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17. Simulation Methods for Developing General Landscape-Level Hypotheses of Single-Species Dynamics

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17.1 Introduction

As described in the introductory chapter (Turner and Gardner, Chapter 1), landscape ecology includes a wide range of concepts. However, one of the dominant themes is the importance of spatial and spatiotemporal heterogeneity in landscape pattern on ecological processes. At the level of the single population, the main aim in studies of landscape ecology is to answer this question: Does our understanding of population dynamics depend on the spatial or spatiotemporal heterogeneity of the landscape in which the population occurs? In this chapter I discuss methods for developing general hypotheses about population dynamics within a landscape.

17.2 Why the Analytical Approach Will Not Work

A major goal of population ecology is the development of central, general hypotheses around which research can focus. Traditional examples are the competitive exclusion hypothesis and density-dependent (logistic) population growth. Such hypotheses usually have originated from simple, analytically tractable mathematical models; reviews of the origins of such models are included in May (1976).

In the present context the term *general* implies that the theory and model from which the hypotheses arise are, in principle, not restricted to one or a few species.

Assuming that they are measurable quantities, the terms used in the model are general enough that they could be measured for any of a broad range of species. The broader this range, the more general is the theory. This kind of generality should not be confused with the actual range of species for which the theory is found to be confirmed. Onstad (1988) uses a more narrow definition of generality; he restricts the generality of a theory to the range of species that actually fits the theory. However, the typical procedure in theoretical ecology is to first propose a theory that is not intrinsically restricted to a narrow range of species (i.e., a general theory). The actual range of applicability is not discovered until after much further work, particularly field studies (Fahrig 1988a).

Many of the simple cornerstone theories and models in ecology have recently undergone a marked loss of credibility, as they have been found to be lacking in their ability to describe observable nature (Hall 1988; Hastings 1988; Ulanowicz 1988). This development is generally attributed to the fact that these models do not include the most critical factors influencing population dynamics (DeAngelis 1988). However, inclusion of such factors often renders the models analytically intractable (Hall 1988).

One factor that makes models of population dynamics intractable is the effect of spatial heterogeneity (Fahrig 1988b). Because landscape ecology explicitly considers spatial heterogeneity, it follows that models of population dynamics in a landscape context, even those that include only simple dynamics, are analytically intractable. A possible alternative is the use of simulation models. Dynamic simulations have been used in landscape ecology to look at the changes in spatial distributions of landscape elements over time (e.g., Sklar and Costanza, Chapter 10; Turner 1987). Many landscape models do not deal with population dynamics, and they usually are specific to a particular study system, making generalization difficult (but see also Hyman et al., Chapter 18; and Merriam et al., Chapter 16).

The question I address in the remainder of this chapter is this: Is it possible to use computer simulation to develop general hypotheses of population dynamics in the landscape context?

17.3 The Simulation Approach: Problems and Preferences

The reason that analytical approaches are still largely preferred for development of general theory in ecology is that, if a solution can be found, the range of parameter values over which the solution is applicable is known perfectly. For example, the solution of the Lotka-Volterra competition equations leads to the simple hypothesis that, if interspecific competition is stronger than intraspecific competition, there is no stable equilibrium point with both species coexisting. If intraspecific competition is stronger, a stable coexistence is possible, but only if $1/a_{21} > K_1/K_2 > a_{12}$, where a_{ij} is a measure of the extent to which species j puts pressure on the resources of species i and K_i is the carrying capacity of the environment for species i.

Simulation models are fundamentally different from analytical models because to run the simulation one must specify values for each parameter in the model.

This means that the outcome of the simulation holds for the particular parameter values selected; it is not known to what extent the outcome may or may not hold for other parameter values.

There are two possible approaches to developing general hypotheses from simulations. The first is advocated by Onstad (1988). He suggests that we "create valid models for one or more specific cases and then attempt to generalize . . . ; models are produced as realistically as possible based on knowledge of a few specific cases; the modeler then attempts to generalize and tests the hypothesis in a variety of other situations." Although this may seem a reasonable approach, there are few, if any, examples of this procedure having been fully carried through. Many specific, detailed models have been developed, but these have not led to generalizations leading to general theories. This is because the detail in the model renders one unable to "see the forest for the trees," and any attempt to generalize is viewed as an oversimplification of the model.

The second possible approach, which I discuss for the remainder of this chapter, is to develop a simple simulation model with a small number of parameters, analogous to an analytical model. The model should be as simple as possible, while remaining faithful to a realistic, if general, picture of the system. The level of detail is greater than if the analytical approach were used because the constraint of analytical tractability has been removed. By conducting a large number of simulations in which the parameters take on different values, one can formulate relationships between the parameters (or combinations of parameters) and the output (i.e., population dynamics) of the model. These relationships are analogous to the general hypotheses that one develops from analytical models.

Although this approach is analogous to the analytical approach, it is not completely equivalent because, even though a large number of simulations is conducted, each simulation represents only one possible point in the parameter space. This space is infinitely large if any of the parameters is continuous or if the range of possible values for any of the parameters is unbounded. In this case it is not possible to cover the whole parameter space, no matter how many simulations are conducted. The descriptions of the relationships between the parameters and the model output (i.e., the general hypotheses) are always subject to the qualification that they may not be reliable for some as yet unsimulated point(s) in parameter space. This problem is particularly important in landscape ecology, where there is a large array of possible landscape configurations in which the population may occur.

The success or failure of the simulation approach, therefore, depends on the choices of parameter values for the many simulations conducted. The simulation experiment is then analogous to an actual experiment in the sense that each simulation run will cost time and money, and one would like to gain the maximum possible amount of information for the number of runs conducted. The set of methods used to determine the best choices of values for the independent variables or factors in an experiment (parameter values in simulation runs) is termed "design of experiments." The principles (e.g., Hicks 1982) apply equally well to actual experiments and simulation experiments.

In the two examples that I describe in this chapter, I illustrate two of the most useful methods for conducting such simulation experiments. The first makes use of the standard factorial experimental design in which a few values are chosen for each parameter, spanning most or all of its range, and at least one simulation is run using each of the possible combinations of the chosen parameter values. The second method makes use of the Latin hypercube design in which Monte Carlo simulations are conducted; random values of the parameters are chosen for each of a large number of simulations. In both cases statistical techniques are then used to relate the parameters to the simulation outcomes.

The latter of these methods is similar to Monte Carlo approaches used in sensitivity analysis (Gardner et al. 1981; Downing et al. 1985) The purpose of sensitivity analysis, however, is different from the purpose of the analysis described here. In the former, the question is this: How sensitive is the model outcome to changes in the estimated value of a parameter? The question here is rather this: What is the qualitative relationship between the model outcome and the parameters over all of the possible parameter space? The general hypotheses are formed from these relationships.

This difference in purpose results in some differences in designs of the simulation experiments and in analyses of the simulation results. In the case of sensitivity analysis, it is usually assumed that there is either a single "correct" parameter value with some error in its estimation or that the parameter may take on a range of values described by a probability distribution with a central tendency (usually a normal distribution; e.g., Gardner et al. 1980; Warwick et al. 1986).

The current analysis differs from this approach because there is no a priori reason to choose any particular parameter value over any other. Each combination of parameter values is viewed as being representative of a particular combination of conditions. This is not to say that some situations are not more common in nature than others, but the goal is to understand the response of the model to all the parameters over all possible values in combination with all possible values of other parameters. This means that simulations must be conducted over the entire possible parameter space. For example, in the case of the Latin hypercube design, parameters are chosen from a uniform distribution that extends over the whole range for that parameter instead of from a normal distribution (as in the sensitivity analysis).

17.4 Two Examples

Since model development always has an intuitive component, it is not possible to present a perfectly standardized methodology. The choices that are made about the structure of the model ultimately depend on the question(s) that the model will be used to explore.

In the development of any simulation model there are four things that need to be resolved at the outset: (1) What are the model components? (i.e., what is in the boxes?); (2) What is the currency in the model (i.e., what is transferred into and out of and between boxes?); (3) What is the spatial scale? (i.e., what is the total spatial area represented in the model; if it is subdivided, what sizes are the pieces?); (4) What is the temporal scale? (i.e., what does one time step in the model represent in actual time?) In a population-level model, the components of the model are populations that may be subdivided by spatial location into local populations or further by age class into local age-classified populations. The currency, then, in a population-level model is the number of individuals moving into or out of or between the local age-classified populations. The appropriate spatial and temporal scales normally depend on the particulars of the species and spatial location that one has in mind.

From this description it is clear that the natural tendency is to develop models that are most appropriate for one or a small number of species, since different species will naturally have different appropriate population subdivisions by space and age class. It is also tempting to make the model specific for a particular spatial location since the same species may react differently to different landscapes. However, this level of specificity is counterproductive when one is attempting to use the model for development of general hypotheses. The challenge is therefore to develop a model that is flexible in terms of the number and kind of local populations, the ways in which individuals can move among local populations, and the spatial and temporal scales that the model can represent. A further challenge is to obtain this flexibility while still using parameters that can be obtained from observed data. In the following example I describe two general models, as well as the methods by which they have been used to develop general hypotheses.

17.4.1 Example 1: Population Response to Disturbance

In the first example I develop general landscape-level hypotheses of population dynamics for the case in which spatial heterogeneity occurs because of local disturbances. The model is a discrete-space and discrete-time simulation model. It is not restricted to a particular spatial scale or temporal scale. Instead, space is divided into a grid of spatial *cells,* and time is divided into time *steps.* The numbers of cells and steps are specified at the start of a simulation.

17.4.1.1 Disturbance

Disturbance frequency is a standard value calculated in field studies of ecological disturbance. However, including a parameter for disturbance frequency in a model is less straightforward than one might suppose. Since the basic spatial unit of the model is the cell, one would like to have a parameter that defines the probability that a cell is disturbed. However, one would also like to have the flexibility to vary the spatial extent of disturbances (i.e., number of cells disturbed) and the duration of disturbances (i.e., number of time steps disturbances last). The disturbance probability per cell would depend not only on the frequency of disturbance events, but also on the spatial extent of disturbances, the total area over which the disturbance frequency is calculated, and the duration of disturbances. Therefore, to standardize disturbance frequency, I use a parameter called the "mean disturbance incidence" (d). This is the mean probability (averaged over all cells and all steps) per time step of a cell being in a disturbed state. This is not the same thing as the probability of a disturbance event. For a particular value of d, the probability of a disturbance event will decrease as the sizes of disturbances increase or as their durations increase.

The size or magnitude of disturbances is determined by the parameter m, which is the number of adjacent cells disturbed by each disturbance event. The choice of which of the cell(s) adjacent to the initially disturbed cell is disturbed is random. The duration of disturbance events, in number of time steps, is specified by the parameter t. If t is 1, the disturbance lasts only one time step; if it is 2, the disturbance lasts 2 time steps, and so on. The parameters m and t are illustrated in Fig. 17.1.

At the beginning of a simulation d, m, and t are specified. The probability of a disturbance event (p) is calculated in each time unit as

$$\frac{d - df}{m(1 - df)}$$

where df is the fraction of cells remaining disturbed from the previous time period (due to disturbance duration; df is 0 if t is 1). In this way, the magnitude or the duration of disturbances can be changed without affecting the mean disturbance incidence (d).

Once the probability of a disturbance event (p) is determined, the decision of whether a particular undisturbed cell becomes disturbed is made by using a uniform random number generator that returns a value between 0 and 1. The cell is disturbed if the random number is less than or equal to the current value of p.

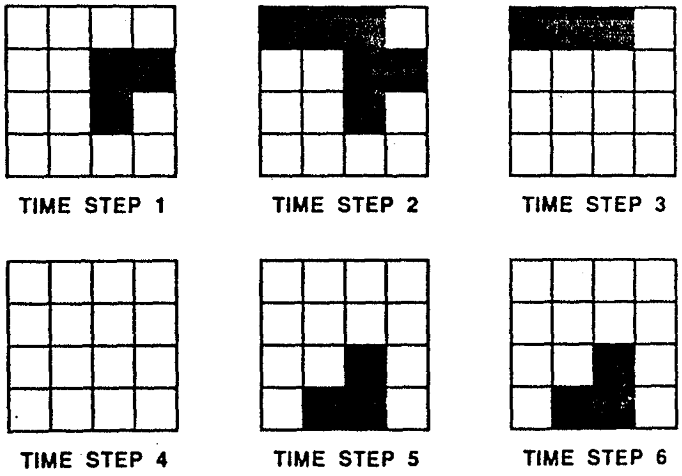

Figure 17.1. Illustration of model parameters disturbance magnitude (m) and disturbance duration (t). A small grid is shown for 6 time steps for m = 3 cells and t = 2 steps.

From these parameters for the disturbance regime, one can calculate the mean time between disturbance events at a cell and the mean distance from a disturbance to the disturbance nearest it. The mean time between disturbance events at a cell (wt) is

$$\frac{(m)\,(t)}{d}\ \text{steps}$$

The mean distance from a disturbance to the disturbance nearest it (i.e., distance between closest edges assuming approximately circular disturbance patches, nn) is

$$-2x + \sum_{z=0}^{\infty} [(z + 2x)\,(1 - (d/m))^{\pi(z+x)^2}(1 - (1 - (d/\mathrm{m})^{\pi(z+3x)^2-\pi(z+x)^2}))]$$

cells, where x is the mean radius of disturbed areas and z is a distance from the center of the disturbance.

17.4.1.2 Within-Cell Population Demographics

The population in each grid cell is age classified; the number of age classes is specified at the beginning of a simulation. Inputs also include age-specific survival rates and birth rates. The number of time steps between reproductive events is also an input parameter; this gives the model the flexibility to include reproductive timing strategies such as dormancy. Although there is no density-dependent adjustment of population growth within cells, there is a ceiling to the cell population size that I call the carrying capacity. The carrying capacity is expressed in units of the smallest age class to allow for age classes having different resource requirements.

17.4.1.3 Dispersal from Cells

Dispersal is set up for species for which the shape of the curve away from the point of dispersal follows a negative exponential function; this assumption appears to be appropriate for many organisms, including plants (Farah et al. 1988) and microorganisms (Lindow et al. 1988). In many cases, dispersal is modeled as a diffusion process (Fleischer et al. 1988; Kareiva and Shigasada 1983; Lande 1987). This approach assumes that the distribution of dispersers follows a Gaussian distribution centered at the starting point of the dispersal. For the current study, in which qualitative questions are being asked, the negative exponential is sufficiently close to the Gaussian so that the conclusions drawn from the simulation experiments should apply to these cases as well. The number of individuals (e.g., seeds) immigrating to a cell is the sum over all the other cells of

$$((dfo\ N_a)/2\pi)e^{-dfo\ s}$$

where dfo is the "density fall-off rate" in the negative exponential, N_a is the number of emigrants leaving the donor cell a, and s is the distance between the recipient cell and the donor cell (DeAngelis et al. 1985).

The equation represents the relative contributions of the cells by calculating the point dispersal. This means that many of the dispersers are "lost" in the calculation. The number lost is the total number that leaves cells minus the total number that disperses into cells. These individuals are allocated among the cells in proportion to the actual immigration rates into the cells. This adjustment works well except when *dfo* is very small. In this case many dispersers should actually leave the grid completely; so the adjustment produces an overestimate of the population sizes in all cells. The mean dispersal distance is then calculated as 2/*dfo*.

Besides the dispersal distance, the other components of dispersal in the model are the dispersal rate or fraction of organisms dispersing per dispersal event (*dr*), the time between dispersal events (*dt*), and the survival probability of dispersing individuals (*ds*). The structure of the model is shown in Fig. 17.2.

17.4.1.4 Experimental Design

The ultimate goal of the development of this model is to predict which categories of species types (described by their life history and dispersal characteristics) are most likely to occur in various types of disturbance regimes. The most straightforward approach to this problem is to conduct a factorial simulation experiment (Hicks 1982). Several values are chosen for each parameter, spanning the relevant range for that parameter. Simulations are then conducted for every combination of each of the parameter values. Although this model is simple compared with specific models of particular species, the level of complexity of the model (required to make it realistic enough to produce believable and testable results) means that it is not possible to conduct a single set of simulations to study this problem.

In fact, the number of possible parameters in the model is large. There are four disturbance parameters, four life history parameters and four dispersal parameters; each of these twelve parameters may have different values for each of any number of different age classes. It is therefore not practical to conduct a complete set of simulations to analyze for the effects of each parameter over its complete range. In addition, there is likely to be a large number of important interactions among the effects of the parameters; a high value of parameter "a" may have a positive impact on predicted population survival if parameter "b" is at a low level but a negative impact if "b" is at a high level. For example, through the use of a different model, Fahrig (1990) showed that there is a predicted interaction between disturbance rate and dispersal rate on population survival.

Even if the number of age classes in the model were limited to two, there would be twenty-four parameters, each of which should be studied over its relevant range and in combination with all other parameters. The required number of simulations would be on the order of 5^{16} (if five levels are used for each parameter), which is not practical, since each model run takes five to thirty min. Even if this could be done, it would certainly lead to intractable results analogous to the results of field studies in which too many factors are simultaneously measured (Caswell 1988).

To deal with this problem I decided not to try to conduct the entire simulation experiment simultaneously but to begin with a subproblem; only a subset of the parameters was varied. Two stages were then required in the simulation experi-

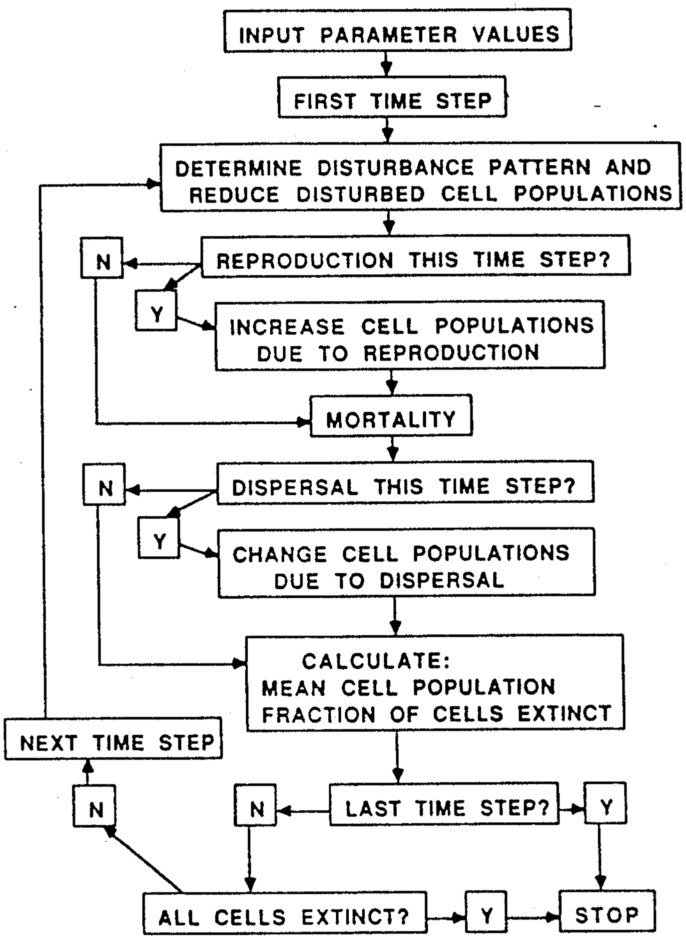

Figure 17.2. Flow diagram of the model of population dynamics in the presence of disturbance.

ment; after the first set of simulations was conducted, it became obvious that the results possibly depended on the particular values chosen for the parameters that were held constant. This realization led to two further simulation experiments.

17.4.1.5 Factorial Simulation Experiment—First Stage

The purpose of the first simulation experiment was to determine the relative effects of the four components of dispersal on population survival in the presence of disturbance. Five hundred simulations were run with the use of a factorial design for the four dispersal parameters (Table 17.1c). Each simulation ran for 150 time steps, and only the last 100 time steps were used in analyses of results. The grid size was 25 by 25 cells in all runs; all of the grid cells were initially assumed to

Table 17.1. Values of Parameters Used in the Simulation Experiment (Example 1)

Parameter	Units	Value(s)	
a. *Disturbance Regime*			
Mean incidence	Rate/cell/step	0.1	
Intensity	Fraction killed	1.0	
Magnitude	Cells	1	
Duration	Steps	1	
b. *Demographics*			
Carrying capacity	Number	500	
Reproductive frequency	Steps	1	
Number of age classes		2	
		Age 1	Age 2
Starting values	Number	10	10
Birth rates	Number per individual	0	1
Survival rates	Fraction	0.8	0.8
c. *Dispersal*			
Rate	Fraction of population	0, 0.25, 0.5, 0.75, 1	
Survival rate	Fraction of population	0, 0.25, 0.5, 0.75, 1	
Time between Dispersal events	Steps	1, 2, 3, 4, 5	
Mean distance	Cells	1, 1.3, 2, 4	

be identical, with spatiotemporal heterogeneity being imposed by the process of disturbance.

I calculated three output values for each simulation: (1) the time at which all populations died (this was 150 for all simulations in which at least one cell was still occupied at the end of the simulation), (2) the mean population size per time step in each cell, and (3) the mean fraction of extinct local (cell) populations per time step before complete extinction (a measure of local extinction probability).

The parameters of the disturbance regime and the within-cell demographics were held constant during all simulations. To set these parameter values in a meaningful range relative to the goal of the simulations, I ran preliminary simulations in which I varied the values of birth rate and disturbance incidence for the cases of no dispersal and maximum dispersal. The goal was to run the simulations under conditions such that the population would not survive without dispersal and would reach near-maximal levels with maximum dispersal. The simulation experiment could then be used to determine which components of dispersal caused the population to shift along this gradient from low to high survival rate.

The FASTCLUS procedure from SAS statistical software (1985) was used to cluster the output data into groups ranging from low success (i.e., low survival rates and population sizes) to high success. Discriminant functions analysis (procedure DISCRIM in SAS [1985]) was then used to ensure that the clusters produced a unique categorization of the data. Finally, I conducted two-way contingency tests with the procedure FREQ from SAS (1985) for the levels of each dispersal component with the clusters. I repeated this procedure with from two to eleven clusters. This allowed me to discover which dispersal components were important for determining population level for those runs in which the population survived.

The cluster analysis led to the delineation of three general categories of simulation outputs: populations were either unsuccessful, moderately successful, or highly successful. The unsuccessful populations had low survival probability. The moderately and highly successful populations had high survival probability, but the latter group had greater population abundances than the former group.

The results of the analysis are summarized in Fig. 17.3A–D. In simulations with no dispersal (i.e., dispersal rate = 0 or disperser survival rate = 0), the populations crashed due to the accumulated effects of disturbed cells that were not recolonized. Even for low dispersal rates, the population sizes jumped to much higher levels, and the mean fractions of extinct cells dropped markedly. For populations that did survive, those with relatively small population sizes had low dispersal rates, low disperser survival rates, and high values of the time between dispersal events. Groups with large population sizes had the reverse.

Dispersal distance is the only dispersal component that had no effect on population size or survival; a possible explanation for this outcome is given in the "Interpretaton of Results" section. Dispersal distance is also the only component that requires the explicit inclusion of space in the model; without it the model would not be a landscape-level model. The question of whether the landscape has an important effect on the population dynamics is the same as asking the question, Under what conditions is the explicit consideration of space a necessary component of the model for understanding population dynamics, and under what conditions is it not? In the context of the current modeling exercise, this is the same thing as asking the question, Under what conditions does the dispersal distance have an important impact on population recovery from disturbance?

17.4.1.6 Factorial Simulation Experiment—Second Stage

The first set of simulations indicated that the spatial component of dispersal, dispersal distance, was not important for population recovery from disturbance. However, it seemed likely that this result might depend on the spatial characteristics of the disturbance regime: disturbance magnitude and disturbance incidence, which controls the distance between disturbed sites.

To study the effect of disturbance magnitude on the relationship between dispersal distance and population size, I ran a factorial simulation experiment with seven values of dispersal distance, ranging from 1.0 to 4.0 cells, and five values of disturbance magnitude ranging from 1 to 9 cells. Analysis of variance (procedure GLM in SAS [1985]) showed that there was a significant positive relationship between dispersal distance and population size for disturbance magnitudes of three cells and above.

To study the effect of disturbance incidence on the relationship between dis-

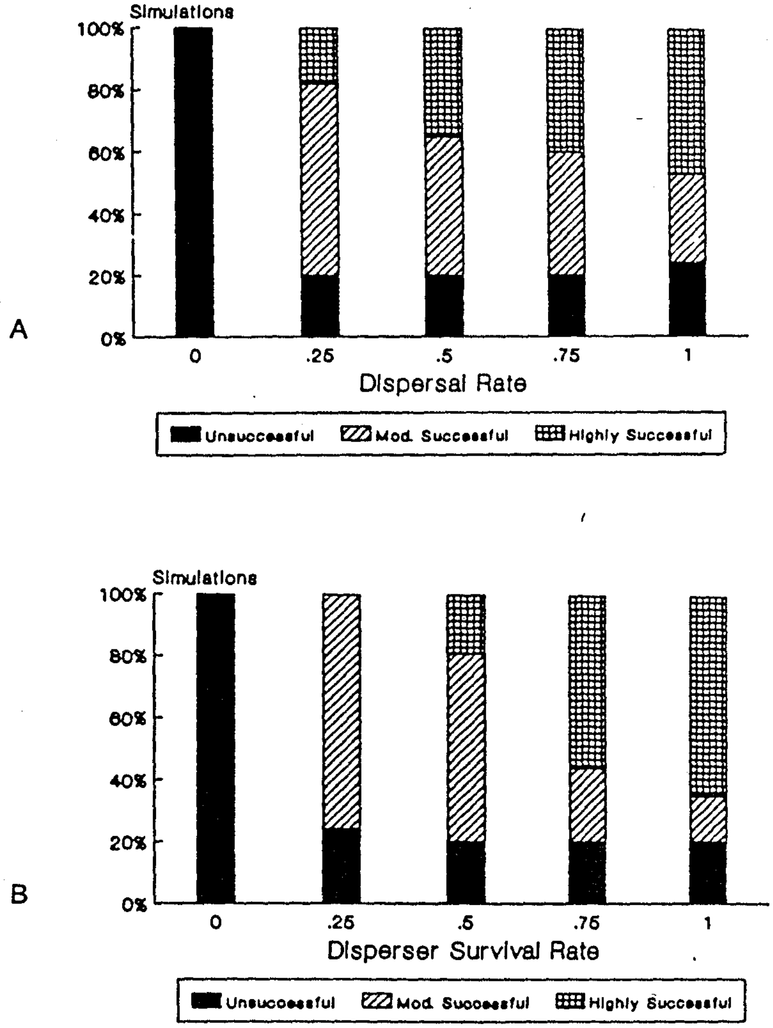

Figure 17.3. Proportions of simulated populations falling into each of three categories: unsuccessful, moderately successful, and highly successful, at various levels of four parameters. (A) Dispersal rate. (B) Disperser survival rate. (C) Time between dispersal events. (D) Dispersal distance.

persal distance and population size, I ran a factorial simulation experiment with sixteen values of dispersal distance, ranging from 1.0 to 4.0 cells, and nineteen values of disturbance incidence fro 0.05 to 0.95. Analysis of variance (procedure GLM in SAS [1985]) showed that there was a significant positive relationship between dispersal distance and population size, but only for high values of disturbance incidence.

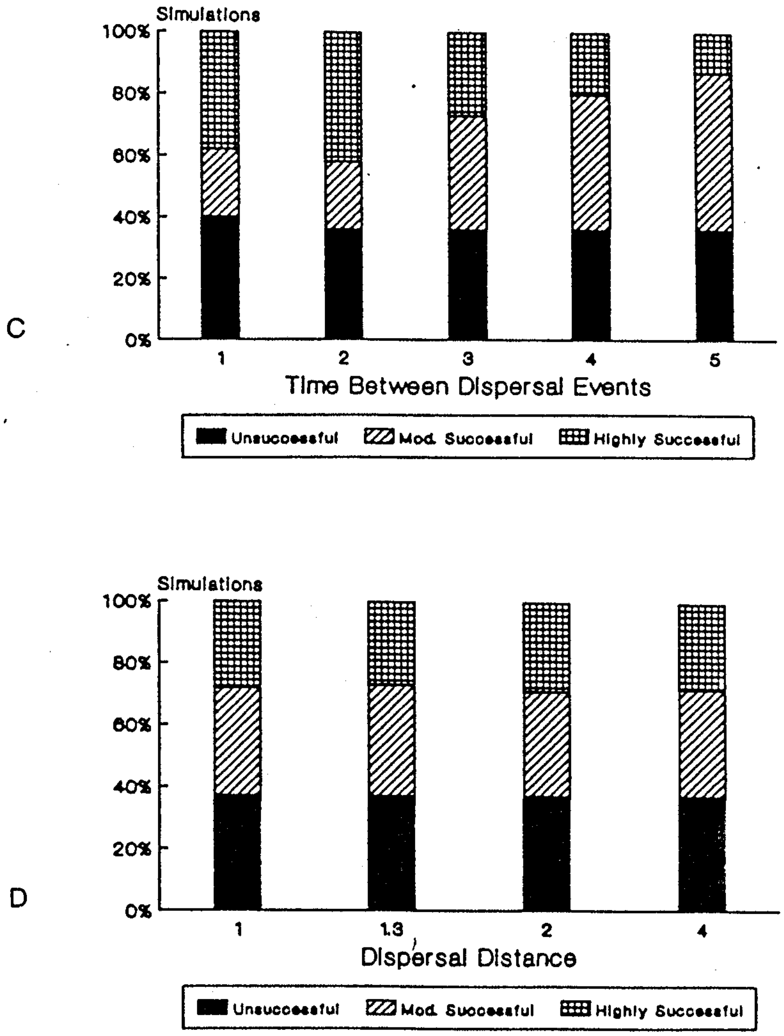

Figure 17.3. *Continued.*

17.4.1.7 General Hypotheses

The results of these simulation experiments can be phrased in terms of a series of landscape-level hypotheses about single-species dynamics in the presence of disturbance: (1) to ensure survival in the presence of disturbance, it is most important for a species to have a high dispersal rate and high disperser survival rate; (2) given that a population has a high survival probability, the highest regional population sizes are obtained by species that have the highest dispersal rates and disperser survival rates and the shortest time intervals between dispersal events; (3) dispersal distance is relatively unimportant for population recovery from disturbance; (4) dispersal distance becomes more important with increasing disturbance incidence and disturbance magnitude; and (5) populations that are frequently disturbed and occur in widespread habitats are unstable at low to moderate levels, so they must maintain high levels to avoid extinction.

In the present context this study serves as an illustration of a simulation experiment that uses the factorial experimental design for development of general landscape-level hypotheses about population dynamics. The following is a brief discussion of the ecological significance of the results.

17.4.1.8 Interpretation of Results

The most obvious pattern in the output is the distinction between successful and unsuccessful populations. In simulations with no dispersal (i.e., *dr* or *ds* = 0), the population crashed due to the accumulated effects of disturbed cells that were not recolonized. Even for low dispersal rates (*dr* or *ds* = 0.25), the population sizes jumped to much higher levels and the mean fractions of extinct cells dropped markedly. This result is similar to that of many others (e.g., May 1974; Reddingius and den Boer 1970; Roff 1974; Vance 1980, 1984; Kuno 1981; Agur and Deneubourg 1985) who have shown that dispersal is important for maintaining regional populations in the face of environmental variability (e.g., disturbance).

However, the result that none of the simulated populations survived with both low sizes and low extinction fractions has not been suggested before. It implies that, for populations that are frequently disturbed but occur in widespread habitats, the population must be able to maintain high levels, or it will go extinct. Note that this result (and the simulations) does not pertain to species that occur in a habitat that is not widespread, such as most fugitive species and species that occur in rare but stable habitats. Patterns observed in field studies of relationships among local population variability, species abundances, and species ranges support this idea (Gaston 1988; Glazier 1986; Grulke and Bliss 1988).

Within the successful category of populations, those in the moderately successful group had low dispersal rates (*dr*), low disperser survival rates (*ds*), and high values for the time between dispersal events (*dt*). The highly successful category had the reverse: high *dr* and *ds* and low *dt*. These results can be explained as follows. If the dispersal rate is high, the population is more evenly spread over all cells. This spreads out the effects of disturbance, leaving room in all cells (relative to their carrying capacities) so that the population can increase over the whole grid. Disperser survival rate has a slightly larger impact than dispersal rate because it incorporates two effects: (1) it enhances overall population size of the regional population and (2) it enhances the effect of high *dr*. The importance of disperser survival was also shown by Levin et al. (1984). The importance of time between dispersal events (*dt*) for distinguishing between moderate and high success has not been shown before. The explanation is straightforward: the more often organisms disperse, the faster they can recolonize empty cells.

The lack of importance of dispersal distance in the outcome of the simulations was somewhat surprising. Previous studies have shown that dispersal distance is important for fugitive species that make use of widely scattered patches of habitat (Platt 1975; Green 1983; Turin and den Boer 1988). Fahrig and Paloheimo (1988) showed that dispersal distance is important for determining the effect of spatial distribution of patches on local population dynamics. The second stage in the simulations was conducted to examine the dispersal distance result in the context of varying disturbance magnitude and incidence. There was a significant positive relationship between population size and dispersal distance for high values of both disturbance magnitude and incidence.

In both cases the results indicated a threshold in the relationship. The result for disturbance magnitude is qualitatively similar to that of simulations by Coffin and Lauenroth (in press) for a prairie grass species. The result for disturbance incidence has not been suggested before. It may be explained as follows. In the first set of simulations, the disturbance incidence (0.1) produced a grid that was composed of disturbed patches surrounded by a matrix of undisturbed habitat. In this situation, even if dispersers move only one grid cell on average, disturbed cells are easily recolonized by the neighboring cells. If the disturbance incidence is much higher, the grid consists of patches of occupied habitat surrounded by a matrix of unoccupied (disturbed) habitat. In this situation, dispersal distance would be important because if the population in a particular patch were to go extinct, it would need to be replenished from another (possibly distant) patch.

The transition point between these two cases may be related to the critical point (p_c) described in percolation theory (Stauffer 1985) and applied to the spread of disturbances across landscapes (Gardner et al. 1987). In this analysis p_c is the disturbance probability at which the disturbed cells on a grid are connected through at least one path from one side of the grid to the other. For random square grids such as the one in the present simulations, this number has been identified as 0.5928. For disturbance rates lower than this, the grid has patches of disturbance surrounded by a matrix of undisturbed habitat. Below this point dispersal distance should have little, if any, effect. This idea is supported by the result here that the population size increased with increasing *dd* only for simulations with $d = 0.55$ or greater.

17.4.2 Example 2: Population Dynamics in a Patchy Landscape

The second example is a study in which general hypotheses of population dynamics were sought for the case where habitat heterogeneity in the landscape is due to the patchy distribution of breeding sites. Details of the model are given in Fahrig (1988b) and Fahrig and Paloheimo (1988). The following is a summary.

The model is a stochastic discrete-time simulation model. Both time and space are in arbitrary units (time steps and spatial units). All parameters are expressed relative to these arbitrary units. The region is assumed to consist of discrete patches of breeding habitat surrounded by nonbreeding habitat. The explicit spatial arrangement of breeding habitat is included; distances between all pairs of patches are required to calculate dispersal rates among the patches.

There are six parameters in the model, which determine the population sizes in each breeding patch at each time step. These are (1) intrinsic population growth rate, (2) patch-carrying capacity, (3) fraction of organisms that disperse from patches in each time unit, (4) dispersal distance relative to the mean distance between patches, (5) distances from which dispersers detect new patches (detection radius) relative to the mean distance between patches, and (6) rate of immigration into the region. A seventh factor, patch detection probability, was calculated for each simulation; this value depends on the detection radius and the dispersal distance (Fahrig and Paloheimo 1988).

Dispersal from each patch is assumed to be, on average, equally likely in all directions, except when one patch is within detection range of another. Dispersal is directly proportional to population size in the patches (i.e., dispersal rate is not assumed to be density dependent). Dispersers from patches are assumed to travel to some mean distance, expressed as a fraction of the average distance among patches. It is not assumed that all dispersers move exactly the mean dispersal distance, but rather that they are spread out over space around the mean.

The distance from which dispersers can detect a new patch (e.g., visually or by chemoreception) is called the detection radius. Although this is a characteristic of the species, for computational ease I refer to the detection zone of patches. This is a circular area around the patch from within which dispersers are able to detect the patch. Patches are assumed to "attract" all those dispersers that, by chance, fall within the detection zone of the patch.

The structure of the model is shown in Fig. 17.4.

17.4.2.1 Experimental Design

The goal of the simulation experiment was to determine the relative importance of the six parameters for the mean population size and the degree to which spatial pattern of patches affects local population size. Simulation runs of ten patches for 150 time steps require about five minutes on the computer. To conduct a factorial experiment with the six parameters at a minimal number of levels (say five) would require about 1300 h of simulations. Since in this case I did not wish to break the problem down into smaller units, I decided to abandon the factorial design in favor of a Latin hypercube design (Iman and Conover 1980). This design allows one to include more factors than the factorial design, for the same number of simulations.

17.4.2.2 Simulation Experiment

Two thousand runs of the model were conducted. In each run there were ten patches and 150 time steps. A different spatial arrangement of ten patches was used for each run. The x and y coordinates of each patch were chosen by a uniform random number generator, and the distances between all pairs of patches were then calculated. The initial population size in all patches and for all runs was 100 organisms. The mean values of the six parameters were chosen at random from a uniform distribution at the beginning of each run. The ranges of these parameters are given in Table 17.2. Stochastic variation in the parameters was included, so that their actual values fluctuated randomly among the 10 patches and between the time periods. The population size in each of the patches was calculated for the 150

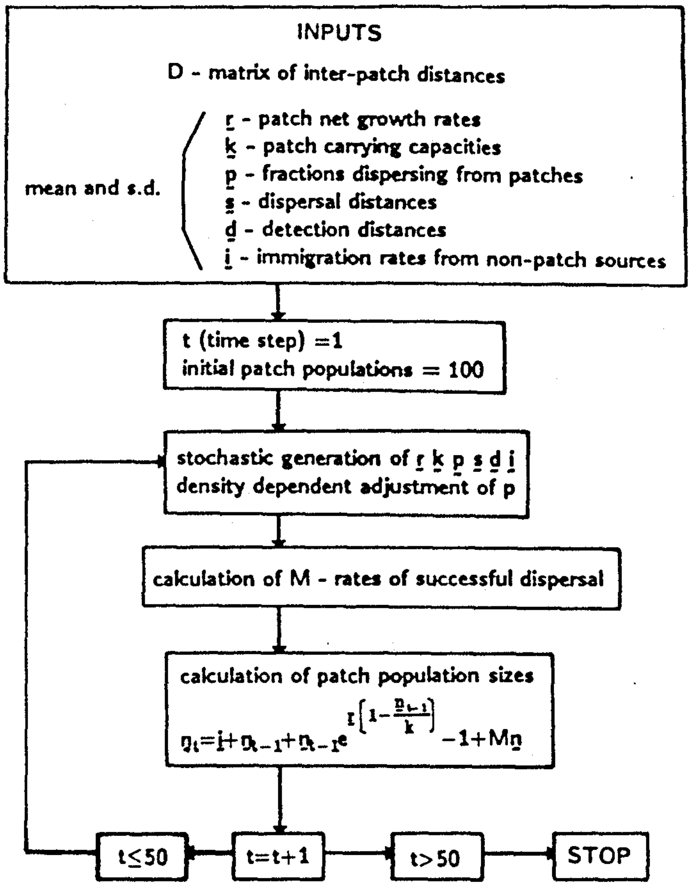

Figure 17.4. Flow diagram of the model of population dynamics in a patchy landscape (Fahrig 1988b).

Table 17.2. Upper Limits of Parameter Values Used in the Simulation Experiments (Example 2)

Parameter	Upper Limit of Mean Value
Growth rate	0.1
Carrying capacity	10000
Dispersal rate	1.0
Dispersal distance/mean interpatch distance	2.0
Dispersal radius/mean interpatch distance	0.3
Immigration rate	1000

Lower limit in all cases is 0, standard deviation/mean is 0.1 (Fahrig and Paloheimo 1988).

time steps. Only the results from the final 100 time steps were included in the analyses.

The following outlines the rationale and procedure used for obtaining a measure of the effect of patch spatial arrangement on local population abundance. If the spatial location of patches has a large impact on local population sizes, one would expect to find large differences among patches due to their spatial relationships with the remaining patches. For example, one might expect the population sizes in centrally located patches to be higher than in peripheral patches if patch spatial arrangement is important. Therefore, the type of variable that is appropriate for measuring the effect of spatial arrangement is one that measures the degree to which populations differ among patches. However, the variability between patches is likely to be significantly correlated with the variability within patches over time. Therefore, a variable that accurately reflects effects of spatial arrangement should measure the variability between patches, corrected for the variability within patches over time. For each run, the mean and coefficient of variation (CV) over the 100 time units for each patch were calculated; then the mean of these CVs was taken as a measure of within-patch variability over time for that run (*tempvar*). The CV among the ten mean patch population sizes was also calculated for each run (*patvar;* i.e., variability between patches). A significant quadratic relationship was found between ln(*tempvar*) and ln(*patvar*). The residuals from the regression are a measure of the variability between patches, corrected for the variability within patches. They are therefore a measure of the importance of patch spatial arrangement on local population size or the pure spatial variability.

The purpose of analyzing the simulation results was to determine which types of organisms (i.e., species characterized by which combinations of independent variables) are predicted to have small or large patch population sizes and a small or large effect of patch spatial arrangement on population abundance. A standard statistical approach to problems in which relationships between several independent variables and one dependent variable are sought is to use the least-squares method to build the best polynomial model relating the independent variables to the dependent variable (Box and Draper 1987). This approach is often used in uncertainty analysis, in which one attempts to measure the sensitivity of model predictions to changes in model parameters. If the relationships between the parameters and the model output are approximately linear, first-order terms will dominate the regression analysis, and the relative importance of parameters can be ranked by using correlation coefficients (Gardner et al. 1981; Gardner 1984).

In the present analysis, however, the results of such polynomial regression analyses were not interpretable; relationships between the parameters and the model output were nonlinear and complex. The resulting polynomial regression models consisted of large numbers of statistically significant terms (fifteen to twenty), most of them higher order interactions involving two or three parameters and each of them explaining only a small portion of the total variation. Therefore, although the analyses resulted in adequate empirical models, in this case they did not aid in understanding of the qualitative relationships between the independent and dependent variables. In particular, they did not result in an estimate of the relative importance of each parameter in explaining variation in the model output.

The following method was used for analyzing the simulation results. First, polynomial regression equations were calculated for each of the dependent variables (i.e., population size and spatial variability) on each of the independent variables (i.e., the six parameters plus detection probability). This provided estimates of the forms of the underlying relationships. To determine the relative importance of the independent variables, the polynomial regression equations were then used as polynomial variables in stepwise regressions of the dependent variables.

The polynomial variables for mean patch detection probability and mean dispersal rate were the most important factors determining average local population size, with partial R^2 values of 0.3890 and 0.2923, respectively. The polynomial regression equations for the parameters are plotted in Figs. 17.5A and B. The polynomial variable for mean dispersal distance was the most important factor determining the spatial variation among local populations, with a partial R^2 value of 0.1404. The equation for this variable is shown in Fig. 17.5C.

17.4.2.3 General Hypotheses

This simulation experiment led to the following hypotheses about single-species dynamics in a patchy landscape: (1) the most important determinants of mean local population size are the probability of dispersers detecting new patches (positive relationship) and the fraction of organisms dispersing from the patches (negative relationship); and (2) the main factor that determines whether a local population will be influenced by exact spatial relationships among patches is its dispersal distance (negative relationship).

In the present context this study serves as an illustration of a simulation that uses the Latin hypercube experimental design for development of general landscape-level hypotheses about population dynamics. A detailed discussion of the results and their significance is in Fahrig and Paloheimo (1988). The following is a brief summary of the points made there.

17.4.2.4 Interpretation of Results

The most important factor determining patch population size was the probability that dispersers successfully detect new patches. This result is analogous to that of Levin et al. (1984), who found that the optimal level of dispersal increases with an increase in the probability of a dispersing propagule successfully attaining a new site. The relative unimportance of dispersal distance and detection radius results from the fact that the effects of these two parameters are largely encompassed by the effect of detection probability. The importance of the dispersal rate (fraction of local population dispersing) reflects the high risk associated with dispersal; high dispersal rates generally result in lower mean patch population sizes, unless the probability of dispersers detecting new patches is very high. A

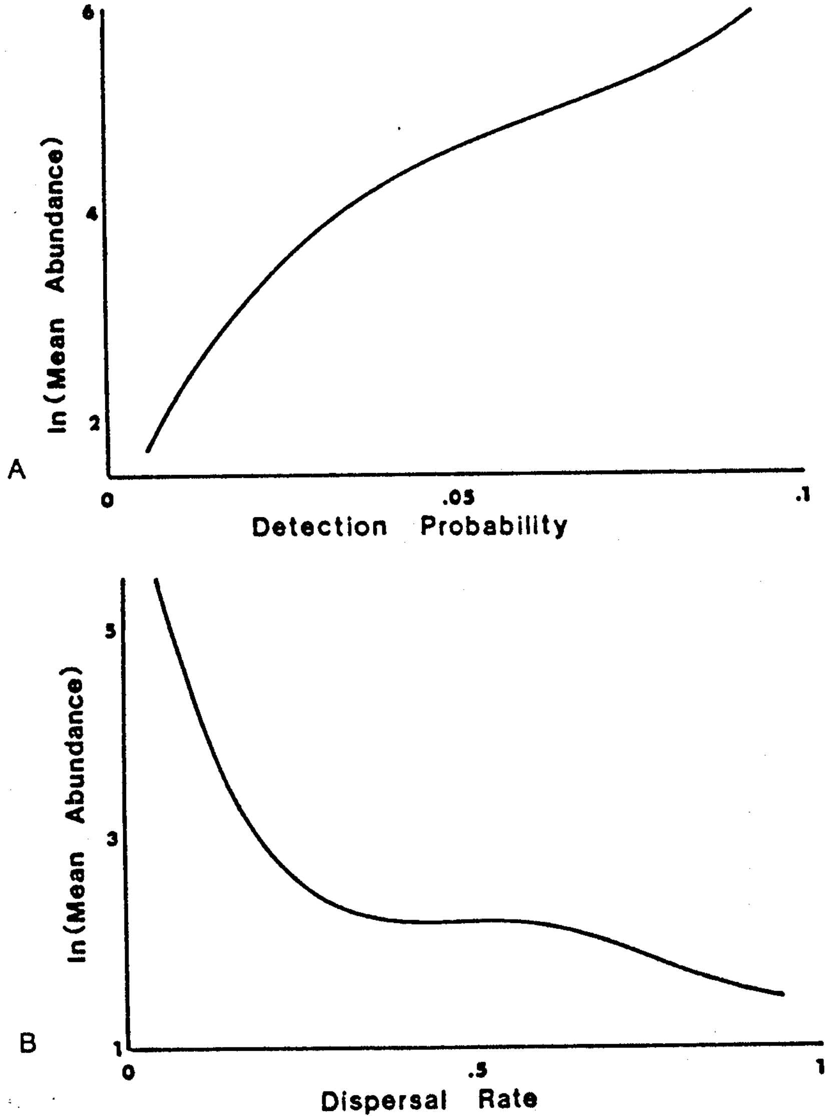

Figure 17.5. (A) Relationship between patch detection probability and log-transformed values of average patch population abundance (averaged over 10 patches). (B) Relationship between dispersal rate of organisms from patches and log-transformed values of average patch population abundance (averaged over 10 patches). (C) Relationship between dispersal distance and spatial variation among 10 patch population means due to patch spatial arrangement (Fahrig and Paloheimo 1988).

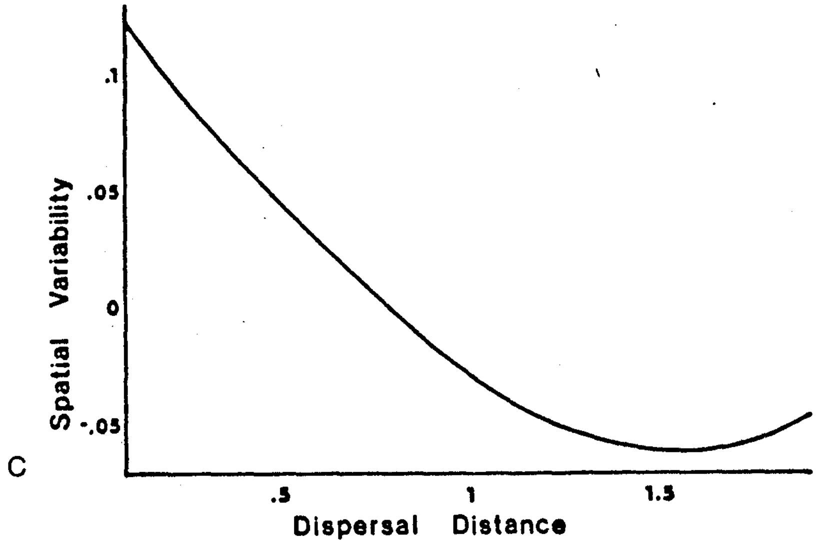

Figure 17.5. *Continued.*

negative relationship between dispersal rate and population size has also been found in studies by Lomnicki (1980) and Roff (1974).

Intrinsic growth rate and carrying capacity were predicted to have little effect on average population sizes in a patchy environment; their effects were almost completely swamped by the dynamics of interpatch dispersal. This result suggests that between-patch processes (i.e., dispersal) will often be more important than within-patch processes (i.e., births and deaths) in determining local population size within a habitat patch.

The results also indicate that the dynamics of dispersal among patches are most important in determining the level of the effect of patch spatial pattern on local population size. The most important factor in this case is the dispersal distance. The greater the dispersal distance, the less important is the spatial arrangement of patches in causing differences among local population sizes. This is because the same number of dispersing organisms is spread over a much larger area when the dispersal distance is large. The result is that dispersal from a particular patch has a more general influence (i.e., affects more patches) for large dispersal distances than for small ones. If the dispersal distance is small, then those patches that have neighbors at close distances receive many more dispersers than those that do not. In this case the spatial relationship among patches is an important determinant of the local population size, and the spatial variation among patch sizes is high.

It is generally believed that migratory bird species disperse shorter distances from their natal site to their reproductive site than do nonmigratory birds (Whitcomb et al. 1981), mainly because the migratory phase uses up time that might otherwise be spent moving between breeding sites. If this is true, the simulation results suggest that the spatial arrangement of bird breeding sites should be a more important determinant of local abundance of migratory species than of nonmigratory species. This pattern was found in a study of birds in woodlots in Maryland (Lynch and Whigham 1984). Also, for species that disperse long distances in the wind, such as small insects (e.g., aphids; Kennedy and Stroyan 1959), small plant seeds, or spores, the result indicates that the spatial pattern of potential breeding sites is unlikely to have much effect on local population abundance.

The reasons for the lack of importance of the rate of immigration from outside the study region are not obvious. One would expect that for high rates of immigration, the effects of interpatch dispersal would be swamped, and in this case the patch spatial arrangement would have less effect on local population size. However, the effect of dispersal distance far outweighed the effect of immigration rate. It is possible that for much higher immigration rates the swamping effect of immigration would be more pronounced. In this study, the upper limit to immigration rate was 1000 individuals per time unit. Relative to the ranges of the other parameters in the model (Table 1; Fahrig and Paloheimo 1988), this represents a large immigration rate. The results indicate therefore, that immigration from outside the study area is not expected to significantly swamp the effects of interpatch dispersal, except possibly at extremely high immigration rates.

17.5 The Possibility of Chaos

Chaotic dynamics are likely to throw a wrench into many types of simulation experiments, particularly those aimed at the development of general hypotheses. Kot et al. (1988) give a summary of the history and current status of the study of chaos. Chaotic behavior has been shown in some of the simplest analytically tractable nonlinear models. Also, several researchers have apparently found chaotic dynamics in real population dynamics (see Table 1 in Kot et al. 1988). Although it is not as commonly noted, chaotic behaviors are now being noticed in some simulation models of particular systems; for example, Rejmanek et al. (1987) found chaotic behavior in a simulation model of forest tent caterpillar.

The problems presented by chaotic behavior can be dealt with by limiting simulations to the parameter space in which the dynamics are not chaotic (Ulanowicz 1988). However, this solution is problematic for the purpose of developing general hypotheses, because one does not know before starting the simulations where the nonchaotic region of parameter space is.

This problem is illustrated in "Example 2: Population Dynamics in a Patchy Landscape" presented above. When the analysis was completed, 78% of the variability in population size and only 23% of the variability in spatial variability were explained by variability in the seven parameters (Fahrig and Paloheimo 1988). Some of this lack of explanatory power may be due to the stochastic nature of the simulations and because the method of postsimulation statistical analysis was not sensitive enough to adequately describe the relationships. However, it is also quite possible that some of the unexplained variability was due to chaotic behavior of the population dynamics for certain values of the parameters. If this is true, the simulation output would appear to be unrelated or only slightly related to the input parameter values, and simulations in these parts of the parameter space would add to the unexplained variability.

To find the areas of parameter space in which chaotic behavior occurs, one would need to conduct an analysis for chaotic behavior of the dynamics of each of a large number of runs then attempt to delineate the chaotic region(s) of parameter space. Parameter values in these regions would represent species types for which the general hypotheses would not be expected to hold. Given the large number of simulations required, conducting such an analysis for anything other than an extremely simple model (e.g, two parameters) would be impractical.

17.6 Summary

I argue that the constraints imposed by simple, analytically tractable models make them unlikely to be of use for the development of general hypotheses of population dynamics in the landscape context. At the other extreme, development of complex simulation models for specific systems is equally unlikely to render general hypotheses. Different situations appear to be less and less comparable as the level of detail in the simulation models increases. The problems associated with extrapolation from detailed models to general hypotheses are analogous to the problems encountered in attempts to extrapolate from detailed field studies to general hypotheses; extrapolation is viewed as oversimplification.

Between these two extremes is the approach I advocate here: (1) state the question; (2) develop the simplest possible simulation model to study the question; (3) design and conduct a simulation experiment(s), using principles of experimental design, to study the effects of each parameter over its relevant range; (4) analyze the output of the simulation experiment as one would analyze the results of an ordinary experiment; and (5) phrase the uncovered relationships between the input parameters and the output in terms of hypotheses of population dynamics.

I illustrate this approach with two examples. The first is a general model of population response to disturbance. By using a factorial experimental design, I ran simulation experiments to develop the following hypotheses about single-species dynamics in the presence of disturbance: (1) to ensure survival in the presence of disturbance, it is most important for a species to have a high dispersal rate and high disperser survival rate; (2) given that a population has a high survival probability, the highest regional population sizes are obtained by species that have the highest dispersal rates and disperser survival rates and the shortest time intervals between dispersal events; (3) dispersal distance is relatively unimportant for population recovery from disturbance; (4) dispersal distance becomes more important with increasing disturbance incidence and disturbance magnitude; and (5) populations that are frequently disturbed and occur in widespread habitats are unstable at low to moderate levels—they must maintain high levels to avoid extinction.

The second example is a general model of population dynamics in a patchy landscape (Fahrig 1988b; Fahrig and Paloheimo 1988). By using a Latin hypercube design, I ran simulation experiments that led to the following hypotheses: (1)

the most important determinants of mean local population size are the probability of dispersers detecting new patches (positive relationship) and the fraction of organisms dispersing from the patches (negative relationship) and (2) the main factor that determines whether a local population will be influenced by exact spatial relationships among patches is the organism's dispersal distance (negative relationship).

Although the method has many advantages, it also has limitations. First, there is always a trade-off between the number of parameters included in the simulation experiment and the accuracy of the results. This is a standard trade-off in real experiments as well, and it is one reason that the first step in the above process (statement of the question) is important. Secondly, one must be aware that this type of simulation is not immune to the possibility of chaotic behavior that has been described for analytical models and is being observed with increasing frequency in nature.

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