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Transient Dynamics in Metapopulation Response to Perturbation

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Transient time in population dynamics refers to the time it takes for a population to return to population-dynamic equilibrium (or close to it) following a perturbation in the environment or in population size. Depending on the direction of the perturbation, transient time may either denote the time until extinction (or until the population has decreased to a lower equilibrium level), or the recovery time needed to reach a higher equilibrium level. In the metapopulation context, the length of the transient time is set by the interplay between population dynamics and landscape structure. Assuming a spatially realistic metapopulation model, we show that transient time is a product of four factors: the strength of the perturbation, the ratio between the metapopulation capacity of the landscape and a threshold value determined by the properties of the species, and the characteristic turnover rate of the species, adjusted by a factor depending on the structure of the habitat patch network. Transient time is longest following a large perturbation, for a species which is close to the threshold for persistence, for a species with slow turnover, and in a habitat patch network consisting of only a few dynamically important patches. We demonstrate that the essential behaviour of the *n*-dimensional spatially realistic Levins model is captured by the one-dimensional Levins model with appropriate parameter transformations. © 2002 Elsevier Science (USA)

Key Words: **metapopulation dynamics; transient time; habitat loss; extinction time; extinction debt.**

1. INTRODUCTION

Natural populations are continuously bombarded by environmental hazards of various kinds and magnitudes. Population dynamic models typically assume that such environmental effects are manifested in time-varying parameter values (Nisbet and Gurney, 1982; Renshaw, 1991; Lande, 1993). In some cases, parameter values may undergo a more permanent and possibly large change. An example is a situation where the carrying capacity of the environment is permanently reduced due to habitat loss. In such cases, an interesting question to ask is how fast the population will approach the new equilibrium state. In a community context, Brooks *et al.* (1999) estimated that it takes roughly 50 years for half of the eventual bird extinctions to occur in 1000 ha fragments of tropical forest following their isolation. The same question may be asked following a major perturbation in population size. For instance, a cold winter may kill a large fraction of individuals, as happened to resident bird populations in the UK in winter 1963, after which it took about 5 years for the song thrush populations to recover (Pimm, 1991).

Population dynamics, especially the equilibrium states and their stability, have traditionally been analysed with mathematical models defined as differential equations or

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difference equations. In this paper we will apply a differential-equation-based metapopulation model to address questions about the transient dynamics in metapopulation response to perturbations. Typically, differential equations predict exponential convergence towards an equilibrium state. As an example, consider the widely applied model of logistic population growth given as

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right), \tag{1}$$

where r is the intrinsic rate of population increase and K is the carrying capacity of the environment. Starting with a small population size N_0, initial growth is exponential with rate r, so that the size of the population at time t is given as $N(t) \approx N_0 \exp(rt)$. When the size of the population approaches the carrying capacity, population growth slows down and eventually converges exponentially to the carrying capacity K, again with a rate proportional to r. Exponential growth and exponential convergence are characteristic of differential equations that are linear around an equilibrium state. The rate of convergence is given by the linear coefficient, or in the case of an n-dimensional model, by the largest eigenvalue of the coefficient matrix. In the case of complex eigenvalues, the approach is oscillatory with exponentially decreasing amplitude. However, convergence towards an equilibrium state may be slower than exponential if the underlying set of equations is essentially non-linear around the equilibrium state. This happens in the current context, if the metapopulation capacity of the habitat patch network (metapopulation theoretic analogue of the carrying capacity; Hanski and Ovaskainen, 2000, Section 3) is close to the threshold value for deterministic persistence. In this case, the set of differential equations is essentially quadratic, leading to slow convergence, the metapopulation size approaching the equilibrium state as $1/t$.

In this paper, we analyse models of classical metapopulation dynamics, that is, we consider highly fragmented landscapes and assume that long-term persistence of the focal species is based on compensation of local extinctions by recolonizations of currently empty habitat patches by migrants from extant local populations. The basic model is due to Levins (1969, 1970), who assumed an infinitely large network of identical and equally connected habitat patches. Using the Levins model, researchers have drawn attention to the delayed extinction of species following habitat loss, dubbed extinction debt (Tilman *et al.*, 1994; Hanski *et al.*, 1996; Tilman and Lehman, 1997; Hanski and Ovaskainen, 2002). Previous studies have examined the threshold condition for persistence as a function of the intrinsic properties of the species and the amount of habitat that is left in the environment. However, these studies have not attempted to quantitatively analyse the length of the transient time, defined as the time it takes for the species to go extinct. Earlier work focusing on the length of the transient has concentrated largely to long-term non-equilibrium behaviour due to non-linearities in the dynamics of local populations (Hastings, 1998; Kaneko, 1998), in contrast to the present case where transient behaviour is caused by an external perturbation represented by a non-equilibrium initial condition.

The Levins model is very simple in ignoring the structure of local populations, the explicit spatial structure of the metapopulation, and stochasticity. All these three elements have been considered in separate studies. Deterministic models with the size structure of local populations have been analysed mathematically, e.g., by Hastings and Wolin (1989), Gyllenberg and Hanski (1992) and Diekmann *et al.* (1998), deterministic models with explicit spatial structure but no population size structure by Adler and Nüernberger (1994) and Hanski and Ovaskainen (2000) and stochastic models with no population size structure nor spatial structure by Gurney and Nisbet (1978) and Hernández-Suárez *et al.* (1999). More complicated models, like stochastic models with explicit spatial structure, have been quantitatively analysed mainly through numerical studies (Hanski, 1994; Day and Possingham, 1995; Frank and Wissel, 1998).

In this paper, we focus on the spatial structure of classical metapopulations. Following Hanski and Gyllenberg (1997), we assume that the habitat patch network consists of n patches with given areas and spatial locations. The extinction proneness of a local population is assumed to decrease with increasing patch area, and the colonization of an empty patch is assumed to become more likely with increasing connectivity to extant populations. These assumptions specify how the dynamics of the metapopulation depend on the structure of the fragmented landscape (Hanski, 1994, 1999).

Our analysis demonstrates that the essential behaviour of the n-dimensional spatially realistic Levins model is described well by the simple one-dimensional Levins model given the appropriate parameter transformations. The extinction and colonization rate parameters of the Levins model are adjusted by factors depending on the interplay between the structure of the habitat patch network and the properties of the species. We show that two factors are needed to describe the effect of the spatial structure of the habitat patch

network. These are the metapopulation capacity of the network, and the effect of the network on the characteristic turnover rate of the species. Based on these findings, we conclude that part of the criticism voiced against the "oversimplified" Levins model (Harrison, 1991, 1994) is not valid. Interpreted in an appropriate way, the one-dimensional Levins model may still be considered as a relevant tool to address a range of ecologically interesting phenomena even in the spatially realistic context.

Our paper is structured in the following manner. The length of the transient time in the simple one-dimensional Levins model is analysed in Section 2. Section 3 introduces the n-dimensional spatially realistic Levins model, and Section 4 shows how the spatially realistic model may be transformed to the one-dimensional model. In Section 5, we apply the transformation to make inferences about the transient time in the spatially realistic model via the results obtained for the one-dimensional model in Section 2. The proofs of the theorems are given in the appendix.

2. THE LEVINS MODEL

The fundamental idea of metapopulation persistence in a balance between stochastic local extinctions and recolonizations of empty patches is captured in the well-known metapopulation model of Levins (1969, 1970). This model assumes an infinitely large network consisting of equally large and equally connected habitat patches, which have two possible states, occupied or empty. The size of the metapopulation is measured by the fraction of patches that are occupied at time t, $0 \leqslant p(t) \leqslant 1$. The existing local populations contribute to the pool of migrants, which are spread out evenly across the entire network. The migrants encounter empty patches in proportion to the number of empty patches. Changes in $p(t)$ are given by

$$\frac{dp}{dt} = cp(1-p) - ep = (c-e)p - cp^2, \qquad (2)$$

where c and e are the colonization and extinction rate parameters, respectively. We note that the Levins model is identical with model (1) for logistic population growth with parameter transformations $r = c - e$ and $K = 1 - e/c$.

An occupancy state p^* for which Eq. (2) is zero is called an equilibrium state. For $c \leqslant e$ metapopulation extinction ($p^* = 0$) is the only equilibrium state, whereas for $c > e$ there is, in addition, a positive equilibrium state given by $p^* = 1 - e/c$.

The Levins model is simple enough to be solved explicitly. Assuming that the fraction of occupied patches at time $t = 0$ is $p(0) = p_0$, the fraction of occupied patches at any time t is given by

$$p(t) = \left\{ \begin{array}{ll} [\frac{1}{p_0}\exp(-(c-e)t) & \\ \quad + \frac{c}{c-e}(1-\exp(-(c-e)t))]^{-1} & \text{for } c \neq e, \\ [\frac{1}{p_0} + et]^{-1} & \text{for } c = e. \end{array} \right\} \qquad (3)$$

If $c > e$, the system converges exponentially to the positive equilibrium state $p^* = 1 - e/c$. If $c \leqslant e$, the system converges to the trivial equilibrium state ($p^* = 0$). For $c < e$, convergence is exponential, whereas in the singular case ($c = e$) the system behaves as $p \sim 1/t$.

This paper is aimed at deriving estimates for the transition time $T(p_0, p_1)$, defined as the time it takes for the metapopulation to move from state p_0 to another state p_1. In the one-dimensional Levins model, analytical expressions for $T(p_0, p_1)$ may be given based on Eq. (3). However, as our main interest will be in the spatially realistic version of the Levins model, where it is not possible to obtain such expressions, we will derive simple approximations to be used in Section 5.

Let us first consider the case $c < e$, for which $p^* = 0$ is the only equilibrium state. It is clear that the term $(c-e)p$ is negligible with respect to $-cp^2$ in Eq. (2) provided that $p(t) \gg d_c = (e-c)/c$, and thus during this far-away (from the equilibrium state) phase the solution behaves qualitatively as $p(t) = 1/(ct + 1/p_0)$. On the other hand, if $p(t) \ll d_c$, model (2) operates in the asymptotic phase, in which the linear term $(c-e)p$ determines the qualitative behaviour, now given by $p(t) = p_0 \exp((c-e)t)$. The analysis may be greatly simplified by considering the far-away and asymptotic phases separately. Around the critical distance d_c from the equilibrium state neither of the phases dominates the other one, and hence ignoring the other component will influence the quantitative result. However, even in this region the qualitative behaviour of the model remains relatively unchanged in spite of the simplification.

Employing similar reasoning to the case $c > e$, we arrive at the following algorithm for estimating the transient time. First, determine the distance d between the current state and the nearest equilibrium state (there may be two of them, including the trivial one).

If $d > d_c = |c - e|/c$, the model is said to be in its far-away phase. If $d < d_c$, the model is said to be in its asymptotic phase, in which case p^* is defined to be the equilibrium state that is closest to the current state. Note that if $c > e$, the asymptotic phase close to the unstable trivial equilibrium state ($p^* = 0$) corresponds actually to the exponential growth away from the equilibrium state.

Transient time may then be estimated as

$$T(p_0, p_1) \approx \begin{cases} \gamma_I(p_0, p_1)/c & \text{in far-away phase,} \\ \gamma_L(p_0, p_1)/|c - e| & \text{in asymptotic phase,} \end{cases} \tag{4}$$

where $\gamma_I(p_0, p_1) = 1/|p_1 - p^*| - 1/|p_0 - p^*|$, and $\gamma_L(p_0, p_1) = |\ln|p_0 - p^*| - \ln|p_1 - p^*||$, the former one measuring distance from the equilibrium state in the sense of inverses, the latter one in the sense of logarithms. Note that $|p_0 - p^*|$ is the distance between the current and the equilibrium states, which can be interpreted as the strength of the disturbance, whereas $|p_1 - p^*|$ is an error term determining how close to the equilibrium solution we want the model to converge before equilibrium is considered to have been reached. If the solution changes the phase at p_c (passes through the critical distance d_c or passes through a point at which the trivial and non-trivial equilibria are at the same distance), the estimates given for the two phases should simply be added together as $T(p_0, p_c) + T(p_c, p_1)$.

The estimates given above for the transient time are illustrated in Fig. 1, where we show the exact value, the estimate (Eq. (4)), as well as simulation results for a range of different situations. The estimates are accurate enough to capture the essential behaviour of the transient dynamics as given by the Levins model. Furthermore, the average transient time in 200 simulations using a network of 30 identical habitat patches is well predicted by the model (Fig. 1), with the exception of a species for which the perturbed environment is close to (either above or below) the threshold for persistence

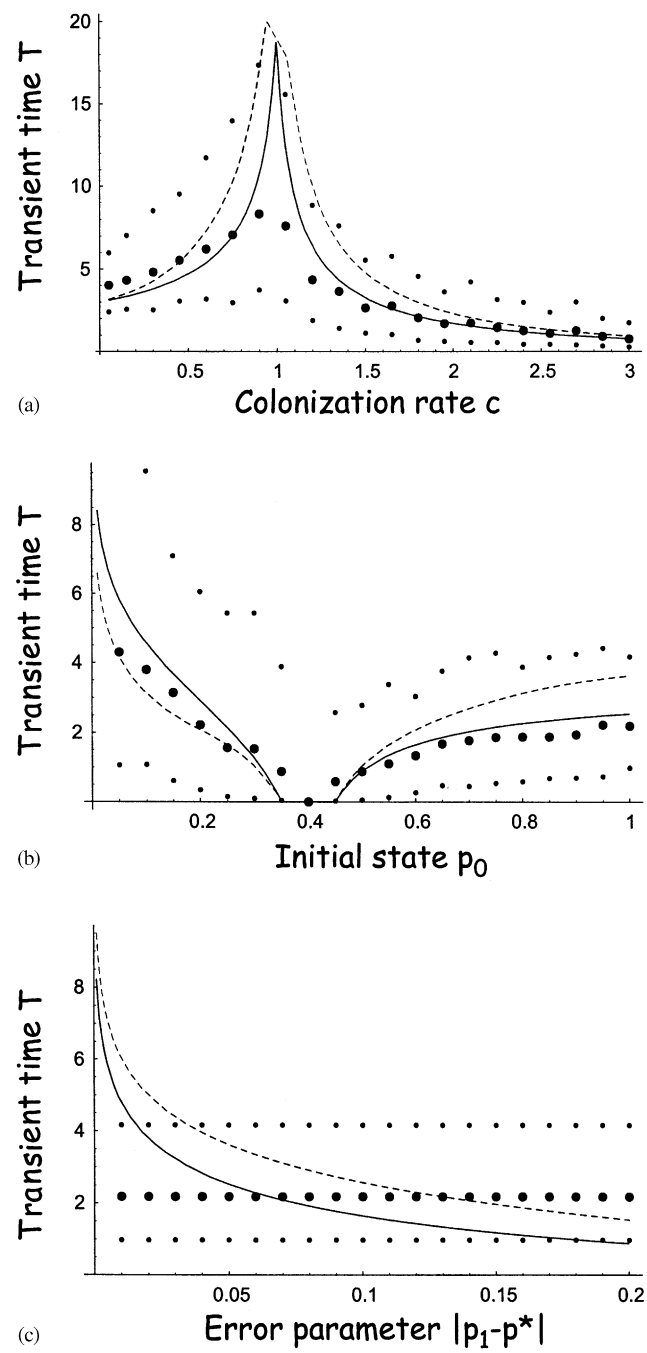

FIG. 1. Transient time according to the (spatially implicit) Levins model. Solid line shows the exact value (according to Eq. (3)), dashed line the estimate (Eq. (4)), and dots the average and 90% confidence intervals of 200 simulations in a network of 30 identical habitat patches. The parameters were fixed to the following values (unless used as a variable): extinction rate $e = 1$, colonization rate $c = \frac{5}{3}$, initial state $p_0 = 1$, and error term $|p_1 - p^*| = 0.05$. The parameter values correspond to metapopulation persistence at an equilibrium state with $p^* = 0.4$. The parameters for the simulation model were chosen so that the simulation would correspond to the spatially implicit Levins model if the number of patches would approach infinity. The simulations were run until the equilibrium value p^* was passed for the first time. Transient time is plotted against **a** the colonization rate c, **b** the initial state p_0, and **c** the error term $|p_1 - p^*|$. In panel **b**, those simulation replicates with $p_0 < p^*$ that went extinct before passing the equilibrium value were excluded. In panel **c**, the simulation results do not depend on the error parameter.

(the peak in Fig. 1a). However, even in this case the qualitative behaviour of the stochastic and deterministic models coincide: the expected length of the transient time is the largest for a species for which the perturbed environment is close to the threshold for persistence. This result is independent of the number of habitat patches, though the variance in the transient time increases with decreasing number of patches.

3. THE SPATIALLY REALISTIC LEVINS MODEL

A simple spatially realistic metapopulation model can be constructed by adding to the Levins model the effects of habitat patch area on extinction rate and connectivity on colonization rate (Hanski, 1999). Assuming a finite number n of patches with given areas and spatial locations, and denoting by $p_i(t)$ the probability that patch i is occupied, the deterministic mean-field approximation for the underlying Markov process is given by

$$\frac{dp_i}{dt} = C_i(p)(1 - p_i) - E_i p_i. \tag{5}$$

Here, C_i are the colonization rates of empty patches and E_i are the extinction rates of extant populations (Hanski and Gyllenberg, 1997).

We will assume that $E_i = e/A_i^{\zeta_{ex}}$, where e is the extinction rate parameter and the scaling factor $\zeta_{ex} \geqslant 0$ describes how sensitive the extinction process is with respect to patch area. This assumption is justified on the grounds that large patches tend to have large populations with a small risk of extinction (Hanski, 1999, and references therein). Furthermore, we will assume that the contributions of the existing populations to the population-dynamic connectivity of patch i depend on the areas of the respective habitat patches and on their distances from patch i as

$$S_i(p(t)) = \sum_{j \neq i} A_j^{\zeta_{em}} \exp(-\alpha d_{ij}) p_j(t), \tag{6}$$

where $1/\alpha$ gives the average colonization distance, d_{ij} is the distance between patches i and j, and $\zeta_{em} \geqslant 0$ is a scaling factor associated with the emigration process. This measure is based on the argument that emigration from patch j, when the patch is occupied, increases with patch area, and the contribution of patch j to immigration to patch i decreases exponentially with distance d_{ij} (Hanski, 1999). The colonization rate is given as $C_i(p(t)) = cA_i^{\zeta_{im}} S_i(p(t))$, where c is the colonization rate parameter and ζ_{im} is a scaling factor associated with the immigration process.

We change to matrix notation by defining the non-negative "landscape" matrix M with elements $m_{ij} = A_i^{\zeta_{ex}+\zeta_{im}} A_j^{\zeta_{em}} \exp(-\alpha d_{ij})$ for $j \neq i$ and $m_{ii} = 0$. In this notation, the differential equation (5) is given as

$$\frac{dp_i}{dt} = E_i \left[\frac{1}{\delta} (Mp)_i (1 - p_i) - p_i \right], \tag{7}$$

where $\delta = e/c$ is the ratio of the extinction and colonization rate parameters. Thus, the equilibrium states are given as fixed points of the map $p \to f(p)$, defined by (Ovaskainen and Hanski, 2001)

$$f_i(p) = (Mp)_i / ((Mp)_i + \delta). \tag{8}$$

Hanski and Ovaskainen (2000) coined the term metapopulation capacity λ_M for the leading eigenvalue of matrix M. A non-trivial equilibrium state of Eq. (5) exists if and only if $\lambda_M > \delta$, in which case the non-trivial equilibrium state is unique and stable and the trivial equilibrium state is unstable. In biological terms, metapopulation capacity describes the capacity of the habitat patch network to support long-term persistence of the focal species. Metapopulation capacity increases with increasing number of habitat patches, with increasing patch areas, and with increasing connectivity between the patches. The threshold value for persistence is set by the species parameter δ, which decreases with the increasing ability of the species to persist as local populations and with the increasing ability of the species to colonize empty habitat. Furthermore, the relative value of patch i (the contribution of patch i to the metapopulation capacity) is given as $V_i = x_i y_i$, where x and y are the right and the left leading eigenvectors of matrix M, scaled as $y^{\mathrm{T}} x = 1$ (Hanski and Ovaskainen, 2000; Ovaskainen and Hanski, 2001). The relative value of a patch increases with increasing patch area and with increasing connectivity of the patch.

4. THE ONE-DIMENSIONAL TRANSFORMATION

Our aim in this chapter is to show that the essential behaviour of the n-dimensional spatially realistic Levins model (Eq. (5)) may be captured by the one-dimensional Levins model (Eq. (2)) with appropriately transformed parameter values. We start by noting that both models always converge to an equilibrium state. In general, an n-dimensional system of differential equations could

also show other types of limiting behaviour, like cycles or chaos. However, in the present case such behaviour is not possible. This assertion is made precise in the following theorem, which has been proved in the epidemiological context by Lajmanovich and Yorke (1976).

THEOREM 4.1. *Let $\lambda_M > \delta$ and let $p(t)$ be the solution to the system of differential equation* (7) *with the initial condition $p(0) = p_0$, where $0 \neq p_0 \in [0,1]^n$. Then $\lim_{t\to\infty} p_i(t) = p_i^*$ where p^* is the unique fixed point of Eq.* (8). *If $\lambda_M \leqslant \delta$, then $\lim_{t\to\infty} p_i(t) = 0$ for all i.*

As will be justified below, an appropriate way to transform the n-dimensional model to a one-dimensional model is obtained by considering a weighted average of the patch occupancy probabilities, the weights being the respective patch values. Letting $\tilde{p}$ denote the weighted average $\tilde{p} = \sum_i V_i p_i$, we will argue that the rate of change in $\tilde{p}$ is approximately given by

$$\frac{d\tilde{p}}{dt} \approx \tilde{c}\tilde{p}(1-\tilde{p}) - \tilde{e}\tilde{p}, \tag{9}$$

where the transformed parameters $\tilde{c}$ and $\tilde{e}$ are defined as $\tilde{e} = 1/(\sum_i V_i/E_i)$ and $\tilde{c} = \tilde{e}\lambda_M/\delta$, and the initial condition $p(0) = \tilde{p}_0$ is given by $\tilde{p}_0 = \sum_i V_i(p_0)_i$. It is helpful to decompose $\tilde{e}$ as $\tilde{e} = e/\omega$, where e is the species-specific extinction rate parameter and $\omega = \sum_i V_i A_i^{ex}$ describes how the spatial structure of the network affects the transformed extinction rate.

Before giving mathematical justification for Eq. (9), we start by noting that the transformation is obtained by forcing the one-dimensional model to mimic the behaviour of the n-dimensional model in two ways. First, in the transformed model, the equilibrium occupancy level is given by $\tilde{p}^* = 1 - \delta/\lambda_M$, which approximates well the averaged equilibrium state of the n-dimensional model (Hanski and Ovaskainen, 2000). Second, in the original homogeneous Levins model, $1/e$ gives the expected lifetime of an occupied patch. In the transformed model, $1/\tilde{e}$ gives the average lifetime of an occupied patch, the average being weighted by the patch values.

The justification for the transformation given by Eq. (9) will be given by the two theorems to follow. In the first one, we show that the transformed model is able to approximate the asymptotic response time of the n-dimensional model for the case $\lambda_M \neq \delta$, and in the second one, we show that the transformation approximates the behaviour of the full model also in the singular case $\lambda_M = \delta$.

Let us first define the asymptotic response time for the spatially realistic Levins model as follows.

DEFINITION 4.1. Let $\lambda_M \neq \delta$. The characteristic response time T is defined as $T = 1/|\lambda_1|$, where λ_1 is the leading eigenvalue of matrix B, where $p' = Bp$ is the linearization of map (5) shifted to the equilibrium state p^*. The characteristic rate of response is defined as $1/T$.

To see that the definition makes sense, we note that the leading eigenvalue of the linearized system gives the slowest component present in the dynamics of the original system near the equilibrium state, and thus in the general case the solution approaches the equilibrium state qualitatively as $\exp(-t/T)$.

THEOREM 4.2. *The characteristic rate of response satisfies*

$$1/T = |\tilde{c} - \tilde{e}| + \mathcal{O}(\lambda_M - \delta)^2. \tag{10}$$

As the linearization of map (9) (shifted to the equilibrium state p^*) is given by $\tilde{p}' = (\tilde{c} - \tilde{e})\tilde{p}$, we conclude that the transformation is able to approximate the asymptotic behaviour of the n-dimensional model.

The next theorem shows that the transformation approximates the behaviour of the n-dimensional model also when $\lambda_M = \delta$. In this singular case, the dynamical system described by the differential equation (7) is non-hyperbolic, and thus stability is not determined by the linearization, but by higher-order terms. The behaviour of the model is characterized in the following theorem.

THEOREM 4.3. *Let $\lambda_M = \delta$. Then for any initial state p_0, there is either a t_0 such that as $t \to \infty$,*

$$p(t) = \frac{x}{k(t+t_0)} + \mathcal{O}(1/t^2), \tag{11}$$

where $k = \tilde{e}\sum_i V_i x_i$ and x denotes the right leading eigenvector of matrix M, or $p(t) = \mathcal{O}(\exp(-\gamma t))$, where $\gamma > 0$ is a constant.

The first and more probable alternative in the theorem corresponds to the behaviour of the system in the centre manifold, whereas the latter one corresponds to the singular case in which the initial state p_0 happens to be purely in the stable manifold. By Theorem 4.3, $\tilde{p} = 1/(\tilde{e}(t+t_0)) + \mathcal{O}(1/t^2)$, which coincides with Eq. (3) for $e = c$.

Figure 2 depicts metapopulation dynamics according to the spatially realistic Levins model (Eq. (5)) and the one-dimensional approximation (Eq. (9)). The three habitat patch networks used as examples were chosen

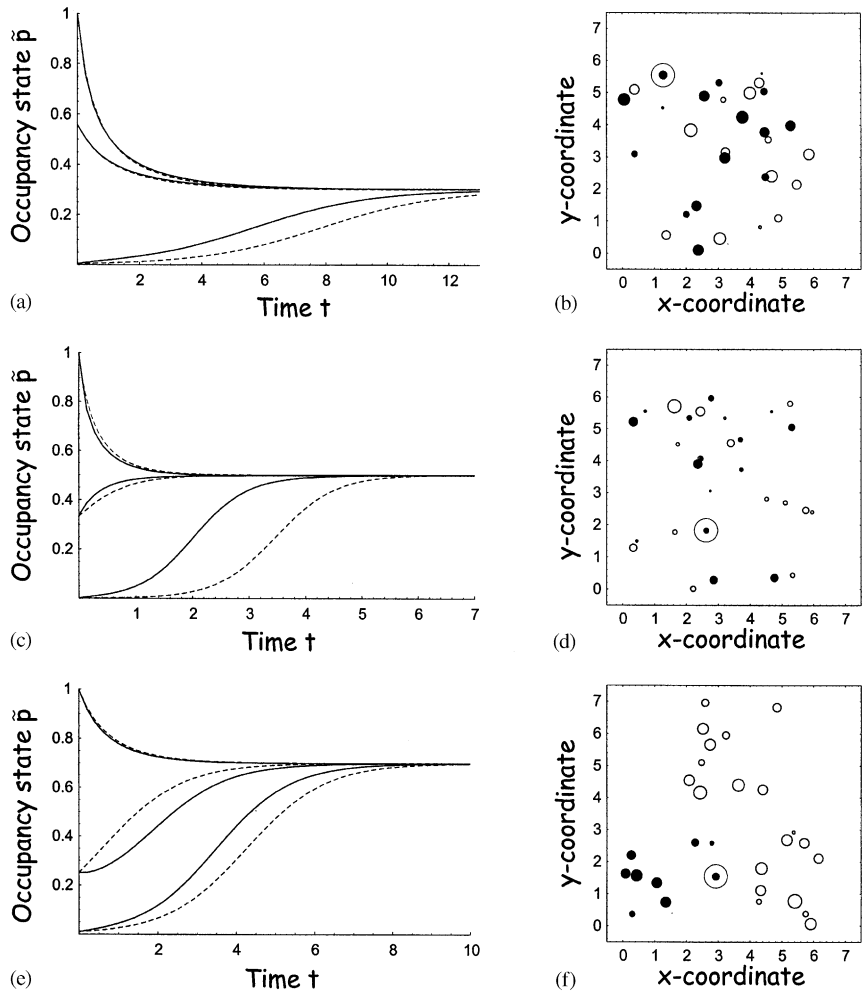

FIG. 2. A comparison between the spatially realistic Levins model (Eq. (5)) and its one-dimensional approximation (Eq. (9)). The habitat patch networks **b**, **d** and **f** (corresponding to metapopulation dynamics depicted in panels **a**, **c** and **e**) were chosen to be heterogeneous both in patch areas and locations, each consisting of 30 patches in a 7×7 square. The average colonization distance was set to $1/\alpha = 1$. In habitat patch networks **b** and **d**, the patches are randomly located within the square, whereas in panel **f** the habitat patch network consists of three clusters of 10 patches each. The solid lines show the weighted average of the patch specific occupancies according to the spatially realistic Levins model, weights being the relative patch values. The dashed lines show the occupancy state according to the one-dimensional approximation. Three different initial conditions were used: a single patch occupied (circled patch), 10–15 patches occupied (filled patches), and all patches occupied. The parameter values where chosen to be $c = 1, \zeta_{ex} = 1, \zeta_{em} = 1, \zeta_{im} = 0$ and $\delta = 0.7\lambda_M$ (panel **a**), $\delta = 0.5\lambda_M$ (panel **c**), $\delta = 0.3\lambda_M$ (panel **e**).

to include considerable variation in patch sizes and connectivities. Although the habitat patch networks and the initial states in these examples are highly heterogeneous, the approximation is typically able to capture the essential behaviour of the spatially realistic model. The only exception occurs when the initial condition is chosen so that only a marginal patch (the relative value of the circled patch in panel **d** is $V_i \approx 6 \times 10^{-4}$) is occupied and all others are empty. The reason for the failure of the one-dimensional approximation in this case is easy to understand. The approximation assumes that the n-dimensional model is sufficiently close to its dominant behaviour, where the occupancy state is roughly proportional to the leading eigenvector (Ovaskainen and Hanski, 2001). This is not the case in the example where the quantitative approximation fails. However, even in this extreme case, the qualitative behaviour of the approximation is correct. We emphasize that Fig. 2 does not show the behaviour of the occupancy probabilities of individual habitat patches but the weighted average $\tilde{p}$ of these probabilities.

5. THE LENGTH OF THE TRANSIENT TIME

We will next utilize the transformation derived in the previous section to make inferences about the length of the transient time in metapopulation response to perturbation. To do this, we first transform the spatially realistic Levins model to the one-dimensional model with parameters $\tilde{e}$ and $\tilde{c}$ and initial value $\tilde{p}_0$, and then use Eq. (4) to obtain an estimate for the length of the transient time.

In the one-dimensional model the system was said to be in an asymptotic phase (far-away phase) if the initial value was close enough to (far enough from) the nearest equilibrium state. As $\tilde{p}$ is defined as a weighted average of the patch occupancy probabilities, it is natural to measure distances between two occupancy states in the spatially realistic Levins model in the weighted L_1-norm:

$$\|p_1 - p_2\| = \sum_i V_i |(p_1)_i - (p_2)_i|. \tag{12}$$

Applying the transformation (Eq. (9)) to Eq. (4), we obtain the following algorithm for the estimation of the length of the transient time. First, determine the distance $d = \|p - p^*\|$ between the current state p and the (nearest) equilibrium state p^*. If d is greater than a critical distance given by $d_c = |\lambda_M - \delta|/\lambda_M$, the model is said to be in its far-away phase. If $d < d_c$, the model is said to be in its asymptotic phase, and p^* is set to be that equilibrium state which is closest to the current state. The transient time is then given by

$$T(p_0, p_1) = \begin{cases} \gamma_I(p_0, p_1)(\omega/e)(\delta/\lambda_M) & \text{in far-away phase,} \\ \gamma_L(p_0, p_1)(\omega/e)(\delta/|\lambda_M - \delta|) & \text{in asymptotic phase,} \end{cases} \tag{13}$$

where $\gamma_I(p_0, p_1) = 1/\|p_1 - p^*\| - 1/\|p_0 - p^*\|$, and $\gamma_L(p_0, p_1) = |\ln\|p_0 - p^*\| - \ln\|p_1 - p^*\||$. In Eq. (13), the factor γ_I (or γ_L) represents the strength of the perturbation, the factor ω/e represents the species- and landscape-specific characteristic turnover time, and the remaining factor measures how close the species is to the threshold for persistence.

Figure 3 illustrates how λ_M, ω and the length of the transient time T depend on the structure of the habitat patch network. In this example, we fixed the total amount of habitat and the shapes of the distributions determining patch locations and areas, and studied how the number of habitat patches into which the fixed area was divided affects these three quantities. In Fig. 3a, λ_M decreases with increasing n. We note in passing that decreasing λ_M with increasing n is not a general result,

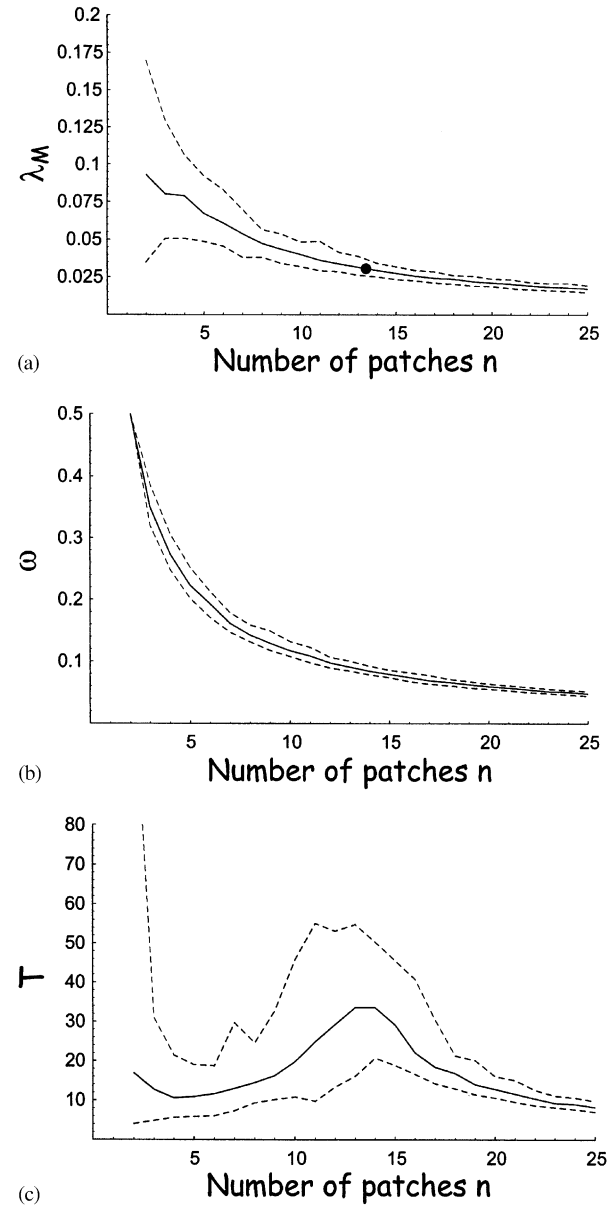

FIG. 3. The behaviour of metapopulation capacity λ_M, the parameter ω, and the length of the transient time T with respect to the structure of the habitat patch network. The $n\,(n = 2, \ldots, 25)$ habitat patches were located randomly within a 2×2 square, the average colonization distance being set to $1/\alpha = 1$. The patch areas were first derived from a uniform distribution in the interval [1,4], then scaled to yield a constant amount of habitat, $\sum_i A_i = 1$. For each value of n, 100 replicate landscapes were generated. The continuous line and the dashed lines show the median value and the 90% confidence intervals of the quantities λ_M (panel **a**), ω (panel **b**) and T (panel **c**). The parameter values where chosen to be $e = 0.03, c = 1, \zeta_{ex} = 1, \zeta_{em} = 1$ and $\zeta_{im} = 0$. The dot in panel **a** corresponds to the threshold condition $\lambda_M = \delta = 0.03$. In panel **c**, the initial condition was set to $p_i = 1\ \forall i$, and the length of the transient time was determined by the condition $\|p(T) - p^*\| = 0.05$.

because the response of λ_M to a change in n depends on how sensitive metapopulation dynamics are to patch area, as described by the value of the patch area scaling factor ζ, defined as $\zeta = \zeta_{ex} + \zeta_{em} + \zeta_{im}$ (Ovaskainen, manuscript). The metapopulation capacity of the landscape decreases with n for $\zeta > 1$, but it increases with n for $\zeta < 1$. The value of ω decreases with increasing n (Fig. 3b), demonstrating that the turnover rate is faster when the landscape consists of a large number of small patches rather than a small number of large patches. Finally, the behaviour of the transient time is non-monotonous with respect to n (Fig. 3c). The behaviour of the transient time is largely set by the distance to the threshold for persistence. The contribution of the factor ω to the transient time is relatively small, though it becomes evident for $\lambda_M \gg \delta$.

6. DISCUSSION

Our analysis shows that the transient time in the spatially realistic metapopulation model is a product of four components: the strength of the perturbation, the ratio between the metapopulation capacity of the landscape and a threshold value determined by the properties of the species, and the characteristic turnover rate of the species, adjusted by a factor depending on the structure of the habitat patch network.

First, transient time increases with the strength of the perturbation, defined by $\|p_0 - p^*\|$. Near the equilibrium state, convergence is exponential and consequently transient time behaves as a logarithm of $\|p_0 - p^*\|$, whereas further away from the equilibrium state transient time decreases in proportion to $1/\|p_0 - p^*\|$. Separation between these two phases occurs when $\|p - p^*\| \approx |\lambda_M - \delta|/\lambda_M$, and thus the far-away phase is relevant only for declining species for which the metapopulation capacity of the environment is close to the threshold for persistence. Second, transient time increases with the ratio δ/λ_M (in far-away phase) or with the ratio $\delta/|\lambda_M - \delta|$ (in asymptotic phase). Thus, in the far-away phase, the more abundant the species is in the landscape at equilibrium (the smaller the ratio δ/λ_M), the faster are the dynamics. In the asymptotic phase, the ratio $\delta/|\lambda_M - \delta|$ is largest and the dynamics the slowest for a species for which the environment after landscape change is close to (either above or below) the threshold for persistence.

Third, transient time increases with $1/e$, the characteristic turnover time of the focal species. And finally, transient time increases with the landscape index ω, which is large for a network consisting of a few large patches as compared to a network consisting of several small patches. These two latter factors may be combined as $1/\tilde{e} = \omega/e$, demonstrating that the characteristic turnover time $1/\tilde{e}$ of a particular species in a particular landscape depends in a multiplicative manner on a property of the species and on the properties of the landscape.

Hanski and Ovaskainen (2000) and Ovaskainen and Hanski (2001) have previously shown that in the spatially realistic model, the threshold condition for long-term persistence is given as $\lambda_M > \delta$, where λ_M is the metapopulation capacity of the landscape and δ is a species parameter. In the one-dimensional Levins model, the threshold condition for metapopulation persistence is given as $h > \delta$, where h is the amount of suitable habitat (Lande, 1988), suggesting that metapopulation capacity plays the same role in the spatially realistic context as the amount of habitat plays in the spatially implicit context. Furthermore, the amount of occupied habitat (out of suitable habitat) is given as $p = 1 - \delta/h$ in the one-dimensional model, and as $\tilde{p} \approx 1 - \delta/\lambda_M$ in the spatially realistic model, where $\tilde{p}$ is the weighted average of the patch-specific occupancies, the weights being the relative patch values.

In this paper, we have shown that the apparent structural similarity of the two models extends beyond the static threshold conditions to the dynamic properties of the models. Both models have a unique stable non-trivial equilibrium state, towards which the system converges starting from any initial condition but the trivial one. By appropriate parameter transformations (Eq. (9)), the one-dimensional Levins model is capable of predicting the behaviour of the spatially realistic Levins model, including both the threshold condition and the speed of the dynamics. Thus, the number of essential degrees of freedom (Dieckmann and Law, 2000) in the n-dimensional spatially realistic Levins model is one, meaning that knowing the weighted average of the current occupancy state (weights being the relative patch values) is sufficient for predicting the behaviour of the system in the future. Based on numerical aggregation techniques, Frank and Wissel (1998) analysed a stochastic metapopulation model, concluding similarly that the parameters describing the spatial configuration of the habitat patch network may be summarized by a few quantities that are sufficient for predicting the expected lifetime of the metapopulation. However, it is important to note that the one-dimensional model imitates only the average behaviour of the spatially realistic model. If occupancy probabilities in individual patches should be modelled, it is clear that it

is not possible to simplify the n-dimensional model to such a great extent.

We conclude by reiterating the practical implications of the approximations derived here for the transient time in metapopulation response to perturbation. First, the length of the transient time can be decomposed into four different factors, each having an intuitive interpretation. Second, for a given species in a given landscape, it is possible to construct a simple one-dimensional metapopulation model, which is able to predict the essential behaviour of the metapopulation in that landscape. From the viewpoint of conservation, the most important message from our analysis is that the transient time is expected to be longest for species for which the perturbed environment is close to the threshold for persistence. Considering such species is critical for conservation, as their long-term persistence is most sensitive to small changes in the environment. The fact that transient time is longest for this class of species suggests that species extinction due to habitat loss may take a long time. The amount of habitat loss and fragmentation that has deteriorated Earth's ecosystems during the past decades gives reason to assume that there is a large number of species prone to go extinct, even in the absence of any further loss and fragmentation of habitats. The only way to save these species is to produce a perturbation in the opposite direction, that is, to improve the quality of the landscape for the species that constitute the current extinction debt.

APPENDIX: PROOFS OF THEOREMS

We will need the following theorem from eigenvalue perturbation theory to prove Theorem 4.2. The proof of the theorem is given in e.g., Stewart and Sun (1990).

THEOREM A.1. *Let λ be a simple eigenvalue of matrix A, with right and left eigenvectors x and y, and let $\tilde{A} = A + F$ be a perturbation of A. Then there is a unique eigenvalue $\tilde{\lambda}$ of $\tilde{A}$ such that*

$$\tilde{\lambda} = \lambda + \frac{y^{\mathrm{T}} F x}{y^{\mathrm{T}} x} + \mathcal{O}(\|F\|)^2. \tag{14}$$

Here $\|F\|$ denotes any consistent matrix norm of F.

Proof of Theorem 4.2. The matrix B is given as $b_{ij} = (1/\delta)E_i m_{ij}(1 - p_i^*)$ for $j \neq i$, and $b_{ii} = -E_i((1/\delta)(Mp^*)_i + 1)$. If $\delta = \lambda_M$, it follows that $p^* = 0$, and consequently $b_{ij} = (1/\lambda_M)E_i m_{ij}$ for $i \neq j$ and $b_{ii} = -E_i$. We will denote this matrix by B_0. It is elementary to see that the leading eigenvalue of B_0 is zero. Furthermore, denoting by x^0 and y^0 the right and the left leading eigenvectors of matrix B_0, direct computation shows that $x^0 = x$ and that the elements of y^0 are given (up to a scaling constant) as $y_i^0 = y_i/E_i$, where x and y are the right and left leading eigenvectors of M.

For $\delta \neq \lambda_M$, we may consider the difference $F = B - B_0$, and utilize eigenvalue perturbation theory. We will consider the cases $\delta > \lambda_M$ and $\delta < \lambda_M$ separately.

First, if $\delta > \lambda_M$, $p^* = 0$, and thus $F = B - B_0$ is given by $f_{ij} = (1/\delta - 1/\lambda_M)E_i m_{ij}$ for $j \neq i$ and $f_{ii} = 0$. The claim of the theorem follows now directly from Theorem A.1.

Second, if $\delta < \lambda_M$, we may utilize the fact that p^* is a positive equilibrium state, and write $b_{ij} = E_i m_{ij} p_i^*/(Mp^*)_i$ for $j \neq i$ and $b_{ii} = -(E_i/\delta)(Mp^*)_i/p_i^*$. Defining the vector a with components $a_i = (Mp^*)_i/p_i^* - \lambda_M$, the components of F are given as $f_{ij} = E_i m_{ij}(1/(a_i + \lambda_M) - 1/\lambda_M)$ for $j \neq i$ and $f_{ii} = -E_i(a_i + \lambda_M - \delta)/\delta$. It has been shown (Ovaskainen and Hanski, 2001) that $a_i = \mathcal{O}(\lambda_M - \delta)$ and $\sum_i a_i x_i y_i = \mathcal{O}(\lambda_M - \delta)^2$, and thus the claim of the theorem follows again by Theorem A.1. ■

Proof of Theorem 4.3. Let us first write the system of differential equations (5) as $p' = Hp + R(p)$, where H is the matrix with elements $h_{ij} = E_i(m_{ij}/\lambda_M)$ for $j \neq i$, and $h_{ii} = -E_i$, and the components of the second-order term $R(p)$ are given as $R_i(p) = -E_i(Mp)_i p_i/\lambda_M$. Direct calculation shows that H has zero as a simple eigenvalue, and all the other eigenvalues have negative real part. Furthermore, denoting by x^0 and y^0 the right and left eigenvectors corresponding to the zero eigenvalue, $x^0 = x$ and the elements of y^0 are given (up to a scaling constant) as $y_i^0 = y_i/E_i$.

By elementary linear algebra, we may transform H to the Jordan canonical form as $T^{-1}HT = J$, where the first row and column of J consist of zeros, and all the eigenvalues of the remaining submatrix have negative real parts. The first column of T is given by the vector x^0, and the first row of T^{-1} is given by the vector $y^{0T}/(y^{0T}x^0)$. Letting $w = (u, v)$ denote a vector in the transformed coordinate system so that $u \in \mathbf{R}$ corresponds to the zero eigenvalue and $v \in \mathbf{R}^{n-1}$ includes the remaining components, we have $w = T^{-1}p$, and the system of differential equations is transformed to $w' = Jw + T^{-1}R(Tw)$. It is straightforward to show that $T^{-1}R(Tw) = -u^2/k + \mathcal{O}(u\|v\| + \|v\|^2)$, where k is given in the theorem. By Theorem 2.1.1 in Wiggings (1990), the dynamics of the transformed system restricted to the

centre manifold are given (for u sufficiently small) by the solution of $u' = -u^2/k + \mathcal{O}(u^3)$, i.e., $u = 0$ or $u = k/t + \mathcal{O}(1/t^2)$. Thus, by Theorem 2.1.2 in the same reference, the solution to the original problem is as given by the theorem. ■

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REFERENCES

Adler, F. R., and Nüernberger, B. 1994. Persistence in patchy irregular landscapes, *Theor. Popul. Biol.* **45**, 41–75.

Brooks, T. M., Pimm, S. L., and Oyugi, J. O. 1999. Time lag between deforestation and bird extinction in tropical forest fragments, *Conservation Biol.* **13**, 1140–1150.

Day, J., and Possingham, H. 1995. A stochastic metapopulation model with variability in patch size and position, *Theor. Popul. Biol.* **48**, 333–360.

Diekmann, O., Gyllenberg, M., Metz, J. A. J., and Thieme, H. R. 1998. On the formulation and analysis of general deterministic structured population models—I. Linear theory, *J. Math. Biol.* **36**, 349–388.

Dieckmann, U., and Law, R. 2000. Relaxation projections and the method of moments, *in* "The Geometry of Ecological Interactions" (U. Dieckmann, R. Law, and J. A. J. Metz, Eds.), pp. 412–455, Cambridge Studies in Adaptive Dynamics, Cambridge University Press, Cambridge.

Frank, K., and Wissel, C. 1998. Spatial aspects of metapopulation survival: from model results to rules of thumb from landscape management, *Landscape Ecol.* **13**, 363–379.

Gurney, W., and Nisbet, R. 1978. Single species population fluctuations patchy environments, *Am. Nat.* **112**, 1075–1090.

Gyllenberg, M., and Hanski, I. 1992. Single-species metapopulation dynamics: a structured model, *Theor. Popul. Biol.* **72**, 35–61.

Hanski, I. 1994. A practical model of metapopulation dynamics, *J. Anim. Ecol.* **63**, 151–162.

Hanski, I., 1999. "Metapopulation Ecology," Oxford University Press, Oxford.

Hanski, I., and Gyllenberg, M. 1997. Uniting two general patterns in the distribution of species, *Science* **275**, 397–400.

Hanski, I., Moilanen, A., Pakkala, T., and Kuussaari, M. 1996. The quantitative incidence function model and persistence of an endangered butterfly metapopulation, *Conservation Biol.* **10**, 578–590.

Hanski, I., and Ovaskainen, O. 2000. The metapopulation capacity of a fragmented landscape, *Nature* **404**, 755–758.

Hanski, I., and Ovaskainen O. 2002. Extinction debt at extinction threshold, *Conservation Biol.*, in press.

Hastings, A. 1998. Transients in spatial ecological models, *in* "Modeling Spatiotemporal Dynamics in Ecology" (J. Bascompte, and R. Solé, Eds.), pp. 189–198, Springer, New York.

Hastings, A., and Wolin, C. L. 1989. Within-patch dynamics in a metapopulation, *Ecology* **70**, 1261–1266.

Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation, *Biol. J. Linn. Soc.* **42**, 73–88.

Harrison, S. 1994. Metapopulations and conservation, *in* "Large-Scale Ecology and Conservation Biology" (P. J. Edwards, R. M. May, and N. R. Webb, Eds.), pp. 111–128, Blackwell Scientific Press, Oxford.

Hernández-Suárez, C. M., Marguet, P. A., and Velasco-Hernández, J. X. 1999. Threshold parameters and metapopulation persistence, *Bull. Math. Biol.* **61**, 341–353.

Kaneko, K. 1998. Diversity, stability, and metadynamics: remarks from coupled map studies, *in* "Modeling Spatiotemporal Dynamics in Ecology" (J. Bascompte, and R. Solé, Eds.), pp. 27–46, Springer, New York.

Lajmanovich, A., and Yorke, J. A. 1976. A deterministic model for gonorrhea in a nonhomogeneous population, *Math. Biosci.* **28**, 221–236.

Lande, R. 1988. Demographic models of the northern spotted owl, *Strix occidentalis caurina*, *Oecologia* **75**, 601–607.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes, *Am. Nat.* **142**, 911–927.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control, *Bull. Entomol. Soc. Am.* **15**, 237–240.

Levins, R. 1970. Extinction, *Lect. Notes Math.* **2**, 75–107.

Nisbet, R. M., and Gurney, W. S. C. 1982. "Modelling Fluctuating Populations," John Wiley & Sons, New York.

Ovaskainen, O., and Hanski, I. 2001. Spatially structured metapopulation models: Global and local assessment of metapopulation capacity, *Theor. Popul. Biol.* **60**, 281–304.

Pimm, S. 1991. "The Balance of Nature?" The University of Chicago Press, Chicago.

Renshaw, E. 1991. "Modelling Biological Populations in Space and Time," University Press, Cambridge.

Stewart, G., and Sun, J. 1990. "Matrix Perturbation Theory," Academic Press, San Diego.

Tilman, D., and Lehman, C. L. 1997. Habitat destruction and species extinction, *in* "Spatial Ecology" (D. Tilman and P. Kareiva, Eds.), pp. 233–249, Princeton University Press, Princeton.

Tilman, D., May, R. M., Lehman, C. L., and Nowak, M. A. 1994. Habitat destruction and the extinction debt, *Nature* **371**, 65–66.

Wiggings, S. 1990. "Introduction to Applied Nonlinear Dynamical Systems and Chaos," Springer-Verlag, New York.