A General Model of Populations in Patchy Habitats

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ABSTRACT

A general model is proposed for study of the effects of the spatial arrangement of habitat patches on population dynamics of resident populations. Previously proposed models are shown to be inadequate or undesirable for the detection of such effects. The proposed model is a stochastic discrete-time simulation model, in which within-patch processes are modeled using a discrete approximation to the logistic equation. The explicit spatial arrangement of patches is included, and the exchange of organisms via interpatch dispersal depends on three sets of parameters: (i) the fraction of organisms which disperse from each patch, (ii) the distance which organisms disperse, and (iii) the distance from which dispersers can detect new patches. A set of simulation experiments was performed, to study the effects of the detection distance [parameter (iii) above] on the effect of the spatial arrangement of habitat patches on population dynamics. It was found that for low and high detection distances patch spatial arrangement is relatively unimportant. However, for intermediate detection distances the spatial arrangement has an important impact on population dynamics.

INTRODUCTION

One of the goals of the landscape ecologist is to find general relationships between types of landscapes and the population dynamics of organisms which inhabit them. However, much of the work to date has focused on the development of large models which provide detailed simulations of specific systems (e.g., [5, 22]). Such models can be valuable, but their results are generally applicable to only a narrow range of situations. To uncover more general relationships, a more general type of modeling approach is necessary.

From the point of view of a single species, a landscape can be thought of as a series of patches of breeding habitat, or "habitat patches," which are spatially distributed in a "matrix" of habitat which the species cannot use as

breeding area. This patchy distribution of breeding habitat generally results in a regionally patchy distribution of the species. At the level of the species, therefore, the above goal can be framed in the following way: can we find general relationships between the spatial arrangement of habitat patches and population dynamics of resident populations?

It is, of course, important to note that the habitat of any species may be patchy on several spatial scales. The researcher's choice of scale will be at least partly subjective. The answer to the above question for a particular species will therefore depend on the scale on which the habitat is defined.

The question can be divided into two subquestions. First, can we find types of species for which the spatial arrangement of habitat patches does not have a significant effect on population dynamics? This question is important for both theoretical ecologists and field ecologists. Generally, the theoretician would like to avoid consideration of spatial heterogeneity whenever reasonable, since it can increase the complexity of a model by several orders of magnitude. The field biologist, on the other hand, needs to decide whether the scale of his observations is appropriate for the question he is asking. A knowledge of potential relationships between habitat spatial arrangement and population dynamics at various spatial scales will help him decide on the appropriate scale.

The second subquestion is: given that the spatial arrangement of habitat patches has an effect on population dynamics for a certain species, can we identify general relationships between "types" of spatial arrangements and population dynamics?

The purpose of this paper is to present a method for modeling patchy populations, and to begin answering the first of the two subquestions mentioned above.

MODEL REQUIREMENTS

Developing a model which can be used to find general relationships between habitat patch spatial arrangement and population dynamics is not a simple task. This is primarily because every spatial arrangement of patches in nature is unique; the number of patches, the sizes of patches, and their relative positions in space will all vary among situations. Also, each species differs from all others with respect to those characteristics of interpatch dispersal which are important determinants of the relationships between patch spatial arrangement and population dynamics. These dispersal characteristics include (i) the fraction of organisms which disperse from each patch, (ii) the average dispersal distance of dispersers, and (iii) the distance from which dispersing individuals can detect new patches.

A model which is to be used to derive general relationships between habitat patch spatial arrangement and population dynamics must therefore be general and flexible enough to encompass most of the possible combinations of patch spatial arrangement and dispersal characteristics of resident populations. Because there will be several important parameters in such a model, the generalities derived from it will have to be derived from a very large number of simulation experiments. Therefore, it is desirable to work with a model which is as simple as possible, while incorporating enough complexity to derive the required relationships.

The main requirements of the model are therefore that it should (i) include the explicit spatial arrangement of habitat patches, (ii) be general and flexible enough to incorporate the majority of spatial arrangements and species, and (iii) be as simple as possible, within the constraints imposed by (i) and (ii).

MODELS OF PATCHY POPULATIONS

Many of the previously proposed models of patchy populations fall into one of three categories, depending on the assumptions which are made concerning dispersal characteristics. I will refer to these as (i) dispersal-pool models, (ii) grid models, and (iii) dispersal-corridor models.

Dispersal-Pool Models

Dispersal-pool models encompass a large number of studies (e.g., [1–4, 11, 15, 17, 18]). Organisms which disperse from patches are assumed to enter a dispersal pool, and are then redistributed among the patches according to a set of rules. The main reason for making the dispersal-pool assumption is that it greatly simplifies the model, sometimes allowing for analytical solutions of equations (e.g., [4]). This type of model has often been used to study the role of dispersal in population stability and survival [16, 18].

Models which contain the dispersal-pool assumption, while useful for some types of investigations, cannot be used to study the effects of the spatial arrangement of habitat patches on population dynamics. This is because, by assuming the presence of a dispersal pool, one ignores the explicit spatial arrangement of patches. A model which is used to find relationships between spatial arrangement and population dynamics must therefore be more complex than a dispersal-pool model; it must include some explicit description of the spatial distribution of the habitat patches.

Grid Models

A second common approach to including spatial heterogeneity is the grid model (e.g., [12, 21]). This is a simulation model, in which an imaginary grid

is placed over the entire region under study, including the habitat patches and the matrix in which they are distributed. The subpopulation within each grid square is explicitly followed through the entire simulation. In the most detailed type of grid model, each individual organism in each grid square is followed (e.g., [13]).

To develop relationships which can be applied to a wide range of possible spatial arrangements and species, one would need to conduct a large number of simulation experiments, with a wide range of parameter values, corresponding to a wide range of situations. If a grid model is used, detailed information concerning the flow of organisms on the grid is necessary for each simulation. At each time step, one would have to calculate the probabilities of organisms in each grid square reaching each of the other grid squares. Over a very large number of simulations, this type of approach, while possibly successful, would be very expensive and time-consuming.

It would clearly be preferable to find some compromise between the dispersal-pool approach, which is too simple to answer the question, and the grid approach, which is probably more complex than necessary to answer the question. A model which includes explicit spatial arrangement of habitat patches, but which does not require that one follow the movements of dispersing organisms through the nonpatch matrix, is desired.

Dispersal-Corridor Models

A model which satisfies both of the above conditions is the dispersal-corridor model [6, 7, 14]. In this model patches in the habitat are represented as nodes, which may be either "connected" or "not connected" to one another. This type of model was shown to be a useful method of modeling populations of small mammals in woodlots, which may be interconnected by fence rows along which dispersing organisms travel [7].

Roff [19, 20] implicitly included the dispersal-corridor assumption by assuming that each of 25 subpopulations was connected by dispersal to its four nearest neighbors. However, this assumption renders his model inappropriate for studying the effect of spatial arrangement on population dynamics, because all 25 patches are spatially equivalent.

Lefkovitch and Fahrig [14] used a dispersal-corridor model to find general relationships between the spatial arrangement of such habitat patches and population survival. Simulations were conducted of populations in all 34 distinct spatial arrangements of 5 habitat patches. Statistical analyses were then performed on the results. It was found that the probability of survival of a population within a patch depends on two factors. First, populations in patches which are completely isolated have lower survival probabilities than those in patches which are connected to other patches. Second, for those patches which are connected to at least one other patch, the probability of
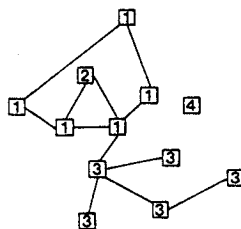
FIG. 1. Illustration of the results of Lefkovitch and Fahrig [14]. Squares represent habitat patches, and lines joining them represent dispersal corridors. Numbers in the squares indicate the relative survival probabilities of populations in the patches ("1" is the highest survival probability). See text for further explanation.

population survival depends on the size of the largest geometric figure of which the patch forms a part. These results are illustrated in Figure 1.

Although the results of Lefkovitch and Fahrig are general relationships between habitat-patch spatial arrangement and population dynamics, they are only general to the extent that the concept of dispersal corridors is a general phenomenon in nature. Apart from the example of mammals in woodlots, it is difficult to find other situations in which this assumption applies. Therefore, to derive truly general relationships, one would prefer to use a model which incorporates a much larger proportion of the dispersal characteristics of real organisms.

From this discussion, three main criteria emerge for a model which can be used to look at general relationships between habitat-patch spatial arrangement and population dynamics. First, it is necessary to include the explicit spatial arrangement of the habitat patches. This precludes use of the dispersal-pool assumption. Second, the model should apply to a wide range of species. This precludes use of the dispersal-corridor assumption. Finally, the model should be as simple as possible, since a large number of simulation experiments must be conducted. This makes a grid type of model undesirable.

THE MODEL

The model which I propose here satisfies the above criteria. The explicit spatial arrangement of habitat is included; distances between all pairs of patches are required to calculate dispersal rates among the patches. The model is not restricted to species which follow dispersal corridors, although it can be modified to include them. Furthermore, it avoids explicit considera-

tion of the spatial locations of organisms in the nonpatch matrix, making it much simpler than the grid approach.

The model is a stochastic discrete-time simulation model. It includes within-patch processes and between-patch dispersal in each time step. Within-patch population dynamics are modeled by a discrete approximation to the logistic growth equation. There are six main parameters in the model, which determine the population sizes in each patch at each time step. These are (i) r: intrinsic population growth rates in the patches, (ii) k: carrying capacities of the patches, (iii) p: fractions of organisms which disperse from each patch in each time unit, (iv) s: dispersal distances relative to the mean distance between patches, (v) d: distances from which dispersers detect new patches (detection radius), and (vi) i: immigration rates. During a particular simulation, the overall value chosen for each parameter is actually the mean of a random variable. The actual values used in the simulation vary stochastically about the means, among the patches, and over the time steps.

The simulation does not follow the fate of each organism; instead, calculations are based on the total population sizes in each patch.

Dispersal from each patch is assumed to be, on average, equally likely in all directions, except when a patch is within detection range of the first. The distances which dispersers move are assumed to be taken from a random normal distribution. Patches are assumed to "attract" all those dispersers which would, by chance, fall within a certain detection radius of the patch. Those dispersing organisms which do not successfully find a new patch in a particular time step are not explicitly followed further. They may die, emigrate from the area, or successfully detect a new patch at some future time step. The net effect of all these possibilities, plus the possibility of immigration of new individuals into the area from outside it, are accounted for in the immigration term i. It is this simplifying assumption which allows one to effectively ignore the nonpatch matrix.

Figure 2 illustrates dispersal from a particular patch (patch 1). Notice that the fraction of dispersers which reach patch 4 is greater than the fraction reaching either patch 5 or 6. Figure 3 is a flow diagram of the model.

In general this model is highly flexible; adjustment of parameter values can result in a dispersal-pool model or a dispersal-corridor model, and a wide range of possibilities in between. However, it is important to note that the model in its present form does not include the large number of species for which dispersal occurs in one predominant direction, such as with a wind or water current, downhill, uphill, or in a particular compass direction. Once general relationships are developed from the present model, it will be appropriate to add this type of overall dispersal directionality to the model, to see if it influences the results.
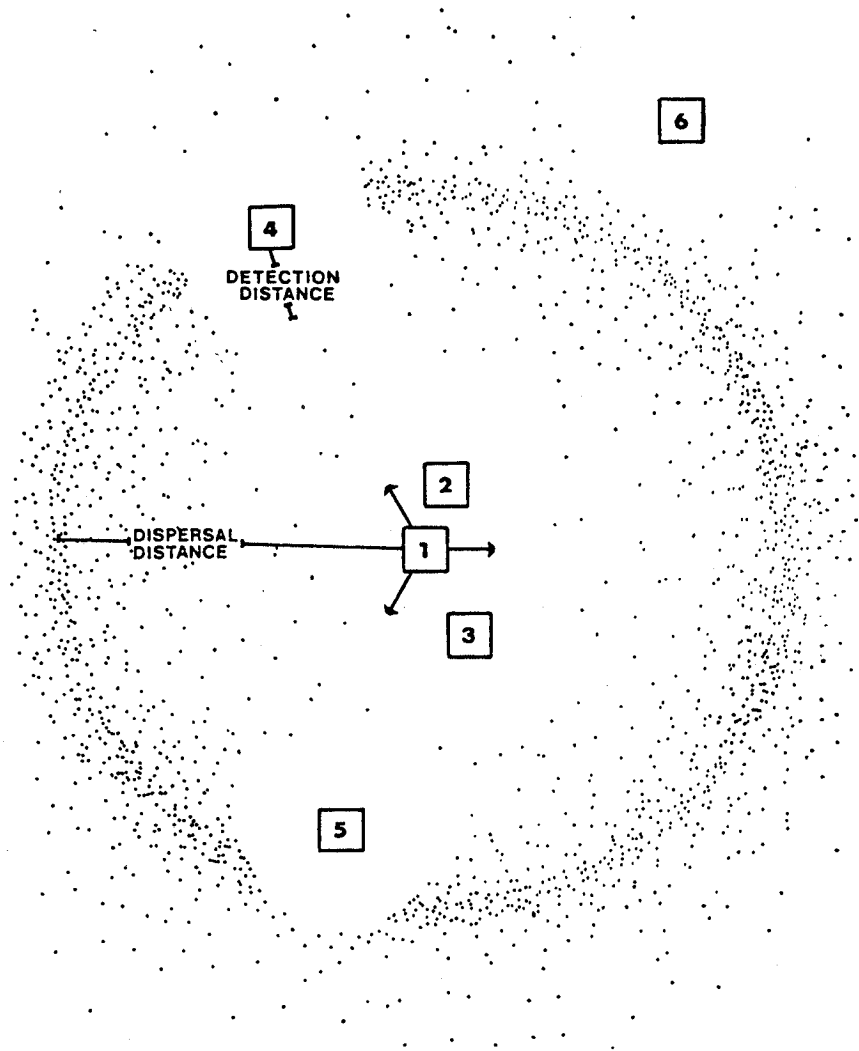
FIG. 2. Illustration of dispersal assumptions. Organisms disperse from patch 1, in the distribution indicated by the speckled pattern. Recipient patches "attract" all dispersers which fall within the detection distance of the patch (represented by the blank circular areas around the patches). Notice that patches 5 and 6 receive fewer dispersers from patch 1 than does patch 4.
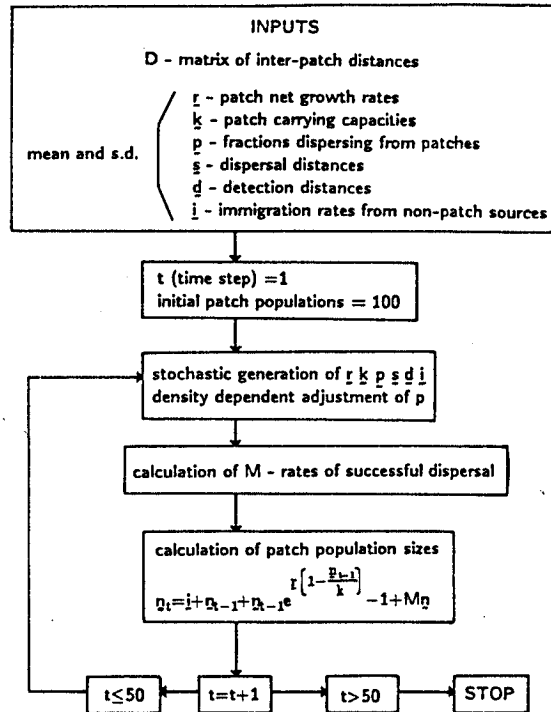
INPUTS

D - matrix of inter-patch distances

mean and s.d.
$\left\{\begin{array}{l}\underline{r}\text{ - patch net growth rates}\\\underline{k}\text{ - patch carrying capacities}\\\underline{p}\text{ - fractions dispersing from patches}\\\underline{s}\text{ - dispersal distances}\\\underline{d}\text{ - detection distances}\\\underline{i}\text{ - immigration rates from non-patch sources}\end{array}\right.$

t (time step) =1
initial patch populations = 100

stochastic generation of $\underline{r}\ \underline{k}\ \underline{p}\ \underline{s}\ \underline{d}\ \underline{i}$
density dependent adjustment of p

calculation of M - rates of successful dispersal

calculation of patch population sizes

$$n_t = i + n_{t-1} + n_{t-1}e^{r\left[1-\frac{n_{t-1}}{k}\right]} - 1 + Mn$$

$t \leq 50$ | $t=t+1$ | $t>50$ | STOP

Fɪɢ. 3. Flow diagram of the model.

Although the model includes stochastic variation in parameter values among patches and over time, there is no correlation over time in the deviations from the means in the parameter values chosen for a particular patch. This means that persistent differences among patches are not included. This assumption is often unrealistic. For example, patches in nature have different shapes (e.g., in the proportion of patch edge to patch area). This may affect parameters in the model such as carrying capacity or dispersal rate. Such consistent differences among patches in parameter values add a level of complexity to the simulations which is best addressed after the simpler situation is studied.

THE EFFECT OF DETECTION DISTANCE

The purpose for proposing the model described here is, as stated, to develop general relationships between the spatial arrangement of habitat
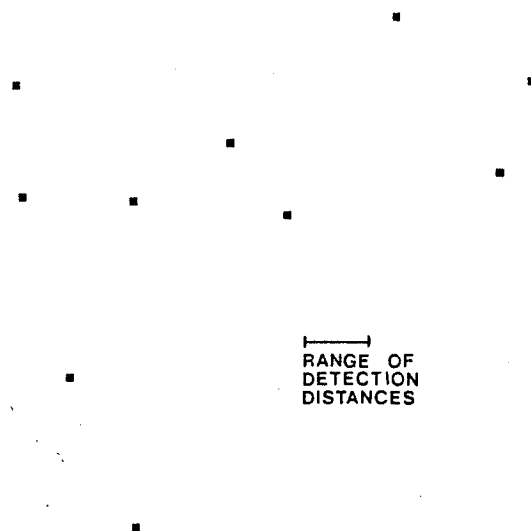
FIG. 4. Spatial arrangement of 10 habitat patches used in simulation experiments.

patches and the population dynamics of resident populations. I report here the results of a limited set of simulations which begin to satisfy this aim.

The impetus for this simulation experiment comes from studies of the cabbage butterfly *Pieris rapae*. This species specializes on host plants in the family Cruciferae, on which the females lay their eggs [9]. The females are highly mobile, and may visit several patches of host plants within a lifetime.

TABLE 1

PARAMETER VALUES USED IN THE SIMULATION EXPERIMENTS

Parameter	Mean value	Standard deviation (%)
Input patch population sizes	100	0
Patch carrying capacities	1000	10
Net population growth rates r	0.1	10
Dispersal distance[a]	0.5	40
Dispersal rate	0.5	10
Detection distance[a]	0-0.2	10
Immigration rate	10	10

[a]As fraction of mean interpatch distance.

Fahrig and Paloheimo [8] found that the females are virtually unable to detect their host plants from a distance, but find them by chance. Therefore, in terms of the model described here, the "detection distance" for this species is 0. The question therefore arises: in general, what affect does the detection distance have on the interaction between the spatial arrangement of habitat patches and population dynamics?

To answer this question, I performed a series of simulation experiments using the model described here. Ten habitat patches were randomly distributed in space (see Figure 4), and the values in the model were arbitrarily set as shown in Table 1. The same spatial arrangement was used for each
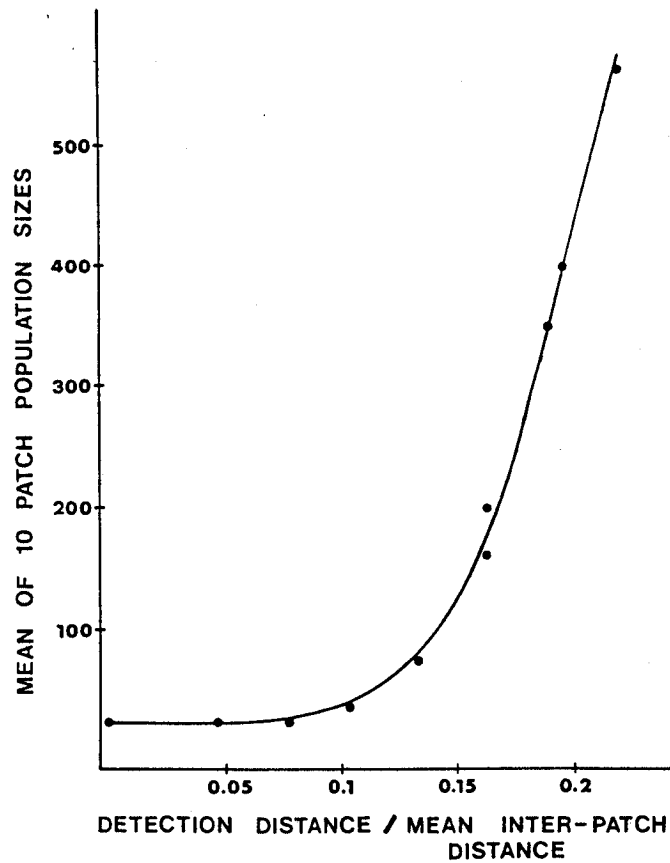
FIG. 5a.   Relationship between mean population abundance in 10 patches, and the distance from which dispersing organisms can detect the patches (detection distance), as derived from simulation experiments.

simulation. In each simulation, the population sizes in each of the patches were calculated for 50 time steps. The mean detection distance was varied from 0 to 20% of the mean interpatch distance. The results of the simulations are shown in Figure 5(a) and (b).

From Figure 5(a), it can be seen that the population size increases as the detection distance increases. This is expected, because more dispersers are successful in finding patches when the detection distance is increased. However, this result does not reveal anything about relationships between the spatial arrangement of habitat patches and population dynamics.

From 5(b), however, one can see a marked effect of the spatial arrangement on population dynamics. This figure illustrates the relationship between
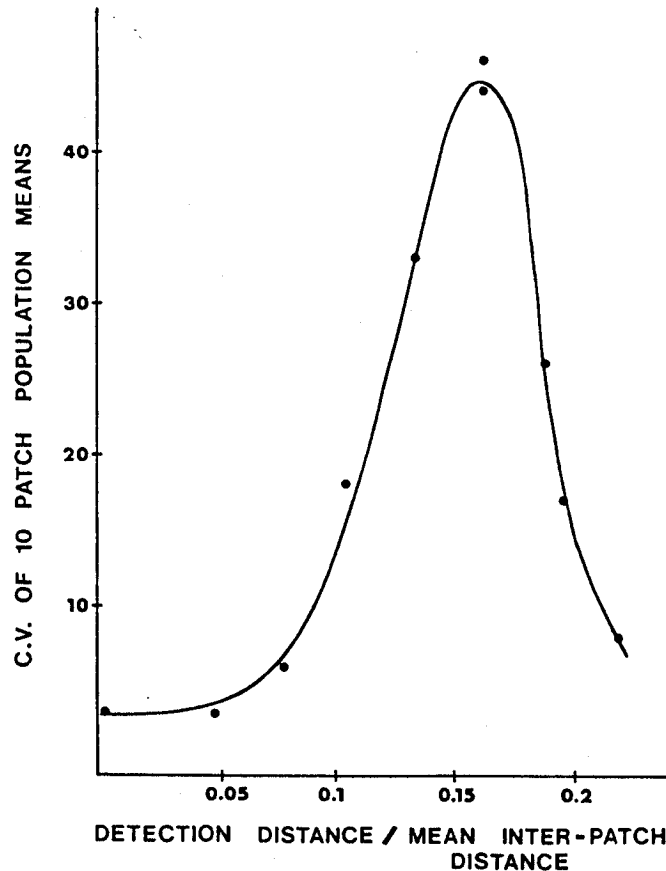
FIG. 5b. Relationship between coefficient of variation among the mean population sizes in 10 patches, and the detection distance, as derived from simulation experiments.

the detection distance and the coefficient of variation (C.V.) among the mean population sizes in the 10 patches. The C.V. is low for very low detection distances, increases as the detection distance increases, and then decreases again for higher detection distances. This can be interpreted as follows. At low detection distances, very few of the dispersing organisms successfully reach new patches. Therefore, the population dynamics in the 10 patches are essentially independent. Any differences among them are due to the effects of stochastic variation in their within-patch population processes. As the detection distance increases, however, a higher proportion of dispersers actually reach new patches. Those patches which are situated at distances near the mean dispersal distance from the other patches will receive more dispersers than those which are not. Therefore, added to the variation due to within-patch processes, the population dynamics in the patches are influenced by their relative spatial locations. This causes an increase in the C.V., which measures the degree to which the populations in the 10 patches differ. Finally, at higher detection distances, the level of interchange among the patches is high enough that any differences caused by the spatial distribution of the patches are damped out. The swamping effect of high dispersal rates was also noted by Hastings [10].

It is important to remember that these results were observed for specific (though arbitrary) values of the five other parameters in the model. Work has begun on the interactions among these parameters, and on finding general types of species for which the spatial arrangement of habitat patches has an important impact on population dynamics. Although this model is rather simple given the complex nature of the questions I am examining, there are still a large number of calculations required for each simulation. In fact, the number of calculations increases exponentially with the number of patches considered. To obtain the desired general results, it will therefore be necessary to run a large number of simulations, with different mean parameter values, but to limit the number of patches in each simulation to a small number, say 10.

For the specific case of the cabbage butterfly, the results here [Figure 5(b)] indicate that it is unlikely that the spatial arrangement of host plant patches has an important impact on population dynamics. The results of a test of this hypothesis will be reported in future.

CONCLUSIONS

I have presented here a model which will be used in future studies to derive general relationships between the spatial arrangement of habitat patches and population dynamics. Although the model is quite general, it

does not include organisms for which dispersal is largely unidirectional due to forces such as wind or water currents. Once general relationships using the model presented here are derived, I will conduct further studies to determine the effects of such directional forces on the relationships.

Finally, I suggest that the model presented here is an appropriate base-level model for studies of specific populations at the landscape level. While it explicitly includes spatial heterogeneity, it is simple enough that higher levels of complexity may be easily added. These higher levels might include (i) studies of several species simultaneously, including interactions among them, (ii) studies of the effects of patch spatial arrangement on the flow of genetic types across a landscape, and (iii) studies of systems in which habitat patches change over time in location, size, and quality.

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