



## **Extinction Dynamics in Mainland–Island Metapopulations: An $N$ -patch Stochastic Model**

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A generalization of the well-known Levins' model of metapopulations is studied. The generalization consists of (i) the introduction of immigration from a mainland, and (ii) assuming the dynamics is stochastic, rather than deterministic. A master equation, for the probability that  $n$  of the patches are occupied, is derived and the stationary probability  $P_s(n)$ , together with the mean and higher moments in the stationary state, determined. The time-dependence of the probability distribution is also studied: through a Gaussian approximation for general  $n$  when the boundary at  $n = 0$  has little effect, and by calculating  $P(0, t)$ , the probability that no patches are occupied at time  $t$ , by using a linearization procedure. These analytic calculations are supplemented by carrying out numerical solutions of the master equation and simulations of the stochastic process. The various approaches are in very good agreement with each other. This allows us to use the forms for  $P_s(0)$  and  $P(0, t)$  in the linearization approximation as a basis for calculating the mean time for a metapopulation to become extinct. We give an analytical expression for the mean time to extinction derived within a mean field approach. We devise a simple method to apply our mean field approach even to complex patch networks in realistic model metapopulations. After studying two spatially extended versions of this nonspatial metapopulation model—a lattice metapopulation model and a spatially realistic model—we conclude that our analytical formula for the mean extinction time is generally applicable to those metapopulations which are really endangered, where extinction dynamics dominates over local colonization processes. The time

evolution and, in particular, the scope of our analytical results, are studied by comparing these different models with the analytical approach for various values of the parameters: the rates of immigration from the mainland, the rates of colonization and extinction, and the number of patches making up the metapopulation.

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## 1. INTRODUCTION

Worldwide anthropogenic activities have been responsible for huge changes on the natural environment for millennia. Currently, change in land use is one of the most important components of global climate change (Vitousek, 1994). As a consequence, natural wild areas are lost and fragmented. Ever smaller fragments of natural habitat are becoming ever more isolated from each other. Therefore, it is reasonable to assume that ever more species are living as fragmented local populations connected by migration. This network of patches inhabited by local populations is called a metapopulation (Levins, 1969, 1970). Cumulative habitat loss and habitat fragmentation has contributed to increase the extinction risk of endangered species. Furthermore, research to date strongly supports the idea that ecosystem functioning is sensitive to biodiversity losses. Plant production, land use, nutrient leaching, and ecosystem reconstruction and stability can all be altered by reductions in biodiversity (Naeem *et al.*, 1999). Thus, it is a general environmental concern to develop analytical tools to predict the dynamics of not only metapopulations, but also ensembles of metapopulations, i.e., metacommunities. In particular, in this paper, a metapopulation stochastic model that considers a mother mainland population feeding a network of  $N$  migration-connected patches is studied. Our aim is to understand how the number of patches affects the regional persistence of the species under different assumptions about how extinction–colonization dynamics takes place.

Harrison (1991) discusses the relevance of the mainland–island metapopulation (MIM) structure in the context of the real metapopulations. Extreme differences in patch sizes make some terrestrial metapopulations very similar in their dynamics to true mainland and islands. Hanski (1999) calls attention again to the importance of this metapopulation structure, and points out that its multispecies version, assuming independent dynamics in the species, is the basis of the dynamic theory of island biogeography of MacArthur and Wilson (1967).

Levins (1969, 1970) introduced an important set of metapopulation models where the fraction of occupied patches results from a dynamic equilibrium between two processes: patch colonization and patch extinction. Gotelli and Kelley (1993) review this topic and classify colonization–extinction Levins-like models into four particular classes. None of these matches the deterministic version of the MIM model we study here. The model in its deterministic form was first written down

by Hanski (1999) and has the following form

$$\frac{dp}{dt} = (m + cp)(1 - p) - ep. \quad (1)$$

Here  $p(t)$  is the fraction of occupied patches at time  $t$  and the constants  $m$ ,  $c$  and  $e$  are the rates of immigration from the mainland, colonization and extinction, respectively. If the immigration from the mainland is absent ( $m = 0$ ), then the classical Levins' model is recovered.

In this mean field approximation local colonization is a metapopulation process that depends on regional occurrence and extinction is independent of regional occurrence. The immigration from the mainland is introduced as a *propagule rain* (Gotelli and Kelley, 1993). Since metapopulations are not completely isolated, some degree of immigration from the biogeographical region that feeds the metapopulation is a very realistic assumption. The arrival of propagules from outside establishes a connection between the internal dynamics of the system under study and the rest of the ecological world. This connection is of paramount importance in the establishment of Hubbell's extension of the dynamic theory of island biogeography (Hubbell, 2001). In particular, within a metapopulation context, not only is this feature very reasonable in itself, but it also increases the mathematical tractability of the stochastic model introduced here. We take advantage of this to find the probability of having  $n$  patches occupied in the steady state, the temporal evolution of that probability, and new analytical expressions for the expected lifetime of the metapopulation as a whole in terms of the number of available patches, the degree of isolation of the metapopulation, and the extinction–colonization parameters.

We note for future reference that the solution for the temporal evolution of the fraction of occupied patches  $p(t)$  of the deterministic model described in (1) can be easily found to be

$$p(t) = \frac{1}{2} \left( \frac{c - e - m}{c} \right) + a \frac{1 + K e^{-2act}}{1 - K e^{-2act}}, \quad (2)$$

where  $K$  is a constant depending on initial condition and  $a$  is given by

$$a = \frac{1}{2c} \sqrt{(c - e - m)^2 + 4mc}. \quad (3)$$

The classical Levins' model describes the temporal evolution of the fraction of local populations that are inhabited by the species under study. The assumptions this model makes can be summarized as follows:

- All patches have the same area.
- All patches are identically connected by migration.

- Local dynamics within a patch is ignored, as is the effect of local dynamics on migration.
- All populations experience an equal extinction risk independently.
- There are an infinite number of patches.

In comparison to the deterministic Levins' model, the stochastic approach adopted here introduces two new features. First, it gives a way to relax the last assumption, and so to study the effect of taking a *finite* number of patches. As a result, such an approach allows one to take into account the intrinsic stochastic extinction–colonization dynamics, i.e., the consequences of demographic stochasticity on metapopulation dynamics. Second, as previously stated, it allows one to consider some degree of immigration from a regional pool of individuals feeding the metapopulation. The stochastic Levins' model, as opposed to the stochastic version of the  $m \neq 0$  model (1), has been previously studied (Gurney and Nisbet, 1978). In that paper the problem of a population persisting in a patchy environment where extinction and colonization occur was examined. Using a 'zero-correlation discrete-state' approach—which is equivalent to our mean field approximation—the patterns of population fluctuations were explained, and mean times to global extinction were estimated.

The stochastic counterpart of the model described in equation (1) is presented in Section 2. In Section 3, we find the stationary probability distribution  $P_s(n)$  analytically, and also find expressions for the mean and variance of the number of occupied patches. The regional persistence of the metapopulation is a temporal process. It is, then, extremely important to address the problem of how the probability distribution,  $P(n, t)$ , evolves in time depending on the parameters. In Section 4 we determine this function when  $N$  is large, by showing how it moves according to the deterministic equation (1), as well as broadening as  $t$  increases. When the tail of this distribution reaches the  $n = 0$  boundary, the approach of Section 4—at least within the Gaussian approximation adopted there—is no longer valid. Therefore, in Section 5 we investigate the probability that no patches are occupied,  $P(0, t)$  (i.e., that metapopulation or regional extinction occurs), for times which are large enough that it is nonzero. Throughout we give comparisons between the analytical approximations, the direct numerical integration of the master equation and numerical stochastic realizations of the model. The final aim of the temporal analysis is to compute the expected time to extinction. However, real metapopulations are not composed of equally connected patches. Therefore, in Section 6, our analytical results are compared to computer simulations of the results obtained from two spatially extended models for metapopulation dynamics: those obtained from a spatially realistic metapopulation (SRM) model and from a lattice metapopulation model, where internal colonization is modeled locally. There are three appendices. In Appendix A, the probability distribution function and the moments in the stationary state are obtained in the limit when  $N$  is large. In the second, the evaluation of the integral, appearing in the formula for the mean time to extinction

of the metapopulation, is given. In the third, the algorithm used to carry out the numerical simulations reported throughout the paper is described in detail.

## 2. THE STOCHASTIC MODEL

Consider  $N$  populations linked by migration together with a source of external immigration, the *mainland*, feeding available patches with immigrants. Suppose also that extinction acts independently in all occupied patches. Then, assuming that  $dt$  is so small that only one event can occur during that time interval, one has the following possible events and their probabilities:

- Probability of having a colonization event in a time  $dt$

$$cn \left( 1 - \frac{n}{N} \right) dt. \quad (4)$$

- Probability of having an extinction event in a time  $dt$

$$endt. \quad (5)$$

- Probability of an external immigration event from the *mainland* in a time  $dt$

$$(N - n) m dt. \quad (6)$$

Putting all of these effects together, we obtain the one-step transition probabilities  $g_n \equiv W(n + 1 | n)$  and  $r_n \equiv W(n - 1 | n)$  as

$$g_n = cn \left( 1 - \frac{n}{N} \right) + m(N - n), \quad (7)$$

and

$$r_n = en. \quad (8)$$

We can now write down a master equation describing this one-step stochastic process (van Kampen, 1981; Gardiner, 1985). If  $P(n, t)$  is the probability of  $n$  of the patches being occupied at time  $t$ , the master equation takes the form

$$\frac{dP(n, t)}{dt} = r_{n+1}P(n + 1, t) + g_{n-1}P(n - 1, t) - (r_n + g_n)P(n, t). \quad (9)$$

Equation (9) is only valid for values of  $n$  not on the boundary (i.e., for  $n \neq 0$  and  $n \neq N$ ); for these values special equations have to be written reflecting the fact that no transitions out of the region  $[0, N]$  are followed. However, from (7) and (8) we see that  $g_N = 0$  and  $r_0 = 0$ , and if additionally we define  $r_{N+1} = 0$  and  $g_{-1} = 0$ , then (9) holds for all  $n = 0, 1, \dots, N$ . To completely specify the system we also need to give an initial condition, which will typically have the form  $P(n, 0) = \delta_{n, n_0}$  for some nonnegative integer  $n_0$ . This completes the formulation of the stochastic process. We now move on to the analysis of this problem, starting with the properties of the stationary state.

### 3. STATIONARY STATE

We begin our investigation by determining the stationary probability distribution,  $P_s(n)$ , of the model. We will then show that  $\langle n^2 \rangle_s$ ,  $\langle n^3 \rangle_s$ , and all of the higher moments in the stationary state, can be expressed in terms of the mean number of patches in the stationary state,  $\langle n \rangle_s$ . We obtain an expression for the mean which is valid in the limit where the total number of patches,  $N$ , is large, but show numerically that in fact this result holds down to even small values of  $N$ .

The stationary state is defined as the state in which  $P(n, t)$  is time independent. Setting  $dP(n)/dt = 0$  in (9), one obtains

$$r_{n+1}P_s(n+1) - g_nP_s(n) = r_nP_s(n) - g_{n-1}P_s(n-1). \quad (10)$$

This is true for all  $n$ , which implies that  $r_nP_s(n) - g_{n-1}P_s(n-1) = J$ , where  $J$  is a constant. Applying the boundary condition at  $n = 0$ , we find that  $J = 0$  and therefore

$$r_nP_s(n) = g_{n-1}P_s(n-1); \quad n = 0, 1, \dots, N. \quad (11)$$

If  $e \neq 0$ , then  $r_n \neq 0$  for all  $n$  such that  $0 < n \leq N$ , and therefore

$$P_s(n) = \frac{g_{n-1}g_{n-2} \cdots g_0}{r_n r_{n-1} \cdots r_1} P_s(0); \quad n = 1, \dots, N. \quad (12)$$

The constant  $P_s(0)$  can be determined from the normalization condition

$$\sum_{n=0}^N P_s(n) = P_s(0) + \sum_{n>0} P_s(n) = 1; \quad (13)$$

$$(P_s(0))^{-1} = 1 + \sum_{n=1}^N \frac{g_{n-1}g_{n-2} \cdots g_0}{r_n r_{n-1} \cdots r_1}. \quad (14)$$

The transition probabilities (7) may be written in the more compact form

$$g_n = e\alpha(n + \beta)(N - n), \quad (15)$$

where

$$\alpha = \frac{1}{N} \frac{c}{e} \quad \text{and} \quad \beta = N \frac{m}{c}. \quad (16)$$

Substituting (15) together with  $r_n = en$ , into (12) and (14) gives

$$P_s(n) = \binom{N}{n} \frac{\Gamma(n + \beta)}{\Gamma(\beta)} \alpha^n P_s(0), \quad (17)$$

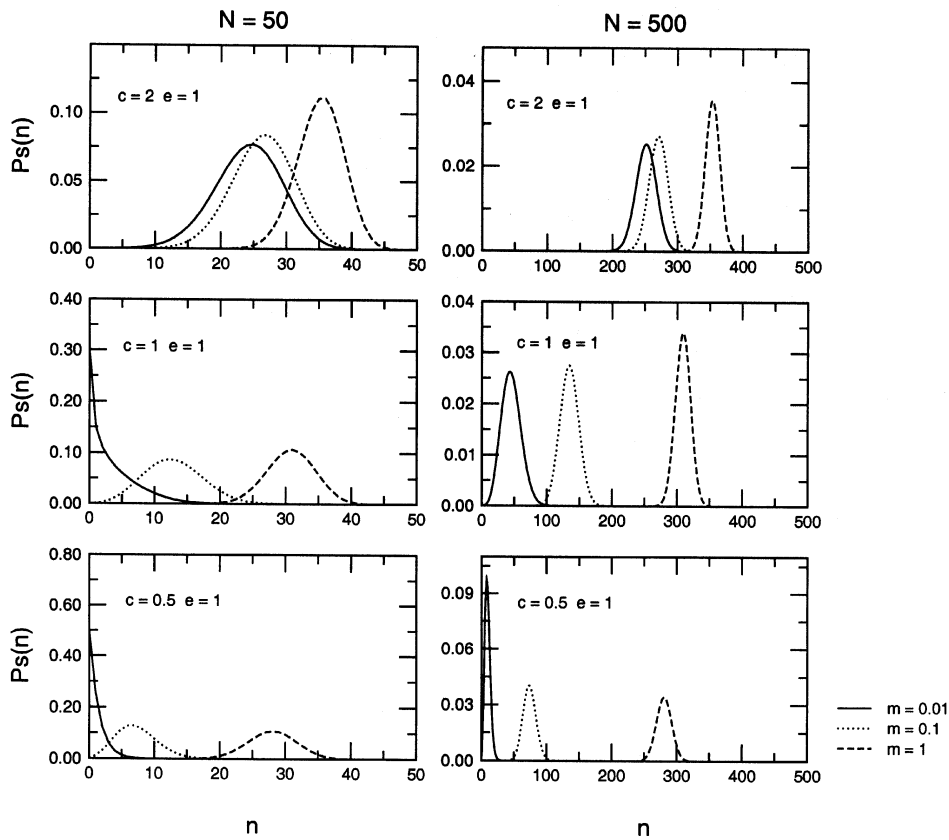


Figure 1. Probability distribution function in the stationary state for different values of external immigration,  $m$ , colonization,  $c$ , extinction,  $e$ , and also for two system sizes. The function  $P_S(n)$  is computed numerically using a suitable modification of the Tridag algorithm (Press *et al.*, 1992).

where

$$(P_S(0))^{-1} = \sum_{n=0}^N \binom{N}{n} \frac{\Gamma(n + \beta)}{\Gamma(\beta)} \alpha^n. \quad (18)$$

Some plots of the stationary distribution  $P_S(n)$  are shown in Fig. 1. The Gaussian form of the curves is apparent as long as immigration from the mainland is high enough. The probability of having zero patches occupied, which can be called *regional extinction* of the metapopulation, increases as the external immigration decreases.

We would also wish to obtain expressions for the moments of this distribution. To do this, let us first derive equations for the time evolution of the moments. Multiplying (9) by  $n^m$ ,  $m = 1, 2, \dots$  and summing over all  $n$  gives

$$\frac{d}{dt} \langle n^m \rangle = \langle [(n + 1)^m - n^m] g_n \rangle + \langle [(n - 1)^m - n^m] r_n \rangle, \quad m = 1, 2, \dots, \quad (19)$$

where we have used the forms of  $g_n$  and  $r_n$  at the boundaries. In the stationary state the left-hand side (l.h.s.) of (19) is zero, which gives for  $m = 1$  and  $m = 2$ :

$$0 = e\alpha\beta N + e[\alpha(N - \beta) - 1]\langle n \rangle_s - e\alpha \langle n^2 \rangle_s \tag{20}$$

$$0 = e\alpha\beta N + e[\alpha(N - \beta) + 2\alpha\beta N + 1]\langle n \rangle_s + e\alpha[2(N - \beta) - 1]\langle n^2 \rangle_s - 2e\alpha \langle n^3 \rangle_s, \tag{21}$$

using the explicit forms for  $g_n$  and  $r_n$ . It is clear that the stationary form of (19) for a given value of  $m$  will involve  $\langle n \rangle_s, \dots, \langle n^{m+1} \rangle_s$ . Therefore, if an explicit form for  $\langle n \rangle_s$  is known, all moments can in principle be found, and those for small values of  $m$  can be found quite easily. For example,

$$\langle n^2 \rangle_s = \beta N + [(N - \beta) - \alpha^{-1}]\langle n \rangle_s. \tag{22}$$

A formal expression for the mean of  $n$  in the stationary state can be easily obtained from (17). It is given by

$$\langle n \rangle_s = \sum_{n=0}^N n P_s(n) = \sum_{n=0}^N \binom{N}{n} \frac{n\Gamma(n + \beta)}{\Gamma(\beta)} \alpha^n P_s(0). \tag{23}$$

Using  $n\Gamma(n + \beta) = \Gamma(n + \beta + 1) - \beta\Gamma(n + \beta)$  together with (18), we find

$$\begin{aligned} \langle n \rangle_s &= \frac{\Gamma(\beta + 1)}{\Gamma(\beta)} \sum_{n=0}^N \binom{N}{n} \frac{\Gamma(n + \beta + 1)}{\Gamma(\beta + 1)} \alpha^n P_s(0) - \beta \\ &= \beta \left\{ \sum_{n=0}^N \binom{N}{n} \frac{\Gamma(n + \beta + 1)}{\Gamma(\beta + 1)} \alpha^n P_s(0) - 1 \right\}. \end{aligned} \tag{24}$$

The sums in (18) and (24) are of the same type and may be expressed in terms of special functions—generalized Laguerre polynomials—as discussed in Appendix A, but this is not especially helpful in understanding the nature of the stationary state as a function of the parameters of the model. Fortunately, approximate forms for  $N$  large are not difficult to derive. For example, it is shown in Appendix A that the first term in the curly brackets in (24) equals  $\epsilon y^*/\mu$  for large  $N$  (and  $\mu N \gg 1$ ) where  $y^*$  is the positive root of  $df/dy = 0$  and

$$f(y) = \mu \ln y + \ln(1 + y) - \epsilon y, \quad \epsilon \equiv \frac{1}{\alpha N} = \frac{e}{c}, \quad \mu \equiv \frac{\beta}{N} = \frac{m}{c}. \tag{25}$$

Solving for  $y^*$  we obtain

$$\frac{\langle n \rangle_s}{N} = \frac{1}{2} \left\{ (1 - \mu - \epsilon) + \sqrt{(1 + \mu - \epsilon)^2 + 4\mu\epsilon} \right\} \left[ 1 + O\left(\frac{1}{N}\right) \right]. \tag{26}$$



The order  $1/N$  corrections to (26) are more complicated, but can still be expressed in terms of the quantities defined in (25):

$$\frac{\langle n \rangle_s}{N} = \mu \left\{ \frac{\epsilon y^*}{\mu} - 1 \right\} + \frac{\epsilon}{2N} \left\{ \frac{2}{y^* f^{(2)}(y^*)} + \frac{f^{(3)}(y^*)}{[f^{(2)}(y^*)]^2} \right\} + O\left(\frac{1}{N^2}\right), \quad (27)$$

where  $f^{(k)}(y)$  is the  $k$ th derivative of  $f(y)$ .

In the case that  $N$  is large, but that  $\mu$  is so small that the condition  $\mu N \gg 1$  is no longer true, we have to proceed in a slightly different manner. The analogous result to (27) can be found from (24), (A.8) and (A.15), and is given by

$$\frac{\langle n \rangle_s}{N} = (1 - \epsilon - \mu) + \frac{\epsilon}{2N} \left\{ \frac{-2(\beta - 1)}{y^* \tilde{f}^{(2)}(y^*)} + \frac{\tilde{f}^{(3)}(y^*)}{[\tilde{f}^{(2)}(y^*)]^2} \right\} + O\left(\frac{1}{N^2}\right), \quad (28)$$

where  $y^*$  is now the positive root of  $d\tilde{f}/dy = 0$  and where  $\tilde{f}(y) = \ln(1+y) - \epsilon y$ . The constant  $\beta$  is given by  $\beta = \mu N$ . Since  $y^*$  is positive only if  $\epsilon < 1$ , this result only holds if  $e < c$ .

As can be seen in Fig. 2, the second-order approximation for the mean agrees well with the exact mean values (l.h.s. plots). The approximation breaks down only for low metapopulation sizes and values of  $\epsilon$  around 1. It can be seen that the approximation works even better than expected, i.e., when the requirements that  $N$  or  $\mu N$  are large, required for the derivation, are not fulfilled. The approximation for the variance obtained using the exact result (22) is not as good as for the mean, because this equation uses the approximate value for the mean in order to estimate the variance.

In summary, the large  $N$  approximation is good at large  $N$ , and in many cases remains reasonable down to quite small values of  $N$ . As mentioned in the introduction, the stochastic approach which we have adopted allows us to study the effect of taking  $N$  to be finite. If we assume that  $\mu$  (or equivalently  $m$ ) is nonzero, then  $\langle n \rangle_s/N$  [given by (26)] approaches  $p^* \equiv p(\infty)$  [the fraction of occupied sites in the deterministic model in the steady state, given by (2) and (3)] as  $N \rightarrow \infty$ , as we would expect. The corrections to this deterministic result, as represented by (26) and (27), are of the form of a power series in  $1/N$ . These conclusions are only true if  $m$  is not zero: as  $m \rightarrow 0$ , (26) and (27) cease to apply. This is because to derive the latter two equations we assumed that  $N$  and  $\mu N$  were large. The latter condition will typically be violated when  $m \rightarrow 0$  and in these cases (28) will instead be applicable. The  $N \rightarrow \infty$  limit of equation (28) for the average number of the fraction of occupied patches in the steady state is now equal to the equilibrium value of the classical Levins' model,  $p^* = 1 - \epsilon$  (the  $m = 0$  version of the deterministic model). The nature of the corrections in this case depends on how  $\mu N$  behaves in the double limit  $\mu \rightarrow 0$  and  $N \rightarrow \infty$ .

These comments show up the subtlety of the  $m \rightarrow 0$  limit. If we simply set  $m = 0$  in the transition probability (7), we see that  $g_0 = 0$  and from (12) we see that

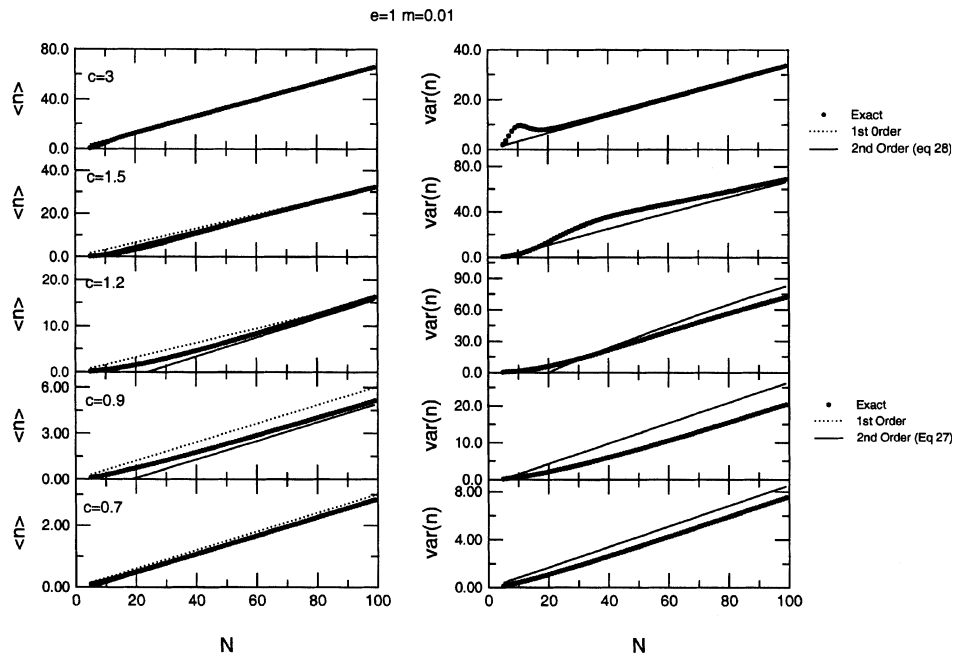


Figure 2. These plots show comparisons between, on the one hand, the large  $N$  approximation for the mean and the variance of the number of occupied patches for different values of connectivity,  $c$ , and metapopulation size,  $N$ , and, on the other, the same values computed directly from the stationary probability distribution,  $P_s(n)$ , which has been found numerically by means of the Tridag algorithm (Press *et al.*, 1992). In the six upper plots, ( $\epsilon < 1$ ), the second-order approximation is calculated using equation (28). In the four lower plots ( $\epsilon > 1$ ), the second-order approximation is calculated using equation (27). In the variance plots, we have only used the second-order approximation, so only two curves are present in these plots.

$P_s(n) = 0$  for  $n > 0$ . Therefore  $P_s(0) = 1$ , which reflects the fact that when there is no immigration, regional extinction is certain in a finite population. However, if a long time elapses before the probability of extinction becomes nonnegligible, there will be a quasi-equilibrium probability distribution, which can also be used to compute different quantities of interest (Renshaw, 1991; Ball and Nasell, 1994; Nasell, 1996). On the other hand if  $m \rightarrow 0$  and  $N \rightarrow \infty$ —so that the population is now formally infinite—extinction is no longer certain, as described earlier. It is also interesting to note that (28) only holds if  $\epsilon < 1$  (a consequence of the breakdown of the steepest descent method described in Appendix A when  $\epsilon > 1$ ). Again this is not too surprising given the nonanalytic behavior of the deterministic ( $N \rightarrow \infty$ ) model for  $\mu = 0$  and  $e > c$ .

In this section we have seen how the large  $N$  limit—apart from the singular regime  $\mu \rightarrow 0$  and  $\epsilon > 1$ —when applied to the mean and variance, gives the deterministic model results to leading order and allows us to calculate corrections to this result. We will now show that the large  $N$  method may also be applied to

the entire evolution equation (9), giving (1) to leading order, and other equations giving the finite  $N$  corrections.

#### 4. TIME DEPENDENCE

Having investigated the properties of the stationary state in the last section, we now move on to the study of the time evolution of the system. The master equation (9) has transition probabilities  $g_n$  which are nonlinear in  $n$ , so that an exact solution for the time-dependent behavior is not possible. However, since very often in the problem of interest  $N$  is large, the possibility of performing a large- $N$  analysis once again suggests itself. In this section we will describe the application of such an analysis—specifically van Kampen’s large- $N$  method (van Kampen, 1981)—to our model. This method has a number of attractive features, for instance, the macroscopic (i.e., deterministic) equation emerges naturally from the stochastic equation as a leading order effect in  $N$ , with the next to leading order giving the Gaussian broadening of  $P(n, t)$  about this average motion. The method is clearly presented by van Kampen (1981), so we will only give a brief outline of the general idea and stress the application to the model of interest in this paper.

If we take the initial condition on (9) to be  $P(n, 0) = \delta_{n,n_0}$ , we would expect, at early times at least,  $P(n, t)$  to have a sharp peak at some value of  $n$  (of order  $N$ ), with a width of order  $N \cdot N^{-1/2} = N^{1/2}$ . It is therefore, natural to transform from the stochastic variable  $n$  to the stochastic variable  $\xi$  by writing

$$n = N\phi(t) + N^{1/2}\xi \tag{29}$$

where  $\phi(t)$  is some unknown macroscopic function which will have to be chosen to follow the peak in time. A new probability distribution  $\Pi$  is defined by  $P(n, t) = \Pi(\xi, t)$ , which implies that

$$\dot{P} = \frac{\partial \Pi}{\partial t} - N^{1/2} \frac{d\phi}{dt} \frac{\partial \Pi}{\partial \xi}. \tag{30}$$

The master equation (9) may be written

$$\dot{P}_n = (\mathcal{E} - 1)r_n P_n + (\mathcal{E}^{-1} - 1)g_n P_n, \tag{31}$$

where  $\mathcal{E}(\mathcal{E}^{-1})$  is an operator which changes  $n$  into  $n + 1(n - 1)$ , e.g., if  $f_n$  is an arbitrary function of  $n$ , then  $\mathcal{E} f_n = f_{n+1}$ . In terms of  $\xi$ :

$$\mathcal{E}^{\pm 1} = 1 \pm N^{-1/2} \frac{\partial}{\partial \xi} + \frac{1}{2!} N^{-1} \frac{\partial^2}{\partial \xi^2} + \dots \tag{32}$$

Using (29)–(32) the original master equation for  $P(n, t)$  can be rewritten as an equation for  $\Pi(\xi, t)$ . A hierarchy of equations can now be derived by identifying terms order by order in powers of  $N^{-1/2}$ . The first two of these are:

$$\frac{d\phi}{dt} = \alpha_{1,0}(\phi) \quad (33)$$

and

$$\frac{\partial \Pi}{\partial t} = -\alpha'_{1,0}(\phi) \frac{\partial}{\partial \xi} (\xi \Pi) + \frac{1}{2} \alpha_{2,0}(\phi) \frac{\partial^2 \Pi}{\partial \xi^2}, \quad (34)$$

where

$$\begin{aligned} \alpha_{1,0}(\phi) &= c\phi(1 - \phi) - e\phi + m(1 - \phi) \\ \alpha_{2,0}(\phi) &= c\phi(1 - \phi) + e\phi + m(1 - \phi). \end{aligned} \quad (35)$$

The first equation, (33), is the macroscopic equation for  $\phi(t)$  and is identical to the deterministic equation (1). Its solution is therefore given by (2) and (3) with  $p(t)$  replaced by  $\phi(t)$  and where  $K$  is an arbitrary constant. This shows that the peak of the distribution moves according to the deterministic dynamics, as we might have expected.

Initially we ask that  $\xi(0) = 0$ , which means that  $\phi(0) = n(0)/N = n_0/N$ . We can use this result to determine the constant  $K$ . Substituting back into (2) gives

$$\phi(t) = \frac{1}{2} \left( \frac{c - e - m}{c} \right) + a \frac{Z + \tanh(act)}{1 + Z \tanh(act)}, \quad (36)$$

where

$$Z \equiv \frac{1}{a} \left[ \frac{n_0}{N} - \frac{c - e - m}{2c} \right]. \quad (37)$$

The second equation, (34), is a linear Fokker–Planck equation whose coefficients depend on time through  $\phi$  given by (36). It is straightforward to show that the solution to this equation is a Gaussian and so it is only necessary to determine  $\langle \xi \rangle_t$  and  $\langle \xi^2 \rangle_t$  to completely characterize  $\Pi(\xi, t)$ . By multiplying (34) by  $\xi$  and  $\xi^2$  and using integration by parts, one finds (van Kampen, 1981)

$$\begin{aligned} \partial_t \langle \xi \rangle_t &= \alpha'_{1,0}(\phi) \langle \xi \rangle_t \quad \text{and} \\ \partial_t \langle \xi^2 \rangle_t &= 2\alpha'_{1,0}(\phi) \langle \xi^2 \rangle_t + \alpha_{2,0}(\phi). \end{aligned} \quad (38)$$

In our case  $\alpha'_{1,0}(\phi) = (c - e - m) - 2c\phi$ , and so

$$\langle \xi \rangle_t = \langle \xi \rangle_0 \exp \left( -2ac \int_0^t \frac{1 + K e^{-2act}}{1 - K e^{-2act}} dt \right) = 0, \quad (39)$$

since we have already assumed that  $\langle \xi \rangle_0 = 0$ . A straightforward, but tedious, calculation now gives

$$\begin{aligned} \langle \xi^2 \rangle_t = & \{ [\lambda + 2ae][1 - e^{-4act}] - 8K[\lambda + ae + a^2c][1 - e^{-2act}]e^{-2act} \\ & + 4acK^2[8a^2c + 6\lambda]te^{-4act} - 8K^3[\lambda - ae + a^2c][1 - e^{-2act}]e^{-4act} \\ & + K^4[\lambda - 2ae][1 - e^{-4act}]e^{-4act} \} / 4ac(1 - Ke^{-2act})^4, \end{aligned} \tag{40}$$

where  $\lambda = e(c - e - m)/c$  and  $K$  is the constant appearing in (2):

$$K = \frac{Z - 1}{Z + 1}. \tag{41}$$

Numerical results (Fig. 3) show that, eventually, the probability distribution deviates from a Gaussian form. While it is true that one could in principle calculate these non-Gaussian effects using van Kampen’s approach (by taking higher order terms in  $N^{-1/2}$  into account), the method gets increasingly cumbersome. Therefore, in the next section, we adopt a totally different approach to the calculation of time-dependence, which will focus on  $P(0, t)$ —the quantity we need to determine if we wish to understand the predictions of the model relating to extinction of the metapopulation.

### 5. MEAN TIME TO EXTINCTION

In this section we will develop an approximate scheme to calculate  $P(0, t)$ , the probability that no patches are occupied at time  $t$ , and compare the results with those obtained numerically. We will also re-examine the behavior of  $\lim_{t \rightarrow \infty} P(0, t) = P_s(0)$ , which was already obtained in Section 3 and in Appendix A within the large  $N$  approximation, as a function of the parameters of the model.

From the lower set of graphs in Fig. 3 we see that the Gaussian approximation of Section 4 is likely to break down when, as  $t$  increases, the left-hand tail of  $P(n, t)$  reaches the  $n = 0$  boundary. At this time,  $P(0, t)$  begins to become significantly different from zero. However, it is also apparent from Fig. 3 that in this case the only values of  $n$  for which  $P(n, t)$  will be significantly different from zero will be small values of  $n$ , specifically those which satisfy  $n \ll N$ . When this condition holds,  $g_n$  given by (15) may be approximated by

$$g_n = e\alpha N(n + \beta) = c(n + \beta). \tag{42}$$

Now both  $g_n$  and  $r_n = en$  are linear in  $n$  and the master equation (9) defines a linear one-step process. This class of problems can be solved exactly by first

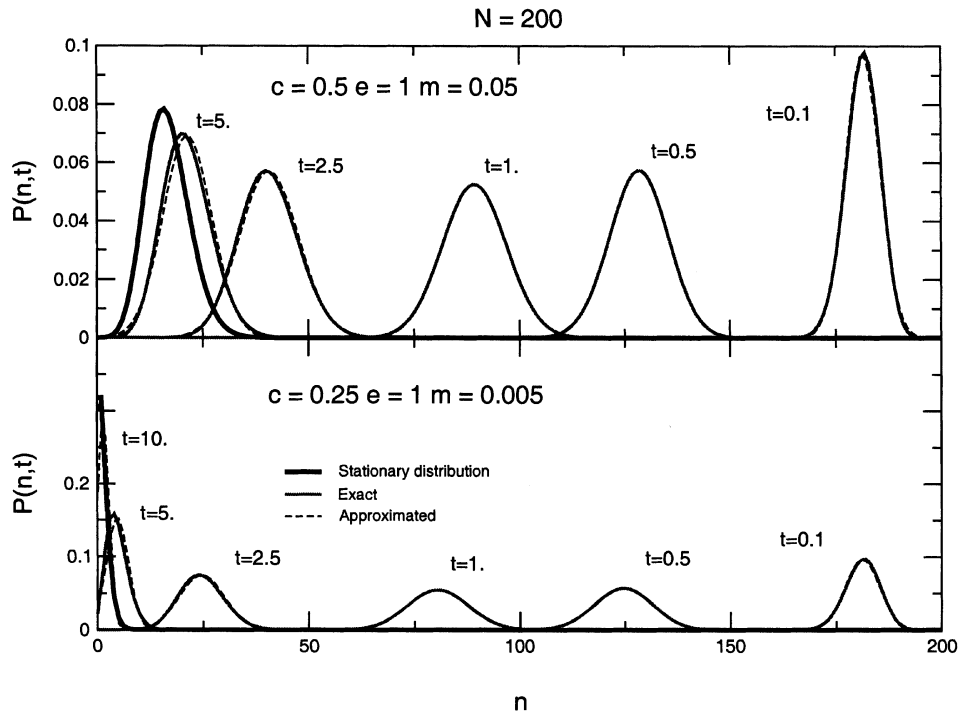


Figure 3. Temporal evolution of the probability distribution function,  $P(n, t)$ , with the initial condition  $P(N, 0) = 1$  and  $P(n, 0) = 0$  for  $n < N$ . The Gaussian approximation is plotted using dashed lines. The probability distribution resulting from the numerical integration of the master equation is plotted in gray and the steady-state solution in bold black. At early times, it is not possible to distinguish the approximation from the exact solution, since both curves coincide.

finding the differential equation satisfied by the generating function

$$F(z, t) = \sum_{n=0}^{\infty} P(n, t)z^n. \tag{43}$$

Note that we have moved the upper boundary from  $N$  to infinity, since  $g_n$  given by (42) no longer vanishes at  $n = N$ . Starting from (9) the derivation of this equation proceeds along standard lines (van Kampen, 1981; Gardiner, 1985) to yield

$$\frac{\partial F}{\partial t} = (1 - z)(e - cz) \frac{\partial F}{\partial z} - c\beta(1 - z)F. \tag{44}$$

The conditions on  $F$  are

$$F(1, t) = 1 \quad \text{and} \quad F(z, 0) = z^{n_0}, \tag{45}$$

and follow from the normalization condition  $\sum_n P(n, t) = 1$  and the initial condition  $P(n, 0) = \delta_{n,n_0}$ , respectively.

The partial differential equation (44) may be solved by the method of characteristics to give

$$F(z, t) = \begin{cases} \frac{1}{(e - cz)^\beta} \Phi\left(\frac{(1 - z)}{(e - cz)} \exp\{-(e - c)t\}\right), & \text{if } e \neq c \\ \frac{1}{(1 - z)^\beta} \Psi\left(ct + \frac{1}{1 - z}\right), & \text{if } e = c \end{cases} \quad (46)$$

where  $\Phi$  and  $\Psi$  are arbitrary functions. The solution to this problem was first obtained by Kendall (1948). To determine  $\Phi$  we impose the initial condition  $P(n, 0) = \delta_{n,n_0}$  using (45). Letting  $x = (1 - z)/(e - cz)$  this gives

$$\Phi(x) = \left(\frac{e - c}{1 - cx}\right)^\beta \left(\frac{1 - ex}{1 - cx}\right)^{n_0}. \quad (47)$$

From (46) and (47) we obtain the solution of (44) with the initial condition  $P(n, 0) = \delta_{n,n_0}$  to be

$$F(z, t) = \left[ \frac{e - c}{(e - cz) - c(1 - z) \exp\{-(e - c)t\}} \right]^\beta \times \left\{ \frac{e(1 - z) \exp\{-(e - c)t\} - (e - cz)}{c(1 - z) \exp\{-(e - c)t\} - (e - cz)} \right\}^{n_0}, \quad (48)$$

and since  $P(0, t) = F(0, t)$ ,

$$P(0, t) = \left[ \frac{e - c}{e - c \exp\{-(e - c)t\}} \right]^\beta \left\{ \frac{e \exp\{-(e - c)t\} - e}{c \exp\{-(e - c)t\} - e} \right\}^{n_0}. \quad (49)$$

A similar analysis can be used to determine the function  $\Psi$  in the special case when  $e = c$ , but the result which is found is the same as taking the limit  $e \rightarrow c$  in (48) and (49).

A comparison of the  $P(0, t)$  calculated in the linearized theory with the numerical integration of the master equation is shown in Fig. 4. A very good agreement is always found. There is close agreement between the approximation and the exact solution for initial times and also for long times. For intermediate times, when  $P(0, t)$  starts increasing, the agreement improves further away from  $\epsilon = 1$ .

As  $t \rightarrow \infty$ , the linearized form of  $P(0, t)$  approaches the stationary distribution of the linear theory, which we will denote by  $P_s^{\text{lin}}(0)$ . It is given by

$$P_s^{\text{lin}}(0) = \begin{cases} \left(1 - \frac{c}{e}\right)^\beta, & \text{if } c < e \\ 0, & \text{if } c \geq e. \end{cases} \quad (50)$$

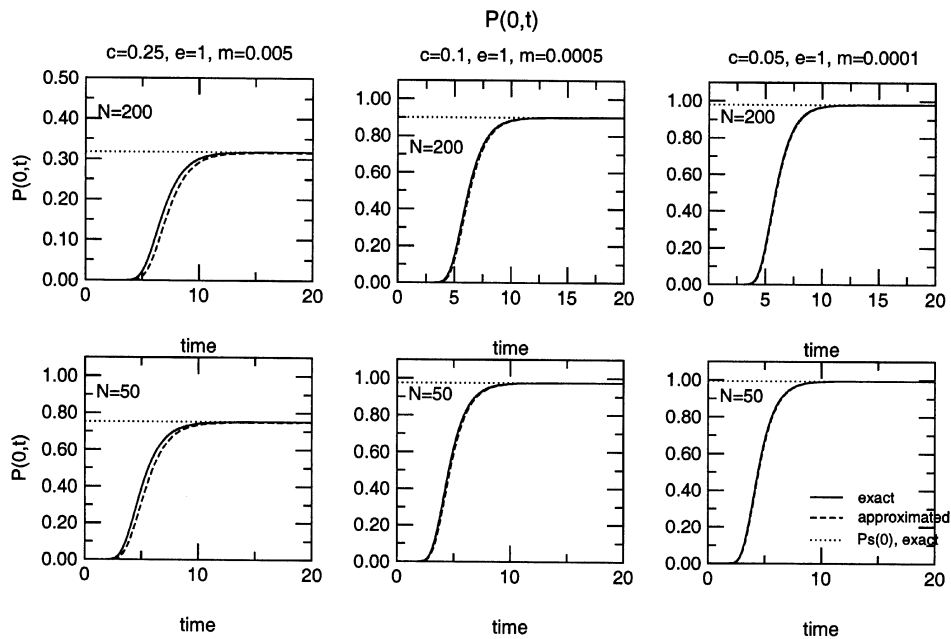


Figure 4. Comparison between the probability of metapopulation extinction,  $P(0, t)$  at time  $t$ , computed from the exact numerical solution, and by using the linear theory (49). A very good agreement is found. The initial condition taken in the calculation shown in this figure is  $P(N, 0) = 1$  and  $P(n, 0) = 0$  for  $n < N$ .

We should check *a posteriori* that the use of the linear approximation is valid. From (50) we see that if  $\epsilon = e/c < 1$ , then the linear approximation predicts that  $P_s(0) = 0$ , which violates the condition which we assumed in the derivation of the approximation. Therefore, we should restrict the use of the linear approximation to the regime  $\epsilon > 1$  and to values of  $m$  that are sufficiently small so that  $P_s(0)$  is nonzero (see Fig. 1). In the limit  $m \rightarrow 0$ , the Levins' model result  $p^* = 1$  for  $\epsilon > 1$  is recovered. Here, unlike when we were discussing this limit in the full model in Section 3, there are no subtleties: the upper boundary has been shifted from  $n = N$  to infinity during the linearization, and so there are no finite-size population effects left. The only place that  $N$  appears in the linear version of the model is in the constant  $\beta = \mu N$ .

In Appendix A, the calculation of  $P_s(0)$  in the full model, that is without the linearization assumption, is presented in the limit of large  $N$ . In exactly the same way as was discussed in Section 3 with regard to the mean and the variance, there are three cases: (i)  $N$  and  $\mu N$  both large; (ii)  $N$  large,  $\mu N$  not large and  $\epsilon < 1$ , and (iii)  $N$  large,  $\mu N$  not large and  $\epsilon > 1$ . The results in cases (i) and (ii) are given in Appendix A. However, the steepest descent procedure fails in the third case. Interestingly, this is exactly the situation where the linearization procedure works, and so the two methods complement each other. The results of these analytic approaches are compared to the exact values obtained from the numerical



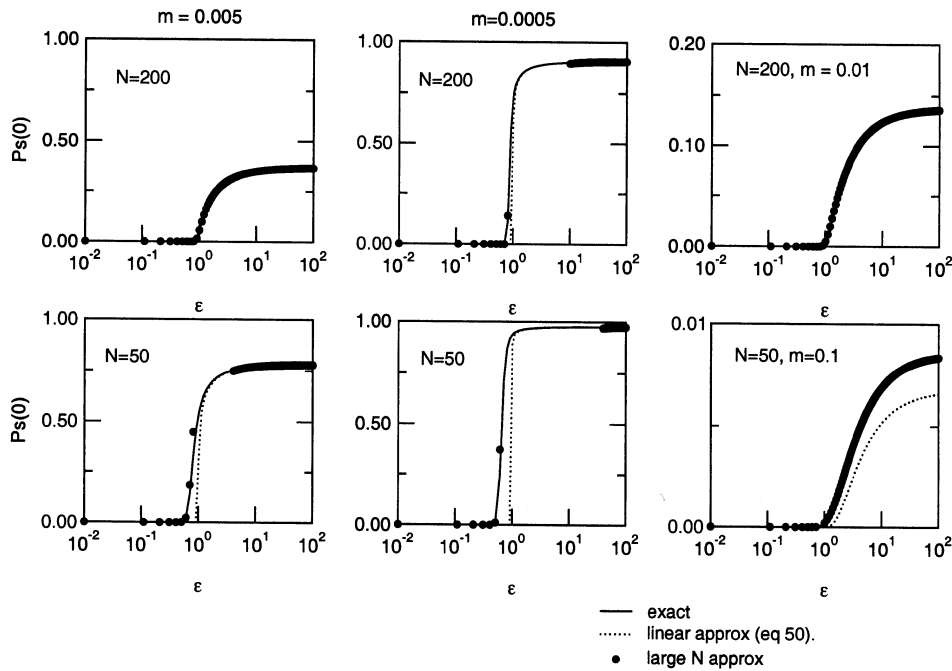


Figure 5. The approximate formula [equation (50)] and the exact probability of regional extinction,  $P_s(0)$ , are plotted against the parameter  $\epsilon = e/c$  for comparison purposes for different values of the external immigration parameter,  $m$ , and metapopulation sizes,  $N$ . The large  $N$  approximation is also shown (as filled circles). We plot the second-order approximation for  $P_s(0)$ , i.e., keeping terms in  $1/N$ , using either equation (A.11) or (A.13) depending on  $\mu N$  if  $\epsilon > 1$ , and using the same formulae except that the functions  $f$  and  $g$  are replaced by  $\tilde{f}$  and  $\tilde{g}$  if  $\epsilon < 1$  (see Appendix A). The large  $N$  approximation is well-behaved around  $\epsilon = 1$ , but if  $\epsilon > 1$ , when  $\mu N$  is too small, it is not possible to get a result because of the failure of the steepest descent method (see Appendix A). In these cases, no point is drawn. This explains why there is a lack of points when  $\epsilon > 1$  in the two central plots and in the lower left-hand plot. The right-hand lower plot ( $N = 50, m = 0.1$ ) is designed to show that the linear approximation we have performed fails if  $m$  is too large [see the derivation of equation (42) from equation (15)].

solution for  $P_s(0)$  using the Tridag algorithm in Fig. 5. In this figure it can be seen to what extent the above-mentioned third case ( $\epsilon > 1$ ) fails to give a good large  $N$  estimate for  $P_s(0)$  as long as  $\mu N$  is too small. There is a very well defined change of behavior at  $\epsilon = 1$ , as long as  $m$  is not too large. We therefore refer to  $\epsilon = 1$  as the *transition value*.

Finally, we use the results of the linear approximation to calculate the mean time to extinction. The probability of a metapopulation persisting to time  $t$  and becoming extinct between times  $t$  and  $t + dt$  is  $(dP(0, t)/dt)dt$  and therefore the mean time to extinction, given that the initial number of patches occupied was  $n_0 \neq 0$ , is

$$T_E(n_0) = \frac{\int_0^\infty t [dP(0, t)/dt] dt}{\int_0^\infty [dP(0, t)/dt] dt} = \int_0^\infty dt t \rho(t), \quad (51)$$

with parameterization

$$\rho(t) = \frac{1}{P_s(0)} \frac{dP(0, t)}{dt}. \quad (52)$$

On the other hand

$$T_E(n_0) = - \int_0^\infty t \frac{d}{dt} \left[ 1 - \frac{P(0, t)}{P_s(0)} \right] dt,$$

and so an integration by parts gives the alternative form (Nisbet and Gurney, 1982)

$$T_E(n_0) = \int_0^\infty \left[ 1 - \frac{P(0, t)}{P_s(0)} \right] dt, \quad (53)$$

where we have used the fact that  $[P_s(0) - P(0, t)]$  decays exponentially at large times.

The analytic evaluation of (53) using the probability distributions (49) and (50) when  $\epsilon > 1$ , is discussed in Appendix B. The main conclusion is that for values of  $\beta \equiv mN/c$  of order 1 (corresponding to the values in Fig. 4), for example,  $\beta = 1$  or  $\beta = 2$ , the dominant  $n_0$  dependence of  $T_E(n_0)$  is logarithmic:  $T_E(n_0) \sim (e - c)^{-1} \ln n_0$ . Here we have used the asymptotic form of the function  $\psi(n_0 + 1)$  (Abramowitz and Stegun, 1965) and assumed that  $n_0$  is not too small.

A population linked to an external source of individuals can never become extinct. After any metapopulation extinction, sooner or later, an individual from the mainland ‘rescues’ the metapopulation. So what is being discussed earlier is actually the time to the extinction of the metapopulation for the first time, given an initial metapopulation occupancy level,  $n_0$ , and this is what is being measured in the simulations. After this first extinction event the metapopulation can be rescued by immigration from the mainland. However there is virtually no chance of metapopulation recovery if extinction exceeds internal colonization. So, from this point on, the metapopulation can effectively be assumed to be ‘dead’. Although some patches will eventually be colonized by external immigrants, these events will be rare if  $m$  is small. In terms of the model, only the ratio of the rates  $e$ ,  $c$  and  $m$  appear in quantities associated with the stationary states [as  $\epsilon$  or  $\mu$  defined in (25)], and the same is true for time-dependent quantities, except that one of the rates will multiply  $t$  and set the time scale. Therefore the phrase ‘ $m$  small’ means specifically  $m \ll c$  and  $m \ll e$ . This is the regime we have investigated when studying the probability of regional extinction.

Having obtained a rather complete description of the model defined by equations (7)–(9), we now move on to consider more realistic versions of the model, specifically those in which the spatial aspects of the metapopulation are taken into account.

## 6. SPATIALLY EXTENDED MODELS

Since patches are made up of individuals which are discrete entities that interact locally, it is of paramount importance to understand how spatial modeling modifies the results obtained by means of both nonspatial models and spatially implicit models (SIMs) (Durrett and Levin, 1994). The potentially critical role of space in determining the output of ecological interactions has recently been highlighted (Bascompte and Solé, 1997; Tilman and Kareiva, 1997; Dieckmann *et al.*, 2000) and it has been found that spatial models often predict intriguing and counterintuitive results. Therefore, in this section we analyze two spatially extended metapopulation (SEM) models in detail. These models are more realistic than the nonspatial models we have considered so far in this paper. However, in general, they are not amenable to analytic treatments and so we have to rely almost entirely on numerical investigations. In the context of spatially extended models, the nonspatial models may be seen as a *mean field approximation*. So we may say that the main purpose of this section is to compare our earlier results (now viewed as the results of a mean field assumption) with two SEM models: the lattice metapopulation model (SEM), and a SRM model. Hanski (1994b) makes a distinction between *spatially realistic* models, which incorporate landscape structure—where every patch in the network is assigned a position and an area—and *spatially explicit* models, such as the lattice model. As a preliminary step, we compare our analytical approximations with exact stochastic realizations of the  $N$ -patch MIM model introduced in Section 2. After this we go on to discuss the lattice model in its usual manifestation: where an empty patch is colonized only from its nearest-neighbor patches. This lattice approach has been often used to study the effect of space on ecological interactions. It is also considered here, because many results involving spatial quantities in metapopulation theory have been obtained using this approach. The lattice metapopulation model may be considered as an example of a contact process (Mollison, 1977; Snyder and Nisbet, 2000) lying within a broad class of stochastic spatial models called interacting particle systems (Durrett, 1999). Finally, and even more usefully for practical purposes, we address a second spatial approach. It is a spatially realistic MIM stochastic model with a finite number of habitat patches which have known areas at particular spatial locations within a region. It is based on previous metapopulation models of this kind (Hanski, 1994a; Hanski and Ovaskainen, 2000). This modeling approach, which started with the incidence function model (Hanski, 1994a), has filled a gap between modeling and empirical studies and, since it was introduced, it has been successfully used for efficient parameter estimation in several empirical metapopulations (Hanski, 1999; Moilanen, 1999). While local dynamics and patch heterogeneity are expected to violate the mean field assumption, we would like to determine by how much analytical mean field predictions differ from numerical estimations of those quantities in models which take into account local dynamics, patch heterogeneity, and patch network structure explicitly.

**6.1. The  $N$ -patch mainland–island metapopulation: a spatially implicit model (SIM).** To build up exact stochastic realizations of the model introduced in Section 2, consider an  $N$ -patch system which at any time will be described by the number of occupied patches at time  $t$ ,  $n_1(t)$ , or equivalently the number of empty patches  $n_0(t) = N - n_1(t)$ . The system is modeled as a continuous-time Markov process in which transitions occur asynchronously so that within a short enough time interval only a single transition can take place (Durrett, 1999). The model contains the following three processes:

- Extinction. The same extinction rate  $e$  is assumed for all sites. Thus the probability of an extinction event within the system is:

$$\Pr\{\mathcal{E}\} = e n_1 dt. \quad (54)$$

- Colonization. Empty sites can be colonized internally at a colonization rate  $c$ . Now, the probability of a colonization event is:

$$\Pr\{\mathcal{C}\} = c \frac{n_1}{N} n_0 dt. \quad (55)$$

- Immigration. Empty sites can be colonized by external immigrants at an immigration rate  $m$ . The probability of an immigration event is:

$$\Pr\{\mathcal{I}\} = m n_0 dt. \quad (56)$$

Equations (54)–(56) are simply a rewriting of equations (4)–(6) in Section 2, but here we have put them in the same form which will be used to discuss the two subsequent models. In Appendix C we formulate the procedure to be used in simulations in a precise and clear way. Our simulation strategy is a natural extension of that given by Renshaw (1991) for a general birth–death process, but based on random patch choice and a rejection method [as described by Press *et al.* (1992)].

**6.2. The  $N$ -patch mainland–island metapopulation: a spatially explicit model (SEM).** In this spatially explicit model, the patch network is modeled as a regular square lattice (see Fig. 6) with periodic boundary conditions. Patches are taken to be sites in the lattice. Thus, each site can be inhabited by one local population. While both the extinction and immigration are still assumed to depend only on the global densities—as in the SIM—the internal colonization is now taken to depend on the local density of occupied sites. The simplest choice is to assume that colonization only takes place from the  $z$  nearest neighbors of an available site, where  $z$  can be either 4 or 8, depending on the neighborhood scheme chosen (either Von Neumann or Moore, respectively). Snyder and Nisbet (2000) have investigated such a model in the absence of immigration. Although this model appears to allow

## LOCAL LATTICE MODEL

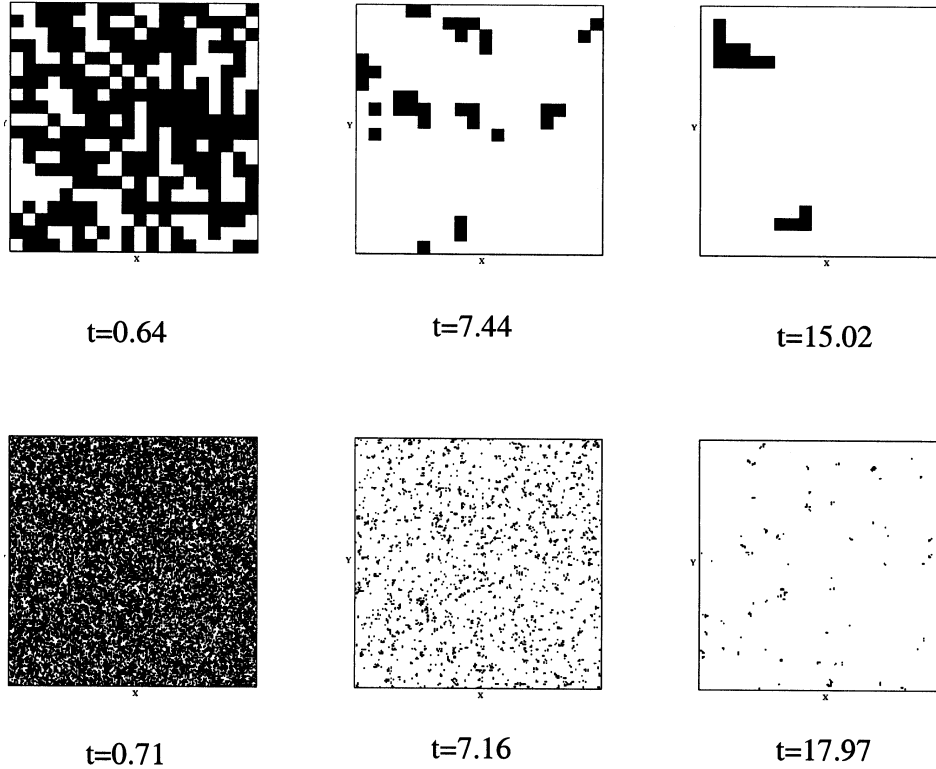


Figure 6. Temporal evolution of two lattices (upper plots,  $20 \times 20$ , and lower ones,  $200 \times 200$ ) for the lattice model (SEM) ( $c = 1$ ,  $e = 1$ ,  $m = 0.0001$ ). The metapopulation begins with all sites populated. As a consequence of local colonization processes, clusters of disconnected occupied sites are formed as time progresses. Three snapshots are shown in each case.

only very local interactions between sites, clusters of occupied sites which are nearest neighbors form extended areas which give rise to much longer range effects.

The system is again modeled as a continuous-time Markov process in which transitions occur asynchronously so that within a short enough time interval only a single transition can take place. Notice that the  $N$ -site lattice system may also be described by the number of occupied sites,  $n_1$ , or by the number of available sites,  $n_0$ . But now, we focus on the available sites and the 0 to  $z$  nearest neighbor populations that can potentially colonize it. Let  $n_{0i}$  be the number of available sites surrounded by  $i$  potential colonizer local populations, so that  $\sum_{i=0}^z n_{0i} = n_0$ . These are the only quantities we need in order to define the probabilities of the three processes occurring within the lattice model:

- Extinction. The same extinction rate  $e$  is assumed for all sites. The proba-

bility of an extinction event is:

$$\Pr\{\mathcal{E}\} = e n_1 dt. \quad (57)$$

- Colonization. Empty sites can be colonized internally at a colonization rate  $c$ . The probability of a colonization event is taken to be proportional to the number of occupied sites surrounding the empty site:

$$\Pr\{\mathcal{C}\} = \sum_{i=0}^z c \frac{i}{z} n_{0i} dt. \quad (58)$$

- Immigration. Empty sites can be colonized by external immigrants at an immigration rate  $m$ . The probability of an immigration event anywhere into the lattice is:

$$\Pr\{\mathcal{I}\} = m n_0 dt. \quad (59)$$

Notice that there is only a slight, but crucial, difference between equations (54)–(56) and equations (57)–(59); the substitution in the colonization rate of a global density (55) for a local density of occupied sites (58). In Fig. 6 the temporal evolution of two lattices is shown.

**6.3. The  $N$ -patch mainland–island metapopulation: a spatially realistic model (SRM).** The spatially realistic version of the  $N$ -patch MIM model we discuss here incorporates the spatial structure of a finite patch network. In this respect it represents a substantial improvement over nonrealistic approaches. As in previous realistic metapopulation models (Hanski, 1994a; Hanski and Ovaskainen, 2000), it considers a finite number of patches, labeled by  $i$ , at given geographic positions. The model is built again as a continuous-time Markov process in which transitions occur asynchronously. By contrast with the SIM and SEM, transitions are now completely patch-dependent. The same three basic processes of extinction, colonization and immigration are again introduced:

- Extinction. Patch extinction rate is known to be inversely proportional to patch area,  $A_i$ . The underlying assumptions here are that population size typically scales like patch area and extinction risk inversely with population size. Thus, the probability of an extinction event in the whole patch network is the sum of extinction probabilities over patches:

$$\Pr\{\mathcal{E}\} = \sum_{i=1}^N E_i p_i dt = \sum_{i=1}^N \frac{\tilde{e}}{A_i} p_i dt \quad (60)$$

where  $E_i$  is the patch-dependent extinction rate:

$$E_i = \frac{\tilde{e}}{A_i}, \quad (61)$$

and where we have defined

$$p_j = \begin{cases} 0, & \text{if patch } j \text{ is empty} \\ 1, & \text{if patch } j \text{ is occupied.} \end{cases} \quad (62)$$

- Colonization. The probability of a colonization event within the patch network is:

$$\Pr\{\mathcal{C}\} = \sum_{i=1}^N C_i(1 - p_i) dt \quad (63)$$

where  $C_i$  is the patch-dependent colonization rate. Empty sites can be colonized internally at a colonization rate which should increase with the number and size of neighboring populations, and decrease with the distance of the focal patch from the colonizing populations:

$$C_i = \tilde{c} \sum_{j \neq i}^N p_j A_j \exp(-\alpha d_{ij}), \quad (64)$$

where  $d_{ij}$  is the Euclidean distance between patches, and  $1/\alpha$  is a constant setting the average migration distance.

- Immigration. The definition of this rate introduces a mainland effect. The probability of an immigration event anywhere into the patch network is:

$$\Pr\{\mathcal{I}\} = \sum_{i=1}^N m(1 - p_i) dt, \quad (65)$$

where  $m$  represents the background colonization rate due to the arrival of immigrants from the mainland which may be viewed as propagule rain (Gotelli and Kelley, 1993).

We have used the same notation for the immigration rate in the SRM as in the SIM and SEM, namely,  $m$ . This is because (65) clearly equals  $mn_0dt$ , if  $n_0$  denotes the number of unoccupied patches, in agreement with (56) and (59). By contrast, although the parameters defined as  $\tilde{e}$  and  $\tilde{c}$  in the SRM resemble the parameters  $e$  and  $c$  arising in the SIM and SEM, they have different meanings, even different physical units. The relationship between them will be discussed in more detail in Section 6.4.

The definitions of the three processes above completely specify the model. However, other variants of the model are possible, and could be investigated using the numerical approach we will shortly describe. For instance, other choices for  $C_i$  which would also be valid include

$$C_i = \tilde{c} \frac{S_i^2}{S_i^2 + y^2}, \quad (66)$$

$$C_i = \tilde{c}(1 - \exp(-yS_i)), \quad (67)$$

$$C_i = \tilde{c} \frac{S_i}{S_i + y}, \quad (68)$$

where  $S_i$  is the number of colonizing individuals—propagule size—arriving at patch  $i$  from any other populated patch in the network. In turn, it is assumed that  $S_i$  is a decreasing function of patch distance and proportional to source patch area:

$$S_i = \sum_{j \neq i}^N p_j A_j \exp(-\alpha d_{ij}). \quad (69)$$

Notice that equation (64) assumes the patch colonization rate to be proportional to propagule size. This linear dependency is the simplest assumption, and has also been adopted by others [for example, Hanski and Ovaskainen (2000)] and is the limiting case of equations (67) and (68), when propagule size is very small. Furthermore, any of the three definitions given by equations (66)–(68) tend toward a constant patch colonization rate in the limit of large propagule size. Although this may be sensible and realistic, there is no need to make this assumption *a priori*, because metapopulation dynamics itself actually leads to asymptotic values of patch colonization rates as soon as the system reaches equilibrium, even under the simple linear dependence assumption. Interestingly, and this is also a reason to keep the linear assumption, if we consider a patch network of equally sized patches and infinite average migration distance ( $\alpha = 0$ ), only the patch dependent colonization rate given by equation (64), ensures that the stochastic SRM model defined through equations (60)–(65) collapses into the SIM model previously described. We will take advantage of this fact when comparing results.

Having defined this model as a continuous-time Markov process in which transitions occur asynchronously, we generate our results by performing stochastic simulations (see Appendix C) and averaging over realizations. This procedure has two advantages. First, it is completely general, since other particular definitions of patch-dependent rates could have been adopted. Secondly, when computing persistence times, this method not only provides averages, but also variances, and even whole lifetime distributions. Furthermore, there is a clear connection between this modeling approach and the theory developed by Hanski and Ovaskainen (2000), although their model is deterministic, rather than stochastic. The assumptions of both models are essentially the same, since the definition of our patch-dependent colonization (64) and extinction rates (61) are exactly those of Hanski and Ovaskainen (2000); the only difference is that the external immigration  $m$  is equal to zero in their model. In order to make this connection even more evident, consider a given patch network configuration. We may define the probability of having the  $i$ th patch populated at time  $t$  as an average over realizations, labeled by  $l$ , when the number of realizations,  $R$ , tends to infinity:

$$f_i(t) = \lim_{R \rightarrow \infty} \frac{\sum_{l=1}^R P_i^l(t)}{R}. \quad (70)$$

Since  $E_i$  is the extinction rate of patch  $i$ ,  $E_i dt$  is the probability of extinction of the  $i$ th patch when populated, within a vanishingly small time interval  $dt$ . Similar



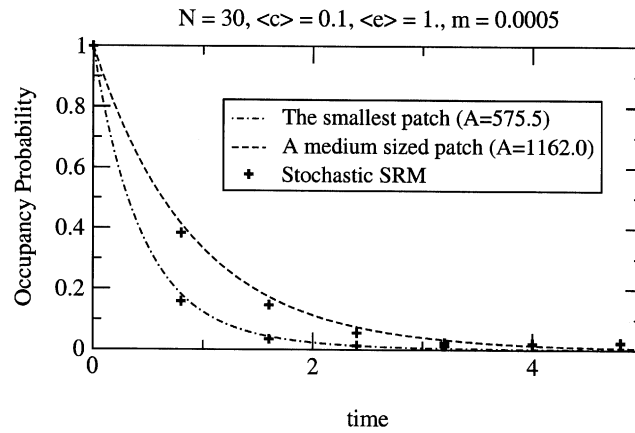


Figure 7. Temporal evolution of the occupation probabilities for two patches of given areas belonging to a pre-defined complex patch network. The patch network has been set up by using the same prescription as given in Section 6.4.1. Temporal evolution is computed through numerical integration, using a 5th order Runge–Kutta method (Press *et al.*, 1992), on the system of ordinary differential equations defined by equations (61), (64) and (72). For comparison purposes, and using the same pre-defined patch network, the estimate of the probabilities [see equation (70)] at discrete times is computed by constructing 50 000 stochastic realizations at each time, making use of the simulation algorithm given in Appendix C.

terms  $C_i dt$  and  $m dt$  give the probability of colonization and immigration. Therefore, the probability of a patch being occupied evolves in time as follows:

$$f_i(t + dt) = [1 - E_i dt] f_i(t) + [C_i + m] dt [1 - f_i], \tag{71}$$

which leads to an equation that gives the rate of change of the probability of a patch being occupied:

$$\frac{df_i}{dt} = (C_i + m)(1 - f_i) - E_i f_i. \tag{72}$$

This equation is the starting point of the theory developed by Hanski and Ovaskainen (2000). Since patch dependent colonization rates depend in general on the probability of the other patches being occupied, what we actually have here is a system of coupled ordinary differential equations. Therefore, given a particular patch network setting, a particular definition of patch rates, and assuming equation (70), we can compare the temporal evolution of the probability of patches being occupied—*occupation probabilities*—computed either by numerical integration of the system (72), or averaging over stochastic realizations. This is exactly what is done in Fig. 7, where a close agreement between the two methods of calculating the corresponding probabilities is shown.

As mentioned earlier, different assumptions lead to different definitions of colonization and extinction rates. However, Hanski and Ovaskainen (2000) develop

a theory which is not restricted to particular functional forms of colonization and extinction rates. They introduce the concept of the metapopulation capacity,  $\lambda$ , and give a condition under which the persistence of the metapopulation is guaranteed:

$$\lambda > \tilde{\epsilon}, \quad (73)$$

where  $\tilde{\epsilon} = \tilde{e}/\tilde{c}$ , a ratio of an extinction to a colonization parameter. Whenever condition (73) is met, there exists an equilibrium solution,  $f_i^*$ , for the system described by equation (72) with  $f_i^* > 0$  for all  $i$ . This means that the whole metapopulation is preserved on this landscape structure. So, at equilibrium, each and every patch of the system has a nonzero probability of hosting the population. However, our approach is different. We are interested in extinction dynamics. So, we are working in the regime where the metapopulation is really endangered ( $\tilde{\epsilon} \gg 1$ ) and declining, and our aim is to determine extinction times by means of various analytical and numerical methods. The quantity of interest to us is, once again,  $P(0, t)$ , the probability of having a global extinction at time  $t$ . Within this theoretical framework, the simplest expression for this quantity is obtained by assuming that the probability of patch  $i$  being occupied is independent of the probabilities of occupation of the other patches. In this case  $P(0, t)$  can be written as the product of the probabilities of each patch being empty:

$$P(0, t) = \prod_{i=1}^N (1 - f_i(t)). \quad (74)$$

Using this result we can now compute the temporal evolution of the probability of having complete extinction by numerical integration of equation (72) (see also Fig. 8). In fact, the occupation probabilities are not independent unless colonization is absent. However, we would expect that as long as immigration and extinction processes dominate over colonization, the occupation probabilities will be only weakly coupled and (74) will be a reasonable approximation to  $P(0, t)$ . In fact, we will see in the next section, that this is the regime where we observe a good agreement between this probability and the same quantity in an equivalent SIM model, where *equivalence* is precisely defined through equations (75) and (76) in the next section. Moreover, this close agreement opens up the possibility of using equation (53) to compute mean times to extinction, even for realistic, complex patch networks, by calculating this integral numerically.

**6.4. Comparison of different approaches.** Given a complex patch network, our purpose is to assess whether we can make use of the analytical mean field results derived from the SIM to determine extinction times in realistic, complex patch networks. Thus, specifically we should compare SIM results and SRM results. We have already remarked that the parameters  $\tilde{e}$  and  $\tilde{c}$  in the SRM differ from  $e$  and  $c$  arising in the SIM and SEM, whereas the external immigration rate  $m$ , by

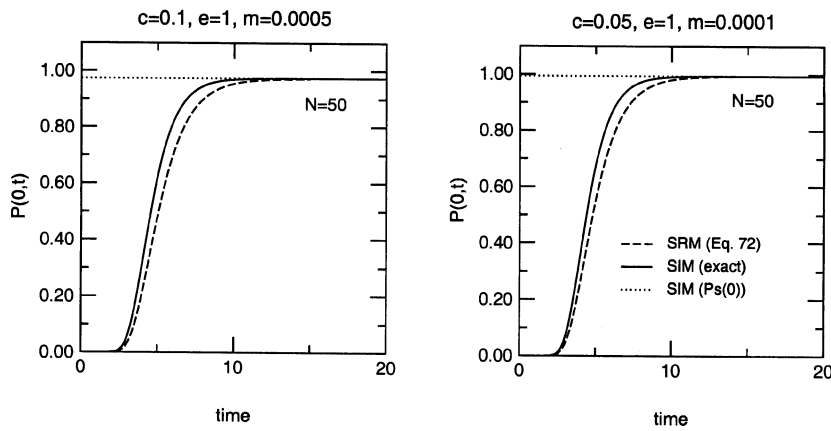


Figure 8. Temporal evolution of the probability of global extinction occurring in a complex patch network created as indicated in Section 6.4.1. The same quantity,  $P(0, t)$ , in an equivalent SIM model defined using equations (75) and (76) is also plotted for comparison purposes.

contrast, has the same meaning for all three models. Therefore, if we want to test our analytical approximations and make comparisons among models, we need to identify quantities in the SRM which play the role of  $e$  and  $c$  in an equivalent SIM.

Let us first consider the extinction rates. In the SIM, described by the master equation (9) and the transition rates derived from equations (54)–(56), the patch extinction rate is patch independent, and is simply the parameter  $e$ . By contrast, in the SRM, since large areas have lower extinction rates, they remain populated longer than smaller areas do. Thus, the contribution of each patch to an average patch extinction rate should be proportional to patch area. So, a properly weighted average patch extinction rate can be defined as follows:

$$\langle e \rangle = \frac{\sum_{i=1}^N E_i A_i}{\sum_{i=1}^N A_i} = \frac{N\tilde{e}}{A_T} = \frac{\tilde{e}}{\langle A \rangle}, \tag{75}$$

where  $\langle A \rangle = A_T/N$  is the average patch area and  $A_T$  is the total patch area. Therefore, patch network extinction dynamics can be roughly characterized by the patch extinction rate corresponding to the network area average  $\langle A \rangle$ .

With regard to colonization, the identification between the models can be made by looking at the case where an empty patch is colonized when the rest of the patches are occupied. In this situation, within the SRM modeling framework, (63) and (64) give a patch-dependent probability  $\tilde{c} \sum_{j \neq i}^N A_j \exp(-\alpha d_{ij}) dt$ . Averaging over patches, we get a patch-independent probability of colonization. Within the SIM framework the probability is not patch-dependent and takes the simple form  $c(N-1)dt/N$ . If we denote the quantity in the SRM which is to be identified with  $c$

in the SIM as  $\langle c \rangle$ , we can make the following straightforward correspondence:

$$\begin{aligned} \frac{\langle c \rangle (N-1) dt}{N} &= \frac{1}{N} \sum_{i=1}^N \left( \tilde{c} \sum_{j \neq i}^N A_j \exp(-\alpha d_{ij}) dt \right) \\ \Rightarrow \langle c \rangle &= \frac{\tilde{c}}{N-1} \sum_{i=1}^N \sum_{j \neq i}^N A_j \exp(-\alpha d_{ij}). \end{aligned} \quad (76)$$

In particular, assuming infinite average migration rate,  $\alpha = 0$ , a little algebra shows that  $\langle c \rangle = \tilde{c} \sum_i A_i$ , which reinforces the idea of  $\tilde{c}$  in the SRM as a colonization rate per unit area.

To sum up, within some parameter regime (see Figs 11 and 12), which turns out to be that characterized by rather strong and rapid extinctions in comparison to internal colonizations, and from the point of view of extinction dynamics, a complex patch network of given areas at fixed spatial locations behaves in the same way as a SIM which is described simply by average extinction and colonization rates given by equations (75) and (76), with the same external immigration rate,  $m$ . Thus, a realistic patch network can effectively be modeled as a SIM, but with these two particular averaged rates acting as the effective extinction and colonization rates.

When comparing results, we need to average over stochastic realizations. For the SRM model, stochastic realizations require the introduction of a complex patch network described earlier. In the next subsection, we describe how patch networks are constructed in practice.

6.4.1. *Complex patch networks.* In the SRM we have, in essence, two kinds of parameters: those fixing the patch network structure (involving the specification of patch areas and patch locations within an overall area which defines the metapopulation) and those which define the model itself (involving the colonization, extinction and migration dynamics, i.e.,  $\alpha$ ,  $\tilde{c}$ ,  $\tilde{e}$  and  $m$ ). In this paper we will fix those parameters concerned with the geometry of the patch network, and will investigate the properties of the model when the second group of parameters change. In other words, our central interest will not be in how patch network geometry influences extinction dynamics. This would make an interesting future investigation.

In every one of our simulations, patches are located at random within a square area ( $7000 \text{ u} \times 7000 \text{ u}$ ), where  $\text{u}$  are arbitrary length units. The specific areas of every patch are chosen at random from a lognormal distribution of average  $1250 \text{ u}^2$  and standard deviation 0.3, a prescription adopted by Moilanen (1999). The  $\alpha$  arising in the colonization rates is taken to have the value of  $1.9 \times 10^{-3} \text{ u}^{-1}$  which implies an average migration distance of  $\approx 500 \text{ u}$ , making internal colonization a rather local process. Any increase in the average migration distance is expected to make the SRM results closer to those from the spatially implicit approach. This

is why we have set up patch networks using this rather low value for the average migration distance: we wanted to test our analytical approximations even under rather local colonization conditions.

6.4.2. *The dimensionless SRM.* So far we have worked with variables and model parameters which have physical units, as seen in the last section where the patch network structure was given in terms of a scale size  $u$ . However, the dynamic behavior of the model cannot depend on the physical units chosen to measure the quantities we use to describe it. So, it is important to rewrite the model in a form which is independent of the units we use. This is very easy to do in this particular case.

Let  $L$  be a linear characteristic dimension of the region where the metapopulation is found. We may define a characteristic time by means of the external immigration,  $m$ :

$$\tau = \frac{1}{m}. \quad (77)$$

Any model parameter involving length and time scales can now be made dimensionless using these two characteristic scales. Some of the more important dimensionless parameters are:

- The relative average migration distance,  $m_d$ :

$$m_d = \frac{1}{\alpha'} = \frac{1/\alpha}{L}. \quad (78)$$

- The relative position of patch  $i$ :

$$\begin{aligned} x_i &= \frac{X_i}{L} \\ y_i &= \frac{Y_i}{L}, \end{aligned} \quad (79)$$

where  $(X_i, Y_i)$  are the physical coordinates of patch  $i$ .

- The relative area of patch  $i$ :

$$a_i = \frac{A_i}{L^2}. \quad (80)$$

- The relative patch internal colonization rate:

$$e_i = \frac{E_i}{m}. \quad (81)$$

- The relative patch extinction rate:

$$c_i = \frac{C_i}{m}. \quad (82)$$

Table 1. Comparison between parameter values of the SRM and its dimensionless counterpart for the same patch network as used in Fig. 7. Rewriting the model in terms of dimensionless parameters allows for easy recognition of, for instance, the degree of locality of the model, or the way patch areas are spread over the whole metapopulation region.

	SRM	Dimensionless SRM
$N$	30	30
Regional area	$4.9 \times 10^7 \text{ u}^2$	1
$m_d$	501 u	0.075
$\langle A \rangle$	$1250 \text{ u}^2$	$2.55 \times 10^{-5}$
$\alpha$	$1.9 \times 10^{-3} \text{ u}^{-1}$	13.3
$\tilde{e}$	1293.7	0.053
$\tilde{c}$	$1.5 \times 10^{-4}$	$1.03 \times 10^7$
$m$	$5 \times 10^{-4}$	1
Equivalent SIM	$\langle c \rangle = 0.1, \langle e \rangle = 1, m = 5 \times 10^{-4}$	$\langle c \rangle' = \frac{\langle c \rangle}{m}, \langle e \rangle' = \frac{\langle e \rangle}{m}, m' = 1$

The definition of the above quantities allows the connection between the SRM parameters, and a new set of dimensionless parameters on which the dimensionless model actually depends, to be made (see Table 1). So, we can rewrite the relative patch-dependent rates in terms of relative quantities as:

$$\begin{aligned}
 e_i &= \frac{\tilde{e}'}{a_i} \\
 c_i &= \tilde{c}' \sum_{j \neq i}^N p_j a_j \exp(-\alpha' d'_{ij}),
 \end{aligned}
 \tag{83}$$

where

$$\begin{aligned}
 \alpha' &= L\alpha \\
 \tilde{e}' &= \frac{\tilde{e}}{L^2 m} \\
 \tilde{c}' &= \frac{\tilde{c} L^2}{m},
 \end{aligned}
 \tag{84}$$

and  $d'_{ij}$  is the distance between patches measured in relative length units.

To sum up, by introducing a characteristic time scale, it is clear that the dimensionless SRM has only two relevant patch rates. Similarly, its relevant spatial lengths (or areas) can be expressed simply as fractions of the characteristic length,  $L$  (or total regional area,  $L \times L$ ) of the metapopulation.

6.4.3. *Stochastic realizations.* At every stage where we have computed averages or distributions over stochastic realizations of the SRM, we have proceeded

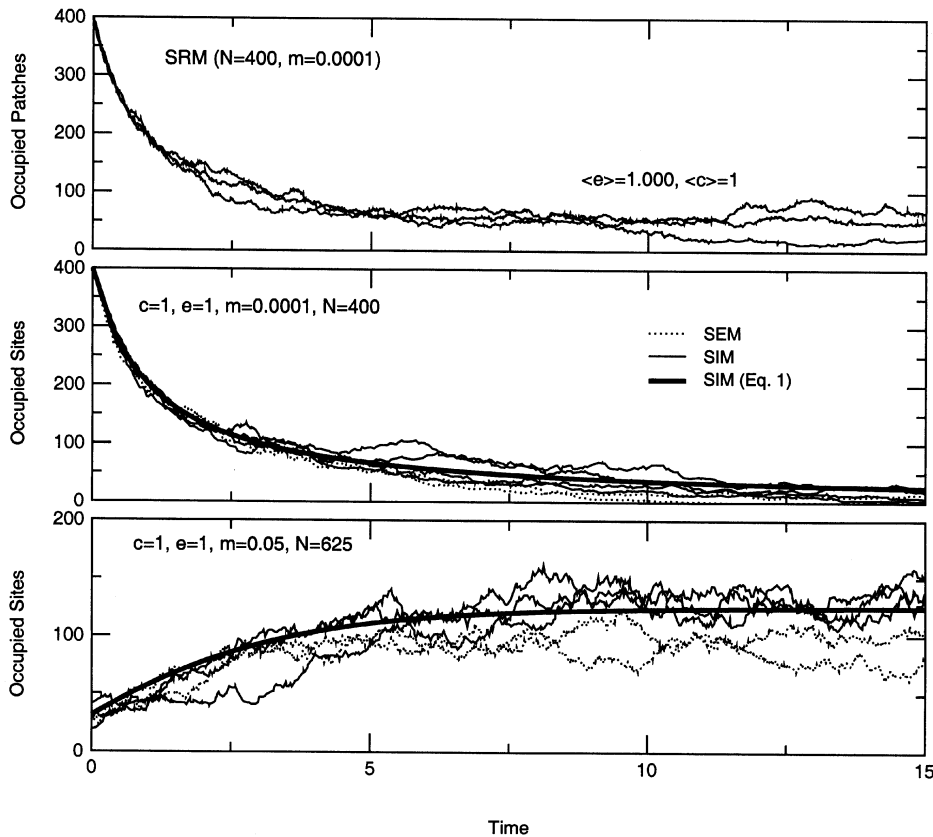


Figure 9. Temporal evolution of the number of occupied patches in different stochastic realizations of the SIM, SEM, and SRM. The evolution of the mean number of occupied patches within the mean field approach [equation (1)] is also plotted in bold black.

in two alternative ways. In the first method, the same patch network was used in every stochastic realization. This was the approach adopted in Fig. 7. By contrast, in Figs 9–12, a new patch network, following the same prescription as given earlier, is constructed for every new stochastic simulation carried out. Finally, and using equations (75) and (76), we choose  $\tilde{e}$  and  $\tilde{c}$  parameters arising in  $E_i$  and  $C_i$ , respectively, in such a way that  $\langle e \rangle$  and  $\langle c \rangle$  match the values of the equivalent SIM, defined by patch-independent extinction and colonization rates,  $e = \langle e \rangle$ , and  $c = \langle c \rangle$ , respectively, and also choose the same external immigration rate,  $m$ . In this way for each computation of a new value of, for instance, the mean time to extinction, we are generating a family of patch networks which share the same spatial geometry in a statistical sense, and which are equivalent to the same spatially implicit  $N$ -patch mainland–island metapopulation model (SIM).

**6.5. Results and discussion.** The main results concerning the temporal behavior of the different approximations we have performed in order to investigate extinc-

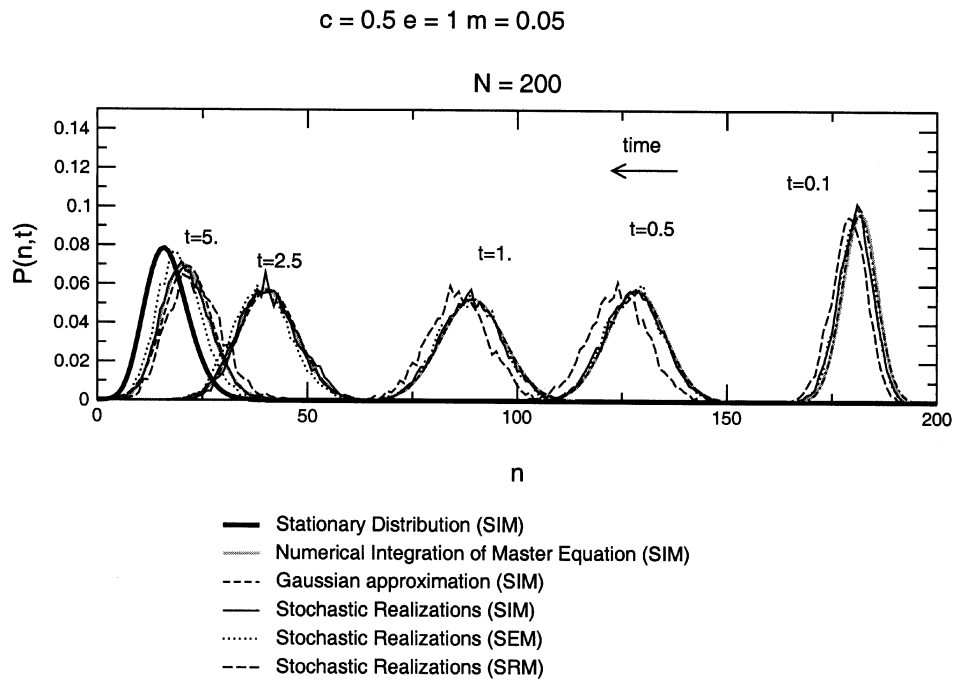


Figure 10. Temporal evolution of the probability of having  $n$  patches occupied at time  $t$  for different models of metapopulation dynamics. In the SRM,  $N = 200$  patches are located at random in the same way as in Fig. 9. The same value for  $\alpha$  was also used. Patch extinction rates  $E_i$  and the colonization parameter  $\tilde{c}$  are chosen to give rise to an equivalent SIM with the same extinction and colonization rates.

tion dynamics and, in particular, estimate persistence times in realistic model metapopulations, are summarized Figs 9–12.

In Fig. 9, some stochastic realizations of the  $N$ -patch MIM model are shown. In the central and lower plots, the stochastic simulations of the SIM are seen to match the average given by the mean field approach, while lattice simulations give values which are significantly lower than those given both by the spatial implicit stochastic realizations and the mean field approach. The evolution of the number of occupied patches in the SRM model is shown in the upper plot. In these three stochastic realizations, the patch network has been set up in such a way that it is equivalent to a SIM with parameters  $\langle c \rangle$ ,  $\langle e \rangle$ , and  $m$ .

In Fig. 10, the temporal evolution of the probability of keeping  $n$  local populations extant at time  $t$  is shown starting with a completely occupied metapopulation, i.e.,  $P(N, 0) = 1$ . The different models agree qualitatively, and even quantitatively, quite well. Notice that most lines corresponding to the SIM overlap at each time, except for the final one ( $t = 5$ ), where slight differences can be seen. The distributions computed using stochastic realizations of an equivalent SRM also quantitatively match those obtained using the spatial implicit approach.



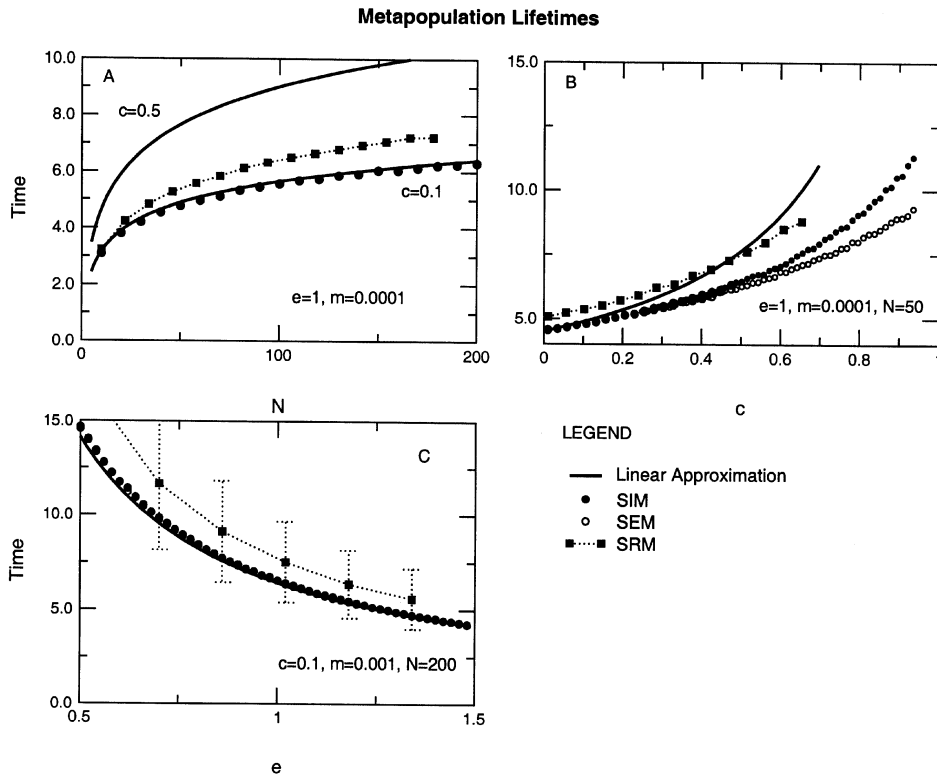


Figure 11. Mean time to extinction. Five thousand stochastic realizations were performed to compute the average of the metapopulation lifetime for each parameter combination.

The time until the last remaining occupied patch (or site) becomes extinct for the first time is defined as the metapopulation lifetime. In other words, lifetime is the persistence time until a global metapopulation extinction event occurs for the first time. In all simulations of Figs 11 and 12, the starting occupation level was always chosen as  $n_0 = N$ . In Fig. 11, we numerically evaluated the integral in (53) when  $c < e$ , and compared the result with the mean time to extinction after performing a large number of numerical simulations for the SIM, SEM, and SRM. For the SRM stochastic simulations, networks were set up following the prescription given in Section 6.4.1, with once again the parameters  $\tilde{c}$  and  $\tilde{e}$  fixed to make the model equivalent to a SIM with parameters  $c = \langle c \rangle$ ,  $e = \langle e \rangle$ , and  $m$ . In plot A, the mean time to extinction (*persistence time*) has been evaluated using the linear approximation (both for  $c = 0.5$  and  $c = 0.1$ ). When  $c = 0.1$ , stochastic realizations are also performed and good agreement is found among all the models and the analytical prediction, as long as the number of patches is not too large ( $N < 40$ ). In any case, the persistence time grows with the size of the network. In plot B, linear approximation curves match values of SIM and SEM (circles) as long as colonization rates have values significantly lower than extinction rates.

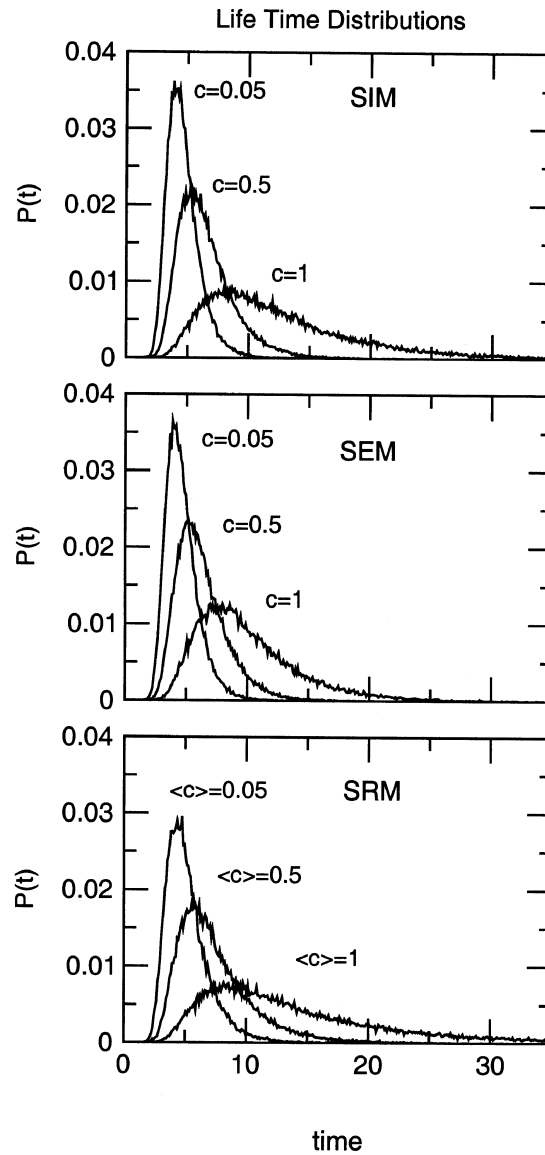


Figure 12. Lifetime distributions of three different metapopulation models. (a) The SIM model of a MIM, where colonization dynamics depends on global densities. (b) The spatially explicit stochastic model (SEM) of a MIM, where colonization takes place locally as in a contact process. (c) The SRM model of a MIM, when colonization depends on network structure, which has been set up following the prescription given in Section 6.4.1. Probability distributions are evaluated by performing 50 000 stochastic realizations of each model.

In plot C,  $\beta = N$ ,  $m/c = 2$ , so the linear approximation has been computed using equation (B.10) of Appendix B. In this case, extinction rates are large enough in comparison with colonization rates that the linear approximation captures the

behavior of the persistence time, at least for the SIM and the SEM. However, SRM realizations give larger estimates than the other two models. This disagreement in metapopulation lifetimes tends to decrease as the ratio of extinction to colonization rates increases.

In general, we notice that SRM realizations give rise to persistence times slightly greater than SIM approximations. Local colonization can be argued to make metapopulations more prone to extinction in comparison to spatially implicit predictions. This is actually what we find in our lattice model (SEM). In a strongly local model such as the lattice SEM, as the metapopulation decays, more and more unconnected empty lattice sites arise. These sites cannot be internally rescued because of isolation, which further accelerates the process of regional extinction. Nevertheless, for our stochastic SRM we find the opposite result: spatial structure and patch heterogeneity linked to local colonization lets realistic model metapopulations persist longer on average. Therefore, any analytically predicted lifetime of a metapopulation using the linear approach [Section 5, equation (53)] within a mean field [and assuming patch extinction and colonization rates to be equal for all patches and given by equations (75) and (76)] will be lower than that obtained by our spatially realistic approach. Since real metapopulations are much more reliably modeled using spatially realistic models, it is probable that our analytical approach will tend to underestimate regional persistence in real situations. However, notice also (see the upper plot of Fig. 11) that there is a parameter regime characterized by strong extinction rates, and also by a low number of patches, where the behavior of the SRM model is well described by the mean field approach. The same idea can also be seen in the tendency of the SRM curve to asymptote to the SIM curves as the ratio  $e/c$  increases (lower plot of Fig. 11).

The lifetime distributions, shown in Fig. 12, display other interesting features. Lifetime distributions were computed for the three different stochastic models we have defined. The shape of lifetime distribution curves,  $P(t)$ , for the different models are comparable. As long as  $c \ll e$ , the variance of the distribution remains small. Whenever  $c \sim e$ , the differences amongst the distributions from different spatially explicit models not only become apparent, but also the lifetime distributions become much broader. Approaching the transition value  $\epsilon = 1$ , the lifetime variance keeps on increasing. Therefore, our approach through the SIM is unable to give good lifetime predictions if the metapopulation is in the regime where extinction and colonization balance out.

## 7. CONCLUSION

In this paper we have carried out an extensive study of a stochastic model of metapopulation dynamics, investigating both its time evolution and its stationary properties, its spatial and nonspatial forms, and used both analytical and numerical calculations in the course of the investigation. The model itself is a generalization

of the classical Levins' model which adds stochastic effects and immigration from the mainland.

We began with the nonspatial version, by deriving a master equation for  $P(n, t)$ , the probability of  $n$  of the patches being occupied at time  $t$ . This equation is of a relatively simple form: it represents a one-step Markov process. The transition probabilities are not linear functions of  $n$ , so it is not exactly soluble, but exact (although rather formal) expressions can be found for the stationary probability distributions  $P_s(n)$ , the mean number of occupied patches in the stationary state  $\langle n \rangle_s$ , as well as the corresponding higher moments. We assumed that the total number of patches was large ( $N \gg 1$ ), in order to obtain relatively simple expressions. These are in good agreement with the results of the numerical solution of the master equation and the direct simulation of the stochastic process, down to surprisingly small values of  $N$ .

The time-dependence can also be well characterized. As long as the probability of extinction of the metapopulation is small ( $P(0, t) \ll 1$ ),  $P(n, t)$  is not strongly influenced by the boundary at  $n = 0$  and, assuming that the effect of the boundary at  $n = N$  is similarly negligible, it consists of a Gaussian distribution whose peak moves according to the deterministic version of the model. The width of this distribution increases with time, and is explicitly calculated in Section 4, at least in the limit when  $N$  can be assumed to be large. As soon as  $P(0, t)$  becomes significant this Gaussian assumption breaks down, but fortunately another approximation now becomes applicable:  $P(n, t)$  only has significant contributions for small  $n$ . This means that  $O(n/N)$  terms in the transition probabilities of the master equation may be neglected and a linear one-step process is obtained. Such processes are exactly soluble, and so exact forms for both  $P(0, t)$  and  $P_s(0)$  may be found in this case. This in turn allows us to calculate the mean time to extinction of the metapopulation, given  $n_0$  patches were initially occupied. Within the linear approximation we found that this mean time was infinite if the colonization rate,  $c$ , was greater or equal to the extinction rate  $e$ , and had the form  $(e - c)^{-1} \ln n_0$  if the extinction rate was greater than the colonization rate and  $n_0$  was not too small. A numerical investigation of the full model, that is, without the linear approximation showed that the linear approximation works well as long as neither the immigration rate from the mainland,  $m$ , nor the number of patches,  $N$ , are not too small. Furthermore, the change of behavior at  $\epsilon = e/c = 1$  in the linearized version persists in the full model, and is sharper the smaller the immigration rate from the mainland,  $m$ , is.

In Section 6 we turned to the investigation of more realistic models—those where the spatial distribution of patches was taken into account. In the context of these models, the nonspatial model situated in the earlier sections of the paper may be viewed as a type of mean field approximation of the spatial models. An analytic treatment of the spatial models is difficult, so our investigations were of a numerical nature, however, these allow us to assess the validity of the mean field approximation by comparing these results to those obtained from the spatially implicit version.

The most obvious, and rather classical, spatial version of the model consists of representing patches as sites on a regular two-dimensional lattice. However, another more interesting version, which has its roots in the study of real metapopulations, is a SRM version for a finite number of habitat patches, that actually admits a formal description that makes it closely related to a model developed by Hanski and Ovaskainen (2000). Although there are many interesting questions relating to these models and to their inter-relation, we focused primarily on the question of the mean time to extinction. Concerning this point, the main conclusion from our numerical investigations is that it is possible to simplify the complexity of a real patch network using equations (75) and (76), and make use of our analytical approximation to estimate mean times to extinction. The results shown in Figs 11 and 12 indicate that there is sufficient agreement between the various models and the mean field approach, that qualitative trends can be identified, and for the range of parameters  $e > c$ , that definite predictions are possible.

We believe that the work, which we have presented here, has extended the scope of metapopulation modeling and hope that by stressing the extinction dynamics of these models, we have contributed to the understanding of the nature of population extinctions.

#### ACKNOWLEDGEMENTS

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#### APPENDIX A

Here we consider the evaluation of sums of the form

$$S_N(\alpha, \gamma) \equiv \sum_{n=0}^N \binom{N}{n} \frac{\Gamma(n + \gamma)}{\Gamma(\gamma)} \alpha^n, \quad (\text{A.1})$$

which are required to obtain expressions for  $P_s(0)$  (the case  $\gamma = \beta$ ) and  $\langle n \rangle_s$  (the case  $\gamma = \beta + 1$ ) in Section 3.

We begin by converting the sum (A.1) to an integral:

$$S_N(\alpha, \gamma) = \frac{1}{\Gamma(\gamma)} \sum_{n=0}^N \binom{N}{n} \int_0^\infty dx x^{n+\gamma-1} e^{-x} \alpha^n$$

$$\begin{aligned}
&= \frac{1}{\Gamma(\gamma)} \int_0^\infty dx x^{\gamma-1} e^{-x} \sum_{n=0}^N \binom{N}{n} (\alpha x)^n \\
&= \frac{1}{\Gamma(\gamma)} \int_0^\infty dx x^{\gamma-1} (1 + \alpha x)^N e^{-x} \\
&= \frac{\alpha^{-\gamma}}{\Gamma(\gamma)} \int_0^\infty dy y^{\gamma-1} (1 + y)^N e^{-(\alpha^{-1})y}. \tag{A.2}
\end{aligned}$$

The integral in (A.2) equals  $\Gamma(\gamma)U(\gamma, N + \gamma + 1; \alpha^{-1})$ , where  $U$  is a confluent hypergeometric function (Abramowitz and Stegun, 1965). A Kummer transformation shows that this may also be written in terms of  $U(-N, 1 - \gamma - N; \alpha^{-1})$  which is related to the generalized Laguerre polynomial  $L_n^{(\lambda)}(z)$  (Abramowitz and Stegun, 1965). So finally we obtain

$$S_N(\alpha, \gamma) = \alpha^N U(-N, 1 - \gamma - N; \alpha^{-1}) = (-1)^N N! \alpha^N L_N^{(-\gamma-N)}(\alpha^{-1}). \tag{A.3}$$

As a check we note that since  $L_N^{(-\gamma-N)}(\alpha^{-1})$  is a polynomial of order  $N$  in  $\alpha^{-1}$ , then  $\alpha^N L_N^{(-\gamma-N)}(\alpha^{-1})$  is a polynomial of order  $N$  in  $\alpha$ . Taking  $\gamma = \beta$  we find from (18)

$$(P_s(0))^{-1} = (-1)^N N! \alpha^N L_N^{(-\beta-N)}(\alpha^{-1}). \tag{A.4}$$

Therefore, from (17)

$$P_s(n) = \binom{N}{n} \frac{\Gamma(n + \beta)}{\Gamma(\beta)} \frac{(-1)^N (\alpha^{-1})^{N-n}}{L_N^{(-\beta-N)}(\alpha^{-1}) N!}. \tag{A.5}$$

Similarly from (24)

$$\langle n \rangle_s = \beta \left\{ \frac{L_N^{(-\beta-1-N)}(\alpha^{-1})}{L_N^{(-\beta-N)}(\alpha^{-1})} - 1 \right\}. \tag{A.6}$$

The expressions (A.4) and (A.6) for  $P_s(0)$  and  $\langle n \rangle_s$  are not very transparent. To obtain more useful equations for these quantities we look at their asymptotic forms when  $N$  becomes large. As we will see, the results we obtain will hold down to even relatively small values of  $N$ .

Trying to obtain the large  $N$  form of the quantities in (A.3) is difficult—for example, in the Laguerre polynomial there is an  $N$  dependence in the order, the upper index and the argument (since  $\alpha = c/eN$ ). Therefore, it is better to begin from (A.2). In the case  $\gamma = \beta$  it can be written as

$$(P_s(0))^{-1} = \frac{\epsilon^{N\mu} N^{N\mu}}{\Gamma(N\mu)} \int_0^\infty \frac{dy}{y} \exp N\{\mu \ln y + \ln(1 + y) - \epsilon y\}, \tag{A.7}$$

where  $\mu$  and  $\epsilon$  are  $N$ -independent constants given by (25). Writing a similar expression for the case  $\gamma = \beta + 1$  and dividing one by the other one finds

$$\sum_{n=0}^N \binom{N}{n} \frac{\Gamma(n + \beta + 1)}{\Gamma(\beta + 1)} \alpha^n P_s(0) = \frac{\epsilon}{\mu} \left\{ \frac{\int_0^\infty dy \exp[Nf(y)]}{\int_0^\infty dy g(y) \exp[Nf(y)]} \right\}, \tag{A.8}$$

where

$$f(y) = \mu \ln y + \ln(1 + y) - \epsilon y, \quad g(y) = \frac{1}{y}. \tag{A.9}$$

In this notation

$$P_s(0) = \frac{\Gamma(N\mu)}{\epsilon^{N\mu} N^{N\mu}} \left\{ \int_0^\infty dy g(y) \exp[Nf(y)] \right\}^{-1}. \tag{A.10}$$

The integrals in (A.8) and (A.10) are in the standard form for the application of the method of steepest descents. There are two steps we need to take:

- (a) Find the values of  $y$  such that  $df/dy = 0$ . It turns out that there is a positive root and a negative root. The integrals in (A.8) and (A.10) will be dominated by values of  $y$  near the positive root which we denote by  $y^*$ .
- (b) To get the contributions near to  $y^*$  we expand about it:  $y = y^* + \hat{y}$  and keep only terms in  $\hat{y}^2$ . The resulting integrals are Gaussian and are easily performed.

Following these steps we find

$$\begin{aligned} P_s(0) = & \frac{\Gamma(N\mu)}{\epsilon^{N\mu} N^{N\mu}} \sqrt{\frac{N|f^{(2)}(y^*)|}{2\pi}} \frac{\exp\{-Nf(y^*)\}}{g(y^*)} \left\{ 1 + \frac{1}{2N} \frac{g^{(2)}(y^*)}{g(y^*)f^{(2)}(y^*)} \right. \\ & + \frac{5}{24N} \frac{[f^{(3)}(y^*)]^2}{[f^{(2)}(y^*)]^3} - \frac{1}{2N} \frac{f^3(y^*)g^{(1)}(y^*)}{[f^{(2)}(y^*)]^2 g(y^*)} - \frac{1}{8N} \frac{f^{(4)}(y^*)}{[f^{(2)}(y^*)]^2} \\ & \left. + O\left(\frac{1}{N^2}\right) \right\} \end{aligned} \tag{A.11}$$

and

$$\frac{\int_0^\infty dy \exp[Nf(y)]}{\int_0^\infty dy g(y) \exp[Nf(y)]} = y^* + \frac{1}{2N} \left\{ \frac{2}{y^* f^{(2)}(y^*)} + \frac{f^{(3)}(y^*)}{[f^{(2)}(y^*)]^2} \right\} + O\left(\frac{1}{N^2}\right). \tag{A.12}$$

There are clearly significant cancellations when the ratio of the two integrals which appear in (A.12) are calculated, which results in a far simple expression for the mean than for the stationary probability distribution.

From (24), (A.8) and (A.12) we find that the approximate form for the mean in the stationary state, valid for large  $N$ , is given by (27).

The result for  $P_s(0)$  can be simplified slightly if  $\mu$  is not too small, so that  $N\mu \gg 1$ . Then an application of Stirling's approximation for the Gamma function gives

$$\begin{aligned}
 P_s(0) = & \frac{\sqrt{|f^{(2)}(y^*)|}}{\sqrt{\mu}g(y^*)} \exp\{-N[f(y^*) + \mu - \mu \ln(\mu/\epsilon)]\} \left\{ 1 + \frac{\mu^{-1}}{12N} + \frac{1}{2N} \right. \\
 & \times \frac{g^{(2)}(y^*)}{g(y^*)f^{(2)}(y^*)} + \frac{5}{24N} \frac{[f^{(3)}(y^*)]^2}{[f^{(2)}(y^*)]^3} - \frac{1}{2N} \frac{f^{(3)}(y^*)g^{(1)}(y^*)}{[f^{(2)}(y^*)]^2g(y^*)} \\
 & \left. - \frac{1}{8N} \frac{f^{(4)}(y^*)}{[f^{(2)}(y^*)]^2} + O\left(\frac{1}{N^2}\right) \right\}. \tag{A.13}
 \end{aligned}$$

If  $\mu$  is so small that the condition  $\mu N \gg 1$  no longer holds, then Stirling's approximation cannot be used and (A.13) no longer holds. However, (A.11) does not hold either, since from (A.7) we see that if  $\mu \sim N^{-1}$  the whole steepest descent procedure fails.

Thus the case  $\mu \sim N^{-1}$  (or less) has to be treated separately; it is a simple modification of the earlier method. Introducing  $\beta = \mu N$ , we rewrite the standard integral appearing in (A.10) as

$$\int_0^\infty dy \tilde{g}(y) \exp[N\tilde{f}(y)],$$

where

$$\tilde{f}(y) = \ln(1 + y) - \epsilon y, \quad \tilde{g}(y) = \frac{y^\beta}{y} = y^{\beta-1}. \tag{A.14}$$

Applying the method of steepest descent gives, in the language of the two-step process described earlier, (a) one value of  $y^*$  only:  $y^* = (1 - \epsilon)/\epsilon$ , which is only positive if  $\epsilon < 1$ , and (b) exactly the same formula (A.11), except that the functions  $f$  and  $g$  are replaced by  $\tilde{f}$  and  $\tilde{g}$ , respectively. In this case, there is obviously no analog of formula (A.13).

So we conclude that the steepest descent method may still be applied to obtain an expression for  $P_s(0)$  for large  $N$  when  $\beta = \mu N$  is not large, but only in the case  $\epsilon < 1$ .

If we wish to calculate the mean in the case where  $N$  is large, but  $\beta$  is not large, we find the analogous result to (A.12) to be

$$\frac{\int_0^\infty dy y^\beta \exp[N\tilde{f}(y)]}{\int_0^\infty dy y^{\beta-1} \exp[N\tilde{f}(y)]} = y^* + \frac{1}{2N} \left\{ \frac{-2(\beta - 1)}{y^* \tilde{f}^{(2)}(y^*)} + \frac{\tilde{f}^{(3)}(y^*)}{[\tilde{f}^{(2)}(y^*)]^2} \right\} + O\left(\frac{1}{N^2}\right), \tag{A.15}$$

where it should be remembered that this result only holds for  $\epsilon < 1$ , and that  $y^*$  is now given by  $y^* = (1 - \epsilon)/\epsilon$ , and not by the value used in (A.12).



**APPENDIX B**

In this short appendix we indicate how the integral appearing in formula (53) for the mean time to extinction may be evaluated for several relevant values of  $\beta = mN/c$  within the linearized theory described in Section 5.

The stationary distribution of the linear theory is given by (50). It is zero if  $e \leq c$ , which means that the population never becomes extinct and the mean time to extinction is formally infinite. We therefore restrict ourselves to the case where  $\epsilon \equiv e/c > 1$ . In this case we have from (49) and (50)

$$\frac{P(0, t)}{P_s(0)} = \frac{(1 - y)^{n_0}}{(1 - \epsilon^{-1}y)^{n_0+\beta}}, \tag{B.1}$$

where  $y = \exp\{-(e - c)t\}$ . Therefore from (53)

$$T_E(n_0) = \frac{I(n_0, \beta)}{(e - c)} \quad \text{where} \quad I(n_0, \beta) = \int_0^1 \frac{dy}{y} \left\{ 1 - \frac{(1 - y)^{n_0}}{(1 - \epsilon^{-1}y)^{n_0+\beta}} \right\}. \tag{B.2}$$

The remainder of the appendix concerns the evaluation of  $I(n, \beta)$ .

First of all, we note that

$$\frac{(1 - y)^n}{(1 - \epsilon^{-1}y)^{n+\beta}} = \frac{(1 - y)^{n-1}}{(1 - \epsilon^{-1}y)^{n-1+\beta}} \left[ 1 - \frac{y(1 - \epsilon^{-1})}{1 - \epsilon^{-1}y} \right], \tag{B.3}$$

and so

$$I(n, \beta) = I(n - 1, \beta) + (1 - \epsilon^{-1}) \int_0^1 dy \frac{(1 - y)^{n-1}}{(1 - \epsilon^{-1}y)^{n+\beta}}. \tag{B.4}$$

Iterating (B.4) and changing variables to  $z = (1 - y)/(1 - \epsilon^{-1}y)$  in the integral gives

$$I(n, \beta) = I(0, \beta) + \sum_{n=0}^{n_0-1} \frac{1}{(1 - \epsilon^{-1})^{\beta-1}} \int_0^1 dz (1 - \epsilon^{-1}z)^{\beta-1} z^n, \tag{B.5}$$

where

$$I(0, \beta) = \int_0^1 \frac{dy}{y} \left\{ 1 - \frac{1}{(1 - \epsilon^{-1}y)^\beta} \right\}. \tag{B.6}$$

We are typically interested in values of  $\beta$  which are of order one (see, for example, the values of  $\beta$  for the graphs in Fig. 4, which range from 0.1 to 4, with two of

them corresponding to  $\beta = 1$ ). In fact, the expression for  $I(n_0, 1)$  is especially simple:

$$\begin{aligned} I(n_0, 1) &= -\epsilon^{-1} \int_0^1 \frac{dy}{1 - \epsilon^{-1}y} + \sum_{n=0}^{n_0-1} \frac{1}{n+1} \\ &= \ln(1 - \epsilon^{-1}) + \psi(n_0 + 1) + \gamma, \end{aligned} \quad (\text{B.7})$$

where  $\psi(x)$  is the logarithmic derivative of the gamma function,  $\Gamma(x)$ , and  $\gamma$  is Euler's constant (Abramowitz and Stegun, 1965).

Expressions for  $I(n, \beta)$  for other values of  $\beta$  which are small positive integers can also easily be found from (B.5) and (B.6). However, it is simpler to use the following recurrence relation in  $\beta$ :

$$I(n_0, \beta + 1) = I(n_0, \beta) - \frac{\epsilon^{-1}}{(1 - \epsilon^{-1})^\beta} \int_0^1 dz (1 - \epsilon^{-1}z)^{\beta-1} z^{n_0}. \quad (\text{B.8})$$

This is proved in exactly the same way as (B.4), but starting from

$$\frac{(1-y)^{n_0}}{(1 - \epsilon^{-1}y)^{n_0+\beta}} = \frac{(1-y)^{n_0}}{(1 - \epsilon^{-1}y)^{n_0+1+\beta}} [1 - \epsilon^{-1}y], \quad (\text{B.9})$$

rather than (B.3). As an example of the use of this result we see that

$$\begin{aligned} I(n_0, 2) &= I(n_0, 1) - \frac{\epsilon^{-1}}{(1 - \epsilon^{-1})} \int_0^1 dz z^{n_0} \\ &= \ln(1 - \epsilon^{-1}) + \psi(n_0 + 1) + \gamma - \frac{1}{\epsilon - 1} \frac{1}{n_0 + 1}. \end{aligned} \quad (\text{B.10})$$

### APPENDIX C

In this appendix we describe a general algorithm for performing stochastic realizations of spatially extended systems. Space must be included in a discrete way, for instance, as sites in a lattice, or as different patches located at particular positions. Each spatial position in the system can be in a finite number of discrete states, which in the particular case of interest to us here is equal to two: patches can be either occupied or available. Transition rates between states define the dynamics. The algorithm is based on the rejection method described by Press *et al.* (1992), and allows us to give a unified picture of all the numerical simulations we have carried out.

Consider a complex  $N$ -patch network (or alternatively a regular lattice of  $N$  sites). Each patch is defined by its spatial position (and other characteristics having any influence on transition rates, for instance, patch areas), and its present state.

Let us assume that each patch can be in any one of  $S$  states. The state of the system,  $\mathbf{n}(t)$ , can be characterized by an  $N$ -vector of states:

$$\mathbf{n} = (n_1, n_2, \dots, n_N), \quad (\text{C.1})$$

where  $n_i = 1, \dots, S$  is the state of the  $i$ th patch. An  $S \times S$  transition matrix defines transition rates among states. In general, transition rates can depend on both the current spatial configuration of the system, and the particular patch  $k$  considered. As a consequence, the temporal dynamics of the system is defined by a set of  $N$  transition matrices:

$$T_k(\mathbf{n}) = (\tau_{ij}^k), \quad (\text{C.2})$$

where  $\tau_{ij}^k$  is the probability per unit time that the  $k$ th patch in state  $j$  changes to state  $i$ . The diagonal elements  $\tau_{ii}^k$  are defined to be zero.

The overview of the algorithm is as follows:

1. Calculation of the total transition rate of the system,  $r$ . This is the probability per unit time that the system changes configuration, as a result of a transition event occurring in any patch within the system.
2. Calculation of the expected time to the next transition. It can be shown that the time to the next event is an exponentially distributed random variable with expectation  $1/r$  (Renshaw, 1991). Sample this distribution in order to estimate when the next event will take place.
3. Rejection method. Choose a patch at random and assess whether this patch can undergo a transition or not. If not, stochastic time is assumed not to advance and nothing happens. If it can, the inter-event expected time calculated in the previous step is accumulated and a particular transition event takes place changing the configuration of the system.
4. Repeat again, starting from step 1.

Let us describe in detail the three main steps enumerated above.

**Total transition rate.** The system transition rate is computed assuming that events at different patches are independent of each other. Thus, the probability of one of them occurring within the system in a time interval  $dt$  is  $r dt$ , where the total transition rate,  $r$ , is given by

$$r = \sum_{k=1}^N \sum_{j=1}^S \tau_{jn_k}^k(\mathbf{n}). \quad (\text{C.3})$$

**Inter-event expected time.** The expected time to the next transition  $t$  can be estimated by sampling an exponential distribution with a parameter  $r$ . So,

$$t = -\log(x)/r, \quad (\text{C.4})$$

where  $x$  is a uniformly distributed random variable. Thus, in this way, we are actually sampling this distribution and estimating when the next event will take place. Accumulating these inter-event times for every stochastic realization we are able to correctly track the time.

**Rejection method.** This is the core part of the algorithm. In principle, a particular patch should not be chosen at random but according to the probability of undergoing a transition to any other state. In general, this probability,  $p_k$ , is patch-dependent. Actually, it also depends on the particular state,  $n_k$ , of that patch. Let us write down the transition rate associated with this probability ( $p_k = r_k dt$ ):

$$r_k = \sum_{j=1}^S \tau_{jn_k}^k(\mathbf{n}). \quad (\text{C.5})$$

Thus, we have a set of  $p_k$  probabilities defining at each step a different discrete probability distribution. We should sample patches according to this distribution. However, the rejection method is designed to do precisely this (Press *et al.*, 1992). In essence, this method requires that we perform the following rejection procedure:

1. Choose a patch at random. Let the  $k$ th patch be the randomly chosen one.
2. Compute the following ratio:

$$x = \frac{r_k}{\max_{k=1, \dots, N}(r_k)}. \quad (\text{C.6})$$

3. Compare the  $x$  value to a randomly chosen number,  $\chi$ , belonging to a uniform distribution lying between 0 and 1. If  $\chi < x$  this patch is accepted and undergoes a transition. If not, the patch is rejected and the rejection procedure is repeated.
4. Once a patch is accepted, a transition is chosen to take place in that patch according to the probabilities:

$$p_j = \frac{\tau_{jn_k}^k(\mathbf{n})}{r_k}; \quad j = 1, \dots, S. \quad (\text{C.7})$$

This is carried out in the standard way. The unit interval (0, 1) is divided into subintervals with lengths  $p_j$ . Finally, a new uniformly distributed random number between 0 and 1 is used to decide which actual event occurs.

In the stochastic models defined throughout this paper (SIM, SEM, and SRM) each patch has just two states:  $p_i = 1$  (occupied) and  $p_i = 0$  (available). Notice that all three can be formulated and simulated in this way by defining the following transition matrices:

$$T_k = \begin{pmatrix} 0 & c\rho^{(k)} + m \\ e & 0 \end{pmatrix}, \quad (\text{C.8})$$

where  $\rho^{(k)}$  is the global occupancy, which is patch-independent in the SIM. Therefore, the subindex  $k$  could be dropped everywhere in this case. In contrast, in the SEM,  $\rho^{(k)}$  is the patch-dependent local occupancy surrounding the  $k$ th site. Finally, in the SRM both rates are patch-dependent, and the transition matrix reads:

$$T_k = \begin{pmatrix} 0 & C_k(\mathbf{n}) \\ E_k & 0 \end{pmatrix}. \quad (\text{C.9})$$

Using these definitions, equation (C.3), and the notation given throughout Section 6, the following total transition rates are easily obtained for the various models:

$$r_{\text{SIM}} = c \frac{n_1}{N} n_0 + m n_0 + e n_1, \quad (\text{C.10})$$

$$r_{\text{SEM}} = \sum_{i=0}^z c \frac{i}{z} n_{0_i} + m n_0 + e n_1, \quad (\text{C.11})$$

$$r_{\text{SRM}} = \sum_{i=1}^N (1 - p_i) C_i dt + m n_0 + \sum_{i=1}^N p_i E_i. \quad (\text{C.12})$$

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