Bulletin of Mathematical Biology (1999) **61**, 341–353
Article No. bulm.1998.0084
Available online at http://www.idealibrary.com on IDEAL

Threshold Parameters and Metapopulation Persistence

CARLOS M. HERNÁNDEZ-SUÁREZ
Centro Universitario de Investigación en Ciencias Básicas,
CGIC, Universidad de Colima,
Gonzalo de Sandoval 444, Colima, Col. 28045 México.
E-mail: cmh2@cgic.ucol.mx

PABLO A. MARQUET
Departamento de Ecología, Facultad de Ciencias Biológicas,
Universidad Católica de Chile, Casilla 114-D, Santiago, Chile
E-mail: pmarquet@genes.bio.puc.cl

JORGE X. VELASCO-HERNÁNDEZ*
Departamento de Matemáticas,
UAM-Iztapalapa, Apartado Postal 55-534, Iztapalapa, D.F.09340
E-mail: jxvh@xanum.uam.mx

A method is presented to estimate the minimum viable metapopulation size based on the *basic reproductive number* R_0 and the expected time to extinction τ_E for epidemiological models. We exemplify our approach with two simple deterministic metapopulation models of the patch occupancy type and then proceed to stochastic versions that permit the estimation of the minimum viable metapopulation size.

1. INTRODUCTION

Minimum viable population size is a key principle in population and conservation biology. The principle refers to the minimum number of individuals within an isolated population necessary to assure its long term persistence (Shaffer, 1981).

Until recently, this concept remained almost unexplored in a metapopulation context. The first analyses on metapopulation persistence times (Nisbet and Gurney (1982) considered a simple stochastic version of Levins' (1969, 1970) patch occupancy model and provided a rough approximation of the expected time to metapopulation extinction [see discussion in Nisbet and Gurney (1982) and Hanski (1989, 1991)]. After this attempt, the major conceptual boost in the calculation of Minimum Metapopulation Size (MMS, hereafter) is due to a model introduced by Nee and May (1992) which considered the effect of patch destruction upon metapopulation persistence. By focusing on patch destruction,

---

*Author to whom all correspondence should be addressed.

0092-8240/99/020341 + 13 $30.00/0

this model allows us to estimate the minimum number or fraction of habitable patches required for metapopulation survival (Nee and May, 1992; Lawton *et al*., 1994; Nee, 1994; Kareiva and Wennergren, 1995; Hanski *et al*., 1996; Nee *et al*., 1997). Conceptually, the extinction of a metapopulation following patch destruction is equivalent to the collapse of a disease epidemic following the removal of susceptible hosts (Lawton *et al*., 1994; Nee, 1994), a process that depends on the eradication threshold (Anderson and May, 1991) or the minimum number of susceptible individuals that allow the disease to persist.

A method that we explore in this note is based on the *basic reproductive number* R_0 and the expected time to extinction τ_E for epidemiological models (Diekman *et al*., 1990; Anderson and May, 1991). We exemplify our approach using two simple deterministic metapopulation models of the patch occupancy type and then proceed to stochastic versions that permit the estimation of the minimum viable metapopulation size.

Patch dynamics as a methodological algorithm has been widely applicable in epidemiology. Typically, a population of hosts is subdivided into discrete classes regarding its disease status. Thus a host population of size N is formed by adding together those individuals that are susceptible to the disease S, those that are infected and infectious I, and those that are recovered from the disease and are immune or dead R. More compartments are possible but here we are only concerned with the simplest subdivisions. The interested reader may consult Anderson and May (1991).

In this context, the patches are the different individual types that interact with an organism, e.g., a pathogen, that invades and colonizes them. Empty patches correspond to susceptible individuals and colonized patches to infective individuals. One of the main problems in epidemiology is to characterize the conditions that determine the invasibility of a host population by a disease agent. In the next section we look in some detail at this problem and establish its connection with metapopulation ecology. The results in Section 2 are all well established in both the metapopulation and the epidemiological literature, and are presented here for the sake of the (useful) analogy. In Section 3 we present our main results.

1.1. ***R_0 in deterministic models.*** The basic reproductive number is one of the most important theoretical concepts developed in epidemiology. It measures the number of secondary infections that a single infectious individual produces when introduced into a completely susceptible population (Diekman *et al*., 1990). If this number is above one, the disease spreads in the host population. Otherwise, no epidemic outbreak ensues and the disease dies out.

The basic reproductive number, usually denoted by the symbol R_0, is an invasion criterion: it determines if a pathogen will be able to survive in a host population once it is introduced. In general, R_0 does not provide information on the long-term persistence of the disease although in simple cases it does. All of the cases discussed below are of this type. In a metapopulation context, R_0 may be interpreted as the number of newly colonized patches arising from a single colonization event in an otherwise empty habitat or set of patches (Gyllenberg *et al.*, 1997; Marquet and Velasco-Hernández, 1997). As in the case of epidemics, one has to assume that at the beginning of the invasion the number of empty patches is large and that extinction and colonization have a negligible impact on the size of the total number of empty patches.

2. LEVINS' METAPOPULATION MODEL

We start our analysis with the metapopulation model proposed by Levins (1969). This model assumes that N, the total number of available patches, is a constant. Let U and O denote the number of unoccupied and occupied patches respectively. In our model an empty patch achieves its carrying capacity immediately following colonization, thus reaching their demographic equilibrium within each patch. Assume that at this equilibrium, each patch produces a total of β propagules per unit time. Therefore βO represents the total number of propagules produced by all occupied patches per unit time. These propagules find unoccupied patches at a rate proportional to their frequency U/N, thus unoccupied patches are 'lost' to colonization at a rate $-\beta OU/N$ per unit time, and occupied patches increase by the same number per unit time. If we assume that occupied patches go extinct at a rate e then eO is the number of occupied patches that go extinct per unit time (i.e., $\tau_E = 1/e$ is the expected time to extinction of any given patch). Also, suppose that extinct occupied patches are immediately available for colonization at the same rate at which they go extinct, implying a closed system. The equations that govern this system are:

$$\begin{aligned} \frac{d}{dt}U &= -\beta O\frac{U}{N} + eO, \\ \frac{d}{dt}O &= \beta O\frac{U}{N} - eO. \end{aligned} \tag{1}$$

Dividing both equations by N and defining $O/N = p$, we note that $U/N = 1 - p$, and the equations reduce to Levins' metapopulation model:

$$\frac{d}{dt}p = \beta p(1 - p) - ep. \tag{2}$$

Levins' model postulates that the total number of patches N is constant, that all patches are equal and that the colonization rate is proportional to the *frequency* of unoccupied patches. These assumptions permit us to follow dynamically the *proportion* of occupied patches instead of their actual *number*; also they allow us to characterize the whole dynamics with two parameters: β and e.

Levins' model predicts that colonization of empty patches is successful whenever $R_0 = \beta/e > 1$. This condition also determines the existence of a nontrivial equilibrium point $pj = 1 - e/\beta$. As we are following *proportions* the value e/β is the fraction of the patch population that is empty (uncolonized). As long as this proportion is not equal to one, the colonization of patches will be successful (the equilibrium pj will exist and will be globally asymptotically stable). Note that the threshold parameter is independent on both total patch population size (N) and propagule initial size.

Suppose that due to evironmental or anthropogenic pressures the extinction rate e is increased to $e + h$ [i.e., τ_E is decreased from $1/e$ to $1/(e + h)$]. We want to determine the maximum possible rate hj_c that still allows pj to be positive, that is, the rate that guarantees persistence of occupied patches. Thus we want

$$\frac{\beta}{e + h} > 1,$$

assuming that $R_0 = \beta/e > 1$. Solving for h, rearranging terms, and using the definition of R_0 we obtain

$$hj_c = e(R_0 - 1).$$

Therefore, we conclude that $h < h_c j$ is a necessary condition to escape extinction. If the number of patches in the metapopulation is N, then we can define the critical rate of patch extinction as $Nh_c j$. If this rate is exceeded, then the empty available patches generated by the extinction process would not be colonized and the metapopulation will disappear.

To appreciate the importance of R_0 as an extinction/persistence indicator, we rescale time by taking as a unit the average time to extinction $1/e$. With this rescaling Levins' equation stands

$$\frac{d}{d\tau} p = R_0 p(1 - p) - p,$$

with τ the new rescaled time.

Obviously, in this deterministic setting, regardless of the initial number of colonized patches, if $R_0 < 1$, $p \to 0$ and if $R_0 > 1$, $p \to 1$. Once again, these properties hold because in this model succesfull colonization ($R_0 > 1$) implies long-term persistence.

2.1. ***Threshold for the total number of patches.*** An alternative model to (1) that also assumes that N, the total number of available patches is a constant, is the following: let U and O denote the number of unoccupied and occupied patches respectively, as N is constant we can write $U = N - O$.

As before, βO represents the total number of propagules produced by all the individuals in the occupied patches. These propagules now find unoccupied patches at a rate proportional to U (*not* to U/N as in Levins' model). The colonization rate is now given by $-\beta OU$ per unit time, and occupied patches increase by the same number per unit time (this form of rate is known as the law of mass action). Let eO be the number of occupied patches that go extinct per unit time and suppose that extinct occupied patches are immediately available for colonization at the same rate.

The change in the colonization rate from frequency-dependent to mass action implies that the threshold condition corresponding to this new case is

$$\bar{R}_0 = \frac{\beta N}{e}.$$

As before, invasion is successful if and only if $\bar{R}_0 > 1$ or, equivalently, if $N > e/\beta$. Thus $Nj = e/\beta$ is the minimum number of empty patches in the metapopulation needed for a succesfull colonization.

The mass action law provides an adequate description for the colonization rate when the total metapopulation size is small. However, a small N introduces the problem of dependence of colonization on the initial number of colonized patches. To deal with this problem we must account for stochastic effects associated with small population size.

3. STOCHASTIC MODELS OF METAPOPULATIONS

During a habitat invasion process, a relatively small number of occupied patches constitute the initial ‘colonizing’ population from which a successful invasion of empty patches may develop. Moreover, the initial number of occupied patches, together with R_0 and N, determine the time during which the habitat will be populated and the average metapopulation size that can be expected during that time. Under a stochastic regime, the initial number of colonized patches i_0 can be a very important determinant of the fate of the invasion event.

3.1. ***Model formulation.*** The stochastic version of the SIS model (Bailey, 1975) is described here in the terminology of patch-dynamics. We present the most basic formulation avoiding technical details. We recommend consulting Bailey (1975) and Nåsell (1995) for complete information.

Let $I(t)$ represent the number of occupied patches at time t in a metapopulation with a fixed number of patches N. $I(t)$ can take values $0, 1, 2, \ldots, N$. Thus, for $m, n = 0, 1, \ldots, N$ the transition probabilities can be written as

$$P_{mn}(s,t) = P[I(t) = n | I(s) = m], \quad 0 \le s \le t,$$

where $P_{mn}(s,t)$ is the probability that $I(t) = n$ at time t given that $I(s) = m$ at time s. The transition rates of the process are

$$\begin{aligned} P_{m,m+1}(t, t+\delta t) &= \beta_m \delta t + o(\delta t), \\ P_{m,m-1}(t, t+\delta t) &= e_m \delta t + o(\delta t) \end{aligned} \qquad (3)$$

where

$$\beta_m = \beta m(1 - m/N), \quad e_m = em.$$

These rates make (3) the stochastic analogous of (1) with β the propagule production rate, and e the patch extinction rate.

Now, given a (small) initial number of newly colonized patches i_0, and given β and e (in other words, given R_0) we can ask: what is the proportion of time in which there are i $(i = 1, \ldots, N)$ occupied patches? What is the expected time to extinction of the metapopulation? What is the probability of extinction of occupied patches?

The stochastic process (3) is a Markov process with a degenerated stationary distribution with all its mass at state 0, that is, the probability of eventual extinction is 1 if N is finite. To answer the previous questions, one should look at the time evolution of the realizations of the stochastic process conditioning in not being absorbed (Nåsell, 1995), obtaining the so-called quasi-stationary distribution (QSD) of the process. This distribution gives the (conditional) proportion of time that the process spends in each state before being absorbed in state 0. Here we describe and use a technique developed by Hernández-Suárez (1997) to compute the distribution of the proportion of time that the process spent in each state before absorption given *any* i_0. The method consists in modifying the original Markov process defined by (3) to one without absorbing states, but where state 0 is now a reflecting state to i_0 (i.e., the original initial propagule size). We will denote this new process the MMP (Modified Markov Process). We will show how to calculate the expected time to extinction τ_E from the stationary distribution of the MMP for any initial propagule size i_0.

3.2. ***The MMP and its stationary distribution.*** In the MMP, transitions to the absorbing state 0 (all patches empty) are substituted with transitions to the initial state i_0. When the process goes from state 1 (one occupied patch) to state i_0 then we say that a cycle has been completed. The MMP is ergodic therefore a limiting distribution exists that can be found using standard methods. Let $\underline{\Pi} = [\pi_1, \pi_2, \ldots, \pi_M]$ be the limiting distribution of the MMP. Now define S_{rj} as the time spent in state r in the jth cycle in the MMP, $j = 1, 2, \ldots$. By the strong law of large numbers, we have that

$$\pi_r = \frac{E(S_r)}{E\left(\sum_i S_i\right)} = \frac{\lim_{n\to\infty} n^{-1} \sum_{j=1}^{n} S_{rj}}{\lim_{n\to\infty} n^{-1} \sum_{j=1}^{n} \sum_{i=1}^{n} S_{ij}}. \tag{4}$$

As $E(S_r)$ is the same for both the original and the modified process, by calculating $\underline{\Pi}$ we can estimate the expected proportion of time that the original process spends on state r, which is π_r. The ergodicity of the MMP guarantees that a distribution $\underline{\Pi}$ exists for each initial state.

In addition, $\underline{\Pi}$ can be used to find the expected time to extinction: note that the expected value for the sum of the time spent in all states in a ‘cycle’ in the

MMP corresponds to the expected time to absorption in the original process, that is $E\left(\sum_i S_i\right) = \tau_E$. From (4) it follows that

$$E(S_r) = \pi_r \tau_E;$$

in particular $E(S_1) = \pi_1 \tau_E$. Using first step analysis (see Appendix) we can show that $E(S_1) = 1/e$, thus obtaining

$$\tau_E = (\pi_1 e)^{-1}$$

Remark 1. It is important to point out the important difference between our method and Renshaw's (1991, p. 58) approximation to the the quasi-stationary distribution of (3). Renshaw used an approximation in which

$$\pi_k \mu_k = \pi_{k-1} \lambda_{k-1} \qquad k = 2, 3, \dots, N$$

where $\lambda(i)$ and $\mu(i)$ are the birth and death rates respectively for state i. Observe that if the initial state is 1 then according to the MMP we change transitions from state 1 to 0 with transitions back to state 1, and we also arrive to the same system of equilibrium equations. Therefore, Renshaw's approximation is a particular case of ours in which the initial state is 1. Because of this, our estimate of τ_E is more general and it agrees with Renshaw's approximation when $i_0 = 1$. In Table 1 we compare both methods to estimate τ_E for different i_0 values. In Fig. 1 we present the comparison between the quasi-stationary distribution of the process (3), and that obtained through MMP for the cases $R_0 > 1$ and $R_0 < 1$. The MMP approach is sensitive to changes in the initial metapopulation size (number of colonized patches).

Table 1 shows the estimated values of τ_E for Renshaw's approach and MMP. In Fig. 2 we show the expected time to extinction τ_E as a function of R_0 for the MMP approach compared with that predicted by Renshaw (1991). Note that both approximations coincide if $i_0 = 1$.

Table 1. Values of τ_E, mean time to extinction for Renshaw's approximation (τ_E^Q), the MMP approximation (τ_E^M) and the average computed over a sufficiently large number of realizations of the process τ_E^*; i_0 indicates the initial propagule size (Renshaw's approximation is insensitive to i_0 and does not change value for fixed R_0 and N).

$R_0 = 1.1,\ N = 50$				$R_0 = 0.9,\ N = 50$			
i_0	τ_E^Q	τ_E^M	τ_E^*	i_0	τ_E^Q	τ_E^M	τ_E^*
1	3.429	3.429	3.520	1	2.179	2.179	2.183
2	···	5.683	5.509	2	···	3.517	3.601
5	···	9.649	9.575	5	···	5.845	5.729
10	···	12.638	12.727	10	···	7.718	7.691

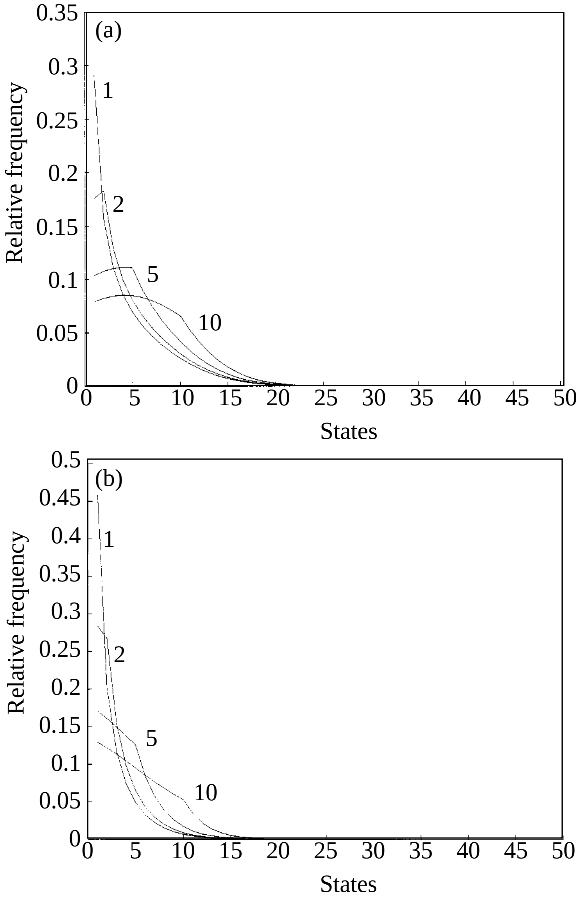

Figure 1. Distribution of the proportion of time that the system spends in state i conditioned to non-extinction (MMP). The numbers 1, 2, 5 and 10 indicate the approximation to the distribution for $i_0 = 1, 2, 5, 10$ respectively, using formula (4) (continuous line). Renshaw's approximation is insensitive to changes in i_0 and coincides with that of the MMP for $i_0 = 1$; (a) Distribution for $R_0 = 1.1$ and total patch size $N = 50$. (b) Distribution for $R_0 = 0.9$ and total patch size $N = 50$.

3.3. ***Probability of extinction.*** By once again using first-step analysis we can calculate an upper bound for the extinction probability of the process. First, to fix ideas, consider the case of a habitat constituted by an infinite number of identical patches that started with a single occupied patch. In order to achieve extinction, all the patches that will be occupied must extinct eventually. Let θ be the probability of extinction. Starting with a single patch we can calculate θ by conditioning in the first event that can occur, which is either extinction of this patch [which happens with probability $e/(e+\beta)$] or it can successfully colonize a new patch, resulting in a total of two colonized patches [with probability $\beta/(e+\beta)$]. In the first case the extinction probability is one, whereas in the second case the extinction probability is θ^2 as we now require extinction of two populations

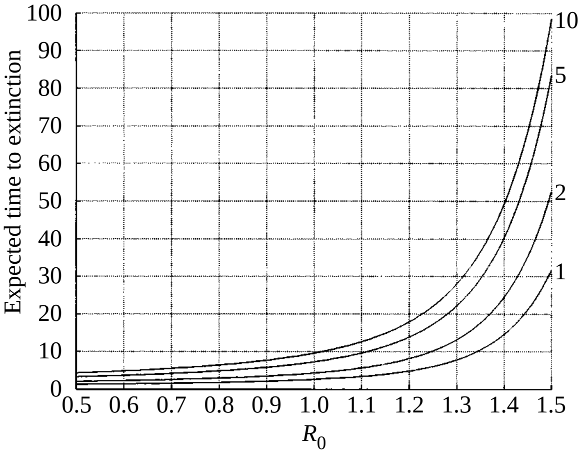

Figure 2. Expected time to extinction τ_E as a function of R_0 calculated using Renshaw's and the MMP approach. The numbers on the right-hand side vertical axis correspond to i_0, the initial number of colonized patches (MMP). Both approximations are identical for $i_0 = 1$.

that started with one single occupied patch each, and we assume independence. Therefore we have:

$$\theta = \left(\frac{e}{\beta + e}\right) + \theta^2 \left(\frac{\beta}{\beta + e}\right).$$

Solving for θ yields $\theta = \min(1, e/\beta)$.

We have claimed that if the population successfully colonizes a second patch, then the probability of extinction is θ^2. This result is correct provided that the habitat is a collection of an infinite number of identical patches, for in that case the probability that a propagule lands on an empty patch tends to one. This does not occur if the number of patches is finite. This means that the estimate $\min(1, e/\beta)$ is only an upperbound for the extinction probability in a habitat with a finite number of patches. Note that $e/\beta = 1/R_0$ in Levins' model. Thus in the stochastic version R_0 is not so much an index of invasion 'success' (growing number of colonized patches) but rather a lower bound for the probability of extinction: the larger R_0 is the lower the per patch probability of extinction, and if $R_0 \leq 1$ then extinction is certain.

4. DISCUSSION

Epidemiology and ecology share the methodological substrate of patch dynamics. This common background can be used to adapt and adopt in reciprocity techniques and conceptual basis for the description, analysis and explanation of particular phenomena. Following the lead of Marquet and Velasco-Hernández

(1997) and Gyllenberg *et al.* (1997), we have shown that the epidemiological concepts of threshold parameters can be applied to metapopulation dynamics. The concept of minimum viable metapopulation size has been used as example. The results that we show here were developed within the context of epidemiology. The classical SIS model has a long tradition in this area and many results are available, both of the stochastic and deterministic kind. Of course, we are still far from understanding even this basic model but the available results can be applied successfully to understand metapopulation dynamics and persistence better.

Models dealing with population extinction processes have usually focused on single populations to model the effects of demographic, environmental and genetic stochasticity [e.g., Richter-Dyn and Goel (1972), Goodman (1987), Wissel and Stocker (1991) and Lande (1993)]. However, real populations usually have a geographic structure composed of a finite number of interconnected subpopulations forming a metapopulation system. This system can go extinct simply because all local populations happen to become extinct at the same time (an analog to the concept of demographic stochasticity in single species models). This process has been termed inmigration–extinction stochasticity by Hanski (1991) and has been shown to be especially important for metapopulations with a small number of subpopulations (Nisbet and Gurney, 1982; Hanski *et al*., 1996). Using a different approach, inspired by epidemiological models, we have shown an interesting alternative for the estimation of expected time to extinction that underscores the importance of immigration–extinction stochasticity.

The role of R_0 as a threshold parameter in deterministic models [e.g., model (1)] changes when dealing with stochastic models. In a deterministic setting, if R_0 is above a threshold then the invasion process will produce a continuous increment in the fraction of the habitat colonized, which will eventually end at an equilibrium level associated with R_0 (in Levins' metapopulation model this equilibrium is of the form $p^* = 1 - 1/R_0$). In the context of stochastic models, R_0 is associated with a lower bound for the per patch probability of extinction, equal to $1/R_0$ if and only if $R_0 > 1$. If this inequality does not hold, then the probability of extinction is 1. In contrast with the results obtained in Section 2 for deterministic models, a successful colonization event depends on N, the total number of patches, i_0, the initial number of colonized patches and R_0.

The minimum viable metapopulation size is defined as the minimum number of occupied patches needed to ensure the long-term persistence of the metapopulation. Of course, in practical terms the 'long term' is an arbitrary length of time. In our stochastic model (3) we characterize this minimum viable size as i_0. In Fig. 2 we can see how, for a fixed number of patches ($N = 50$), the expected time to extinction increases exponentially as a function of R_0, for each choice of i_0. Note that the increase in the expected time to extinction is of about 20 time units when i_0 goes from 1 to 2, but only of 15 when changing from 5 to 10 due to the exponential nature of the increase. We call this property a *diminishing* *return*. In a practical situation a diminishing return threshold should be set based on management criteria, thus there is no *a priori* (model-based) way of setting a time threshold in this model. Nevertheless, model (2) is the simplest stochastic model that captures the basic ideas in Levins' metapopulation model and obviously is far from being applicable to specific field situations. It shows that the determination of a minimum viable metapopulation size involves knowledge of the total number of empty and occupied patches, the intrinsic demographic properties of the target species and an arbitrary time horizon desired for management purposes. As mentioned earlier, Renshaw has produced an analytic approximation for the expected time to metapopulation extinction based on the assumption that $i_0 = 1$. As shown in our simulations (Fig. 2), this approximation largely underestimates the true expected time to metapopulation extinction for all $i_0 \geq 2$. The approximation is even less accurate when the probability of local extinction is small ($R_0 >> 1$).

For the sake of simplicity and mathematical tractability, we have illustrated our approach using a simple metapopulation model, of the patch occupancy type, where no local population dynamics are included. However, this could be extended to more complicated models incorporating different patch types [e.g., Hanski and Gyllenberg (1993) and Marquet and Velasco-Hernández (1997)]. At present, the model could provide a good approximation to understand the process of extinction of plant populations by considering that each site or patch is the size of a single individual (Tilman, 1994). We hope our approach will spur theoretical and empirical work on this subject, thus underscoring the importance of epidemiological theory for metapopulation ecology.

ACKNOWLEDGEMENTS

We thank Professor Roger Nisbet for the useful comments that helped to improve our work. PM acknowledges funding from FONDECYT grant 1951036 (Chile) and a Presidential Chair in Science to Fabian M. Jaksic. JXVH acknowledges also the support from grant CONACYT (Mexico, 1998). CMHS acknowledges support from CONACYT and a Presidential Faculty Award to Carlos Castillo-Chavez.

APPENDIX

Given that process (3) will visit state 1 with probability 1, we can calculate $E(S_1)$, the expected time spent in this state before extinction, assuming that the process is already in state 1. Using first step analysis, we have that the expected time in state 1 is $(\beta + e)^{-1}$ if the patch becomes empty, whereas it is $(\beta + e)^{-1} + E(S_1)$ if the process goes to state 2 (successful colonization of an empty patch). Therefore, by the law of total probability

$$E(S_1) = E(S_1|\text{patch becomes empty})\,P(\text{patch becomes empty})$$
$$+E(S_1|\text{patch remains occupied})\,P(\text{patch remains occupied}).$$

Now, given that

$$P(\text{patch becomes empty}) = \frac{e}{\beta + e} = 1 - P(\text{patch remains occupied})$$

and that

$$E(S_1|\text{patch becomes empty}) = (\beta + e)^{-1},$$

and

$$E(S_1|\text{patch remains occupied}) = (\beta + e)^{-1} + E(S_1),$$

then we have

$$E(S_1) = (\beta + e)^{-1}\frac{e}{\beta + e} + ((\beta + e)^{-1} + E(S_1))\frac{\beta}{\beta + e}.$$

Solving for $E(S_1)$ yields

$$E(S_1) = 1/e.$$

REFERENCES

Anderson, R.M. and R.M. May. (1991). *Infectious Diseases of Humans*, Oxford, Oxford Science Publications.

Bailey, N.T.J. (1975). *The Mathematical Theory of Infectious Diseases and its Applications*, London, Charles Griffin.

Diekman, O., J.A.P. Hesterbeek and J.A.J. Metz. (1990). On the definition and computation of the basic reproductive ratio R_0 in models for infectious diseases in heterogeneous populations. *J. Math. Biol.* **28**, 365–382

Goodman, D. (1987). The demography of chance extinctions, in *Viable Populations for Conservation*. M.E. Soulé, (ed.) pp. 11–43. New York, Cambridge University Press.

Gyllenberg, M., I. Hanski and A. Hastings (1997). Structured metapopulation models. In *Metapopulation Biology: Ecology, Genetics, and Evolution.* I. Hanski, and M.E. Gilpin (eds), pp. 93-122. New York, Academic.

Hanski, I (1989). Metapopulation dynamics: does it help to have more of the same? *Trends Ecol. Evol.* **4**, 113–114.

Hanski, I (1991). Single-species metapopulation dynamics: concepts, models and observation. *Biol. J. Linn. Soc.* **42**, 17–38.

Hanski, I. and M. Gyllenberg (1993). Two general metapopulation models and the core-satellite species hypothesis. *Am. Naturalist* **142**, 17–41.

Hanski, I., A. Moilanen and M. Gyllenberg (1996). Minimum viable metapopulation size. *Am. Naturalist* **147**, 527–541.

Hernández-Suárez, C.M. (1997). Problems in the theory and application of models of infectious diseases. PhD Thesis, Biometrics Unit Cornell University.

Kareiva, P. and U. Wennergren (1995). Connecting landscape patterns to ecosystem and population processes. *Nature*, **373**, 299–302.

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

Lawton, J.H., S. Nee, A.J. Letcher and P.H. Harvey (1994). Animal distributions: patterns and processes, in *Large Scale Ecology and Conservation Biology*, P.J. Edwards, R.M. May, and N.R. Webb (eds), pp. 41–58. Oxford, Blackwell Scientific.

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

Levins, R. (1970). Extinction. *Lectures on Mathematics in the Life Sciences 2*. Providence, American Mathematical Society, RI.

Marquet, P.A. and J.X. Velasco-Hernández (1997). A source–sink patch occupancy metapopulation model. *Revista Chilena de Historia Natural*, **70**, 371–380.

Nåsell, I. (1995). The threshold concept in deterministic and stochastic models, in *Epidemic Models: their Structure and Relation to Data*, D. Mollison (ed.), Cambridge, Cambridge University Press.

Nee, S. (1994). How populations persist. *Nature*, **367**, 123–124.

Nee, S. and R.M. May. (1992). Dynamics of metapopulations: habitat destruction and competitive coexistence. *J. Animal Ecol.* **61**, 37–40.

Nee, S., R.M. May and M.P. Hassell. (1997). Two-species metapopulation models. In *Metapopulation Biology: Ecology, Genetics, and Evolution*, I. Hanski and M.E. Gilpin (eds), pp. 123–147. New York, Academic.

Nisbet, R. and W.S.C. Gurney (1982). *Modeling Fluctuating Populations*. Chichester, Wiley.

Renshaw, E. (1991). *Modeling Populations in Space and Time*. Cambridge, Cambridge University Press.

Richter-Dyn, N. and N.S. Goel (1972). On the extinction of a colonizing species. *Theor. Pop. Biol.* **3**, 406–433.

Shaffer, M.L. (1981). Minimum population sizes for species conservation. *BioScience*, **31**, 131–134.

Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology*, **75**, 2–16.

Wissel, C. and S. Stocker (1991). Extinction of populations by random influences. *Theor. Pop. Biol.* **39**, 315-328.

Received 30 July 1997 and accepted 29 October 1998