A patch-based spatial modeling approach: conceptual framework and simulation scheme

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Abstract

Patchiness is ubiquitous across a wide range of scales, and spatial pattern and ecological processes are interdependent and interactive. However, traditional approaches have not been able to incorporate spatial patchiness and pattern-process interactions into modeling frameworks because of their assumptions of homogeneity, equilibrium and determinism. Recently, different modeling approaches have been developed to take into account of spatial heterogeneity and its effects on ecological processes. In this paper, we present a conceptual framework and simulation scheme for a spatially explicit patch dynamic modelling approach. The model structure consists primarily of two submodels: a spatially-explicit, age-/size-structured patch demographic model and a multi-specific population dynamic model. We demonstrate the modeling approach through an example, and also present alternative formulations and algorithms for implementing different parts of the model. While most existing spatial models are grid-based, the patch-based spatial modeling approach provides a unique, alternative way of studying pattern and process in ecological systems. © 1997 Elsevier Science B.V.

Keywords: Framework; Simulation scheme; Spatial modeling

1. Introduction

Ecological systems exhibit patchiness in structure, function, and dynamics across a range of spatial, temporal, and organizational scales (Ko-

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lasa and Pickett, 1991; Wu and Loucks, 1995). Coupling spatial pattern with ecological processes has recently become a major theme in both theoretical and empirical ecology (Levin, 1992; Wiens et al., 1993; Wu and Levin, 1994). Patch dynamics emphasizes spatial and temporal heterogeneity, non-equilibrium properties, and scale-dependence of ecological systems, and facilitates the coupling between pattern and process (Levin and Paine,

1974; Pickett and White, 1985; Levin et al., 1993; Wu and Loucks, 1995).

In linking spatial pattern with ecological processes, spatial models are indispensable. Levin and Paine (1974) argued that the patch is the natural unit for modeling many marine and terrestrial systems, exhibiting dynamics on characteristic spatial and temporal scales that control system behavior. Still, most spatial models are grid or raster based, in which patches are considered as single cells or aggregates of multiple cells within a regularly divided grid (e.g. Smith and Urban, 1988; Turner and Gardner, 1991). Such a raster approach is difficult or unrealistic in dealing with overlapping among patches that are dynamic. On the other end of the spectrum, individual-based spatial models keep track of the location and dynamics of all individual organisms (e.g. Pacala and Silander, 1985). The application of this approach can be seriously limited by increased model complexity and computational demand as the study area expands, and a central challenge is to aggregate to simplify. Here we, therefore, present a patch-based spatial modeling approach that deals with patch overlap explicitly.

2. Model conceptualization: ecological systems as hierarchical dynamic mosaics of patches

Ecological systems have typically been perceived and studied in terms of populations, communities, and ecosystems. While these organizational units can facilitate both theoretical and empirical studies in several ways, their internal homogeneity is frequently assumed implicitly. In general, the validity of this assumption is dependent on the questions being addressed; but for a wide variety of questions, spatial heterogeneity has been shown to be essential to understanding system dynamics. In recent years, there has been a shift in attention in ecology, from equilibrium to non-equilibrium, from homogeneous to heterogeneous, from deterministic to stochastic, and from consideration of single scales to the relations among scales (see discussions in Wu and Loucks, 1995). With this transition, there has been increasing recognition that ecological systems are hierar-

chical mosaic systems of patches that differ in size, shape, and successional stage (Levin and Paine, 1974; Loucks et al., 1985; Kotliar and Wiens, 1990; Wu and Loucks, 1995). In this approach, the patch becomes a fundamental structural and functional unit. This conceptualization is not contradictory but complementary to the traditional organizational hierarchy.

The patch dynamics concept dates back to the 'pattern-process hypothesis' by Watt (1947). Since the 1970s, patch dynamics has become a central theme in ecology through a number of theoretical and empirical studies at different organizational levels (See Levin and Paine, 1974; Paine and Levin, 1981; Pickett and White, 1985; Levin et al., 1993; Wu and Loucks, 1995 for reviews). Such a perspective is particularly ostensible in the 'waveform dynamics' hypothesis (Loucks, 1970), the intertidal landscape patch model (Levin and Paine, 1974, 1975), the patch mosaic concept for plant communities (Whittaker and Levin, 1977; Steele, 1978), the 'minimum dynamic area' concept for terrestrial ecosystems (Pickett and Thompson, 1978), the 'shifting mosaic steady state' hypothesis (Bormann and Likens, 1979), and the mosaic-cycle concept of ecosystems (Remmert, 1991). The patch dynamics perspective has had pervasive influences on a wide range of studies in community ecology (e.g. Pickett and White, 1985; Collins, 1989), metapopulation dynamics (Levins, 1970; Gilpin and Hanski, 1991; Levin et al., 1993; Wu et al., 1993; Wu and Levin, 1994), and landscape ecology (e.g. Forman and Godron, 1986; Wu and Levin, 1994).

Based on the patch dynamics perspective, many ecological systems may be considered as hierarchical, dynamic patch mosaics, generated and maintained by processes of patch formation, patch development, and disappearance (Fig. 1). Both natural and anthropogenic disturbances (e.g. fire, grazing, fragmentation) are frequently responsible for these processes (Wu and Loucks, 1995). Usually, disturbances create patchiness in ecological systems through physical destruction, in which the type, intensity, and frequency of disturbances may all play an important role. Within-patch succession or patch development, which is affected by numerous biological and physical factors, takes
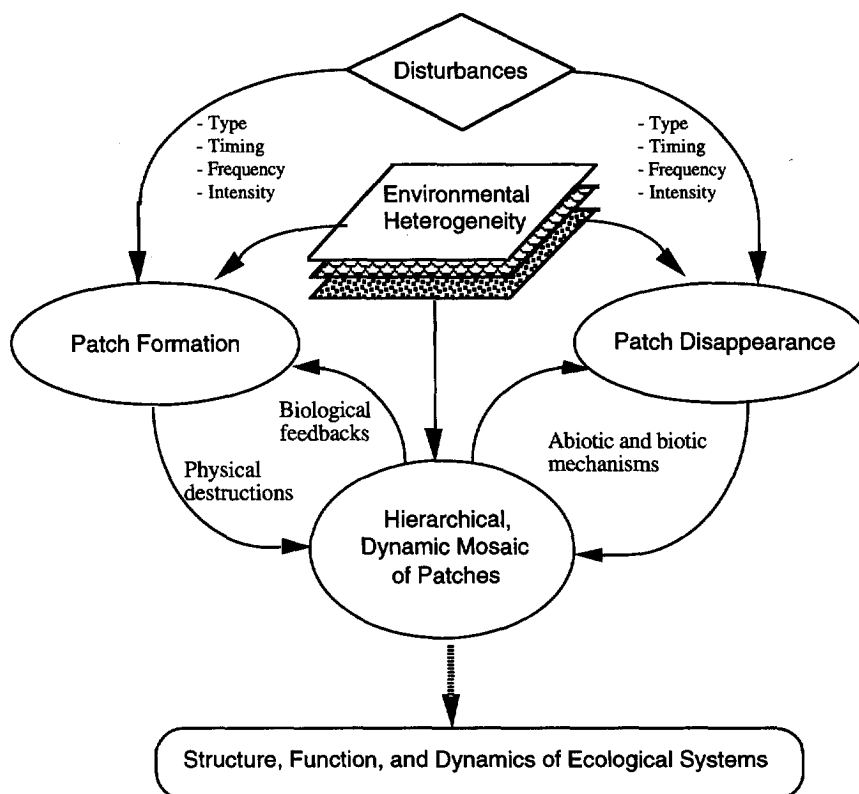
Fig. 1. A patch dynamics conceptualization of ecological systems (e.g. populations, communities, ecosystems, or landscapes). Natural and anthropogenic disturbances and environmental heterogeneity on different scales frequently induce patchiness in time and space. The structure, function, and dynamics of an ecological system are determined by individual patches and their interactions at different hierarchical levels.

place following disturbances. Feedbacks exist between the patch dynamic processes and the existing ecological mosaic system, although their importance may vary in different ecosystems. All these aspects may be complicated further by heterogeneity in underlying physical environment (e.g. topography, soil, and climatic factors). The structure, function, and dynamics of an ecological system are determined by individual patches and their interactions at different hierarchical levels.

A general bottom-up approach to modelling such patchy ecological systems involves accounting for the dynamics of pattern and processes on a range of distinct levels (Wu, 1993): the local individual patch, the patch aggregate, and the landscape (Fig. 2). The local patch dynamics model (or the patch dynamics model unit,

PDMU) is composed of a mechanistic or phenomenological model of processes (e.g. population dynamics or nutrient cycling) and a model of disturbance patch demography. Environmental factors that affect the processes of study at the local scale are also considered in the PDMU. By incorporating pattern and processes that operate on larger scales, these local patch models can be scaled up to give rise to a landscape-level patch dynamics model (Fig. 2). Although this conceptual framework holds for many systems and is useful to model-building, the biological connotation of patch dynamics and mathematical details may vary greatly depending on questions to be addressed. In the following section, we illustrate how to implement this modeling approach based on a grassland ecosystem. Because the basic struc-
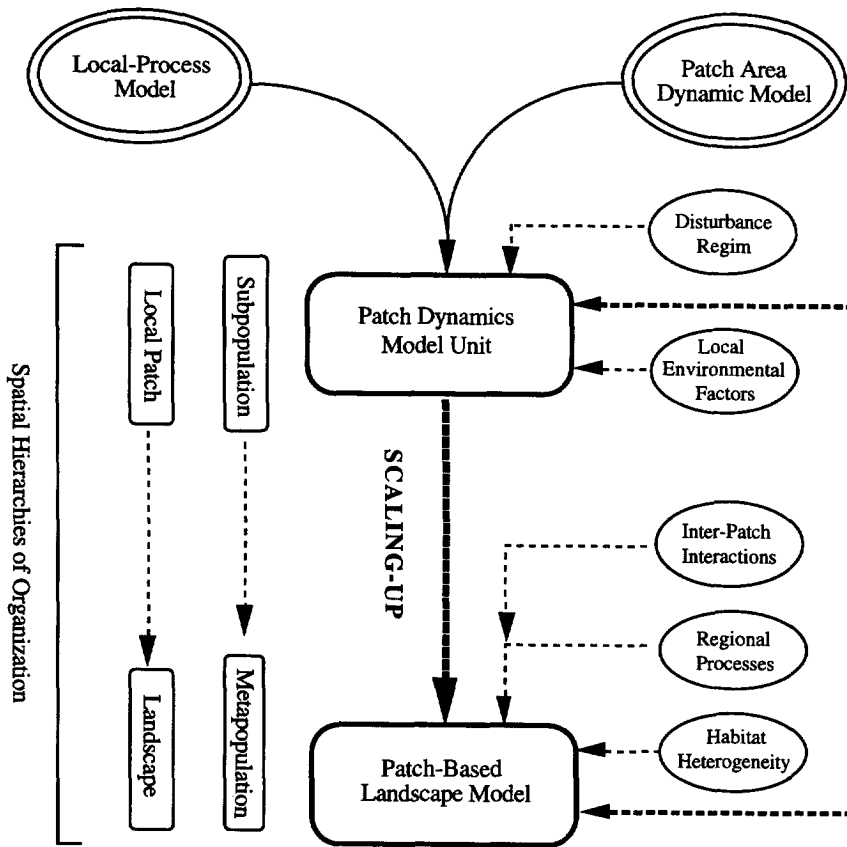
Fig. 2. A hierarchical patch dynamics modeling framework, illustrating how patch-level processes scale up to the landscape level.

ture and simulation results of the spatial patch dynamic grassland model were presented elsewhere (Wu, 1993; Wu and Levin, 1994), here we will focus on several modeling aspects with alternative mathematical formulations that have not been discussed in detail previously.

3. Model structure and implementation: an example from the Jasper Ridge serpentine grassland

In this section, we will demonstrate how the spatial patch-based modelling approach can be implemented through an example based on the serpentine annual grassland in the Jasper Ridge Biological Preserve of Stanford University in San Mateo County, California. Because a general de-

scription of the model has been given elsewhere (Wu and Levin, 1994), here we will focus primarily on several key modelling processes that were not covered or only briefly discussed previously. Alternative algorithms will be presented whenever appropriate.

The serpentine grassland is dominated by a relatively high diversity of annual native forbs (e.g. *Lasthenia californica*, *Plantago erecta*, and *Calycadenia multiglandulosa*) and perennial bunch grasses (e.g. *Stipa pulchra*, *Sitanion jubatum*; see McNaughton, 1968 and Hobbs and Mooney, 1985 for descriptions of the soil, plant communities, and landscape characteristics). As in many other ecosystems, localized disturbances play an important role in shaping the structure and function of this annual grassland. In particular, the burrowing activities of western pocket gophers

(*Thomomys bottae*) account for a major component of the disturbance regime. By bringing excavated soil material from underneath to the surface, gophers create approximately round mounds of bare soil of up to 50 cm in diameter. 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. This apparently resembles the situation of treefalls in many forests where a similar sequence of ecological processes operate, which is often called 'gap dynamics' (Runkle, 1981, 1982; Shugart, 1984) or 'mosaic cycle' (Remmert, 1991; Wissel, 1991). These disturbance-induced patches exhibit a series of different phases: nudation or patch formation, dispersal and colonization, plant establishment, intraspecific and interspecific competition, and achievement of the pre-disturbance state. Gopher disturbances continue throughout the year, with higher intensities in April and July. Each year as much as more than 20% of the total area is turned over by gopher activity, resulting in changes in vegetation composition and spatio-temporal distribution of plant species (Hobbs and Mooney, 1985, 1991).

We chose the Jasper Ridge serpentine annual grassland as the model system for several reasons. First of all, the dynamics of gopher mounds, like tree gaps in forests, can be easily conceptualized following the patch dynamics perspective. Secondly, gopher mounds are easy to observe and quantify in terms of number, size, and distribution. In addition, the rapid dynamics of annual plant populations and availability of field data make possible the parameterization of the simulation model. Thus, the annual grassland landscape is conceptualized as a patch mosaic of gopher mounds of different size, age, and species composition.

In general, the spatial patch dynamic model is composed of two submodels: a spatially-explicit, age-/size-structured patch demographic model, which is a spatial extension of the Levin-Paine model (1974, 1975), and a multi-specific plant population dynamic model of a non-equilibrium island biogeographic type. The spatial patch demographic submodel simulates the dynamics of disturbance regime (rate and spatial and temporal distribution of disturbance) and the change of the age- and size-structured gopher mound population in both time and space. The plant population dynamic submodel keeps track of spatial and temporal changes in plant density within each individual patch. Parameterization of the model is based mostly on available field data, while, for some whose values are not obtainable from the existing field information, biologically sensible estimation is applied as indicated herein. In the following, we present a more detailed description of the spatial patch dynamic model, with alternative formulations for several model components.

3.1. Modelling disturbance patch demography

Disturbance patches (gopher mounds in this case) are classified into two groups: obsolete patches and effective patches. Obsolete patches refer to patches that are older than a maximum patch age and essentially represent the non-patch (undisturbed) areas. The maximum patch age is an indicator of change in soil conditions of the gopher mounds. We realize that it may be affected by within-patch vegetation dynamics through biological feedback, but the current version of the model does not take this into account for simplicity. Effective patches are those whose age is smaller than the maximum patch age. Patch age is related to soil conditions, which significantly affect plant growth processes. While the obsolete patches are treated as the same, effective patches of different age essentially represent different microhabitats for plant populations. To simulate the spatial and temporal dynamics of the disturbance patch population, we develop a spatially explicit, age- and size-structured model.

3.1.1. Patch shape, size distribution, and disturbance rate

Based on field observation, we assume that all individual patches at birth are circular in shape. A lognormal size distribution for new patches is used in the model (see Paine and Levin, 1981), with the minimum and maximum sizes being 10 and 50 cm in diameter, respectively. That is,

$$\ln A \sim N(m, \sigma^2), \tag{1}$$

where A is the patch area at birth, and m and σ are the mean and standard deviation of the normal distribution. m is obtained using the mean patch diameter, and σ is determined in such a way that the resulting lognormal distribution of patch size fit the range reasonably well. For example, when the mean patch diameter is 30 cm, $m = 6.5608$, and $\sigma = 0.35$. Truncation at the tails is necessary and can be done easily by considering the minimum and maximum size of new patches. The assumption of patch size distribution is consistent with field data showing that intercepted patch length along a one-dimensional transect in the serpentine grassland appears to follow a lognormal distribution (Moloney, 1993). This assumption also was found plausible for tree gaps in some old-growth mesic forests of eastern North America (Runkle, 1982) and wave-generated patches in an intertidal landscape (Levin and Paine, 1975; Paine and Levin, 1981). However, note that, after birth, patches may change greatly in both shape and size because they may be overlapped by younger patches.

Field observations show considerable interannual variability in disturbance rate (Hobbs and Mooney, 1991). Here disturbance rate is defined as the percentage of the total area of study disturbed by gopher activities per year. Disturbance rate may be modelled as temporally uncorrelated or correlated events. For this particular system, a lognormal model (Fig. 3) seems plausible in that smaller gopher mounds are more frequently found than larger ones in the field (Hobbs and Mooney, 1991; Moloney et al., 1992).

3.1.2. Spatial pattern of disturbance patches

Field observations show that new gopher mounds are usually positively correlated to those formed in the previous years in their spatial locations (Hobbs and Mooney, 1991). This correlation in space and time may be related to the behavioral characteristics of gophers (see Cox, 1990; Reichman et al., 1982). Positive spatial autocorrelation may be introduced by assigning conditional probability to new patches according to the distance to patches formed in the previous year. To do this,

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

$$\begin{cases} \varphi_p(L_p) = 0 & L_p < L_{min} \\ \varphi_p(L_p) = \lambda_p e^{-\lambda_p(L_p - L_{min})} & L_p \ge L_{min}, \end{cases} \tag{2}$$

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
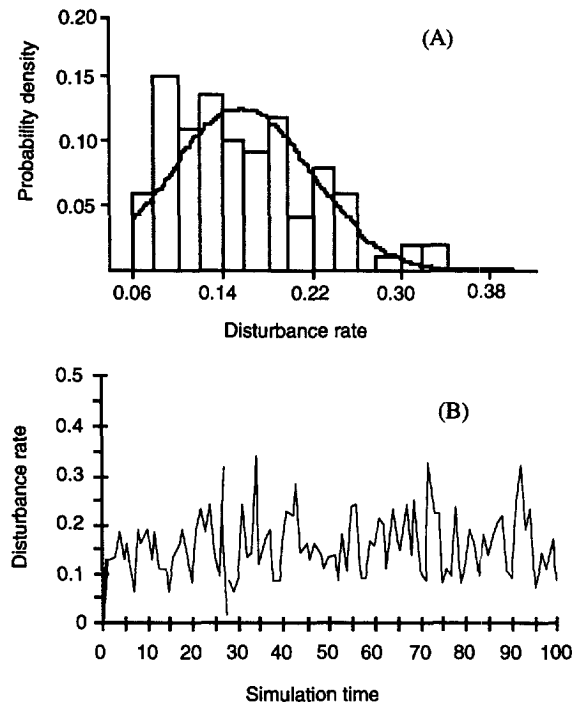

Fig. 3. Probability density function with respect to disturbance rate and a time series of disturbance rate obtained from a simulation. Disturbance rate is modelled using a lognormal distribution (i.e. $\ln R \sim N(m, \sigma^2)$, where R is disturbance rate, $m = -1.897$ (i.e. a mean disturbance rate of 0.15), and $\sigma = 0.4$. Truncation is applied at disturbance rate of 0.05 and 0.35, respectively.

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 previous year 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 2π 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 the bounds set for 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; therefore, spatial patterns of disturbance patches revealed from aerial photos or other remotely sensed images can be simulated. Alternatively, a patch influence index method may be used (see Appendix A).

The overlap of a new gopher mound with an existing mound is likely to increase with the age of the existing mound (Wu and Levin, 1994), perhaps due to the scarcity in food supply. As a first approximation, a hyperbolic relationship equation may be used to describe such an effect. We 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

$$OLR_{max}(\tau) = \frac{1}{1 + \left(\dfrac{1}{OLR_0} - 1\right) e^{-\gamma(\tau - 1)}},$$

$$\tau = 1, 2, ..., a_{max}, \tag{3}$$

where $OLR_{max}(\tau)$ is the overlap ratio, OLR_o 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.

3.1.3. Definition and estimation of the effective patch area

The spatial patch dynamics modelling approach entails the calculation of the effective size of each patch in the landscape at each simulation time 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 of concern 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, we must calculate the overlapping areas of a varying number of patches of different size and age (see Appendix B). In general, the effective area of a patch that is submerged in a mosaic of patches of different age and size can be written as

$$A_j^* = A_i \cap \left(\bigcup_{j=1, j \neq 1}^{m} A_j \right)^c \tag{4}$$

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.

Eq. (4) 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. When the number of patches involved is larger than two, an analytical solution for overlapping areas among them be-

Table 1
List of parameters used in the model simulations

Microhabitat	Species name	Max fecundity (seeds/plt)	Germination rate (%)	Survivorship (%)	Above-ground biomass (mg)
Undisturbed	*Bromus*	11.00	0.30	0.50	39.60
	Lasthenia	22.00	0.15	0.60	10.20
Gopher Mounds	*Bromus*	16.00	0.40	0.80	—
	Lasthenia	27.00	0.20	0.75	—

Values are obtained from Hobbs and Mooney (1985, 1991) and Hobbs and Hobbs (1987).

comes extremely difficult, if ever possible (see Appendix B). We have developed a 'second-order overlapping moving window' algorithm using a Monte Carlo integration method to estimate the overlaps among any number of patches. The basic idea is 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 overlap them (the second-order overlapping patches). Then, effective sizes for the patches affected by the new disturbance are calculated through a Monte Carlo integration within the restricted region. We found that the accuracy in calculating patch areas was very satisfactory. For example, a sample output showed that when the actual patch area was 63.62% of the entire model landscape, the estimated value using the Monte Carlo integration method was 63.08%.

3.2. Modelling plant population dynamics at the patch level

The patch-based, multiple-specific plant population dynamic model simulates demographic processes, including germination, survival, and seed reproduction, which are affected by microhabitat conditions (represented by different patch age classes). Within patches, both intraspecific and interspecific competition are considered as they influence the seed production 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. For the sake of demonstrating the modeling approach, only two species, *Bromus mollis* and *Lasthenia californica*, will be included in the simulations discussed in this paper. Table 1 lists the values of demographic parameters for the two species in undisturbed and disturbed areas.

3.2.1. Plant population demography

The plant population dynamics at the patch scale is modelled as:

$$N_{i,t+1} = (N_{i,t}f_{i,t} + I_{i,t} - D_{i,t})(A_{t+1}/A_t)g_i s_i, \quad (5)$$

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 sizes at times $t+1$ and t, respectively ($A_{t+1} \leq A_t$). 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 proportionally decreases the plant population size in that patch.

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

$$f_i = \text{RMP}_i \, \text{AMP}_i f_i^*(H)\left(1 + \alpha_i\left(\sum_{j=1}^{m} B_{ij}n_j\right)\right)^{-q_i},$$
$$(6)$$

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, $1/n_{\mathrm{crit}}$ 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 $1/n_{\mathrm{crit}}$. 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.:

$$\beta_{ij} = \alpha_w \frac{W_j}{W_i},\tag{7}$$

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.

3.2.2. Effect of environmental resources on demographic parameters

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. The recovery of soil conditions may take place rather rapidly at first after disturbance and then slow down when the predisturbance 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:

$$\frac{\mathrm{d}Y_G(\tau)}{\mathrm{d}\tau} = -\eta(Y_G(\tau) - Y_u),\tag{8}$$

or

$$Y_G(\tau) = Y_u + (Y_G^* - Y_u)\,\mathrm{e}^{-\eta(\tau - 1)},\tag{9}$$

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 η is a constant that determines the pace of the exponential decay. All the above parameters are species-specific.

Let $\mathrm{AMP} = Y_G(\tau)/Y_G^*$ and call this ratio the patch age multiplier; then we have

$$\mathrm{AMP} = \frac{Y_u}{Y_G^*} + \left(1 - \frac{Y_u}{Y_G^*}\right)\mathrm{e}^{-\eta(\tau - 1)}.\tag{10}$$

AMP is equal to 1 when patch age is 1 and asymptotically approaches Y_u/Y_G^* when patch age gets larger (Fig. 4A). Of course, AMP is also species specific. For computational convenience, we set AMP to Y_u/Y_G^* when patch age is larger than $\tau_{\max}$, which is the empirically estimated, maximum time for the difference in soil characteristics between the different microhabitats to disappear (see Fig. 4a).

To estimate η, we assume that it takes t_r years for $Y_G(\tau)$ to decrease to a fraction ζ of the predisturbance level. That is, when $\tau = t_r + 1$

$$\frac{Y_{\mathrm{G}}(\tau)}{Y_{\mathrm{u}}} = \xi. \tag{11}$$

From Eq. (9), we have

$$\eta = \frac{1}{t_{\mathrm{r}}} \ln \frac{Y_{\mathrm{G}}^* - Y_{\mathrm{u}}}{(\xi - 1)Y_{\mathrm{u}}}. \tag{12}$$

Alternatively to Eq. (8), if plant demographic parameters change gradually at a constant rate, then we have:

$$Y_{\mathrm{G}}(\tau) = Y_{\mathrm{G}}^* = Y_{\mathrm{G}}^* - \frac{(Y_{\mathrm{G}}^* - Y_{\mathrm{u}})}{(\tau_{\max} - 1)},$$

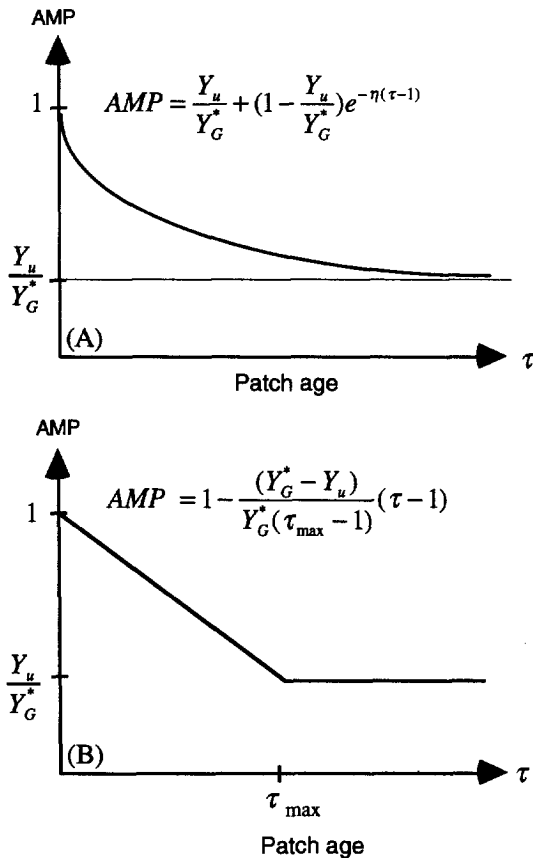$$\text{for } \tau = 1, 2, \ldots, \tau_{\max} \tag{13}$$

Fig. 4. Relationship between plant demographic parameters and patch age. (A) An exponential model, and (B) A linear model. 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).

$$Y_{\mathrm{G}}(\tau) = Y_{\mathrm{u}}, \qquad \text{for } \tau > \tau_{\max}. \tag{14}$$

Then,

$$\text{AMP} = 1 - \frac{(Y_{\mathrm{G}}^* - Y_{\mathrm{u}})}{Y_{\mathrm{G}}^*(\tau_{\max} - 1)} (\tau - 1), \tag{15}$$

i.e.

$$\text{AMP} = 1 - \left(1 - \frac{Y_{\mathrm{u}}}{Y_{\mathrm{G}}^*}\right) \frac{(\tau - 1)}{(\tau_{\max} - 1)}$$

$$\text{for } \tau = 1, 2, \ldots, \tau_{\max} \tag{16}$$

and

$$\text{AMP} = Y_{\mathrm{u}}/Y_{\mathrm{G}}^* \qquad \text{for } \tau > \tau_{\max} \tag{17}$$

AMP assumes values between $Y_{\mathrm{u}}/Y_{\mathrm{G}}^*$ (when $\tau \geq \tau_{\max}$) and 1 (when $\tau = 1$; see Fig. 4B).

3.3. Seed dispersal in mosaics of patches

Disturbance patches of different age are essentially different microhabitats in which plant demographic parameters (e.g. germination, survivorship, and fecundity) vary. To take into account this heterogeneity, seed dispersal has to be modelled on the individual patch basis in terms of both source and target patches. Modelling of dispersion of organisms and their propagules is necessary for many studies ranging from population dynamics to landscape ecology, and different types of models have been proposed (e.g. Frampton et al., 1942; Werner, 1975; DeAngelis et al., 1986; Okubo and Levin, 1989). Nevertheless, modelling dispersal in mosaics of heterogeneous patches of different size and shape poses both conceptual and computational challenges. In the following, we will discuss how dispersal is modelled in such patch mosaics.

The relationship between the number of dispersed seeds and travel distance from the source is an important part of the dispersal model. Although this relationship may be affected by numerous physical and biological factors (e.g. the terminal settling velocity, wind speed and turbulence, seed release height, and specific morphological adaptations for dispersal; see Augspurger and Franson, 1987; Okubo and Levin, 1989), two simple phenomenological models (the negative exponential and the inverse power equation) have

long been used with reasonable success for modelling dispersal. The negative exponential model is preferable in a mathematical sense because the solution to the equation is bounded when distance is approaching zero. We will use the exponential model to develop the simulation algorithm for seed dispersal, although different dispersal-distance relationships may be more suitable for certain situations.

The exponential dispersal model can be written as:

$$\varphi(L) = \lambda\, e^{-\lambda L}, \tag{18}$$

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. The probability density function can be easily integrated to obtain the cumulative probability function,

$$\Phi(L) = \int \varphi(L)\, \mathrm{d}L = 1 - e^{-\lambda L}, \tag{19}$$

which approaches unity when L approaches the positive infinity.

Obviously, λ must be estimated before this model can be used to determine how far a particular seed will fall. λ can be readily obtained from field data as follows. Suppose that the probability for a seed to fall within a distance of L_x is ω: then

$$\omega = 1 - e^{-\lambda L_x}, \tag{20}$$

and, thus,

$$\lambda = -\frac{1}{L_x} \ln(1 - \omega). \tag{21}$$

The probability ω may 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. Table 2 gives the
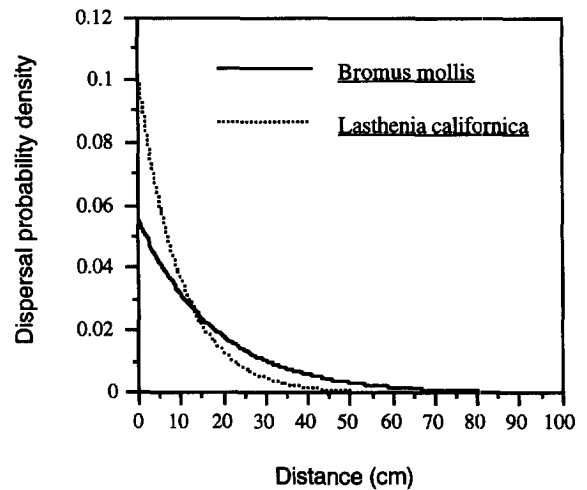

Fig. 5. The probability density functions of seed dispersal with respect to distance for *Bromus mollis* and *Lasthenia californica*.

values of λ for two species in the serpentine grassland, and the probability density functions with respect to distance are illustrated in Fig. 5.

We have developed a general procedure for seed dispersal in this patchy system that is based on the following assumptions. First, seeds disperse away from the center of the source patch with equal probability in all directions. Second, dispersal probability decreases exponentially with distance away from the source patch. Third, seeds are randomly distributed within a patch. Fourth, each patch in the landscape may be both a source and recipient patch during dispersal. We have developed a procedure for each seed to be dispersed. The procedure includes seven steps in a loop (see Fig. 6 for a schematic representation of the variables and their relations):

1. select a source patch in which there is at least one seed present at the dispersal time;
2. locate a random position within the effective area of the source patch;
3. randomly determine a dispersal angle (θ) between 0 and 2π;
4. determine dispersal distance (e.g. from $L(\varphi) = 1/\lambda \ln \lambda/\varphi$, where $0 \le \varphi \le \lambda$);
5. determine the spatial position of the landing point for a given pair of θ and L (from equations: $x = x_0 + L \cos\theta$, $y = y_0 + L \sin\theta$, where $0 \le \theta \le 2\pi$);

Table 2
Estimation of λ by assuming a negative exponential dispersal function, based on field data (Hobbs and Mooney, 1985)

Species	Inflorescence height (cm)	Proportion of seeds within a 25 cm radius (%)	Dispersal decay coeff λ (per cm)	Critical pop density n_{crit} (no. indiv./cm^2)	Fecundity density coeff α (cm^2/plant)	Initial max pop density (no. indiv./cm^2)
Bromus	19.90	75	0.0555	0.02	25.00	0.2
Lasthenia	12.20	90	0.0921	0.25	8.00	0.35

6. identify the recipient patch according the spatial location determined in the previous step and update its seed bank; and

7. repeat the above steps until seeds in all patches have been dispersed.

Dispersing all seeds one by one following the above procedure may become formidably demanding in computation if the number of seeds is considerably large. Therefore, we have tried to develop an algorithm that reduces the computing time by 'dispersing' seedlings or adults instead of seeds. If all patches in a landscape have the same demographic parameters (i.e. belonging to the same type of microhabitat), this can be easily done. In such a case, dispersing seeds among patches is essentially the same as dispersing seedlings (or adults) by multiplying a universal germination rate (or the product of germination rate and survivorship) to the total number of seeds produced in a source patch. However, in reality germination rate and survivorship may vary in different patches; thus the abovementioned method becomes unrealistic.

To account for microhabitat heterogeneity, the algorithm involves two separate sets of Bernoulli trials with each seed to be dispersed (Fig. 7). We
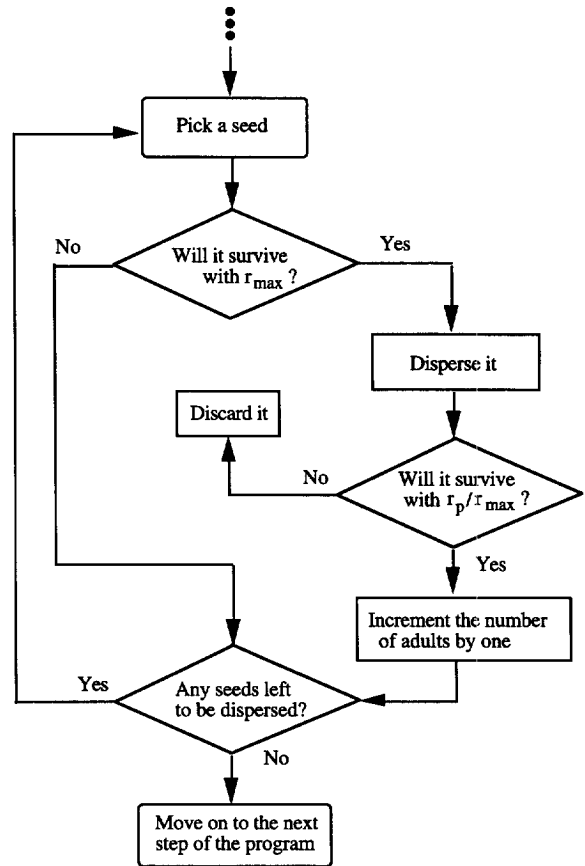

Fig. 7. The flow chart for the dispersal algorithm involving two sets of Bernoulli trials. The first reduces the total number of seeds to be dispersed eventually to the number of adult plants out of these seeds; second adjusts the number of adults to the particular microhabitat. The algoroithm minimizes the computational time for dispersal while retaining dispersal stochasticity at the individual level.

$$x = x_0 + L\cos\Theta, \; y = y_0 + L\sin\Theta \;\; (0 \le \Theta \le 2\pi)$$

Fig. 6. A schematic representation of the relation among a source pathc, a recipient patch, dispersal angle Θ, and seed travel distance L. It also illustrate how dispersal parameters are determined in a Cartesian system.

define plant recruitment rate for species i as the product of its germination rate and survivorship (i.e. $r_i = g_i s_i$). The first uses the maximum recruitment rate ($r_{max} = g_{max} s_{max}$) as the probability for dispersal, which reduces the number of dispersal events from the total number of seeds to the number of adult plants that will 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
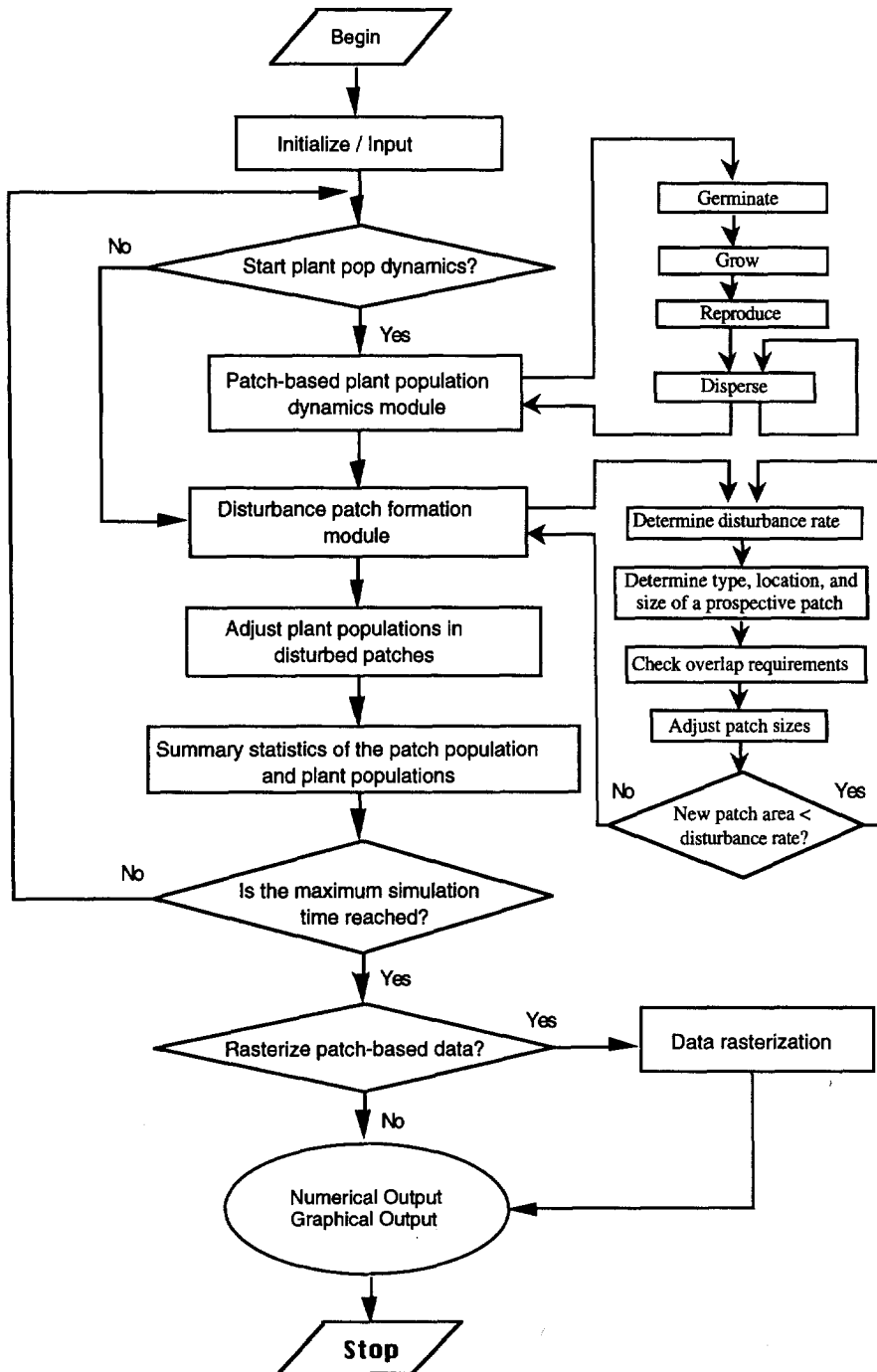
Fig. 8. The flow chart of the spatially explicit patch dynamic model for the Jasper Ridge serpentine grassland (PatchMod).

reduced to the product of r_{max} and the total number of seeds to be dispersed.

3.4. Model simulation

Fig. 8 is a flowchart depicting the scheme to link the disturbance patch population model with the plant population model, and to scale local patch dynamics to the landscape level. The model 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. First of all, the model landscape is initialized and input data are read in. A simulation may either start with generating the first patch in an 'empty' landscape, or begin with a landscape that is already entirely covered by various patches. The second approach requires landscape initialization.

If the initialization option is chosen, the current version of the model uses the 'patchy blanket method' which covers the entire landscape with four layers of patches in the first four time steps before staring the plant population dynamics model (see Fig. 9). The patches in the first three layers are identical, whose diameters are equal to the length of the reference window (a square cell of the reference grid overlaid on the model landscape for programming convenience). The first layer includes $(R \times C)$ identical patches, where R and C are the numbers of rows and columns of 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 in the reference grid. The third layer consists of $2(R - 1) + 2(C - 1)$ patches, which are arranged along the four edges of the reference grid. Only four smaller identical patches at the corners make up the fourth layer, whose diameters are one fourth of the reference window length. Fig. 9 gives an example in which the model landscape consists of 5×5 reference windows.

The plant population module begins with initializing all patches, except those formed at this time step, in the landscape with randomly determined population densities (Fig. 8). The initial number of plant adults in each patch is randomly chosen between 0 and the maximum observed in the field for each species. 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 newly formed ones, its plant population abundance is adjusted based on the remaining area (see Eq. (5)).

Spatial models of this type can produce a wide range of information that is pertinent to understanding pattern and process dynamics in ecological systems. In particular, the outputs of the model PatchMod include the number and size of different types of patches, current size and spatial location of individual patches, plant population density in each patch, metapopulation density of modelled species at the landscape level, and spatial distribution of disturbance patches and plant populations. All the patch-based outputs may come out in both numerical and graphical forms. Some examples of the simulation results from
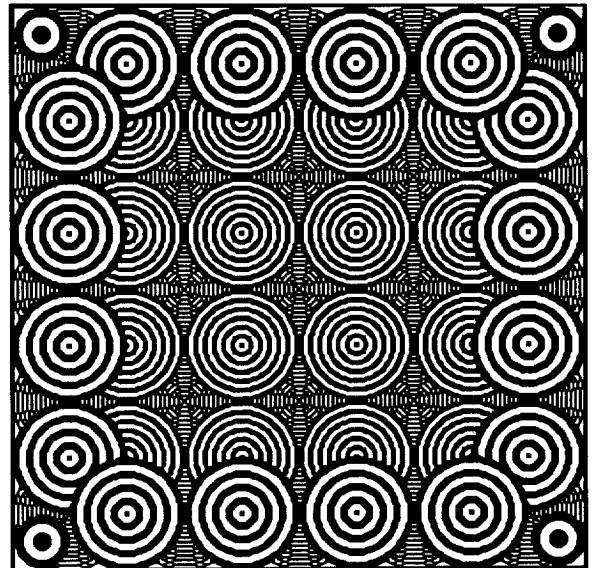

Fig. 9. An example of landscape initialization using the 'patchy blanket method,' where the model landscape contains 25 (5×5) reference windows.
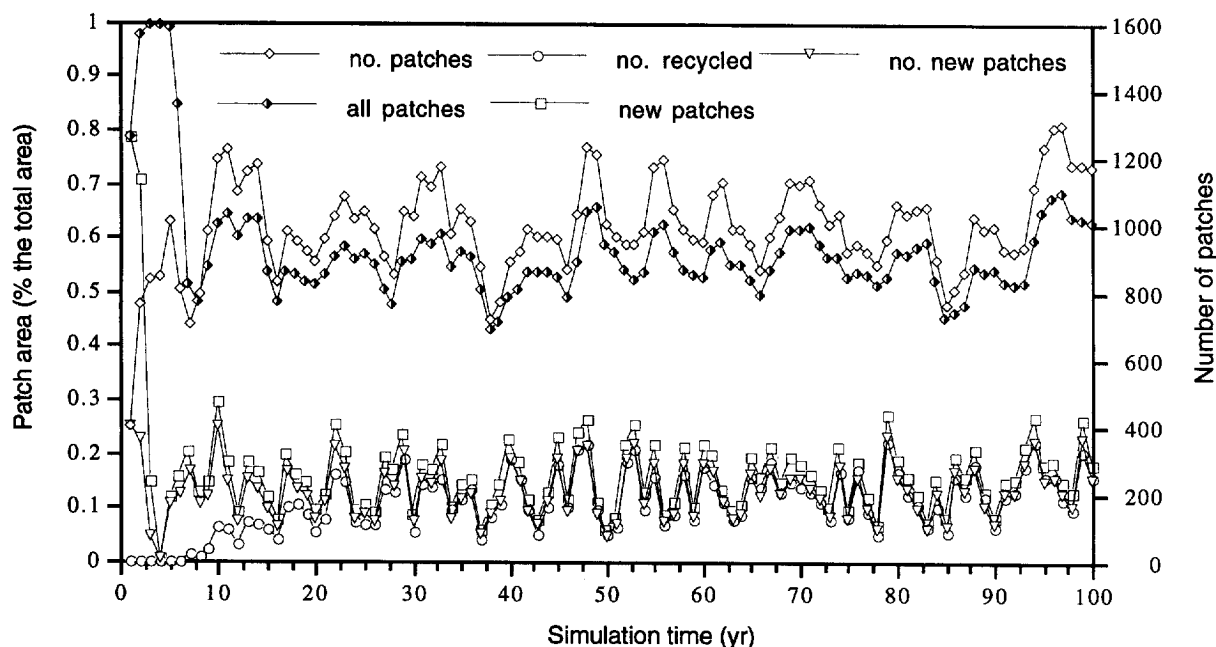
Fig. 10. Simulated temporal dynamics of the area and number of differnet types of patches, where all patches include obsolete and effective patches, new patches are those formed in the year, and recycled patches are those that are completely buried by younger ones in the past 5 years.

PatchMod are given in Figs. 10–13. Fig. 10 illustrates the temporal dynamics of the area and number of different types of patches. Fig. 11 and Fig. 12 show the dynamics of plant populations at the patch and landscape levels in different simulation scenarios. The simulator generates 'bull's eye' maps to display spatial data (see Wu and Levin, 1994) and, in addition, the patch-based information can be rasterized for further data visualization and analysis (Fig. 13). These simulated spatial patterns of plant populations are in good agreement with field observations (see Wu and Levin, 1994).

A series of questions concerning pattern-process dynamics can be readily addressed by simulating this model. For example, how do the mean size, total number, and total area of patches change in time with different disturbance rate functions? Given a spatial patch pattern generated by a known process (e.g. random, clustering, or regular), how does the disturbance scale up? How is vegetation pattern at the landscape level related to local patch dynamics? How is a particular

functional relationship (e.g. plant weight-seed production or population density-biomass relation) at the local scale manifested at the landscape scale? Based on preliminary simulation results, these questions have briefly been addressed in Wu and Levin (1994) in relation to the Jasper Ridge serpentine grassland. More systematic and detailed investigations are to be conducted of the above research questions using this spatial patch dynamic modeling approach.

4. Discussion and conclusions

Patch dynamics as a conceptual framework has increasingly been used in ecological studies across a range of scales, and provided much insight into evolutionary biology, population ecology, community ecology, and landscape dynamics (Levin et al., 1993; Wu and Loucks, 1995). Numerous empirical and theoretical studies have demonstrated that many ecological systems may more appropriately be viewed as mosaics of various patches. The
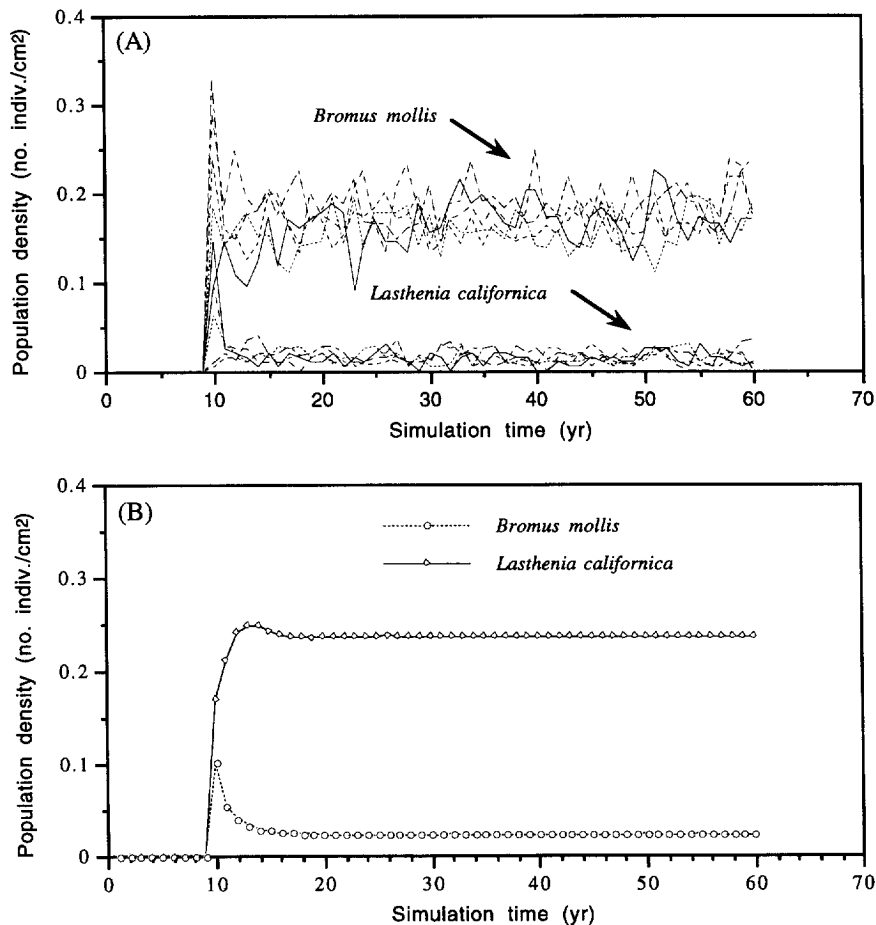
Fig. 11. Simulated population dynamics when feedbacks between the two species are discoupled (i.e. no interspecific competition). (A) Local population dynamics at the patch level for five arbitrarily chosen individual patches; and (B) metapopulation dynamics at the landscape level.

spatial patch dynamic modelling framework presented here provides a sensible and effective way of transforming the patch dynamics conceptualization into a mathematical model for studying pattern-process dynamics in ecological systems. Based on the Jasper Ridge serpentine grassland, we also have discussed in detail the structure and implementation of this modeling approach. In general, the modeling 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 the spatial complexity of patch mosaics. Although the model is developed for an annual grassland, the modeling framework should be suitable for other ecological systems in which patch dynamics are fundamental. Such an approach may be used for modelling species competition, predator-prey interactions, insect-plant interactions, vegetation dynamics, and landscape-level phenomena.

The complexity of models usually increases with model resolution in the spatial dimension, although non-spatial models can be rather intricate when they are overwhelmed with detailed processes (e.g. Jørgensen, 1992). Validation of complex spatial models may be facilitated by comparing alternative modelling approaches. The
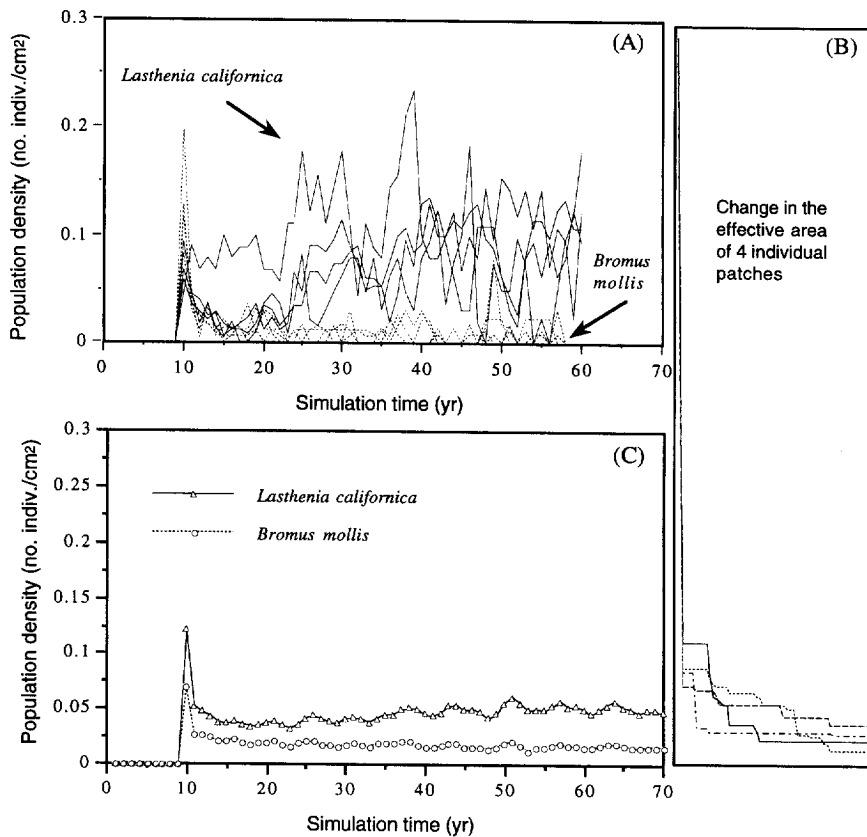
Fig. 12. Simulated population dynamics at the patch and landscape levels when interspecific competition is considered. (A) Local population dynamics at the patch level for four arbitrarily chosen individual patches; (B) Changes in the effective patch size for the four patches during simulation; and (C) metapopulation dynamics at the landscape level.

problem and modelling objectives, to large extent, define the degree of spatial aggregation. Nevertheless, because patchiness is ubiquitous in nature, realistic ecological theories are more likely to emerge from models that adequately address the problem of spatial heterogeneity. Linking spatial pattern with process is still a challenge in ecological modeling, but it also represents an opportunity for greatly enhancing our understanding of the structure, function, and dynamics of ecological systems across scales.
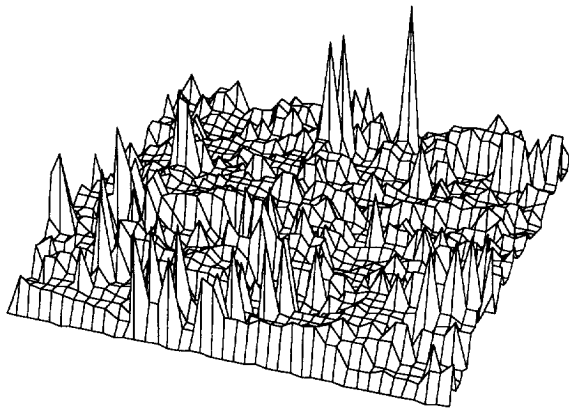
Acknowledgements
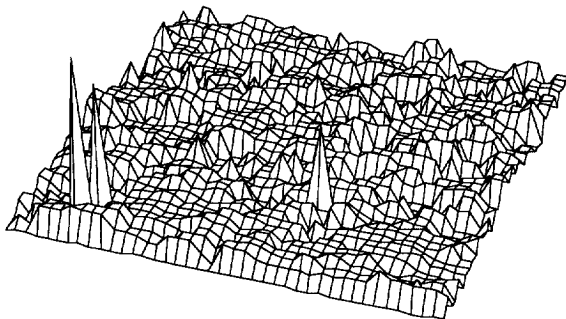
Appendix A. The patch influence index method

An alternative method to the patch probability method is the patch influence index method. This method is similar to the modelling scheme for

(A) Age- and size-structured disturbance patch population
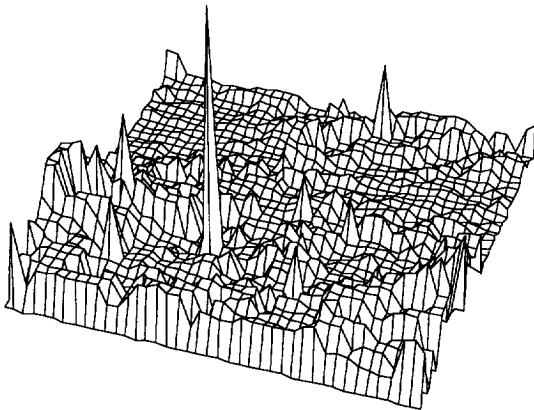
(B) Spatial distribution of Lasthenia californica

(C) Spatial distribution of Bromus mollis

Fig. 13.

generating clumped point patterns used by Nuern-berger (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 next year in its vicinity is assumed to decrease exponentially with the distance away from it. This is formally expressed as:

$$\psi(D) = e^{-\gamma D}, \qquad (A1)$$

where M 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:
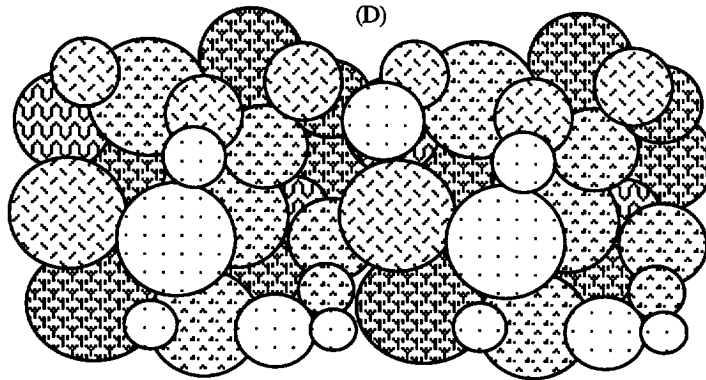
$$\Psi(P) = \frac{1}{M} \sum_{k=1}^{M} e^{-\gamma D_{Pk}}, \qquad (A2)$$

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, $\Psi(P)$ is an indicator of the average crowdedness relative to point P in the landscape, and takes values between 0 and 1. To generate a clumped pattern of patch centers, $\Psi(P)$ 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.

Fig. 13. Spatial distributions of disturbance patches and plant populations at the end of a simulation run. (A) spatial pattern of the age- and size-structured disturbance patch population, in which the height of peaks represents the age of patches; (B) spatial pattern of *Lasthenia californica*; and (C) spatial pattern of *Bromus mollis*. In (B) and (C) the height of peaks is proportional to plant density. These surface plots were generated using Spyglass™ based on rasterized output from Patch-Mod.

(A)

(B)

$$\angle PO_1Q = \alpha_1 \leq \pi \quad \angle PO_2Q = \alpha_2 < \pi \qquad \angle PO_1Q = \alpha_1 > \pi \quad \angle PO_2Q = \alpha_2 < \pi$$

(C)
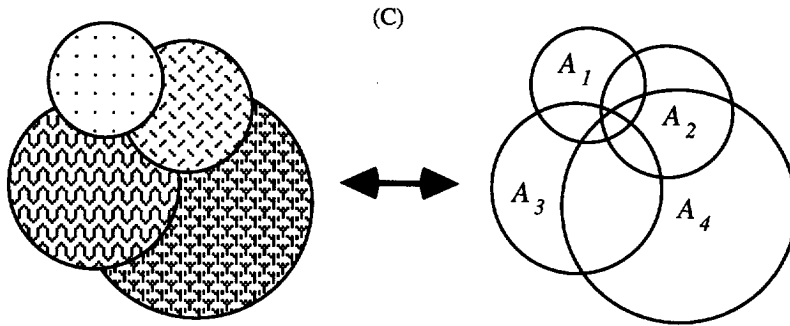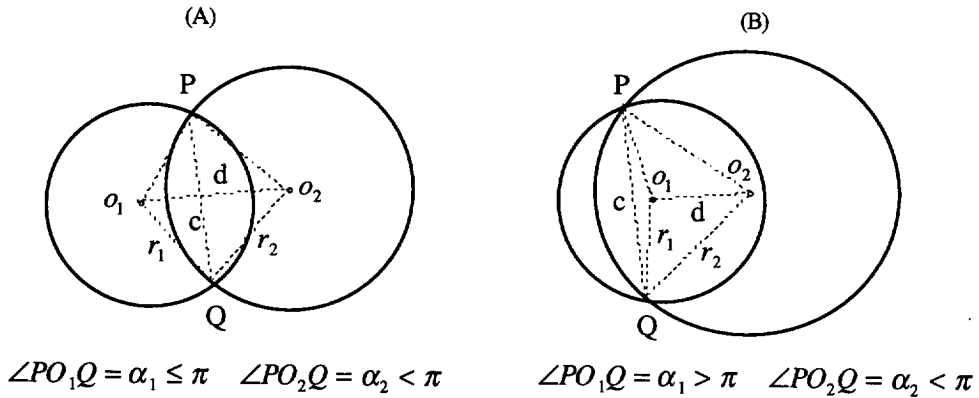
$$A_4^* = A_4 \bigcap \left(A_1 \bigcup A_2 \bigcup A_3 \right)^c = A_4 \bigcap A_3^c \bigcap A_2^c \bigcap A_1^c$$

(D)

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

Fig. 14. Illustration of mosaics of overlapping patches of differnet size and age and calculation of effective areas of individual patches. Patches are circular in shape and differ in size at birth. The effective sizes of patches can be calculated analytically when only two of them are involved (A and B), but a Monte Carlo simulation method becomes necessary when more patches interact (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.

Appendix B. Computation of the effective area of individual patches

We have developed the following general formula for calculating the effective area of a patch that is submerged in a mosaic of patches of different age and size:

$$A_j^* = A_i \cap \left(\bigcup_{j=1, j \neq 1}^{m} A_j \right)^c = A_i \cap \left(\bigcap_{j=1, j \neq 1}^{m} A_j^c \right) \quad \text{(B1)}$$

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 (Fig. 14).

When $A_i \not\subset A_j$ and $A_i \cap A_j \neq \phi$ ($i, j = 1, 2$ and $i \neq j$), the overlapping area can be analytically computed from the formulas:

(a) when $\angle PO_1Q = \alpha_1 \leq \pi$ and $\angle PO_2Q = \alpha_2 < \pi$,

$$A_{\text{overlap}} = \tfrac{1}{2}(r_1^2 \alpha_1 + r_2^2 \alpha_2 - cd) \quad \text{(B2)}$$

(b) when $\angle PO_1Q = \alpha_1 \geq \pi$ and $\angle PO_2Q = \alpha_2 < \pi$,

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

$$+ \tfrac{1}{2}c\left(\sqrt{r_1^2 - \left(\frac{c}{2}\right)^2} - \sqrt{r_2^2 - \left(\frac{c}{2}\right)^2} \right) \quad \text{(B3)}$$

with

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

$$\alpha_1 = 2 \arccos\left(\frac{1}{2dr_1}(d^2 + r_1^2 - r_2^2) \right),$$

$$\alpha_2 = 2 \arccos\left(\frac{1}{2dr_2}(d^2 + r_2^2 - r_1^2) \right),$$

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. 14).

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