

**EPIDEMIOLOGY MEETS ECOLOGY:
THRESHOLD PARAMETERS AND METAPOPOPULATION PERSISTENCE**

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Abstract

We discuss the analogies that exist between models of infectious diseases and those of metapopulation dynamics. Both deterministic and stochastic approaches are considered. We apply the equivalent mathematical framework of the stochastic *SIS* epidemiological model and the Richard Levins classic metapopulation model to the computation of expected time to extinction given an arbitrary initial number of colonized patches. We discuss the implications that result regarding the determination 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 (Schaffer, 1981).

This concept has been almost unexplored in a metapopulation context although there are some rough results on its estimation (Nisbet and Gurney, 1982; Hanski, 1989, 1991).

An alternative 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 using recent results of Hernández-Suárez (1996).

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, 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 to this problem and establish its connection with metapopulation ecology.

1.2 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 in 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. It is important to point out that R_0 is computed assuming that all individuals in the population are susceptible since it measures the ability of the pathogen to spread initially. It is obvious that whenever a disease invades a susceptible population, the number of infected individuals increases and the number of susceptible individuals decreases. This hypothesis is supported by a time scale argument: within the time scale at which the infection process occurs, and given a large population size, demographic and infection processes have negligible impact on the number of susceptibles in the population. In general, R_0 does not provide information on the long term persistence of the disease although in simple cases it does. Some of these cases are discussed below.

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. 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 in 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. Immediately upon colonization of an empty patch the organisms achieve their carrying capacity, 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 $-\beta O U/N$ per unit time, while occupied patches increase at the same number per unit time. If we assume that occupied patches become 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:

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

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:

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

Levins' model postulates that the total number of (homogeneous) patches N is constant. These assumptions permit to dynamically follow 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 .

For Levins' model $R_0 = \beta/e$. Colonization of empty patches is successful whenever $R_0 = \beta/e > 1$. This condition also determines the existence of a nontrivial equilibrium point $p^* = 1 - e/\beta$. Since 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 p^* will exist and will be globally asymptotically stable).

Suppose that due to environmental 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 h_c^* that still allows p^* 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

$$h_c^* = e(R_0 - 1).$$

Therefore, we conclude that $h < h_c^*$ 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^* . 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

$$\frac{d}{d\tau}p = R_0p(1-p) - p,$$

with τ the new rescaled time.

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

2.1 The minimum viable metapopulation size

The next model also assumes that N , the total number of available patches is a constant. As before, let U and O denote the number of unoccupied and occupied patches respectively. Since 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 the Levins' model). The colonization rate is given by $-\beta O U$ per unit time, and occupied patches increase by the same number per unit time. 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 equations that govern this system are:

$$\begin{aligned} \frac{d}{dt}U &= -\beta O U + eO, \\ \frac{d}{dt}O &= \beta O U - eO. \end{aligned} \tag{2}$$

The threshold condition corresponding to this model is

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

As before, invasion is successful if and only if $\bar{R}_0 > 1$. In this case the threshold parameter is $\bar{R}_0 = \beta N/e$. Note also that since $\bar{R}_0 > 1$ is a threshold condition for invasion it provides a formula for the minimum metapopulation fraction of empty patches U_c^*/N needed to have a successful invasion of an empty habitat, and persistence. Observe that, at the start of an invasion $N \approx U$, *i.e.* the total number of patches is approximately equal to the number of empty patches. With this in mind define

$$q_c^* = U_c^*/N = \frac{e}{\beta}$$

as the critical fraction of empty patches such that if $U/N > q_c^*$ invasion takes place (moreover, it can be shown that in this case, as in Levins' model, the invasibility threshold is also the long term persistence threshold for the metapopulation). On the other hand, if $U/N < q_c^*$ the metapopulation goes extinct. As expected, the greater the magnitude of β/e , the smaller the minimum viable metapopulation fraction q_c^* need be. q_c^* can also be thought of as the minimum fraction of patches in a metapopulation needed to ensure its persistence at a positive equilibrium level. If U/N were smaller than q_c^* , the parameter \bar{R}_0 would be less than 1, and the metapopulation would become extinct .

To illustrate the nature of q_c^* as a minimum metapopulation size to escape extinction, we rescale time into units of average time to extinction $1/e$, as we did in the previous section: The equation that results is

$$\frac{d}{d\tau}p = \frac{\beta N}{e}p(1-p) - p,$$

with τ the rescaled time and $p = O/N$.

Obviously, regardless of the initial proportion of colonized patches, if $U/N < q_c^*$, $p \rightarrow 0$ and if $U/N > q_c^*$, $p \rightarrow 1 - e/\beta N$.

3. Stochastic models of infectious diseases

During a disease invasion process, a relatively small number of infective individuals constitute the initial 'colonizing' population from which an epidemic outbreak may develop. Moreover, the initial infective size together with R_0 and N , determine the so-called average infective population before extinction characterized as the average population size achieved during the time that the disease was present in the population. It is intuitively obvious that under an stochastic regime, the initial infective size i_0 should be very important determinant for the fate of the epidemic. We have discussed in section 2 the analogies between the *SIS* and Levins' metapopulation deterministic models where the asymptotic dynamics depends on β and e but not on $p(0) = i_0$, the initial proportion of occupied patches. In this section we present the stochastic versions and address the problem of successful colonization of patches in the context of metapopulation dynamics.

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 formula-

tion avoiding technical details. We recommend to consult Bailey (1975) and Nasell (1993) 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 $0, 1, 2, \dots, N$. Thus, for $m, n = 0, 1, \dots, N$ the transition probabilities can be written as

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

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

$$\begin{aligned} P_{m,m+1}(t, t + \delta t) &= \lambda_m \delta t + o(\delta t), \\ P_{m,m-1}(t, t + \delta t) &= \mu_m \delta t + o(\delta t) \end{aligned} \quad (3)$$

where

$$\lambda_m = \beta m(1 - m/N), \quad \mu_m = em.$$

These rates make Model (3) the stochastic analogous of Model (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) and a future time T , what is the proportion of T in which there are i ($i = 1, \dots, N$) occupied patches?

The stochastic process (3) is a Markov process with a unique absorbing state (stationary distribution) at 0, that is, the probability of extinction in infinite time is 1 (hardly a useful result). To compute meaningful statistics of Model (3), *e.g.* τ_E the expected time to extinction, one sets a time T in the future, and looks at the time evolution of the realizations of the stochastic process within that time interval conditioned on not being absorbed (Cavender, 1978) obtaining the so-called quasi-stationary distribution (QSD) of the process. This distribution gives the (conditional) proportion of the time that the process spends in each state. From it, the expected time to extinction τ_E can be estimated (Nisbet and Gurney, 1982).

We use a technique developed by Hernández-Suarez (1996) to compute the distribution of the proportion of the time that the process spent in each state given *any* i_0 . This 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 approach by MMP (modified Markov process).

In Figure 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 population size (inoculum).

Nisbet and Gurney (1982) and Renshaw (1991) discuss a particular *approximation* to the quasi-stationary distribution from which τ_E can be computed. It can be shown (Hernández-Suárez, 1996) that this approximation is a modification of the Markov process (3) to one where state 0 is a reflecting state to state 1. Using this approximation the expected time to extinction can be estimated (Table 1).

Alternatively, MMP allows the calculation of τ_E as follows. Let $\Pi' = (\pi_1, \dots, \pi_N)$ the limiting distribution of the modified Markov process (MMP) characterized above. Assume that the process evolves for a large time T . Then π_i is the total proportion of the time T that the process spends in state i . In particular π_1 is the proportion of time that the MMP was in state 1. Thus, the average time to extinction of the *original* process (3) can be computed as (Hernández-Suárez, 1996)

$$\tau_E = \frac{1}{\pi_1 \mu_1} \equiv \frac{1}{\pi_1 e}. \quad (4)$$

Expression (4) allows the computation of τ_E . The dependence of the initial propagule size (*i.e.*, initial infectious population) is implicit in π_1 .

Table 1 shows the estimated values of τ_E for the Nisbet and Gurney approach and MMP. The former consistently under-estimates the expected time to extinction for $i_0 > 1$. The inaccuracy of this approximation is, not surprisingly, worst for large initial populations. In Figure 2 we show the expected time to extinction τ_E as a function of R_0 for the MMP approach compared with the one predicted by Nisbet and Gurney (1982) and Renshaw (1991). It is obvious that this method produces estimates of τ_E that are insensitive to differences in i_0 . Note that the approximation suggested by Nisbet and Gurney (1982) and with the MMP above coincide if $i_0 = 1$.

4. Discussion

Epidemiology and ecology share the methodological substrate of patch dynamics. This common background can be used to adapt and adopt in reciprocity technics and conceptual basis for the description, analysis and explanation of particular phenomena. In this work 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 shown 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 type. We are still far from understanding even this basic model but the available results can be applied successfully to better explain metapopulation dynamics and persistence.

Models dealing with population extinction processes have usually focus 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, 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 population models). This process has been termed immigration-extinction stochasticity by Hanski (1991) and have been shown to be specially important for metapopulations with a small number of subpopulations (Nisbet and Gurney 1982). Using a different approach, inspired by epidemiological models, we have shown a interesting alternative for the estimation of the expected time to extinction that underscores the importance of immigration-extinction stochasticity.

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 is included. However, this could be extended to more complicated models incorporating different patch types (e.g., Hanski and Gyllenberg, 1993; Marquet and Velasco-Hernández 1996). At present, the model can 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.

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Figure and Table Captions

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). The distribution of the QSD approximation (insensitive to changes in i_0) is also shown; **a)** Distribution for $R_0 = 1.2$ and total patch size $N = 50$. **b)** Distribution for $R_0 = 0.9$ and total patch size $N = 50$.

FIGURE 2 Expected time to extinction τ_E as a function of R_0 for the ‘Nisbet and Gurney’ (line 1) and MMP (continuous lines) approaches. The numbers in the left hand side vertical axis correspond to i_0 , the initial population size (MPP). Both approximations are identical for $i_0 = 1$.

TABLE 1 Values of τ_E , mean time to extinction for the Nisbet and Gurney 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 (Nisbet and Gurney approximation is insensitive to i_0 and does not change value for fixed R_0 and N); **a)** Results for $R_0 = 1.2$ and total patch size $N = 50$; **b)** Results for $R_0 = 0.9$ and total patch size $N = 50$.

Table 1

a) $R_0 = 1.1, N = 50$

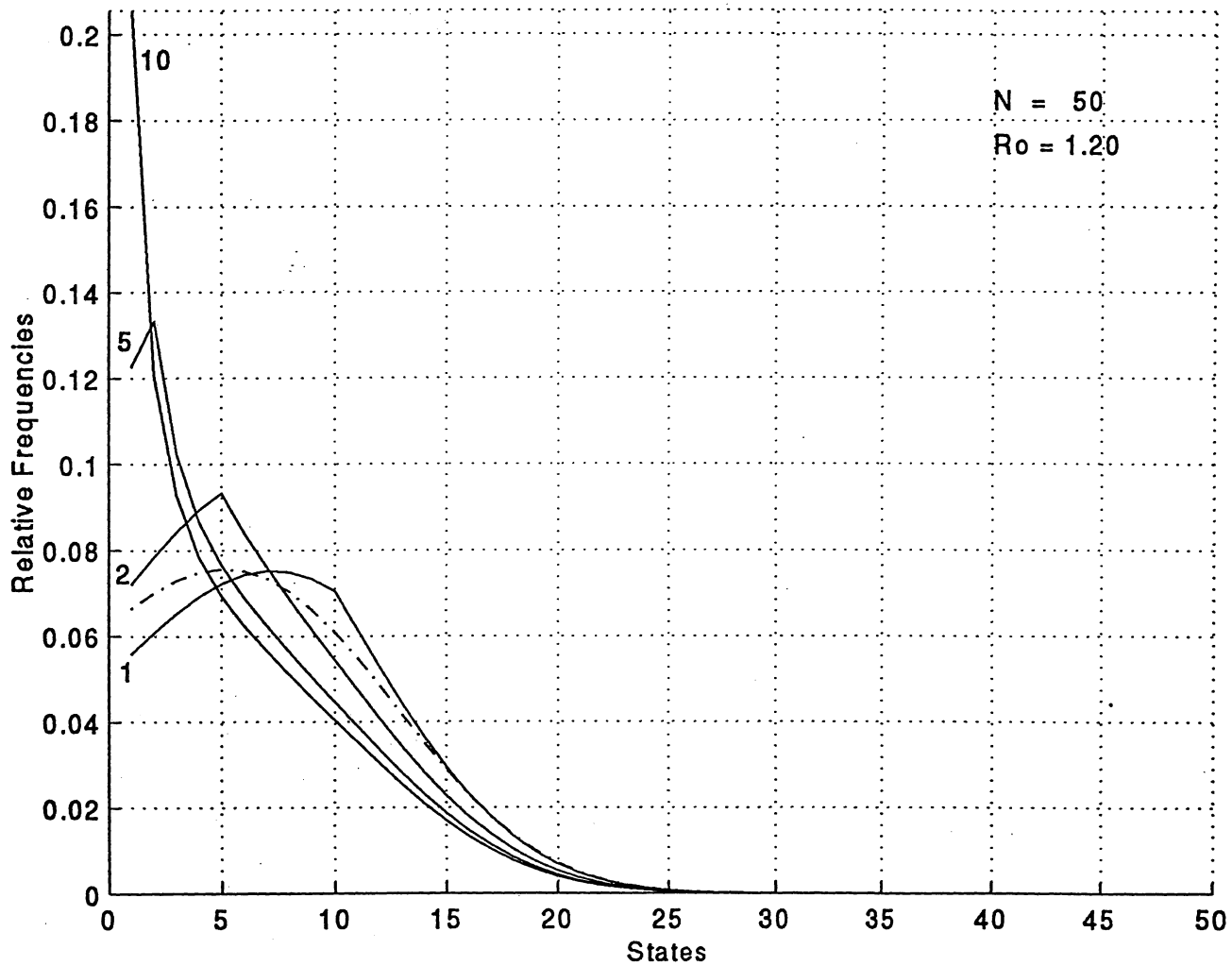
i_0	τ_E^Q	τ_E^M	τ_E^*
1	3.429	3.429	3.520
2	...	5.683	5.509
5	...	9.649	9.575
10	...	12.638	12.727

b) $R_0 = 0.9, N = 50$

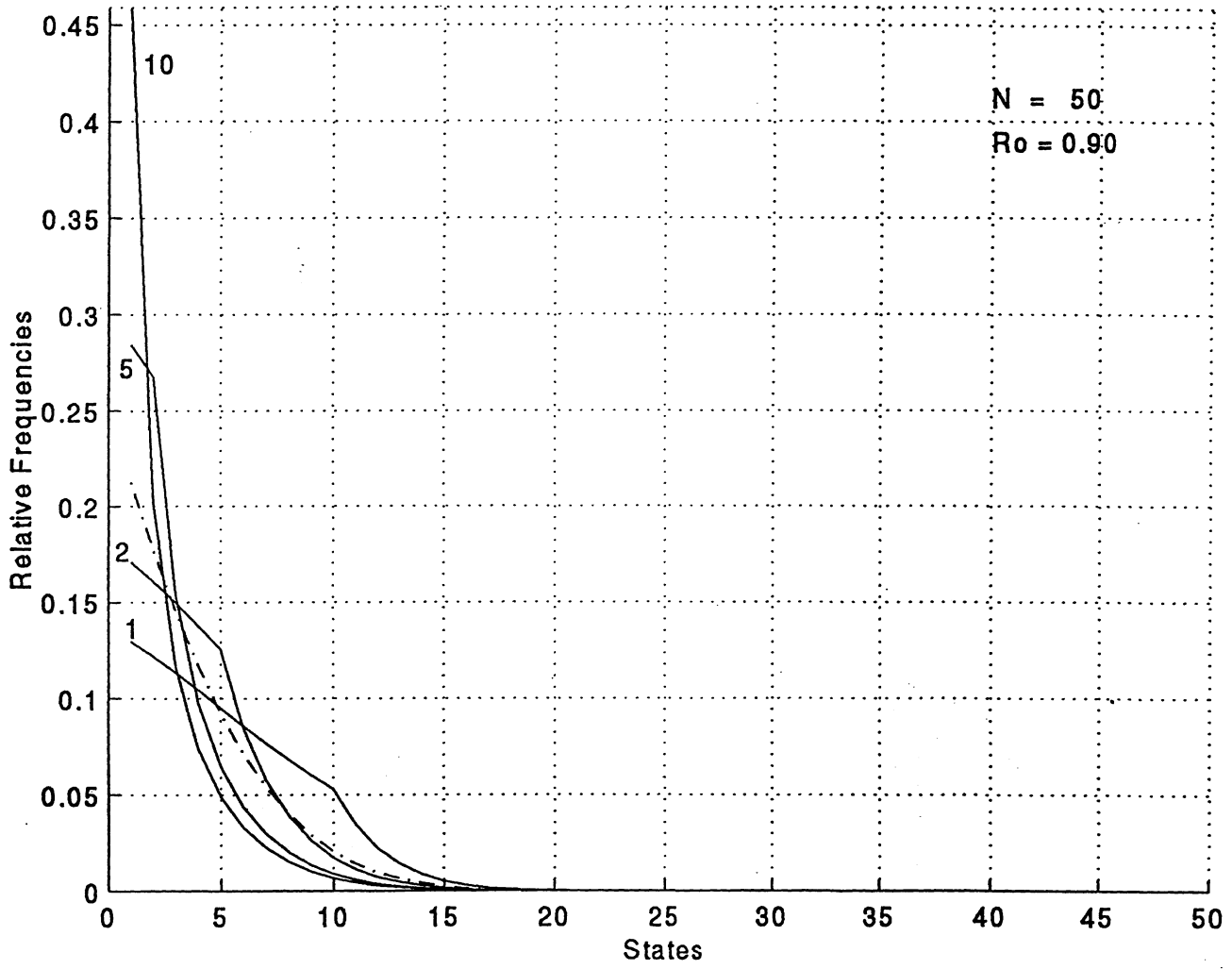
i_0	τ_E^Q	τ_E^M	τ_E^*
1	2.179	2.179	2.183
2	...	3.517	3.601
5	...	5.845	5.729
10	...	7.718	7.691

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Comparsion between QSD and MSD



Comparsion between QSD and MSD



Comparison of Expected time to Extinction

