

Persistence in Patchy Irregular Landscapes

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This paper presents a simulation and three approximations designed to study the effects of spatial clumping of patches in a metapopulation linked by costly dispersal. Assuming that all patches are identical and that each experiences a simple regime of density-independent uncorrelated extinction, we demonstrate that clumping enhances persistence of the population. We find a persistence threshold which depends on the leading eigenvalue of the matrix describing dispersal success between each pair of patches and show that this eigenvalue exceeds the mean dispersal success. An averaged approximation that uses a single statistic to describe each path, rather than the full matrix, successfully predicts the regional population size produced by the simulation and predicts a simple linear relationship between this statistic and the patch immigration rate. An approximation which ignores the detailed spatial structure fails to accurately predict the simulation results. © 1994 Academic Press, Inc.

1. INTRODUCTION

The life span of many local, semi-isolated populations is limited. Their disappearance may be caused by relatively sudden biotic or abiotic disturbances or by a gradual and predictable decline in habitat quality. Yet, a species may persist regionally over extensive time periods provided that local extinctions are balanced by colonization events elsewhere. Such

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dynamics lead to a shifting mosaic of more or less transient populations (Cockerell, 1934; Andrewartha and Birch, 1954; den Boer, 1968).

The key to prolonged regional persistence lies in the range of movement of the organisms relative to the scale at which disturbances occur (Crowley, 1977). If dispersal movements cover a wide area, then many disturbances will be perceived as local, and their effect on a subdivided population will be offset by favorable conditions elsewhere. Thus, dispersal beyond the correlation length of local conditions can act effectively to average over conditions and promote species persistence. In this case, the regional mean population size may be fairly constant despite pronounced variation in local abundance (Reeve, 1990).

Two approaches to evaluating the influence of spatial patterning on population dynamics have been taken: simple theoretical models and more detailed simulation models. Theoretical models typically consider discrete patches of habitat in a sea of unfavorable terrain so that the dynamics can be modeled on two distinct spatial and temporal scales. The within-patch component comprises population growth, interactions with other species, and the occurrence of disturbances. A separate set of assumptions governs the processes of dispersal and colonization by which the patches are interconnected.

The first and simplest such model is due to Levins (1969, 1970) and is termed a metapopulation model. It tracks only the fraction p of occupied patches in a landscape with a large number of identical patches. If m represents the rate of production of dispersers per occupied patch and e represents the rate at which occupied patches go extinct, the dynamics of p follow

$$\frac{dp}{dt} = mp(1-p) - ep. \quad (1.1)$$

This model has a threshold dispersal rate below which the equilibrium at $p=0$ (corresponding to global extinction) is globally stable and above which an equilibrium with a positive fraction of patches occupied is globally stable. The threshold occurs at $m=e$, where the expected number of disperser produced by a patch before extinction equals 1.

Considerations of persistence, occupancy, stability, and thresholds have continued to be the focus of investigation of more complex models which relax the many assumptions embodied in this simple caricature (Kareiva, 1990; Hanski, 1991). We focus on two of these assumptions: the equal connectivity of all pairs of patches and the drastically simplified population dynamics within patches.

The two most widely considered models of patch connectivity might seem to present two extremes: the island model (Wright, 1951), which

assumes identical connections between all pairs, and the stepping-stone model (Kimura and Weiss, 1964), which assumes that only neighboring patches exchange dispersers. Both migration regimes have in common that they assume homogeneity in the connectedness of habitat (Doak *et al.*, 1992), although some consideration has been given to edge effects in stepping-stone models (Allen, 1987; Seno, 1988). When colonization probabilities are equal across patches, patch occupancy and the production of dispersers are independent of location. Due perhaps to this fundamental similarity, the results of island models and stepping-stone models have proven rather similar in general (Gurney and Nisbet, 1978; Comins *et al.*, 1980; Ray *et al.*, 1991).

If dispersal distances are limiting and the arrangement of habitat in the landscape is irregular, then more isolated patches will be less important in the overall dynamics than those surrounded by close neighbors (Wilcove *et al.*, 1986; Eberhard, 1991; Sjögren, 1991). DeAngelis *et al.* (1979) used M -matrix theory to derive conditions for persistence as a function of the full set of patch interconnections. They showed that an entire system will persist if a single subsystem persists. However, they did not consider the effects of clumping on individual patches. The effects of differing degrees of isolation within a single model have been modeled only recently. One group found, through a combination of field experiment and simulation, that populations in patches near other patches show more rapid growth than isolated populations (Fahrig and Merriam, 1985; Fahrig and Paloheimo, 1988b) and that persistence is enhanced by higher connectivity (Lefkovich and Fahrig, 1985; Fahrig and Paloheimo, 1988a), but that these effects become less important as dispersal distances increase (Fahrig and Paloheimo, 1988a). Phenomological models of colonization rates as a function of isolation (Wilcove *et al.*, 1986; Hanski, 1991) show that increased average isolation can decrease persistence. Simulations have also shown that clumping can enhance persistence (Herben *et al.*, 1991) and that patches in clusters have higher occupancy (Verboom *et al.*, 1991).

The effect of isolation is accentuated if dispersal entails a cost that increases with the distance that an organism has to travel before it reaches a new site (Doak *et al.*, 1992). In this case, the prospects of a dispersing animal depend largely on its point of departure. If it starts from an isolated patch, it has no choice but to travel far, facing a high risk of death in transit. In contrast, emigration from a patch surrounded by close neighbors may not be very risky at all. The distribution of these success probabilities varies depending on the arrangement of habitat in the landscape. Evenly spaced habitat patches generate a low variance in this distribution, while the variance is maximized in patterns consisting of a mix of clustered and isolated patches. It is this distribution that links the dynamics of the species to the landscape pattern.

In this paper we demonstrate the importance of habitat arrangement in a metapopulation in which regional persistence is threatened by local uncorrelated catastrophes. While holding the overall density of habitat patches constant, we vary the spatial pattern from regular to random to clumped. A simple search mechanism is assumed to govern the movement of dispersers through unfavorable terrain, with movement range limited by a distance-dependent cost of dispersal. Population densities are followed in detail in each patch, with local dynamics dependent upon an intrinsic growth rate, the departure of dispersers, and the arrival of dispersers. The analysis is guided by the following questions. First, what are the critical features of the landscape and life history that determine persistence? Second, when a species can persist, how will individuals and dispersers be distributed across the landscape?

To address these questions, we present first a simulation model and then a series of increasingly simple analytical approximations of its dynamics. We compare the results of the simulation with the approximations and use the approximations to derive answers to the above questions in particular cases. We conclude by discussing additional factors which can be analyzed using the approximations.

2. THE SIMULATION MODEL

To focus on the effects of landscape pattern on dispersal, we describe a model with a fairly detailed dispersal rule. Table I summarizes the variables and parameters used in the simulation and lists the numerical values used. The simulation and its results are discussed in more detail in Nuernberger (1991).

The landscape consists of largely unsuitable area into which are strewn 50 habitat patches of equal size and carrying capacity. We assume that the dimensions of the landscape are vast relative to the size of the patches. In order to exclude confounding edge effects, the simulations are run

TABLE I
Parameters Used in the Simulation

Symbol	Description	Values used
k	Number of patches	50
K	Finite rate of growth	1.5, 1.8
K	Carrying capacity of a patch	200
d	Fraction of individuals dispersing per generation	0.03, 0.25, 0.5
b	Movement range of dispersing individuals	2, 3, 6
x	Probability of extinction of a patch each generation	0.05

on a torus. Compared to the case in which dispersers "fall off the edge" of an isolated plane, fewer potential colonizers are lost in transit in the torus version, favoring persistence. Simulation results show that the bias that the periodic geometry introduces is quantitative rather than qualitative.

A variety of different habitat arrangements were generated by a computer algorithm, while others were designed by hand. The algorithm iteratively rearranges an initial random (Poisson) distribution by picking up and relocating patches based on local crowding. Clumped patterns were generated by biasing patch repositioning toward existing clusters, while regular patterns were produced by biasing patch repositioning away from existing clusters (see Appendix for details). This technique generates patterns of more or less continuously varying local densities with no need to define landscape elements and their spatial scale in advance. Figure 2.1 shows three example landscapes whose dynamics will be analyzed in some detail below.

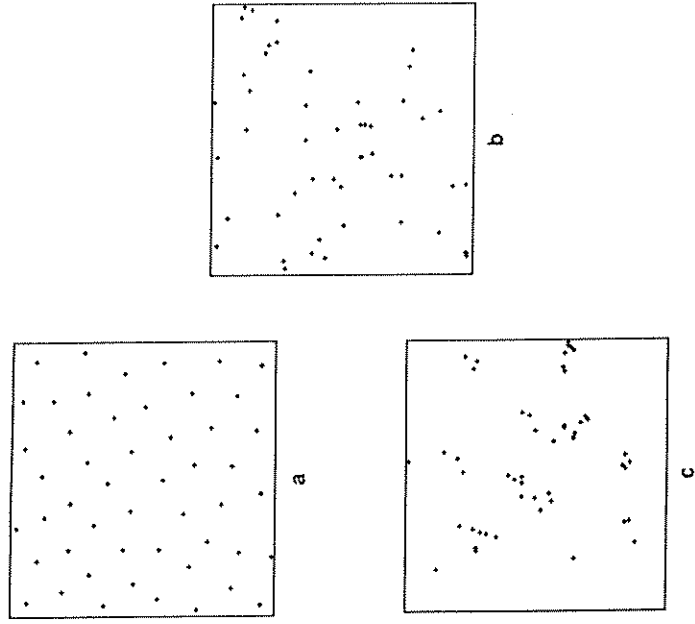


Fig. 2.1. Three landscapes used in the simulation and results: (a) regular, (b) random, (c) clumped.

The movement rules assume that dispersers have no way of assessing the properties of the entire landscape. Instead, an individual disperser leaves its home patch in a random direction and moves away on a straight path. It finds and settles the first patch it approaches within a given detection radius. A large detection radius biases dispersal toward short-range movement to neighbors, while a small detection radius produces a more porous ring of close neighbors around the home patch and longer average dispersal distances. In this study, the detection radius remains fixed throughout, with magnitude intermediate between an overly large value, in which case the separate patches are perceived as one, and an overly small value, in which case dispersers almost invariably leave the region. If the distance between two patches is shorter than the detection radius, half of the possible departure directions from each path are assumed to lead dispersers to the other.

Fahrig and Paloheimo (1988a) base their dispersal rule on search following dispersal by a fixed average distance. Because dispersers hop over nearby patches, small clumps are less important with this rule. The dispersers modeled by Doak *et al.* (1992) follow a random walk on a two-dimensional grid, a behavior leading to relatively short dispersal distances which can enhance the importance of clumps.

Departure direction determines the target patch. Dispersal success depends on the distance to that target. The probability that a disperser will successfully travel the distance D_{ij} from patch i to patch j , a_{ij} , is assumed to decline exponentially with distance according to

$$a_{ij} = \left(\frac{1}{2}\right)^{D_{ij}/b},$$

as in Wilcove *et al.* (1986). Thus b sets the movement range of the organisms relative to the dimensions of the landscape, being equal to the distance that can be successfully traversed with probability 0.5. The exponential form formalizes the assumption that the probability of death in transit is constant per unit distance moved. Three levels of b are used in the simulations.

The combined rules determining dispersal destination and success reflect the fact that the intrinsic movement abilities of the organism and the spatial distribution of available habitat sites combine to generate the observed pattern of immigration. We set λ_{ij} to be the fraction of individuals leaving patch j in any direction which arrive successfully in patch i , combining the two elements of the dispersal process.

In each generation, a fixed proportion of the individuals in each patch disperses, independent of local density. We refer to this fraction as the dispersal rate, denoted by d . Three different values of d are used in the

stochastic simulation, ranging from low (0.03) to medium (0.25) to high (0.5). Denoting population size in patch i before dispersal by $N_{i,t}$, the population size after dispersal, $N_{i,t+h}$, is the nearest integer to

$$N_{i,t+h} = (1-d)N_{i,t} + d \sum_{j=1}^k \lambda_{ij} N_{j,t}. \quad (2.1)$$

Upon arrival in an existing population, an immigrant has the same chance of reproduction as any resident. Population enhancement by immigrants has been shown to have important effects on the dynamics (Hanski, 1991; Hastings, 1991). If immigration leads to the recolonization of a previously vacant patch, the founding propagule will grow deterministically. Population size after growth, $N_{i,t+1}$, is assumed to follow a discrete approximation of the logistic equation (Begon and Motimer, 1986), or

$$N_{i,t+1} = \frac{RN_{i,t+h}}{1 + (R-1)N_{i,t+h}/K}, \quad (2.2)$$

where R is the finite rate of growth and K is the carrying capacity per patch. K was set to 200 throughout the simulations. As in all steps of the simulation, function values representing counts of individuals are rounded to the nearest integer. The magnitude of R determines whether a single immigrant can initiate population growth. As long as R exceeds 1.5 (and K is sufficiently large), a single gravid female may recolonize a patch by laying eggs. Otherwise, two individuals are needed to start a new population. These values correspond roughly to mating before and after dispersal. Stochastic simulation at the individual level would be more precise, but was impossible within our computational constraints. The two values of R used in the model (1.5 and 1.8) were chosen from both sides of this threshold. Population growth then proceeds until either K is reached or the patch is hit by an extinction event. The growth trajectories for populations initiated by the minimum propagule with a range of fixed immigration and dispersal rates are plotted in Fig. 2.2 to illustrate the time scale of the within-patch dynamics.

The population in each patch has an equal probability x per generation of being obliterated by a catastrophe. We set this probability to be 0.05 throughout the simulations and assume that disturbances are spatially and temporally uncorrelated.

At the beginning of each simulation, all patches are filled to carrying capacity. The simulations cycle through dispersal, extinction, and growth every generation for 1000 generations. In simulations in which the species persisted to the end, the regional mean population size changed very little

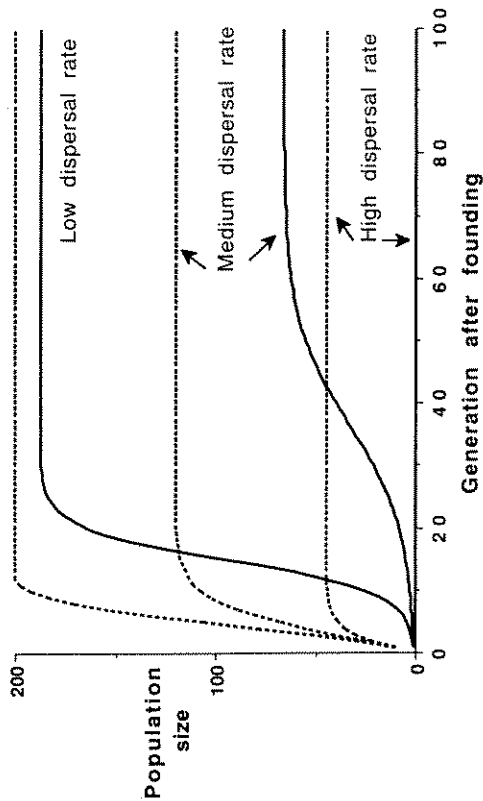


FIG. 2.2. Growth trajectories for $R = 1.5$, three different dispersal rates (0.03, 0.25, 0.5), and two constant immigration rates (0 shown by solid lines and 10 per generation shown by dotted lines). Note that the population with high dispersal and no immigration never gets established.

after an initial period of 200 to 300 generations, suggesting that the system had settled at a stochastic equilibrium. Regional extinction followed either a rapid decline in the total number of individuals or a more prolonged period of fluctuations around a low overall mean abundance. We found no evidence for multiple stable states and a non-zero threshold in any of the simulations, a result discussed in more length in the following section. It thus appears that the simulation length of 1000 generations was sufficient to determine whether or not a given combination of parameter values allowed for long-term persistence. In addition, this cut-off point is motivated by the idea that the parameters governing the process are themselves subject to change, if on a much slower time scale. Simulations over several thousand generations may therefore exceed the "lifetime" of the system as defined by these parameters, and phenomena that take excessively long to emerge may never be realized in nature.

Of the three life history parameters, the dispersal rate has the most interesting effect on the regional abundance of individuals. Since dispersers face a considerably higher risk of death than their non-dispersing conspecifics, emigration is only partially compensated by immigration. The regional abundance of individuals after 1000 generations is much less than the total carrying capacity of the entire landscape. Total population size is maximized at an intermediate dispersal level, since an overly low dispersal cannot compensate for the effects of local extinctions through rapid

recolonization, while an overly high dispersal rate saturates the environment with dispersers risking their lives in a vain quest for empty patches.

Growth rate and dispersal success affect abundance and persistence in the manner that intuition suggests. Faster local population growth leads to an increased production of dispersers, and the losses due to emigration in a given patch are more quickly replenished. Less costly dispersal produces higher rates of immigration which promote the growth of small populations and diminish the losses due to emigration.

To study the effect of landscape pattern on persistence, simulations were run with different landscapes of varying degree of clumpedness (including the ones depicted in Fig. 2.1). For each pattern, we determined persistence for all possible combinations of the three life history variables (i.e., a $2 \times 3 \times 3$ factorial experiment). Each parameter combination was replicated 50 times per landscape. This design explores only a very small subset of the parameter space, a limitation dictated by the computing time required for each run. Ideally, one could delineate the region of persistence inside the cube defined by the three independent variables and compare size and

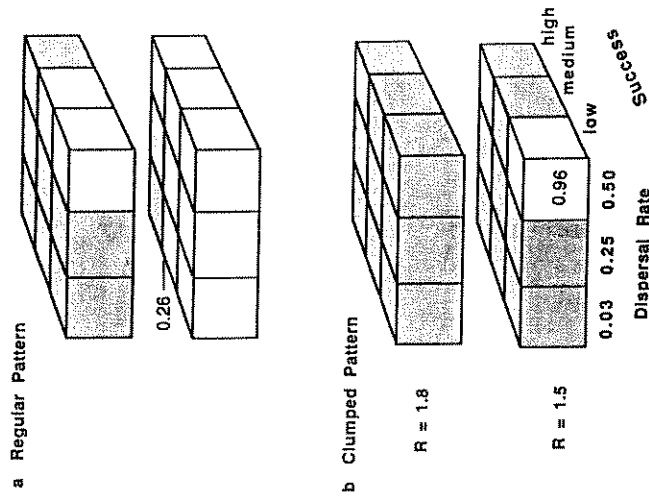


FIG. 2.3. Species persistence as a function of the three life history parameters for a regular and clumped landscapes (Figs. 2.1a and 2.1c). Shaded boxes indicate persistence and white boxes extinction in all 50 replicate runs.

shape of this volume for different landscapes. Nevertheless, the simulations clearly distinguish the potential of different patterns to sustain species with various life histories and provide a suitable basis for comparison with the less computer-intensive approximation (Fig. 2.3). While virtually all parameter combinations allow for persistence in case of the clumped pattern, regional extinctions are the rule over a large part of the parameter space in the regular pattern. This corresponds with earlier results (DeAngelis *et al.*, 1979), in which a system could persist based solely on the persistence of a single clump. The most "threatened" combination of life history traits consists of low growth and success rates and a high dispersal rate.

Within a single landscape, the degree of isolation of a patch determines the rate at which it is reached by dispersers. Low immigration rates can lengthen the time period between extinction and recolonization events and slow the growth of newly established populations. To demonstrate these two consequences of location, the dynamics of three isolated patches were compared with those of three patches in clusters, all of which were chosen from the clumped landscape of Fig. 2.1c.

The time from extinction to recolonization differed little with the parameters chosen, but we expect more separation if the supply of colonizers were more limiting. Nonetheless, the patch-specific growth trajectories show a clear response to the degree of isolation (Fig. 2.4). Patches

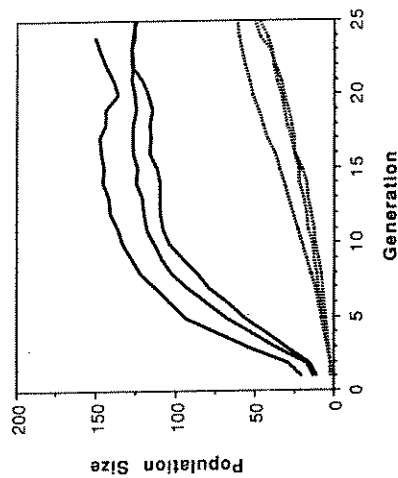


Fig. 2.4. Mean growth trajectories of populations as a function of their location in the landscape. Each curve shows the average population size as a function of time since colonization in a particular patch taken from the clumped landscape (Fig. 2.1c). Solid lines are for patches in clusters and broken lines for isolated patches, with data compiled over three replicate runs from generation 500 to 1000, using $R = 1.5$, $d = 0.25$, $b = 6$. Compare with Fig. 2.2. Note that sample sizes decline with time because more and more populations are hit by catastrophes (minimum sample size is 5).

located in clusters are colonized by larger propagules, which shortens the initial lag phase, and accelerates the rise of the logistic growth curve (cf. Fig. 2.2). In contrast, the three isolated patches are typically colonized by very few individuals. The growth rate of such newly founded populations is much reduced because emigration is only partially balanced by immigration.

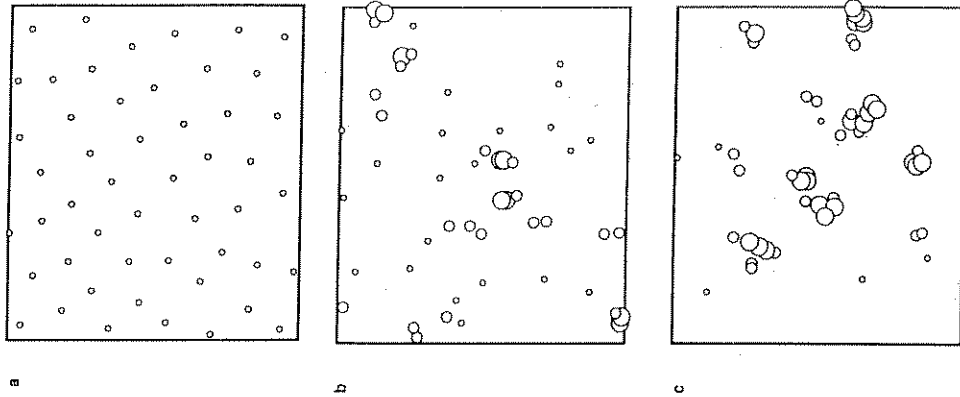


Fig. 2.5. Spatial distribution of mean population sizes in the landscapes of Fig. 2.1. Data compiled from generation 500 to 1000 with $R = 1.5$, $d = 0.25$, $b = 6$. Small dots indicate average population sizes between 20 and 59, medium dots between 60 and 99, and large dots between 100 and 140.

Figure 2.5 summarizes the consequences of these dynamics for the spatial distribution of average population sizes in the three example landscapes. Each patch in a cluster typically maintains a large average population and produces many dispersers that rapidly recolonize neighboring patches. Furthermore, such clusters are rich sources of colonizers to surrounding more isolated sites. Species persistence is thus strongly bolstered by these core clusters.

The simulations show that clumping of patches increases the persistence of metapopulations and give some insight into the process by which clusters buoy the population. They show that the distance-dependent movement rules produce clusters of population in clusters of patches.

3. THE ANALYTIC APPROXIMATIONS

In this section, we provide several approximations to the simulation. They are designed to predict whether a population of organisms can persist in a given landscape and the distribution of organisms and dispersers if it can. Unfortunately, we were unable to derive error bounds for these methods. We seek to understand what level of detail regarding the system is necessary to capture important features of the dynamics. The most detailed approximation, termed the "full matrix approximation," uses the entire matrix of interpatch connections λ_{ij} to estimate average population sizes. A second, the "averaged approximation," uses a single number to describe each patch. This number, the "immigration potential," is the sum of the strengths of all connections to a patch. Finally, we compare these results with those of the "homogeneous connection approximation," in which the detailed structure is ignored except for a single scaling constant.

Our approximation method is essentially that used by Hastings and Wolin (1989), which ignores spatial and temporal autocorrelations in patch occupancy. This also corresponds to what Gurney and Nisbet (1978) term the "zero-correlation" assumption, the assumption that such autocorrelations produce only small effects upon long-term patterns and can be ignored. The method of approximation begins by estimating the mean occupancy level of a patch with a given fixed immigration rate. We then pretend that this patch produces dispersers at a constant rate equal to the product of the dispersal rate d and the mean size. Imposing the condition that the mean number of immigrants arriving in a patch must equal the number of dispersers destined to arrive there safely produces a set of equations which can be solved for the average population sizes in the patches.

TABLE II
Variables Used in the Approximations

Symbol	Description
$N_{i,t}$	Population size of patch i at time t
$N_{i,t+h}$	Population size of patch i after dispersal at time t
λ_{ij}	Probability that disperser leaving patch j arrives safely at patch i
A	Matrix of the λ_{ij}
s_j	Immigration potential into patch i , $\sum_j \lambda_{ij}$
μ	Leading eigenvalue of A
g	Growth rate as a function of population size
p_t	Probability that a patch was recolonized t generations ago without an intervening extinction
n_t	Approximate size of a patch recolonized t generations ago without an intervening extinction
$v(q)$	Approximate average population size of a patch as a function of average immigration rate q
q_i	Full matrix approximate immigration rate into patch i
N_i	Full matrix approximate mean population size of patch i
\bar{N}	Full matrix approximate overall mean population size
E	Mean immigration potential
V	Variance of the immigration potentials
$\hat{\mu}$	Averaged approximate leading eigenvalue $= E + V/E$
\hat{q}_i	Averaged approximate immigration rate into patch i
\bar{N}_i	Averaged approximate mean population size of patch i
\bar{N}	Averaged approximate overall mean population size
q^*	Homogeneous connection approximate immigration rate
N^*	Homogeneous connection approximate mean population size

The Full Matrix Approximation

Consider a patch with mean immigration rate, or mean number of arrivals per generation, of q . The mean occupancy of such a patch can be estimated by following patch age (Hastings, 1991). We first compute the probability that the patch survives a certain number of generations after colonization, and then compute the population size at this time. Let $\pi(q)$ be the probability that the patch, when empty, is colonized by a disperser. If dispersers arrive independently, the number of arrivals will be Poisson distributed with probability of at least one arrival per generation of

$$\pi = 1 - e^{-q}, \quad (3.1)$$

where we have suppressed the explicit dependence of π on q . Ignoring the possibility that a patch is emptied by coincidental simultaneous emigration,

patches are emptied in a given generation with probability x . The patch will then be empty, on average, a fraction p_0 of the time satisfying

$$p_0 = \frac{x}{x + \pi}, \tag{3.2}$$

and be occupied the rest of the time. Let p_t give the probability that the patch has been colonized for exactly t generations without an intervening extinction. Then $p_{t+1} = (1-x)p_t$ for $t \geq 1$, so that

$$\begin{aligned} 1 - p_0 &= \frac{\pi}{x + \pi} \\ &= \sum_{t=1}^{\infty} p_t \\ &= \sum_{t=1}^{\infty} (1-x)^{t-1} p_1 \\ &= \frac{p_1}{x} \end{aligned}$$

implying that

$$p_t = (1-x)^{t-1} \frac{x\pi}{x + \pi}. \tag{3.3}$$

Let n_t be the expected population size just after colonization. If q is small, this will be 1, otherwise it might be larger due to multiple immigrations. Let n_t be the expected population size t generations after successful colonization if no intervening extinctions have occurred. Then we have that

$$n_{t+1} \approx g((1-d)n_t + q), \tag{3.4}$$

where we use g to denote the growth function, the discrete logistic of Eq. (2.2). This expression is not exact since this equation uses the average value of immigration inside the growth function rather than averaging over different values of immigration after growth (cf. Chesson, 1981). This introduces only a small bias with reasonable parameter values.

The expected population size of the patch, denoted by $v(q)$, is then

$$v(q) = \sum_{t=1}^{\infty} p_t(q) n_t(q). \tag{3.5}$$

Figure 3.1 shows the behavior of this function for three different dispersal rates. This function will have a negative second derivative unless there is a

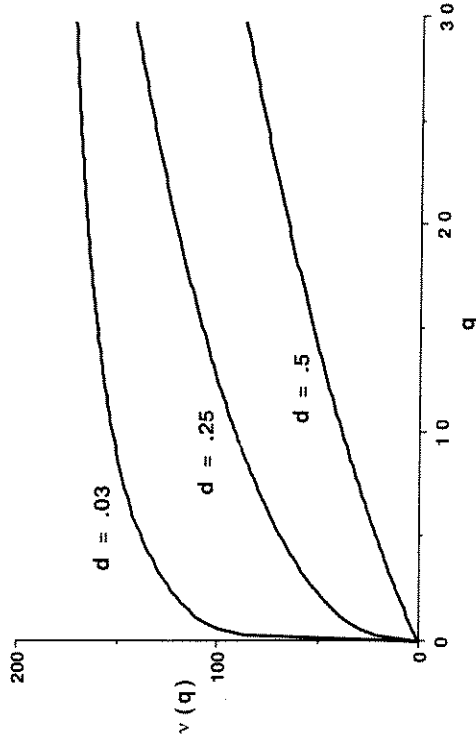


FIG. 3.1. The expected population size of a patch with constant immigration of q individuals per generation and finite rate of growth $R = 1.5$ for three values of the dispersal rate.

strong Allee effect or density-dependent dispersal at low population size (Hanski, 1985; Hastings, 1991). In the first case, immigration must exceed some non-zero threshold in order for a patch to be reestablished. In the second, a newly settled metapopulation cannot persist, due to lack of sufficient dispersal to counterbalance extinction.

If patch i has mean immigration rate q_i , we expect the mean population size of the patch, N_i , to approximately satisfy

$$N_i = v(q_i) \tag{3.6}$$

for $i = 1, \dots, k$. Consistency requires that

$$\begin{aligned} q_i &= d \sum_{j=1}^k \lambda_{ij} N_j \\ &= d \sum_{j=1}^k \lambda_{ij} v(q_j). \end{aligned}$$

This gives a set of k equations for the q_i .

It is convenient to express this in vector notation as follows. Let \mathbf{N} denote the vector of the N_i and \mathbf{q} the vector of the q_i . Then

$$\mathbf{q} = d\mathbf{A}\mathbf{N}. \tag{3.7}$$

If we define the vector function \mathbf{v} by

$$(\mathbf{v}(\mathbf{q}))_i = v(q_i), \quad (3.8)$$

we have that

$$\mathbf{N} = \mathbf{v}(\mathbf{q}). \quad (3.9)$$

Eliminating \mathbf{N} from Eq. (3.7) gives

$$\mathbf{q} = dA \mathbf{v}(\mathbf{q}). \quad (3.10)$$

Solution of this equation, which is straightforward numerically, yields an approximation of the mean immigration rates into each patch at equilibrium, from which mean population sizes can be found from Eq. (3.9).

Equation (3.10) always has the solution $\mathbf{q} = 0$, corresponding to extinction. When will it also have a positive solution? As with the Levins (1969, 1970) model, one expects to find a threshold value of the parameters below which the zero solution is unique and stable and above which a positive solution exists and is stable. In this case, the existence of a positive solution is equivalent to persistence of the species of interest.

The threshold corresponds to a transcritical bifurcation of a dynamical system (Hirsch and Smale, 1974) and occurs when the first colonist into an empty system produces, on average, more than one successfully dispersing offspring. Such a bifurcation occurs only when v is concave down. In the case where multiple immigrants are required to found a population and v is sigmoidal, a different bifurcation produces two new equilibria. The lower one acts as a threshold population size below which the population decreases deterministically to the stable equilibrium at zero, and above which it increases to a positive stable equilibrium (cf. Hastings, 1991). As noted above, in the absence of negative density dependence (lower reproduction or lower dispersal rate at low population size), this case will not arise.

We begin by linearizing Eq. (3.10) as

$$\mathbf{J} = dA \mathbf{v}'(0), \quad (3.11)$$

where \mathbf{v}' denotes differentiation. From Eq. (3.5) we have that

$$\mathbf{v}'(q) = \sum_{i=1}^{\infty} (p'_i(q) n_i(q) + p_i(q) n'_i(q)).$$

Since $p_0 = 1$ when $q = 0$,

$$\mathbf{v}'(0) = \sum_{i=1}^{\infty} p'_i(0) n_i(0).$$

Using Eq. (3.3) and (3.1) gives

$$p'_i(0) = (1-x)^{i-1},$$

so that

$$\mathbf{v}'(0) = \sum_{i=1}^{\infty} (1-x)^{i-1} n_i(0). \quad (3.12)$$

Recall that $n_i(0)$ gives the population size of a patch i generations after colonization if no further immigration and no extinction occurs in the interim. Thus $\mathbf{v}'(0)$ is just the total population size, conditional on founding, for a patch receiving no further dispersers. The number of dispersers expected to be produced by such a patch will then be $d\mathbf{v}'(0)$.

The condition for persistence is that μ , the leading eigenvalue of A , satisfies

$$d\mathbf{v}'(0) \mu > 1. \quad (3.13)$$

The eigenvalue μ expresses the appropriately averaged probability that a disperser will arrive somewhere successfully; thus inequality indicates that the system can persist if a newly settled patch produces more than one successful disperser on average. Below this threshold, the only equilibrium is extinction; above it, there is an equilibrium with each patch occupied at least some of the time in a fully connected system. The threshold condition corresponds to that found in epidemiological situations (Diekmann *et al.*, 1990) and in earlier work on spatially structured populations (Chesson, 1984).

In terms of the model parameters, the threshold condition separates neatly into two components. The term $d\mathbf{v}'(0)$ depends only on the life history parameters of the organism (R , K , and d) and on the extinction rate (x), while μ depends only on the properties of the landscape (the movement range b , and the pattern of patches). If one fixes the life history parameters and the extinction regime, the threshold depends only on μ , making it easy to study the fate of a given organism over a range of landscapes.

The Averaged Approximation

In this section we develop an approximation for the leading eigenvalue and the patch occupancies based only on the immigration potentials. We first show that the leading eigenvalue μ separates approximately into two components, the sum of the mean and the variance to mean ratio of the set of immigration potentials. The derivation presented here is valid only for symmetric migrations matrices, but the approximation works well for the roughly symmetric migration matrices which arise in the simulation.

Our main result is the following. Define

$$s_i = \sum_{j=1}^k \lambda_{ij} \quad (3.14)$$

to be the immigration potential for patch i . It can be thought of as the expected number of dispersers which would arrive in patch i if one disperser departed from each patch and thus acts as a measure of patch connectedness purely dependent on landscape features. Isolated patches have lower immigration potentials than patches in clusters. Let E be the average of the immigration potentials and V be their variance. We will show that

$$\hat{\mu} = E + \frac{V}{E} \quad (3.15)$$

approximates the true eigenvalue μ .

There are thus two factors involved in producing a large eigenvalue. The first is a large mean immigration potential, which can be thought of as high dispersal success. The second, if the mean dispersal probability is fixed, is a high variance in dispersal success, which translates into clumpiness. For a fixed average dispersal success, the minimum eigenvalue occurs when the variance vanishes, as has been shown in an epidemiological context (Adler, 1992). Moving patches into a more clumped arrangement generally increases both E and V , making the operation of the factors difficult to separate. Doak *et al.* (1992), on the other hand, consider a random walk movement rule and find that increased clumping produces a decreased value of E and increased V .

We now derive Eq. (3.15). Let \mathbf{u} denote the vector of 1's. The vector \mathbf{s} of immigration potentials can be written as $\mathbf{s} = A\mathbf{u}$, and the mean and variance of the immigration potentials can be expressed as

$$E = \frac{\sum_{i=1}^k s_i}{k} = \frac{(A\mathbf{u}, \mathbf{u})}{k} \quad (3.16)$$

$$V = \frac{\sum_{i=1}^k s_i^2}{k} - E^2 = \frac{(A\mathbf{u}, A\mathbf{u})}{k} - E^2. \quad (3.17)$$

This leads to the convenient expression

$$E + \frac{V}{E} = \frac{(A\mathbf{u}, A\mathbf{u})}{(A\mathbf{u}, \mathbf{u})}. \quad (3.18)$$

The following derivation is based upon the "power method" of numerical analysis (Golub and Van Loan, 1983), which uses the fact that the

sequence of vectors generated by iterated application of a matrix tends to converge to the eigenvector with leading eigenvalue. Slightly modifying formula 7.3-3 from Golub and Van Loan (1983), we have that the leading eigenvalue μ satisfies

$$\mu = \lim_{n \rightarrow \infty} \frac{(A^n \mathbf{u}, \mathbf{u})}{(A^{n-1} \mathbf{u}, \mathbf{u})} \quad (3.19)$$

as long as \mathbf{u} has a component in the direction of the leading eigenvector \mathbf{v} . The expression on the right-hand side of Eq. (3.18) is simply the expression on the right-hand side of Eq. (3.19) evaluated at $n=2$, where we have used the assumed symmetry of A to equate $(A^2 \mathbf{u}, \mathbf{u})$ with $(A\mathbf{u}, A\mathbf{u})$. Also by symmetry, A has an orthogonal basis of eigenvectors, and \mathbf{u} has a component in the direction of \mathbf{v} as long as their inner product is non-zero. The Perron-Frobenius theorem guarantees that \mathbf{v} can be chosen to have nonnegative components and that at least some components will be positive if the matrix is primitive (Grantmacher, 1989). It therefore has a positive inner product with \mathbf{u} . Rapid convergence of the limit in Eq. (3.19) is enhanced by two factors: near colinearity of \mathbf{v} and \mathbf{u} and small absolute value of the other eigenvalues relative to the leading eigenvalue. The first factor appears generally to be operative in the context of this model, since the immigration potentials associated with the different patches do not differ too much.

Our next task is to use this approximate eigenvalue and the immigration potentials to find an approximate solution of Eq. (3.10). Such a solution depends on A only through the immigration potentials.

We begin by expanding $\mathbf{v}(q_i)$ to first order (Kaplan, 1984) around some value q^* to be specified later, giving

$$\mathbf{v}(q_i) \approx \mathbf{v}(q^*) + (q_i - q^*) \mathbf{v}'(q^*)$$

or, in vector notation,

$$\mathbf{v}(\mathbf{q}) \approx \mathbf{v}(q^*) \mathbf{u} + (\mathbf{q} - q^* \mathbf{u}) \mathbf{v}'(q^*).$$

Substituting $\mathbf{q} = dA \mathbf{v}(\mathbf{q})$ from Eq. (3.7) gives

$$\begin{aligned} \mathbf{q} &\approx dA(\mathbf{v}(q^*) + (\mathbf{q} - q^* \mathbf{u}) \mathbf{v}'(q^*)) \\ &= d\mathbf{v}(q^*) \mathbf{s} + d\mathbf{v}'(q^*) (A\mathbf{q} - q^* \mathbf{s}). \end{aligned}$$

We seek to pick q^* to make $\mathbf{q} \approx d\mathbf{v}(q^*)\mathbf{s}$ by minimizing the second term of this expression.

If $\mathbf{q} \approx d\mathbf{v}(q^*)\mathbf{s}$, then

$$A\mathbf{q} \approx d\mathbf{v}(q^*)\Lambda\mathbf{s} \approx d\mathbf{v}(q^*)\hat{\mu}\mathbf{s},$$

where we have used the fact that \mathbf{s} approximates the leading eigenvector of A [see Eq. (3.19)]. Then

$$A\mathbf{q} - q^*\mathbf{s} \approx (d\hat{\mu}\mathbf{v}(q^*) - q^*)\mathbf{s},$$

which vanishes when

$$q^* = d\hat{\mu}\mathbf{v}(q^*). \quad (3.20)$$

This equation is precisely Eq. (3.10) in a landscape where each $s_i = \hat{\mu}$ and has a threshold at $d\hat{\mu}\mathbf{v}'(0) > 1$, the averaged approximate version of Eq. (3.13). We set

$$\hat{q}_i = d\mathbf{v}(q^*)s_i, \quad (3.21)$$

and

$$\hat{N}_i = \mathbf{v}(\hat{q}_i). \quad (3.22)$$

Note that this approximation depends only on the immigration potentials when the approximate $\hat{\mu}$ of Eq. (3.15) is used. This is the averaged approximation.

We also define $N^* = \mathbf{v}(q^*)$ to be “homogeneous connection approximation.” This is the mean occupancy in a model with leading eigenvalue equal to that in the averaged approximation, but in which all patches have equal immigration potential. As noted in the introduction, the island model and stepping-stone model are two examples of this sort.

4. RESULTS

We begin by comparing the results of the approximations with those from the simulation, showing that the approximations successfully capture the global features of the dynamics. We then use the approximations to illustrate some results regarding mean dispersal success and population size as a function of the dispersal rate.

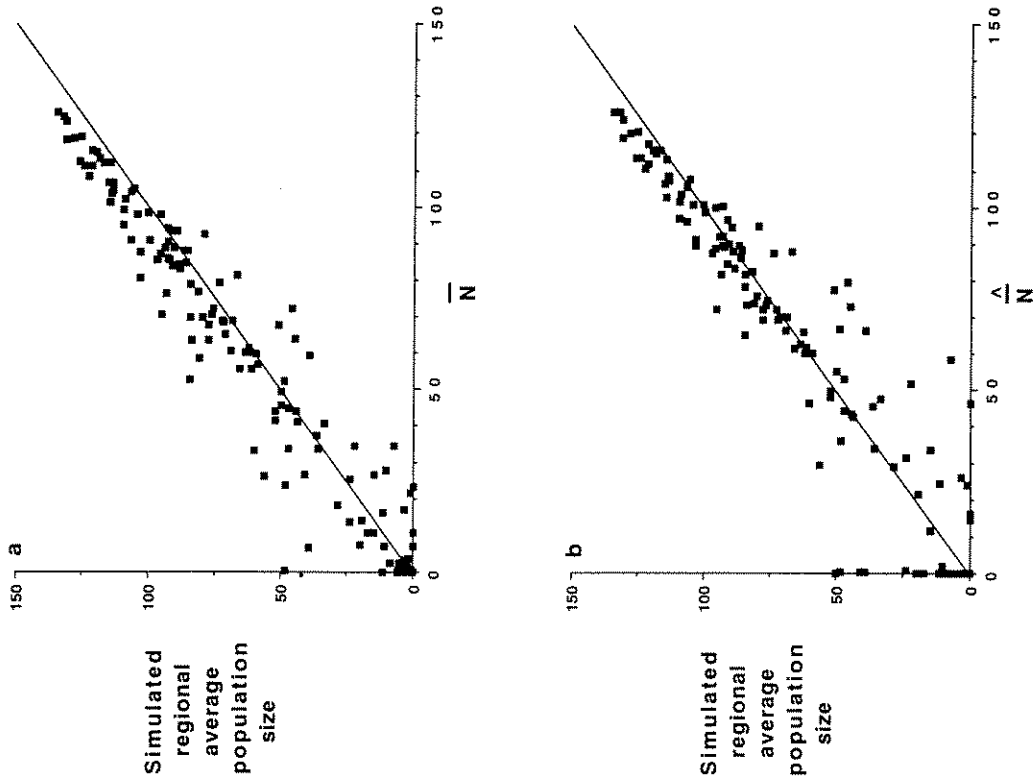


FIG. 4.1. The three approximations as predictors of simulated regional average population size. Seven different patterns and 18 parameter combinations were used. The diagonal lines indicate equality of simulation and prediction.

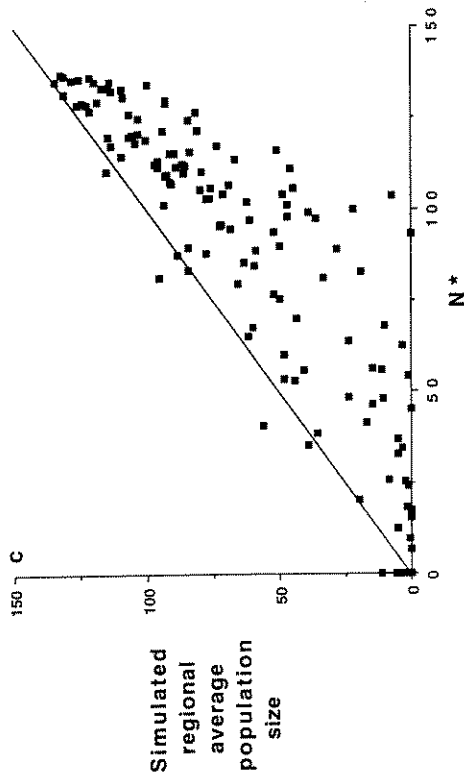


FIG. 4.1.—Continued

Testing the Approximations

The approximations make global and patch-by-patch predictions of the dynamics of the simulation. The global prediction is the regional mean population in a system, with a particular focus on whether it is positive. Patch-by-patch predictions regard mean population sizes and immigration rates of patches within a given landscape.

We first define the regional mean populations predicted by the three approximations. The full matrix approximation uses the full matrix A to compute \bar{N}_i [defined by Eq. (3.7)], whose average we denote by \bar{N} . The averaged approximation uses only the immigration potentials to compute \bar{N}_i [defined by Eq. (3.21)], whose average we denote by \bar{N} . The homogeneous connection approximation uses only the approximate eigenvalue μ to compute N^* for each patch of the appropriately averaged unclumped model. Figure 4.1 illustrates the accuracy of these three approximations in capturing the behavior of the simulation for a variety of patterns and a range of parameter values. Although there are some discrepancies at lower population sizes, both \bar{N} and \bar{N} predict the general trend very well. Note that N^* consistently overestimates regional population sizes as explained below.

The second global prediction is the threshold given in Eq. (3.13). Figure 4.2 shows the simulated regional population size as a function of $d\mu v'(0)$, the threshold in the averaged approximation. Although this quantity has little predictive value overall (Fig. 4.2a), it is successfully picks out the point where simulations tend to persist (Fig. 4.2b). The threshold calculation ignores the stochastic effects of low population size, referred to

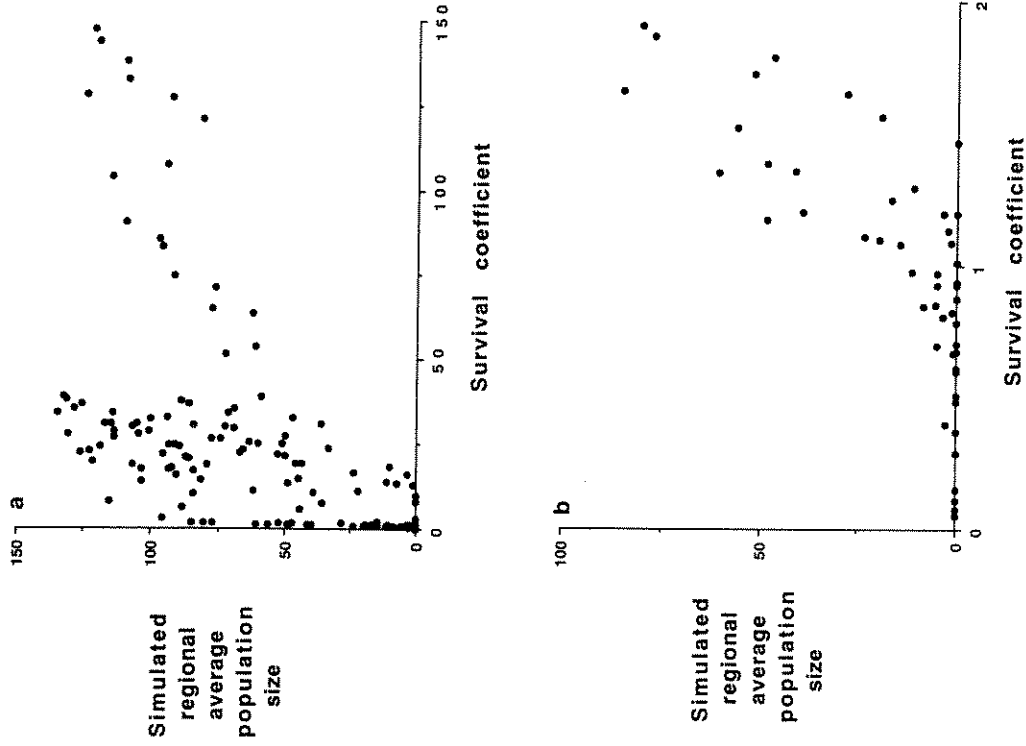


FIG. 4.2. The survival coefficient $d\mu v'(0)$ [Eq. (3.13)] as a predictor of simulated regional average population size. (a) Blow-up of (a), near the threshold at 1.

as "immigration-extinction stochasticity" (Hanski, 1991), which would be expected to produce extinction in simulations near the threshold (Gurney and Nisbet, 1978). Using methods from population genetics, one of us has shown that the approximate expected time to extinction in a finite version of the Levins (1970) metapopulation model (1.1) begins a rapid exponential increase near the threshold represented in Eq. (3.13) (Adler, 1991).

The patch-by-patch predictions are less impressive. Figure 4.3 shows the size predicted by the full matrix approximation (N_i) plotted against three replicates of the simulation for the three patterns shown in Fig 2.1. The simulations average over the last 500 generations of a 1000-generation run. There is great variability among replicates, and although the predictions fall within this range, the correspondence between the predicted and simulated patch sizes is never strong, even with the clumped pattern. More interesting is the prediction that immigration rates are related linearly to the immigration potentials [Eq. (3.21)]. Figure 4.4 shows the full matrix approximation (q_i) along with two replicates of the simulations plotted against the immigration potentials of the patches. The results of the full matrix approximation lie right along the line predicted by the averaged approximation in each case, but only with the more heterogeneous random and clumped patterns do the simulated results follow this pattern. There are a few mysterious outliers in each case. Note that the simulated immigration rates are generally better behaved than the simulated population sizes.

Using the Approximations to Predict Dispersal Success

We illustrate several results which can be easily established using the averaged approximation. We discuss in detail the effects of different dispersal rates on the distribution of the population and of dispersers and then briefly address the effects of movement range.

The fraction of successful dispersers in the averaged approximation is

$$f = \frac{\hat{q}}{d\hat{N}},$$

where \hat{q} is the mean of the q_i and \hat{N} is the mean of the \hat{N}_i as above. From Eqs. (3.20) and (3.21), we have that

$$\hat{q} = dv(q^*) E = q^* \frac{E}{\bar{\mu}} \leq q^*.$$

Also

$$\hat{N} = \mathbf{E}(v(\hat{q}_i)) \leq v(\mathbf{E}(\hat{q}_i)) = v(\hat{q}) \leq v(q^*) = N^*,$$

Where \mathbf{E} represents expectation. The first inequality follows from Jensen's inequality (Billingsley, 1986) when v has a negative second derivative, and

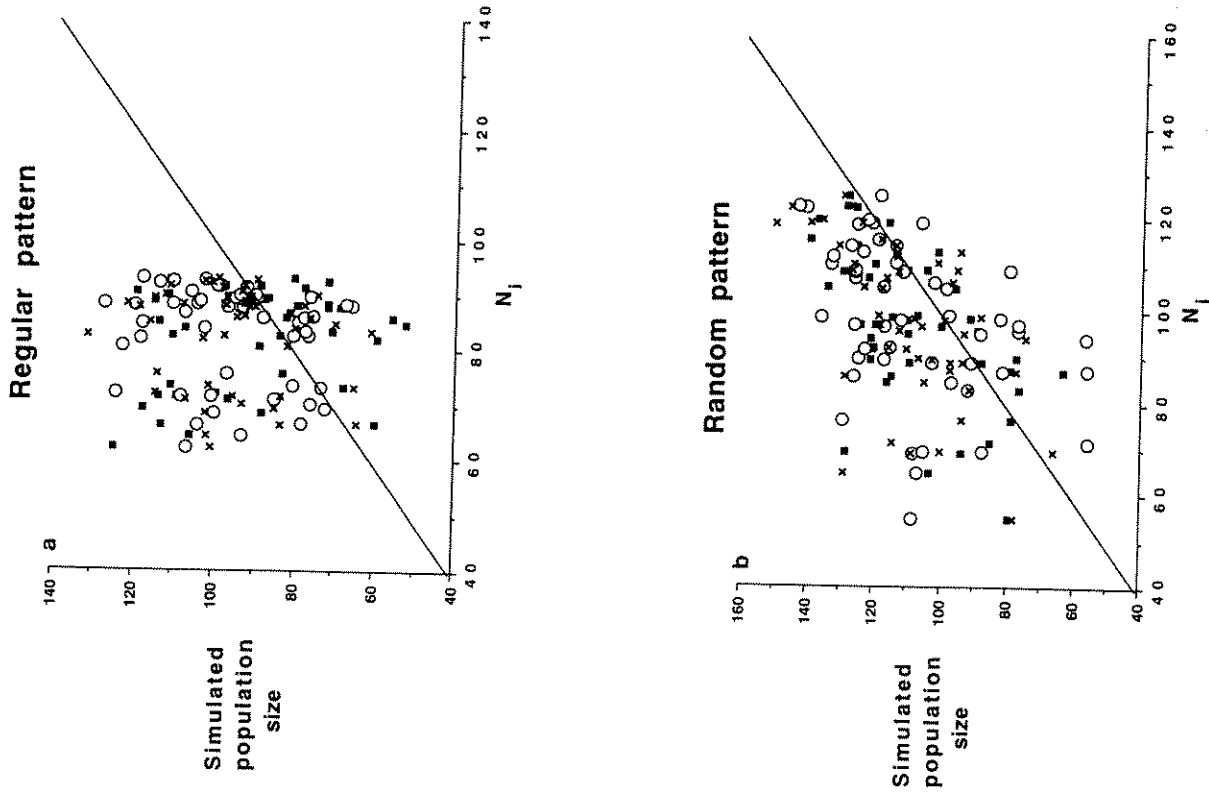


Fig. 4.3. The full matrix approximate average patch population sizes (N_i) as predictors of simulated average patch size for three different replicates of the simulation. Note the large variability among simulation results.

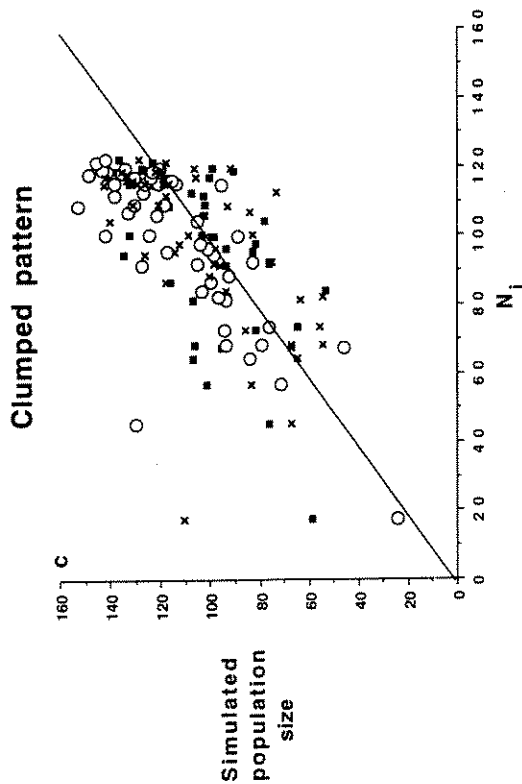


Fig. 4.3.—Continued

the second follows because v is an increasing function. This explains the general overestimation of simulated population size by the homogeneous connection approximation. It is a consequence of the greater local crowding, and thus decreased local growth rate, experienced by a clustered population with density-dependent growth (Lloyd, 1967).

Substituting into the expression for f gives

$$\begin{aligned}
 f &= \frac{\hat{q}}{d\hat{N}} \\
 &= \frac{q^*E}{d\hat{\mu}\hat{N}} \\
 &= E \frac{v(q^*)}{\hat{N}} \\
 &= E \frac{N^*}{\hat{N}} \gg E.
 \end{aligned}$$

This shows that the mean dispersal success of the population at its equilibrium distribution exceeds that if individuals were distributed uniformly and thus indicates that individuals are concentrated in clumps. Furthermore, if the third derivative of v were positive, it can be shown that $f \leq \hat{\mu}$. Although this is not generally true, $\hat{\mu}$ provides another convenient comparison.

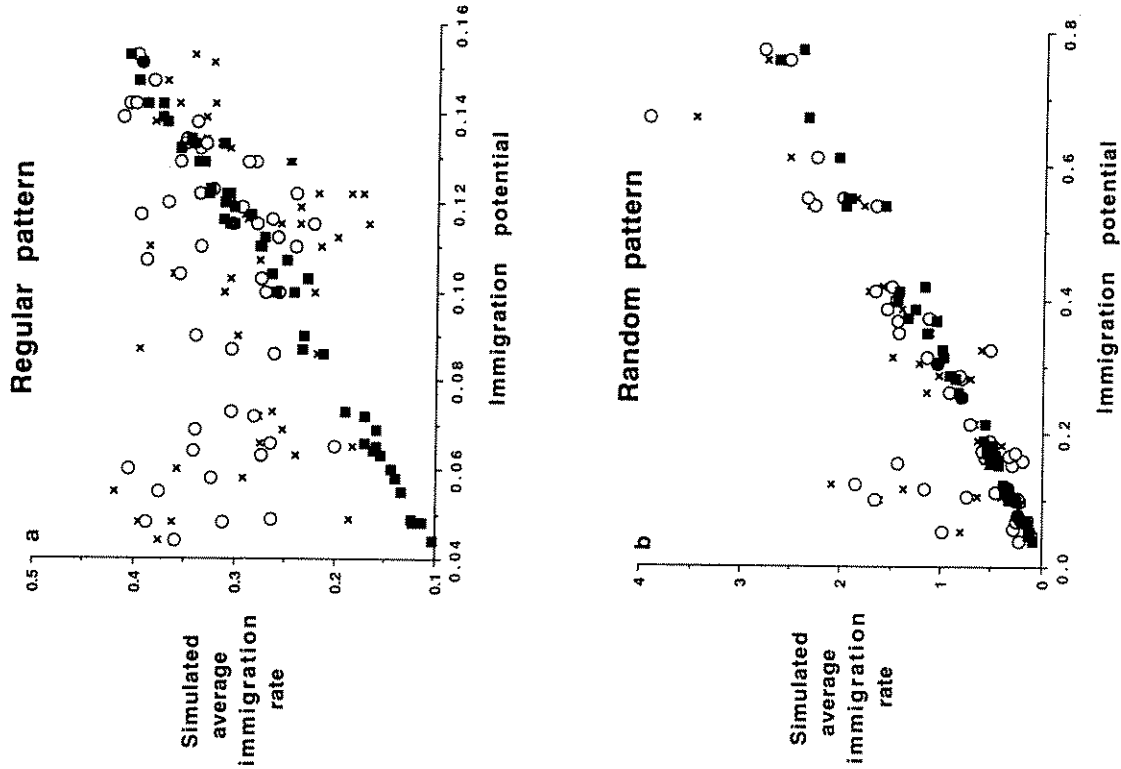


Fig. 4.4. The average number of immigrants arriving in a patch per generation for two replicates of the simulation (X, O) and the average immigration rate q_i (■) predicted by the full matrix approximation plotted against the immigration potentials (s_i). In each case, the full matrix approximation lies along the line predicted by the averaged approximation [Eq. (3.21)]. With the more heterogeneous landscapes (note the different ranges of the immigration potentials), the simulations also follow this pattern.

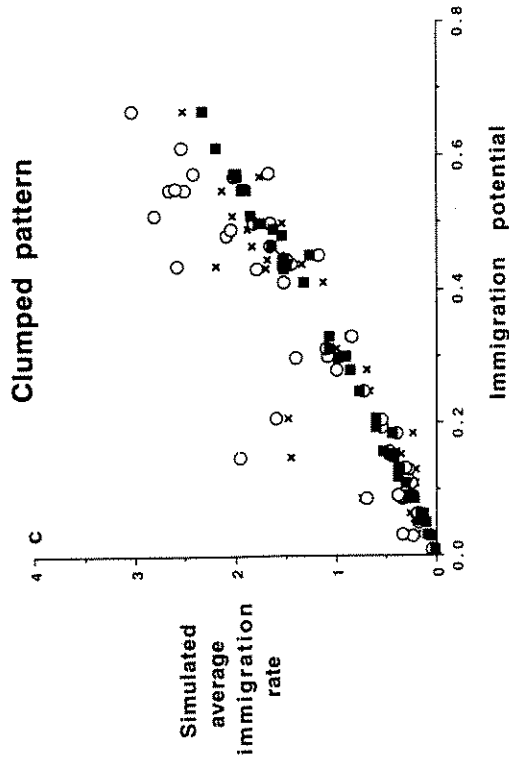


Fig. 4.4.—Continued

Figure 4.5 compares the fraction of successful dispersers with E , $\hat{\mu}$, and the coefficient of variation of mean population sizes across the landscape of Fig. 2.1b for a range of dispersal rates. With these parameters, the

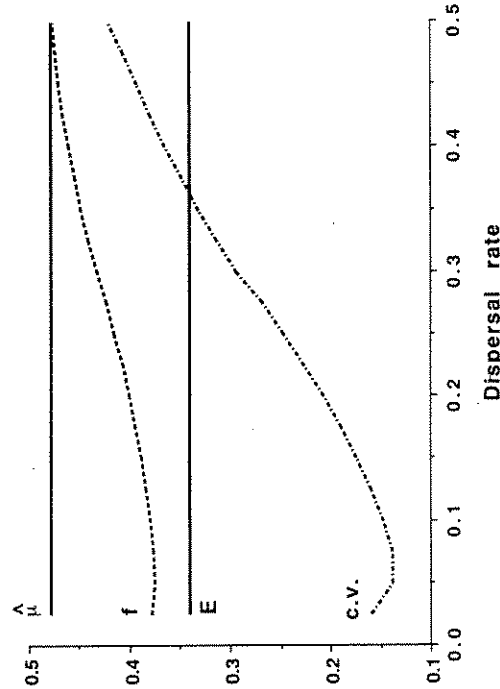


Fig. 4.5. The fraction of successful dispersers (dotted line) and the coefficient of variation (c.v.) of the average population sizes (dot-dashed line) predicted by the averaged approximation plotted against dispersal rate for a random pattern (Fig. 2.1b). The lower solid line is the average immigration potential E , and the upper solid line is the averaged approximate eigenvalue $\hat{\mu}$.

coefficient of variation of the population distribution mirrors the pattern of success. Note that increased average success is associated with small populations, because such populations are restricted to clusters.

Increasing the dispersal range b increases average success in all landscapes. Although the spatial pattern has a diminished effect when dispersal range is large, as in Fahrig and Paloheimo (1988a), the differences do not disappear even with a very large dispersal range. This is due to the fact that clusters are important as "traps" with our dispersal rule, because nearby patches act to hide more distant patches and keep populations clustered.

5. DISCUSSION

This paper presents the results of a simulation and its approximation designed to study the effects of spatial clumping of patches on a metapopulation linked by costly dispersal. Assuming that all patches are identical and that each experiences a simple regime of density-independent uncorrelated extinction, we demonstrate that clumping enhances persistence of the population.

The first approximation, the full matrix approximation, pretends that each patch interacts with its neighbors only through their average behavior and requires complete knowledge of dispersal between each pair of patches. It predicts the existence of a persistence threshold and gives values for the average population size and immigration rate for each patch in the landscape. A second, the averaged approximation, estimates these quantities using only a single measure of connectedness for each patch. This measure is the immigration potential, defined as the expected number of immigrants arriving in a patch if each other patch sent forth one disperser. The third, the homogeneous connection approximation, uses only a single number from the averaged approximation to create a normalized model with no variance in immigration potential. Both the full matrix and averaged approximations do well in predicting the persistence and mean landscape occupancy of the simulations, while the homogeneous connection approximation shows a consistent bias.

The persistence threshold derived with the full matrix approximation depends linearly on the leading eigenvalue of the connection matrix. This eigenvalue is approximated in the averaged approximation by the sum of the mean and variance to mean ratio of the set of immigration potentials. This implies that of two landscapes with the same mean immigration potential (the same average probability of successful dispersal between randomly chosen pairs of patches), the one with the larger variance among the immigration potentials will persist with higher probability. In such a

system, organisms will tend to be concentrated in clusters and experience higher dispersal success than if they were distributed uniformly. Local dispersal alone, as in a stepping-stone model, does not produce different levels of connectance and thus leads to dynamics similar to those of a globally connected island model. Further analysis of the averaged approximation indicates that the immigration potential of a patch in a given landscape is proportional to the average rate of immigration into that patch.

The full matrix approximation works well when there are sufficiently many patches to average over some of the variability. Our simulations used only 50 patches, with each patch receiving significant numbers of dispersers from far fewer, indicating that the necessary numbers are not unreasonably large. More importantly, the approximation requires that there are no spatial correlations in the pattern of catastrophes (Harrison and Quinn, 1989). The averaged approximation requires in addition that the immigration process be additive in the sense that the population founding or enhancement depends only on the number of immigrants and not on their source.

Although the model has major simplifying assumptions, reviewed below, it can be used to guide measurement of parameters of existing populations and to make predictions regarding persistence in novel or modified environments. We show that calculation of the function v [Eq. (3.5)] depends on an understanding of the local growth, extinction, and dispersal parameters. Estimates of this function could be combined with measurements of average dispersal to test the key findings of the model. Recall that the more general full matrix approximation can be used when the local dynamics vary among patches. More predictively, knowledge of the demographic parameters in an existing population and estimates of the dispersal parameters (such as the immigration probability) in a new region can be used to predict persistence and the distribution of dispersers [Eq. (3.21)]. Estimates of dispersal parameters in the potential new region could be measured directly, through mark-recapture studies, or indirectly by extrapolation from existing knowledge. To evaluate the effects of modifying an existing habitat, the approximations can be used to estimate the importance of existing patches for the population by considering the effects of patch loss on dispersal success.

Like Hastings and Wolin (1989), we find that catastrophes produce a hierarchy of population sizes at any given time, due to the different lengths of time since extinction. Here we show that spatial position can produce a hierarchy of average population sizes. However, simulations show that these averages can take an extremely long time to settle down (over 25 extinction-recolonization cycles) and will thus be difficult to distinguish in the field. Similarly, Hansson (1991) notes that short-range dispersal in a homogeneously connected environment can lead to a more clumped distribution of occupied patches, and the drift of these clumps through the

landscape could produce a highly unpredictable pattern. The approximations predict that patches in clusters have higher average immigration rates, and this measure appears to be better behaved than average population size. Furthermore, this measure is predicted in the simplified case analyzed in this paper to be linearly related to the immigration potential, a relationship which could be examined in the field given sufficient knowledge of the dispersal regime.

Our predictions depend in varying degrees upon the simplifying assumptions. In particular, the importance of spatial arrangements depends upon the strictly local catastrophes and short-range movements, the latter a consequence of the search rule and the distance-dependent cost of movement. The scale of dispersal is roughly the size of a patch cluster, while the scale of disturbance is smaller. Spatial correlation of catastrophes, or catastrophes encompassing entire clusters of nearby patches, would eliminate the benefits of clusters and mediate against persistence (Harrison and Quinn, 1989). Variability in extinction rates over time decreases persistence in a way parallel to the increase due to clumping (Levins, 1969). Dispersal rules involving active search for unoccupied patches or long-range movement increase the scale of dispersal relative to cluster size and would diminish to importance of clusters. Conspecific attraction, biasing dispersal toward occupied sites, would have the opposite effect (Ray *et al.*, 1991).

Differences among patches in characteristics other than spatial connectivity, such as size, stability, or quality, would produce other gradients of occupancy. Although these could be overlaid upon the patterns described in this paper using the full matrix approximation, detailed knowledge about the patches would be required to make qualitative predictions about the interaction of multiple factors. Unless position and quality were highly correlated, as they might be near the edge of a species range (more isolated patches being of lower quality), no approximation of simplicity comparable to that of the averaged approximation would be possible.

More complex local dynamics, including demographic stochasticity at low population size or stochasticity in growth trajectories, could be included if more detailed knowledge were available. Demographic stochasticity, or any factor inhibiting small populations, would enhance the importance of clusters by making necessary large founding propagules (Hastings, 1991).

A potentially important element in persistence is the lack of density dependence in the dispersal rate. Density-dependent dispersal would allow small populations to grow more quickly because they would not lose individuals to dispersal and would thus make dispersal more punctuated in space and time. Only relatively few populations might produce emigrants in a given generation and colonization might be restricted to certain parts of the landscape (Hanski, 1985). It is unclear what effect this factor would

have upon the importance of clusters or upon the power of the approximations.

More complicated biological interactions might occur in a subdivided system (Hanski, 1991). Particular attention has been paid to predator-prey systems (Reeve, 1990; Nachman, 1991; Sabelis *et al.*, 1991), although more complex trophic interactions have been described (Levin *et al.* 1977). In such cases, where complex dynamics are common, the simple equilibrium approximations presented here are unlikely to be accurate.

Once established in a certain area, a species life history is likely to evolve according to the spatiotemporal pattern of habitat distribution (Cohen and Levin, 1991), with dispersal rates and movement ranges adjusting to the conditions set by the landscape (Ehrlich, 1984). Landscape pattern and spatial strategy are independent only to a first approximation. An interesting follow-up to the present model would be to use the simulation and approximation to study the effects of landscape on evolutionarily stable dispersal strategies. If, for example, most organisms are found in a few clustered patches, then the specific pattern of variability perceived from within these clusters might dominate the regional dispersal strategy. This strategy might not be very effective for the exploitation of isolated patches, but adaptations that improved utilization of these sites might be ineffective in populating the center cluster. Alternatively, one could imagine clustering allowing coexistence of different dispersal types, one specializing on well-connected clusters and another persisting as a spatial fugitive in more marginal areas.

Such a landscape could also alter the genetic structure of the population (Slatkin, 1981; Gilpin, 1991). Genetic differentiation among patches in a model like the one presented here could have important implications for evolution and warrants further study.

The complexity of spatially structured metapopulations might seem to be a curse for both modelers and empiricists due to the detail necessary to produce a model or interpret measurements. We show in this paper that the information encoded in such systems can be a blessing when that information can be used to derive statistics that tease apart the processes interacting to produce pattern.

APPENDIX

This appendix describes the algorithm used to generate clumped and regular patterns.

The algorithm begins with an initial random distribution of patches. Every point in the landscape is then assigned as crowding index the sum of the distance weighted effects of all patches. We assume that the influence

of a particular patch on any given point in the landscape declines exponentially with the distance between them to mimic the distance-dependent effects of dispersal. The crowding index for a point x is then

$$G(x) = \sum_{i=1}^k e^{-\alpha D_{ix}},$$

where D_{ix} represents the distance from patch i to point x .

An existing patch and a potential new location are then picked at random. The patch is relocated to the new location based on the value of the crowding index at that new location. To create a clumped pattern, the probability of relocating is an increasing function of crowding, such as a linear increase from 0 at the minimum value of G to 1 at the maximum. Regular patterns are created by setting the probability of relocating to be a decreasing function of crowding. This procedure is iterated until the desired degree of clumping, as measured by the variance in the G values, is attained.

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