Abstract. Phenomena such as disturbance play a major role in structuring ecological systems by producing a spatiotemporal mosaic of patches at different successional states. The distribution of species within the resulting mosaic depends upon an interaction between species’ life history traits and the spatial and temporal structure of the ecological processes controlling species’ distributions. We have used a spatially explicit simulation model (JASPER) of a serpentine grassland to examine the importance of some of these relationships, focusing primarily on the role of disturbance. The model JASPER is hierarchical in design and was developed to simulate the population dynamics of three interacting plant species: Bromus mollis, Calycadenia multiglandulosa, and Plantago erecta. Population dynamics were modeled as occurring within local sites, which were then arranged in a square array to form a landscape. Connections among sites within a landscape were made primarily through seed dispersal.

Several components of disturbance architecture were varied systematically among model runs to determine their impact on population dynamics at the scale of the landscape. We considered three levels of organization in modeling disturbance: (1) overall rate of disturbance, (2) size of individual disturbances, and (3) temporal and spatial autocorrelation among individual disturbances. The results demonstrate that the impact of disturbance depends upon a complex interaction between the life history characteristics of the species making up the community and the spatial and temporal structure of the disturbance regime. For example, we found that the biggest impact on species abundance occurred in response to a shift in the temporal autocorrelation structure of the disturbance regime. Also, species diversity was found to increase at intermediate levels of disturbance (as has been shown in several other studies). However, what can be considered an intermediate level of disturbance depends as much upon the temporal autocorrelation structure of the disturbance regime as it does upon the absolute rate of disturbance. These results suggest that predicting the impact of disturbance on ecological communities will require an explicit understanding of at least some aspects of the spatial and temporal architecture of the disturbance regime.

Key words: dispersal; disturbance; disturbance rate; disturbance size; landscape; life history; population dynamics; serpentine grassland; simulation model; spatial autocorrelation; temporal autocorrelation.

INTRODUCTION

The importance of spatial relationships and disturbance as factors affecting ecological systems has been recognized at least since Watt (1947) considered these influences together in his seminal paper on pattern and process. Although a large number of subsequent theoretical and empirical studies have examined the impact of disturbance on ecological systems, the spatial pattern of disturbance has in general been ignored, with attention being restricted to understanding only the effects of varying the rate and intensity of disturbance (e.g., Huston 1979, Hastings and Wolin 1989, Clark 1991a, b, Frelich and Lorimer 1991, Colasanti and Grime 1993, Turkington et al. 1993). Disturbance rate is generally represented only by the proportion of habitat affected by disturbance over a set time period or the temporal frequency with which disturbances occur (cf. definitions in Pickett and White 1985). Intensity is most often considered to be the proportion of damage (usually in terms of mortality or loss of biomass) caused by a localized disturbance. However, neither rate nor intensity of disturbance explicitly consider the spatial structure of the disturbance regime.

Recently, in the theoretical and empirical literature the traditional, non-spatial approach towards studying the impact of disturbance on ecological processes has been broadened to include an explicit consideration of the impact of varying the size of individual disturbances on ecological processes (Runkle 1982, Runkle and Yetter 1987, Armstrong 1988, Foster 1988a, b, Coffin and Lauenroth 1989, McConnaughay and Bazzaz 1990, 1991). This discussion has included an ex-
plicit consideration of the potential for disturbance size to influence community composition through an interaction with species’ life history attributes (Brokaw and Scheiner 1989, Halpern 1989, Spies and Franklin 1989, Whitmore 1989). And, in a few of these cases, there has also been careful consideration of the joint distribution of frequency and size of disturbances in a broadly based spatial context (Levin and Paine 1974, Paine and Levin 1981). In these studies, disturbance is most often viewed as occurring at random within a homogeneous landscape: the effect is to reset the local successional clock, producing a spatiotemporal mosaic of sites within the landscape. However, the successional processes occurring after disturbance are in general not treated as being dependent on the spatial structure of the system or of the disturbance regime (although see Lawton and Putz 1988, Coffin and Lauenroth 1989, Frellich et al. 1993).

The spatial context of disturbance regimes has received some attention in the metapopulation dynamics literature, an offshoot of the theory of island biogeography. Here, habitat suitable for occupation by species is viewed as being composed of islands separated by a matrix of uninhabitable landscape (Lefkovitch and Fahrig 1985, Fahrig 1988, Fahrig and Paloheimo 1988). Disturbance acts to remove populations from individual islands of habitat at a specified rate and/or with a specified intensity, and recolonization is a function of spatial location and dispersal geometry. In this view, the spatial structure of the landscape is static (although see Fahrig 1992), with populations periodically going extinct, and the question of interest is to determine the impact of different spatial architectures and dispersal geometries among islands on survival probabilities of the metapopulation as a whole. In general, the literature does not consider the much broader class of ecological processes that occur within a highly interconnected landscape (the traditional concern of the disturbance literature).

A systematic approach needs to be taken towards understanding the impact of varying spatial and temporal structures of disturbance regimes on ecological patterns and process in continuous landscapes. What does this entail? First, a scheme must be developed that allows a classification of disturbance regimes according to their spatial and temporal structure. Once this is accomplished, a systematic exploration of the impact of varying the spatial and temporal structure of the disturbance regime on ecological systems can be undertaken.

There are essentially three levels of organization to consider in classifying a disturbance regime and in characterizing its impact upon ecological landscapes: (1) the basic, non-spatial components of disturbance: rate and intensity; (2) spatial components of individual disturbances: size and shape; and (3) spatial and temporal components of groups of disturbances: temporal and spatial autocorrelation among individual disturbances. The non-spatial factors—rate and intensity—determine the immediate impact a disturbance regime has upon an ecological landscape. The rate of disturbance, for example, determines the proportion of the landscape that is reset to an earlier successional state; intensity determines how far back the successional clock is set. However, the manner in which a landscape recovers from disturbance, and ultimately the longterm ecological dynamics of the system, may depend critically upon the temporal and spatial structure of the disturbance regime. The size and shape of individual disturbances and the correlation structure among individual disturbances will ultimately determine the rate at which disturbed sites can be recolonized by species of varying life history characteristics and will set the long term structure of the resulting spatiotemporal ecological mosaic.

In this paper we will systematically explore the impact of varying the rate of disturbance, the size of individual disturbances, and the temporal and spatial autocorrelation among individual disturbances on the distribution and abundance of plant species. This will be done by means of a simulation model that has been developed to characterize the ecological dynamics of an annual serpentine grassland located at Jasper Ridge, California (Moloney et al. 1991). We will also relate model results to what is known about disturbance and the distribution and abundance of plant species at Jasper Ridge.

The advantage of the modeling approach is that we can explore a broader range of spatial and temporal scales than is possible in other contexts, such as experimentation and field observation. A modeling approach also allows us to examine a wider range of disturbance architectures under controlled conditions than would otherwise be possible.

**Model Description**

JASPER is a simulation model based upon the ecological dynamics occurring in an annual, serpentine grassland located at Jasper Ridge in the foothills of the Santa Cruz Mountains of California (see Moloney et al. (1991) and Hobbs and Mooney (1985) for a detailed description of the system). Results from an earlier version of the model have been presented elsewhere (Moloney et al. 1991; see also Wu and Levin 1994 for a complementary, patch-based modeling approach). JASPER has since been modified to allow for a more systematic exploration of the impact of the spatial and temporal structure of disturbance events on the demographic dynamics of plant species, and to include density-dependent competitive interactions among plant species. The earlier version of the model considered only intraspecific interactions, and used a negative exponential functional form to model density effects. In the current version of the model a commonly used density–yield function is employed instead (cf. Watkinson 1986, Seber and Wild 1989), allowing extension...
to interspecific interactions. A description of the current structure of the model will be presented in the following, with further details available in Moloney et al. (1991).

**General model structure**

**JASPER** is a hierarchical, spatially explicit simulation model constructed at two basic organizational scales, local and landscape (Fig. 1). At the local scale, **JASPER** consists of a submodel characterizing the demographic dynamics of plant species within a spatially homogeneous area of 0.01 m² (a 10 × 10 cm model cell at the landscape scale). An area of this size in the serpentine grassland at Jasper Ridge is small enough that the local microenvironment is roughly uniform, yet population densities are high enough to allow the study of intraspecific and interspecific interactions (Hueneke et al. 1990, Moloney et al. 1991). At the second level of organization, **JASPER** characterizes ecological dynamics at the scale of the landscape. The landscape-level model consists of a square grid of cells (typically 100 × 100 cells), with each cell in the grid containing a copy of the demographic submodel. In the following, a cell located at position (x, y) of the grid at timestep t will be referred to by z ∈ (x, y, t). Connections among cells in the landscape occur through dispersal of seeds. Disturbance also enters through a submodel at the scale of the landscape, and represents the effects of mound building activities by the western pocket gopher (*Thomomys bottae* Mewa). Boundaries are treated as periodic with the landscape forming a torus with respect to dispersal and disturbance. This is done for computational convenience alone, and to minimize boundary affects, and will have minimal effect on pattern for sufficiently large landscapes. The model is updated on an annual cycle with each model run lasting 200 cycles. All analyses were conducted on the last 100 cycles. We analyzed the last 100 cycles, in part, to avoid incorporating the initial transient behavior of the model into our results. [Preliminary studies of the detailed behavior of the model show that transient behavior at the beginning of a model run lasts, on average, 10 to 20 cycles, after which point the model settles down into its long-term dynamics (Moloney et al. 1991).]

**Disturbance submodel**

The disturbance submodel is patterned after the mound building activity of the western pocket gopher within the Jasper Ridge grassland and is structured to allow study of the impact of spatial and temporal patterns of disturbance on demographic processes. Gopher activity is widespread at Jasper Ridge and typically involves two spatial components: individual mounds, which are circular in shape, and mound clusters, which can consist of varying numbers of individual mounds in a localized region of the grassland (Moloney 1993). At this time little is known about year-to-year patterns of disturbance at Jasper Ridge. (A more detailed description of the disturbance regime at Jasper Ridge will be presented below in the discussion of model results.)

The aspects of the disturbance regime characterized by the disturbance submodel include: (i) timing of disturbance within the growing season, (ii) overall rate of disturbance, (iii) size of individual disturbances, (iv) probability of disturbances reoccurring within the same region at successive timesteps (temporal autocorrelation), and (v) spatial clustering of individual disturbances (spatial autocorrelation).

Individual disturbances are categorized as either early or late disturbances. The ratio of early to late disturbances was 3:1 in all model runs, corresponding to natural patterns of disturbance activity through the growing season. Early disturbances are modeled as occurring prior to seed production and dispersal by all of the species in the model. As a result, no seed is produced on these sites, but all species can recolonize through dispersal in the first year after disturbance. Late disturbances are modeled as occurring after seed production and dispersal by early flowering species, but prior to seed production and dispersal by late flowering species. Early flowering species can produce seed on these sites, but only late flowering species can recolonize during the first year after disturbance.

The overall rate of disturbance, defined to be the average proportion of cells in the model affected by disturbance during a time step, was varied among model runs but held constant within any given run. As with disturbance rate, the size of individual disturbances was held constant within each model run but could be varied among runs. Individual disturbances were always square in shape, with a 4 × 4 cell disturbance being the closest approximation to the size of naturally occurring mounds.

Three versions of the disturbance submodel were used to explore the impact of varying different aspects of disturbance architecture on population level dynamics within the simulated landscape. This resulted in three simulation experiments where disturbance rate (average number of cells disturbed) was varied independently of one other component of disturbance architecture in a series of model runs. The experiments examined (1) disturbance size vs. disturbance rate, (2) temporal autocorrelation vs. disturbance rate, and (3) spatial autocorrelation vs. disturbance rate.

**Disturbance size vs. disturbance rate.**—In this experiment, individual disturbances were of fixed size within any given model run, but varied in size among model runs. Size of individual disturbances ranged from a 2 × 2 cell area in runs with the smallest disturbances to a 16 × 16 cell area for runs with the largest disturbances. Disturbance rate within a model run was fixed by setting the probability *p*₀ that an individual cell in the landscape would be an initiation site for a disturbance. During each timestep individual distur-
Local Demographic Model

![Diagram of a local demographic model](image)

**FIG. 1.** Basic structure of the simulation model JASPER including a flow chart of the principal demographic processes occurring in individual cells. Flowering is a density-dependent stage involving intra- and interspecific competition.

Individual disturbances were initiated within regions using the same protocol as in the disturbance size vs. disturbance rate experiment subsection above, using \( p_R \) instead of \( p_D \) as the test value. No disturbances were initiated in cells lying outside of the disturbance regions. The number of regions of disturbance activity varied among model runs, but was held constant within any particular model run. The landscape-level disturbance rate for a given model run was effectively a function of the number of disturbance regions entering into the model, since \( p_R \) was fixed at a value of 0.10.

At the beginning of each model run the disturbance regions were distributed at random within the landscape. During subsequent timesteps, each region was repositioned at random with probability \( p_M \), which will be referred to as the disturbance turnover rate. We varied \( p_M \) from 0.0 (no repositioning) to 1.0 (repositioning at each timestep) among different model runs to alter the temporal autocorrelation of the disturbance regime. At low values of \( p_M \) there was a high probability that a cell that was impacted by a disturbance during one timestep would also be impacted during following timesteps, due to little repositioning of disturbance

Dispersal POOL

Disperse?

Seed Bank

Germinate

Survive?

Gopher Disturbance

Flower Census

Flower

Generation Counter

Initialize

Gopher Disturbance

Census

Landscape Scale Grid

In this experiment, the size of individual disturbances was set to be a 4 × 4 cell area in all of the model runs. Temporal autocorrelation among disturbances was modeled as a two-stage process. In the first stage, regions of disturbance activity were positioned on the landscape grid, with each region consisting of a 20 × 20 cell area. In the second stage, each of the cells in a disturbance region became an initiation site for an individual disturbance with probability \( p_R \). The value of \( p_R \) was set to 0.10 for all of the model runs in this experiment. There was an intermediate degree of spatial autocorrelation among individual disturbances in the model runs of this experiment, due to the clustering of disturbances in the disturbance regions.

Temporal autocorrelation vs. disturbance rate.—In this experiment, the size of individual disturbances was set at random by drawing a random number \( p^* \) for each cell in the landscape; if \( p^* < p_D \) then a disturbance was initiated in that cell, with the top left corner of the disturbance being located in the initiating cell. The landscape-level disturbance rate was effectively a function of disturbance size and \( p_D \), the initiation probability. There was no spatial or temporal autocorrelation among individual disturbances in this version of the disturbance submodel.

Temporal autocorrelation vs. disturbance rate.——In this experiment, the size of individual disturbances was set at a 4 × 4 cell area in all of the model runs. Temporal autocorrelation among disturbances was modeled as a two-stage process. In the first stage, regions of disturbance activity were positioned on the landscape grid, with each region consisting of a 20 × 20 cell area. In the second stage, each of the cells in a disturbance region became an initiation site for an individual disturbance with probability \( p_R \). The value of \( p_R \) was set to 0.10 for all of the model runs in this experiment. There was an intermediate degree of spatial autocorrelation among individual disturbances in the model runs of this experiment, due to the clustering of disturbances in the disturbance regions.
regions. Under these circumstances there was a high degree of temporal autocorrelation in the disturbance regime at the level of the cell. At high values of \( p_M \) disturbance regions had a high probability of being relocated randomly across timesteps leading to very little temporal autocorrelation in the disturbance regime.

Spatial autocorrelation vs. disturbance rate.---As in the previous experiment, the size of individual disturbances was set to be a 4 \( \times \) 4 cell area in all of the model runs. Although spatial autocorrelation among disturbances could have been modeled using the two step process described in the temporal autocorrelation vs. disturbance rate experiment above, we took a different approach that allowed more precise control of the level of spatial autocorrelation over the entire landscape. Essentially, we adopted the midpoint displacement method (the algorithm MidPointFM2d presented as pseudocode in Saupe 1988) for generating random two-dimensional fractal landscapes, and used output from this algorithm to determine where disturbances would occur within the model landscape. (Landscapes produced by this algorithm were 128 \( \times \) 128 cells in size, instead of the standard 100 \( \times \) 100 cells, due to constraints imposed by the algorithm.) We will briefly describe the algorithm below as it pertains to generating spatially correlated disturbances. A more detailed description of the theory behind the algorithm and its implementation can be found in Burrough (1983) and Saupe (1988). Palmer (1992) also provides an extremely interesting example of the midpoint displacement algorithm as used in a spatial modeling context.

The midpoint displacement algorithm models a two-dimensional stochastic process \( Z \) that has the following properties (Saupe 1988):

\[
E(Z(x_1) - Z(x_2)) = 0 \tag{1}
\]

and

\[
\text{var}(Z(x_1) - Z(x_2)) = E[(Z(x_1) - Z(x_2))^2] = \sigma^2 \| x_1 - x_2 \|^{2H}, \tag{2}
\]

where \( x_i \) is location in two-dimensional space, \( Z(x) \) is the value of the stochastic process at location \( x \), \( \| x_1 - x_2 \| \) is the Euclidean distance between two locations, \( H \) is a parameter determining the fractal dimension of the process, and \( \sigma^2 \) is a variance term. As can be seen in Eq. 2, the degree of spatial autocorrelation in \( Z \) across the model landscape can be controlled by varying the parameter \( H \) from a value of 0.00 (no spatial autocorrelation and a fractal dimension of 3) to a value of 1.00 (strong spatial autocorrelation and a fractal dimension of 2) to a value of 1.00 (strong spatial autocorrelation and a fractal dimension of 2) to a value of 1.00 (strong spatial autocorrelation and a fractal dimension of 2) to a value of 1.00 (strong spatial autocorrelation and a fractal dimension of 2). Intermediate values of \( H \) can be used to generate landscapes with varying degrees of spatial autocorrelation in \( Z \), and fractal dimensions between 2 and 3.

We used the midpoint displacement algorithm to generate disturbances in the following way: We fixed the value of \( H \) for any particular model run and generated a new fractal landscape at each timestep. We then selected a set proportion (\( p_d \)) of the cells from the landscape to serve as potential initiation sites for individual disturbances. Half of the sites selected came from the 1/2 \( p_s \) highest values of \( Z \) and the other half from the 1/2 \( p_s \) lowest values of \( Z \). Once the potential initiation sites were identified, individual disturbances were produced at these sites at random with probability \( p_s \), where \( p_s \) was held constant for individual model runs. As a consequence, the landscape-level disturbance rate was a function of both \( p_s \) and \( p_s \). The value of \( p_s \) set the upper limit for the local (within region) disturbance rate, whereas the value of \( p_s \) set the overall proportion of the landscape that could be affected by disturbances. For \( H = 0.00 \), the sites selected were randomly distributed as individual cells or very small clusters of cells within the landscape (Fig. 2). For \( H = 1.00 \), the sites selected were located in large clusters of contiguous cells. Intermediate values of \( H \) produced intermediate levels of clustering consistent with the spatial autocorrelation structure indicated in Eq. 2 above. There was effectively no temporal autocorrelation in the disturbance regime for the model runs in this experiment.

Demographic submodel

The demographic submodel of JASPER included three species---*Bromus mollis*, *Calycadenia multiglandulosa* and *Plantago erecta*---which were chosen to represent different life history types found at Jasper Ridge. (A fourth species, *Lasthenia californica*, was included in the original version of JASPER, but was not included here due to inconsistencies in data availability for parameterizing the model with respect to interspecific competition.) *Calycadenia multiglandulosa* is a late flowering annual forb with moderate reproductive output, high rate of dispersal, and strong competitive ability. *Plantago erecta* is an early flowering annual forb with a low dispersal rate, high reproductive output, and strong competitive ability. *Bromus mollis* is an early flowering annual grass, with high dispersal ability, high seed output, and poor competitive ability on serpentine soils. *Bromus mollis* is also one of the few exotic species that has been able to invade the serpentine grassland at Jasper Ridge. However, *Bromus*' ability to invade and persist is highly variable, changing dramatically with shifts in rainfall patterns (Hobbs and Mooney 1991).

Three demographic transitions for each species \( i \) were included in the demographic submodel: (a) germination, (b) survival to flowering, and (c) seed production (Fig. 1). Germination rates \( g \), were constant for each species within and among model runs, and were based on data from Hobbs and Mooney (1985), Hobbs and Hobbs (1987), and Gulmon (1992) (Table 1). Sur-
The potential initiation sites were determined by the midpoint displacement algorithm, with parameter values set as follows: For model runs with $H = 0.00$ and 0.50, $p_L$ was set equal to 0.10; for model runs with $H = 1.00$, $p_L$ was set equal to 0.15; and, in all of the examples, $p_S = 0.10$. The parameter $H$ determines the fractal dimension of the landscape; $p_L$ determines the proportion of cells in the landscape that are potential initiation sites for a disturbance; and $p_S$ is the probability that a disturbance will actually be produced at a particular site and timestep in the model run. These parameter settings resulted in average landscape-level disturbance rates of 0.13, 0.100, and 0.13 for $H = 0.00$, 0.50, and 1.00, respectively. (See Model description: Disturbance submodel: Spatial autocorrelation vs. disturbance rate for a more detailed explanation of the protocol used in setting disturbances.)

Survivability $s_i(\delta(z))$ was a function of recent disturbance history $\delta(z)$, with values being determined from data published in Hobbs and Mooney (1985). The dummy variable $\delta(z) \in 0, 1, 2$ represents recent disturbance history at cell location $z$, where 0 = no disturbance; 1 = early disturbance; and 2 = late disturbance (or early and late disturbance combined). Seed production $w_i(z)$ is based on a density—yield function incorporating both inter- and intraspecific density effects:

$$w_i(z) = m_i(\delta(z)) \times \left[ 1 + \sum_k \alpha_{i,k}n_k(z) \right]^{-\beta_i}.$$  

Here, $m_i(\delta(z))$ represents maximum seed production for species $i$ with recent disturbance history $\delta(z)$, $n_k(z)$ the abundance of flowering individuals of species $k$, $\alpha_{i,k}$ the competitive effect of species $k$ upon species $i$, and $\beta_i$ a parameter controlling the intensity of the competitive effect. ($\beta_i$ is often considered to be related to resource use efficiency (Watkinson 1986).) Parameters for the above equation were determined from a series of competition experiments conducted in lysimeters containing serpentine soils, which were exposed to ambient environmental conditions at Jasper Ridge (K. Moloney and N. Chiariello, unpublished data).
TABLE 1. Demographic parameters used for the three species—Bromus, Calycadenia, and Plantago—in the Jasper spatial simulation model of population dynamics at Jasper Ridge, California. (See Model description: Demographic submodel and Dispersal submodel for details on the source of the values used to fit the parameters.)

<table>
<thead>
<tr>
<th>Demographic process</th>
<th>Parameter</th>
<th>Species i</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Bromus</td>
</tr>
<tr>
<td>Germination rate</td>
<td>$g_i$</td>
<td>0.98</td>
</tr>
<tr>
<td>Survivorship, $s(k)$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>No disturbance ($k = 0$)</td>
<td>$s_i(0)$</td>
<td>0.49</td>
</tr>
<tr>
<td>Early disturbance ($k = 1$)</td>
<td>$s_i(1)$</td>
<td>0.90</td>
</tr>
<tr>
<td>Late disturbance ($k = 2$)</td>
<td>$s_i(2)$</td>
<td>0.47</td>
</tr>
<tr>
<td>Maximum seed production, $m_i(k)$</td>
<td>[no. seeds/individual]</td>
<td></td>
</tr>
<tr>
<td>No disturbance ($k = 0$)</td>
<td>$m_i(0)$</td>
<td>179.39</td>
</tr>
<tr>
<td>Early disturbance ($k = 1$)</td>
<td>$m_i(1)$</td>
<td>237.33</td>
</tr>
<tr>
<td>Late disturbance ($k = 2$)</td>
<td>$m_i(2)$</td>
<td>351.40</td>
</tr>
<tr>
<td>Competition coefficient ($\alpha_i$)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bromus ($j = 1$)</td>
<td>$\alpha_1$</td>
<td>1</td>
</tr>
<tr>
<td>Calycadenia ($j = 2$)</td>
<td>$\alpha_2$</td>
<td>1.2</td>
</tr>
<tr>
<td>Plantago ($j = 3$)</td>
<td>$\alpha_3$</td>
<td>1.003</td>
</tr>
<tr>
<td>Competition exponent</td>
<td>$\beta_i$</td>
<td>1.08</td>
</tr>
<tr>
<td>Local dispersal</td>
<td>$d_1$</td>
<td>0.11</td>
</tr>
<tr>
<td>Long-distance dispersal</td>
<td>$d_2$</td>
<td>0.29</td>
</tr>
</tbody>
</table>

A simple, non-spatial, difference equation model of the system can be written using the above definitions:

$$n_i(t + 1) = n_i(t) \times m'_i \times \left[1 + \sum \alpha_i n_i(t)\right]^{-\alpha_i} \tag{4}$$

where $m'_i = g_i \times s_i(l) \times m_i(l)$. Here, the dummy variable $l$ was held at a constant value of 0, 1, or 2, producing three different versions of Eq. 4 that reflect environmental conditions associated with sites recently affected by no disturbance, early disturbance, or late disturbance, respectively. This formulation represents a model with no direct, mechanical effects of disturbance on seed production and the seed bank, and no dispersal out of the local cell. The utility of this approach was to allow us to examine the potential effects on long term demographic processes of the different environmental conditions associated with disturbance, without including the added complexities of spatial interactions and disturbance-related mortality.

Dispersal submodel

Dispersal for each species was modeled as consisting of three fractions: the stay-at-home fraction $d_h$ (no dispersal), a local dispersal fraction $d_l$ (local dispersal), and a long-distance dispersal fraction $d_d$ (bath dispersal). In bath dispersal, the long-distance fraction was accumulated from each model cell into a landscape-level seed pool. The number of seeds in the pool was then divided by the number of cells in the model to determine the mean number of seeds available for distribution to each cell. Seeds from the long-distance seed pool were then distributed to each cell at random using a Poisson distribution characterized by the landscape-level mean. The local fraction of dispersing seed was evenly divided among the eight cells adjacent to each cell. The remainder of the seed produced in a cell remained in the cell. The long-distance and local dispersal fractions were determined from data presented in Hobbs and Hobbs (1987).

SIMULATION EXPERIMENTS

We conducted an analysis of the non-spatial version of the model JASPER and three simulation experiments. The results from the analysis of the non-spatial model were used to provide insight into the potential contribution each type of site (undisturbed, early disturbance, and late disturbance) had on population dynamics in the fully specified, spatial model. As indicated above, the three simulation experiments were designed to explore the importance of disturbance architecture in determining species distributions within the modeled landscape. In each experiment, disturbance rate was varied independently of one other aspect of the spatial or temporal architecture of the disturbance regime. All other aspects of the disturbance regime were held fixed.

For each of the three simulation experiments, a series of model runs was conducted varying the two variables of interest across a broad range of values (e.g., disturbance size and landscape-level disturbance rate in the disturbance size vs. disturbance rate experiment). Only one model run was conducted for each combination of parameter values to enable a more extensive exploration of parameter space. We feel that this was a reasonable approach since landscapes were either 100 X 100 cells or 125 X 125 cells in size and summary statistics were calculated over the last 100 timesteps of a model run, incorporating information from either 1 000 000 or 1 562 500 individual cells in each calcu-
TABLE 2. Equilibrium solutions to Eq. 4, with and without Bromus, assuming survivorship rates for environmental conditions occurring under each of three types of recent disturbance history.

<table>
<thead>
<tr>
<th>Disturbance history</th>
<th>With Bromus</th>
<th>Without Bromus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>None</td>
<td>Early</td>
</tr>
<tr>
<td>Plant density (inds./0.01 m²)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bromus</td>
<td>-0.4</td>
<td>47.9</td>
</tr>
<tr>
<td>Calycadenia</td>
<td>24.3</td>
<td>43.5</td>
</tr>
<tr>
<td>Plantago</td>
<td>32.0</td>
<td>39.7</td>
</tr>
<tr>
<td>λ₁</td>
<td>1.01</td>
<td>0.68</td>
</tr>
</tbody>
</table>

*λ₁ is the eigenvalue of greatest magnitude for the linearization matrix A associated with Eq. 4 for each of the models examined here (see Simulation experiments: Non-spatial model for a more complete description of the analysis). Equilibria are stable if |λ₁| < 1.

TABLE 3. Equilibrium solutions to Eq. 4 in the absence of interspecific competition for environmental conditions occurring under conditions produced by each of three disturbance types. (Equilibria are stable if |λ₁| < 1.)*

<table>
<thead>
<tr>
<th>Disturbance history</th>
<th>None</th>
<th>Early</th>
<th>Late</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>Density (inds./0.01 m²)</td>
<td>Density (inds./0.01 m²)</td>
<td>Density (inds./0.01 m²)</td>
</tr>
<tr>
<td>Bromus</td>
<td>60.92</td>
<td>-0.10</td>
<td>139.90</td>
</tr>
<tr>
<td>Calycadenia</td>
<td>26.54</td>
<td>0.04</td>
<td>48.87</td>
</tr>
<tr>
<td>Plantago</td>
<td>43.50</td>
<td>-0.29</td>
<td>63.33</td>
</tr>
</tbody>
</table>

*λ₁ is the eigenvalue of greatest magnitude for the linearization matrix A associated with Eq. 4 for each of the models examined here (see Simulation experiments: Non-spatial model for a more complete description of the analysis).

Non-spatial model

The non-spatial version of JASPER was analyzed to determine the three-species equilibrium points and their associated stability properties for each set of conditions associated with recent disturbance history (Table 2). We also analyzed a version of the model that suppressed interspecific density effects (αᵢⱼ = 0 for i ≠ j in Eq. 4) to determine equilibrium values for the species in the absence of interspecific competition (Table 3). Any differences in equilibrium values predicted for the three versions of the non-spatial model would be primarily a function of differences in rates of survivorship and seed production, as these were the parameters affected by recent disturbance history (Table 1).

The methodology we used in determining equilibrium points and their stability was as follows: Equilibrium points satisfy \( n_i(t + 1) = n_i(t) \) in Eq. 4. Non-trivial equilibria therefore satisfy

\[ \mathbf{n} = \mathbf{A}\mathbf{n}^*, \]

in which \( \mathbf{n} \) and \( \mathbf{n}^* \) are vector quantities and \( \mathbf{A} \) is a matrix, with \( \mathbf{n} = (n_i^*, n_j^*, \ldots, n_k^*, 1) \), \( \mathbf{A} = (\alpha_{ij}) \), and \( \mathbf{n}^* = (n_i^*) \). Here, \( n_i^* \) represents the equilibrium population size for species \( i \). We solved for \( \mathbf{n}^* \) and conducted a stability analysis for each set of conditions in the non-spatial model using standard analytical and numerical techniques (e.g., Edelstein-Keshet 1988). The eigenvalue of greatest magnitude \( (\lambda_1) \) for each linearization matrix was determined. The equilibrium point is stable if \( |\lambda_1| < 1 \) and unstable if \( |\lambda_1| > 1 \). Linearization, and the ability to assess stability without a more detailed analysis, fails if \( |\lambda_1| = 1 \).

Bromus had the highest density of the three species in the early disturbance version of the non-spatial model. In contrast, Bromus went extinct under conditions of no disturbance and late disturbance (Table 2). Bromus thus was not able to coexist with Calycadenia and Plantago under the environmental conditions imposed under no disturbance or late disturbance versions of the model. The results for Bromus can be explained primarily by differences in survivorship among the...
March 1996

DISTURBANCE EFFECTS ON LANDSCAPES

three versions of the model, and by the relatively strong competitive effects of *Calycadenia* and *Plantago* (Table 1).

Without *Bromus*, the equilibrium point for the community of *Calycadenia* and *Plantago* is stable, and stable to invasion by *Bromus* (Table 2).

The equilibrium values for *Plantago* in the three-species model were similar under environmental conditions associated with no disturbance and late disturbance, and somewhat higher for conditions associated with early disturbance (Table 2). However, in the absence of interspecific competition, *Plantago* had the highest equilibrium density under conditions associated with late disturbance (Table 3). Predicted equilibrium values for *Calycadenia* varied threefold among the three versions of the three-species model, with the highest value being associated with late disturbance and the lowest with no disturbance. And, unlike those for *Plantago*, the predicted equilibrium values for *Calycadenia* didn’t differ much between the versions of the model having no competition and three-species competition.

The observed patterns for *Plantago* and *Calycadenia* resulted from greater seed production by both species in disturbed sites, particularly late disturbance, which ultimately led to an intensification of competition. For *Plantago*, intensification of competition led to a decrease in seed production, due to density effects, and eventually to a decrease in realized carrying capacity (Tables 2 and 3). This was due in large part to the relatively strong competitive effect of *Calycadenia* on *Plantago* and in part to the relatively large value of $\beta$ for *Plantago* (Table 1; also see Begon and Mortimer (1986) for a discussion of the relationship between the magnitude of $\beta$ and the resulting density effects). On the other hand, the impact of increasing competition had little effect on *Calycadenia* due to the weak competitive effect of *Plantago*. These relationships gave *Calycadenia* a distinct advantage over *Plantago* under conditions of increasing density. However, competitive displacement of *Plantago* by *Calycadenia* did not occur under any of the conditions modeled. The latter would be expected on theoretical grounds given that the interspecific density effects were always less than the intraspecific density effects for these two species.

**Disturbance size vs. disturbance rate**

The first simulation experiment was designed to explore the impact of varying the size and rate of disturbances on population dynamics. The size of individual disturbances and the landscape-level rate of disturbance were held fixed in each model run, but were varied independently among model runs. Individual disturbances were always square in shape and varied in area among model runs from 4 cells to 256 cells. The average landscape-level disturbance rate varied from 0.00 to 0.99.

Species richness at the level of the landscape was a function of both disturbance rate and disturbance size (Fig. 3). The greatest level of species richness (3 species) was observed for model runs with an intermediate disturbance rate, although the range of disturbance rates over which all three species were present varied among disturbance sizes. At lower disturbance rates, *Bromus* was absent from the community and at higher rates *Plantago* dropped out. At even higher disturbance rates *Calycadenia*, and subsequently *Bromus*, dropped out.

Mean abundance for two of the species, *Plantago* and *Calycadenia*, declined under increasing disturbance rates (Fig. 4). *Plantago* survived only at disturbance rates <0.19, with the one exception of disturbances of the smallest size (4 cells), and exhibited an approximately linear decline in average abundance with increasing rates of disturbance. In contrast, *Calycadenia* was able to survive at very high disturbance rates (0.87 as a maximum), and exhibited a curvilinear
FIG. 4. Mean abundance per cell and the coefficient of variation for mean abundance per cell for the species Bromus, Calycadenia, and Plantago calculated over the last 100 timesteps in simulations incorporating varying combinations of disturbance rate and disturbance size in the model JASPER. See Simulation experiments for details concerning the calculation of these statistics. Symbols used for size treatments are the same as in Fig. 3.

decline in abundance that was more gradual at lower disturbance rates and increased at higher rates.

Bromus exhibited a more complex abundance pattern than the other two species under changing disturbance rates. At disturbance rates <0.18, Bromus was not able to coexist with the other two species. However, Bromus was able to survive at higher disturbance rates, exhibiting an initial increase in abundance up to a disturbance rate of ~0.27, and then declined linearly in abundance beyond this point. A slight increase in mean abundance for Bromus was observed for all disturbance sizes at disturbance rates >0.87. This corresponded to the disappearance of Calycadenia from the model and a subsequent release from competition.

The effect of varying disturbance size on mean abundance was minimal, with one notable exception. The mean abundance of Plantago increased for model runs consisting of the smallest disturbances (4 cells). There was also a concomitant decrease in the mean abundance of Bromus under these circumstances due to an increase in the competitive effects of Plantago. The increased success of Plantago in the smallest disturbances was primarily a function of Plantago’s low dispersal rates. Plantago could successfully recolonize all of the cells of a disturbance of size 4 at lower disturbance rates, as most of the cells in disturbances were adjacent to undisturbed sites already occupied by Plantago. In larger disturbances, there could be a considerable delay in recolonization of the interior cells by Plantago due to the slow rate of dispersal, putting Plantago at a competitive disadvantage (Fig. 5).

Temporal variability in mean abundance increases
with increasing rates of disturbance and with increasing disturbance size for all three species (see coefficient of variation in Fig. 4). One apparent anomaly occurred at a disturbance rate of 0.27, where Plantago exhibited an abnormally high degree of variability for disturbances of size 16. However, this result was an artifact of Plantago going extinct over the last 100 timesteps of the simulation, inflating the variance due to the non-stationarity of the process.

Temporal autocorrelation vs. rate of disturbance

The second simulation experiment examined the joint effects of temporal autocorrelation in the disturbance regime and overall disturbance rate on plant species distributions. The amount of temporal autocorrelation in the disturbance regime was varied among model runs systematically by altering the turnover rate \( p_d \) from 0.0 to 1.0 in increments of 0.2. (As explained in Model: General model structure: Temporal autocorrelation vs. disturbance rate description, turnover rate is inversely proportional to the degree of temporal autocorrelation in the disturbance regime.) The landscape-level disturbance rate was varied from 0.0 to \( \approx 0.95 \).

The abundance curves and species richness curves in this experiment were similar in shape to the curves observed for the size vs. rate experiment discussed above (Figs. 6 and 7). However, turnover rate had a large impact on species abundances, contrasting sharply with the minimal response observed for changes in disturbance size. There was also a strong interaction between disturbance rate and turnover rate in determining species richness. All three species occurred only when there were "moderate" rates of disturbance (e.g., Fig. 8). However, what could be considered "moderate" shifted toward lower disturbance rates in response to increasing turnover rates (lower temporal autocorrelation). The same shift towards lower disturbance rates for the transitions to one or no species in the landscape was observed with increasing turnover rates.

The nature of the response to changes in turnover rates differed among the three species. The average abundance for Plantago declined with an increase in the turnover rate, whereas Calycadenia's abundance increased. With no turnover in regions of disturbance activity, Plantago was able to persist at very high disturbance rates (>90%). In this situation, the landscape was effectively composed of two habitat types, disturbed and undisturbed, with Plantago finding refuge in undisturbed habitat. In landscapes with even a minimal chance of having all sites impacted by disturbance (turnover rates as low as 0.20), Plantago could only persist at low to moderate disturbance rates.

Bromus exhibited a more complex response to changing disturbance rates than the other two species (Fig. 7). Its abundance curves shifted towards lower disturbance rates with an increase in the turnover rate. In the case of no turnover \( (p_d = 0) \), Bromus was not able to coexist with the other two species at any disturbance rate. Bromus' abundance was apparently enhanced at moderate levels of disturbance under conditions that promoted the availability of recently disturbed habitat that had subsequently been released from...
the influence of disturbance. This would also explain the lower abundances at high disturbance rates, as compared to the first experiment, where there should have been more edge sites available for a given disturbance rate due to lower spatial autocorrelation among individual disturbances.

Temporal variance in the abundance of Calycadenia and Plantago (scaled by mean abundance) had a general tendency to decline with decreasing turnover rates (Fig. 7). However, for Bromus this was only true at higher disturbance rates. Variance in Bromus exhibited a bimodal distribution with peaks in variance associated with both low and high disturbance rates. These two regions corresponded to circumstances under which mean abundances were low.

Spatial autocorrelation vs. rate of disturbance

The third simulation experiment examined the joint effects of spatial autocorrelation among individual disturbances and disturbance rates on plant species distributions. The parameter $H$ was varied from 0.00 to 1.00 in increments of 0.25, with $p_5$ equal to 0.10, and the proportion of the landscape sites selected to be initiation points for individual disturbances ($p_i$) varied from 0.01 to 1.00. This produced disturbance rates over a range of values from 0.014 to 0.79. Further simulations were conducted by setting $p_i = 1.00$ and varying $p_S$ from 0.11 and 0.15 in increments of 0.01. The latter was done to push landscape-level disturbance rates above the maximum obtainable ($≈ 0.79$) by setting $p_S = 0.10$.

There was little, if any, effect of changes in the spatial autocorrelation structure of the disturbance regime on the mean abundance or normalized variance of Calycadenia (Fig. 9). Plantago went extinct at lower disturbance rates in landscapes characterized by greater degrees of clustering of individual disturbances (high values of $H$). In these cases, Plantago was not able to recolonize disturbed sites readily due to its poor dispersal ability. Bromus exhibited a bimodal response to the degree of spatial autocorrelation. At high rates of disturbance, Bromus decreased in abundance with increases in spatial autocorrelation in the disturbance regime. At lower rates of disturbance, Bromus showed a non-linear, but minimal, response to changes in spatial clustering of disturbances.

Species richness was again highest for “intermediate” disturbance rates (Fig. 10); intermediate rates in this context shifted towards lower disturbance rates for higher levels of spatial clustering in the disturbance regime (i.e., higher values of $H$).

SYNTHESIS

Simulation experiments

We found that all three of the species modeled in the non-spatial version of JASPER could survive in the absence of interspecific competition under the conditions of no disturbance, early disturbance, or late disturbance. In fact, equilibrium densities of all three species increased under environmental conditions associated with disturbances. These results are primarily a function of the parameterization of the model, which reflects increasing rates of survivorship and fecundity on sites associated with recent disturbances, as determined from field data presented in Hobbs and Mooney (1985).

It is important to understand the derivation of the parameters for survivorship and fecundity to be able to interpret the results of the spatial and non-spatial versions of JASPER appropriately. These parameters were derived from observations taken on and off mounds under natural field conditions (Hobbs and Mooney 1985). As such, they reflect conditions associated with differences in the soil environment produced by the formation of gopher mounds and with differences in community structure resulting from disturbance. Because of this, the dynamics of the model
March 1996

DISTURBANCE EFFECTS ON LANDSCAPES

387

Fig. 7. Mean abundance per cell and the coefficient of variation for mean abundance per cell for the species *Bromus*, *Calycadenia* and *Plantago* calculated over the last 100 timesteps in simulations incorporating varying combinations of disturbance rate and turnover rate in the disturbance regime (turnover rate as defined in Model description: Disturbance submodel: Temporal autocorrelation vs. disturbance rate). See Simulation experiments for details concerning the calculation of these statistics. Symbols used for turnover rates are the same as in Fig. 6.

implicitly include the differential effects of interspecific competition among the different types of sites. The net effect is to discount seed production and survivorship more heavily on undisturbed sites, due primarily to an increase in interspecific competition because of higher overall plant densities (Hobbs and Mooney 1985, Koide et al. 1987). The primary effect of soil differences among sites of different disturbance histories alone would be to decrease growth rates on mound sites due to a decrease in N and P concentrations and a decrease in the Ca:Mg ratio (Koide et al. 1987). As such, what we are really modeling is the detailed interactions occurring among three species imbedded within a community matrix whose structure is affected by disturbance history.

The outcome of the non-spatial version of the model changed dramatically when interspecific competition was introduced. Equilibrium densities of all three species declined under most conditions, although the decline was minimal for *Calycadenia* as compared to the other two species. None of the results from this version of the model were surprising and could have been predicted by inspection of model parameters (see Begon and Mortimer (1986) and Watkinson (1986) for a discussion of the relevant theory). What we gain from this analysis is an understanding of the potential contribution of sites of different disturbance history to overall population densities in the spatially explicit model. Only sites characterized by recent disturbance early in the growing season would be expected to have a long
term positive influence on population densities of *Bromus* in the presence of *Plantago* and *Calycadenia*. All of the sites would be expected to have a positive influence on the abundance of *Calycadenia*, increasing in the order of no disturbance→early disturbance→late disturbance. *Plantago*, on the other hand, would be predicted to benefit most from sites impacted by a recent, early disturbance.

What we gain from adding a spatially explicit component to the model is the ability to explore the impact of the mechanical effects of disturbance under different spatial and temporal disturbance architectures. Models characterized by the same disturbance rate had approximately the same proportion of sites under conditions of no disturbance, early disturbance, and late disturbance. However, the spatial and temporal relationships among these sites varied among models with different disturbance architectures. By comparing model outcomes at a fixed disturbance rate we can develop a clear understanding of the effect of disturbance architecture on the dynamics of the species in our model ecosystem, and perhaps gain a general understanding of the factors regulating species distributions at Jasper Ridge.

The biggest effect on model outcome, for a fixed disturbance rate, was produced by changing the temporal autocorrelation structure of the disturbance regime. For *Bromus* and *Plantago*, the impact of increasing the degree of temporal autocorrelation (decreasing the value of $p_M$) was effectively the same as decreasing the landscape-level disturbance rate. The opposite was true for *Calycadenia*. Perhaps the most interesting result was produced in model runs for which $p_M$ was set equal to zero. Under these circumstances two distinct habitats were produced, a habitat consisting of clusters of cells that had a high probability of being disturbed during each timestep and a habitat consisting of clusters of cells that were never disturbed. For these simulations, *Bromus* could not coexist with the two other species at any disturbance rate and *Plantago* was able to persist at very high disturbance rates. Under all other versions of the model examined, *Bromus* was present at intermediate disturbance rates and *Plantago* disappeared from the landscape at low to intermediate disturbance rates.

Although the effect on model outcome of changing the size of individual disturbances, or changing spatial autocorrelation among individual disturbances, was less dramatic than the effect of changing temporal autocorrelation, there were some important impacts produced by altering these characteristics of the disturbance regime. Most notably, *Plantago* was able to persist at higher disturbance rates when individual disturbances either were small or were randomly distributed rather than clustered. Under both of these circumstances *Plantago*, a poor disperser, was able to reinvade disturbed sites more rapidly since most disturbed sites were close to undisturbed sites and not imbedded in a large area of disturbance. In contrast, *Bromus* declined in abundance under similar circumstances, due to increased competition with *Plantago*.

**The interaction between life history attributes and disturbance architecture**

Clearly, the impact of disturbance on the distribution of species within a landscape is highly dependent upon the spatial and temporal architecture of the disturbance regime. It is also clear that the impact of disturbance on the distribution of individual species depends critically on individual life history characteristics. The response by *Plantago* to changes in disturbance architecture can be explained almost entirely by its poor dispersal ability. As disturbance becomes more widespread in the landscape, *Plantago* is incapable of invading sites rapidly enough after disturbance to make up for direct losses to its population, so its population level declines, eventually leading to extinction even under moderate rates of disturbance. However, with even a few sites protected from disturbance ($p_M = 0$), *Plantago* can persist in the community at very high disturbance rates, as it is never completely removed from the system (Fig. 7).

*Calycadenia* can persist under all but the most extreme disturbance regimes. It is a very good disperser and is relatively immune to competition from *Plantago* or *Bromus*. A further advantage for *Calycadenia* is that it produces seed late in the season and is the only species able to invade late season disturbances immediately, whereas the other two species are delayed by at least one growing season (Fig. 8).

The major life history characteristics determining the response by *Bromus* to disturbance are its good dispersal ability, relative insensitivity to the presence of *Calycadenia*, and its poor performance in competition with *Plantago*. Because of these characteristics the abundance of *Bromus* at low disturbance rates is influenced primarily by competitive interactions with *Plantago* and only indirectly by the disturbance regime. Once *Plantago* is eliminated from the system at “moderate” disturbance rates, the abundance of *Bromus* is influenced directly by disturbance and declines under increasing rates of disturbance.

**Relationship to natural dynamics at Jasper Ridge**

Although the primary goal of the simulation experiments presented here has been to explore, in an abstract sense, the impact of varying disturbance architecture on the distribution of species within a landscape, we have patterned the model after the dynamics occurring within the Jasper Ridge grassland. One reason for this approach has been to develop a conceptual model of the processes operating at Jasper Ridge that can, in turn, produce testable predictions and hypotheses. One of the simplest tests of the validity of the model would be to compare model output to field mea-
FIG. 8. Distribution of disturbances and species abundances across a 100 cell × 100 cell landscape in a run of the model JASPER. The 4 panels are from one timestep in a model run for the experiment examining the relationship between disturbance rate and temporal autocorrelation in the disturbance regime. The mean disturbance rate in this example was 0.19 with model parameters set as follows: six 20 cell × 20 cell regions of disturbance activity; 0.60 turnover rate (p_i); and 0.10 initiation probability for individual disturbances within a disturbance regime (p_d). The location of disturbances is color coded as follows: dark blue for disturbances early in the growing season, intermediate blue for late disturbances, and light blue for cells impacted by both early and late disturbances. Species abundances are color coded as indicated in the figure. Sites with the highest abundance of Calycadenia (yellow and orange) during the timestep illustrated here were disturbed during the previous timestep, indicating a rapid increase in abundance by Calycadenia immediately following disturbance.
measurements; in the present case this would be primarily a comparison of predicted and observed species abundances. An exact test of this nature would require output from a model run with the disturbance architecture specified to closely approximate the present disturbance regime at Jasper Ridge. However, a complete characterization of the spatial and temporal architecture of the disturbance regime at Jasper Ridge is difficult to accomplish and has not yet been completed. In the absence of an exact test, a general evaluation of the model can be obtained by examining the qualitative agreement between model predictions and species abundances in the field, considering only model runs that fall within the range of possibilities for the disturbance regime at Jasper Ridge.

The easiest aspect of the disturbance regime to characterize at Jasper Ridge is the size and shape of individual disturbances. Individual gopher mounds are circular areas with a mean diameter of 37.6 ± 3.4 cm covering an area of ≈ 0.10 m² (Hobbs and Mooney 1985). Individual mounds in all of the simulation runs (with the exception of runs in the size vs. rate experiment) occupy an area slightly larger than natural disturbances (≈ 0.16 m²), but well within the range of natural variation. Disturbance rates at Jasper Ridge are more difficult to estimate accurately. Current estimates range from 5% to 30%, depending in part on the location and spatial scale considered by individual investigators. The 5% estimate comes from an analysis of a digitized image of recent gopher disturbances that covers approximately one-quarter of the Jasper Ridge grassland (K. Moloney, unpublished). Higher estimates of a 20–30% disturbance rate have been obtained in smaller regions characterized by high rates of gopher
activity (Hobbs and Mooney 1985, 1991). Local rates of disturbance can also vary markedly from year to year and from place to place, as some areas of the grassland are characterized by very high rates of disturbance and others remain virtually undisturbed due to shallow soils (Hobbs and Mooney 1991; A. Lobo, unpublished data). This type of spatial heterogeneity has not been included in JASPER, but would be of future interest.

The most difficult aspect of the disturbance regime to characterize at Jasper Ridge is the spatial and temporal autocorrelation structure. There is a high degree of spatial autocorrelation due to the burrowing behavior of gophers (Deichman et al. 1982, Hobbs and Mooney 1991, Moloney 1993). Transects across a digitized image of newly formed gopher mounds at Jasper Ridge found lengths of continuous disturbance ranging from 0.025 m (the resolution of the image) to 1.8 m, corresponding to individual mound edges and regions with a high degree of spatial clustering, respectively (Moloney 1993). Spatial autocorrelation in the disturbance regime, as determined from the digitized image, was found to decay exponentially over the same range of scales. We have bracketed the observed range of scales of spatial clustering in the various model runs. At one extreme, individual disturbances were distributed at random with no spatial autocorrelation: the size vs. rate experiment. In the temporal autocorrelation experiment, individual disturbances were clustered in 2.0 × 2.0 m square regions producing a high degree of spatial autocorrelation. We also explored a continuous range of autocorrelation structures through the spatial autocorrelation experiment. Which of these scenarios is closest to the field situation is not clear and demands further study.

The temporal autocorrelation structure of the disturbance regime in the field is even more poorly characterized than the spatial autocorrelation structure. Experimental studies conducted over a 6-yr period in a very small sample region found that the average return time between disturbances in 0.25 × 0.25 m quadrats was 1.6 ± 0.1 yr; however this is an underestimate as a large proportion of the quadrats (38–40%) either were undisturbed, or were disturbed only once, over the course of the study (Hobbs and Mooney 1991). Another study indicates that regions that are highly disturbed during one year are less likely to be disturbed in the following year, but are often disturbed 2 yr later (A. Lobo and K. Moloney, unpublished data). The temporal dynamics might be quite complicated, as mounds may be related to both feeding and burrow maintenance activities (Huntley and Reichman 1994). Burrow systems are maintained over long periods of time, which may result in mound production in the same locations year after year (cf. Reichman et al. 1982). Mounds produced through feeding activity, however, may shift in space due to depletion of food resources during years of heavy local above- and belowground grazing, decreasing the amount of temporal autocorrelation in the disturbance regime. Clearly, more information is needed to adequately characterize this aspect of the disturbance regime.

Given all of the above considerations, we have compared the predicted species abundances for disturbance rates of 5% to 20% with abundances estimated from field data appearing in Hobbs and Mooney (1985) (Table 4). Only abundances predicted for Plantago closely approximate the field data. The model apparently overestimates abundance of Calycadenia by an order of magnitude, and underestimates the abundance of Bromus. The overestimates for Calycadenia are the most likely related to the choice of species used in the simulations. Of the three species, Calycadenia is a more deeply rooted plant species that produces seed late in the growing season, due to its ability to obtain water deeper in the soil. This minimizes the interaction with

---

**Fig. 10.** Species richness under varying combinations of disturbance rates and spatial autocorrelation in the disturbance regime.
TABLE 4. Mean abundances for *Bromus*, *Calycadenia*, and *Plantago* at disturbance rates of 5%, 10%, and 20% as predicted from the simulation model JASPER and determined from field data gathered at Jasper Ridge, California.*

<table>
<thead>
<tr>
<th>Disturbance rates (%)</th>
<th>5</th>
<th>10</th>
<th>20</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Abundance (inds./0.01 m²)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Bromus</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Model</td>
<td>0</td>
<td>0</td>
<td>0–15</td>
</tr>
<tr>
<td>Field</td>
<td>2.5</td>
<td>2.6</td>
<td>3.0</td>
</tr>
<tr>
<td><em>Calycadenia</em></td>
<td>22–23</td>
<td>22–24</td>
<td>20–23</td>
</tr>
<tr>
<td>Model</td>
<td>2.9</td>
<td>2.8</td>
<td>2.8</td>
</tr>
<tr>
<td>Field</td>
<td>24.8</td>
<td>24.1</td>
<td>22.7</td>
</tr>
<tr>
<td><em>Plantago</em></td>
<td>27–31</td>
<td>22–28</td>
<td>12–24</td>
</tr>
</tbody>
</table>

* Field estimates were calculated from Hobbs and Mooney (1985: Table 3c) assuming a 3:1 ratio of early- to late-season disturbances. Model estimates are presented as a range of values corresponding to all model runs at a particular disturbance rate. All abundance values correspond to the area of an individual cell in the simulation model, 0.01 m².

*Conclusions*

The results from this study strongly suggest that predictions about the impact of disturbance on ecological processes at the landscape scale need to account for more than the rate and intensity of disturbance. Temporal and spatial autocorrelation patterns may play a great role in determining the response to disturbance. The response will also depend on the life history characteristics of individual species and on community composition.

After disturbance rate, we found that the most important factor determining the response to disturbance was the temporal autocorrelation structure of the disturbance regime. Spatial factors, such as the size of individual disturbances and spatial autocorrelation among disturbances appeared to play a minor role, although this may, in part, be an artifact of the dispersal model used. A more detailed dispersal model, for example one incorporating exponential decay with distance, might increase the sensitivity of species to the spatial details of the disturbance regime. Under these conditions, we would hypothesize that optimal dispersal distances would be closely linked to the average size of individual disturbances and to the spatial autocorrelation structure among disturbances.

One motivation for developing models of the sort described here is to determine what aspects of an ecological system need to be considered in making predictions at a broader geographic scale. In the present example, a prediction of species abundances at the scale of the serpentine grassland at Jasper Ridge, an area of approximately 40 ha (Gulmon et al. 1983), would require information about the rate of disturbance and the temporal autocorrelation structure of the disturbance regime at the scale of the simulated landscapes, 0.01 ha. However, a detailed understanding of the spatial autocorrelation structure or an accurate estimate of the size of individual disturbances may not be required.

Four thousand estimates at the 0.01-ha scale would be required to fully characterize the disturbance regime of the Jasper Ridge grassland, although further aggregation might be possible if different regions of the grassland can be classified into discrete disturbance categories for the purposes of prediction. These estimates could be obtained from a temporal series of aerial photographs of the grassland. This information could then be used to predict species abundances, with no need to measure the details of demographic processes at the same scale.

This is clearly an idealization of what would be required to make accurate predictions using a model such as JASPER. We currently have a good model of disturbance dynamics, but would be able to gain a deeper understanding of the Jasper Ridge serpentine grassland by modifying other aspects of the model. More species should be included, particularly if we want to predict...
the abundance of Calycadenia more accurately. We might also want to characterize demographic variability in response to variability in weather patterns. This information could then be used to make predictions over a series of years by incorporating knowledge about prevailing weather patterns. Or, it might be best to determine the role that spatially heterogeneous environmental factors (e.g., soil depth, topographic relief, and nutrient availability) play in modifying the disturbance regime and local demographic dynamics across the grassland. As with disturbance, we may find that some of this additional information is essential for making accurate predictions at the landscape scale, while some may not be required at all.

ACKNOWLEDGMENTS

We would like to thank Bob Gardner for providing invaluable insights into modeling spatial autocorrelation; Nona Chiariello for providing the data used in parameterizing the competition equations and for enhancing our understanding of the Jasper Ridge grassland; Hal Mooney and Richard Hobbs for earlier work that provided the basis for developing the simulation model; Linda Buttel for her contributions to earlier versions of the model; Agustin Lobo for being so amiable; and Brent Danielson for helpful suggestions on an early draft of the manuscript. The comments of two anonymous reviewers and the editor, Don DeAngelis, were also extremely helpful in clarifying the text. The use of the Cornell National Supercomputer Facility (CNSF) at the Center for Theory and Simulation in Sciences and Engineering, Cornell University, is gratefully acknowledged. This work was supported in part through grants from the Andrew W. Mellon Foundation and the National Aeronautics and Space Administration (NAGW-3124).

LITERATURE CITED


