A SPATIAL PATCH DYNAMIC MODELING APPROACH TO PATTERN AND PROCESS IN AN ANNUAL GRASSLAND[1]

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Abstract. Landscapes are hierarchical mosaics of patches that differ in their age, size, shape, content, and other aspects. The Jasper Ridge serpentine grassland exemplifies hierarchical patchiness and pattern–process interactions that are common features of natural ecosystems. Gopher mounds formed each year destroy all the plant individuals underneath and result in conspicuous spatial pattern in the landscape. A snapshot of the system is, therefore, a reflection of the patch mosaic of gopher mounds that are different in age and species composition and abundance. Based on a patch dynamics perspective, we have developed a spatially explicit patch-based modeling approach to studying landscape pattern and process dynamics. The simulation model (PATCHMOD) has two major components: a spatially explicit, age- and size-structured patch demographic model and a multiple-species plant population dynamic model. We use this simulation model to examine the spatiotemporal dynamics of the disturbance patches and of populations of two species on the local and landscape scales.

The spatial patch dynamic model can relate spatiotemporal dynamics of plant populations to the age- and size-structured disturbance patch population, taking into account variability in microhabitats, complexity in patch overlap, and patch-based plant competition. The localized gopher disturbances can significantly structure the vegetation dynamics at the landscape level. Local populations at the patch level may go extinct frequently, though metapopulations may show little fluctuation. Disturbance promotes coexistence of *Bromus mollis* and *Lasthenia californica* by divorcing local competitive exclusion and global extinction. The functional representation of an ecological relationship such as density-dependent fecundity at the local patch scale may be transmuted by patchiness at the landscape scale.

Key words: competitive exclusion; disturbance; Jasper Ridge serpentine grassland; metapopulation; patch dynamics; PATCHMOD; population dynamics; scale; spatial modeling.

INTRODUCTION

With drastically increasing anthropogenic perturbations, one of the most conspicuous spatial phenomena of the world's landscapes is habitat fragmentation, a major threat to global biological diversity. For example, in North America and Europe, human alterations of the previously continuous forested landscapes have resulted in forest fragments or forest islands that are surrounded by a matrix of agricultural and urban lands (Curtis 1956, Wilcove et al. 1986, Wu and Vankat 1991). In fact, both anthropogenic and natural processes create patchiness across a range of spatial scales, resulting in complex landscape structures. Tree gaps in a forest, mounds created by ants and gophers in a grassland, wave-generated gaps in an intertidal community, and plankton aggregates in an aquatic system all constitute hierarchical mosaics of patches. Patchiness is ubiquitous and scale dependent (Kotliar and Wiens 1990, O'Neill et al. 1991, Levin 1992, Levin et al. 1993).

Studying ecological processes in context and searching for pattern based on understanding of ecological processes represent a central issue in ecology (Levin 1989, 1992, Levin et al. 1989, Wu 1992, 1993, Wu et al. 1993). Process modifies existing pattern and creates new pattern; pattern enhances or constrains ecological processes. This dual relationship makes necessary the consideration of spatial heterogeneity in studies of ecological processes. Traditionally, many investigations attempt to understand nature by distinguishing different organizational levels such as individuals, popula-

tions, communities, and ecosystems without explicitly considering relationships among scales. While such an organizational hierarchy is convenient and helpful as a starting point, a patch dynamics perspective allows one to make critical linkages among scales.

A patch dynamics paradigm in ecology has been emerging since the 1970s (Wu 1992, 1994). The conceptualization of ecological systems as mosaics of patches is evident in the "pattern–process hypothesis" (Watt 1947), the intertidal landscape pattern dynamic model (Levin and Paine 1974, 1975, Paine and Levin 1981), the patch mosaic dynamics perspective (Whittaker and Levin 1977), the "shifting mosaic steady state" hypothesis (Bormann and Likens 1979), the mosaic-cycle concept of ecosystems (Remmert 1985, 1991), the patch dynamics literature in terrestrial community ecology (Pickett and Thompson 1978, Loucks et al. 1985, Pickett and White 1985, White 1987, Collins 1989, Collins and Glenn 1991), and metapopulation theory (Levins 1970, Gilpin and Hanski 1991, Wu et al. 1993, Wu 1994). Loucks' (1970) "wave-form dynamics" hypothesis provides a parallel patch dynamic example in the time domain. While the physical or biological meaning of a patch may vary substantially across biological systems, the effect of spatial patchiness on pattern and process in marine ecosystems has long been recognized (see Hutchinson 1953, Steele 1978). Patch dynamics as a conceptual framework has been central to landscape ecology in theory and practice since its emergence in North America (Forman and Godron 1981, 1986, Risser et al. 1984, Vankat et al. 1991, Wu 1994).

While the patch dynamics perspective has provided insights into ecological studies at population, community, and landscape levels, a great challenge is to apply it to develop quantitative and predictive models. In fact, the conceptualization has been inspirational to the development of models that are different from traditional population or ecosystem counterparts. Levin and Paine (1974; also see Paine and Levin 1981) first constructed a quasi-spatial patch demographic model to characterize and predict the dynamics of distribution pattern of an age- and size-structured patch population on an intertidal landscape. Clark (1991*a, b*) and Kohyama (1993) developed quasi-spatial patch models to couple disturbance patch demography with tree species population dynamics on a shifting mosaic landscape. These above-mentioned models all ignore the spatial locations and overlaps of patches, but allow the consideration of localized interactions and stochastic events (see also Chesson 1981). The quasi-spatial patch models also include a group of computer models of forest dynamics, which have been called gap simulation models (see Shugart 1984). Recently, spatially explicit gap models have also been developed based on gap modeling principles (e.g., Smith and Urban 1988, Coffin and Lauenroth 1989) and the mosaic-cycle concept of ecosystems (Wissel 1991). These models take a grid-based approach in which patches are considered as single grid cells or aggregates of multiple cells within a regularly divided grid. There may be situations, for example those in which patches are not clearly defined entities but simply inhomogeneities in a continuum, for which the grid-based approach is to be preferred. These grid-based models may become inadequate and impractical when overlapping among patches is common and complex, which is often the case in many ecological systems. More importantly, they miss the essential features of the patch as an important level of biological interaction, clearly distinct from the background.

Visualizing the serpentine grassland as a hierarchical system of patches that differ in age, size, and internal composition, we have developed a simulation model for the system, using a spatially explicit patch dynamics modeling approach that has several unique features. First, the approach transforms the patch dynamics conceptualization of ecological systems into a quantitative and predictive model in a biologically sensible way. Second, in contrast with other existing modeling approaches, this patch-based modeling approach treats patches as individual objects changing continuously in size and spatial location. In contrast with the arbitrary cell boundaries in some grid-based models, the boundaries of patches in this approach are ecologically meaningful. Third, the approach more realistically deals with complex overlaps in a mosaic of patches of different age and size. The model is primarily composed of two modules: a spatially explicit disturbance patch demographic module and a spatially explicit, multiple-species, patch-based population dynamic module. The parallel formulation of the patch population model and species population model enables 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.

Our objectives are (1) to develop a general spatial patch dynamics modeling platform for studying pattern and process dynamics at local and landscape scales, (2) to examine the spatiotemporal patterns of the age- and size-structured disturbance patch (gopher mound) population, and (3) to examine how local disturbance and patch dynamics affect vegetation pattern at the landscape scale. The emphasis here is to illustrate the spatially explicit patch dynamics approach through modeling a specific ecological system. Although we establish functional relationships and estimate model parameters based on available field data as closely as possible, there are places where educated guesses are employed. However, the qualitative conclusions that emerge from the study seem robust. Ultimately, the model must be tested, refined, and calibrated against

broad-scale distributional data; even in this initial stage, however, it provides a tool for investigating landscape-scale consequences of smaller scale processes.

THE JASPER RIDGE SERPENTINE GRASSLAND

The spatially explicit patch dynamic model is based on the serpentine annual grassland within the Jasper Ridge Biological Preserve of Stanford University in San Mateo County, Northern California. The grassland is dominated by a relatively high diversity of annual native forbs and perennial bunch grasses (Hobbs and Mooney 1985, 1991). The most abundant annual forbs include *Lasthenia californica, Plantago erecta,* and *Calycadenia multiglandulosa.* Scarcity of nutrients, low Ca : Mg ratio, and high concentrations of heavy metals in the serpentine soil effectively keep most non-native grass species from successfully invading the system. In fact, the only non-native grass present on the serpentine soil in any abundance is the annual species *Bromus mollis.* While the species differ in their phenology, field studies show that there are very few seeds carried over from year to year, and the range of seed dispersal of most of the annual species is usually <100 cm (Hobbs and Mooney 1985, Hobbs and Hobbs 1987).

The activities of western pocket gophers (*Thomomys bottae* Mewa) 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 >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. Previous field experimental studies by Hobbs and Mooney (1985, 1991) have indicated that gopher activities exert a strong influence on the spatial pattern and temporal dynamics of the serpentine grassland, through their effects on the population processes of individual species such as germination, survival, and seed production. In general, the importance of such small mammals as pocket gophers in structuring a variety of plant communities has been increasingly appreciated (see Korn 1991 for a recent review).

The Jasper Ridge serpentine annual grassland is an ideal system for developing a spatial patch dynamics modeling approach for several reasons. First of all, the observed pattern and process in this particular system can be well conceptualized according to the patch dynamics perspective. Similar to tree gaps in forests, the mound patches represent fundamental spatial units in the vegetation dynamics. The patches exhibit a series of different phases: nudation or patch formation, dis-

persal and colonization, plant establishment, intraspecific and interspecific competition, and achievement of the predisturbance state. This chain process may be interrupted at any phase and, as a consequence, succession starts all over again. Therefore, a snapshot of the grassland vegetation is essentially a hierarchical mosaic of different-sized patches at different succession stages. Secondly, the disturbance patches (gopher mounds) are conspicuously visible and easy to quantify in terms of number, size, and distribution. Third, the rapid dynamics of annual plant populations make the system a good choice for modeling. Finally and importantly, the existing field studies on the site make possible the parameterization and validation of the simulation model.

We conceptualize the annual grassland landscape as a patch mosaic of gopher mounds of different size, (successional) age, and species composition and have constructed a spatially explicit patch dynamic model to relate the landscape pattern to the underlying process at the individual patch scale. Estimation of parameters in the model is based on available field data, while, for parameters whose values are not obtainable from the existing field information, biologically sensible educated guesses are applied as indicated where they take place. Although the model is developed for the serpentine annual grassland, the modeling approach and structure should be suitable for other ecological systems in which patch dynamics are fundamental; indeed, many aspects in principle parallel the approach of Levin and Paine (1974), who two decades ago applied a patch dynamics approach to an intertidal landscape.

STRUCTURE OF THE SPATIALLY EXPLICIT PATCH DYNAMIC MODEL

The spatial patch dynamics model consists of two major submodels: a spatially explicit, age- and size-structured patch demographic model and a multiple-species 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 patch in the landscape.

Disturbance patch demographic model

Based on the rate of disturbance (patch formation) and the spatiotemporal distribution of gopher mounds, the spatial patch demographic model generates an age- and size-structured gopher mound (patch) population. It is capable of keeping track of the effective size (i.e., a patch's area that is not covered by any younger patches) of all individual disturbance patches in a constantly shifting patch mosaic, using an approach combining both analytical and Monte Carlo simulation methods

(see Wu 1993 for details of the computing algorithm). The capability of providing information on effective sizes of individual patches in the dynamic mosaic of overlapping patches of different age and size at each time step is a salient characteristic of the modeling approach. This ability facilitates a patch area-based modeling of plant population dynamics following the patch mosaic conceptualization.

Shape, size, and types of patches. — A new patch is represented as a circle in shape at its birth time, which, to large extent, resembles a gopher mound in the field. The individual gopher mounds usually range from 20 to 50 cm in diameter and are frequently clumped into areas of 1 m² or larger (Hobbs and Mooney 1991). 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. This lognormal assumption seems supported by field observations of intercepted patch length along a one-dimensional transect (Moloney 1993) and parallels observations made in the intertidal (Paine and Levin 1981). 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; these essentially represent the nonpatch (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 relationship between patch age and the maximum overlapping areas will be discussed in the following section. New patches are further divided into two types: early patches and late patches. The early patches are the new gopher mounds formed in April, whereas the late patches are those formed in July. The average area ratio of the early to late patches is 3:1 (Moloney et al. 1992).

The distinction between the two subtypes within new patches is necessary for two reasons. First, most species in the serpentine grassland flower and release most of their seeds by the end of June, so that the patches formed in July apparently can experience only a portion of the seed rain of these species each year. In light of the potential importance of seed dispersal in vegetation dynamics on larger scales, the differential timing of patch formation cannot be neglected. Seed-trapping field experiments by Hobbs and Mooney (1985) indicate that *B. mollis* continues to release seeds from summer well into November, whereas *L. californica* peaks in seed release before July and drops rapidly afterwards (Hobbs and Mooney 1985: fig. 2). Second, gopher mounds formed in July may retain a certain amount of seeds in the soil because species have already started reproducing seeds before July. On the other hand, April gopher mounds essentially do not contain any seeds produced in the current year at the time of formation. This fact may cause significant differences in the local population dynamics (Levin et al. 1989). We, therefore, model seed dispersal in such a way that in their first year patches of type 2 only experience a fraction of the total seed rain for species *L. californica* (say, 40%).

Spatial distribution of patches. — Field observations (Hobbs and Mooney 1991) indicate a strong clumping of new gopher mounds; this may result from the tunneling behavior of gophers. For examining effects of spatial configurations of patches on population and community processes, we have used patterns of disturbance with different degrees of aggregation in model simulations.

For clumped patterns of spatially autocorrelated patches, the following method is used. We start with the assumption that the probability for an existing patch to have a new patch the next year in its neighborhood decreases exponentially with distance beyond a certain threshold. Because of food shortage and other factors, the patch formation probability may be negligibly small within a certain distance of the parental patch. In addition, the probability is assumed equal in all directions around the patch. Therefore, we have

$$\begin{cases} \varphi_p(L_p) = 0 & L_p < L_{min} \\ \varphi_p(L_p) = \lambda_p e^{-\lambda_p(L_p - L_{min})} & L_p \geq L_{min} \end{cases} \quad (1)$$

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} (< radius of the parental patch) 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.

Patch overlap constraints represent another important aspect in patch formation. From field observation, the overlaps between a newly formed gopher mound and existing mounds seem to vary considerably, though they are frequently clumped together. It appears consistent with field observation that new gopher mounds tend to overlap less with themselves and younger mounds than with older mounds. 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); when a new patch is formed in our model, we do not permit it to exceed this value. We express the maximum overlap fraction that a new patch may have with an existing patch by

$$OLR_{max}(\tau) = \cfrac{1}{1 + \left(\cfrac{1}{OLR_0} - 1\right)e^{-\gamma(\tau-1)}},$$
$$\tau = 1, 2, \ldots, a_{max} \tag{2}$$

where $OLR_{max}(\tau)$ is the overlap ratio, OLR_0 is the overlap ratio when the age of the existing patch is 1 (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. γ is determined by solving Eq. 2 for a given set of parameters of OLR_0, $OLR_{max}(\tau)$, and τ, which are predetermined empirically. For the ecological questions addressed here, OLR_0 and γ do not appear sensitive to the conclusions. 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 cannot exceed $OLR_{max}(\tau)$; if it does, the candidate new patch is obliterated. This overlapping constraint exerts some degree of negative spatial autocorrelation in patch formation.

The general procedure of patch formation may be briefly described as follows. 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 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 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 the disturbance rate has been reached 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.

Disturbance rate. — Disturbance rate is defined and measured as the percent of the total area of study disturbed by gopher activities per year. Field observations show that there is considerable interannual variability in disturbance rate, which is perceived to be important in the dynamics of the vegetation (Hobbs and Mooney 1991). Disturbance rate may be temporally uncorre-lated (white noise) or temporally autocorrelated. The current version of PatchMod deals only with constant and uncorrelated random disturbances. In particular, a lognormal distribution in time of disturbance rate (truncated at 0.05 and 0.35) is used to reflect the idea that, extremes being least likely, smaller disturbances occur more frequently than larger ones.

Multiple-species population dynamic model

The multiple-species 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 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.

Patch-based multiple-species plant population dynamic model.—The patch-based population model takes the following form:

$$N_{i,t+1} = (N_{i,t}f_{i,t} + I_{i,t} - D_{i,t}) \cdot$$
$$(A_{t+1}/A_t)g_i s_i, \tag{3}$$

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, respectively $(A_{t+1} \le A_t)$. The values of $I_{i,t}$ and $D_{i,t}$ at each time step are obtained by keeping track of each patch in the landscape and updating the number of seeds dispersed in and out during every dispersal event of a patch. The ratio of patch size, A_{t+1}/A_t, adjusts the population size in a patch if the size of the patch changes, on the assumption that as a first approximation, the reduction in patch size proportionally decreases the plant population size in that patch.

While the possible density-dependent factors affecting germination and survivorship are not explicitly taken into account for the current version of the model, plant fecundity is modeled as a density-dependent variable on the individual patch level. The model equation for per-plant seed production is, in form, essentially the same as those found in Watkinson (1981, 1986), Silander and Pacala (1985), and Pacala (1986):

$$f_i = RMP_i AMP_i f_i^*(H)\left[1 + \alpha_i \left(\sum_{j=1}^{m} \beta_{ij}n_j\right)\right]^{-q_i}, \tag{4}$$

where f_i^* is the fecundity of species i without neighbors, RMP_i is the rainfall multiplier that reflects the effect

AMP

$$\text{AMP} = \frac{Y_u}{Y_G^*} + (1 - \frac{Y_u}{Y_G^*})e^{-\eta(\tau-1)}$$
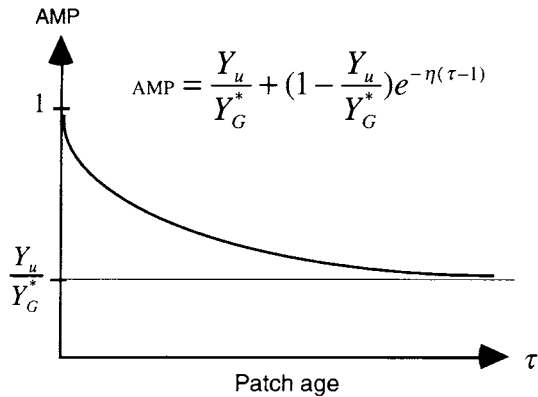
Patch age

FIG. 1. 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).

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 (i.e., patches of different age), α_i and q_i are species-specific constants (a value of 1 for q_i is used for all species in the simulations presented here), 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 (cf. Watkinson 1980). 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, which is dominated by relatively short annual forbs, soil resources are most likely to be the main limiting factors for plant growth and reproduction (see Whittaker 1954, Huenneke et al. 1990). A first approximation is to estimate the interspecific competition coefficients based on the aboveground biomass of the adult plants of the species. For simplicity and also limited by data availability, we calculate β_{ij} as the ratios of aboveground biomass between two competing species, i.e.:

$$\beta_{ij} = \alpha_w \frac{W_j}{W_i}, \tag{5}$$

where α_w is a scaling constant, and W_i and W_j are the aboveground biomass for the adult plants of species i and j. The values of W_i used for estimation of interspecific competition coefficients are those observed for undisturbed areas (Hobbs and Mooney 1985).

Effect of patch age on plant demographic parameters.—Germination rate, survivorship, and fecundity of plants are different on gopher mounds of different age. Survivorship and fecundity for species modeled are, in general, considerably higher on gopher mounds than undisturbed areas, probably due to increased resource availability and/or reduced competition on the former (Hobbs and Mooney 1985). On an average, soil characteristics appear to come back to the predisturbance state in a few years (R. Hobbs, personal communication).

There are no data available to specify what the trajectory of the recovery of soil physical conditions looks like. We postulate that the recovery 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 (Fig. 1). In particular, if $Y_G(\tau)$ is the value of a plant demographic parameter (i.e., germination rate, survivorship, or fecundity) for a particular species in a gopher mound of age τ, Y^*_G is the value of a plant demographic parameter in a newly formed gopher mound, and Y_u is the value in an undisturbed area, then AMP$_i = Y_G(\tau)/Y^*_G$ (patch age multiplier) is assumed to decay exponentially according to the formula

$$\text{AMP}_i = \frac{Y_u}{Y^*_G} + \left(1 - \frac{Y_u}{Y^*_G}\right)e^{-\eta(\tau-1)}. \tag{6}$$

For computational convenience, we set AMP$_i$ 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 among the different microhabitats to disappear. Ideally, values of each parameter should be estimated based on field data for each species. Because of the limitation in available field information, however, for the purpose of laying out a modeling framework we use Eq. 6 to describe changes of three parameters (germination, survivorship, and fecundity).

Seed dispersal.—There are several different ways to model the dispersal of seeds (see DeAngelis et al. 1985, Fahrig and Paloheimo 1988, Okubo and Levin 1989, Wu 1993). The relationship between the number of dispersed seeds with distance from source is, in general, affected by such factors as the terminal settling velocity, seed release height, wind speed and turbulence, and specific morphological adaptations for dispersal (Augspurger and Franson 1987, Okubo and Levin 1989).

Two phenomenological models, the negative exponential decay and the inverse power equation, long have been used for dispersal of different types of organisms and seem to fit data well in many cases (e.g., Frampton et al. 1942, Werner 1975, DeAngelis et al. 1985, Coffin and Lauenroth 1989, Okubo and Levin 1989, Fahrig 1991). The exponential model has the advantage that the solution to the equation is bounded when distance is approaching zero, which may be expressed as:

$$\mathcal{P}(L) = \lambda e^{-\lambda L}, \qquad (7)$$

where $\mathcal{P}(L)$ is the dispersal probability density function, L is the distance between the centers of a donor patch and the recipient patch, $\mathcal{P}(L)$ 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 Coffin and Lauenroth 1989, Okubo and Levin 1989). Both $\mathcal{P}(L)$ 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,

$$\Phi(L) = \int \mathcal{P}(L)dL$$
$$= 1 - e^{-\lambda L}, \qquad (8)$$

which approaches unity when L approaches infinity. λ can be estimated from data.

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. The following algorithm is used to alleviate this problem. We define plant recruitment 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
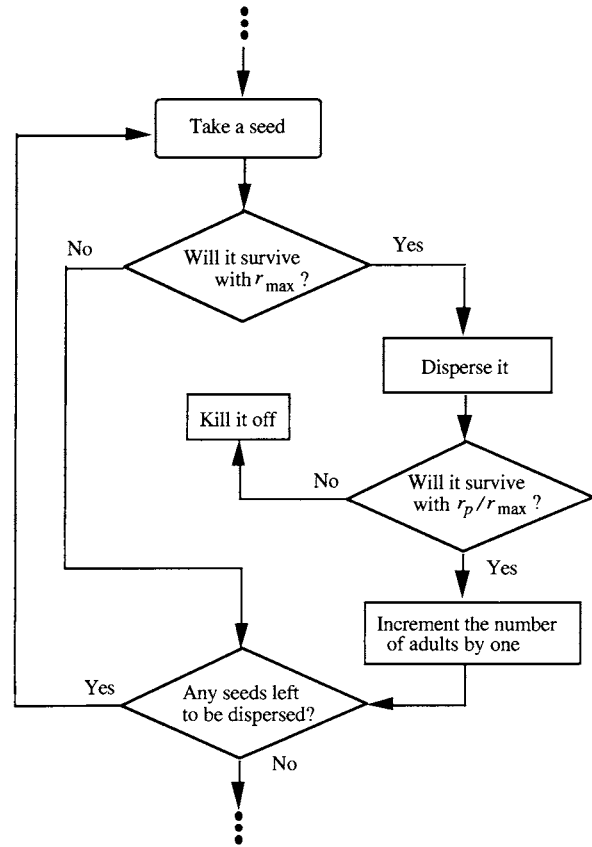

FIG. 2. A flow chart illustrating the dispersal algorithm involving two sets of Bernoulli trials. The first reduces the total number of seeds to be dispersed eventually to the number of adult plants out of these seeds; the second adjusts the number of adults to the particular microhabitat. The algorithm minimizes the computational time for dispersal while retaining dispersal stochasticity at the individual level.

trials are conducted with each seed to be dispersed. The first uses the maximum recruitment rate ($r_{max} = g_{max}s_{max}$) 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 recruit-

TABLE 1. List of parameters used in the model simulations. The information is primarily based on Hobbs and Mooney (1985, 1991) and Hobbs and Hobbs (1987).

Microhabitat	Species name	Max. fecundity (no. seeds/plt)	Germination rate (%)	Survivorship (%)	Aboveground 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	...

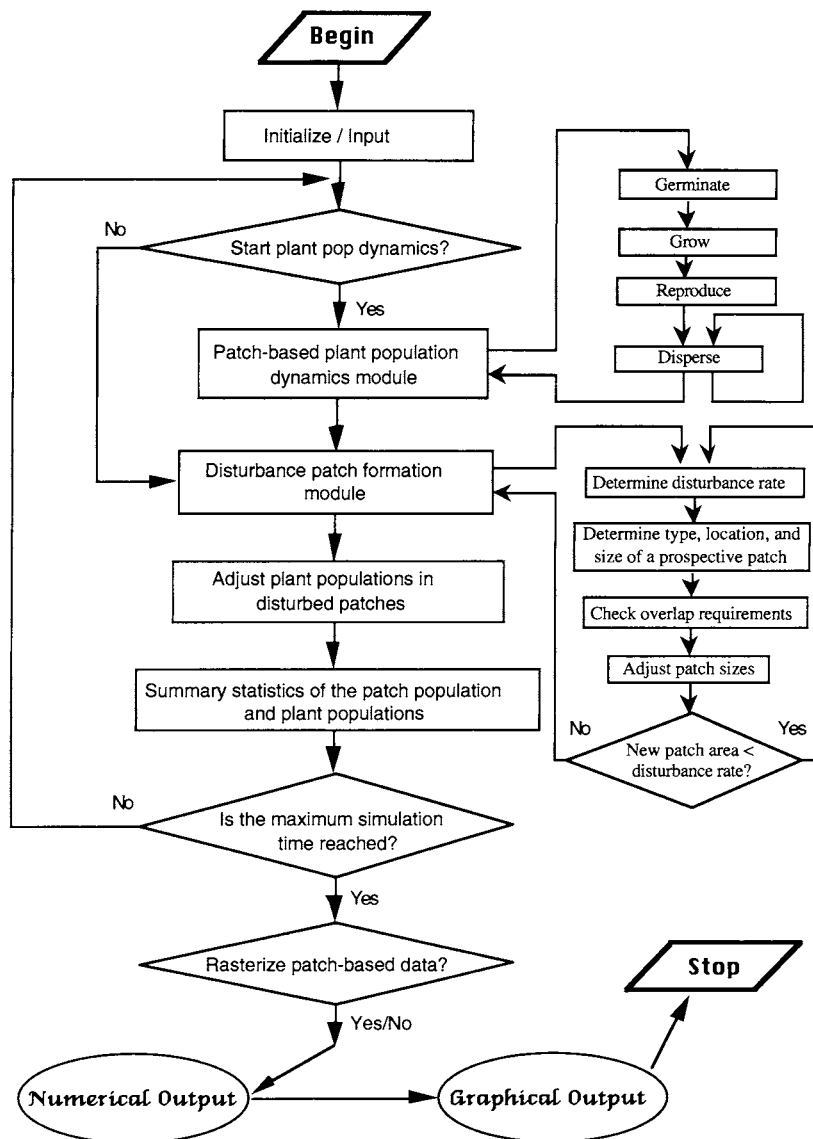| Microhabitat	Species name	Critical plant pop. density (no. plts/cm²)	Fecundity–density coeff. (cm²/plt)	Initial max. plant pop. density (no. plts/cm²)	Dispersal decay coeff. (1/cm)
Gopher mounds	*Bromus*	0.0200	25.0000	0.2000	0.0555
	Lasthenia	0.2500	8.0000	0.3500	0.0921

FIG. 3. Flow chart of the spatial patch dynamic model, PATCHMOD.

ment (r_p) in patch type p to the maximum rate as the dispersal probability and 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. 2. With respect to seed dispersal, we have treated the model boundary as absorbing. That is, a seed that falls off the boundaries will disappear without a trace.

MODEL SIMULATIONS

We parameterized the spatially explicit patch dynamic model, PATCHMOD, using information obtained from field observations and experiments (Hobbs and Mooney 1985, 1991, Hobbs and Hobbs 1987). A list

of parameters and their values is given in Table 1. Several different simulation scenarios were conducted to demonstrate uses of the model to address a range of questions regarding the spatiotemporal dynamics of the gopher mound population and the plant populations. Differences among the scenarios involve the manipulation of the disturbance rate and the spatial distribution patterns of gopher mounds within the disturbance patch demographic submodel and the alteration of some plant demographic parameters in the multiple-species plant population dynamic submodel.

Simulation scheme

The computer program of the spatial patch model is written in C. A flow chart of the model is shown in Fig. 3. It outlines how the spatial patch dynamic model
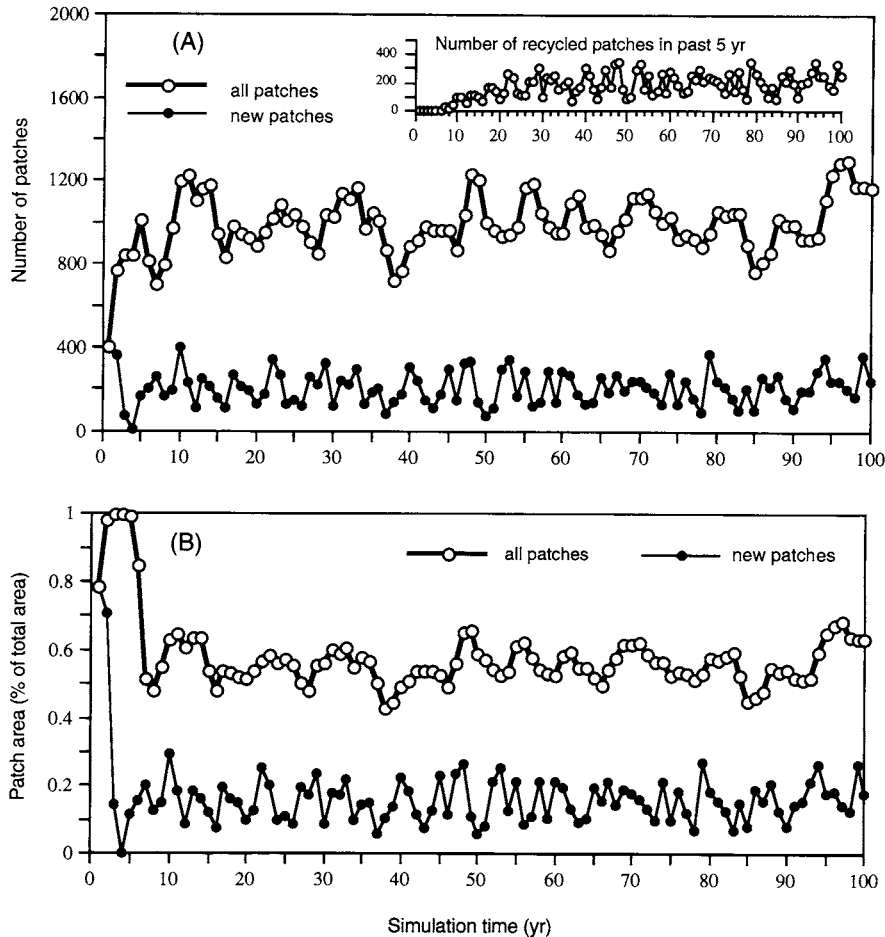
FIG. 4.   Dynamics of the number and area of patches when the temporal distribution of annual disturbance rate and patch size distribution are modeled as truncated lognormal probability functions. (A) Three curves are shown for all effective patches (———O———), newly formed patches (———●———), and patches that have been completely covered by one or more younger patches in the last 5 yr (inset). (B) Percentage areas covered by all effective patches (———O———) and by newly formed patches (———●———) are compared. The simulated area is 100 m².

is constructed and how its different model components are connected. The model may be run without invoking the plant population dynamic module, to simulate only 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.

A simulation may start either with generating the first patch in a landscape that has previously had no patch or 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. 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. The plant population module begins with

the initialization of all but newly formed patch units (including obsolete ones) in the landscape with population abundances 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 go-
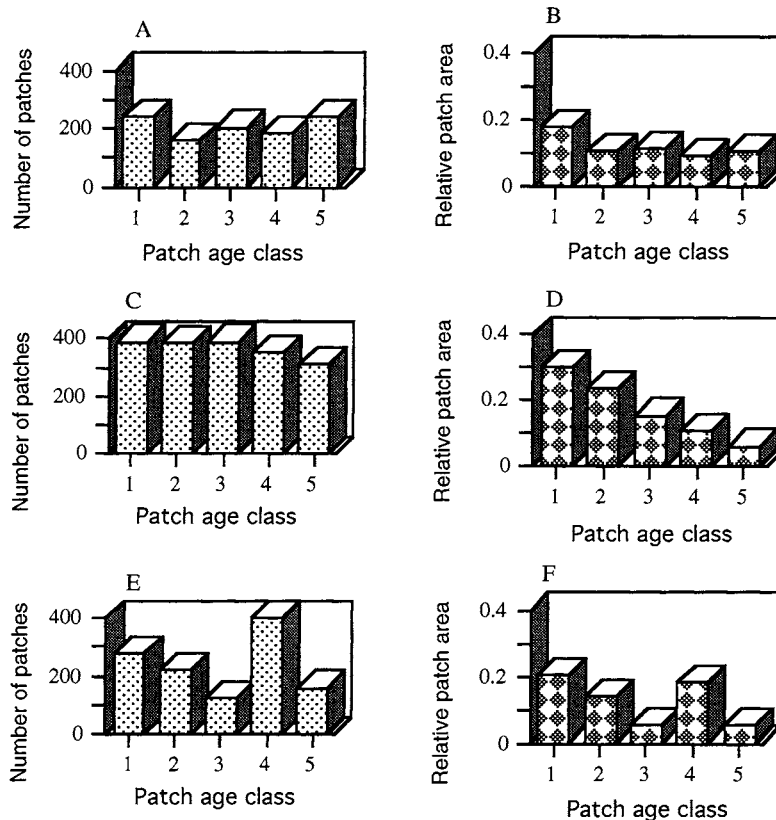
FIG. 5. Age distributions of the disturbance patch population: (A–B) the spatial pattern of patches is random and the annual disturbance rate is lognormally distributed in time; (C–D) the spatial pattern of patches is clumped, with a constant and high annual disturbance rate (30%); and (E–F) the spatial pattern of patches is clumped and the annual disturbance rate is lognormally distributed in time.

pher mounds and plant populations. In addition, the patch-based information can be rasterized at the end of the simulation for data visualization and analysis, if desired.

Dynamics of the disturbance patch population

Temporal dynamics of the number and area of patches.—One of the salient features of the model is its ability to predict the dynamics of the age- and size-structured disturbance patch (gopher mound) population in time and space. Fig. 4 shows the temporal patterns in the number and area of patches when the annual disturbance rate changes according to a lognormal distribution function truncated with the minimum and maximum values observed in the field. Total patch number is the number of all effective patches (i.e., gopher mounds ≤5 yr of age), and the total patch area refers to the area covered by effective patches in the landscape. The simulation starts with an area of 100 (10 × 10) m², which is fully covered with patches of different age in the first four time steps (see Fig. 4B). Within this simulated landscape the number of all existing patches under 5 yr of age may reach the order of 10³ at a given time, while the number of all existing patch units, including both obsolete and effective

patches, may exceed 3000. The numbers of new, effective, and recycled patches all seem to fluctuate randomly around a mean, while the initial increases in total and recycled patch numbers are due to the time lag related to the maximum patch age (Fig. 4A). The areas covered by new and all effective patches show a similar pattern (Fig. 4B).

Age profiles of the disturbance patch population.— The age profiles of the gopher mound population can be examined in terms of both the number and area of patches according to age classes. The age distributions of patch number and area change in time and also differ with spatial distribution patterns of disturbance patches (Fig. 5). For random disturbance the two age profiles tend to be similar (Fig. 5A, B), while clumped disturbance with a constant and high annual disturbance rate (30%) results in two rather different age distributions for patch number and area (Fig. 5C, D). Comparing the age profile of patch number with that of patch area, one can immediately get a rough idea about the average patch sizes across age classes. For example, the average patch sizes for the clumped high disturbance rapidly decrease with patch age (Fig. 5C, D), but this is not the case for the random and clumped disturbances (see Fig. 5A, B, E, F).
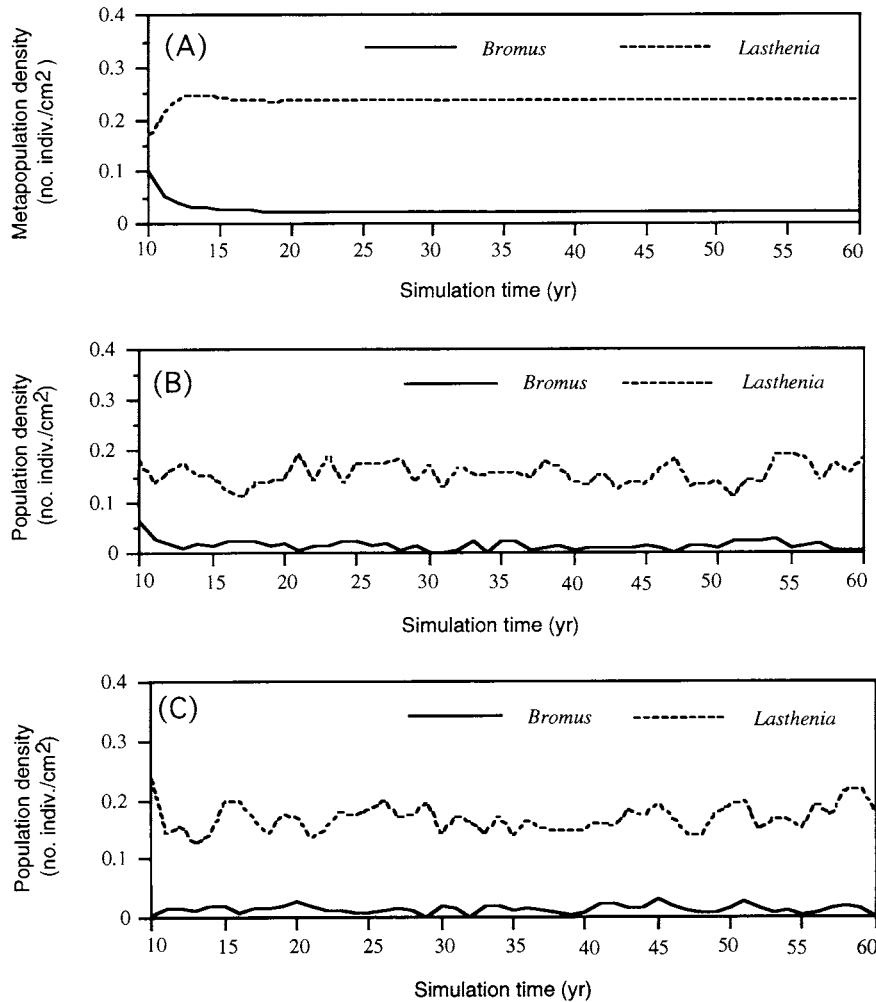
FIG. 6. Single-species population dynamics: model simulations without interspecific competition. Both populations of *Bromus mollis* and *Lasthenia californica* rapidly reach a steady state with little variation at the landscape scale (A), but show appreciable fluctuations at the local patch scale though the steady-state feature still appears evident (B, C). While thousands of patches are present in the simulated landscape, the two individual patches (B, C) are chosen arbitrarily as examples. Note that the plant population dynamic module starts running at simulation year 10.

Patch dynamics of plant populations

Single-species population dynamics.—While both within-species and between-species competition are considered in the patch-based plant population model, it is apparent from its mathematical formulation (Eqs. 3 and 4) that the population of a species will exhibit density-dependent behavior even in the absence of other species. For the purpose of comparison and as part of the model verification, the single-species population dynamics of *B. mollis* and *L. californica* are simulated by omission of interspecific competition from the model. At the landscape scale, both species quickly reach a steady state and *L. californica* has a much higher equilibrium population density (Fig. 6A). At the patch scale, on the other hand, populations show apparent fluctuations and even local extinctions for *B. mollis*, though the steady-state feature is still evident (Fig. 6B,

C). The fluctuations in the population densities at the local scale are consequences of stochasticities in seed dispersal and formation of new disturbance patches.

Population dynamics of competing species.—We also study effects of interspecific competition and disturbance on plant population dynamics and persistence through simulations, which take into account two fundamental different scales. Without disturbance *L. californica*, because of its much higher fecundity, outcompetes *B. mollis*, and as a result only one species can persist in the system (Fig. 7A). This is a landscape-level consequence of the local plant competitive exclusion that takes place within individual patches. On the other hand, disturbances enable the two species to coexist for long times in the same landscape, though the steady-state metapopulation density for *L. californica* is much lower (Fig. 7A). These simulation results suggest that competitive exclusion may occur for plants
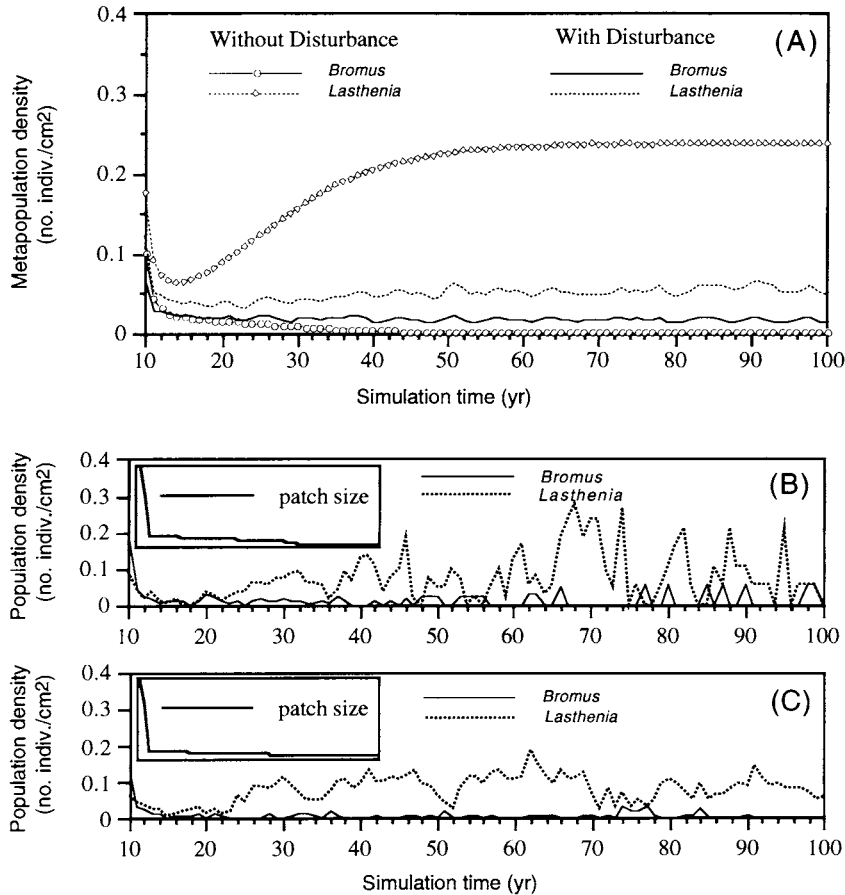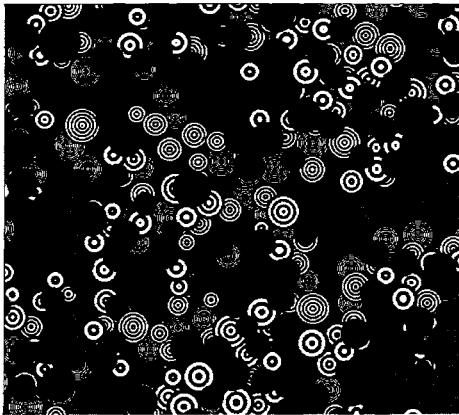
FIG. 7. Population dynamics of two competing species at the landscape and patch scales: effect of disturbance on plant population dynamics and persistence (A), and examples of the local dynamics of individual patches (B, C). The insets in (B) and (C) depict the temporal changes in the effective size of the particular individual patch. The patch-based plant population dynamic module starts running at simulation year 10.

that are weak competitors, but its consequences may depend on both spatial scale and spatiotemporal aspects of the disturbance regime.

It is evident from Fig. 7 (B, C) that the local populations of both species at the patch scale fluctuate drastically and are subject to frequent local extinctions. However, disturbance can effectively decouple local competitive exclusion and global extinction. Continuous generation of new disturbance patches favors the persistence of *B. mollis* because this species has an advantage in dispersal (a larger portion of seeds move

farther) and is more competitive on an individual basis (inferred from its higher aboveground biomass) compared to *L. californica*. This is consistent with the regeneration niche hypothesis (Grubb 1977) where species coexistence is enhanced by localized disturbances through constantly providing a dynamic shifting mosaic of regeneration niches. The effect of disturbance on the population dynamics of the two species is spatiotemporal, which becomes clearer when the spatial patterns of disturbance patch population and plant populations are compared in the following section.
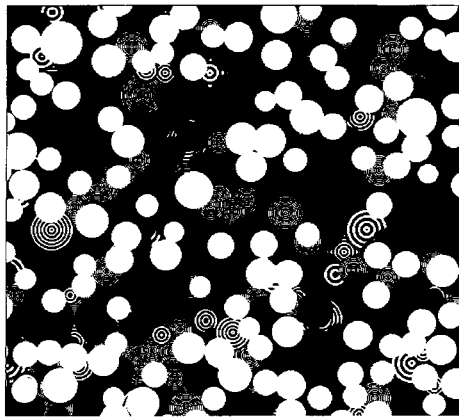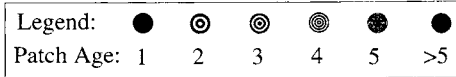
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FIG. 8. Spatial distributions of the disturbance patch population and plant populations: (A–C) for initial conditions at simulation time 10 (the plant population dynamic module starts running at simulation year 10), and (D–F) for results at simulation time 100. (A) and (D) are for the disturbance patch population, (B) and (E) are for the plant density of *Bromus mollis*, and (C) and (F) for the plant density of *Lasthenia californica*. In the disturbance patch maps (A, D), the inside lines of bull's eye diagrams are thicker when patches are younger and black discs represent newly formed disturbance patches. Patches whose age is >5 are all drawn in gray, forming the background in the maps. In contrast, the line thickness of bull's eye diagrams for plant density distribution (B, C, E, and F) increases with the plant density in patches. Patches with no plants are all left as white spaces. The actual area shown by these bull's eye diagrams is some 25 m² (5 × 5 m).
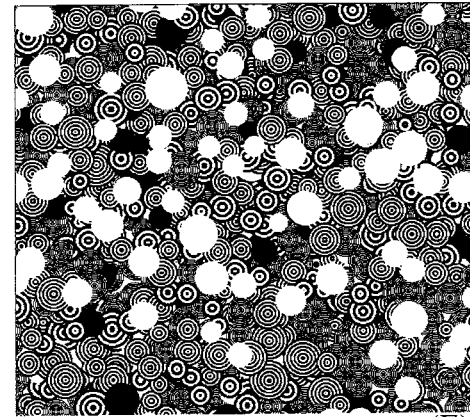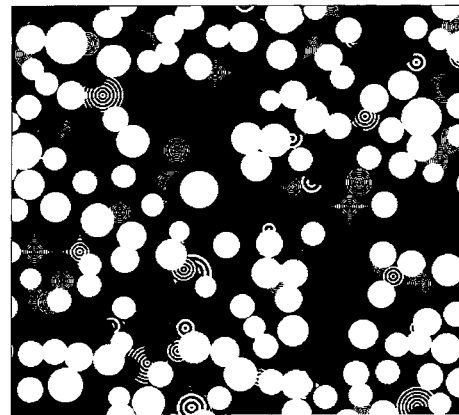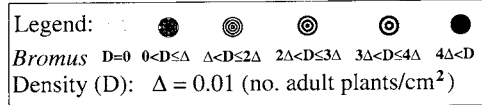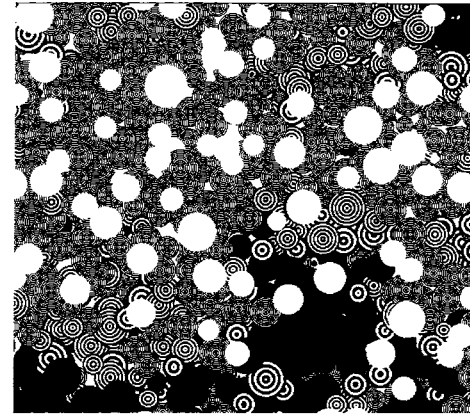
(A)

(D)

Legend:	●	◉	◎	◍	⦿	●
Patch Age:	1	2	3	4	5	>5

(B)

(E)

Legend:	⦿	◎	◎	◎	●
Bromus Density (D):	D=0	0<D≤Δ	Δ<D≤2Δ	2Δ<D≤3Δ	3Δ<D≤4Δ	4Δ<D

Δ = 0.01 (no. adult plants/cm²)

(C)

(F)

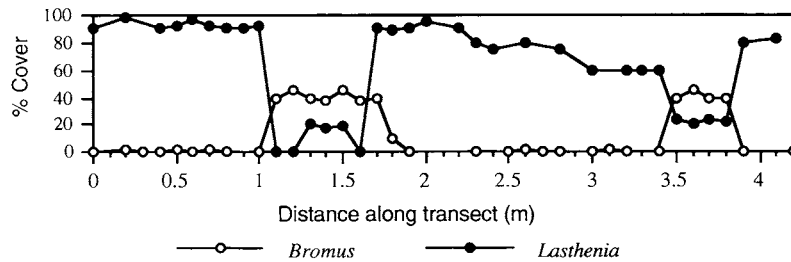| Legend:	⦿	◎	◎	◎	●
Lasthenia Density (D):	D=0	0<D≤Δ	Δ<D≤2Δ	2Δ<D≤3Δ	3Δ<D≤4Δ	4Δ<D

Δ = 0.01 (no. adult plants/cm²)
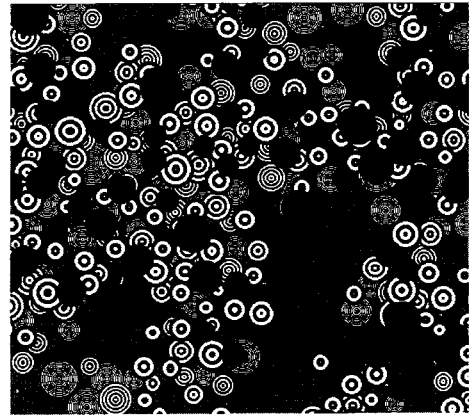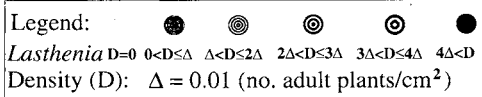
FIG. 9. Observed spatial distribution pattern of *Lasthenia californica* and *Bromus mollis* in the Jasper Ridge serpentine annual grassland: percentage cover of *L. californica* and *B. mollis* in 10 × 10 cm quadrats along a 4-m transect (redrawn from Hobbs and Mooney 1985).

Spatial patchiness and pattern of the disturbance population and plant populations

Spatial pattern in the shifting mosaics of patches. — The disturbance patch demographic module of PatchMod can generate a range of spatial patterns, including random and clumped ones. For illustrative purposes, we discuss one particular simulation run where disturbance patches are generated using the patch-formation probability method (see *Structure of the spatially explicit patch dynamic model: Disturbance patch demographic model* section above). Though rasterized spatial output data from the model may be easily displayed using common visualization packages (e.g., SPYGRASS, GRASS), we use the bull's eye diagrams because they are more precise (no data rasterization necessary) and preserve the uniqueness of the approach. Fig. 8A shows the spatial distribution of the age- and size-structured disturbance patch population at simulation time step (year) 10 when the plant population module starts to run. The initial plant population densities and their spatial distributions for species *L. californica* and *B. mollis* are displayed in Fig. 8 (B, C). Because the initial plant densities of both species in each patch (except the newly formed) are determined randomly between 0 and the maximum value observed, there is no appreciable difference between their initial distributions.

The serpentine grassland is composed of shifting mosaics of gopher mounds that differ in age, size, and plant composition. Fig. 8D is the distribution map of the disturbance patch population at simulation time year 100 for the exactly same area as in Fig. 8A. At this time the system as a whole has reached a steady state in metapopulation densities of the species modeled (see Fig. 7A). Although patches are evidently clumped in both the maps (Fig. 8A, D), the mosaics with highly aggregated patches have changed in space. Overall, the plant densities at the steady state have reduced appreciably for both species (compare Fig. 8B, C with Fig. 8E, F). The most interesting is, however, the correlation between the spatial distributions of the gopher mound population and the plant populations, which emerges from the bull's eye diagrams (Fig. 8A–

C). While *B. mollis* finds its higher densities mostly on effective gopher mounds (but not newly formed ones; see Fig. 8E), higher population density patches for *L. californica* seem to correspond to the areas covered by obsolete patches that are older than 5 yr (Fig. 8F). This simulated spatial distribution pattern of plant populations appears to be in good agreement with the alternating plant cover pattern observed in the field that species *B. mollis* has a higher percentage of plant cover on younger gopher mounds while *L. californica* dominates areas that have not recently been disturbed (Fig. 9). The existence of old patches with none or only few individuals of either species may well be a result of the limitation in seed dispersal.

The spatial patterns of gopher mound population and plant populations, in conjunction with their temporal dynamics, suggest that *L. californica* should be a superior competitor over *B. mollis* in areas that have not been disturbed in recent years (i.e., obsolete patches) and that *B. mollis,* on the other hand, outcompetes *L. californica* on relatively young gopher mounds (effective patches). This implies that the extinction of *B. mollis* in undisturbed or lightly disturbed areas should be frequent and that gopher activity seems necessary for this species to coexist with *L. californica.*

Effect of spatial patchiness on an ecological process on different scales. — Due to logistic constraints or limited perspectives, most ecological studies are characterized by a scale of investigation, frustrating across-scale comparison. Modeling work such as this allows the investigation of how particular properties scale from smaller scales to larger ones.

There are several ways of scaling an ecological process or relationship across spatial scales, and they usually involve changing the grain size (resolution) and/or the extent (the total study area; King 1991, Rastetter et al. 1992). For example, consider the observed relationship between population density and plant fecundity. At the local patch scale, plant fecundity decreases with population density exponentially, according to the assumptions of the model (Eq. 4, also see Fig. 10A). At the metapopulation and landscape scales, a quite different relationship is observed (Fig. 10B); because of clustering, measurement of landscape scale density does not translate easily into a spectrum of local
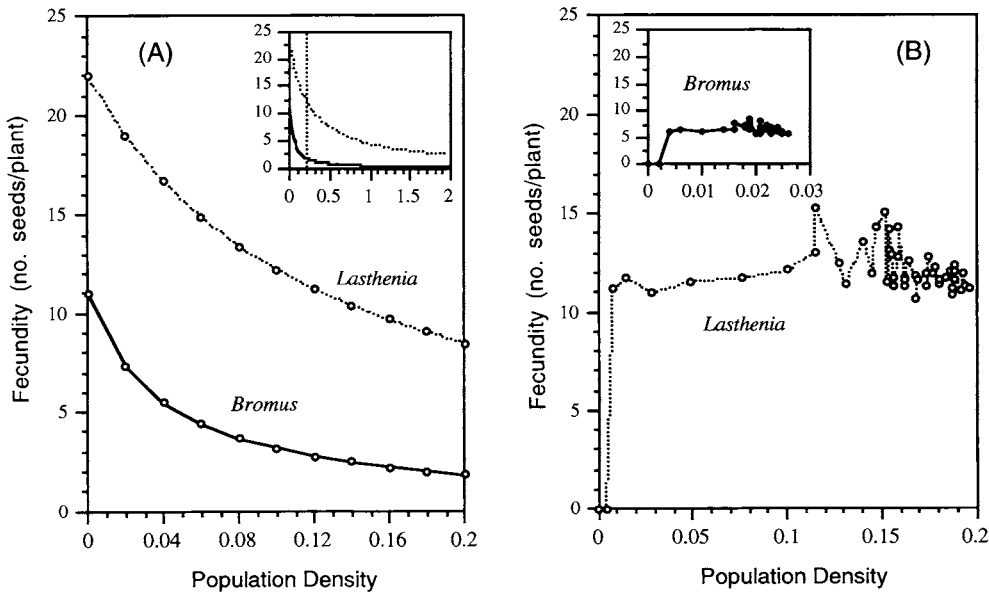
FIG. 10.   The relationship between population density and fecundity for *Bromus mollis* and *Lasthenia californica*: (A) at the local patch scale and (B) at the landscape scale. The inset of (A) represents a more complete picture of the local population density–fecundity relationship. The relationship seems similarly distorted for the two species due to spatial patchiness generated by localized disturbance and subsequent plant successional processes, though *B. mollis* actually experienced a much narrower range of metapopulation densities during the simulation (inset of B).

densities. Indeed, as we see from Fig. 10, after an initial transient phase, most patches are either saturated or empty regarding a particular species. The observed landscape-level relationships are dominated by a weighted average of two density levels and their effects.

Such change in the functional representation of an ecological process across spatial scales is sometimes termed "spatial transmutation" (sensu O'Neill 1979, King et al. 1991). The change in the fecundity–density relationship is a consequence of interactions between plant demographic processes and spatial patchiness created by localized disturbances on multiple scales. The negative feedback loop linking fecundity and population density at the local scale is transmuted due to aggregation, so that fecundity does not respond to the metapopulation density in the same way as it does to local population density. The annual grassland is a fast dynamic system in which steady states in population densities are rapidly reached on both the local and landscape scales (Figs. 6 and 7). The slower scale metapopulation dynamics are, therefore, dominated by flips among alternative local equilibria. This suggests the possibility of reducing the local plant population model to an interacting particle system (Durrett and Levin 1994), in which patches are treated simply as occupied or not. The fluctuations in fecundity at the landscape scale, on the other hand, reflect the stochasticities in the disturbance regime and plant demographic processes.

The spatial transmutation of the population density–fecundity relationship implies: (1) local density-depen-

dent relationships that are usually common to plants may not be detected when the grain size of samples is too large or when properly sampled data are improperly lumped over a larger spatial extent; (2) spatial patchiness distorts ecological relationships as scale changes and therefore makes scaling up more complex; and (3) our ability to predict the consequences or dynamics at a larger scale based on information at a local scale may well depend on how spatial heterogeneity "transmutes" the ecological process under consideration.

DISCUSSION AND CONCLUSIONS

Patch dynamics as a concept has been widely used in population and community ecology and provided new insights into problems of population dynamics and persistence, community structure and stability, and landscape dynamics since the early 1970s. Numerous 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 structure and functionality of the ecological system. For example, the size of a tree gap in a forest, a wave-created opening in an intertidal community, or a gopher mound in a grassland represents such a fundamental spatial scale. As a conceptual framework, patch dynamics provides a new way to view ecological systems by emphasizing spatial heterogeneity, transient dynamics, and relationships among hierarchical levels.

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 we have developed a spatially explicit, patch dynamics model that is built on the natural spatial unit, i.e, the patch. Our model 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 such an approach has to be computationally demanding, rapid development in computing technology has made this possible and practical.

The main purpose of this paper is to present the model as a tool for exploring ecological relationships; investigation of those relationships, in general, is reserved for future papers. However, to demonstrate the power of the approach, it is useful to give examples of the kinds of conclusions that are possible. In particular, our spatial patch dynamic model of the Jasper Ridge serpentine grassland can effectively relate spatiotemporal dynamics of plant populations to the age- and size-structured disturbance patch population. The simulations show (1) that local dynamics of disturbance patches can significantly contribute to the landscape-level pattern of *B. mollis* and *L. californica* populations; (2) that while metapopulations exhibit much less fluctuation in dynamics at the landscape scale, local populations of both species may be subject to frequent extinctions at the patch scale; (3) localized disturbances create areas in the landscape where patch return time is shorter than that required for local competitive exclusion, thus rendering regeneration niches for *B. mollis* and promoting coexistence of the two species modeled; and (4) density-dependent relations at the local patch scale may be transmuted between different spatial scales due to patchiness in the system.

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