MODELING THE LANDSCAPE AS A DYNAMIC MOSAIC OF PATCHES: SOME COMPUTATIONAL ASPECTS

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ABSTRACT

The only thing that is certain and absolute about Nature is its patchiness. Patchiness is ubiquitous, occurring across systems, organizational levels, and spatio-temporal scales. Traditional modeling approaches in ecology often fail to recognize spatial patchiness because they usually assume spatial homogeneity. A landscape may be viewed as a hierarchical mosaic system of patches that are different in their age, size, shape, content and other aspects. The spatial change of the patch mosaic results in the landscape pattern, whereas the phase change of individual patches at the local scale and temporal change in patch mosaics at larger scales give rise to the landscape dynamics. Following such a patch dynamics conceptualization, a spatially explicit patch dynamic modeling approach has been developed based on a serpentine annual grassland. The model has two basic submodels: a spatially-explicit, age-/size- structured patch demographic model and a multi-specific plant population dynamic model of a non-equilibrium island biogeographic type. In this paper, the basic structure and some computational aspects of the model are discussed.

Key words: spatial modeling, patch dynamics, landscape modeling, patch maps, overlapping circles, dispersal, plant population dynamics

I. INTRODUCTION

Patchiness is ubiquitous in nature, occurring in both terrestrial and aquatic ecological systems across all spatio-temporal scales. The concept of patchiness emphasizes the spatial patterns of physical and biological entities and their variations. With enormously increasing awareness of and research emphasis on spatial heterogeneity, the study of patchiness and patch dynamics is becoming a major them in both marine and terrestrial ecology (e.g., Levin, 1976, 1988, 1989, 1992; Wiens, 1976; Pickett and Thompson, 1978; Steele, 1978; Forman and Godron, 1981, 1986; Pickett and White, 1985; Collins, 1989; Kotliar and Wiens, 1990; Collins and Glenn, 1991; Kolasa and Pickett, 1991; Wu, 1992; Wu et al. 1990, 1993). Patch dynamics represents not only a field of study, but a new emerging ecological paradigm as well. It represents a view that emphasizes spatial and temporal heterogeneity, non-equilibrium properties, hierarchical structure, and scale-dependence of ecological systems. A great challenge for ecologists is to relate small-scaled processes to large-scaled phenomena, or vice versa. Efforts have been made to develop mathematical models that reflect the characteristics of patchiness of natural systems. Three major types of patch models may be identified based on the degrees of their spatial explicity.

1. Non-Spatial Patch-Implicit Models (or Non-Spatial Patch Models)

They include mainly the so-called patch-occupancy models in which the state variables are usually the proportions of patches occupied and unoccupied by a species' populations or by different species (Levins, 1970; Gilpin and Hanski, 1991). These models deal with a large number of patches and involve both single-species dynamics and multi-species interactions. Mathematically, patch-occupancy models mostly take the analytical approach. The simplest model of this type is of the form

$$\frac{dp}{dt} = m \, p \, (1 - p) - e \, p \tag{1}$$

where p is the proportion of patches occupied by the species and m and e are constants that are related to the colonizing ability and extinction rate of the species, respectively.

2. Quasi-Spatial, Patch-Explicit Models (or Quasi-Spatial Patch Models)

They may be further broken into three subcategories: diffusion-reaction models, patch demographic models, and gap models. Diffusion-reaction models usually have population densities as state variables and take into account such spatial aspects as patch size and interpatch distance indirectly (e.g., Levin, 1976; Okubo, 1980). A general formulation of these models is as follows (as per Levin, 1976):

$$\frac{dY_i^u}{dt} = f_i^u \, Y^u, X^u + \left(net \ exchange \ with \ other \ patches\right) + \left(net \ exchange \ with \ matrix\right) \tag{2}$$

in which Y^u is the vector (Y_1^u, Y_2^u, ..., Y_n^u) of state variables for a given patch u, X^u the vector (X_1^u, X_2^u, ..., X_n^u) of parameters accounting for the same patch, and f^u the specific functional relationship. A simple example of the continuous model may be in a PDE form of

$$\frac{\partial n(x,t)}{\partial t} = n \, f(n) + \frac{\partial [D \, \partial n(x,t)]}{\partial x^2} \tag{3}$$

where $n(x,t)$ is the population density relative to the spatial position x, D is the diffusion rate of individuals of the population, and $f(n)$ is the population growth rate (Hastings, 1990). The corresponding discrete model may be written as

$$\frac{dn_i}{dt} = N_i f(n_i) + \sum_{j \neq i} [d_{ij} (n_j - n_i)] \qquad (4)$$

where d_{ij} is the exchange rate of individuals between patch i and patch j and n_i and n_j are population sizes in the two patches, respectively (Levin, 1974).

Patch demographic models explicitly consider the distributions of the age, size and other characteristics of patches. The general formulation is given by Levin and Paine (1974):

$$\frac{\partial \rho}{\partial t} + \frac{\partial \rho}{\partial \alpha} + \frac{\partial}{\partial \xi} (g \rho) = -\mu(t, \alpha, \xi) \rho \qquad (5)$$

$$\frac{d\xi}{dt} = g(t, \alpha, \xi) \qquad (6)$$

where $\rho(t, \alpha, \xi)$ is the probability density function which describes the frequency distribution of patches of age t and size ξ at time t, $\mu(t, \alpha, \xi)$ is the mean extinction rate of patches of age α and size ξ at time t (due to intrapatch succession), and $g(t, \alpha, \xi)$ is the mean growth rate of patches of age α and size ξ at time t (due to patch shrinkage or expansion). Population density or other variables of interest may be coupled with the patch demographic model in the following general form (Levin 1976):

$$\bar{n}_j(t) = \frac{1}{A(t)} \left\{ [A(t) - \int_0^\infty \int_0^\infty \xi \rho(t,\alpha,\xi) \, d\alpha d\xi] \varphi_j^o(t) + \int_0^\infty \int_0^\infty \xi \rho(t,\alpha,\xi) \varphi_j(t,\alpha,\xi) \, d\alpha d\xi \right\} (7)$$

where $\bar{n}_j(t)$ is the overall population density over the landscape, $\varphi_j(t, \alpha, \xi)$ is the expected population density of species j within a patch of age a and size at time t, $\varphi_j^o(t)$ is the population density of the same species in the non-patch area, and $A(t)$ is the total area of consideration at time t.

Gap models include a large host of computer simulation models of forest dynamics (e.g., Botkin et al., 1972; Shugart and West, 1977). These models usually spatially explicit only on the vertical dimension; the simulation plot -- gap is explicitly considered, but not the entire model area. A detailed and comprehensive review on these models can be found in Shugart (1984).

3. Spatially Explicit Patch Models (Spatial Patch Models)

Satial patch models are still in their early stage of development. Most of these models usually take a grid-based approach in which patches are considered as single grid cells or aggregates of multiple cells within a regularly divided grid (e.g., the spatially explicit forest gap model by Smith and Urban, 1988 and a grassland parallel by Coffin and Lauenroth, 1989). They do not contain an explicit patch demographic submodel, so it is difficult or impossible to directly relate biological properties of the system under study to the disturbance patch demogranphy. In addition, the raster approach becomes inadequate and unrealistic when overlapping among patches is common and varying continuously in space, which is often the case in nature.

Based on the conceptualization of a landscape as a hierarchical system of patche mosaics and the mathematical framework of the Levin-Paine model, I have developed a spatially explicit patch dynamics modeling approach that has several unique features. First of all, the approach best fits the patch dynamics conceptualization of ecological systems while it transforms such a qualitative conceptualization into a quantitative and predictive model. Second, in contrast with existing modeling approaches this patch-based modeling approach treats patches as individual objects changing continuously in real numbers in size and spatial location. Third, the approach more realistically deals with complex overlaps in a mosaic of patches of different age and size. Fourth, the model is primarily composed of two modules: a spatially explicit disturbance patch demographic module and a spatially explicit, multispecific, patch-based population dynamic module. Finally, the parallel formulation of the patch population model and species population model enables a scrutiny of the dynamics and spatial pattern of both the gopher mound and plant populations; this also makes the modeling framework suitable for studying a range of problems, such as population dynamics in a fragmented environment where patches are habitats and plant-parasite and plant-insect interactions where patches are individual plants.

II. ECOLOGICAL SYSTEM USED FOR DEVELOPING THE SPATIAL PATCH DYNAMICS MODELING APPROACH

The serpentine annual grassland within the Jasper Ridge Biological Preserve of Stanford University in San Mateo County, Northern California has been used for developing and implementing the spatially explicit patch dynamic modeling approach. The grassland is dominated by a relatively high diversity of annual native forbs and perennial bunch grasses (Hobbs and Mooney 1985, 1991). The activities of western pocket gophers account for a major component of the disturbance regime within the serpentine grassland. By bringing excavated soil material from underneath to the surface, these burrowing gophers periodically create approximately round mounds of bare soil, ranging from 30 to 50 cm in diameter. The formation of gopher mounds is concentrated in April and July, though gopher activities are found throughout the year. Field estimation indicates that as high as over 20% of the total area is turned over by gopher activity each year (Hobbs and Mooney 1985, 1991). When new mounds are formed, the plants buried up to 10 cm beneath are essentially killed and plant succession on these "microhabitat islands" takes place subsequently.
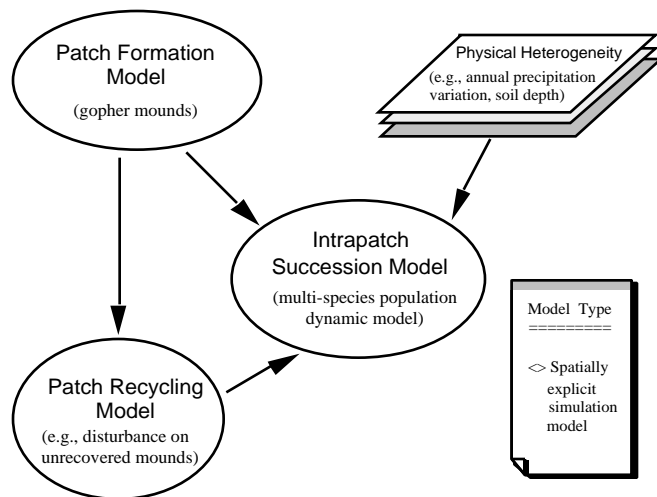

Fig. 1. Components of the spatial patch dynamics model.

The basic model structure for the Jasper Ridge serpentine grassland is diagmatically outlined in Fig. 1. The spatial patch dynamics model consists of two major submodels: a spatially explicit, age- and size-structured patch demographic model and a multi-specific plant population dynamic model of a non-equilibrium island biogeographic type. While the patch population model mimics the spatiotemporal changes of gopher mounds, the plant population model simulates the dynamics of vegetation pattern by keeping track of the growth and reproductive processes of species populations in each and every gopher mound in the landscape. In the following sections, I shall focus on some computational aspects of the model.

III. GENERATION OF PATCH MOSAICS

Field observations show that new gopher mounds are usually positively correlated to those formed in the previous years in their spatial locations. This spatial correlation may be related to the behavioral characteristics of the gophers. Positive spatial autocorrelation may be introduced by assigning conditional probability to new patches according to the distance to patches produced in the previous year. Two methods may be used to generate clumped patterns: patch probability method and patch influence index method.

1. Patch Probability Method

This method assumes that the probability for an existing patch to have a new patch the next year in its neighborhood decreases exponentially with distance. Because of food shortage and other factors, the patch formation probability may be negligibly small within certain distance to the parental patch. In addition, the probability is assumed equal in all directions around the patch. Therefore, we have

$$\varphi_p(L_p) = 0 \qquad\qquad L_p < L_{\min}$$
$$\varphi_p(L_p) = \lambda_p e^{-\lambda_p(L_p - L_{\min})} \qquad\qquad L_p \quad L_{\min} \tag{8}$$

where φ_p is the patch-formation probability at a point, L_p is the distance of the point from the center of the parental patch, $L_{\min}$ is the distance within which the probability is zero, and λ_p is the exponential decay coefficient that determines how fast this probability drops with distance. This method creates a positive spatial autocorrelation among patches generated.

As the initial condition, patches are generated with their centers randomly distributed and the total number of patches is recorded. During the next simulation time step, the following steps are implemented sequentially when a new patch is generated: (1) choose a last year's patch randomly, (2) calculate a distance value for a randomly chosen φ_p according to the distance-dependent probability density function of patch formation, (3) determine an angle between 0 and 2 randomly, (4) determine the x, y coordinates for the point based on the angle and the distance to the center of the parental patch, (5) dismiss the seed if x and/or y is out of bounds set by the model (absorbing boundary), and (6) return to step (1) if the new patch would overlap too much with any existing patch. The above steps are repeated until all patches have been generated for the time step.

By changing the value of λ_p, we can produce patch maps with different degrees of aggregation, exploring theoretically the consequences of clumping, or simulating the spatial pattern of disturbance patches as deduced from aerial photos or other remotely sensed images.

2. Patch Influence Index Method

This method is based on a modeling scheme for generating clumped point patterns used by Nuernberger (1991). Based on the field observation that new gopher mounds seem positively correlated to those formed in the past year in their spatial locations, the influence for a patch of this year on having a new patch in next year in its vicinity is assumed to decrease exponentially with the distance away from it. This is formally expressed as:

$$\psi(D) = e^{-\gamma D} \tag{9}$$

where $\psi(D)$ is the influence function, D is the distance away from the center of the existing patch, and γ is the exponential decay coefficient which determines the rate of decrease in the tendency.

For a given point in the landscape, the mean cumulative influence index is calculated from the following equation:

$$(P) = \frac{1}{M} \sum_{k=1}^{M} e^{-\gamma D_{Pk}} \tag{10}$$

where M is the total number of last year's patches, and D_{Pk} is the distance between the point $P(x,y)$ and the center of an existing patch k. So, (P) is an indicator of the average crowdness relative to point P in the landscape. To generate a clumped pattern of patch centers, (P) is used as the probability for a randomly chosen point $P(x,y)$ to be a candidate for the center of a new patch. However, in order for this new patch to be actually formed all other requirements for patch formation (e.g., age-related overlapping constraints) must be also satisfied. The initial condition for starting the pattern generation is set by determining the centers of patches through drawing uniform pseudo-random numbers for x-y pairs.

A lognormal distribution for the size of new patches at birth is used in the model, with the minimum and maximum sizes being 10 and 50 cm in diameter, respectively. Although they are circular when formed, patches after birth may be very different in both shape and size from their original because they may have been overlapped by other patches occurring subsequently. Therefore, to update the patch sizes it is necessary to develop an efficient algorithm capable of taking into account the complex and changing shapes of existing patches.

Two major categories of patches are distinguished: obsolete patches and effective patches. Obsolete patches refer to patches that are older than the maximum patch age and essentially represent the non-patch (undisturbed) areas. The maximum patch age is mainly an indicator of change in soil conditions of the gopher mounds and may be affected by the vegetation dynamics in the patches through biological feedback, but the current version of the model does not address this possibility. Effective patches are those whose age is smaller than the maximum patch age. The model assumes that the age of a patch correlates with the soil conditions of the patch, which significantly affect plant demographic parameters. Also, patches of different ages have different maximum overlapping areas with a new patch.

The overlap of a new gopher mound with an existing mound is likely to increase with the age of the existing mound. Part of the reason for this may have to do with the scarcity in food supply on new mounds, besides the animal's behavioral idiosyncrasy. As a first approximation, a logistic equation may be used to describe such a relationship. I define the maximum overlap ratio ($OLR_{max}(\tau)$) as the fraction of area of the new patch that overlaps an existing patch (i.e., the overlap divided by the area of the new patch). Then the relation between the maximum overlap ratio between a new patch and another patch of any age may be expressed as

$$OLR_{max}(\tau) = \frac{1}{1 + (\frac{1}{OLR_0} - 1)e^{-\gamma(\tau-1)}} \qquad \tau = 1, 2, ..., a_{max} \tag{11}$$

where $OLR_{max}(\tau)$ is the overlap ratio, OLR_0 is the overlap ratio when the age of the existing patch is one (which is the minimum overlap), τ is the age (in years) of the existing patch encountered by the new patch, and γ is a coefficient adjusting the rate of increase in the overlap ratio with patch age. Therefore, each time a new patch is generated during the simulation, its overlap with any existing patch of age τ in the landscape is checked, so that the actual overlap ratio is equal to or smaller than $OLR_{max}(\tau)$. Conceivably, this overlapping constraint exerts some degree of negative spatial autocorrelation in the patch formation.

IV. CALCULATION OF PATCH OVERLAPS

The spatial patch dynamics modeling approach entails the calculation of the effective size of each and every patch in the landscape at each simulation itme step. The effective size of a patch in a mosaic of overlapping patches of different age and size is defined as its remaining area that is not covered by any younger patches. To compute the effective size of a patch, it is necessary to know the number of other patches that overlap and are overlapped by the patch and the spatial and age relationships among all of them. The portions of the patch in consideration overlapped by other patches should be appropriately subtracted at each simulation time step from its original patch size. To do that, one has to be able to calculate the overlapping area among a varying number of patches of different size and age.

Let A_i^* and A_i be the effective size and the original size of patch i at its birth, respectively. When only two patches are involved (see Fig. 2A,B), the effective patch sizes can be readily calculated as follows.

(i). When $A_1 \bigcap A_2 = \phi$ (i.e., the overlap between the two patches is zero), the effective size of each patch is identical to its original:

$$A_1^* = A_1$$
$$A_2^* = A_2$$

(12)

(ii). When $A_1 \quad A_2$ or $A_1 \quad A_2$, the overlap is equal to the size of the smaller patch (either A_1 or A_2). The effective area of each patch can be obtained from:

$$A_i^* = A_i \qquad (\text{when patch i is younger})$$
$$A_i^* = A_i \bigcap A_j^c \qquad (\text{otherwise})$$

(13)

$$i, j = 1, 2 \text{ and } i \quad j.$$

where A_j^c is the complement of set A_j.

(iii). When $A_i \quad A_j$ and $A_i \bigcap A_j \quad \phi$ (i, j = 1, 2 and i   j), the overlapping area can be analytically computed from the following formulas:

(a) when $PO_1Q = \alpha_1 \quad \pi$ and $PO_2Q = \alpha_2 < \pi$ (Fig. 2A):

$$A_{overlap} = \frac{1}{2} \left(r_1^2 \alpha_1 + r_2^2 \alpha_2 - cd \right)$$

(14)

(b) when $PO_1Q = \alpha_1 > \pi$ and $PO_2Q = \alpha_2 < \pi$ (Fig. 2B):

$$A_{overlap} = r_1^2 \pi - \frac{1}{2} (r_1^2 \alpha_1 - r_2^2 \alpha_2) + \frac{1}{2} c \sqrt{r_1^2 - (\frac{c}{2})^2} - \sqrt{r_2^2 - (\frac{c}{2})^2}$$

(15)

with

$$c = \sqrt{2 r_2^2 (1 - \cos \alpha_2)}$$

(16)

$$\alpha_1 = 2\arccos \frac{1}{2dr_1}(d^2 + r_1^2 - r_2^2) \tag{17}$$

$$\alpha_2 = 2\arccos \frac{1}{2dr_2}(d^2 + r_2^2 - r_1^2) \tag{18}$$

where A_{over} is the overlap area, r_1 and r_2 are the radii of the two patches, d is the distance between the two centers, α_1 and α_2 are the central angles of the two patches, and c is the chord for the overlapped area (see Fig. 2A,B).
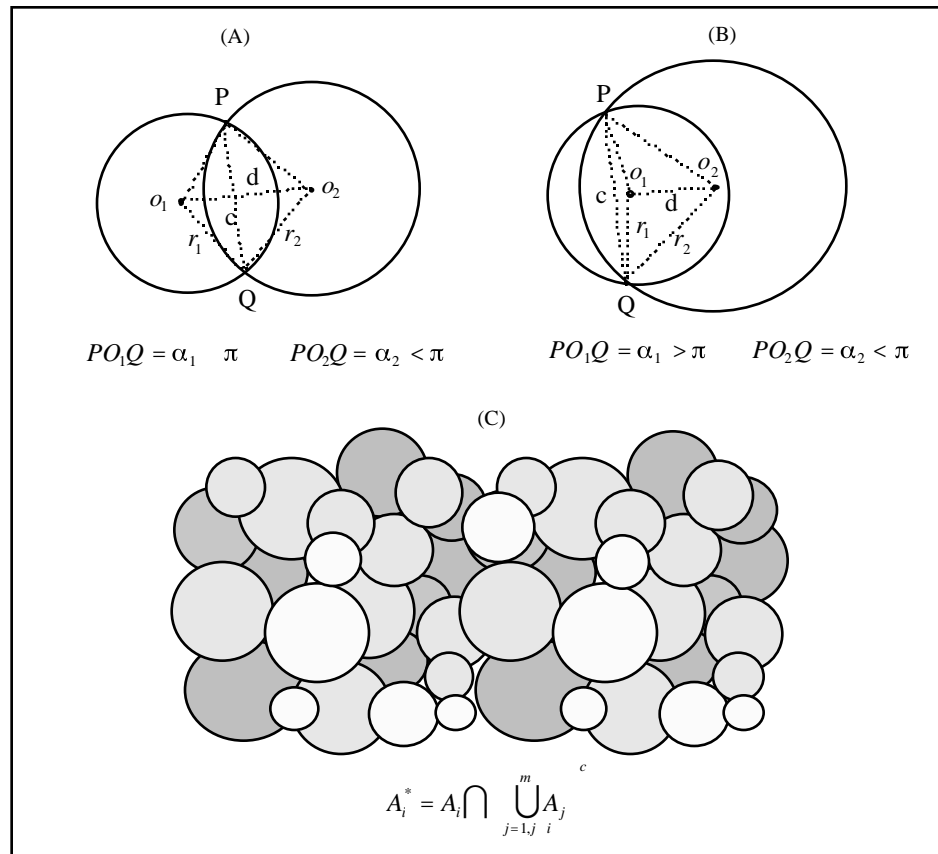

Fig. 2. Illustration of mosaics of overlapping patches. Patches are circular in shape and vary in size and age and different shading patterns represent different ages of the patches. The effective sizes of patches can be calculated analytically when only two of them are involved (A and B), but they have to be computed using a Monte Carlo simulation method when more patches are involved (C). A_i^* is the effective size of patch i, A_i is the birth-time size of patch i, A_j^c is the complement of set A_j, and m is the number of patches that are younger than patch i.

When the number of patches involved is larger than two, an analytical solution for overlapping areas among them becomes extremely difficult, if possible (see Fig. 2C). A Monte Carlo simulation method, however, can be used to estimate the overlaps among any number of patches. We have developed a computer algorithm which updates the effective sizes of patches at each time step. For each patch whose size is changed by formation of a new patch, the algorithm first identifies all the patches overlapping and overlapped by it, then delineates a rectangle enclosing

only the patches relevant to the area calculation of the patch, and finally compute the effective size of the patch through a Monte Carlo integration. The effective size of a patch in an age-structured patch mosaic can be expressed in terms of set algebra as follows:

$$A_i^* = A_i \bigcap \left(\bigcup_{j=1,j \ne i}^{m} A_j \right)^c = A_i \bigcap \bigcap_{j=1,j \ne i}^{m} A_j^c \tag{19}$$

where A_i^* and A_i are the effective size and the birth-time size of patch i, respectively, A_j^c is the complement of set A_j, and m is the number of patches younger than patch i (see Fig. 2C).

Equation (19) provides an understanding of the relationship among an existing patch and all other patches that overlap it with regard to its effective size. But, it does not directly render a computer-implementable algorithm. To develop an efficient computer algorithm for updating the effective sizes of all individual patches involved after each disturbance in the landscape is, however, no trivial matter both technically and ecologically. I have developed a "second-order overlapping moving window" algorithm which is rather accurate and efficient. The basic idea goes as follows. After each new patch is generated, all patches directly touched by this new patch are identified with information on their spatial locations, original sizes, ages, and sequential patch ID numbers. Afterwards, a rectangular window is selected in such a way that it contains all the patches that directly overlap the patch under adjustment and all others that over-lap them (the second-order overlapping patches). Then, effective sizes for the patches affected by the new disturbance are calculated through a Mente Carlo integration within the restricted region.

V. PATCH-BASED PLANT POPULATION DYNAMIC MODEL

The multiple-specific plant population dynamic model is patch-based. Plant demographic processes including germination, survival and seed reproduction as affected by microhabitat conditions (represented by different patch age classes) are taken into account. Within patches, both intraspecific and interspecific competition are considered as they influence the seed produc-tion through density-dependent mechanisms. Among patches, local plant populations interact with each other through seed dispersal, resulting in the dynamics of species metapopulations at the landscape level. The patch-based population model takes the following form:

$$N_{i,t+1} = (N_{i,t} f_{i,t} + I_{i,t} - D_{i,t}) (A_{t+1} / A_t) g_i s_i \tag{20}$$

where $N_{i,t+1}$ and $N_{i,t}$ are the population size (number of plant adults) for species i at time $t+1$ and t, respectively, f_i is the fecundity function, $I_{i,t}$ is the number of seeds received by the patch, $D_{i,t}$ is the number of seeds dispersed out of the patch, g_i is the germination rate, s_i is the seedling survivorship of species i, and A_{t+1} and A_t are the patch size at time $t+1$ and t, respec-tively $(A_{t+1} \le A_t)$. The ratio of patch size, A_{t+1}/A_t, adjusts the population size in a patch if the size of the patch changes, assuming as a first approximation that the reduction in patch size pro-portionally decreases the plant population size in that patch.

Plant fecundity is modeled as a density-dependent variable on the individual patch level as follows:

$$f_i = RMP_i AMP_i f_i^*(H) \left[1 + \alpha_i \left(\sum_{j=1}^{m} \beta_{ij} n_j \right) \right]^{-q_i} \tag{21}$$

where f_i^* is the fecundity of species i without neighbors, RMP_i is the rainfall multiplier which reflects the effect of annual precipitation variation on the fecundity of species i (set to 1 for simulations discussed in this paper), AMP_i is the gopher mound recovery multiplier, H denotes the different microhabitat types, α_i and q_i are species-specific constants, β_{ij} is the interspecific interference coefficient, m is the number of species modeled, and n_j is the population density of plant species j in the patch.

The maximum fecundity for each species differs between effective patches (gopher mounds) and obsolete patches (non-mound areas), and also changes with patch age. The constant α_i has the dimension of [area per plant] and, thus, $1/\alpha_i$ may be conceived as a measure of the critical population density, n_{crit}, at which fecundity becomes appreciably reduced by crowding effects. In particular, we assume α_i to be directly proportional to $1/n_{crit}$. The values of n_{crit} for different species are based on Hobbs and Hobbs (1987). All the aforementioned density-dependence relationships can be evaluated by regression against field data, and the best fit parameters can be, therefore, determined (e.g., Pacala and Silander 1985, 1990).

The competition coefficients β_{ij} essentially define the equivalence among the species in the same community. In the Jasper Ridge serpentine grassland community, dominated by relatively short annuals forbs, soil resources are most likely to be the main limiting factors for plant growth and reproduction. A first approximation is to estimate the interspecific competition coefficients based on the above-ground biomass of the adult plants of the species. For simplicity and also limited by data availability, we calculate β_{ij} as the ratios of above-ground biomass between two competing species, i.e.:

$$\beta_{ij} = \alpha_w \frac{W_j}{W_i} \tag{22}$$

where α_w is a scaling constant, and W_i and W_j are the above-ground biomass for the adult plants of species i and j.

Germination rate, survivorship and fecundity of plants are different on gopher mounds of different age, and survivorship and fecundity for species modeled are, in general, considerably higher on gopher mounds than undisturbed areas due to increased resource availability and/or reduced competition on the former (Hobbs and Mooney 1985). The recovery of soil physical conditions may take place rather rapidly at first after disturbance and then slow down when the pre-disturbance state is approached. A negative exponential decay model is used to account for the change in plant demographic parameters due to soil properties of gopher mounds (Fig. 3):

$$\frac{dY_G(\tau)}{d\tau} = -\eta(Y_G(\tau) - Y_u) \tag{23}$$

or

$$Y_G(\tau) = Y_u + (Y_G^* - Y_u)e^{-\eta(\tau-1)} \tag{24}$$

where τ is the patch age, $Y_G(\tau)$ is the value of a plant demographic parameter (i.e., germination rate, survivorship or fecundity) in a gopher mound of age of τ, Y_G^* is the value of a plant demographic parameter in a newly formed gopher mound, Y_u is the value in an undisturbed area, and is a constant which determines the pace of the exponential decay. All the above parameters are species specific.

Let $AMP = Y_G(\tau) / Y_G^*$ and call this ratio the patch age multiplier:

$$AMP = Y_G(\tau) / Y_G^* \tag{25}$$

$$AMP = \frac{Y_u}{Y_G^*} + (1 - \frac{Y_u}{Y_G^*})e^{-\eta(\tau-1)} \tag{26}$$

AMP is equal to 1 when patch age is 1 and asymptotically approaches Y_u/Y_G^* when patch age gets larger. Of course, AMP is also species specific. For computational convenience, we set AMP to Y_u/Y_G^* when patch age is larger than τ_{max} which is the empirically estimated, maximum time for the difference in soil characteristics between the different microhabitats to disappear.
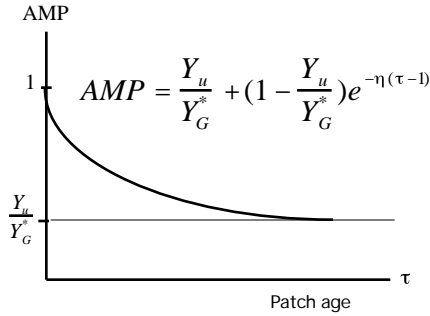
Fig. 3. Relationship between patch age and plant demographic parameters. AMP is the patch age multiplier, τ is the patch age, Y_G^* is the value of a plant demographic parameter (i.e., germination rate, survivorship or fecundity) in a newly formed gopher mound, Y_u is the value in an undisturbed area (obsolete patch).

To estimate , we assume that it takes t_r years for $Y_G(\tau)$ to decrease to a fraction ξ of the predisturbance level. That is, when t = t_r

$$\frac{Y_G(\tau)}{Y_u} = \xi \tag{27}$$

Then, according to equation (24), we have

$$\eta = \frac{1}{t_r} \ln \frac{Y_G^* - Y_u}{(\xi - 1)Y_u} \tag{28}$$

VI. SEED DISPERSAL IN A MOSAIC OF PATCHES

In a homogeneous environment, dispersing seeds among patches would be essentially the same as dispersing seedlings after multiplying a universal germination rate to the total number of seeds produced in any source patch. However, this is not the case for the dispersal of seeds and other propagules if the landscape under study is composed of a number of patches with differential germination rates. Because dispersing all the seeds one by one in a spatially explicit fashion may become formidably time-consuming in a simulation model if the number of seeds is considerably large, an algorithm analogous to that in homogeneous environment would make the expicit simulation of dispersal much more efficient and effective.

A phenomenological exponential model is used to determine the distance related probability of seed dispersal:

$$\varphi(L) = \lambda e^{-\lambda L} \tag{29}$$

where $\varphi(L)$ is the dispersal probability density function, L is the distance between the centers of a donor patch and the recipient patch, $\varphi(L)$ is the probability of a seed falling at the distance L,

and λ is the exponential decay constant, which is a measure of the dispersability of the seeds in a specific set of field conditions (see Okubo and Levin 1989). Both $\varphi(L)$ and λ have the dimension [1/L]. The reciprocal of λ is the characteristic length of the negative exponential function which is, in the case of dispersal, the mean dispersal distance for the species under consideration. In this simple case, the probability density function can be easily integrated to obtain the cumulative probability function,

$$(L) = \quad \varphi(L)dL$$
$$= 1 - e^{-\lambda L}$$

(30)

which approaches unity when L approaches infinity.

If the probability for a seed to fall within a distance of L_x is ω, then

$$\omega = 1 - e^{-\lambda L_x}$$

(31)

Thus,

$$\lambda = -\frac{1}{L_x}\ln(1 - \omega)$$

(32)

The probability ω may then be estimated from the proportion of seeds dispersed within the distance L_x. Therefore, the value of λ can be calculated for any given pair of ω and L_x. The probability density functions for two species modeled are illustrated in Fig. 4.
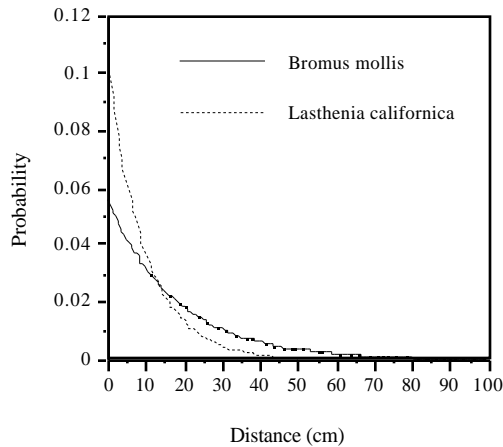

Fig. 4. Probability density function for seed dispersal with respect to distance.

Each patch in the landscape may be both a source and recipient in terms of dispersal. We assume that seeds are randomly distributed within a patch and that they disperse in equal probabilities in all directions. Dispersal stochasticity at the individual level may result in significant consequences for local patch populations with a small number of individuals. To retain this stochasticity it is necessary to disperse seeds individually which greatly increases the computational demand. For each seed to be dispersed, dispersal angle, seed travel distance, landing point, and target patch all have to be calculated or determined (Fig. 5).
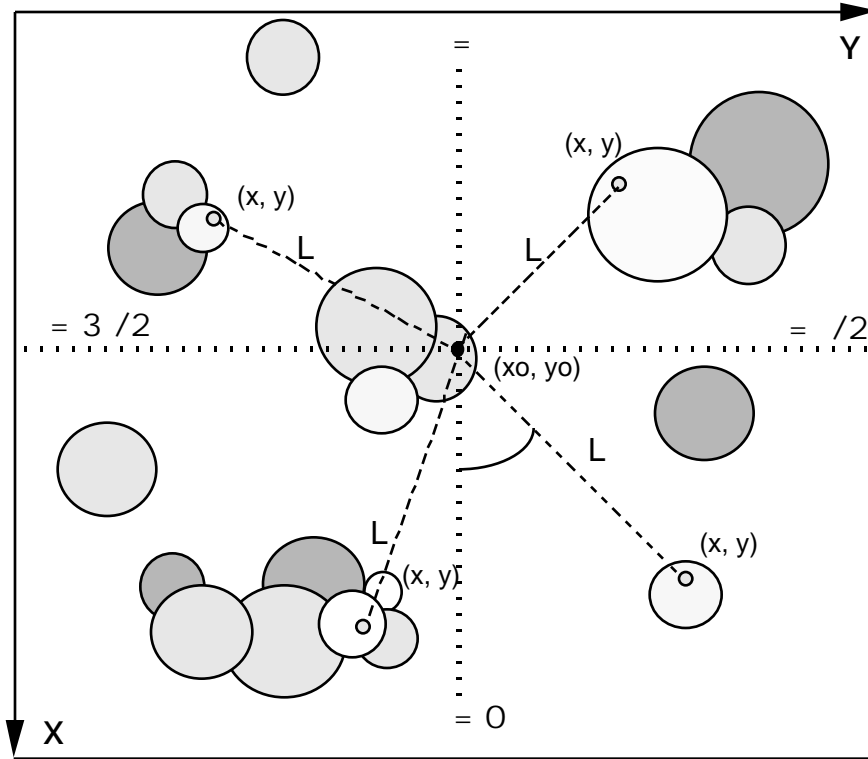
Fig. 5. Illustration of the relation between dispersal angle   and dispersal distance L and the way they are dtermined in the Cartesian system used in the model.

The following algorithm is used to alleviate this problem. We define plant recuitment rate for species i as the product of its germination rate and survivorship (i.e., $r_i = g_i s_i$). Two separate sets of Bernoulli trials are conducted with each seed to be dispersed. The first uses the maximum recruitment rate (r_{max}, $r_{max} = g_{max} s_{max}$)   as the probability of a dispersal event, and reduces the total number of seeds to be dispersed to the number of adult plants that come from these seeds. The second takes the ratio of the actual rate of recruitment (r_p) in patch type p to the maximum rate as the dispersal probability, and this makes an adjustment on the number of adults according to the particular microhabitat. As a result, the number of seeds actually dispersed is reduced to the product of r_{max} and the total number of seeds to be dispersed. The approach is illustrated in Fig. 6.

VII. SIMULATION SCHEME

The spatially explicit patch dynamic model of the Jasper Ridge serpentine grassland has been implemented in C. Fig. 7 depicts the scheme to relate local patch dynamics to landscape level phenomena in this model. A flow chart of the model is shown in Fig. 8, which outlines how the spatial patch dynamic model is constructed and how its different model components are connected. The mode may be run without invoking the plant population dynamic module, which would only simulate the spatiotemporal dynamics of the age- and size-structured gopher mound population. When both disturbance patch and plant population modules are in operation, the model assumes the following simulation scheme.
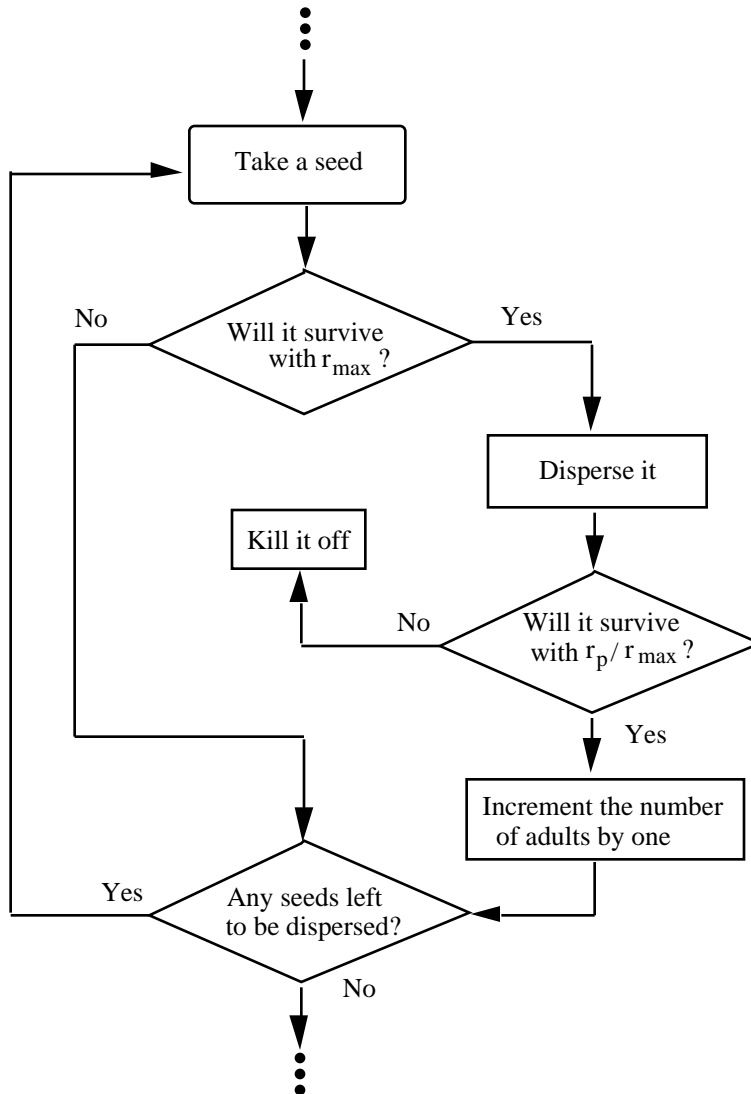
Fig. 6. An illustration for the dispersal algorithm involving two sets of Bernoulli trials. The first reduces the total number of seeds to be dispersed eventually to the number of adult plants out of these seeds; second adjusts the number of adults to the particular microhabitat. The algorithm minimizes the computational time for dispersal while retaining dispersal stochasticity at the individual level.

First of all, the model landscape, represented by a two-dimensional array of bi-directional linked lists, is initialized and input data are read in. A simulation may either start with generating the first patch in a landscape that has previously had no patch, or start with a landscape already covered entirely by various obsolete and effective patches. This landscape initialization -- blanketing the model system with a variety of patches, is accomplished in the first four time steps in the simulation as follows.

To cover the entire landscape with patches before staring the plant population dynamics module, four layers of circular patches are overlaid on another in separate time steps. The patches in the first three layers of the initial blanket are identical, whose diameters are equal to the length of the reference window. The first layer includes (R x C) identical patches where R and C are the numbers of rows and columns of the windows in the reference grid. The centers of these patches are the same as the geometric centers of the reference window. The second layer is composed of (R-1)(C-1) patches whose centers are the intersection points along the reference window boundaries. The third layer consists of [2(R-1)+2(C-1)] patches which are arranged along the four edges of the reference grid. Only for smaller identical patches at the corners make up the fourth layer, whose diameters are one fourth of the reference window length. For a reference grid with 5 x 5 windows, the initial blanket is illustrated in Fig. 9.

Except for initialization, the annual disturbance rate is determined from a probability function at each time step, and the type (April or July mound), spatial location (Cartesian coordinates of the center) and size of a prospective patch are then determined (see previous section). If the overlap between this patch-to-be and any other existing patch is consistent with the maximum overlap ratio requirement, it then becomes a new patch and the sizes of all other patches overlapped by it are consequently adjusted. This patch formation process is repeated until the annual disturbance rate is met.
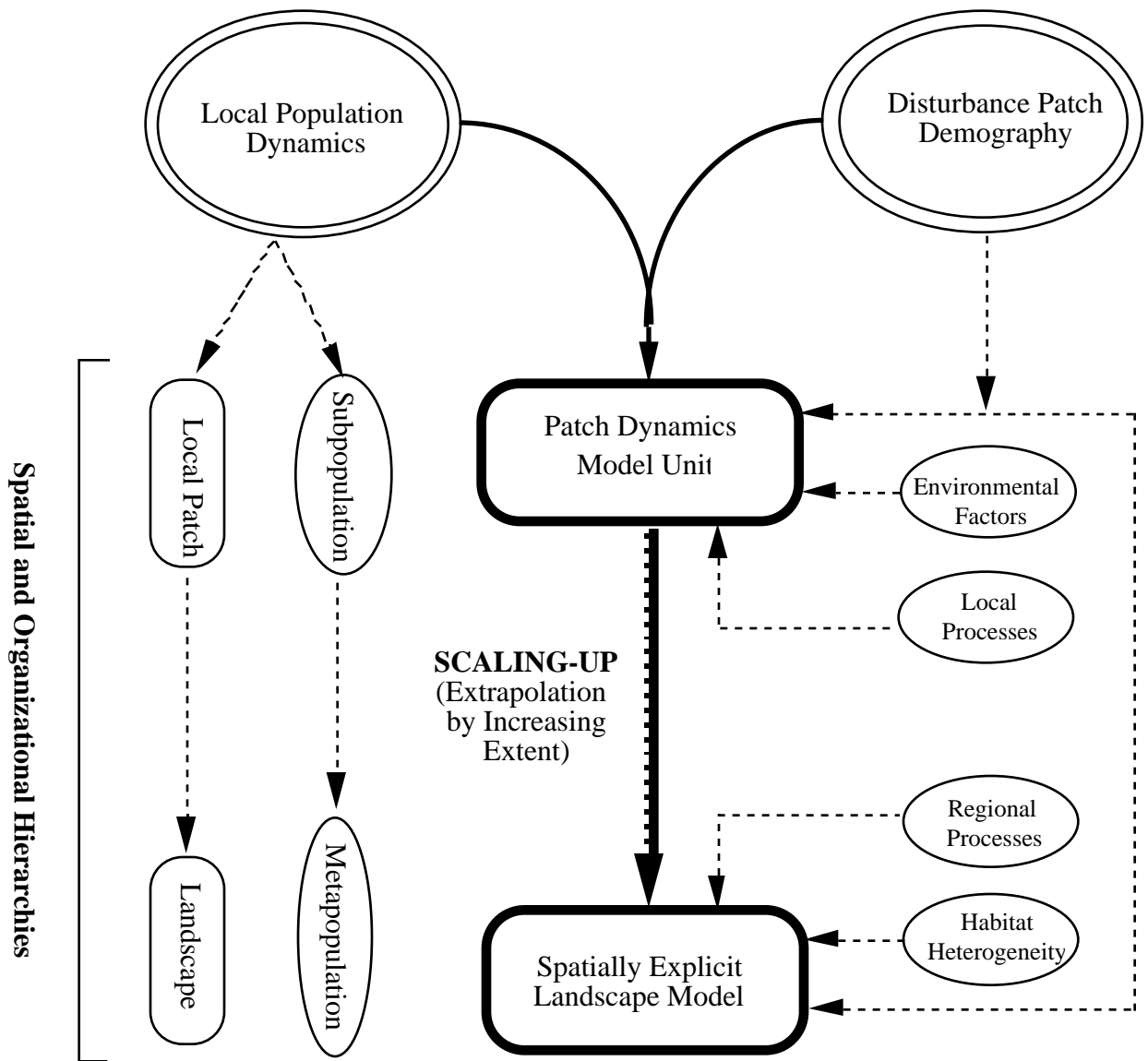
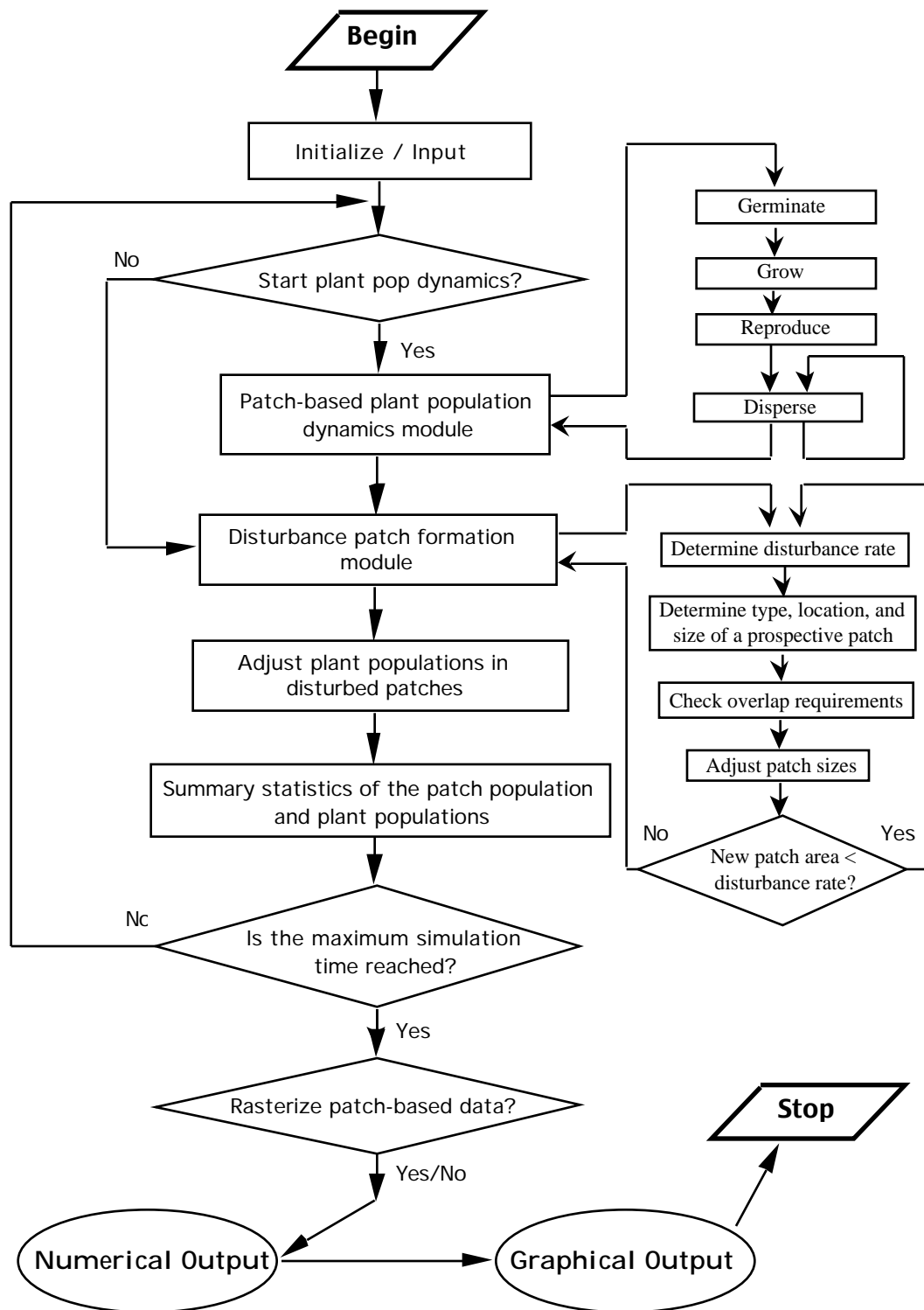Fig. 7. A conceptual scaling framework of the spatical patch dynamics model

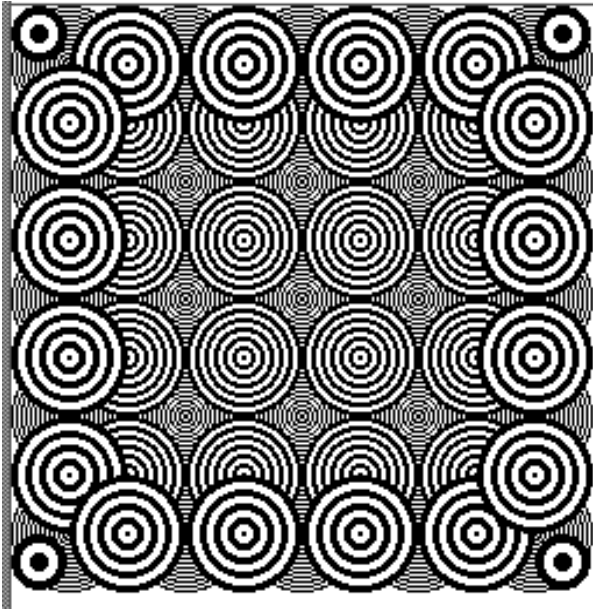FIG. 8. Flow chart of the spatial patch dynamic model.

Fig. 9. Initial "patchy blanket" when the landscape has 25 (5 by 5) reference windows, which are used for computational convenience.

The plant population module begins with the initialization of all, but newly formed, patch units (including obsolete ones) in the landscape with population abundance of species modeled. The initial number of plant adults in each patch is randomly chosen between 0 and the maximum observed in the field for each species (Hobbs and Hobbs 1987). The same sequence of germination, growth, reproduction and dispersal is then repeated once again at each time step. If an existing patch is overlapped by a newly formed one, its plant population abundance is adjusted based on the remaining area. At each specified time step, the simulation model provides a set of statistics of the disturbance patch population and plant populations, including the total number and size of different types of patches, the current size and spatial location of each individual patch, plant population density in each existing patch, and metapopulation density at the landscape level for each species. The final outputs include both numerical and graphical forms. "Bull's eye" maps are generated to depict the spatial distributions of gopher mounds and plant populations. In addition, the patch-based information can be rasterized at the end of simulation for data visualization and analysis.

VIII. Discussion

Patch dynamics as a conceptual framework has increasingly been used in ecology and provided numerous insights into problems of species evolution and adaptation, population dynamics and persistence, community structure and stability, and landscape dynamics since the early 1970's. Field studies have demonstrated that many natural communities can be viewed as mosaics of various patches. While patches of different types often occur on distinct spatial and temporal scales, there are scales on which patches are fundamental to the ecological system. Efforts have been made to apply the patch dynamics conceptualization to development of mathematical models of vegetation dynamics since the work by Levin and Paine (1974). Yet, so far most of these models have been quasi-spatial or spatial on a regular grid. Here I present a spatially explicit patch dynamics modeling approach that is based on the natural spatial unit -- patch. Such an approach is capable of simulating the spatiotemporal dynamics of both an age- and size-structured disturbance patch population and patch-based plant populations, taking into account complexity in disturbance patch distribution and overlapping. While the approach may be computationally demanding, rapid development in today's computing technology has made this possible and practical.

Acknowledgments

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