Extinction threshold in metapopulation models

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The term extinction threshold refers to a critical value of some attribute, such as the amount of habitat in the landscape, below which a population, a metapopulation, or a species does not persist. In this paper we discuss the existence and behavior of extinction thresholds in the context of metapopulation models. We review and extend recent developments in the theory and application of patch occupancy models, which have been developed for assessing the dynamics of species inhabiting highly fragmented landscapes. We discuss the relationship between deterministic and stochastic models, the possibility of alternative equilibria, transient dynamics following perturbations from the equilibrium state, and the effect of spatially correlated and temporally varying environmental conditions. We illustrate the theory with an empirical example based on the Glanville fritillary butterfly (*Melitaea cinxia*) metapopulation in the Åland Islands in southwest Finland.

Introduction

Habitat loss and habitat fragmentation have been widely recognized as the main threats for the survival of species both locally and worldwide (Barbault & Sastrapradja 1995). However, convincing empirical studies demonstrating extinctions due to habitat loss and fragmentation are scarce (Andrén 1994, 1996), mainly due to the long time scales and large spatial scales that would be involved in conducting such studies. Experimentalists have overcome the problem by demonstrating the effects of habitat loss and fragmentation on extinction in microbial (Burkey 1997, Debinski & Holt 2000) and other small-scale model systems (Gonzales *et al*. 1998, Gonzales & Chaneton 2002). To assess the long-term and large-scale consequences of habitat loss and fragmentation for the vast majority of species for which there will never be enough data for a rigorous empirical analysis, a robust and general theoretical framework is needed.

Human-caused habitat loss and fragmentation transform more continuously varying landscapes to networks of discrete habitat fragments. Metapopulation theory, with its focus on the dynamics and persistence of assemblages of local populations inhabiting such fragmented landscapes, has gained much attention as a potential tool for assessing the ongoing biodiversity crisis. Metapopulation theory may be used both to provide general insights into how species respond to habitat fragmentation (e.g. Levins 1969, Gyllenberg *et al*. 1997, Ovaskainen & Hanski 2001, Ovaskainen *et al*. 2002) and as a part of spatially extended population viability analyses (e.g. Lindenmayer & Possingham 1996, Gaona *et al*. 1998, Hanski 1999, Sjögren-Gulve & Hanski 2000).

The fundamental prediction made by most metapopulation models is that a metapopulation will go deterministically extinct when the amount of habitat left in a fragmented landscape is below a critical level. This was the key conclusion of Levins (1969, 1970), who formulated the first and most widely used metapopulation model. As Levins formulated his model as a patch occupancy (presence-absence) model for a network of infinitely many identical and equally connected habitat patches, the main contribution of his model was to provide qualitative insight to metapopulation dynamics, though subsequently some empirical applications have been based on the original Levins model (Lande 1987, Doncaster & Gustafsson 1999, Carlson 2000). Over the years, the Levins model has been extended in various directions to incorporate more biological realism. First, models structured by the size of local populations (Hastings & Wolin 1989, Hanski 1985, Hastings 1991, Gyllenberg & Hanski 1992, Gyllenberg *et al.* 1997, Casagrandi & Gatto 1999, 2002) have relaxed the simple presence-absence description of local populations by including mechanistic submodels for the dynamics of local populations. Second, stochastic models assuming finite networks of habitat patches (Nisbet & Gurney 1982, Andersson & Djehiche 1998, Lande *et al.* 1998, Hernández-Suárez *et al.* 1999, Ovaskainen 2001, Alonso & McKane 2002) have shifted the emphasis from deterministic extinction thresholds to the distribution of the time to extinction due to extinction-colonization stochasticity. Third, spatially realistic models (Moilanen *et al.* 1998, Hanski 1999, Hanski & Ovaskainen 2000, Ovaskainen 2002a) have extended the Levins model to heterogeneous networks in which the habitat patches may differ from each other e.g. in terms of their size, quality and connectivity to the remaining network.

In this paper we review the literature on extinction thresholds in metapopulation dynamics and present some extensions to the current theory. We will restrict our discussion to patch occupancy models, which ignore the dynamics and structure of local populations. While this simplification restricts the range of situations to which the theory can be applied, it makes the models both tractable for rigorous mathematical analysis (Ovaskainen & Hanski 2001, 2002,

Ovaskainen 2001, 2003) and turns them to effective tools that are increasingly used in empirical studies (Moilanen 1999, 2000, Hanski 1999, Hanski & Ovaskainen 2000, ter Braak & Etienne 2003). We start with theory based on deterministic models, which are most appropriate for relatively large patch networks. After describing the basic threshold conditions, we extend the discussion to patch values (the contributions that the individual habitat fragments make to the dynamics and persistence of the metapopulation), to models that possess alternative equilibria, and to the connections between metapopulation theory and the theory of infectious diseases. Next, we turn to stochastic models, which are needed to estimate the time that a metapopulation living in a finite patch network is expected to persist. We show how correlated local dynamics increase the extinction risk and discuss transient dynamics following a perturbation. Finally, we illustrate both the deterministic and the stochastic theories by analyzing the extinction threshold of a large metapopulation of the Glanville fritillary butterfly in a highly fragmented landscape.

Extinction in deterministic metapopulation models

The Levins model and its spatial extensions

The classic model of metapopulation dynamics was formulated by Levins (1969, 1970), who used the logistic model to analyse patch occupancy dynamics in an infinitely large network of identical habitat patches. Lande (1987) extended Levins's model by assuming that only fraction *h* of the patches is suitable for occupancy, though migrating individuals still continue to arrive also at the unsuitable patches. Habitat loss is thus represented by $1 - h$ in Lande's model, and the rate of change in the fraction of occupied patches *p* (out of suitable patches) is given by

$$dp/dt = chp(1 - p) - ep, \qquad (1)$$

where *e* and *c* are the extinction and colonization rate parameters. In this model the equilibrium value for the fraction of occupied patches is

$$p^* = 1 - \delta/h, \qquad (2)$$

where $\delta = e/c$. Thus, the species will persist, in the sense that there is a non-trivial equilibrium state $p^* > 0$, only if

$$h > \delta. \qquad (3)$$

In Eq. 3, h represents the amount of habitat, and is thus a property of the landscape, whereas δ is a species parameter, measuring how good the species is in colonizing empty patches and in persisting in the occupied patches. The fundamental message from Eq. 3 is that if the amount of habitat h is reduced below the threshold value δ, the metapopulation goes extinct even though there still is suitable habitat for occupancy.

The models of Levins and Lande and their multi-species extensions have been widely applied in theoretical studies (Levins & Culver 1971, Slatkin 1974, Levitt 1978, Hanski 1983, Nee & May 1992, Tilman *et al.* 1994, Hanski *et al.* 1996, Lei & Hanski 1997, Etienne 2000, Ovaskainen 2001, Ovaskainen & Hanski 2002), but their applicability to real metapopulations has remained questionable because of the blatantly unrealistic assumptions made by the models (Harrison 1991, 1994). Most importantly, real landscapes do not consist of an infinite number of identical and equally connected patches, but habitat patch networks are typically highly heterogeneous. As an attempt to overcome this limitation of the original model, we (Hanski & Ovaskainen 2000, Ovaskainen 2002a, 2002b, 2003, Ovaskainen & Hanski 2001, 2002, 2004, Ovaskainen *et al.* 2002) have extended the Levins model to a model termed the spatially realistic Levins model (SRLM), which does not model just the overall fraction of occupied patches but also the probabilities that the individual patches are occupied. Letting $p = \{p_i\}_{i=1}^{n}$ denote the vector with the element p_i giving the probability that patch i is occupied, the SRLM is defined by (Hanski & Ovaskainen 2000, Ovaskainen & Hanski 2001)

$$dp_i/dt = C_i(p)(1 - p_i) - E_i p_i, \qquad (4)$$

where $C_i(p)$ is the colonization rate of patch i when the patch is empty, and E_i is the extinction rate of the local population in patch i when the patch is occupied.

The spatially realistic model applies to heterogeneous patch networks, where the patch-specific colonization and extinction rates are assumed to depend on the spatial configuration of the network. The theory applies to a large family of functional forms of the colonization and extinction rates (Ovaskainen & Hanski 2001), but here we restrict the analysis, for the sake of illustration, to simple but biologically justified forms that have been used before (Ovaskainen 2002a, 2002b, Ovaskainen & Hanski 2004). We assume that the extinction rate E_i is given as $E_i = e/A_i^{\zeta_{ex}}$, where e is a species-specific extinction rate parameter, A_i is the area of patch i, and ζ_{ex} describes how patch area affects the risk of extinction. The reasoning behind this formula is that the expected population size increases with patch area, and the risk of extinction generally decreases with increasing population size. The colonization rate C_i of an empty patch i is given as $C_i(p) = \Sigma_{j \neq i} c_{ij} p_j$, where c_{ij} is the contribution that an occupied patch j makes to the colonization rate of the empty patch i. We assume that $c_{ij} = c A_i^{\zeta_{im}} A_j^{\zeta_{em}} f(d_{ij})$, where c is a colonization rate parameter, and $\zeta_{im} \geq 0$ and $\zeta_{em} \geq 0$ describe how patch area affects immigration and emigration, respectively. The function f describes the dispersal kernel, i.e., the effect of the interpatch distance d_{ij} on migration success. We will use the exponential dispersal kernel $f(d_{ij}) = e^{-\alpha d_{ij}}$, where α is a parameter determining the scale of dispersal distances. The reasoning behind the assumptions made about the colonization rate is that only occupied patches may contribute to the colonization of an empty patch, that large patches are expected to send out more emigrants than small patches, that large empty patches are expected to attract more immigrants, and that dispersal success decreases with increasing distance.

The fundamental prediction made by the model (4) is that the species will persist in the long-term if and only if the condition

$$\lambda_M > \delta \qquad (5)$$

is met. In Eq. 5, $\delta = e/c$ is a species parameter as in Eq. 3, and λ_M a quantity called the metapopulation capacity of the fragmented
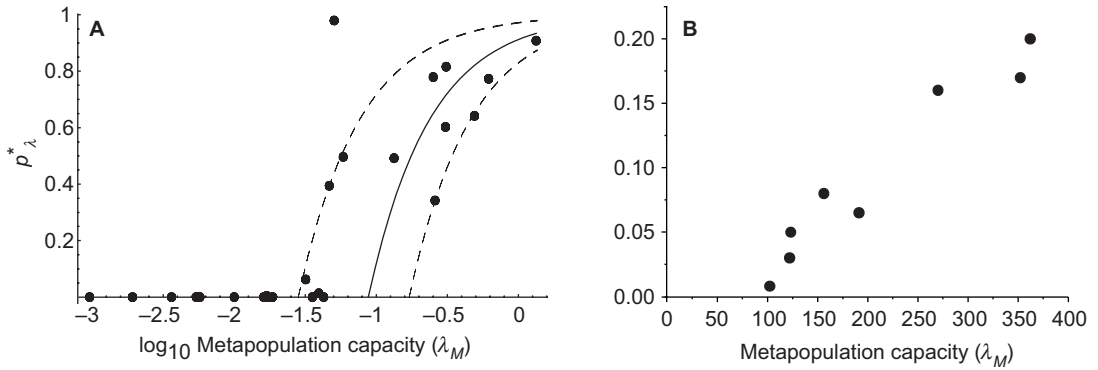
Fig. 1. Empirical evidence for the extinction threshold. Each dot corresponds to a network of habitat patches. The horizontal axis gives the metapopulation capacity λ_M of the patch network, whereas the vertical axis shows an appropriately weighted fraction of occupied patches as derived from presence-absence data. (**A**) The Glanville fritillary butterfly (from Hanski & Ovaskainen 2000), (**B**) the three-toed woodpecker (from Pakkala *et al.* 2002).

landscape (Hanski & Ovaskainen 2000). The metapopulation capacity is given as the leading eigenvalue of matrix **M**, the elements of which are defined by $m_{ii} = 0$ and $m_{ij} = A_i^{\zeta_{ex} + \zeta_{im}} A_j^{\zeta_{em}} f\left(d_{ij}\right)$ for $j \neq i$. Here the factor $A_i^{\zeta_{ex}}$ is proportional to the expected lifetime of the local population in patch i, and $A_i^{\zeta_{im}} A_j^{\zeta_{em}} f\left(d_{ij}\right)$ is proportional to the rate at which immigrants originating from patch j succeed in colonizing patch i.

Comparison with Eq. 3 suggests that λ_M is analogous to the amount of habitat h in the non-spatial model, but in addition λ_M takes into account the effect of the spatial configuration of the habitat on metapopulation persistence. A further analogy is given by the fact that an appropriately weighted (*see* below) average of the equilibrium fraction of occupied patches p_λ is given by an equation that is analogous to Eq. 2,

$$p_\lambda{}^* = 1 - \delta/\lambda_M. \qquad (6)$$

The spatially realistic model has been applied to the study of two species, the Glanville fritillary butterfly (Hanski & Ovaskainen 2000, Ovaskainen 2002a, Ovaskainen & Hanski 2004) and the three-toed woodpecker (Pakkala *et al.* 2002). In both cases, the metapopulation capacity successfully ranked multiple networks of habitat patches in terms of the occurrence of the species (Fig. 1). In the case of the butterfly, many networks were below the apparent deterministic extinction threshold, providing convincing empirical evidence for the extinction threshold.

Patch values

While the threshold condition (Eq. 5) characterizes the viability of an entire metapopulation, one might also like to consider more localized measures to assess the contributions that individual habitat fragments make to metapopulation dynamics and persistence. For example, in the management of natural metapopulations inhabiting fragmented landscapes, metapopulation viability analysis has been used as a tool to choose those fragments that should be conserved to maximize the conservation benefits from a limited amount of resources (Lindenmayer & Possingham 1996, Keitt *et al.* 1997, Verboom *et al.* 2001, Moilanen & Cabeza 2002). Patch values in the sense of the contributions that individual patches make to the dynamics and persistence of the metapopulation have most often been derived by simulating alternative scenarios with a metapopulation model that has been parameterized for the focal species (e.g. Hanski 1994: fig. 3).

As an alternative for the simulation-based approach, we have developed mathematical theory aimed at enhancing the general understanding of patch values in the context of patch occupancy models (Hanski & Ovaskainen 2000, Ovaskainen & Hanski 2001, Ovaskainen 2003). As "patch value" and "the contribution that a patch makes to metapopulation dynamics" are ambiguous terms, it is important to make it explicit exactly how one wishes to assess the value of a patch. We (O. Ovaskainen & I.

Hanski unpubl.) have suggested four biologically relevant definitions for patch value. First, patch value V_i denotes the contribution that patch *i* makes to the metapopulation capacity of the landscape, defined as the reduction in λ_M following the destruction or deterioration of patch *i*. Second, we denote by U_i the contribution of patch *i* to the size of the metapopulation, measured as the decrease in the fraction of occupied patches (possibly weighted by patch area or other such attribute) following the destruction or deterioration of patch *i*. Third, t_i denotes the contribution of patch *i* to metapopulation persistence, measured as the decrease in the mean time to metapopulation extinction following the destruction or deterioration of patch *i*. And fourth, we denote by W_i the long-term contribution of patch *i* to colonization events in a patch network. Patch values turn out to be given by eigenvectors of appropriate matrices (Ovaskainen & Hanski 2001, Ovaskainen 2003). For example, the metapopulation dynamic measure $W = \left\{ W_i \right\}_{i=1}^{n}$ is given as the left leading eigenvector of matrix **B**, the elements of which are defined as

$$b_{ij} = \frac{p_j^* c_{ij}}{\Sigma_{k \neq i} p_k^* c_{ik}}. \qquad (7)$$

Here b_{ij} measures the direct contribution that patch *j* makes to the colonization rate of patch *i*, while the left leading eigenvector **W** accounts for the chain of colonizations through time and thus measures the long-term contribution of patch *j* to the colonization events in the entire network (O. Ovaskainen & I. Hanski unpubl.). In addition to being helpful for applications, patch values also facilitate the construction of metapopulation theory by allowing a compact description of the size of a metapopulation in a heterogeneous network with a single number, p_λ. This can be done by defining p_λ as the weighted fraction of occupied patches, $p_\lambda = \Sigma_i W_i p_i$, where the weights are the patch values W_i.

Alternative equilibria

The Levins model is structurally simple, as it assumes that the extinction rate of an occupied patch is independent of and the colonization rate of an empty patch depends linearly on the state of the remaining metapopulation. There are two main reasons why this might not be the case in many real metapopulations. First, the rescue effect may decrease the rate at which local populations go extinct, as immigrants may supplement a local population and thus decrease the local extinction risk (Brown & Kodric-Brown 1977). Second, if local dynamics involve an Allee effect (Allee *et al*. 1949) the colonization rate of an empty patch may be especially low when the occupancy state of the remaining metapopulation is low leading to low rate of immigration. This may happen e.g. in such sexually reproducing species in which the number of immigrants arriving at a patch has to exceed a threshold level before successful colonization is likely. Both the rescue effect and the Allee effect have been modelled mechanistically in metapopulation models that are structured by local population size (Gyllenberg *et al*. 1997, Etienne 2000).

We will illustrate these concepts here by modifying the structure of the Levins model as follows. First, we model the rescue effect by assuming that the extinction rate *e* of an occupied patch is reduced to $e / \left(1 + \sqrt{cp} \right)$. Second, we model the Allee effect by assuming that the colonization rate *cp* of an empty patch is reduced to cp^2. These functional forms are somewhat arbitrary, and they have been chosen mainly to illustrate the possible qualitative consequences that such structural modifications of the Levins model may lead to. The model with a rescue effect (model B in Fig. 2) predicts a higher equilibrium state for given parameter values than the basic Levins model (model A). This is to be expected, as the rescue effect decreases the extinction rate of local populations. Likewise, the model with an Allee effect (model C in Fig. 2) predicts a lower occupancy state than the basic Levins model, as the Allee effect decreases the colonization rate of empty patches. Both modifications lead to alternative equilibria, as illustrated by the unstable equilibria depicted by dashed lines in Fig. 2. The unstable equilibria act as watersheds; if the initial state of the metapopulation is above the unstable equilibrium, the metapopulation will converge upwards to the stable equilibrium p^*, whereas in the opposite case it will converge to metapopulation extinction ($p^* = 0$). In model C, alternative equilibria are present for all values of
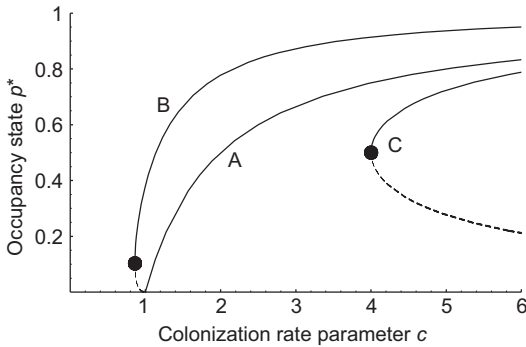
Fig. 2. Alternative equilibria due to structural modifications of the Levins model. Continuous lines depict stable equilibria and dashed lines unstable equilibria. The letters A, B and C stand for the basic Levins model, the Levins model with a rescue effect and the Levins model with an Allee effect. The dots show bifurcation points. Parameter $e = 1$.

the parameter c, whereas in model B the unstable equilibrium disappears for $c > 1$. In the terminology of Ovaskainen and Hanski (2001), models B and C possess a weak and a strong Allee effect at the metapopulation level, respectively. Although empirical demonstration of alternative equilibria remains a challenge (though *see* Hanski *et al.* 1995), the theoretical analyses (Gyllenberg *et al.* 1997, Ovaskainen & Hanski 2001) suffice to make a point of general importance. The message is that even a large metapopulation with a relatively high level of patch occupancy may have a substantial risk of extinction. If population dynamics include non-linearities such as the ones considered above, a perturbation e.g. in the form of an exceptionally unfavourable year may drive the metapopulation below the unstable equilibrium, after which the metapopulation has a deterministic tendency to go exinct.

Threshold conditions for disease eradication

Epidemiological models describing the dynamics of a disease in a host population are closely analogous to metapopulation models (Grenfell & Harwood 1997). In a basic epidemiological model, a group of host individuals corresponds to a habitat patch network, disease transmission corresponds to colonization of empty patches,

and the recovery of an individual corresponds to the extinction of a local population (alternatively one may consider a host population corresponding to a patch, in which case a clustered set of such populations comprises a patch network). While metapopulation models have been used to elucidate the conditions that would ensure the long-term persistence of a species, epidemiological theory has been employed to find out conditions under which the disease incidence would drop below the eradication threshold. In epidemiology, the analogy for habitat loss is reduction in the number of susceptibles, which is typically achieved through vaccination or other such intervention measures. The eradication threshold is generally written as

$$R_0 < 1, \tag{8}$$

where R_0 is the basic reproductive rate of an infection, defined as the average number of secondary cases produced by one primary case in an entirely susceptible population. The simplest epidemiological model, the homogeneous SIS-model (susceptible-infected-susceptible), is exactly analogous to Lande's metapopulation model, the variable $1 - h$ now denoting the fraction of immunized individuals.

In analogy with most landscapes being highly heterogeneous, host individuals typically differ greatly in their number of contacts with other hosts as well as in their susceptibility and infectiousness. Host heterogeneity may be due to age-dependent, genetic, spatial, behavioral or other such factors. Including this heterogeneity into epidemiological models has received much attention (Anderson & May 1991, Brunham 1997, Thomas & Smith 2000, Anderson & Garnett 2000, Diekmann & Heesterbeek 2000). The main result is familiar from metapopulation theory, namely that the threshold condition $R_0 < 1$ is still valid, provided that the definition of the basic reproductive rate R_0 is appropriately extended to the heterogeneous case. Typically, R_0 is given as the leading eigenvalue of an appropriate matrix or operator (Anderson & May 1991, Diekmann & Heesterbeek 2000). Comparing Eqs. 5 and 8, we observe that the basic reproductive rate is given as $R_0 = \lambda_M/\delta$ in metapopulation theory. While λ_M/δ in the metapopulation theory

increases with the number of habitat patches and with the colonization ability of the species, the value of R_0 in the epidemiological theory grows with increasing number of contacts between the individuals and with increasing level of infectiousness and susceptibility.

The development of effective intervention methods is a major goal for epidemiological theory. Analogously with metapopulation management, where patch values have been used to seek for cost-effective conservation measures, epidemiological research aims at determining those individuals who should be targeted for e.g. vaccination to make intervention as effective as possible (Anderson & May 1985, 1991, Diekmann & Heesterbeek 2000). Ovaskainen & Grenfell (2003) used the analogy between the heterogeneous SIS model and the spatially realistic Levins model combined with the theory of patch values to assess the contributions that different social groups make to the spread and persistence of sexually transmitted diseases.

Extinction in stochastic metapopulation models

The models of Levins and Lande predict that a metapopulation will go extinct only if the threshold condition $h > \delta$ is not met. These models are based on the assumption that there are infinitely many patches, and the models thus ignore stochastic fluctuations in patch occupancy. If the number of patches is small, the relative effect of such fluctuations may be large, and thus a small metapopulation may be vulnerable to extinction even if the deterministic threshold condition is met.

To examine the effect of stochasticity, we consider the stochastic logistic model, which is the stochastic analogue of the Levins model, and assumes a finite network of n habitat patches. In this model, an occupied patch will turn empty at rate $E = e$. Depending on the underlying biological processes, the colonization rate C of an empty patch may be assumed to behave either as $C = ck$ or as $C = ck/n$, where c is a colonization rate parameter and k is the number of occupied patches. If the number of habitat patches n is kept fixed, the two forms are equivalent, as the

factor $1/n$ may be included in the parameter c. However, as the two forms scale differently with respect to the number of patches, we will consider both cases separately.

The first alternative, which we call the occupancy-number model, assumes that the colonization rate of an empty patch is proportional to the number of occupied patches in the network: $C = ck$. This may be the case if the size of the landscape (area within which the habitat patches are located) is constant irrespective of the number of habitat patches. The occupancy-number model seems particularly appropriate if furthermore dispersal is global (propagules from each patch are distributed randomly within the entire landscape) and happens via a passive propagule rain, so that the propagules do not distinguish between the habitat patches and the landscape matrix. The second alternative, called the occupancy-frequency model, assumes that the colonization rate of an empty patch is proportional to the fraction of occupied patches in the network: $C = ck/n$. This model follows if we modify the above assumptions so that the size of the landscape and thus the area to which the propagules are distributed scales with the number of habitat patches, so that the density of patches (number per unit area) remains constant. Although these two examples represent idealizations of any real situation, the occupancy-number and occupancy-frequency models serve as toy models that need to be understood before a stochastic model in an explicit spatial setting will be analyzed.

In the deterministic mean-field approximation, the metapopulation capacity λ_M (or the amount of habitat h in Lande's model) of the occupancy-number model is $\lambda_M = h = n - 1$, whereas in the occupancy-frequency model it is $\lambda_M = h = (n - 1)/n$ (the term -1 arises because once empty, a patch cannot send migrants and thus cannot contribute to its own colonization rate). Thus, in the occupancy-number model, there is a threshold number of habitat patches, $n = e/c + 1$, above which the metapopulation will persist in the deterministic sense, whereas in the occupancy-frequency model the threshold condition $e/c < (n - 1)/n \approx 1$ is almost independent of the number of habitat patches. This happens because in the occupancy-frequency model,
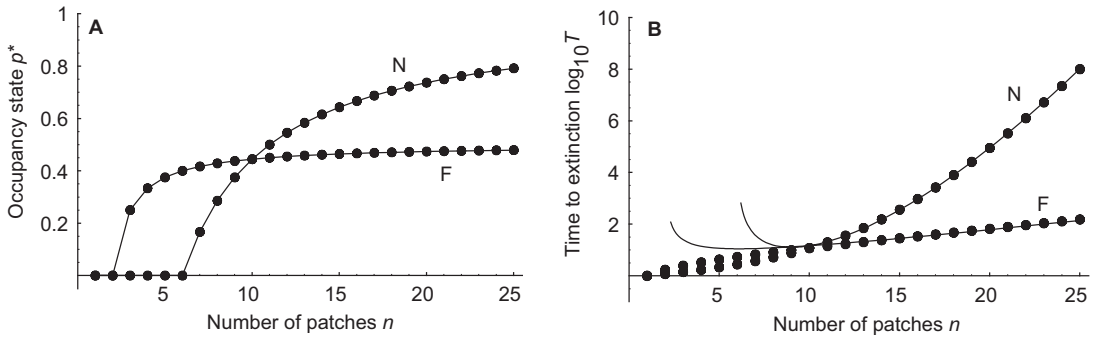
Fig. 3. The behavior of the stochastic logistic model with respect to the number of habitat patches. (**A**) The equilibrium state p^* predicted by the deterministic mean-field approximation. The dots and the lines are based on the Levins model. (**B**) Mean time to extinction. The dots depict the exact result derived from the stochastic transition matrix, whereas the lines are based on the approximation formula given by Eq. 9. The letters N and F refer to the occupancy-number model and the occupancy-frequency model, respectively. Parameter values $e = 1$ and $c = 0.2$ (occupancy-number model) or $c = 2$ (occupancy-frequency model).

adding more patches does not increase patch density but just enlarges the landscape, which is not expected to largely affect the fraction of occupied patches if the landscape was not very small to start with.

As the stochastic logistic model is a Markov process, its qualitative behavior is easy to describe. Metapopulation extinction is an absorbing state, which the process will eventually reach with probability one. However, if the metapopulation is above the deterministic threshold, the mean time to extinction T may be much longer than the time to local extinction. In this case, the state of the metapopulation is expected to converge to a quasi-stationary distribution π, which is obtained as the limiting distribution conditioned on non-extinction. Assuming that the initial state is derived from the quasi-stationary distribution, the mean time to extinction T is given by the subdominant eigenvalue of the stochastic transition matrix $\mathbf{P}$. Furthermore, the quasi-stationary distribution π is obtained as the corresponding left eigenvector. In this simple model, an asymptotically ($n \to \infty$) exact formula for the mean time to metapopulation extinction may be derived analytically, and is given by (Andersson & Djehiche 1998, Ovaskainen 2001)

$$T = \sqrt{\frac{2\pi}{n}} \frac{e^{-(n-1)p^*}}{p^{*2}\left(1 - p^*\right)^{n-1}}, \qquad (9)$$

where $p^* = 1 - \delta/\lambda_M$ is the equilibrium fraction of occupied patches. Figure 3 shows how p^* and

T increase with an increasing number of habitat patches in the occupancy-number and occupancy-frequency models. The figure assumes that the metapopulation has been parameterized in a situation in which there are $n = 10$ habitat patches (hence the two curves intersect at this point). If the occupancy-number model is assumed, the metapopulation is predicted to go deterministically extinct if the number of habitat patches is reduced to $n = 6$, whereas in the occupancy-frequency model the metapopulation does not go deterministically extinct until only $n = 2$ patches remain. The dissimilar behaviors of the two models are also seen in Fig. 3B, where time to extinction is more sensitive to the number of patches in the occupancy-number model than in the occupancy-frequency model. Figure 4 examines time to extinction from a different viewpoint, asking how many patches are needed to make the time by which the metapopulation is expected to go extinct at least 100 times as long as the expected lifetime of a single local population. As the 'critical' number of patches is now plotted against the equilibrium state p^* of the metapopulation, the result is the same for both the occupancy-number and occupancy-frequency models (Eq. 9).

It is worth noting here that the usual interpretations of Lande's model (Eq. 1) as a description of the metapopulation consequences of habitat loss are in the spirit of the occupancy-number model (Nee 1994, Hanski *et al.* 1996, Carlson

2000, Hanski & Ovaskainen 2000). In this case, the extinction threshold depends strongly on both the properties of the landscape (density of habitat patches) and the properties of the species (extinction-proneness and colonization ability). It is indeed clear that the occupancy-number model is more appropriate than the occupancy-frequency model for the situations usually considered by ecologists, with an emphasis on increasing isolation of the remaining habitat patches in increasingly fragmented landscapes. Most importantly, however, more convincing stochastic models of habitat loss can only be constructed with explicit and realistic assumptions about the dependence of colonization rate on the spatial structure of the landscape, in the spirit of the spatially realistic metapopulation theory.

Correlated local dynamics

The theory that we have just outlined predicts that the time to extinction increases exponentially with the number of habitat patches, which implies that sufficiently large metapopulations have a negligible risk of extinction. However, there are a number of reasons why this conclusion might not hold for most real metapopulations. Most importantly, local population dynamics are seldom completely independent of each other as assumed in the model. In this section we will examine how correlation in local dynamics affects the behavior of the stochastic logistic model.

As correlations are more naturally defined for probabilities than for rates, we will first consider a discrete-time version of the model. To do this, we assume that during a short time step Δt, an occupied patch goes extinct with probability $E(p) = e\Delta t$, and an empty patch becomes occupied with probability $C(p) = cpn\Delta t$ (occupancy-number model) or $C(p) = cp\Delta t$ (occupancy-frequency model), where $p = k/n$ is the fraction of occupied patches.

As the model assumes identical patches, we are not interested in which particular patches are occupied, just on temporal changes in the fraction of occupied patches p. The leading dynamic behavior of p may be described by the expected value and the variance of Δp, which is the random variable measuring the change in p
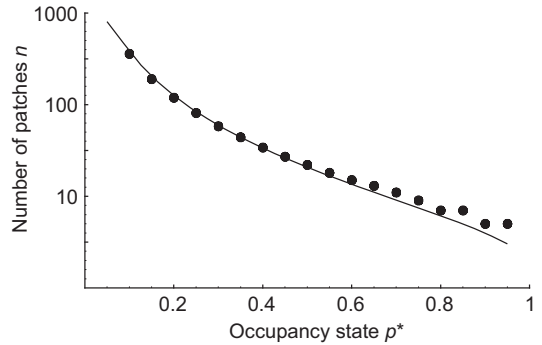

Fig. 4. The number of habitat patches needed to make the mean time to metapopulation extinction at least 100 times longer than the mean time to local extinction. The dots show the exact result derived from the generator matrix of the stochastic logistic model, while the line is based on the approximation formula given by Eq. 9.

during one time step. It is straightforward to see that if extinctions and colonizations are independent of each other, the expected value $E[\Delta p]$ and the variance $\text{Var}[\Delta p]$ are given by (Ovaskainen 2002a)

$$E[\Delta p] = (1 - p)C(p) - pE(p), \qquad (10)$$

$$\text{Var}[\Delta p] = \frac{(1-p)C(p)[1-C(p)] + pE(p)[1-E(p)]}{n}. \ (11)$$

We will next assume that local population dynamics are correlated with each other. To do this, we denote by $O_i \in \{0,1\}$ the occupancy state of patch i, and by $\Delta O_i \in \{-1,0,1\}$ the random variable measuring the change in O_i during one time step. Depending on the biological processes that actually generate the correlation, either extinctions, colonizations, or both are correlated. To keep this analysis as simple as possible, we will assume that the correlation between ΔO_i and ΔO_j is a constant ρ independently of the occupancy states of patches i and j, which means that extinctions and colonizations are similarly correlated. This assumption is justified e.g. in situations where environmental conditions vary between favourable and unfavourable. Under favourable conditions, extinctions are expected to be rare and colonizations are expected to be frequent, while under unfavourable conditions the opposite is true. This mechanism produces a positive correlation between extinctions ($\Delta O_i = \Delta O_j = -1$), a positive correlation between
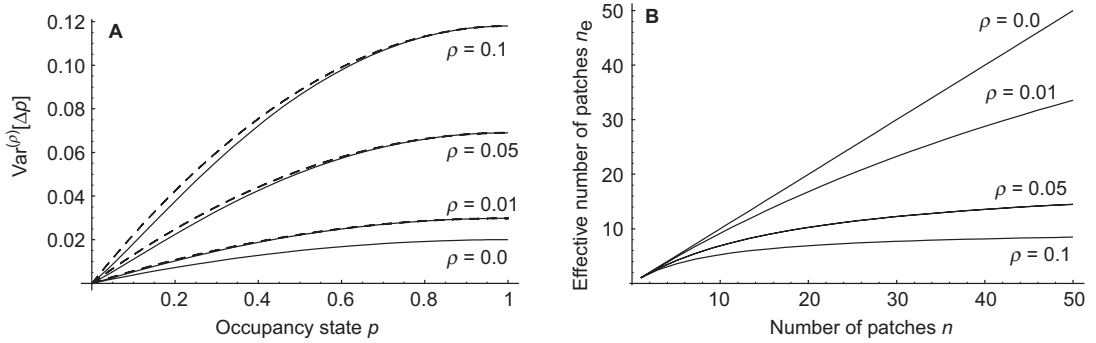
Fig. 5. The effect of correlated local dynamics in the stochastic logistic model. (**A**) The variance $\mathrm{Var}^{(\rho)}[\Delta p]$ for different values of the correlation coefficient ρ. Continuous lines show the exact result (Eq. 13) and dashed lines the approximation (Eq. 14). Parameter values $n = 50$, $e = 1$ and $\Delta t = 10^{-6}$. (**B**) The effective number of habitat patches as a function of the actual number of patches and the value of the correlation coefficient ρ.

colonizations ($\Delta O_i = \Delta O_j = 1$), and a negative correlation between extinctions and colonizations ($\Delta O_i = 1$, $\Delta O_j = -1$).

Assuming the above-described correlation structure, we denote the expected value and the variance of Δp by $E^{(\rho)}$ and $\mathrm{Var}^{(\rho)}$, respectively. As the expected value of Δp depends linearly on $C(p)$ and $E(p)$, it is not affected by the correlation structure, and hence

$$E^{(\rho)}[\Delta p] = E[\Delta p]. \qquad (12)$$

The change in variance may be derived as follows.

$$
\begin{aligned}
\mathrm{Var}^{(\rho)} &= (1-p)\mathrm{Var}[\Delta p] \\
&+ \rho\left[(1-p)\sqrt{C(p)[1-C(p)]} + p\sqrt{E(p)-[1-E(p)]} \right]^2 \quad (13) \\
&= \left[(n-1)\rho+1\right]\mathrm{Var}[\Delta p] \\
&- \rho p(1-p)\left[\sqrt{C(p)[1-C(p)]} - \sqrt{E(p)-[1-E(p)]} \right]^2 \\
&\approx \left[(n-1)\rho+1\right]\mathrm{Var}[\Delta p], \qquad (14)
\end{aligned}
$$

where the final step is justified by the following reasoning. In the quasi-stationary state, colonizations of empty patches are typically as likely as extinctions of occupied patches, suggesting that $C(p) \approx E(p)$, in which case the term inside the brackets is small. If the metapopulation is not close to the equilibrium, the above reasoning does not hold. However, in the extreme cases in which p is close to zero or one, the factor $p(1 - p)$ is small, and the approximation holds again. Figure 5A shows that the approximation is typically very good also for other values of p.

Comparing Eqs. 12 and 14 with Eqs. 10 and 11, we conclude that the effect of correlated dynamics is largely captured by changing the actual number of habitat patches n to an effective number of habitat patches n_e, which is given by

$$n_e = \frac{n}{(n-1)\rho+1} \qquad (15)$$

To see that the formula for n_e is intuitive, note first that if extinctions and colonizations happen independently ($\rho = 0$), the effective number of habitat patches equals the actual number of patches ($n_e = n$). In the other extreme, in which $\rho = 1$, all patches are in complete synchrony, and thus the network behaves essentially as a single patch ($n_e = 1$). If $0 < \rho < 1$, the effective number n_e increases with the true number n, converging asymptotically to the finite value $1/\rho$ as $n\to\infty$ (Fig. 5B).

Let us next return to the continuous-time model, the dynamics of which are approximated by a diffusion process with drift $\mu(p) = E[dp]/dt$ and infinitesimal variance $\sigma^2(p) = E[dp^2]/dt$. In the case $\rho = 0$, these are given by (Karlin & Taylor 1981, Sæther *et al.* 1999, Ovaskainen 2002a)

$$\mu(p) = C(p)(1-p) - E(p)p, \qquad (16)$$

$$\sigma^2(p) = \frac{C(p)(1-p) + E(p)p}{n}. \qquad (17)$$

Assuming that Δt is infinitesimally small (in which case we may denote it by dt), the above argument for the discrete-time model extends to the continuous-time model, and thus the formula
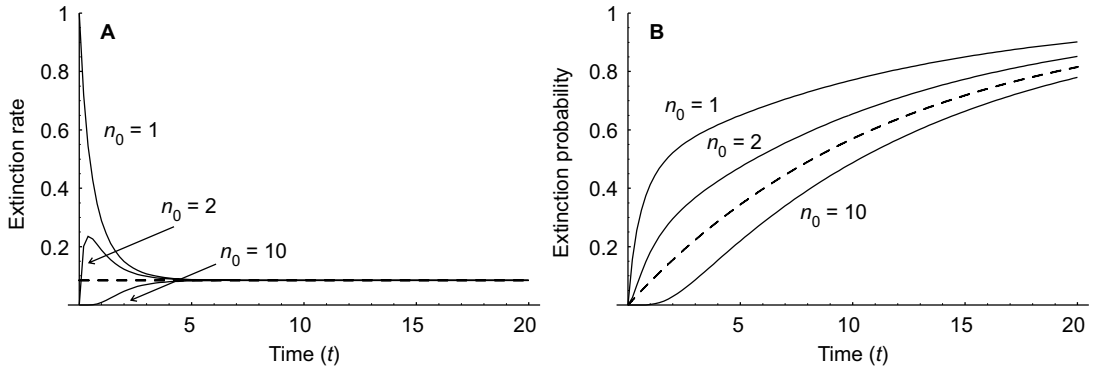
Fig. 6. Transient dynamics in the stochastic logistic model. — **A**: the extinction rate at time *t* conditioned on the metapopulation not having gone extinct before time *t*; — **B**: the cumulative probability that the metapopulation has gone extinct by time *t*. The continuous lines correspond to three different initial conditions, in which either 1, 2 or 10 out of the *n* = 10 patches are occupied at time *t* = 0. The dashed lines correspond to the situation in which the initial condition has been drawn from the quasi-stationary distribution. Parameter values *e* = 1 and *c* = 0.2 (occupancy-number model).

(Eq. 15) holds also in this case. Substituting the value for n_e to Eq. 9 we may examine how the mean time to extinction behaves as the number of patches increases. We find that in the occupancy-frequency model, for $\rho > 0$ the mean time to extinction approaches a finite asymptote, the value of which decreases with an increasing value of ρ. To see why this should be the case, note that the effective number of patches approaches a finite asymptote, and that in the occupancy-frequency model the deterministic drift is essentially independent on the actual number of patches. In the occupancy-number model, the time to extinction is found to behave according to a power-law $T \sim n^{1/\rho}$. This result is analogous to what has been found for extinction models for single populations, in which environmental stochasticity changes the scaling of the extinction risk with respect to carrying capacity from exponential scaling to a power law scaling (Lande 1993, Foley 1994). Note that correlated stochastic local dynamics represent a form of stochasticity in metapopulation dynamics (called regional stochasticity) that is analogous to environmental stochasticity in local dynamics (Hanski 1991).

Transient dynamics

The mean time to extinction discussed in the previous section was derived without specify-

ing how many of the patches were initially occupied. By assuming that the initial state of the metapopulation was derived from the quasi-stationarity distribution π, we actually assumed that the metapopulation had already persisted for a long time before the point in time from which the mean time to extinction was measured. However, it is often of interest to account explicitly for the initial condition, and the study of transient dynamics has gained a lot of interest (*see* e.g. Alonso & McKane 2002, Etienne & Nagelkerge 2002). For example, if a species is to be introduced into an initially empty patch network, the number of patches into which it is translocated in the first place may make a big difference to the probability that the species will successfully invade the network (Hanski 1999: fig. 10.7). This is illustrated in Fig. 6, in which we analyze extinction in the stochastic logistic model with different initial conditions. As expected, an initial occupancy state with a small number of occupied patches leads to a transient period with an exceptionally high extinction rate, whereas a high initial occupancy state leads to a transient period with an exceptionally low extinction rate. In the course of time, the effect of the initial condition decreases, and the extinction rate (conditioned on non-extinction by that time) converges to the extinction rate that is given by the quasi-stationary distribution (Fig. 6A). Nonetheless, the initial condition still has an effect on
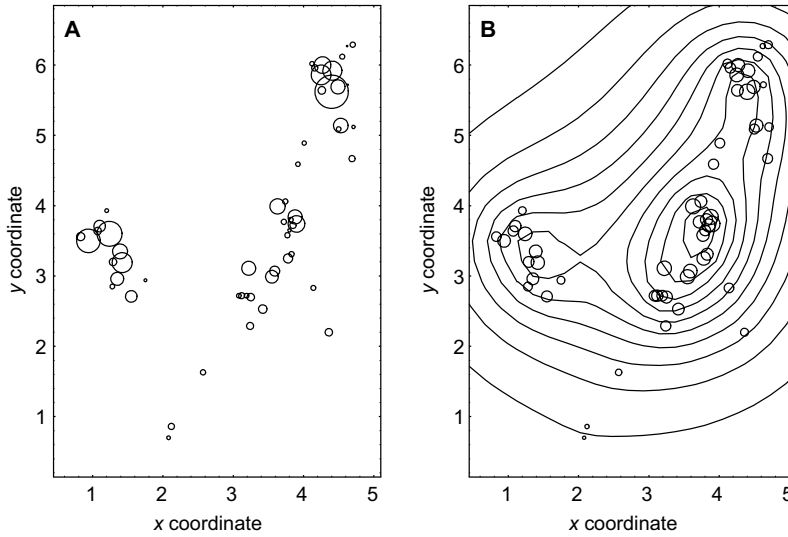
Fig. 7. A network of habitat patches inhabited by the Glanville fritillary butterfly in the Åland Islands in SW Finland. The sizes of the dots are proportional (**A**) to the areas of the habitat patches and (**B**) to the values *W* of the habitat patches. The contour lines in panel **B** indicate the relative value which a hypothetical patch would attain if added to a particular location within the network. The spatial unit is km. Parameter values are given in the text.

the cumulative distribution describing the probability that the metapopulation has gone extinct before a given time (Fig. 6B).

We have previously used the spatially realistic Levins model to analyze how the length of the transient period following an environmental or population dynamic perturbation depends on the interplay between the properties of the species and the structure of the fragmented landscape (Ovaskainen & Hanski 2002). We concluded that the length of the transient period may be written as the product of four factors. First, as illustrated in Fig. 6, the length of the transient period increases with the distance between the present state and the equilibrium state. Second, the length of the transient period is longer for species which have slow dynamics (e.g. due to long life-span) than for species with fast dynamics. Third, the length of the transient period is longer in a patch network which has a few large patches than in a network with many small patches, as the turnover rate is slower for larger patches. Finally, and most importantly, the length of the transient period is expected to be especially long for species that are located close to their extinction threshold following the perturbation. This fourth point has the important consequence that land-

scapes that have experienced recent habitat loss may have a number of species that are located below their deterministic extinction threshold. The number of such species that are doomed to extinction but have not yet had time to go extinct has been termed the extinction debt (Tilman *et al*. 1994, Hanski & Ovaskainen 2002).

An empirical example

In this section we illustrate the theory described in the previous sections with an empirical example on the Glanville fritillary butterfly (*Melitaea cinxia*) metapopulation in the Åland Islands in southwest Finland (Hanski 1999). The habitat patch network for this species in Åland consists of ca. 4000 patches (dry meadows), but we will here consider just one sub-network of 56 patches (Fig. 7A). As the species has an annual life-cycle, we will model its metapopulation dynamics with a discrete-time version of the SRLM. This is otherwise the same model as the continuous-time SRLM, but the colonization rate C_i and the extinction rate E_i are replaced by the colonization and extinction probabilities $1 - e^{-C_i}$ and $1 - e^{-E_i}$, respectively (Ovaskainen 2002a).
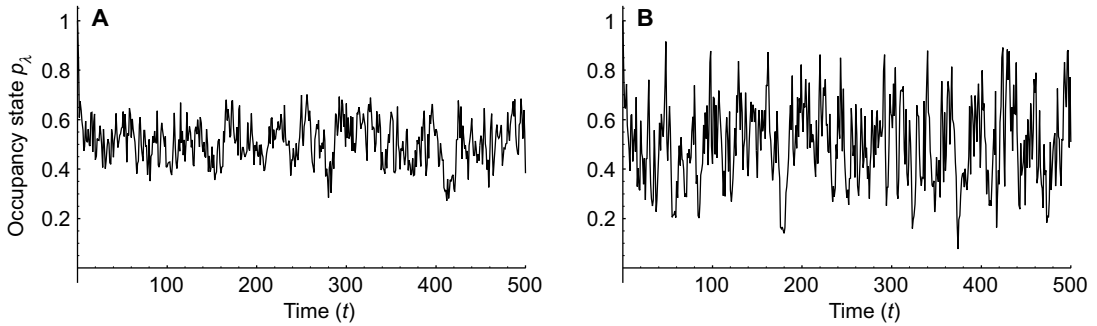
Fig. 8. Simulation runs of the Glanville fritillary model. Panels **A** and **B** show the results for models with constant and temporally varying parameter values, respectively. The temporally varying parameter values e = (0.24, 0.48, 0.33, 0.34, 0.17, 0.30, 0.53, 0.04) and c = (0.14, 0.10, 0.10, 0.33, 0.08, 0.08, 0.06, 0.22) were estimated separately for the 8 annual transitions.

To parameterize the model, we use presence-absence data for the occurrence of the butterfly in the patch network in the period 1993–2001. These data have been collected in each autumn in the course of a long-term project (Hanski 1999). We parameterized the model with the maximum likelihood method using data on the 8 annual transitions. The parameter estimates thus obtained were α = 0.84, ζ_{ex} = 0.17, ζ_{em} = 0.07 and ζ_{im} = 0.30 (using data from the entire Åland Islands), and e = 0.38 and c = 0.083 (using data from the network shown in Fig. 7A). The parameters α, ζ_{ex}, ζ_{em} and ζ_{im} represent structural model parametes, and hence they were estimated from the entire Åland data set, whereas the parameters e and c may be considered to be network specific, as the different networks in the Åland Islands vary in terms of habitat quality (Hanski 1999).

The model predicts that the equilibrium occupancy state is p_λ^* = 0.51, and thus the metapopulation is well above the deterministic threshold for persistence. The contributions that the individual habitat patches make to metapopulation dynamics are illustrated by the measure W in Fig. 7B. As expected, patch values are high for large and well-connected patches.

To illustrate the actual dynamics of the metapopulation, we start by showing a single simulation run (Fig. 8). In panel B in Fig. 8, we have accounted for regional stochasticity by estimating the parameters e and c separately for the 8 annual transitions in the data set. As expected, based on the theoretical results discussed in the
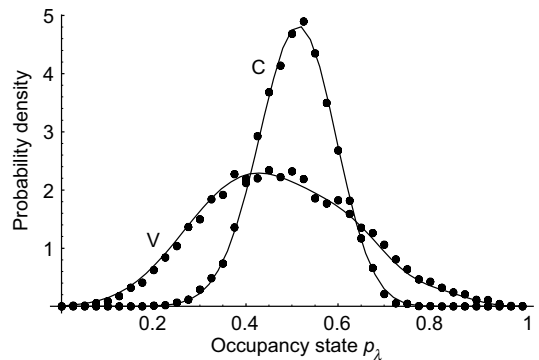

Fig. 9. The quasi-stationary distribution of the Glanville fritillary model. The dots are based on a long simulation of the spatially realistic model, the lines show the analytical result based on the effective metapopulation size method (Ovaskainen 2002a). The letters C and V refer to models with constant and temporally varying parameter values, respectively.

previous section, regional stochasticity increases stochastic fluctuations and thus increases the extinction risk of the metapopulation. This is clearly seen in Fig. 9, which depicts the quasi-stationary distributions for the two models. The extinction risk is determined by the left-hand tail of the quasi-stationary distribution, and is 6.6×10^7 years for the model without regional stochasticity and 7770 years for the model with regional stochasticity (estimates based on the effective metapopulation size method, *see* Ovaskainen 2002a).

The Glanville fritillary butterfly has been classified as an endangered species in Finland (Hanski 1999, Rassi *et al*. 2001). The extinction
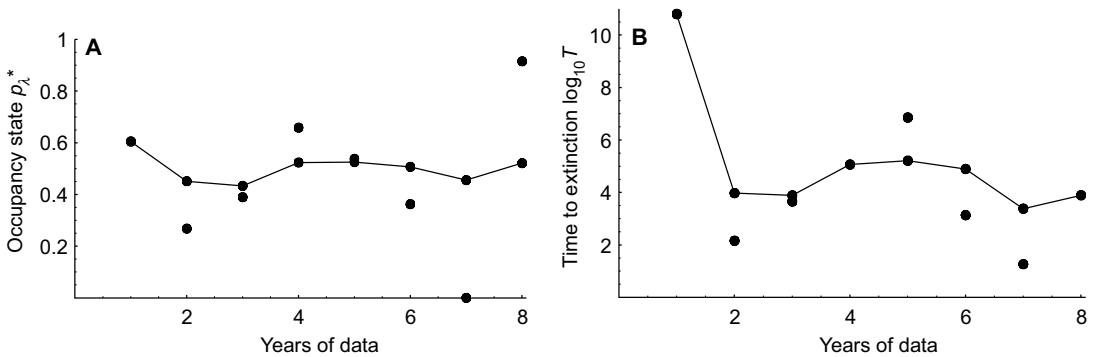
Fig. 10. The behavior of the Glanville fritillary model as a function of increasing amount of data used for estimating the measures calculated. The two panels show (**A**) the equilibrium state p_λ^* and (**B**) the mean time to extinction T. The joined dots are based on cumulative data (up to that year) and the unjoined dots on data for a single transition. The mean time to extinction was estimated by calculating the effective size of the metapopulation (*see* Ovaskainen 2002a for details) except for the single transition for year 7, for which the estimate $T(7) = 18.4$ is an average of 1000 simulation runs initiated with all patches occupied (and is thus an overestimate of T). The values $T(4) = 1.2 \times 10^{19}$ and $T(8) = 1.4 \times 10^{41}$ based on data for single transitions are not shown in the figure.

risk we have just estimated seems negligible in the time scale of tens or even hundreds of years, which raises the question whether the species has been misclassified. There are several reasons why this is not the case. First, changes in land use have greatly reduced the numbers of dry meadows that are suitable for the species in Finland. In fact, the Glanville fritillary has already gone extinct from the mainland Finland, apparently because of habitat loss and fragmentation (Hanski 1999). The species is currently restricted to an area within 2000 km² in the Åland Islands (Hanski 1999), which is a sufficient reason to classify it nationally endangered. Land use practices have changed less drastically in the Åland Islands than in mainland Finland, but nonetheless some changes have occurred (Hanski *et al.* 1996) and the present occupancy pattern may be somewhat optimistic due to the possibility that the species is presently in a transient state following habitat reduction. Another reason why the small extinction risk estimated above has to be interpreted with caution is that the empirical data for parameter estimation consist of only 8 annual transitions in patch occupancy, which themselves show much variation (Fig. 10). As the extinction risk of most (meta)populations is determined by the occurrence of exceptionally unfavorable years, it may well be that our estimates are severe underestimates simply because the empirical data set happens to lack especially

bad years. In several years in the 1990s, the butterfly populations could have performed extremely poorly had the periods of summer drought lasted one or two weeks longer than they actually happened to do (I. Hanski unpubl.).

We can perform a limited analysis of whether our estimate of the long-term extinction risk is an underestimate, by examining how much the extinction risk estimate changes with an increasing amount of data. The results show that the estimate of p_λ^* stabilizes quickly (Fig. 10), and hence it seems likely that the present estimate $p_\lambda^* = 0.51$ is relatively robust with respect to regional stochasticity and that the metapopulation is indeed well above the deterministic threshold for persistence. Note, however, that the most pessimistic single annual transition would predict $p_\lambda^* = 0$. In contrast, the estimate of the mean time to metapopulation extinction remains highly variable even after several years of data (note the logarithmic scale). For example, one exceptionally bad year (transition number 7) dropped the estimate of T to a small fraction (3%) only of what it was before that observation. Thus it seems impossible to reliably estimate the extinction risk of this metapopulation with the amount of data presently available, even if a 9-yr data set for hundreds of local populations is much better than what is typically available for most species. These results reinforce the opinion of many other authors that estimating the long-term risk of extinction is next to imprac-

tical for most species (Beissinger & Westphal 1998, Ludwig 1999, Hanski 2002), and is likely to be useful only when an exceptional amount of data is available and extinction is imminent (e.g. Engen *et al.* 2001).

Concluding remarks

In this paper, we have discussed extinction thresholds in the context of metapopulation models. We have examined the behavior of extinction thresholds with respect to the properties of the species, the properties of the landscape, and variation in environmental conditions. We conclude by summarizing our main results as five ecologically relevant messages.

First, the qualitative behaviors of stochastic and deterministic models differ fundamentally from each other. Deterministic models predict a simple threshold condition $\lambda_M > \delta$, above which the metapopulation is expected to persist forever, and below which the metapopulation is doomed to extinction. In contrast, a finite metapopulation will always go extinct with probability one in a stochastic model, where the "extinction threshold" must be interpreted via the distribution of the time to extinction. In a stochastic model, a metapopulation may be viewed to be above the extinction threshold if it is unlikely to go extinct within a relevant time period. To calculate the time to extinction, one needs to account for the stochastic fluctuations around the deterministic mean-field dynamics. As the relative role of stochasticity increases with decreasing number of habitat patches, small metapopulations in particular may have a substantial extinction risk although they would be well above the deterministic extinction threshold.

Second, in the spatially realistic context, the contributions that the habitat patches make to the persistence of the metapopulation — that is, its distance from the extinction threshold — do not depend only on the size and quality of those patches but also on their locations within the patch network. This is illustrated in Fig. 7B, in which the contour lines reveal the core area of the patch network.

Third, while the Levins model, which is the archetypal metapopulation model, pre-

dicts that the metapopulation will respond in a simple manner to environmental and population dynamic perturbations, more complicated models may represent a different picture. In particular, introducing biologically motivated modifications such as the Allee effect or the rescue effect may lead to more complex dynamics, including the possibility of alternative stable equilibria (Fig. 2), which may lead to abrupt "unexpected" extinctions from a high occupancy state.

Fourth, transient dynamics should be explicitly considered whenever the metapopulation or the environmental conditions have not remained stable for a long period of time. This is especially relevant in human-modified landscapes, many of which have experienced recent and ongoing habitat loss and fragmentation. Ignoring transient dynamics may lead to overestimation of the capacity of the landscape to support a viable metapopulation of a particular species, and thus ignoring transient dynamics in situations where landscapes have changed greatly gives an overly optimistic view of the persistence of metapopulations.

Fifth, environmental stochasticity may be spatially correlated. Such correlation (regional stochasticity) does not affect the mean-field dynamics and hence leaves the deterministic threshold condition unchanged, but regional stochasticity may greatly amplify stochastic fluctuations (Fig. 8) and thus increase the extinction risk. Furthermore, the presence of regional stochasticity makes it difficult to reliably assess the risk of extinction (Fig. 10).

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