

# Merging Spatial and Temporal Structure within a Metapopulation Model

Yssa D. DeWoody,<sup>1,2,\*</sup> Zhilan Feng,<sup>2,†</sup> and Robert K. Swihart<sup>1,‡</sup>

1. Department of Forestry and Natural Resources, Purdue University, West Lafayette, Indiana 47907-2061;

2. Department of Mathematics, Purdue University, West Lafayette, Indiana 47907-1395

Received September 7, 2004; Accepted March 14, 2005;  
Electronically published May 11, 2005

---

**ABSTRACT:** Current research recognizes that both the spatial and temporal structure of the landscape influence species persistence. Patch models that incorporate the spatial structure of the landscape have been used to investigate static habitat destruction by comparing persistence results within nested landscapes. Other researchers have incorporated temporal structure into their models by making habitat suitability a dynamic feature of the landscape. In this article, we present a spatially realistic patch model that allows patches to be in one of three states: uninhabitable, habitable, or occupied. The model is analytically tractable and allows us to explore the interactions between the spatial and temporal structure of the landscape as perceived by the target species. Extinction thresholds are derived that depend on habitat suitability, mean lifetime of a patch, and metapopulation capacity. We find that a species is able to tolerate more ephemeral destruction, provided that the rate of the destruction does not exceed the scale of its own metapopulation dynamics, which is dictated by natural history characteristics and the spatial structure of the landscape. This model allows for an expansion of the classic definition of a patch and should prove useful when considering species inhabiting complex dynamic landscapes, for example, agricultural landscapes.

*Keywords:* metapopulation models, patch dynamics, spatially realistic models, dynamic landscape, persistence, fragmentation.

---

Within the metapopulation framework, two structures have emerged as critical in the study of species persistence within patchy landscapes. The importance of spatial struc-

ture (i.e., heterogeneity) has been supported by many studies (Durrett and Levin 1994; Moilanen and Hanski 1995; With and Crist 1995; Bascompte and Solé 1996; Hanski 1998; Bevers and Flather 1999; Hill and Caswell 1999; With and King 1999; Hanski and Ovaskainen 2000) that show that spatial features such as patch connectivity, patch size, and the assumption of local dispersal are essential to understanding the dynamics of a population. In addition to the spatial structure of the landscape, recent research also has touted the importance of the temporal structure of the landscape (Merriam et al. 1991; Gyllenberg and Hanski 1997; Marquet and Velasco-Hernández 1997; Brachet et al. 1999; Hanski 1999; Keymer et al. 2000; Crone et al. 2001; Johst et al. 2002; Marquet et al. 2003). The general consensus is that temporal components interact with the spatial components to determine metapopulation persistence (Fahrig 1992; Hanski 1999; Keymer et al. 2000; Johst et al. 2002).

Many natural landscapes are dynamic (e.g., prairie pot-holes subjected to periodic drought, canopy gaps in forests), and landscapes dominated by humans often exhibit temporal changes in structure as well (e.g., crop rotations in agricultural ecosystems, schedules of timber harvest in managed forests). The prevalence of dynamic landscapes requires a closer consideration of patch dynamics in the persistence of metapopulations. In this article, we develop a metapopulation model that integrates both the spatial heterogeneity and temporal dynamics of patches within the landscape.

## Models

Our model is an analytically tractable patch model that incorporates both the spatial and temporal structure of the landscape by blending two previous models. We chose to capture the spatial structure of the landscape by following a spatially realistic Levins model (SRLM; Moilanen and Hanski 1995). Temporal structure was added by emulating a dynamic landscape model (DLM; Keymer et al. 2000). In this section, we provide a brief review of each of these previous models, followed by an overview of our

\* E-mail: dewoodyy@purdue.edu.

† E-mail: zfeng@math.purdue.edu.

‡ E-mail: rswihart@purdue.edu.

**Table 1:** Definitions of frequently used symbols

Model/symbol	Definition
Spatially realistic Levins model (SRLM):	
$n$	Number of patches in the landscape
$p_i(t)$	Probability of patch $i$ being occupied at time $t$
$C_i(\cdot)$	Colonization rate of patch $i$
$E_i(\cdot)$	Extinction rate of patch $i$
$d_{i,j}$	Distance between patch $i$ and $j$
$A_i$	Area of patch $i$
$c$	Colonization rate constant
$e$	Extinction rate constant
$1/\alpha$	Average migration distance
$\vec{p}^*$	Equilibrium vector of patch occupancy probabilities, $p_i^*$
$\mathbf{M}; \lambda_M$	Landscape matrix; metapopulation capacity
$P_A^*$	Expected landscape occupancy; weight average of $p_i^*$ 's
$d$	Amount of destroyed habitat relative to original landscape
Dynamic landscape model (DLM):	
$S = \{0, 1, 2\}$	Patch states: uninhabitable, habitable but empty, occupied
$P_j(t)$	Proportion of patches in each state $j \in S$
$\lambda$	Patch creation rate
$\beta$	Patch destruction rate
$\tilde{e}$	Patch extinction rate
$\tilde{c}$	Propagule production rate
$P_j^*$	Equilibrium proportion of patches in state $j \in S$
$P^*$	Equilibrium proportion of occupied habitable patches
$\tilde{s}$	Long-term expected amount of suitable habitat
$\tilde{\tau}$	Long-term expected life span of habitable patches
$R_0$	Basic reproductive number
$\hat{R}_0$	Reproductive number adjusted for DLM
Spatially realistic dynamic landscape model (SRDLM):	
$q_{ij}(t)$	Probability of patch $i$ being in state $j \in S$ at time $t$
$\beta_i; \beta$	Destruction rate of patch $i$ ; destruction rate for landscape
$\lambda_i; \lambda$	Creation rate of patch $i$ ; creation rate for landscape
$\vec{q}_2(t)$	Vector containing the probabilities that each patch is occupied, $q_{i2}t$
$\vec{q}$	State vector of reduced system
$B_i$	Relative destruction rate of patch $i$
$\vec{O}^*$	Trivial equilibrium of reduced system
$\hat{\mathbf{M}}; \lambda_{\hat{\mathbf{M}}}$	Alternative landscape matrix; metapopulation capacity
$s$	Long-term expected amount of suitable habitat
$\tau$	Long-term expected life span of habitable patches
$\hat{R}_0$	Reproductive number adjusted for SRDLM
$q_{ij}^*$	Equilibrium probability that patch $i$ is in state $j \in S$
$q_i^*$	Expected occupancy probability for habitable patch $i$
$Q_j^A$	Average weighted probability of patches being in state $j \in S$
$Q_A^*$	Expected landscape occupancy; weighted average of $q_i^*$ 's
$\hat{d}$	Long-term expected amount of destroyed habitat

model, which incorporates the interaction of spatial and temporal structures while remaining analytically tractable. (See table 1 for definitions of frequently used symbols.)

### Spatial Structure

The SRLM (Moilanen and Hanski 1995; Hanski and Ovaskainen 2000; Ovaskainen and Hanski 2001) is a contin-

uous-time patch model that incorporates the effects of the spatial landscape into classical metapopulation dynamics. This model assumes a finite number of  $n$  patches. Each patch has an associated area as well as a connectivity rating based on the distance of the patch in question to all other patches in the network. The model retains the basic flavor of the Levins model (Levins 1969) by assuming that meta-

population dynamics are governed by the balance between colonization and extinction. Let  $p_i(t)$  be the probability of patch  $i$  being occupied at time  $t$ , where  $i = 1, \dots, n$ . Then

$$\frac{dp_i(t)}{dt} = C_i(t)[1 - p_i(t)] - E_i(t)p_i(t), \quad (1)$$

where  $C_i(\cdot)$  and  $E_i(\cdot)$  are the colonization and extinction rates for patch  $i$ . Spatial structure is incorporated by invoking two canonical assumptions. First, the colonization rate of each patch is assumed to be proportional to patch connectivity, which is dependent on the patch areas, interpatch distances, incidence of patches, and a species' intrinsic dispersal ability (Adler and Nürnbergger 1994; Hanski 1994, 1998). Second, extinction rates are assumed to decrease as a function of patch area, reflecting the belief that larger areas support larger populations and that extinction risk should decrease as a population grows (Gilpin and Diamond 1981; Hanski 1992). Based on these assumptions, the rates governing metapopulation dynamics can be quantified as

$$C_i(\vec{p}) = c \cdot \sum_{j \neq i} e^{-\alpha d_{ij}} A_j p_j(t), \quad (2)$$

$$E_i = \frac{e}{A_i}, \quad (3)$$

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:  $1/\alpha$  is the average migration distance, and  $c$  and  $e$  are constants that scale colonization and extinction rates, respectively.

Ovaskainen and Hanski (2001) concluded that a stable nontrivial equilibrium  $\vec{p}^* = (p_1^*, p_2^*, \dots, p_n^*) > 0$  exists for SRLM if and only if

$$\lambda_M > \frac{e}{c}, \quad (4)$$

where  $\lambda_M$  is defined as the leading eigenvalue of a landscape matrix,  $\mathbf{M}$ . Under the model assumptions stated above, they derived  $\mathbf{M}$  to be

$$\mathbf{M} = \begin{bmatrix} 0 & e^{-\alpha d_{12}} A_1 A_2 & e^{-\alpha d_{13}} A_1 A_3 & \cdots & e^{-\alpha d_{1n}} A_1 A_n \\ e^{-\alpha d_{21}} A_2 A_1 & 0 & e^{-\alpha d_{23}} A_2 A_3 & \cdots & e^{-\alpha d_{2n}} A_2 A_n \\ e^{-\alpha d_{31}} A_3 A_1 & e^{-\alpha d_{32}} A_3 A_2 & 0 & \cdots & e^{-\alpha d_{3n}} A_3 A_n \\ \vdots & \vdots & \vdots & \cdots & \vdots \\ e^{-\alpha d_{n1}} A_n A_1 & e^{-\alpha d_{n2}} A_n A_2 & e^{-\alpha d_{n3}} A_n A_3 & \cdots & 0 \end{bmatrix}. \quad (5)$$

The matrix  $\mathbf{M}$  is unique not only to the landscape and focal species but also to assumptions specific to SRLM

(Hanski and Ovaskainen 2000; Feng and DeWoody 2004). This persistence threshold, equation (4), is analogous to Levins' Rule,  $h > e/c$ , which states that the proportion of habitable patches  $h$  must exceed the fraction of empty patches at equilibrium (Hanski et al. 1996). Thus, heuristically,  $\lambda_M$  is a measure of the amount of suitable habitat in the landscape—hence the term “metapopulation persistence capacity” (Ovaskainen and Hanski 2001). Another term defined by Ovaskainen and Hanski (2001) is the “metapopulation invasion capacity,” denoted  $\lambda_I$ , which defines the ability of an empty network to be invaded by a single local population. For Levins-type models, that is, models with no Allee effect (Allee 1931),  $\lambda_I = \lambda_M$ , and the quantity can simply be called “metapopulation capacity” (Ovaskainen and Hanski 2001). Since  $\alpha$ ,  $e$ , and  $c$  remain constant for a given species, the metapopulation capacity provides a way to rank different landscapes in terms of a species' invasibility and persistence (Hanski and Ovaskainen 2000).

Note that the SRLM provides a means of monitoring the expected probability of occurrence for a species at two scales: patch and landscape. At the patch level, transient and long-term occurrence probabilities exist for each patch,  $p_i(t)$  and  $p_i^*$ , respectively. At the landscape level, the following weighted average of the  $p_i^*$  values reflects expected landscape occupancy:

$$P_A^* = \sum_{i=1}^n \frac{A_i p_i^*}{A_T}, \quad (6)$$

where  $A_T$  is the total patch area in the landscape.

### Temporal Structure

Keymer et al. (2000) proposed to explore the consequences of spatial and temporal heterogeneity by allowing patches to change in quality. Building on earlier work (Marquet and Velasco-Hernández 1997), Keymer et al. (2000) developed a lattice metapopulation model based on interacting particle systems (IPS). This new model incorporated both spatial and temporal structure. Unfortunately, their analytic thresholds were derived from a mean field approximation that neglected spatial structure and concentrated on the dynamic nature of the landscape. We will refer to this approximate model as the dynamic landscape model (DLM). They concluded that persistence thresholds were dependent on and often dominated by the rate of habitat destruction.

In the DLM of Keymer et al. (2000), each patch can be in one of three possible states,  $S = \{0, 1, 2\}$ . These patch states are defined as uninhabitable, habitable but empty, and occupied, respectively. Let  $P_i(t)$  denote the proportion of patches in each state,  $i \in S$ . The model has four pa-

parameters: the rate of patch creation ( $\tilde{\lambda}$ ), the rate of patch destruction ( $\tilde{\beta}$ ), the rate of propagule production ( $\tilde{c}$ ), and the extinction rate for local populations ( $\tilde{e}$ ). The first two parameters describe the patch dynamics, that is, the transition between habitable and uninhabitable patches, whereas the last two parameters refer to metapopulation dynamics, that is, extinction and colonization dynamics. Figure 1 depicts how these transition rates change the state of the patches. The DLM can be described by

$$\begin{aligned} \frac{dP_0}{dt} &= \tilde{\beta}(P_1 + P_2) - \tilde{\lambda}P_0, \\ \frac{dP_1}{dt} &= \tilde{\lambda}P_0 - \tilde{c}P_1 - \tilde{e}P_2 - \tilde{\beta}P_1, \\ \frac{dP_2}{dt} &= \tilde{c}P_1 - (\tilde{e} + \tilde{\beta})P_2. \end{aligned} \quad (7)$$

System (7) has a unique globally stable nontrivial equilibrium ( $P_2^* > 0$ ):

$$\begin{aligned} P_0^* &= \frac{\tilde{\beta}}{\tilde{\lambda} + \tilde{\beta}}, \\ P_1^* &= \frac{\tilde{e} + \tilde{\beta}}{\tilde{c}}, \\ P_2^* &= 1 - \frac{\tilde{\beta}}{\tilde{\lambda} + \tilde{\beta}} - \frac{\tilde{e} + \tilde{\beta}}{\tilde{c}}. \end{aligned} \quad (8)$$

The expected amount of suitable habitat is given by

$$\tilde{s} = 1 - P_0^* = \frac{\tilde{\lambda}}{\tilde{\lambda} + \tilde{\beta}}, \quad (9)$$

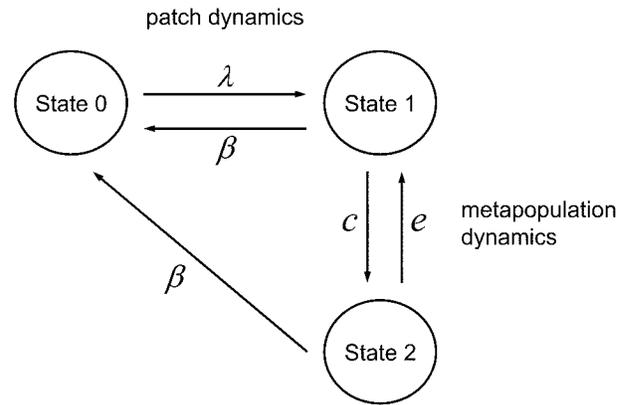
and the expected lifetime of a habitat is given by

$$\tilde{\tau} = \frac{1}{\tilde{\beta}}. \quad (10)$$

Define  $P^* = P_2^*/\tilde{s}$  as the equilibril proportion of habitable patches occupied by a species:

$$P^* = 1 - \frac{1}{\tilde{c}\tilde{s}}\left(\tilde{e} + \frac{1}{\tilde{\tau}}\right). \quad (11)$$

Thus,  $P^*$  reflects landscape-level occupancy. Notice that metapopulation persistence under this model depends not only on habitat suitability,  $\tilde{s}$ , but also on patch lifetime,  $\tilde{\tau}$ . When  $R_0$  is defined as the basic reproductive number (i.e., the average number of propagules an individual pro-



**Figure 1:** Transition diagram between patch states. States 0, 1, and 2 correspond to patches being uninhabitable, habitable but empty, and occupied, respectively. Patch dynamics are governed by destruction and creation rates  $\beta$  and  $\lambda$ , while metapopulation dynamics are governed by colonization and extinction rates  $c$  and  $e$ .

duces in a lifetime), then a requirement for metapopulation persistence is given by  $R_0 > 1$  (Anderson and May 1992). If this is put in terms of the DLM, two interdependent thresholds emerge:

$$P^* > 0,$$

or equivalently,

$$\tilde{R}_0 = \frac{\tilde{c}\tilde{s}}{\tilde{e} + 1/\tilde{\tau}} > 1$$

if and only if

$$\tilde{s} > \tilde{s}_{\min} = \frac{1}{\tilde{c}}\left(\tilde{e} + \frac{1}{\tilde{\tau}}\right) \quad (12)$$

if and only if

$$\tilde{\tau} > \tilde{\tau}_{\min} = (\tilde{c}\tilde{s} - \tilde{e})^{-1}. \quad (13)$$

Conditions (12) and (13) must be satisfied in order to achieve metapopulation persistence. Thus, “effective” colonization and extinction rates are given by  $\tilde{c}\tilde{s}$  and  $\tilde{e} + 1/\tilde{\tau}$ , respectively. Although the IPS model of Keymer et al. (2000) was spatially explicit, all spatial structure is lost in their mean field DLM. Their comparisons of the IPS and DLM revealed that the DLM consistently overestimated the expected patch occupancy  $P^*$  as well as the threshold conditions, and these estimates worsened as  $\tilde{R}_0$  approached 1 (Keymer et al. 2000).

### Merging Spatial and Temporal Structure

In this section, we combine the approaches of Hanski and Ovaskainen (2000) and Keymer et al. (2000) to develop a metapopulation model that permits examination of patch dynamics in conjunction with connectivity via a spatially realistic patch model. Consider a landscape composed of  $n$  patches with each patch in one of the three possible states,  $j \in S = \{0, 1, 2\}$  (uninhabitable, habitable but empty, occupied). Let  $q_{i0}(t)$  = probability of patch  $i$  being uninhabitable at time  $t$ ,  $q_{i1}(t)$  = probability of patch  $i$  being habitable yet empty at time  $t$ ,  $q_{i2}(t)$  = probability of patch  $i$  being occupied at time  $t$ ,  $\beta_i$  = destruction rate of patch  $i$ ,  $\lambda_i$  = creation rate of patch  $i$ ,  $C_i(\vec{q}_2(t))$  = colonization rate of patch  $i$ , and  $E_i(\vec{q}_2(t))$  = extinction rate of patch  $i$ , where  $C_i$  and  $E_i$  are smooth functions of  $\vec{q}_2(t) = (q_{12}, q_{22}, \dots, q_{n2})$  (i.e., a vector containing the probabilities of each patch being occupied at time  $t$ ) for  $i = 1, 2, \dots, n$ . Then our model is described by the following equations:

$$\begin{aligned} \frac{dq_{i0}}{dt} &= \beta_i(q_{i1} + q_{i2}) - \lambda_i q_{i0}, \\ \frac{dq_{i1}}{dt} &= \lambda_i q_{i0} - C_i(\vec{q}_2)q_{i1} + E_i(\vec{q}_2)q_{i2} - \beta_i q_{i1}, \\ \frac{dq_{i2}}{dt} &= C_i(\vec{q}_2)q_{i1} - (E_i(\vec{q}_2) + \beta_i)q_{i2}, \end{aligned} \quad (14)$$

where  $i = 1, 2, \dots, n$ .

We will henceforth refer to this system as the spatially realistic dynamic landscape model (SRDLM). Using the constraint  $q_{i0} + q_{i1} + q_{i2} = 1$  for  $i = 1, 2, \dots, n$ , we can reduce the dimension of this system (14) by eliminating the  $q_{i1}$  equations in the following manner:

$$\begin{aligned} \frac{dq_{i0}}{dt} &= \beta_i(1 - q_{i0}) - \lambda_i q_{i0}, \\ \frac{dq_{i2}}{dt} &= C_i(\vec{q}_2)(1 - q_{i0} - q_{i2}) - (E_i(\vec{q}_2) + \beta_i)q_{i2}, \end{aligned} \quad (15)$$

where  $i = 1, 2, \dots, n$ . Define the state of the reduced SRDLM by the vector  $\vec{q}(t) = (q_{10}, q_{20}, \dots, q_{n0}, q_{12}, q_{22}, \dots, q_{n2})$ ,  $\Omega = \{(q_i) \in \mathbf{R}^n: 0 \leq q_i \leq 1\}$ ,  $\Sigma = \{(q_i) \in \mathbf{R}^n: 0 \leq q_i \leq 1 - B_i\}$ , where  $B_i = \beta_i/(\beta_i + \lambda_i)$  is the relative destruction rate of patch  $i$ . Consider the following general assumptions on colonization and extinction.

First,  $C_i(\vec{0}) = 0$ ,  $C_i(\vec{q}_2) > 0$  for all nontrivial  $\vec{q}_2$  in  $\Omega \setminus \{0\}$ , and  $C_{ij}(\vec{q}_2) = [\partial C_i(\vec{q}_2)/\partial q_{j2}] \geq 0$  whenever  $1 \leq i \neq j \leq n$  for all  $\vec{q}_2$  in  $\Sigma$ . In biological terms, this means we assume no migration from outside the metapopulation, no patch is completely isolated, and the colonization prob-

ability of an empty patch is independent of or increased by the occupancy of other patches.

Second,  $E_i(\vec{q}_2) > 0$  for all nontrivial  $\vec{q}_2$  in  $\Omega \setminus \{0\}$ , and  $E_{ij}(\vec{q}_2) = [\partial E_i(\vec{q}_2)/\partial q_{j2}] \leq 0$  whenever  $1 \leq i \neq j \leq n$  for all  $\vec{q}_2$  in  $\Sigma$ . In biological terms, this means we assume that each local population has some vulnerability to extinction and that the extinction rate of extant patches is independent of or reduced by the occupancy of other patches.

Under these assumptions, the reduced system (eq. [15]) yields a trivial equilibrium,  $\vec{O}^* = (B_1, B_2, \dots, B_n, 0, 0, \dots, 0)$ . The stability of  $\vec{O}^*$  is determined by the eigenvalues of  $\mathbf{H}_1 - \mathbf{D}_1$ , where  $\mathbf{D}_1 = \text{diag}(E_i(\vec{0}) - (1 - B_i)C_{ii}(\vec{0}))$  and

$$\mathbf{H}_1 = \begin{bmatrix} 0 & (1 - B_1)C_{12}(\vec{0}) & \cdots & (1 - B_1)C_{1n}(\vec{0}) \\ (1 - B_2)C_{21}(\vec{0}) & 0 & \cdots & (1 - B_2)C_{2n}(\vec{0}) \\ \vdots & \vdots & \ddots & \vdots \\ (1 - B_n)C_{n1}(\vec{0}) & (1 - B_n)C_{n2}(\vec{0}) & \cdots & 0 \end{bmatrix}.$$

As proved by Diekmann et al. (1990),  $\mathbf{H}_1 - \mathbf{D}_1$  has at least one eigenvalue with a positive real part if and only if

$$\lambda_{\mathbf{H}_1, \mathbf{D}_1^{-1}} = \text{the leading eigenvalue of } \mathbf{H}_1 \mathbf{D}_1^{-1} > 1.$$

Since a species will persist if and only if the trivial equilibrium  $\vec{O}^*$  is unstable, then the criteria for persistence is  $\lambda_{\mathbf{H}_1, \mathbf{D}_1^{-1}} > 1$ . An extension of this argument provides conditions that insure the existence of a unique, nontrivial equilibrium,  $\vec{q}^* \neq \vec{O}^*$ , that is globally asymptotically stable (D. Xu, Z. Feng, L. Allen, and R. Swihart, unpublished manuscript).

Now consider the following specific forms for the transition probabilities. Let the patch colonization and extinction rates be defined in the traditional manner:

$$C_i(\vec{q}_2) = c \sum_{j \neq i} e^{-\alpha d_{ij}} A_j q_{j2}(t), \quad (16)$$

$$E_i(\vec{q}_2) = \frac{e}{A_i}, \quad (17)$$

where once again  $1/\alpha$  is the average dispersal distance for the species,  $d_{ij}$  is the intrapatch distances, and  $e$  and  $c$  are constants that scale extinction and colonization rates. If we further assume area-dependent rates for patch creation and destruction, then

$$\begin{aligned} \lambda_i &= \frac{\lambda}{A_i}, \\ \beta_i &= \frac{\beta}{A_i}, \end{aligned} \quad (18)$$

with  $i = 1, 2, \dots, n$ ; where  $\lambda$  and  $\beta$  are the background creation and destruction rates of the landscape, then spe-

cific persistence thresholds can be derived (Feng and DeWoody 2004). In this case,  $\mathbf{H}_1\mathbf{D}_1^{-1}$  can be written as

$$\mathbf{H}_1\mathbf{D}_1^{-1} = \frac{c[\lambda/(\lambda + \beta)]}{e + \beta} \hat{\mathbf{M}},$$

where

$$\hat{\mathbf{M}} = \begin{bmatrix} 0 & e^{-\alpha d_{12}}A_2^2 & e^{-\alpha d_{13}}A_3^2 & \cdots & e^{-\alpha d_{1n}}A_n^2 \\ e^{-\alpha d_{21}}A_1^2 & 0 & e^{-\alpha d_{23}}A_3^2 & \cdots & e^{-\alpha d_{2n}}A_n^2 \\ e^{-\alpha d_{31}}A_1^2 & e^{-\alpha d_{32}}A_2^2 & 0 & \cdots & e^{-\alpha d_{3n}}A_n^2 \\ \vdots & \vdots & \vdots & \cdots & \vdots \\ e^{-\alpha d_{n1}}A_1^2 & e^{-\alpha d_{n2}}A_2^2 & e^{-\alpha d_{n3}}A_3^2 & \cdots & 0 \end{bmatrix}. \quad (19)$$

Let

$$\lambda_{\hat{\mathbf{M}}} = \text{the leading eigenvalue of } \hat{\mathbf{M}}.$$

We found that a nontrivial equilibrium  $\vec{q}^* \neq \vec{0}^*$  exists and is stable if and only if

$$\lambda_{\hat{\mathbf{M}}} > \hat{\delta} = \frac{e + \beta}{c[\lambda/(\lambda + \beta)]}. \quad (20)$$

Note the similarity between the SRDLM threshold and the SRLM, equation (4). Although the matrix  $\hat{\mathbf{M}}$  differs slightly from Hanski and Ovaskainen's landscape matrix  $\mathbf{M}$  given by equation (5), it can be shown through the following similarity transform— $\hat{\mathbf{M}} = \mathbf{A}^{-1}\mathbf{M}\mathbf{A}$ , where  $\mathbf{A} = \text{diag}(A_i)$ —that both matrices share a common set of eigenvalues (Horn and Johnson 1985). It follows then that  $\lambda_{\mathbf{M}} = \lambda_{\hat{\mathbf{M}}}$ . Thus, the thresholds are consistent, provided there is no dynamic destruction of habitat (i.e.,  $\beta = 0$ ).

In a fashion similar to Keymer et al. (2000), we define

$$s = 1 - q_{i0}^* = \frac{\lambda}{\lambda + \beta}, \quad (21)$$

$$\tau = \frac{1}{\beta}, \quad (22)$$

$$R_0 = \frac{c\lambda_{\hat{\mathbf{M}}}s}{e + 1/\tau}, \quad (23)$$

to be the long-term probability that any patch is suitable, the expected lifetime of a habitat patch of unit area, and the effective reproduction number as the ratio of the effective colonization rate (i.e.,  $c\lambda_{\hat{\mathbf{M}}}s$ ) to the effective extinction rate (i.e.,  $e + 1/\tau$ ), respectively. Thus, in context of a dynamic landscape, effective landscape capacity is given by  $\lambda_{\hat{\mathbf{M}}}s$ . From equation (20), we obtain the following

two interdependent thresholds for metapopulation persistence:

$$s > s_{\min} = \frac{1}{c\lambda_{\hat{\mathbf{M}}}} \left( e + \frac{1}{\tau} \right) \quad (24)$$

if and only if

$$\tau > \tau_{\min} = (c\lambda_{\hat{\mathbf{M}}}s - e)^{-1}. \quad (25)$$

Comparing these thresholds with (12) and (13), which are corresponding thresholds for the model without landscape connectivity, we can see how metapopulation capacity  $\lambda_{\hat{\mathbf{M}}}$  affects the two thresholds by scaling the amount of suitable habitat, which changes colonization ability. These thresholds now incorporate the spatial structure of the landscape through the  $\lambda_{\hat{\mathbf{M}}}$  and  $s$ , the temporal landscape structure through  $\tau$ , and the natural history characteristics of the target species through  $\alpha$  (embedded in  $\lambda_{\hat{\mathbf{M}}}$ ),  $c$ , and  $e$ .

This model can monitor species occupancy on both the patch and landscape level with the following statistics. On the patch level, we define the expected occupancy of patch  $i$  as the long-term probability of patch  $i$  being occupied, given that it is habitable; that is,

$$q_i^* = \frac{q_{i2}^*}{(1 - q_{i0}^*)} = \frac{q_{i2}^*}{s}, \quad (26)$$

where  $q_{i2}^*$  and  $q_{i0}^*$  are the long-term, that is, equilibrial, probabilities that patch  $i$  is occupied and uninhabitable, respectively. On the landscape level, we define occupancy as the long-term average of the patch occupancy probabilities weighted by the patch area; that is,

$$Q_A^* = \sum_{i=1}^n \frac{A_i}{A_T} q_i^*, \quad (27)$$

where  $A_i$  is the area of patch  $i$  and  $A_T$  is the total area in the landscape. Thus,  $Q_A^*$  reflects the expected occupancy of the landscape and is analogous to  $P_A^*$  of the SRLM and  $P^*$  of the DLM.

### Comparison of Models

All three models provide a means of evaluating a landscape in terms of its ability to support a viable population; however, the emphasis of each model is on a different structure of the landscape. In this section, we show how our model reduces to the two parent models under certain conditions. We then contrast the different thresholds when these conditions are altered. These comparisons are done on a re-

alistic landscape (fig. 2), which resembles the habitat of the butterfly, *Melitaea cinxia*, in Finland (Hanski and Thomas 1994). This landscape was chosen because it has served as an illustration of a landscape with complex spatial structure that is known to support a viable metapopulation (Hanski et al. 1994).

#### Comparison with the Dynamic Landscape Model

The DLM of Keymer et al. (2000) has at least three implicit assumptions: an infinite number of patches, homogeneous patches, and unlimited dispersal of the species (i.e., colonization is modeled as a mass action). Our model, SRDLM, has relaxed all three assumptions by permitting a finite number of patches, patch-specific transition rates, and connectivity-dependent colonization that is mitigated by the limited dispersal ability of the species and the spatial attributes of the landscape.

We can compare the two models through the following summary statistics of our patch model. Let  $Q_j^A$  be the average probability of a patch being in state  $j$  weighted by patch area; that is,

$$Q_j^A = \frac{\sum_{i=1}^n A_i}{\sum_{i=1}^n A_T} q_{ij} \quad j \in \{0, 1, 2\},$$

where  $A_i$  is the area of patch  $i$ ,  $A_T$  is the total patch area in the landscape, and  $q_{ij}$  is defined in equation (14). Consider our model under the assumptions of homogeneous patches and unlimited dispersal ability; that is,  $A_i = A$  for  $i = 1, 2, \dots, n$  and  $\alpha = 0$ . Under these assumptions,  $Q_j^A$  is just an average. The dynamics of the statistics  $Q_j^A$  can be reduced to the following system:

$$\begin{aligned} \frac{dQ_0^A}{dt} &= \frac{\beta}{A}(Q_1^A + Q_2^A) - \frac{\lambda}{A}Q_0^A, \\ \frac{dQ_1^A}{dt} &= \frac{\lambda}{A}Q_0^A - (cAn)Q_2^AQ_1^A + \frac{e}{A}Q_2^A \\ &\quad - \frac{\beta}{A}Q_1^A + \frac{cA}{n} \sum_{i=1}^n q_{i2}q_{i1}, \\ \frac{dQ_2^A}{dt} &= (cAn)Q_2^AQ_1^A - \left(\frac{e}{A} + \frac{\beta}{A}\right)Q_2^A - \frac{cA}{n} \sum_{i=1}^n q_{i2}q_{i1}. \end{aligned} \quad (28)$$

Note that equation (28) is analogous to equations (7) with the exception of the term  $cA/n \sum_{i=1}^n q_{i2}q_{i1}$ ; this term represents the inability of a patch to colonize itself. Thus, it is reasonable to consider  $Q_j^A$  of the SRDLM as the proportion of the habitat in state  $j$  and to compare it with  $P_j$  of the DLM,  $j \in \{1, 2, 3\}$  when model parameters are equivalent; that is,  $\beta_j = \beta/A = \tilde{\beta}$ ,  $\lambda_j = \lambda/A = \tilde{\lambda}$ ,  $e_j =$

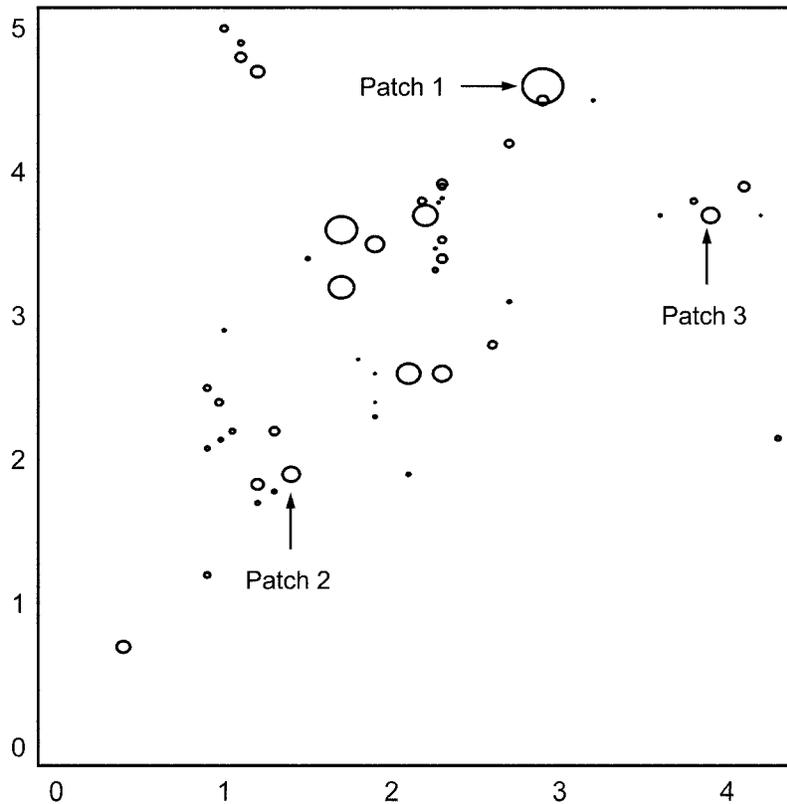
$e/A = \tilde{e}$ , and  $cAn = \tilde{c}$ . Under these conditions, it is possible to compare the persistence thresholds for these two models:

$$\begin{aligned} s > \frac{1}{c\lambda_{\tilde{M}}}\left(e + \frac{1}{\tau}\right) &= \frac{1}{[\tilde{c}/(A \cdot n)][A^2(n-1)]} \\ &\quad \times \left[ (A \cdot \tilde{e}) + \left(A \cdot \frac{1}{\tilde{\tau}}\right) \right] \\ &= \left(\frac{n}{n-1}\right)\tilde{s}, \end{aligned}$$

where  $\lambda_{\tilde{M}} = A^2(n-1)$ . Thus, under the conditions of homogeneous area and unlimited dispersal, our model still requires a larger amount of suitable habitat when  $n$  is small. However, the two thresholds become equivalent as  $n$  becomes large, that is, as the limiting assumption of an infinite number of patches becomes more reasonable.

How does the added spatial realism improve our understanding of the metapopulation dynamics? First we consider the effect of heterogeneous area. If rates of patch creation and destruction are dictated by equation (18), then the smaller patches are more ephemeral (compare  $\beta_i$ 's); however, the probability of any patch being suitable,  $s = 1 - q_{i0}^* = \lambda/(\lambda + \beta)$ , is constant for each patch and independent of area. Heterogeneity of area also affects patch extinction and colonization rates. Patch heterogeneity always increases the occupancy above that of a homogeneous landscape and extends persistence thresholds (fig. 3) because larger patches are assumed to have a larger carrying capacity. These larger local abundances not only decrease the focal patch's extinction risk but also increase the connectivity of surrounding patches by creating a larger pool of potential emigrants. These effects are realized even when species have unlimited dispersal ability ( $\alpha = 0$ ) and are summarized by a decrease in metapopulation capacity, that is,  $\lambda_{\tilde{M}} = 29.8217$  with heterogeneous patch area, whereas  $\lambda_{\tilde{M}} = 8.40116$  with homogeneous patch area.

This disparity between results of homogeneous and heterogeneous patch areas is amplified as dispersal ability becomes more limited (fig. 3). Clearly, limited dispersal reduces colonization ability, thus restricting occupancy and persistence thresholds by decreasing metapopulation capacity. Limited dispersal magnifies the importance of the spatial layout of the landscape by scaling interpatch distances. Whereas colonization in the DLM is reduced to one parameter,  $\tilde{c}$ , colonization in our model is parameterized by a species' dispersal ability,  $\alpha$ , and its colonization potential,  $c$ , given its ability to arrive at a patch. Thus, the more limited the dispersal ability becomes, the more critical the spatial structure of the landscape. In general, mean



**Figure 2:** Location and relative sizes of 50 habitat patches in the *Melitaea cinxia* metapopulation. Patches range from 12 m<sup>2</sup> to 46 ha, and the average patch area is 0.414 ha. (Hanski and Thomas 1994). Patches 1, 2, and 3 are considered in figure 5.

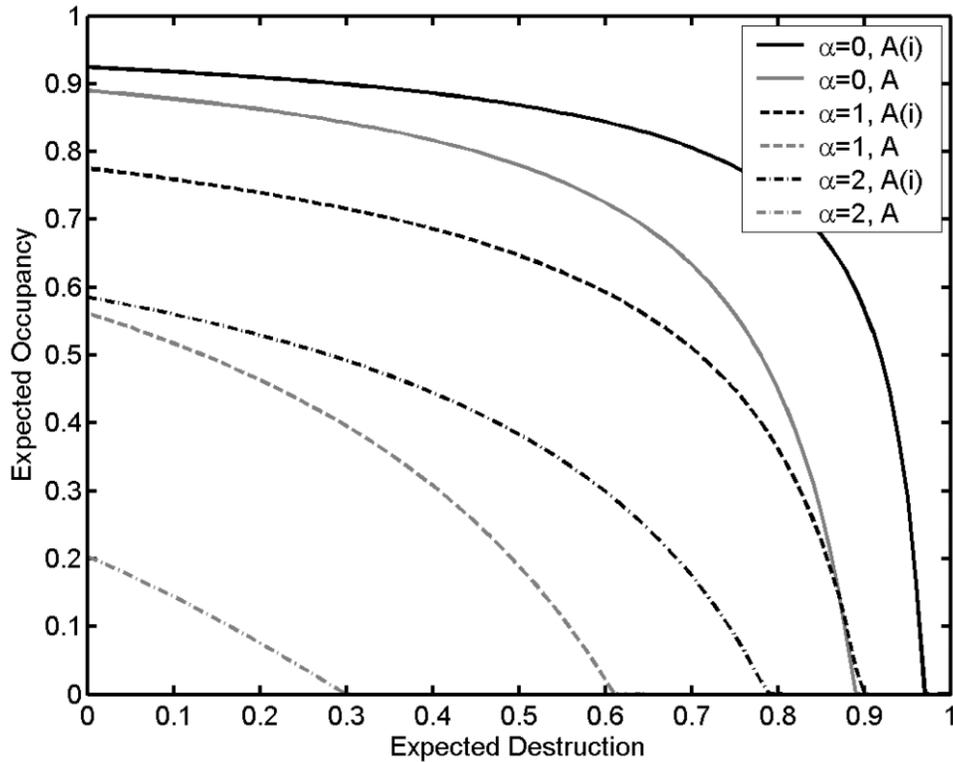
field models have overestimated occupancy and persistence thresholds because of their neglect of spatial correlations as a result of unlimited dispersal (Lande 1987; Bascompte and Solé 1996; Tilman et al. 1997; Brachet et al. 1999; Keymer et al. 2000), but the spatial realism in our model allows one to define the scale of spatial correlations in occupancy, thus reducing inaccuracies in the estimated occupancy and persistence thresholds.

Intertwined with the spatial structure is the temporal structure of the landscape. The rate of change of the landscape signified by the mean lifetime of a patch,  $\tau$ , is quite important (fig. 4). Connectivity in space-time is limited as the landscape changes at a faster rate, that is, by decreasing  $\tau$ . Sensitivity to  $\tau$  increases as dispersal ability becomes more limited (cf. fig. 4A, 4B). All other factors being equal, a species with more colonization potential (higher  $c$ ) is better equipped to deal with a more ephemeral habitat. Note also that once  $\tau$  exceeds its critical threshold, the occupancy of a better colonizer is more sensitive to changes in  $\tau$  than the occupancy of a poorer colonizer. Thus, the poorer colonizer is more constrained by its abil-

ities, whereas the better colonizer is more constrained by the limitations of the landscape.

#### *Comparison with the Spatially Realistic Levins Model*

The essential difference between our model and SRLM is habitat variability. Whereas our model allows for uninhabitable patches and defines the lifetime of a patch in terms of its destruction rate, SRLM assumes that a patch is always habitable. Thus, the definition of a patch is fundamentally different in the two models. However, our model does reduce to the SRLM when the mean lifetime of each patch is infinite, that is,  $\tau = \infty$ , implying a static landscape in which all patches are habitable and either empty or occupied. Habitat destruction in the SRLM is static and signifies a change in the landscape (e.g., patch area is reduced or a patch is lost from the landscape) leading to a permanent alteration in the connectivity of patches and metapopulation capacity. In our model, habitat destruction and creation (or restoration) are ephemeral. Although the landscape or metapopulation capacity



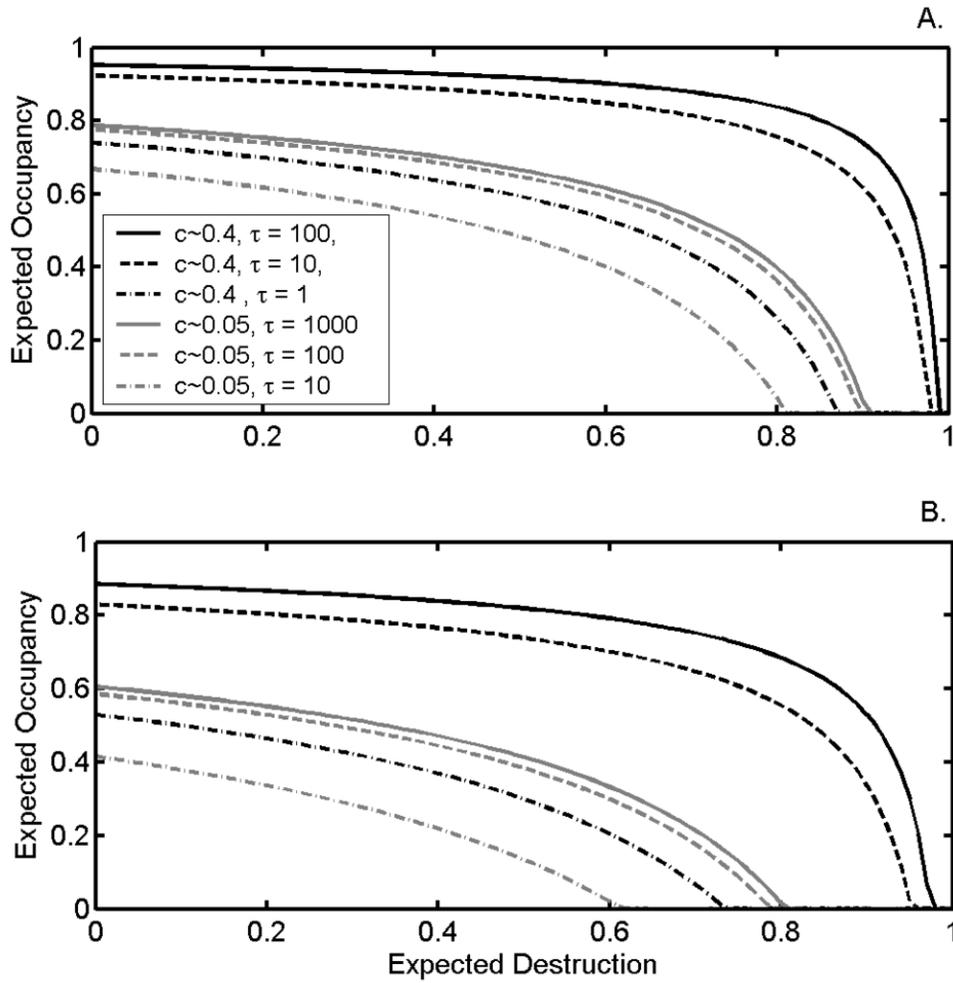
**Figure 3:** Expected landscape occupancy of the spatially realistic dynamic landscape model,  $Q_A^*$ , as a function of expected destruction,  $\hat{d} = 1 - s = q_{i0}^* = \beta/(\lambda + \beta)$ , for the landscape depicted in figure 2. Focal species is described by parameters  $e = 0.0414068$  ( $\bar{e} = .1$ ) and  $c = 0.0483012$  ( $\bar{c} = 1$ ). Mean lifetime of a patch is  $\tau = 100$ . Black and gray lines contrast the effects of heterogeneity versus homogeneity in patch area as dispersal ability becomes limited. Note that the solid gray line closely approximates results from dynamic landscape model due to homogeneity in patch area and unlimited dispersal.

is viewed as fixed, the relative impact of capacity is scaled by the probabilistic amount of suitable habitat,  $s$ . Moreover, connectivity is allowed to morph in response to suitability and occupancy.

We compare ephemeral habitat destruction with static destruction by introducing destruction into the SRLM through the use of nested, altered landscapes. Following Hanski and Ovaskainen (2000), we considered the effect of incorporating two types of static destruction into the SRLM: decreasing the area of patches and random removal of patches. Once again we utilized the realistic landscape depicted in figure 2. To facilitate comparisons, we kept the long-term expected amount of destroyed habitat in the SRDLM,  $\hat{d} = 1 - s = \hat{p}_{i0}$ , equal to the actual amount of destroyed habitat  $d$  in the SRLM, calculated as  $d = 1 - (\text{total area in the altered landscape})/(\text{total area in original landscape})$ . We compare landscape-level occupancies,  $Q_A^*$  of the SRDLM (eq. [27]) and  $P_A^*$  of the SRLM (eq. [6]). For the SRLM, patch areas  $\tilde{A}_i$  are defined in terms of the altered landscape and reflect destruction. For our model, patch area is always defined in terms of the

original landscape, and destruction is reflected by a decline in the amount of suitable habitat  $s$ . We considered two rates of patch dynamics for the SRDLM: a rapidly changing landscape where  $\tau = 10$  and a slowly changing landscape where  $\tau = 1,000$ .

When considering shrinking patch areas in the SRLM, each patch was statically decreased by the same proportional amount,  $d = \hat{d} = q_{i0} = \beta/(\beta + \lambda)$ , where  $d$  ranged from 0 to 1. For each destruction level, equilibrium patch probabilities were calculated for each model. We compared the patch occupancies of our model,  $q_i^*$ , given by equation (26), with the long-term probability of occupancy,  $p_i^*$ , of the SRLM model in the statically reduced landscape. Both models show the same qualitative effect of area and isolation on the probability that a particular patch is occupied (fig. 5). At low destruction, the SRLM more closely corresponds to the predictions of our model within a slowly changing landscape; however, at higher destruction rates, the SRLM more closely corresponds to our model in a rapidly changing landscape (fig. 5). We also compared the landscape-level occupancies of each model,  $Q_A^*$  versus

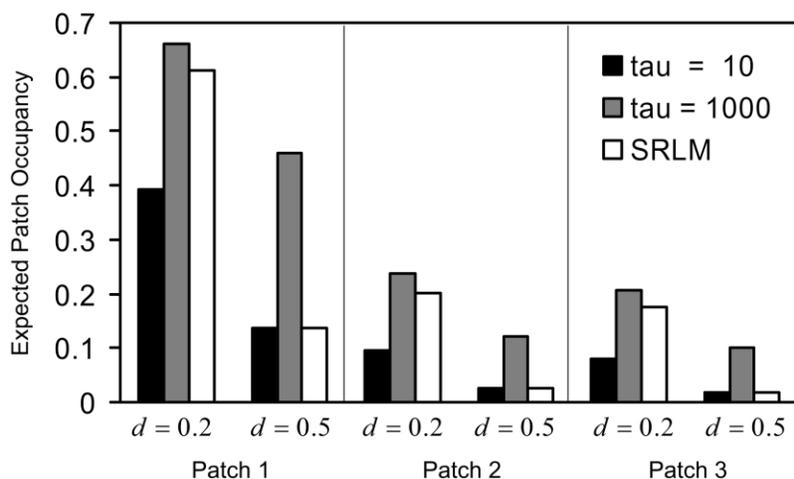


**Figure 4:** Expected landscape occupancy of the spatially realistic dynamic landscape model,  $Q_A^*$ , as a function of expected destruction,  $\hat{d} = 1 - s = q_{\hat{a}}^* = \beta/(\lambda + \beta)$ , for the landscape depicted in figure 2. Dispersal ability is varied between the panels: A,  $\alpha = 1$ ; B,  $\alpha = 2$ . Solid and dashed lines contrast results for a species with good ( $c = 0.38641$  or  $\tilde{c} = 8$ ) versus moderate ( $c = 0.04830$  or  $\tilde{c} = 1$ ) colonization abilities where  $e = 0.0414068$  ( $\tilde{e} = .1$ ) is fixed. Solid versus dashed versus dash-dotted lines show the effects of altering the rate at which the landscape changes, which is signified by mean patch lifetime  $\tau$ .

$P_A^*$ , as described above. Modeling destruction as the reduction of patch area in the SRLM produces a steeper decline in occupancy than predicted by our model regardless of the rates at which the landscape changes (fig. 6). Note that a slowly changing landscape has the potential to greatly improve occupancy and extend persistence thresholds beyond what is predicted by statically declining patch area, even when the effective area of the landscape is the same.

When considering random removal of patches in the SRLM, 100 different nested landscapes were considered. To create sequences of nested landscapes  $\{\mathcal{L}_i^j\}_{j=0}^{50}$ , where  $i = 1, \dots, 100$ , the 50 patches from figure 2 were arranged in a random order such that  $\mathcal{L}_i^0 = \{A_{i_j}\}_{j=1}^{50}$  represented the

unaltered landscape for all  $i$ . Nestedness was achieved by sequentially removing the patches from the landscape,  $\mathcal{L}_i^0 \supset \mathcal{L}_i^1 \supset \mathcal{L}_i^2 \supset \dots \supset \mathcal{L}_i^{50} = \emptyset$ , where  $\mathcal{L}_i^j = \mathcal{L}_i^{j-1} \setminus \{A_{i_j}\} = \{A_{i_k}\}_{k=j+1}^{50}$  and  $j = 0, 1, 2, \dots, 49$ . After each patch removal, destruction  $d$  was increased by an amount equal to that patch's relative contribution to the original landscape. Thus, each (degraded) landscape  $j$  within the nested sequence  $i$  defines a certain amount of destruction  $d_i^j$  and a certain landscape-level occupancy  $P_A^*$  where the weights are derived from  $(\mathcal{L}_i^j)$  for each  $i = 1, \dots, 100$  and  $j = 0, \dots, 50$ . Note it is possible for average occupancy in the SRLM to increase after the removal of a patch if that patch exhibits a low probability of occupancy or a small area. Each pair  $(d_i^j, P_A^*)$  is represented by a point on figure 6.



**Figure 5:** Occupancy probabilities for patches 1, 2, and 3 of figure 2 from the spatially realistic dynamic landscape model (SRDLM) and the spatially realistic Levins model (SRLM). The first and second sets of bars in each panel display long-term results when  $\hat{d} = d = 0.2$  and  $\hat{d} = d = 0.5$ , respectively. Black and gray bars contrast SRDLM results from rapidly versus slowly changing landscapes, whereas the white bars represent SRLM results from static reduction in patch area. Focal species is described by parameters  $c = 0.04830$ ,  $e = 0.0414068$ , and  $\alpha = 2$ .

The effect of random patch removal on the SRLM was calculated as a moving average of these points. The occupancy curves from our model under the assumptions for a rapidly versus slowly changing landscape provide reasonable bounds for the variation produced from the SRLM under random patch removal. However, there clearly are catastrophic orderings that produce early extinction events in the SRLM.

### Conclusion

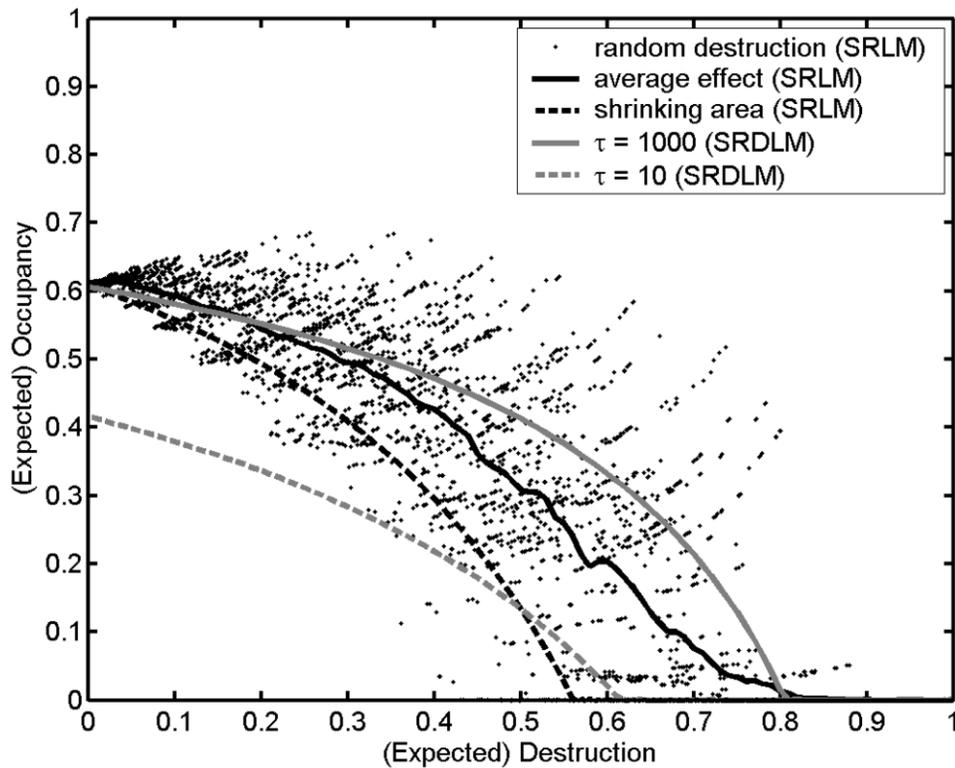
All three models provide a means of evaluating a landscape in terms of its ability to support a viable population; however, the emphasis of each model is on a different structural component of the landscape. The SRDLM provides a means for studying ephemeral destruction within fragmented landscapes while taking into account both the spatial and temporal structure of the landscape. It can be used to examine both global and local aspects of persistence and occupancy within an analytic framework.

We found that long-term metapopulation persistence depends on the relationship between the scale of metapopulation dynamics and landscape dynamics. A species is able to tolerate more ephemeral destruction provided the rate of destruction does not exceed the scale of its own metapopulation dynamics. Indeed, colonization potential is scaled by the rate of patch dynamics, and reductions in occupancy are due to the cumulative effects of extinction and loss of habitat suitability. Thus, our model reinforces

the role of spatiotemporal connectivity in metapopulation dynamics.

The thresholds and landscape matrix presented in this article are based on the assumption that patch destruction and creation rates are normalized by patch area (eq. [18]). This was a convenient assumption because it allowed for the reduction and easy comparison of our model to previous contributions. However, these assumptions are not necessary, and different assumptions can be made that lead to different persistence thresholds, different measures of metapopulation capacity, and different dynamics (table 2; fig. 7). Note that occupancy is most resilient to destruction when patch destruction rates are inversely proportional to area and patch creation rates are independent of area, whereas occupancy is most sensitive to destruction when this assumption is reversed; that is, patch destruction rates are independent of area, and patch creation rates are inversely proportional to patch area. Both of these assumptions produce an area dependence in the long-term expected probability of a patch being suitable. Modeling patch destruction and creation rates separately emphasizes the fact that destruction and creation (or restoration) are different dynamic processes that can affect persistence and occupancy in singular ways. We concur with Fischer (2001) in that our results indicate that under certain assumptions, restoration might be less effective than previously assumed in that it compensates only for loss of habitat but not the harmful effect of patch dynamics (fig. 7, *solid line*).

Although we have focused on comparisons between the



**Figure 6:** Expected landscape occupancy of the spatially realistic dynamic landscape model (SRDLM) and the spatially realistic Levins model (SRLM) as a function of (expected) destruction of habitat. Each dot corresponds to the point  $(d_j^i, P_{\lambda}^i)$  derived from the SRLM within the  $i$ th nested landscape after the removal of patch  $j$ . The solid black line depicts the average effect of random patch removal from the SRLM calculated as a moving average of the points  $(d_j^i, P_{\lambda}^i)$ . The dashed black line depicts expected landscape occupancy,  $P_{\lambda}^i$ , of the SRLM as a consequence of static reduction in patch area. The gray lines depict the expected landscape occupancy,  $Q_{\lambda}^i$ , calculated from SRDLM within a rapidly ( $\tau = 10$ ) and slowly ( $\tau = 1,000$ ) changing landscape. Focal species is described by parameters  $c = 0.04830$ ,  $e = 0.0414068$ , and  $\alpha = 2$ .

SRDLM model and its two parent models, SRLM (Moilanen and Hanski 1995; Hanski and Ovaskainen 2000) and DLM (Keymer et al. 2000), other comparisons are possible. Gyllenberg and Hanski (1997) also studied the effects of dynamic destruction on metapopulation persistence, and their threshold (expression [7.1]) is consistent with our threshold (24) when amount of the suitable habitat is described by metapopulation capacity as opposed to their  $h$ . All models discussed so far have ignored the timescale of local population growth. In contrast, Johst et al. (2002) used a spatially explicit metapopulation model that combined local population and patch dynamics to study persistence in a dynamic landscape. They found that persistence was independent of the local population growth rate provided that this rate insured “fast” local dynamics. Assuming fast local dynamics, our model is also comparable to theirs, and many of our results were consistent. For example, both models confirm the dependence of occupancy and persistence on rate of destruction and that sensitivity to colonization and dispersal ability increases as

the frequency of patch destruction increases. However, they ultimately concluded that, indeed, four rates (or timescales) interact and determine long-term persistence of metapopulations in dynamic landscapes: rate of patch destruction, rate of patch creation (or regeneration), local population growth rate, and colonization rate (Johst et al. 2002).

The utility of our model lies in its flexibility. For instance, these rates of patch dynamics could easily incorporate a spatial component allowing for autocorrelation, thus allowing a separation of demographic stochasticity,  $e$ , from regional or environmental stochasticity,  $\beta$  and  $\lambda$ . Moreover, the patch-specific nature of these parameters provides the flexibility to explore the consequences of subsets of patches operating under different rates of change, situations that are commonplace in landscapes subjected to multiple ownership. Neighboring subsets of patches may experience substantially different management regimes, leading to effects due to ownership fragmentation that may include variation in temporal dynamics. Even within the

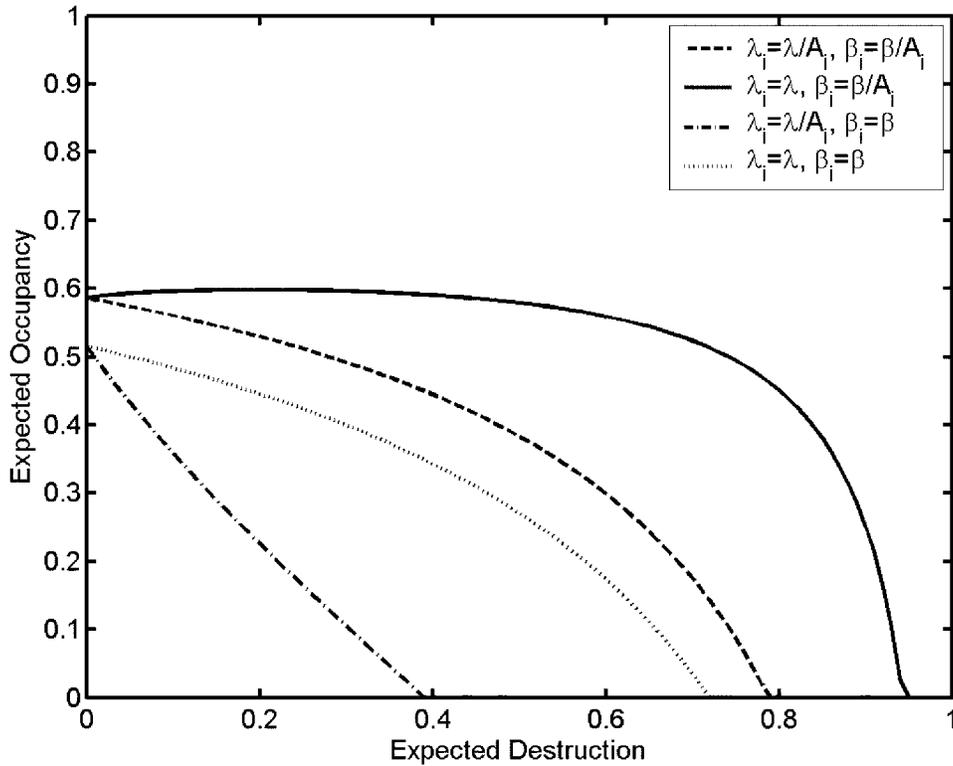
**Table 2:** Corresponding extinction threshold and landscape matrix for the spatially realistic dynamic landscape model based on different functional forms for patch destruction and creation rates where  $\phi_{ij} = \exp(-\alpha d_{ij})$

Destruction rate	Creation rate	Threshold	Landscape matrix
$\beta_i = \frac{\beta}{A_i}$	$\lambda_i = \frac{\lambda}{A_i}$	$\lambda_{\hat{M}} > \frac{e + \beta}{c[\lambda/(\lambda + \beta)]}$	$\hat{m}_{ij} = \phi_{ij} A_j^2$
$\beta_i = \frac{\beta}{A_i}$	$\lambda_i = \lambda$	$\lambda_{\hat{M}} > \frac{e + \beta}{c\lambda}$	$\hat{m}_{ij} = \phi_{ij} A_j^2 \left( \frac{1}{A_i \lambda + \beta} \right)$
$\beta_i = \beta$	$\lambda_i = \frac{\lambda}{A_i}$	$\lambda_{\hat{M}} > \frac{1}{c\lambda}$	$\hat{m}_{ij} = \phi_{ij} A_j^2 \left( \frac{1}{\lambda + A_i \beta} \right) \left( \frac{1}{e + A_i \beta} \right)$
$\beta_i = \beta$	$\lambda_i = \lambda$	$\lambda_{\hat{M}} > \frac{1}{c[\lambda/(\beta + \lambda)]}$	$\hat{m}_{ij} = \phi_{ij} A_j^2 \left( \frac{1}{e + A_i \beta} \right)$

context of a predominantly static landscape, the patch-specific nature of  $\beta_p$ ,  $\lambda_p$ ,  $C_p$ , and  $E_i$  enables exploration of broader definitions of a patch that could include temporary refugia.

Viewing habitat alteration as potentially ephemeral also provides greater flexibility in addressing practical issues associated with conservation in human-dominated land-

scapes. For instance, suppose that within a landscape a certain amount of habitat must be used for agricultural production. What potential benefits might accrue to metapopulations adapted to early successional habitats if fallow periods were included in crop rotation schemes? What critical rates and spatial configurations would be most conducive to attaining these benefits for species of con-



**Figure 7:** Expected landscape occupancy of the spatially realistic dynamic landscape model,  $Q_{\lambda}^*$ , as a function of expected destruction,  $\hat{d} = 1 - s = q_{\hat{d}}^* = \beta/(\lambda + \beta)$ , under four different assumptions about patch dynamics. See table 2 for details on how these assumptions alter the persistence thresholds. Mean lifetime of a patch is  $\tau = 100$ , and focal species is described by parameters  $c = 0.04830$ ,  $e = 0.0414068$ , and  $\alpha = 2$ .

ervation concern? The model we have described has the potential to address these questions.

### Acknowledgments

Financial support for the project was provided by James S. McDonnell Foundation. This is article number 2005-17583 of the Purdue University Agricultural Research Programs.

### Literature Cited

- Adler, F. R., and B. Nürnbergger. 1994. Persistence in patchy irregular landscapes. *Population Biology* 45:41–75.
- Allee, W. C. 1931. *Animal aggregations: a study in general sociology*. University of Chicago Press, Chicago.
- Anderson, R. A., and R. M. May. 1992. *Infectious diseases of humans: dynamics and control*. Oxford University Press, Oxford.
- Bascompte, J., and R. Solé. 1996. Habitat fragmentation and extinction thresholds in explicit models. *Journal of Animal Ecology* 55: 61–76.
- Bevens, M., and C. Flather. 1999. Numerically exploring habitat fragmentation effects on populations using cell-based coupled map lattices. *Theoretical Population Biology* 65:465–473.
- 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.
- Crone, E. E., D. Doak, and J. Pokki. 2001. Ecological influences on the dynamics of a field vole metapopulation. *Ecology* 82:831–843.
- Diekmann, O., J. A. P. Heesterbeek, and J. A. J. Metz. 1990. On the definition and the computation of the basic reproduction ratio in models for infectious diseases in heterogeneous population. *Journal of Mathematical Biology* 28:365–382.
- Durrett, R., and S. A. Levin. 1994. The importance of being discrete (and spatial). *Theoretical Population Biology* 46:363–394.
- Fahrig, L. 1992. Relative importance of spatial and temporal scales in a patchy environment. *Theoretical Population Biology* 41:300–314.
- Feng, Z., and Y. DeWoody. 2004. Conservation thresholds derived from metapopulation models. Pages 49–68 in R. K. Swihart and J. E. Moore, eds. *Conserving biodiversity in agricultural landscapes: model-based planning tools*. Purdue University Press, West Lafayette, IN.
- Fischer, M. 2001. Landscape dynamics can accelerate metapopulation extinction. *Trends in Ecology & Evolution* 16:225–226.
- Gilpin, M. E., and J. M. Diamond. 1981. Immigration and extinction probabilities for individual species: relation to incidence functions and species colonization curves. *Proceedings of the National Academy of Sciences of the USA* 78:392–396.
- Gyllenberg, M., and I. Hanski. 1997. Habitat deterioration, habitat destruction, and metapopulation persistence in a heterogeneous landscape. *Theoretical Population Biology* 52:198–215.
- Hanski, I. 1992. Inferences from ecological incidence functions. *American Naturalist* 139:657–662.
- . 1994. A practical model of metapopulation dynamics. *Journal of Animal Ecology* 63:151–162.
- . 1998. Metapopulation dynamics. *Nature* 396:41–49.
- . 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. *Oikos* 87:209–219.
- Hanski, I., and O. Ovaskainen. 2000. The metapopulation capacity of a fragmented landscape. *Nature* 404:755–758.
- Hanski, I., and C. D. Thomas. 1994. Metapopulation dynamics and conservation: a spatially explicit model applied to butterflies. *Biological Conservation* 68:167–180.
- Hanski, I., M. Kuussaari, and M. Nieminen. 1994. Metapopulation structure and migration in the butterfly *Melitaea cinxia*. *Ecology* 75:747–762.
- Hanski, I., A. Moilanen, and M. Gyllenberg. 1996. Minimum viable metapopulation size. *American Naturalist* 147:527–541.
- Hill, M. F., and H. Caswell. 1999. Habitat fragmentation and extinction thresholds on fractal landscapes. *Ecology Letters* 2:121–127.
- Horn, R. A., and C. R. Johnson. 1985. *Matrix analysis*. Cambridge University Press, New York.
- Johst, K., R. Brandl, and S. Eber. 2002. Metapopulation persistence in dynamic landscapes: the role of dispersal distance. *Oikos* 98: 263–270.
- Keymer, J. E., P. A. Marquet, J. X. Velasco-Hernández, and S. A. Levin. 2000. Extinction thresholds and metapopulation persistence in dynamic landscapes. *American Naturalist* 156:478–494.
- Lande, R. 1987. Extinction thresholds in demographic models of territorial populations. *American Naturalist* 130:624–635.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomology Society of America* 15:237–240.
- Marquet, P. A., and J. K. Velasco-Hernández. 1997. A source-sink patch occupancy metapopulation model. *Revista Chilena de Historia Natural* 70:371–380.
- Marquet, P. A., J. K. Velasco-Hernández, and J. E. Keymer. 2003. Patch dynamics, habitat degradation, and space in metapopulations. Pages 239–254 in G. A. Bradshaw and P. A. Marquet, eds. *How landscapes change: human disturbance and ecosystem fragmentation in the Americas*. Springer, New York.
- Merriam, G., K. Henein, and K. Stuart-Smith. 1991. Landscape dynamics models. Pages 399–416 in M. G. Turner and R. H. Gardner, eds. *Quantitative methods in landscape ecology*. Springer, New York.
- Moilanen, A., and I. Hanski. 1995. Habitat destruction and coexistence of competitors in a spatially realistic metapopulation model. *Journal of Animal Ecology* 64:141–144.
- Ovaskainen, O., and I. Hanski. 2001. Spatially structured metapopulation models: global and local assessment of metapopulation capacity. *Theoretical Population Biology* 60:281–302.
- Tilman, D., C. L. Lehman, and C. Yin. 1997. Habitat destruction, dispersal, and deterministic extinction in competitive communities. *American Naturalist* 149:407–435.
- With, K. A., and T. O. 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.

Associate Editor: Donald L. DeAngelis  
Editor: Jonathan B. Losos