

# Habitat Destruction, Environmental Catastrophes, and Metapopulation Extinction

Renato Casagrandi<sup>1</sup> and Marino Gatto

*Dipartimento di Elettronica e Informazione, Politecnico di Milano, Via Ponzio 34/5, 20133 Milano, Italy*

E-mail: [casagran@elet.polimi.it](mailto:casagran@elet.polimi.it), [gatto@elet.polimi.it](mailto:gatto@elet.polimi.it)

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The extinction process of fragmented populations, characterized by a small number of conspecifics inhabiting each patch, is heavily affected by natural and human disturbance. To evaluate the risk of extinction we consider a network of identical patches connected by passive or active dispersal and hosting a finite, discrete number of individuals. We discuss three types of disturbance affecting the metapopulation: permanent loss of habitat patches, erosion of existing patches, and random catastrophes that wipe out the entire population of a patch. Starting from an infinite-dimensional Markov model that fully accounts for demographic stochasticity, we reduce it to finite dimension via moment closure with negative-binomial approximation. The compact models obtained in this way account for the dynamics of the fraction of empty patches, the average number of individuals in occupied patches, and the variance of their distribution. After comparing the performance of these compact models with that of the infinite-dimensional model in the case of no disturbances, we then proceed to computing persistence–extinction boundaries as bifurcation lines of the compact models in the space of demographic and disturbance parameters. We consider bifurcations with respect to demographic and environmental parameters and contrast our results with those of previous theories. We find out that environmental catastrophes increase the risk of extinction for both frequent and infrequent dispersers, while the random loss of patches has a much larger influence on frequent dispersers. This influence can be counterbalanced by active dispersal. Local erosion of habitat fragments has a larger influence on infrequent than on frequent dispersers. We finally discuss the important synergistic effects of disturbances acting simultaneously. © 2002 Elsevier Science (USA)

**Key Words:** threshold; moment closure; bifurcation analysis; habitat loss; patch erosion; environmental disasters.

## 1. INTRODUCTION

Understanding the influence of disturbance, both natural and anthropogenic, on metapopulation persistence is of paramount importance for conservation. In fact, the occurrence of random catastrophes—such as local epidemics or abrupt abiotic changes—and the habitat destruction induced by man activities considerably

increase the extinction risk of populations living in fragmented habitats. Several modeling approaches have been adopted to describe and analyze the effect of disturbances on metapopulations (Lande, 1987; Fahrig, 1992; Gyllenberg and Hanski, 1992; Adler and Nüernberger, 1994; Olivieri *et al.*, 1995; Kareiva and Wennergren, 1995; Bascompte and Solé, 1996; Fahrig, 1997; Hill and Caswell, 1999; Gyllenberg and Hanski, 1997; Hanski and Ovaskainen, 2000). Unfortunately, the comparison between the effects induced by environmental disasters and those caused by habitat destruction has

<sup>1</sup>To whom correspondence should be addressed. Fax: +39 02 23993412.

been rarely done (Lande, 1993): studies analyzing the consequences of the first source of risk usually neglect the latter, while other studies consider the latter risk only (but see the simulation model by Fahrig, 1998, as a good exception). Therefore, in this paper we want to study and compare the effects of the various types of disturbance on metapopulations characterized by different demographic parameters and dispersal ability.

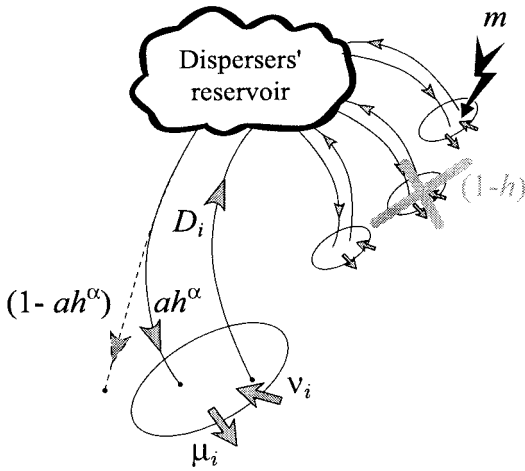
Elsewhere (Casagrandi and Gatto, 2002) we have shown the usefulness of the metapopulation models pioneered by Chesson (1981, 1984), which consider local discrete populations described by Markov chains connected by dispersal. The state variables of these systems are the probabilities that each patch hosts an integer number of individuals. Demographic stochasticity is thus naturally incorporated in the models and the population extinction corresponds to the death of the last surviving individual. For these model metapopulations (which are infinite-dimensional) it is possible to state a simple persistence criterion: the expected number  $E_0$  of successful dispersers from a patch begun with one individual and to which immigration is excluded must be greater than unity. However, this criterion, to our knowledge, cannot be easily extended to metapopulations subject to disturbance. Also, detailed statistics on local population numbers may be unavailable, thus making the infinite-dimensional Markov model unfit to describe the great majority of available metapopulation data. For this reason, here we resort to simpler models that had been already outlined in another paper (Casagrandi and Gatto, 1999). These are derived from the Markov model and describe only a few characteristics of the metapopulation under study, typically the fraction of empty patches and the average number of individuals [and their variance] in occupied locations. The simplified models have the advantage that persistence extinction boundaries in the space of model parameters can be easily found by bifurcation techniques for finite-dimensional dynamical systems (Kuznetsov, 1995). We can thus analyze the effects of both random environmental catastrophes, which hit local populations, and permanent habitat destruction. In particular, we consider two patterns of habitat destruction: random loss of entire habitat fragments and erosion of the areas of existing patches (Hanski and Ovaskainen, 2000).

The paper is organized as follows. First, we suitably modify the infinite-dimensional nonlinear Markov model of the metapopulation (introduced in Casagrandi and Gatto, 2002) to incorporate the disturbances due to environmental catastrophes and habitat destruction. Active vs passive dispersal is described by a parameter that modulates the function linking the colonization

probability with the available habitat. Subsequently, we derive finite-dimensional models through a moment closure technique (as in Anderson and May, 1978) and a negative-binomial approximation of the distribution of numbers in each patch. These approximate models describe the dynamics of at most three variables: the probability of patch occupancy and the mean and variance of abundance in occupied patches. By studying the equilibria of the finite-dimensional models and using nonlinear analysis (Kuznetsov, 1995) for systems of ordinary differential equations, we easily determine the persistence–extinction boundaries as transcritical bifurcations in the plane of two parameters: dispersal rate and intrinsic rate of population increase. Then, to evaluate the performance of the approximate models, we consider the case of no disturbance and compare the boundaries obtained from the infinite-dimensional model via the criterion  $E_0 = 1$  against those obtained via bifurcation analysis. As the performance turns out to be satisfactory, we finally proceed to studying the sensitivity of persistence–extinction boundaries to the parameters describing the intensity and frequency of disturbance, both environmental and anthropogenic. More precisely, the local carrying capacity is considered as an indicator of the extant patch size after erosion, the fraction of undestroyed patches as an indicator of permanent habitat loss, and the rate of complete destruction of local populations as an indicator of the frequency of environmental catastrophes. We consider the various kinds of disturbance both separately and as acting simultaneously and show that there can be important synergistic effects on persistence–extinction boundaries.

## 2. THE INFINITE-DIMENSIONAL MARKOV MODEL

The infinite-dimensional Markov model on which we base our analysis is an extended version of the birth–death–dispersal nonlinear system described in Casagrandi and Gatto (2002) suitably modified to take environmental and anthropic disturbances into account (Fig. 1). The state variables of the model are the probabilities  $p_i(t)$  that any patch of the infinite network of undestroyed habitat fragments be occupied by precisely  $i$  individuals ( $i = 0, 1, 2, \dots$ ). The key demographic parameters for describing the dynamics of abundance in a patch containing  $i$  individuals are the per capita rates of birth ( $v_i$ ), death ( $\mu_i$ ), and dispersal ( $D_i$ ). We assume (see again Fig. 1) that the dispersing organisms first reach a common pool and then emigrate uniformly toward the



**FIG. 1.** A schematic diagram of the model metapopulation composed by an infinite network of equal patches subject to disturbance.  $v_i$  and  $\mu_i$  are local fertility and mortality rates for populations of size  $i$ .  $D_i$  is the rate of dispersal from the patches. A fraction  $(1-h)$  of the patches is permanently destroyed because of habitat loss while some local populations can be wiped out by environmental disasters (which occur at a rate  $m$ ). The propagule rain from a common reservoir of dispersers can rescue from extinction any local population via colonization, whose success depends on the colonizing probability  $a$ , the fraction  $h$  of undestroyed patches, and the ability to search for suitable patches (described by parameter  $\alpha$ ).

patches (global dispersal). Thus the average number of dispersers per patch is given by

$$S_p(t) = \sum_{i=1}^{\infty} D_i \cdot i \cdot p_i(t).$$

However, not all of these dispersers will successfully reach another patch. In another paper (Casagrandi and Gatto, 2002) we have shown that, without habitat loss, the average number  $F(t)$  of dispersers ending up in a patch is given by the simple linear relationship

$$F(t) = a \cdot S_p(t), \quad 0 \leq a \leq 1,$$

where the colonizing probability  $a$  is an aggregate parameter negatively related to the mortality during the period spent in the common pool and proportional to the landing success of the propagules into suitable habitat. However, if the immigration from the common pool is toward a landscape on which man acts by permanently destroying part of the patches, the colonizing success depends also on the fraction  $h$  of undestroyed patches (out of the original habitat). The parameter  $h$  is an indicator of habitat loss:  $h=0$  means that landscape has been completely altered and made unsuitable for the species under study, while  $h=1$  indicates that all the

original patches are preserved. With habitat loss the average number  $F(t)$  of dispersers ending up in a patch is then given by

$$F(t) = a\phi(h) \cdot S_p(t),$$

where  $\phi(h)$  is a measure of success during colonization ( $0 = \phi(0) \leq \phi(h) \leq \phi(1) = 1$ ). More precisely, it is a monotonically increasing function of  $h$  because the probability of finding a suitable habitat before dying decreases with the decreasing amount of available habitat. The analytical form of  $\phi(h)$  depends upon the species ability to recognize suitable habitat fragments, and, in general, the following properties hold,

$$\frac{d\phi(h)}{dh} > 0, \quad \frac{d^2\phi(h)}{dh^2} \leq 0,$$

because search for a suitable habitat is often nonrandom. The last assumption implies, in fact, the concavity of  $\phi(h)$ . A simple form of  $\phi(h)$  that satisfies the above conditions is  $\phi(h) = h^\alpha$  with  $\alpha$  positive, constant, and  $\leq 1$ . The parameter  $\alpha$  is inversely related to the species ability to distinguish between suitable and unsuitable habitats:  $\alpha = 1$ , for example, means that the dispersal process is passive (e.g., through seeds). A somewhat similar approach was taken by Lande (1987), who considered the ability of dispersing animals to search up to a certain number of territories before perishing. This maximum number could be considered an indicator of colonizing ability.

In addition to the permanent disturbance represented by habitat destruction, we also consider random catastrophic disturbances that hit local populations without destroying their habitat (such as local epidemics or microclimatic vagaries). The effect of these environmental catastrophes can be incorporated in the Markov model in many ways. For example, one may imagine that, when a disaster occurs in a patch, only a fraction of the local population is killed (partial disasters; Metz, *personal communication*) or that all the individuals are unable to survive through these extreme episodes (total disasters; see Gyllenberg and Hanski, 1992; Adler and Nüernberger, 1994; Olivieri *et al.*, 1995). We follow this latter approach and introduce a single parameter  $m$ , the rate of catastrophic occurrences, to describe the phenomenon.

By considering that habitat loss reduces the chance of successfully occupying a patch (see the function  $\phi(h)$  above) and that an environmental disaster can drastically reduce the local abundance of a patch to zero, one can

modify the model discussed in Casagrandi and Gatto (2002) as

$$\dot{p}_0(t) = -ah^\alpha \cdot S_p(t) \cdot p_0(t) + (\mu_1 + D_1) \cdot p_1(t) + m \cdot (1 - p_0(t)) \quad (1a)$$

$$\begin{aligned} \dot{p}_i(t) = & [v_{i-1} \cdot (i-1) + ah^\alpha \cdot S_p(t)] \cdot p_{i-1}(t) \\ & - [(v_i + \mu_i + D_i) \cdot i + ah^\alpha \cdot S_p(t) + m] \cdot p_i(t) \\ & + (\mu_{i+1} + D_{i+1}) \cdot (i+1) \cdot p_{i+1}(t) \quad (i \geq 1) \end{aligned} \quad (1b)$$

where  $p_i(t)$ —we remind the reader—are the probabilities that a suitable patch be occupied by  $i$  individuals. Also, we assume that the rate of local demographic increase  $v_i - \mu_i$  vanishes in correspondence to a number  $K$ , which we will call the local carrying capacity. The parameter  $K$  can be considered an indicator of patch size. Thus habitat erosion, the further kind of permanent disturbance we consider, can be described as a decrease of this carrying capacity. The species habitat can in fact be destroyed not only by eliminating a fraction of the suitable patches, but also by reducing the area of the patches (Hanski and Ovaskainen, 2000). To study this case, we will consider values of the carrying capacity  $K$  that are reduced to  $(1 - \eta)K$ , where  $\eta$  is the fraction of eroded habitat.

It is worthwhile to remark that Eq. (1a), which describes how the fraction of empty patches varies through time, is Levins-like. In fact, the model proposed by Levins (1969) can be written as

$$\dot{p}_0(t) = -cp_0(t)(1 - p_0(t)) + e(1 - p_0(t)), \quad (2)$$

where  $p_0$  represents the fraction of empty patches, and  $c$  and  $e$  represent rates of colonization and extinction of occupied patches, respectively. Note that the first terms of the right-hand sides of Eqs. (1a) and (2) describe the rescue of empty patches due to dispersal and colonization while the other terms describe the extinction process. However, the rationale behind the two models is a bit different. In our model, the rescue effect depends not only upon the fraction of occupied patches but also upon their population densities via  $S_p(t)$ . Also, Eq. (1a) details the extinction process by splitting it into a demographic component and an environmental component. This latter is modeled in the same way as the second term of Levins' Eq. (2), with the rate  $m$  of catastrophes replacing Levins' extinction rate  $e$ . Instead, the demographic component accounts for the fact that only those patches that are occupied by one individual can become extinct in a short time interval. The remaining equations (1b)

describe the dynamics of numbers in occupied patches, a feature that is neglected in Levins-like models.

Performing a detailed analysis of metapopulation persistence under different disturbance scenarios with the infinite-dimensional model (1) could be possible, but is quite cumbersome for many reasons. First of all, that model consists of a set of infinite equations for the  $p_i$ 's, which is not very manageable. Even if we approximate them by truncation at say twice the carrying capacity we are anyway left with several scores of equations for values of  $K$  as small as 10 or 20. Second, an analytical expression for the equilibrium distribution, such as the closed form pointed out in Casagrandi and Gatto (2002), is unavailable if the environmental disaster rate is non-negligible. This implies that the criterion  $E_0 = 1$  ( $E_0$  being the number of successful dispersers emigrating from a patch initially occupied by one individual and to which subsequent immigration is excluded), which we used there to compute the persistence–extinction boundaries, cannot be used here as is. Third, model (1) may not be the most appropriate to match the available data collected by field biologists. In fact, it is quite difficult to record the exact dynamics of numbers in all patches and consistently derive the distribution of local abundances, while simpler information such as the frequency of empty patches and the average and variance of abundance per occupied patch may be more readily available. For all these reasons, we now introduce some approximate, more compact models that involve only a finite number of state variables.

### 3. COMPACT MODELS

A first way to derive finite-dimensional models from the infinite Markov model (1) could be that of grouping adjacent state variables of the sequence  $p_i(t)$  (where  $i = 0, 1, 2, 3, \dots$ ). The resulting grouped sequence  $p_{\mathcal{J}}$  (where  $\mathcal{J} = \text{I, II, III, IV, } \dots, N_{\max}$ ) would then represent the probability that a patch be occupied by a number of individuals within the range  $i_{\min}^{\mathcal{J}} - i_{\max}^{\mathcal{J}}$  characterizing the  $\mathcal{J}$ th class. This technique, known as the binning technique (Gilpin, 1992; Stephan and Wissel, 1994; Gilpin and Taylor, 1994; Kokko, 1996), has been successfully used to discuss the probability of extinction in linear Markovian models of populations living in homogeneous landscapes. The main reason for which we do not follow this approach here is that in a non-linear Markov model it would be quite difficult to determine the transition probabilities from one bin to another.

A second way for approximating model (1) by more compact models is that of using a moment closure technique. This approach has been successfully used over the past decades to face many ecological problems, ranging from host–parasite dynamics (Anderson and May, 1978) to biodiversity and ecosystem functioning (Norberg *et al.*, 2001). The idea, better detailed hereafter, is that of deriving from (1) the equations for the dynamics of the first few central moments of the distribution of the  $p_i$ 's. More precisely, we derive compact models that account for the extinction risk ( $p_0$ , namely the probability that a patch be empty) and the first two moments of the distribution of abundances in occupied patches.

As a first step, it is necessary to state model (1) in terms of the probabilities  $\delta_i$  conditional on a patch being occupied by one or more individuals. They are defined as

$$\delta_i = \frac{P_i}{1-p_0}. \quad (3)$$

Since the following relationship holds

$$\dot{\delta}_i = \frac{\dot{P}_i}{(1-p_0)} + \frac{\dot{p}_0}{(1-p_0)} \delta_i,$$

we obtain from Eq. (1)

$$\dot{p}_0 = [-ah^\alpha \cdot S_\delta \cdot p_0 + (\mu_1 + D_1) \cdot \delta_1 + m] \cdot (1-p_0) \quad (4a)$$

$$\begin{aligned} \dot{\delta}_i &= [v_{i-1} \cdot (i-1) + ah^\alpha \cdot (1-p_0) \cdot S_\delta] \cdot \delta_{i-1} \\ &\quad - [(v_i + \mu_i + D_i) \cdot i + ah^\alpha \cdot S_\delta - (\mu_1 + D_1) \cdot \delta_1] \cdot \delta_i \\ &\quad + (\mu_{i+1} + D_{i+1}) \cdot (i+1) \cdot \delta_{i+1}, \quad i \geq 1, \end{aligned} \quad (4b)$$

where  $\delta_0 = p_0/(1-p_0)$  and  $S_\delta$  is the average number of dispersers from occupied patches, namely

$$S_\delta = \sum_{i=1}^{\infty} D_i \cdot i \cdot \delta_i(t) = \frac{S_p}{1-p_0}.$$

Note that the dynamics of  $\delta_i$ 's (4b) does not directly depend upon the environmental disaster rate  $m$ , because these probabilities are conditional on patches being occupied. Starting from model (4), through some algebraic calculations (see Appendix for details), one can derive the equations for the dynamics of the first two central moments

$$M_\delta(t) = \sum_{i=1}^{\infty} i \cdot \delta_i(t) \quad (5)$$

$$\sigma_\delta^2(t) = \sum_{i=1}^{\infty} (i - M_\delta)^2 \cdot \delta_i(t) \quad (6)$$

which represent the conditional mean and variance of abundance in occupied patches, respectively. Truncating the infinite-dimensional model (4) at the first two moments provides

$$\dot{p}_0 = [-ah^\alpha \cdot S_\delta \cdot p_0 + (\mu_1 + D_1) \cdot \delta_1 + m] \cdot (1-p_0) \quad (7a)$$

$$\begin{aligned} \dot{M}_\delta &= \sum_{i=1}^{\infty} [v_i - \mu_i - D_i] \cdot i \cdot \delta_i \\ &\quad + ah^\alpha \cdot (1-p_0 \cdot M_\delta) \cdot S_\delta + (\mu_1 + D_1) \cdot \delta_1 \cdot M_\delta \end{aligned} \quad (7b)$$

$$\begin{aligned} \dot{\sigma}_\delta^2 &= 2 \sum_{i=1}^{\infty} (v_i - \mu_i - D_i) \cdot i \cdot (i - M_\delta) \cdot \delta_i \\ &\quad + \sum_{i=1}^{\infty} (v_i + \mu_i + D_i) \cdot i \cdot \delta_i \\ &\quad + [-ah^\alpha \cdot S_\delta \cdot p_0 + (\mu_1 + D_1) \cdot \delta_1] (\sigma_\delta^2 - M_\delta^2) \\ &\quad + ah^\alpha \cdot S_\delta \cdot (1 - 2p_0 \cdot M_\delta). \end{aligned} \quad (7c)$$

Approximate models can then be obtained by a suitable closure of the truncated model. This requires two different kinds of hypotheses. First, some specific assumptions about the density dependence of  $v_i$ ,  $\mu_i$ , and  $D_i$  have to be made to express the right-hand sides of Eqs. (7b) and (7c) as functions of  $\delta_1$  and the moments of  $\delta_i$ . Table I shows the resulting equations for density-dependent or density-independent dispersal and logistic demography, namely

$$v_i - \mu_i = r \cdot \left(1 - \frac{i}{K}\right) \quad \text{with} \quad v_i + \mu_i = \beta + \gamma \cdot i, \quad (8)$$

where the intrinsic rate of increase  $r$ , the carrying capacity  $K$ , and  $\beta$  are positive, while  $\gamma$  can also be negative (see Casagrandi and Gatto, 2002, for details).

Second,  $\delta_1$  and the moments of third order or greater must be specified as functions of  $M_\delta$  and  $\sigma_\delta^2$ . To this end, we have to assume that at any instant  $t$  the conditional distribution  $\delta_i$  equals a theoretical discrete distribution  $\Delta$  for the numbers of individuals in occupied patches, namely

$$\delta_i(t) = \Delta(i, M_\delta(t), \sigma_\delta^2(t)).$$

For example, if the theoretical distribution is specified by its first moment only (e.g., Poisson or negative binomial with fixed clumping), then  $\delta_1$ ,  $\sigma_\delta^2$ , and the third moment are functions of  $M_\delta$  (see Table II for examples) and the compact model consists of two equations which specify

**TABLE I**  
The General Structure of the Mesoscale Models for Logistic Demography and Density-Independent or Density-Dependent Dispersal

$$\begin{cases} \dot{p}_0 = (1-p_0)[(\mu_1 + D) \cdot \delta_1 - ah^x \cdot p_0 \cdot S_\delta + m] \\ \dot{M}_\delta = rM_\delta \cdot \left(1 - \frac{M_\delta}{K}\right) - \frac{r}{K} \sigma_\delta^2 + (\mu_1 + D) \cdot \delta_1 \cdot M_\delta - S_\delta \cdot [(1 - ah^x) + ah^x \cdot p_0 \cdot M_\delta] \\ \dot{\sigma}_\delta^2 = \beta M_\delta + 2r\sigma_\delta^2 + S_\delta \cdot [1 + ah^x(1 - 2p_0 \cdot M_\delta)] + \left(\gamma + 2 \frac{r}{K} M_\delta\right) \cdot (M_\delta^2 + \sigma_\delta^2) \\ \quad + [(\mu_1 + D) \cdot \delta_1 - ah^x \cdot S_\delta \cdot p_0](\sigma_\delta^2 - M_\delta^2) - 2 \frac{r}{K} \sum_{i=1}^{\infty} i^3 \cdot \delta_i + F \end{cases}$$

$$\mu_1 = \frac{\beta + \gamma}{2} - \frac{r}{2} \left(1 - \frac{1}{K}\right)$$

**Density-independent dispersal**

$$D_i = D \Rightarrow S_\delta = D \cdot M_\delta$$

$$F = -2D \cdot \sigma_\delta^2$$

**Density-dependent dispersal**

$$D_i = D \cdot i \Rightarrow S_\delta = D \cdot (M_\delta^2 + \sigma_\delta^2)$$

$$F = 2 \left[ M_\delta \cdot S_\delta - D \cdot \sum_{i=1}^{\infty} i^3 \cdot \delta_i \right]$$

*Note.* They can account for the dynamics of the frequency of empty patches ( $p_0$ ) and the mean ( $M_\delta$ ) and variance ( $\sigma_\delta^2$ ) of abundance in occupied patches for the metapopulation of Fig. 1. To obtain analytically closed forms for these models, it is necessary to assume a theoretical distribution for the  $\delta_i$ 's (See Table II).

the dynamics of the probability of patch occupancy and of average abundance in nonempty patches. If the theoretical distribution depends on the first two moments (e.g., negative binomial with varying clumping), then  $\delta_1$  and the third moment are functions of  $M_\delta$  and  $\sigma_\delta^2$  (see again Table II): a three-dimensional model with a further equation for the dynamics of abundance

variance is thus obtained from (7a)–(7c). A large number of compact models can be deduced from combining different assumptions.

#### 4. PERFORMANCE OF THE COMPACT MODELS

One of the main advantages of using compact models instead of the full Markov model is that persistence–extinction boundaries in the space of model parameters (such as  $r$ ,  $D$ , or  $K$ ) can be viewed as transcritical bifurcations of equilibria. While crossing the boundary from the extinction to the persistence region, in fact, the equilibrium associated with extinction, i.e.,

$$\bar{p}_0 = \lim_{t \rightarrow \infty} p_0(t) = 1,$$

loses its stability in favor of another equilibrium which was infeasible ( $p_0 > 1$ ) and becomes feasible and stable. The advantage is that bifurcation curves of equilibria are easily computable, because there is a well-established body of literature on the analysis of nonlinear finite-dimensional dynamical systems (Arnold, 1982;

**TABLE II**  
Relationships Necessary to Close the Mesoscale Models of Table I under the Hypothesis of Poisson or Negative Binomial Distribution (Clumping Parameter  $\mathcal{K}$ ) for the  $\delta_i$ 's.

	Poisson	Negative binomial
$\delta_1$	$e^{-(M_\delta-1)}$	$\left(1 + \frac{M_\delta-1}{\mathcal{K}}\right)^{-\mathcal{K}}$
$\sigma_\delta^2$	$M_\delta - 1$	$(M_\delta - 1) + \frac{(M_\delta - 1)^2}{\mathcal{K}}$
$\sum_{i=1}^{\infty} i^3 \cdot \delta_i$	—	$M_\delta^3 + 3M_\delta \cdot \sigma_\delta^2 + 2 \frac{\sigma_\delta^4}{M_\delta - 1} - \sigma_\delta^2$

*Note.* In the negative-binomial three-dimensional models, the clumping parameter  $\mathcal{K}$  varies through time and is computed via the relationship that links  $\sigma_\delta^2$  to  $M_\delta$ .

Guckenheimer and Holmes, 1983; Kuznetsov, 1995). Many packages are now available to numerically explore the behavior of dynamical systems composed by few state variables (Doedel and Kernévez, 1986; Khibnik *et al.*, 1993; Kuznetsov *et al.*, 1996). If the models under study exhibit equilibria only, using specialized software for bifurcation analysis does not require knowledge of the sophisticated mathematics underlying the code. This means that the opportunity of evaluating the extinction risk for metapopulations is open even to nonmathematically oriented scientists. Another and perhaps more important advantage of the compact models is that the analysis on how all the parameters qualifying the model affect metapopulation persistence can be performed in a few seconds, whereas the numerical analysis of the infinite-dimensional model is computationally expensive.

The use of compact models is, however, predicated on their performance being not much worse than that of the infinite-dimensional model. In order to compare the former models with the latter we consider the case of no disturbance ( $h = 1, m = 0$ ) for which persistence–extinction boundaries can be obtained from both the criterion  $E_0 = 1$  (infinite-dimensional model) and a bifurcation analysis (compact models). Figure 2 shows the persistence–extinction boundaries in the  $(D, r)$  plane obtained for some approximate models through a bifurcation analyzer (Khibnik *et al.*, 1993). The parameter plane  $(D, r)$  is particularly significant because these parameters summarize the demographic potential and the dispersal power of a given species. The comparison against the Markov model (1) shows that the Poisson approximation is perhaps too crude, while the negative-binomial (NB) truncations are much more accurate. In fact, the second-order NB model tends to overestimate the lower dispersal threshold for metapopulation persistence, but the overall picture is qualitatively preserved, while the result obtained by using the three-dimensional NB compact model does not differ significantly from that deduced via the infinite-dimensional model, even from a quantitative point of view. The use of the two-dimensional NB approximation requires an estimate of the clumping parameter, which could be obtained from data, while this estimate is not necessary with the 3D model. From the data on the abundances of some beetle species living in fragmented landscapes from den Boer (1990) and Whitlock (1992) (see Fig. 2 in Casagrandi and Gatto, 2002), for example, one can deduce that the clumping parameter is lower than unity, and ranges approximately from 0.1 to 0.8. In other cases, however, it can be higher: the clumping of the distributions conditioned on patch occupancy calculated from some data of birds, as reported by Haila *et al.* (1993), reaches 9. It is

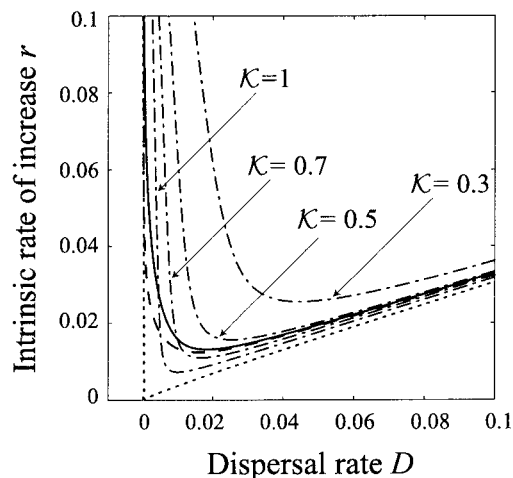


FIG. 2. Persistence–extinction boundaries of different compact models with logistic demography and density-independent dispersal ( $D_i = D$ ) in parameter space  $(D, r)$ , for the case of no disturbance ( $h = 1, m = 0$ ). Metapopulation is persistent ( $\bar{p}_0 < 1$ ) above the lines. The solid line, corresponding to the extinction boundary for the infinite-dimensional model (1), is reported as a reference. The dotted line is the boundary calculated with a compact model (7) in which a Poisson distribution is assumed as the theoretical distribution for moment closure. The dash-dotted lines are the boundaries obtained in the negative-binomial distribution case, when the clumping parameter  $\mathcal{K}$  is fixed to different values. The dashed line is the boundary for a three-dimensional model characterized by a negative-binomial distribution with varying clumping parameter and third moment dependent on the first two moments (see Table II). Other parameters are set to  $a = 0.75$ ,  $K = 10$ ,  $\beta = 0.2$ ,  $\gamma = 0.001$ , and  $\alpha = 1$ .

worthwhile to remark that all the simulations we have run up to now with the third-order NB model (for which the clumping parameter, calculated as  $(M_\delta - 1)^2 / (\sigma_\delta^2 - (M_\delta - 1))$ , is a function of time) have shown that at equilibrium the clumping varies between 0.1 and 10.

## 5. THE EFFECT OF DISTURBANCES ON METAPOPOPULATION PERSISTENCE

The flexibility of the compact models and the relative simplicity of their analysis allow us to study how the persistence of a metapopulation is influenced by disturbance, either permanent (habitat loss and erosion) or temporary (random environmental catastrophes), and by the species dispersal being passive or active. As we remarked above, it would be difficult to discuss these points with the infinite-dimensional model, because this would require extensive simulations. With the compact models, instead, we can quickly rerun the bifurcation analysis in the  $(D, r)$  plane with different values of the

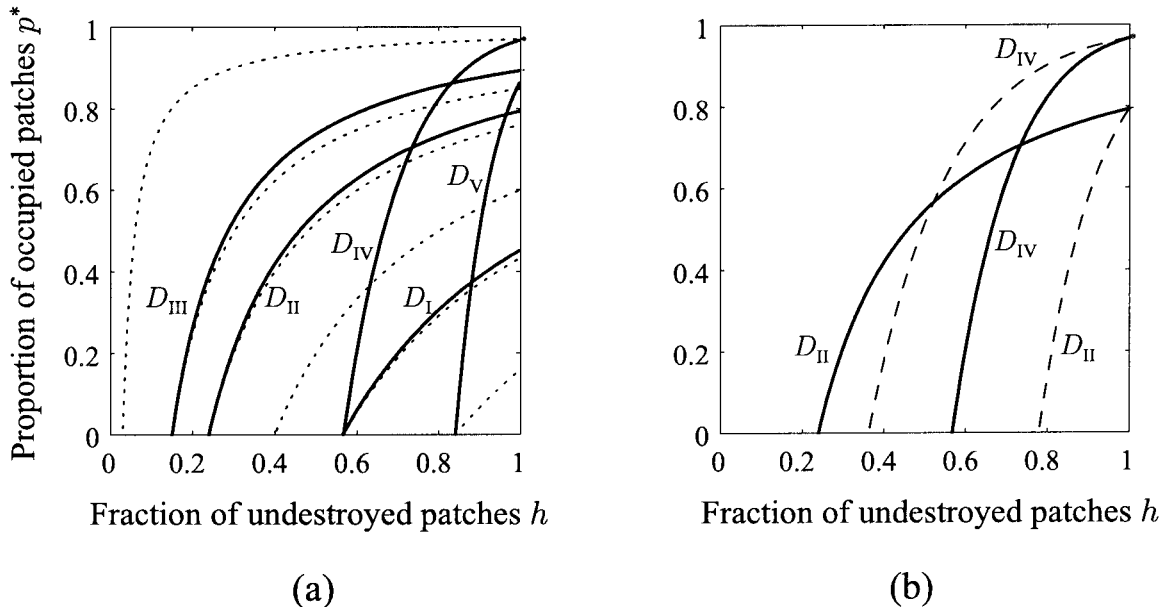
parameters characterizing disturbance. We can thus see how the shape and the area of the persistence region (an indicator of the global risk for all the species affected by disturbances) are affected by the disturbance intensity. We can also calculate for each species the fraction of occupied patches at equilibrium  $p^* = 1 - \bar{p}_0$  and see how this fraction varies under different disturbance scenarios. Before considering the synergistic effects of the various disturbances we first analyze how habitat destruction per se affects the extinction risk of fragmented populations. In doing this we compare our results with those obtained mainly by Lande (1987) and Hanski and Ovaskainen (2000).

### 5.1. The Random Loss of Habitat Patches

A first important effect of habitat destruction is the random loss of entire patches that were originally available for the species. In our models this amounts to considering values  $h$  of the remaining suitable habitat that are smaller than unity ( $1-h$  is the fraction of lost patches). This problem was tackled by using the simple Levins model (see Eq. (2)) in many previous studies (May, 1991; Nee and May, 1992; Lawton *et al.*, 1994; Moilanen and Hanski, 1995; Kareiva and Wennergren 1995). It turned out that the metapopulation is doomed to

extinction for values of  $h$  smaller than  $e/c$  (see again Eq. (2)), while the fraction  $p^*$  of occupied patches increases hyperbolically with  $h$  beyond the threshold value  $e/c$ . A more thorough analysis with a model of dispersing territorial populations was conducted by Lande (1987), who considered the problem of evaluating the minimum amount of suitable habitat that is required for persistence. In Lande's model a fraction  $\varepsilon$  of juveniles inherits the parental territory, while a fraction  $1-\varepsilon$  (which is comparable to our  $D$ ) disperses and then the juveniles can or cannot find a suitable unoccupied territory in which to settle. Lande found a threshold for  $h$  ( $p^* = 0$  for  $h \leq h_{\text{thr}}$ ), which was related to what he called demographic potential, and calculated that the fraction  $p^*$  of occupied patches displays a hyperbolic increase with  $h$ , similar to what is obtained by Levins-like models. Moreover, the influence of dispersal (Lande's  $1-\varepsilon$ ) is such that increasing dispersal implies uniformly lower values of  $p^*$  for any  $h$  as we show in Fig. 3a (family of dotted hyperbolas).

In particular the threshold  $h_{\text{thr}}$  is an increasing function of dispersal, which equals zero for low values of dispersal. A spatially explicit version of Lande's model was introduced by Bascompte and Solé (1996), who obtained higher values of  $h_{\text{thr}}$  with respect to the implicit model. It is to be remarked that Levins-like and Lande's models



**FIG. 3.** The influence of habitat destruction on the proportion of occupied patches at equilibrium. (a) The solid curves represent  $p^* = 1 - \bar{p}_0$  as a function of  $h$  according to the 3D NB compact model (i.e., Eqs. (7) with negative-binomial closure). Increasing values of the dispersal parameter  $D$  are indicated by roman numerals labeled on each curve. Dotted curves, plotted for reference, are computed as in Lande (1987). (b) Comparison between random loss of patches (represented by solid curves as in (a)), and erosion of patch size (dashed curves; the fraction of undestroyed patches  $h$  is  $1 - \eta$ ). The values of the dispersal parameters are  $D_I = 0.000366$ ,  $D_{II} = 0.001$ ,  $D_{III} = 0.002$ ,  $D_{IV} = 0.05$ , and  $D_V = 0.1$ ;  $r$  is set to 0.05 and all other parameters are as in Fig. 2.

predict a threshold for the available habitat that is exactly equal to the percentage of unoccupied patches in an undestroyed landscape, namely  $h_{\text{thr}} = 1 - p^*(h = 1)$ .

By contrast, the analysis of our own model points out that the effects of random habitat loss can be more complex than those predicted by previous models. Figure 3a shows that the curve relating  $p^*$  with the fraction  $h$  of suitable habitat is not simply hyperbolic and  $h_{\text{thr}}$  can be much larger than  $1 - p^*(h = 1)$ . Also, the influence of dispersal on the metapopulation extinction risk is much more articulated than one would expect. In fact,  $p^*$  does not uniformly decrease for any  $h$  with increasing  $D$ . At very low dispersal rate, demographic stochasticity brings the population to extinction ( $p^* = 0$  for any  $h$ ). Higher, but still low, dispersal rates allow the rescue effect due to immigration from other patches to counterbalance local extinction. As a result,  $p^*$  is uniformly larger for larger values of  $D$  (compare the curves at  $D = D_I$ ,  $D_{II}$ , and  $D_{III}$  in Fig. 3a). At even higher dispersal rates the negative effect of dispersing organisms ending up in unsuitable habitat starts showing up: the risk of extinction is now higher for organisms that disperse too much (compare curve at  $D = D_{IV}$  against that at  $D = D_{III}$  in Fig. 3a). However, the effect is not negative over the whole range of  $h$ 's. Its main consequence is to increase the minimum amount  $h_{\text{thr}}$  of suitable habitat required for persistence (actually, note that in Fig. 3a the curves at  $D = D_{III}$  and that at  $D = D_{IV}$  do intersect at high  $h$ 's). More precisely, Fig. 4 (solid line) shows that  $h_{\text{thr}}$ , as calculated from our model, is not an increasing function of  $D$  as predicted by Lande's territorial model, rather it is a valley-shaped function. The reason for this discrepancy is that the

territorial populations considered by Lande were not affected by demographic stochasticity and therefore the importance of dispersal to rescue local populations from extinction was not evidenced. By contrast, our model incorporates both the positive (at low  $D$ ) and the negative effects (at high  $D$ ) of dispersal.

## 5.2. Habitat Erosion and Its Consequences

It is easy to find out how the metapopulation persistence is affected by habitat erosion by evaluating the proportion of occupied patches with different values of the local carrying capacity. The results are shown in Fig. 3b, which displays two curves (corresponding to low and high dispersal rates) relating  $p^*$  to the fraction  $1 - \eta$  of suitable habitat out of the original habitat. The main features of the curves are quite similar to those obtained with random loss of habitat patches ( $p^*$  vanishes below a threshold and then increases with the amount of noneroded habitat). However, the detailed comparison of the two mechanisms of habitat destruction points out very interesting differences. In fact, if we draw also the corresponding curves due to random loss of habitat patches (these are obtained by setting  $h = 1 - \eta$  with all the other parameters being equal), we realize that at low dispersal ( $D = D_{II}$ ) habitat erosion is more harmful than random loss of entire patches, while at high dispersal rates ( $D = D_{IV}$ ) it is just the converse. This is to be compared with Hanski and Ovaskainen's (2000) conclusion that habitat erosion can in general be more harmful. Quite likely, this is due to the small dispersal distance used by Hanski and Ovaskainen in their simulations of a spatially explicit Levins-like model. Figure 4 (dashed line) clarifies the effect of different dispersal rates even better. It reports the values of the threshold (in terms of  $h$  or  $1 - \eta$ ) as a function of  $D$ . It is clear that the minimum fraction of suitable habitat necessary for persistence is higher for habitat erosion than for random loss of patches at low dispersal, while this threshold is lower for habitat erosion at high dispersal. Therefore, if we draw a distinction between frequent and infrequent dispersers (species with  $D > r$  vs species with  $D < r$ ; Casagrandi and Gatto, 2002), we can say that frequent dispersers are more hit by random loss of entire patches, and infrequent dispersers are more hit by habitat erosion.

## 5.3. The Effect of Nonrandom Habitat Search

In the previous subsections we have considered only passive dispersal. However, an accurate description of the different species' ability at recognizing suitable

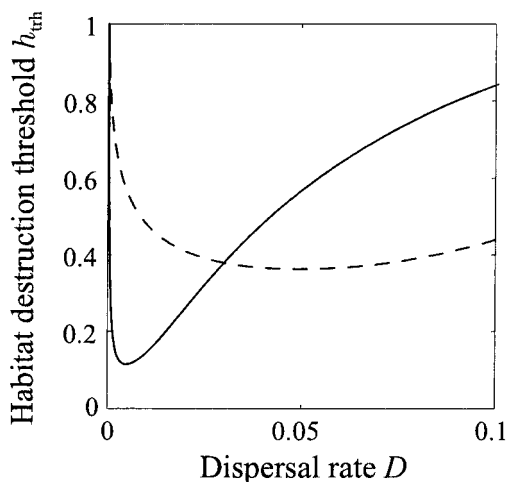


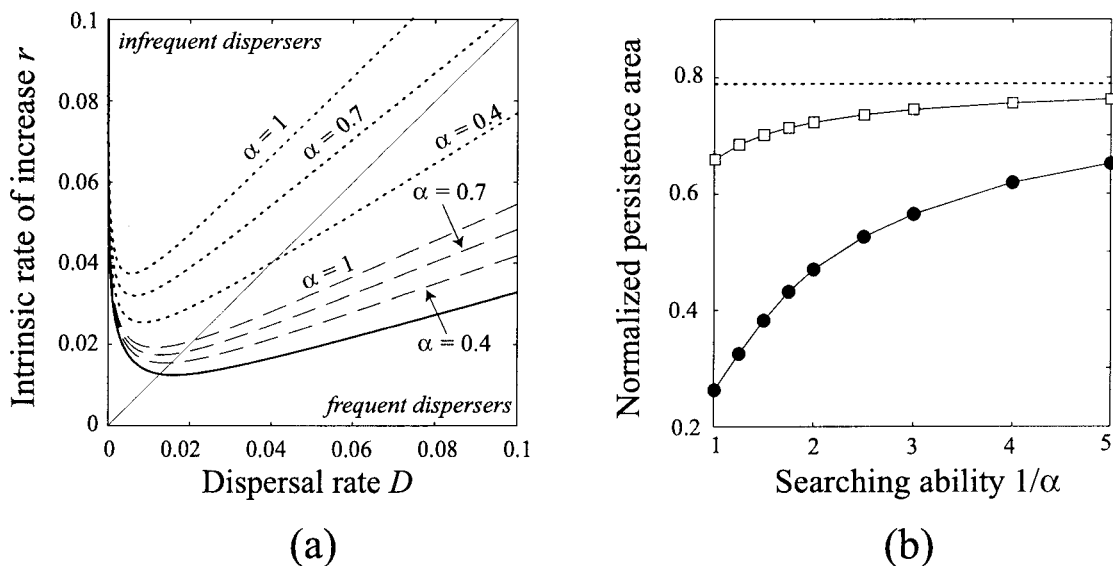
FIG. 4. Minimum fraction of remaining suitable habitat, below which metapopulation becomes extinct, as a function of dispersal  $D$ . Solid line: random loss of patches; dashed line: habitat erosion. Unspecified parameters are as in Fig. 3.

patches of a fragmented habitat has been recently proposed as a new frontier in metapopulation ecology (Travis and French, 2000). While random dispersal patterns are surely appropriate for seed-dispersing organisms, this is obviously a simplification of reality when applied to most animal species. Animals can use different strategies to recognize suitable patches, from the simple “coming back” to the natal site, after a period spent exploring the surrounding environment, to the use of biochemical cues toward a good place to live in (Browne *et al.*, 1998). Accounting for this “cleverness” of dispersers is usually avoided in available models (but see Ruxton and Rohani, 1998). Here, we have introduced a very simple way to consider active dispersal by assuming that the colonization success  $\phi$  is a nonlinear function of the amount  $h$  of available habitat. The characteristics of  $\phi$  are summarized in a single parameter  $\alpha$ , which is inversely related to the searching ability of the species. Up to now, we had set  $\alpha = 1$ ; by running bifurcation analyses for different values of  $\alpha$  we have been able to establish that nonrandom search can considerably increase the chance of persistence. However, the influence of active dispersal very much depends on the fraction of destroyed habitat. More precisely, the effect on persistence of the species’ ability to avoid dispersing to unsuitable habitats is illustrated in Fig. 5: we consider increasing levels of active dispersal in two cases, one with low random

habitat loss ( $h = 0.8$ ), and the other with high random habitat loss ( $h = 0.3$ ). Figure 5a shows how highly nonrandom search can make a big difference in the size of the extinction region when the proportion of destroyed habitat is large. Also, nonrandom search considerably decreases the risk of extinction mainly for frequent dispersers ( $D > r$ ). To further illustrate the effect of nonrandom search, we have calculated which proportion of the parameter space ( $0 \leq D \leq 0.1$ ,  $0 \leq r \leq 0.1$ ) is occupied by the persistence region. Figure 5b shows this proportion as a function of  $1/\alpha$  (a measure of cleverness) for the two levels of random habitat loss. The proportion is obviously increasing with searching ability, but its rate of increase is significantly larger when the amount of habitat lost is high. All these results point out how active dispersal can be of paramount importance to salvage a species subject to heavy habitat degradation.

#### 5.4. Environmental Catastrophes and Synergistic Effects

Our model incorporates not only permanent habitat loss, but also temporary random catastrophes (such as local epidemics) that do not destroy the habitat, but wipe out some local populations entirely. It is particularly interesting to discuss the effect of permanent vs temporary disturbance on the persistence of a fragmented



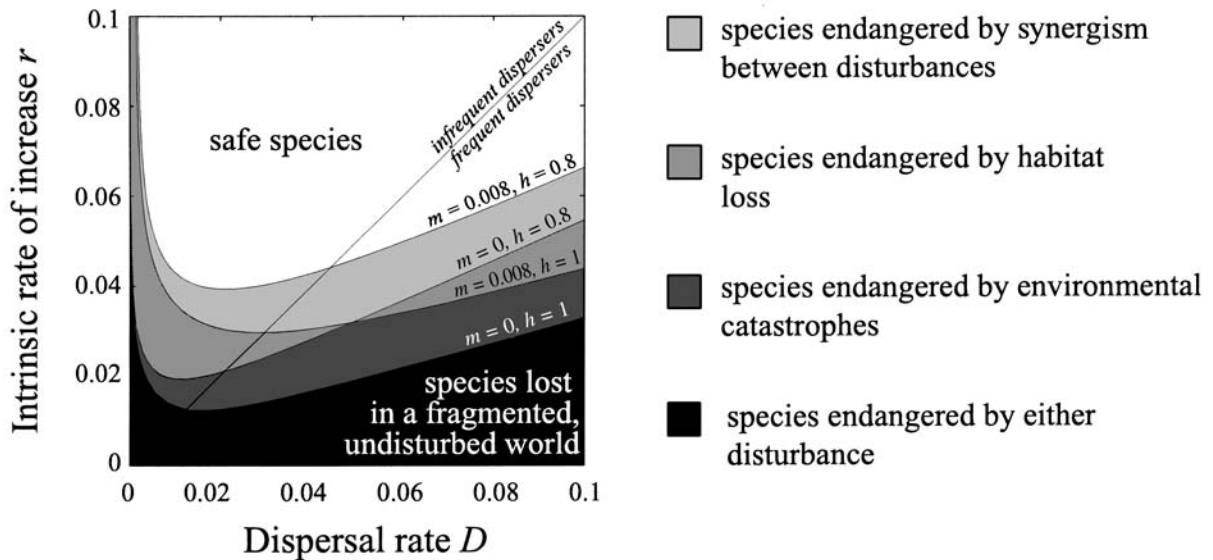
**FIG. 5.** The effect of species’ ability to distinguish between suitable and unsuitable patches (which is inversely related to the parameter  $\alpha$ ): (a) Persistence–extinction boundaries of the 3D NB compact model in the  $(D, r)$  parameter space for the cases of low habitat loss (dash,  $h = 0.8$ ) and high habitat loss (dot,  $h = 0.3$ ). (b) Proportion of parameter space ( $0 \leq D \leq 0.1$ ,  $0 \leq r \leq 0.1$ ) occupied by the persistence region as a function of the species searching ability ( $1/\alpha$ ) in the two cases of low habitat loss ( $h = 0.8$ ) and high habitat loss (black circles,  $h = 0.3$ ). The dotted line represents the same proportion in the case of undestroyed habitat ( $h = 1$ ). All unspecified parameters are set as in Fig. 2.

population and, in addition, to explore whether there are important synergistic effects between the two kinds of disturbances. In fact, distinguishing the characteristics of the species that can be more affected by either of the two main sources of disturbance is a key point for conservation. In Fig. 6, we show how this comparative analysis can be easily performed with our compact models, for which we have run bifurcation analyses for different values of the parameters  $m$  and  $h$ . In fact, for given estimates of the occurrence rate  $m$  of environmental catastrophes and the fraction  $h$  of suitable habitat, we can compute the persistence–extinction boundary corresponding to: (1) environmental catastrophes only, (2) habitat loss only, and (3) the combined action of the two disturbances. The white region in Fig. 6 identifies the safe species: all these species persist in presence of both disturbances. The species belonging to the light-gray region are doomed to extinction because of the synergism between environmental catastrophes and habitat loss. The dark-gray region corresponds to species that would irreversibly decline in the presence of one or the other of the two disturbances, while species in the black region would become extinct even without disturbance. Regions shaded in gray intermediate between light and dark correspond to species that can withstand one disturbance, but not the other. Therefore, random loss of entire patches and environmental catastrophes have a quite

different effect on persistence–extinction boundaries. Habitat loss mainly drives frequently dispersing species to extinction, whereas frequent and infrequent dispersers are equally endangered by environmental catastrophes.

## 6. CONCLUSION

In this paper we have analyzed the impacts of anthropogenic and natural disturbances on the persistence of metapopulations. Our analysis has been performed by using a few compact models—i.e., models composed by two or three equations—which have been derived via moment closure from an infinite-dimensional Markov model. As the Markov model naturally describes demographic stochasticity, this phenomenon is also included in the compact models, which, therefore, account for the positive role of dispersal to salvage a fragmented population. On the other hand, we also model explicitly the disadvantage of too much dispersal. In fact, our metapopulations can become extinct because too many dispersing organisms can die before finding a suitable habitat to colonize. The important study by Lande (1987) contained this latter effect, but did not include demographic stochasticity and the possible rescue, due to dispersal, of patches that have become empty. This is the main reason why Lande (1987) found



**FIG. 6.** Summary of various contributions to metapopulation extinction in parameter space ( $D$ ,  $r$ ). Synergistic effects of environmental catastrophes and habitat loss ( $m = 0.008$ ,  $h = 0.8$ ) sentence to extinction all the species corresponding to the light-gray region. Species corresponding to regions shaded in light and dark-gray can withstand one disturbance, not the other. One or the other of the two disturbances (either  $m = 0.008$ ,  $h = 1$  or  $m = 0$ ,  $h = 0.8$ ) leads to the extinction of species in the dark-gray region. Species corresponding to the black region ( $m = 0$ ,  $h = 1$ ) would be lost even in a pristine world. All unspecified parameters are set as in Fig. 2.

that the minimum amount of suitable habitat necessary for persistence is monotonically increasing with dispersal, while we showed that this threshold can decrease at low levels of dispersal and increase at high levels. Therefore, we hypothesize that habitat destruction should selectively favor species or genotypes characterized by intermediate dispersal power.

Another important feature of our models is that the percentage of occupied patches is not hyperbolically increasing with the amount of remaining suitable habitat. In particular, we predict that the threshold habitat necessary for metapopulation persistence is higher than the percentage of unoccupied patches in an undestroyed landscape. This result was already found by Bascompte and Solé (1996), who utilized a different model, namely a cellular automaton that mimicked Lande's mechanisms. As our model is not spatially explicit, we suspect that the effect is actually due to demographic stochasticity (which is implicitly modeled by Bascompte and Solé's (1996) cellular automaton), not to the spatial description of dispersal.

Our analysis demonstrates that the most useful classification to understand whether a species subject to disturbance will persist is between frequent and infrequent dispersers (in frequent dispersers the rate of dispersal exceeds the intrinsic rate of demographic increase, in infrequent ones it is just the opposite). In fact, we found that random loss of patches is more detrimental than erosion of patch sizes for frequent dispersers, while the converse is true for infrequent dispersers. By contrast, environmental catastrophes increase the extinction risk for both frequent and infrequent dispersers. The synergism between permanent habitat destruction and temporary disturbance can considerably increase the risk of extinction for both frequent and infrequent dispersers.

Finally, our models easily incorporate the effects of active vs passive dispersal. We obtain the obvious result that actively dispersing organisms are less prone to extinction than passive dispersers. Less obvious are the predictions that nonrandom search can considerably decrease the risk of extinction for frequent dispersers and when the proportion of destroyed habitat is large. Whether all these predictions are sufficiently robust as to be applied to real landscapes and populations may be a matter of debate. Surely, they need to be tested against experimental evidence which is still inadequate. Nevertheless, the advantage of our approach is that the models we have proposed are reasonably simple, yet flexible enough to account for the many different processes that affect fragmented populations. Also, there is still room for further refinements which may lead to

other interesting predictions concerning the fate of metapopulations subject to disturbance.

## APPENDIX

### The Dynamics of the Average and Variance of Abundance in Occupied Patches

Here we show how to obtain Eqs. (7b) and (7c) starting from model (4). The dynamics of the average abundance in occupied patches ( $M_\delta = \sum_{i=1}^{\infty} i \cdot \delta_i$ ) is given by

$$\dot{M}_\delta = \sum_{i=1}^{\infty} i \cdot \dot{\delta}_i = C_1 - C_2 + C_3, \quad (9)$$

where

$$C_1 = \sum_{i=1}^{\infty} i \cdot [v_{i-1} \cdot (i-1) + ah^\alpha \cdot (1-p_0) \cdot S_\delta] \cdot \delta_{i-1}$$

$$C_2 = \sum_{i=1}^{\infty} i \cdot [(v_i + \mu_i + D_i) \cdot i + ah^\alpha \cdot S_\delta - (\mu_1 + D_1) \cdot \delta_1] \cdot \delta_i$$

$$C_3 = \sum_{i=1}^{\infty} i \cdot (\mu_{i+1} + D_{i+1}) \cdot (i+1) \cdot \delta_{i+1}.$$

The three terms  $C_1$ ,  $C_2$ , and  $C_3$  can be written explicitly as

$$C_1 = \sum_{i=1}^{\infty} v_i \cdot i^2 \cdot \delta_i + \sum_{i=1}^{\infty} v_i \cdot i \cdot \delta_i + ah^\alpha \cdot (1-p_0) \cdot S_\delta \cdot M_\delta + ah^\alpha \cdot S_\delta$$

$$C_2 = \sum_{i=1}^{\infty} (v_i + \mu_i + D_i) \cdot i^2 \cdot \delta_i + ah^\alpha \cdot S_\delta \cdot M_\delta - (\mu_1 + D_1) \cdot \delta_1 \cdot M_\delta$$

$$C_3 = \sum_{i=1}^{\infty} (\mu_i + D_i) \cdot i^2 \cdot \delta_i - \sum_{i=1}^{\infty} (\mu_i + D_i) \cdot i \cdot \delta_i.$$

By algebraically summing the three terms above, one finally gets

$$\dot{M}_\delta = \sum_{i=1}^{\infty} [v_i - \mu_i - D_i] \cdot i \cdot \delta_i + ah^\alpha \cdot (1-p_0 \cdot M_\delta) \cdot S_\delta + (\mu_1 + D_1) \cdot \delta_1 \cdot M_\delta,$$

namely Eq. (7b). As for the dynamics of variance, it is easier to deal with the second noncentral moment of the  $\delta_i$ 's, namely

$$V_\delta = \sum_{i=1}^{\infty} i^2 \cdot \delta_i.$$

In fact, its time derivative has the form

$$\dot{V}_\delta = \sum_{i=1}^{\infty} i^2 \cdot \dot{\delta}_i = V_1 + V_2 + V_3, \quad (10)$$

where

$$V_1 = \sum_{i=1}^{\infty} v_{i-1} \cdot (i^3 - i^2) \cdot \delta_{i-1} + ah^\alpha \cdot (1 - p_0) \cdot S_\delta \cdot \sum_{i=1}^{\infty} i^2 \cdot \delta_{i-1}$$

$$V_2 = -\sum_{i=1}^{\infty} (v_i + \mu_i + D_i) \cdot i^3 - ah^\alpha \cdot S_\delta \cdot V_\delta + (\mu_1 + D_1) \cdot \delta_1 \cdot V_\delta$$

$$V_3 = \sum_{i=1}^{\infty} (\mu_{i+1} + D_{i+1}) \cdot (i+1) \cdot i^2 \cdot \delta_{i+1}.$$

By simple algebraic manipulations, one can express  $V_1$  as

$$\sum_{i=1}^{\infty} v_i \cdot [i^3 + 2i^2 + i] \cdot \delta_i + ah^\alpha \cdot S_\delta \cdot [(1 - p_0) \cdot V_\delta + 2M_\delta \cdot (1 - p_0) + 1]$$

and  $V_3$  as

$$\sum_{i=1}^{\infty} (\mu_i + D_i) \cdot [i^3 - 2i^2 + i] \cdot \delta_i.$$

The sum of the three terms above provides

$$\begin{aligned} \dot{V}_\delta &= 2 \sum_{i=1}^{\infty} (v_i - \mu_i - D_i) \cdot i^2 \cdot \delta_i + \sum_{i=1}^{\infty} (v_i + \mu_i + D_i) \cdot i \cdot \delta_i \\ &+ (\mu_1 + D_1) \cdot \delta_1 \cdot V_\delta \\ &+ ah^\alpha \cdot S_\delta \cdot [2M_\delta \cdot (1 - p_0) + 1 - p_0 \cdot V_\delta]. \end{aligned} \quad (11)$$

Deducing Eq. (7c) from (11) is then just a simple algebraic exercise, since

$$\dot{V}_\delta = \frac{d}{dt} (\sigma_\delta^2 + M_\delta^2) = \dot{\sigma}_\delta^2 + 2 \cdot M_\delta \cdot \dot{M}_\delta.$$

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## REFERENCES

- Adler, F. B., and Nüernberger, B. 1994. Persistence in patchy irregular landscapes, *Theor. Popul. Biology* **45**, 45–71.
- Anderson, R. M., and May, R. M. 1978. Regulation and stability of host–parasite population interactions—I–II, *J. Anim. Ecol.* **47**, 219–247, 249–267.
- Arnold, V. I. 1982. "Geometrical Methods in the Theory of Ordinary Differential Equations," Springer-Verlag, New York, NY.
- Bascompte, J., and Solé, R. V. 1996. Habitat fragmentation and extinction thresholds in spatially explicit models, *J. Anim. Ecol.* **65**, 465–473.
- Browne, K. A., Tamburri, M. N., and Zimmer-Faust, R. K. 1998. Modelling quantitative structure–activity relationships between animal behaviour and environmental signal molecules, *J. Exp. Biol.* **201**, 245–258.
- Casagrandi, R., and Gatto, M. 1999. A mesoscale approach to extinction risk in fragmented habitats, *Nature* **400**, 560–562.
- Casagrandi, R., and Gatto, M. 2002. A persistence criterion for metapopulations, *Theoret. Popul. Biol.* **61**, 115–125.
- Chesson, P. L. 1981. Models for spatially distributed populations: The effect of within-patch variability, *Theor. Popul. Biol.* **19**, 288–325.
- Chesson, P. L. 1984. Persistence of a Markovian population in a patchy environment, *Wahrscheinlichkeitstheor.* **66**, 97–107.
- den Boer, P. J. 1990. Density limits and survival of local populations in 64 carabid species with different power of dispersal, *J. Evol. Biol.* **3**, 19–48.
- Doedel, E. J., and Kernévez, J. P. 1986. AUTO: Software for continuation and bifurcation problems in ordinary differential equations, Applied Mathematics Report, California Institute of Technology, Reading, MA.
- Fahrig, L. 1992. Relative importance of spatial and temporal scales in a patchy environment, *Theor. Popul. Biol.* **41**, 300–314.
- Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction, *J. Wildlife Management* **61**, 603–610.
- Fahrig, L. 1998. When does fragmentation of breeding habitat affect population survival? *Ecol. Model.* **105**, 237–292.
- Gilpin, M. E. 1992. Demographic stochasticity: A Markovian approach, *J. Theor. Biol.* **154**, 1–8.
- Gilpin, M. E., and Taylor, B. 1994. Reduced dimensional transition matrices: Extinction distributions from Markovian dynamics, *Theor. Popul. Biol.* **46**, 121–130.
- Guckenheimer, J., and Holmes, P. 1983. "Nonlinear Oscillations, Dynamical Systems and Bifurcations of Vector Fields," Springer-Verlag, New York, NY.
- Gyllenberg, M., and Hanski, I. 1992. Single-species metapopulation dynamics: A structured model, *Theor. Popul. Biol.* **42**, 35–61.
- Gyllenberg, M., and Hanski, I. 1997. Habitat deterioration, habitat destruction, and metapopulation persistence in a heterogeneous landscape, *Theor. Popul. Biol.* **52**, 198–215.
- Haila, Y., Hanski, I. K., and Raivio, S. 1993. Turnover of breeding birds in small forest fragments: The sampling colonization hypothesis corroborated, *Ecology* **74**, 714–725.

- Hanski, I., and Ovaskainen, O. 2000. The metapopulation capacity of a fragmented landscape, *Nature* **404**, 755–758.
- Hill, M. F., and Caswell, H. 1999. Habitat fragmentation and extinction thresholds on fractal landscapes, *Ecol. Lett.* **2**, 121–127.
- Kareiva, P., and Wennergren, V. 1995. Connecting landscape patterns to ecosystem and population process, *Nature* **373**, 299–302.
- Khibnik, A. I., Kuznetsov, Y. A., Levitin, V. V., and Nikolaev, E. V. 1993. Continuation techniques and interactive software for bifurcation analysis of ODEs and iterated maps, *Physica D* **62**, 360–371.
- Kokko, H. 1996. Finding the probability of extinction: Error analysis and optimal use of Markovian population models, *J. Theor. Biol.* **183**, 77–87.
- Kuznetsov, Y., Levitin, V., and Skovoroda, A. 1996. “Continuation of Stationary Solutions to Evolution Problems in CONTENT,” Technical Report AM-R9611, Centrum voor Wiskunde en Informatica, Kruislaan 413, 1098 SJ Amsterdam, The Netherlands.
- Kuznetsov, Y. A. 1995. “Elements of Applied Bifurcation Theory,” Springer-Verlag, New York, NY.
- Lande, R. 1987. Extinction thresholds in demographic models of territorial populations, *Am. Nat.* **130**, 624–635.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes, *Am. Nat.* **142**, 911–927.
- Lawton, J. H., Nee, S., Letcher, A. J., and Harvey, P. H. 1994. Animal distributions: Patterns and processes, in “Large-Scale Ecology and Conservation Biology” (P. J. Edwards, R. M. May, and N. R. Webb, Eds.), pp. 41–58, Blackwell Sci., Oxford, UK.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control, *Bull. Entomol. Soc. Am.* **15**, 237–240.
- May, R. M. 1991. The role of ecological theory in planning re-introduction of endangered species, *Symp. Zool. Soc. London* **62**, 145–163.
- Moilanen, A., and Hanski, I. 1995. Habitat destruction and coexistence of competitors in a spatially realistic metapopulation model, *J. Anim. Ecol.* **64**, 141–144.
- Nee, S., and May, R. M. 1992. Dynamics of metapopulations: Habitat destruction and competitive coexistence, *J. Anim. Ecol.* **61**, 37–40.
- Norberg, J., Swaney, D. P., Dushoff, J., Lin, J., Casagrandi, R., and Levin, S. A. 2001. Biodiversity and ecosystem functioning in changing environments: A theoretical framework, *Proc. Natl. Acad. Sci. USA* **98**, 11376–11381.
- Olivieri, I., Michalakis, Y., and Gouyon, P. H. 1995. Metapopulation genetics and the evolution of dispersal, *Am. Nat.* **146**, 202–228.
- Ruxton, G. D., and Rohani, P. 1998. Fitness-dependent dispersal in metapopulations and its consequences for persistence and synchrony, *J. Anim. Ecol.* **67**, 530–539.
- Stephan, T., and Wissel, C. 1994. Stochastic extinction models discrete in time, *Ecol. Model.* **75/76**, 183–192.
- Travis, J. M. J., and French, D. R. 2000. Dispersal functions and spatial models: Expanding our dispersal toolbox, *Ecol. Lett.* **3**, 163–165.
- Whitlock, M. C. 1992. Nonequilibrium population structure in forked fungus beetles: Extinction, colonization and the genetic variance among populations, *Am. Nat.* **139**, 952–970.