

MULTIPLE STABLE EQUILIBRIA IN GRASSLANDS MEDIATED BY HERBIVORE POPULATION DYNAMICS AND FORAGING BEHAVIOR

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Abstract. Plant community structure is often the result of interactions between succession, disturbance, and dispersal. While some disturbances may be highly stochastic (e.g., flooding or landslides), other types of disturbance are closely linked to the current successional state of the community (e.g., fire or herbivory). For example, when herbivores preferentially feed on early successional species they may generate conditions favorable for these species and thus create a positive feedback. Positive feedbacks may create multiple stable equilibria within plant communities. We demonstrate the presence of these positive feedbacks using experiments conducted in a restored California grassland. We found that pocket gophers (*Thomomys bottae*) preferentially forage in areas dominated by annual species, and gopher foraging activity increases the abundance of annual plants. We use a Markov chain model to identify how the foraging behavior, dispersal behavior, and population dynamics of territorial herbivores can structure a plant community across multiple spatial scales. The model is loosely based on the biology of pocket gophers, though it is general enough to be applicable to other territorial herbivores with foraging preferences. We find that a foraging preference for early successional species can generate multiple plant communities that persist within a herbivore's territory. If juveniles are selective when searching for territories during their dispersal phase, then herbivores can also generate persistent and distinct plant communities over larger spatial scales. In this case, fixed regions of the landscape may become occupied by herbivores for long periods (many herbivore generations) and be composed of a range of successional plant species, whereas the remaining landscape is abandoned by herbivores and becomes dominated by late successional species. This structuring of the landscape occurs even though we assume that the entire landscape is intrinsically identical.

Key words: alternate stable states; disturbance; foraging; grasslands; herbivory; herbivore population dynamics; multiple stable state; pocket gophers; spatial structure; succession; territoriality *Thomomys bottae*.

INTRODUCTION

Many patterns in plant communities arise from the interactions between succession, disturbance, and dispersal (Cowles 1899, Gleason 1926, Clements 1936, Moloney and Levin 1996, Wiegand et al. 1998). While the rate and magnitude of some types of disturbances are primarily controlled by exogenous factors (e.g., flooding, landslides, and hurricanes), in many cases, disturbance rate and magnitude are linked to the current successional state of the plant community and thus can be considered as endogenous processes (e.g., wildfires, tree throw, and herbivory) (Mutch 1970, Petraitis and Latham 1999). In this paper, we focus on herbivory, a disturbance that is important in structuring many plant communities. Although individual herbivores generate small-scale disturbances (e.g., at the bite scale), their effects on plant communities may vary because they often make frequent attacks and respond to their en-

vironment in complex ways through social interactions and foraging preferences (Coughenour 1991, Laca et al. 1992, Gibb et al. 1997, Seabloom and Reichman 2001). For example, when foragers target early successional plants they may generate a positive feedback by generating conditions favorable for the recruitment of their preferred food. Theory has demonstrated that systems with positive feedbacks can generate complex spatial structure (Murray 1989). Hence, forage preference has the potential to play an important role in spatially structuring plant communities.

A number of systems show distinct plant communities located side by side in apparently similar environments (Peterson 1984, Petraitis and Latham 1999). One explanation for this is that such systems exhibit multiple stable equilibria (MSE), and the plant community present at a given locality depends on its initial condition. Sufficiently large disturbances may perturb an otherwise stable plant community to a state that allows an alternative stable community to develop and establish. This prediction is often observed in simple models of plant community dynamics. A classic ex-

ample comes from models where a fixed number of grazers are introduced into a monospecific pasture (Noy-Meir 1975). If grazers are introduced at a time when plant biomass is sufficiently low, then grazers may keep biomass at a low level; however, if grazers are introduced when biomass is high, then they may not be able to control biomass. Instead, biomass reaches some stable high level because grazers become limited by handling time. MSE are also possible when herbivore population dynamics are introduced and herbivore growth rate is severely limited when plant biomass is high (van De Koppel et al. 1996). In these simple models the state of a plant community is described by total biomass; however, in many natural systems plant communities may also be distinguished by their species composition. In this paper we are interested in the common situation where herbivores forage within a habitat containing multiple plant species and they have a preference for a particular species (or plant type).

Plant-herbivore interactions occur across a multitude of spatial scales (Sousa 1984, White and Pickett 1985, Coffin and Lauenroth 1988). At the smallest scale, herbivore attacks remove plant biomass at the individual bite level. If herbivores form groups, biomass loss may be rapid but spatially confined in the short-term. On the other hand, if herbivores form territories, local biomass loss may be less rapid but spread over a large area. Social interactions that result in herbivores avoiding each other may create refuges for plants along the boundaries of adjacent territories (Robertson 1989, Seabloom and Reichman 2001).

Comparing theoretical results regarding MSE with empirical observations on natural systems is nontrivial because herbivory is typically composed of multiple processes that act at distinct spatial scales. Systems observed at a small spatial scale may show substantial variation in plant biomass and species composition, whereas systems observed over a very large spatial scale may show little overall change. At intermediate scales, communities at different localities may appear to be quite distinct and relatively stable (Pascual and Levin 1997, Petraitis and Latham 1999). An additional complication is that natural systems are stochastic and thus always exhibit some degree of variation. Recently, a number of plant community models have been constructed that explicitly consider the spatial scales and uncertainty associated with disturbance regimes, and demonstrated their importance for structuring plant communities (e.g., Moloney and Levin 1996). In this paper we present a plant-herbivore model that is stochastic and explicitly incorporates processes that operate at distinct spatial scales (e.g., localized foraging and territoriality). We have chosen to keep the model general and simple enough so that its dynamics can be readily analyzed. We are particularly interested in the situation where herbivores are territorial and have a foraging preference, and thus plant disturbances have some degree of predictability both spatially and tem-

porally. The model allows us to identify when MSE are most likely to occur and their spatial scale.

Pocket gophers are well-studied territorial herbivores that generate strong effects on plant communities (Howard and Childs 1959, Olff 1994, Zinnel and Tester 1994, Reichman and Seabloom 2002). In the absence of gopher disturbance, grasslands often become dominated by perennial grasses. The soil tailings that pocket gophers deposit on the soil surface while constructing foraging tunnels increase the abundance of annual plants, their preferred food (Laycock 1958, McDonough 1974, Tilman 1983, Hobbs and Mooney 1985, Hobbs and Hobbs 1987, Inouye et al. 1987, Peart 1989, Hunt 1993, Davis et al. 1995, Kitajima and Tilman 1996). Pocket gophers' reliance on annual forbs is strong enough that using an herbicide to eliminate forbs from a Colorado grassland reduced pocket gopher populations up to 90% due to starvation (Keith et al. 1959, Ward and Keith 1962, Tietjen et al. 1967, Tietjen 1973). As a result of their feeding preferences, pocket gopher disturbances are clustered in high-productivity areas or areas dominated by preferred species (Tilman 1983, Inouye et al. 1987, Huntly and Inouye 1988, Benedix 1993, Steuter et al. 1995, Wasley 1995). Because of their territoriality and positive effect of their foraging activities on the abundance of their preferred species, pocket gophers have the potential to generate MSE.

The remainder of this paper is structured as follows. We start by describing two experiments in which we look for empirical evidence of a positive feedback between pocket gopher feeding behavior and dominance by annual species. Specifically, we use two experiments to test (1) whether pocket gopher activity increases the abundance of annual species, and (2) whether pocket gophers focus their foraging efforts in annual-dominated areas. We began both of our experiments *de novo*, the controls have no historical effects of subterranean animals. In contrast, most studies of effects of subterranean herbivores remove and exclude animals from an area; an approach that confounds the effects of historical burrowing activity in the "controls" with the removal effects (Andersen 1987).

We then introduce a Markov chain model of plant-herbivore population dynamics. We model herbivore behavior based on our understanding of pocket gopher dynamics; however, we have kept the formulation of the model general enough to make it applicable to many territorial herbivores. The model incorporates the following processes: territorial behavior, forage preference, and juvenile dispersal, each of which operates at a distinct spatial scale. We then vary the strength and scale of each process to identify their effect on plant community structure.

EXPERIMENTAL METHODS

Study site

We conducted these experiments at the 2382-ha Sedgwick Natural Reserve, which is located in Santa

Barbara County in California, USA. This site has a Mediterranean climate with cool wet winters and hot dry summers. Mean annual rainfall is 380 mm. We set up the experiments in an abandoned agricultural field on a floodplain terrace composed of sandy, clay, loam soils. We plowed the fields and added seeds of five native perennial grasses (500 seeds·m⁻²·species⁻¹) typical of relict natural grasslands on the reserve (*Bromus carinatus*, *Elymus glaucus*, *Nassella cernua*, *N. pulchra*, and *Poa secunda*). Seeds were purchased from a local supplier (S&S Seeds, Carpinteria, California) and were grown in a nursery located a few kilometers from the reserve.

Effects of pocket gophers on plant community composition

The objective of this experiment was to determine if pocket gopher activity increased the abundance of annual species in a restored perennial grassland (i.e., are pocket gophers selective foragers). We conducted this experiment in six 20 × 20 m pocket gopher exclosures established in 1998 and 1999. These exclosures were constructed by digging a 1.5 m deep trench around each exclosure, placing a barrier of steel fencing (1.25-cm mesh) in the trench and refilling the trench. A 30-cm "T" of steel fencing was attached to the bottom of the fence to prevent pocket gophers from digging under the barrier. The fences extended 0.5 m aboveground. The few pocket gophers that colonized the plots during the construction of the pens were live-trapped and relocated. In the winter of 2000, during the third growing season, we introduced four pocket gophers (*Thomomys bottae*) into each exclosure. We repeated the introductions during the winter of 2001 in pens that did not show signs of recent gopher activity.

We monitored plant community composition in three randomly placed 1-m² quadrats in each exclosure. We also added one or two additional quadrats in actively disturbed areas to ensure that our sampling included disturbed areas. In each quadrat, we estimated the percent cover of all species, as well as litter and pocket gopher mounds using the pinframe method. To do this, we recorded all species that touched a vertical wire located at each of the 100 nodes of a regular 10-cm grid. In our analysis, we compare the composition of quadrats that contain some (at least one point contacts a gopher mound) disturbance to those that were undisturbed.

Effects of plant community composition on pocket gopher activity

The objective of this experiment was to determine if there were higher levels of pocket gopher activity in annual-dominated or perennial-dominated plots. We conducted this experiment in the same restored grasslands used for the previous experiment in areas open to colonization by pocket gophers. We established five 3 × 3 m annual-dominated communities in 2000 using

a short-lived herbicide (Roundup, Scott Company, Columbus, Ohio) to kill the perennial grasses in randomly located plots in the restored grassland. We added seed collected from neighboring exotic-dominated grasslands to ensure rapid colonization. The 10 most common species in the annual-dominated plots in order of abundance were *Bromus hordeaceus*, *Bromus diandris*, *Brassica nigra*, *Elymus glaucus*, *Bromus carinatus*, *Bromus madritensis*, *Hordeum murinum*, *Erodium cicutarium*, *Vulpia myuros*, and *Cirsium* sp. Note that *E. glaucus* and *B. carinatus* are native perennial species that were present in low densities in the annual-dominated plots. Each of these annual-dominated plots was paired with a stand of undisturbed restored-perennial grassland. We sampled community composition and gopher disturbance in a 1-m² quadrat using the pinframe method described above.

EXPERIMENTAL RESULTS

We used logistic regression to compare the proportional cover of annual plants and pocket gopher mounds in the two experiments in the spring of 2002. In these analyses, we used a quasi-likelihood approach to adjust for over- or underdispersion in the data (McCullagh and Nelder 1989). We found that pocket-gopher-disturbed areas in the gopher pens had almost twice the cover of annual species when compared with plots having no gopher disturbance ($P = 0.0309$; Fig. 1a). In addition, on average, annual-dominated plots had more than 20% of their area covered with pocket gopher disturbance, while we did not find any pocket gopher activity in the perennial-dominated plots ($P < 0.0001$; Fig. 1b). At the time of sampling, annual species comprised 81.1% of the total plant cover in the annual-dominated plots and only 35.2% of the plant cover in the perennial-dominated plots. This result illustrates that pocket gophers have clear preference for annual-dominated areas. It should be noted that there is pocket gopher activity in perennial-dominated areas, but the density was low enough that we did not detect it in our sampling plots. In addition, one of the pairs of annual- and perennial-dominated plots was located in an area that has not yet been colonized by pocket gophers and was excluded from the analysis. Inclusion of this pair of plots did not change the significance of the result, though mean cover of gopher mounds in annual-dominated areas was lowered to 16.9%.

THE MODEL

We used a Markov chain model to explore how foraging behavior and herbivore dispersal can alter the diversity and spatial structure of a plant community. A Markov chain model is a discrete-state model where the probability of entering any given state depends only on the state in the previous time step. Each model simulation begins with an initial probability distribution of states. In a system with S possible states, the initial condition is represented by an S -element vector con-

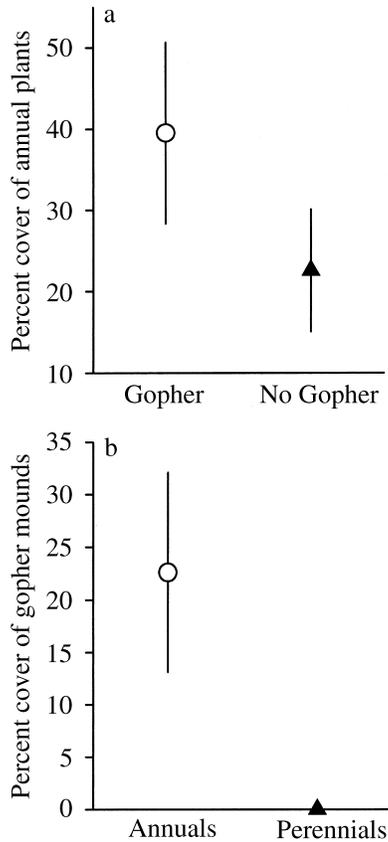


FIG. 1. Effects of pocket gophers on abundance of annual plants and effect of annual plant abundance on pocket gopher foraging activity. In the first experiment (a), pocket gophers were introduced into a 3-yr-old restored perennial grassland from which they had been previously excluded. Areas disturbed by pocket gophers had higher abundance of annual plants. In the second experiment (b), pocket gopher activity was higher in experimentally established annual-dominated plots than in perennial-dominated plots. Error bars represent ± 1 SE.

taining probabilities that sum to 1. The probability that the system is in each of the S states in the next time step is determined by multiplying this vector by a $S \times S$ element transition matrix containing the probabilities of switching among each of the S states. This process can be iterated in time, and in our case, the system eventually reaches a steady-state probability distribution. In the following sections we describe how the transition probabilities are evaluated.

Consider an herbivore that sets up territories that may be occupied by a single individual. The landscape may be thought of as a collection of occupied and unoccupied territories (Fig. 2). These territories are subdivided into N patches, which may be dominated by (1) bare ground, (2) annuals, or (3) perennials. A patch is larger than an individual plant but small enough to model within-territory plant heterogeneity. Because patches are larger than an individual plant, we say

patches are dominated by either bare ground, annuals, or perennials; thus, a bare patch may still contain some plants but at very low density. N describes the size of the territory (in terms of the number of patches) and may represent the area that an herbivore can defend. The vegetative state of a territory is described by a triplet indicating the number of patches in each of the three states. Ignoring the spatial configuration of patches, the possible number of states a territory may be in is $S = (N + 1)(N + 2)/2$, and these states are ranked from $i = 1$ to $i = S$. Let b_i , a_i , and p_i denote the number of patches in the bare, annual, and perennial-dominated state, when the territory is in state i ($1 \leq i \leq S$). Note that $b_i + a_i + p_i = N$. Let $u_{p,t}$ and $o_{p,t}$ denote the probability a territory is in state i at the start of time step t and is unoccupied and occupied by a herbivore, respectively. These probabilities satisfy

$$\sum_{i=1}^S (u_{i,t} + o_{i,t}) = 1 \quad (1)$$

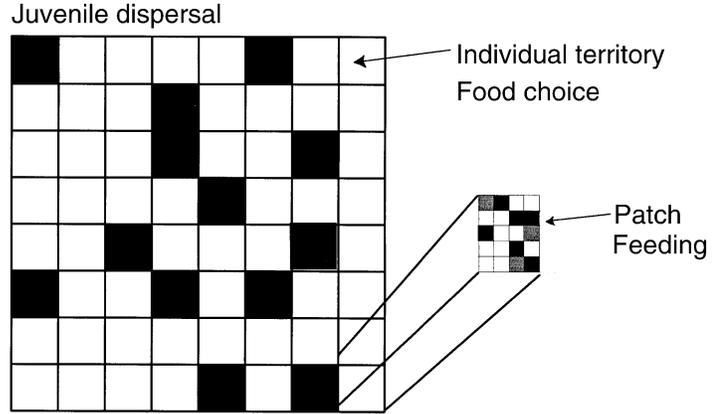
for all t (Fig. 3). The state of the system at the start of time step t is denoted by the vectors $\mathbf{o}_t = (o_{1,t}, \dots, o_{S,t})$ and $\mathbf{u}_t = (u_{1,t}, \dots, u_{S,t})$. In this paper, vectors and matrices are given in bold face and scalars in light face type. We consider a landscape consisting of an infinite number of territories, and hence the probabilities presented in Eq. 1 represent the fraction of territories in each state. The fraction of territories occupied by herbivores at time t is the sum of the probabilities contained in the vector \mathbf{o}_t , which we denote O_t .

Plant succession and population dynamics of the herbivore are described using a discrete-time Markov model. Each time step is divided into the following sequence of events: (1) herbivory, (2) herbivore mortality, (3) plant succession, and (4) herbivore births and offspring dispersal. The vectors \mathbf{o}_t and \mathbf{u}_t describe the probability that a territory is in each of the S possible state after offspring dispersal (event 4) and before herbivory (event 1). The four events are now described in detail.

Herbivory

During a time step, herbivores forage and affect vegetation at the scale of a patch, reducing it to the bare-dominated state (i.e., herbivory resets patches to an early-successional state). Herbivore foraging preference is modeled by assuming each patch state has a weighting indicating its propensity to be attacked. These weightings are denoted w_b , w_a , w_p , for the bare, annual, and perennial-dominated states, respectively. Let H_{ij} denote the probability that an herbivore attack moves a territory from state j to state i during a time step. An attack can move a territory to one of three states depending on the type of patch attacked. If a bare patch is attacked, the state of the territory remains unchanged; otherwise, the number of bare patches increases by one and the number of patches in the state

FIG. 2. Conceptual view of how the model represents space. The entire landscape available to herbivores is represented by a large number of potential territories, some occupied (black squares), others unoccupied (white squares). Each territory is subdivided into patches, which may be in one of three vegetational states: dominated by (1) bare ground, (2) annuals, or (3) perennials. Offspring dispersal occurs at the landscape scale, food choice occurs at the within-territory scale, and feeding occurs at the patch scale.



attacked is reduced by one. These transition probabilities are calculated using

$$H_{ij} = \begin{cases} \omega_{bj} & \text{if } i = j \\ \omega_{aj} & \text{if } b_i = b_j + 1, a_i = a_j - 1, \text{ and } p_i = p_j \\ \omega_{pj} & \text{if } b_i = b_j + 1, a_i = a_j \text{ and } p_i = p_j - 1 \\ 0 & \text{otherwise} \end{cases} \quad (2)$$

where

$$\omega_{xj} = \frac{w_x x_j}{(w_b b_j + w_a a_j + w_p p_j)} \quad (3)$$

is the probability an herbivore attacks a patch in state x ($x = b, a, p$) when the territory is in state j . The probabilities H_{ij} form the matrix \mathbf{H} .

Herbivore mortality

Herbivores experience a probability of dying each time step, that may be related to the state of the patch it just attacked (e.g., if states differ in food quantity or quality). Let m_b , m_a , and m_p denote the probability that an herbivore dies if it attacks a patch in the bare, annual, or perennial state, respectively. If an herbivore dies, its territory moves to the unoccupied state. The density of territories in state i at time t that experience an herbivore death, denoted $m_{p,t}$ are calculated using

$$\mathbf{m}_t = \mathbf{M}\mathbf{o}_t \quad (4)$$

where the elements of \mathbf{M} are given by

$$M_{ij} = \begin{cases} \omega_{bj} m_b & \text{if } i = j \\ \omega_{aj} m_a & \text{if } b_i = b_j + 1, a_i = a_j - 1, \text{ and } p_i = p_j \\ \omega_{pj} m_p & \text{if } b_i = b_j + 1, a_i = a_j, \text{ and } p_i = p_j - 1 \\ 0 & \text{otherwise} \end{cases} \quad (5)$$

and represent the probability that an herbivore moved the territory from state j to state i after it attacked a patch and then died.

This model assumes a feedback between foraging and mortality that occurs at the time scale of a time step. In the scenarios described below, we set the probability of herbivore mortality to be low each time step ($0.05 \leq m_b, m_a, m_p \leq 0.1$), and hence herbivores live on average between 10 to 20 time steps. Thus, an herbivore that attacks a poor-quality patch does not necessarily suffer dire consequences, and herbivore fitness is typically related to the distribution of patch quality across its territory.

Plant succession

Transitions in patch state due to plant succession are assumed to be probabilistic. Plant succession is modeled by assuming that, in each time step, (1) bare-dominated patches may become dominated by annuals or perennials, and (2) annual-dominated patches may become dominated by perennials. Perennials are assumed to be the better local competitors (Tilman 1983), and, in the absence of herbivore disturbance, patches, and hence the entire landscape, eventually become dominated by perennials. Each time step is divided into two periods. First, annuals convert bare patches to annual-dominated with probability $C_a(\alpha)$, where α is the number of annual patches in the territory. Second, perennials convert bare and annual patches to perennial-dominated patches with probability $C_p(\beta)$, where β is the number of patches in the perennial state within the territory at the start of the time step. These transition probabilities are assumed to have the form

$$C_a(\alpha) = 1 - \exp[-(a_g + a_1 \alpha)] \quad (6)$$

$$C_p(\beta) = 1 - \exp[-(p_g + p_1 \beta)] \quad (7)$$

where a_1 , a_g , p_1 , and p_g are constants describing colonization from local plants (i.e., plants within a territory) and global plants (i.e., plants external to the territory). If $a_g > 0$ or $p_g > 0$, then the territories are open systems. In this model, annuals can coexist with perennials only if herbivores are present and $a_g > 0$. For simplicity, we have assumed that the rate of global colonization is constant and not dependent on plant densities across

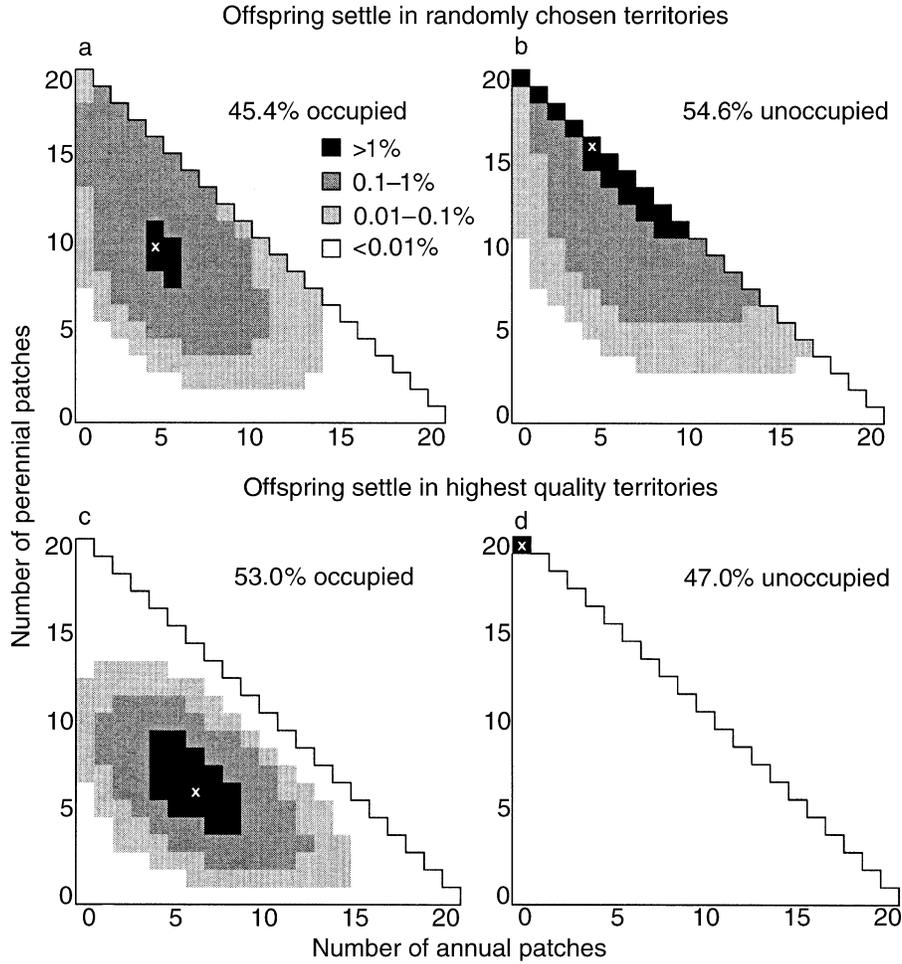


FIG. 3. Steady-state distributions of occupied and unoccupied territories. The top two panels describe the case where offspring disperse and settle in randomly chosen territories. At steady state, (a) 45.4% of territories are occupied, and (b) 54.6% are unoccupied. The bottom two panels describe the case where offspring preferentially settle in the higher quality territories. In this case, at steady state, (c) 53.0% of territories are occupied, and (d) 47% are unoccupied. All parameter values are presented in Table 1. The gray scale shows the percentage of territories in each vegetative state, and the white \times shows the most common state.

the entire landscape. This might be the case when species have widely dispersed seeds or a seed bank.

Let S_{ij} denote the probability plant succession moves a territory from state j to state i during a time step. These transition probabilities form the succession matrix \mathbf{S} (of size $S \times S$). We now construct this matrix. Let A_{ij} denote the probability that colonization by annuals changes a territory from state j to state i . This probability is given by

$$A_{ij} = \begin{cases} B[b_j, b_j - b_i, C_a(a_j)] & \text{if } b_i \leq b_j \text{ and } p_i = p_j \\ 0 & \text{otherwise} \end{cases} \quad (8)$$

where $B[b_p, b_j - b_i, C_a(a_j)]$ is the binomial given by

$$B(Z, z, q) = \binom{Z}{z} q^z (1 - q)^{Z-z}. \quad (9)$$

In Eq. 8, $(b_j - b_i)$ of the b_j bare patches become colonized and dominated by annuals. Similarly, let P_{ij} denote the probability that colonization by perennials changes a territory from state j to state i :

$$P_{ij} = \begin{cases} B[b_j, b_j - b_i, C_p(p_j)]B[a_j, a_j - a_i, C_p(p_j)] & \text{if } b_i \leq b_j, a_i \leq a_j \text{ and} \\ & p_i = p_j + b_j - b_i + a_j - a_i. \\ 0 & \text{otherwise.} \end{cases} \quad (10)$$

In this case $(b_j - b_i)$ and $(a_j - a_i)$ are the number of bare and annual patches colonized by perennials, respectively. The succession matrix is simply

$$\mathbf{S} = \mathbf{PA} \quad (11)$$

where \mathbf{A} and \mathbf{P} are matrices having elements A_{ij} and P_{ij} , respectively.

The state of the system immediately after plant succession (event 3) and before offspring birth (event 4) is denoted and evaluated using

$$\mathbf{o}'_t = \mathbf{S}[\mathbf{H}\mathbf{o}_t - \mathbf{m}_t] \quad (12)$$

$$\mathbf{u}'_t = \mathbf{S}[\mathbf{u}_t + \mathbf{m}_t]. \quad (13)$$

Herbivore births and offspring dispersal

At the end of each time step, surviving females may give birth to a single offspring that disperses to another territory. As with mortality, the probability that females give birth may depend on the state of the patch they just attacked; and these probabilities are given by r_b , r_a , and r_p , for bare, annual, and perennial patches, respectively. Assuming females are not male-limited and offspring have equal sex ratio, the per-territory density of offspring produced at the end of a time step is given by

$$y_t = \frac{1}{2} \sum_{i=1}^S [\omega_{bi}r_b(1 - m_b) + \omega_{ai}r_a(1 - m_a) + \omega_{pi}r_p(1 - m_p)]o_{it}. \quad (14)$$

Eq. 14 states that half of the occupied patches contain a female who gives birth to a single offspring based on the type of patch she recently foraged in, provided she survived the time step.

Offspring are assumed to disperse globally and experience a probability of mortality that is proportional to the fraction of patches currently occupied (i.e., dispersal mortality is density dependent). We consider two types of dispersal that differ in the ability of dispersers to evaluate territory quality before settling permanently (Pulliam and Danielson 1991, Sutherland 1996). First, we assume dispersers are unable to evaluate territory quality; they settle in randomly chosen territories and die if that territory is already occupied. We then assume the other extreme, where dispersers rank territories according to their quality and preferentially settle in the highest quality unoccupied territories. In this case, we refer to juvenile herbivores as being selective. Territory quality is equal to the expected number of offspring a female would have if the territory stayed in its current state. A territory in state i has quality

$$q_i = \frac{\omega_{bi}r_b(1 - m_b) + \omega_{ai}r_a(1 - m_a) + \omega_{pi}r_p(1 - m_p)}{(\omega_{bi}m_b + \omega_{ai}m_a + \omega_{pi}m_p)} \quad (15)$$

(see Appendix). The numerator in Eq. 15 is the probability that a female survives a time step and gives birth. The denominator is the probability that a female dies during a time step.

For both types of dispersal, the y_t offspring are distributed among the updated territory densities \mathbf{o}'_t and \mathbf{u}'_t that give the state of the system at the start of the following time step, namely \mathbf{o}_{t+1} and \mathbf{u}_{t+1} . In many systems we might expect dispersing juveniles to choose

patches according to some rules that lie between the two extremes considered in this paper.

Patch return times

Preferential foraging may cause herbivores to use a limited number of patches within their territory. To evaluate the degree to which individuals localize their feeding within a territory, we calculate the mean number of time steps it takes a forager to return to the same patch if the patch is currently in the perennial-dominated state. The expected return time if the territory stays in state i is denoted T_i and given by

$$T_i = N + \left(\frac{w_b}{w_p} - 1\right)b_i + \left(\frac{w_a}{w_p} - 1\right)a_i. \quad (16)$$

If foraging is random (i.e., there is no foraging preference) then $w_b = w_a = w_p$ and $T_i = N$; however, if foragers prefer annuals (i.e., $w_a > w_p > w_b$) then the return time to a perennial-dominated patch is dependent on territory state. If $T_i > N$, feeding is concentrated in the nonperennial patches implying that foragers tend to farm a fixed group of patches.

MODEL RESULTS

A wide range of plant–herbivore dynamics can be generated by the model presented above. In this section we consider several special cases and identify processes that generate different spatial and temporal patterns within the plant community. Specifically, we develop a series of increasingly complex scenarios that demonstrate the effects of feedbacks between herbivore behavior and plant succession. We start by describing the dynamics of the system in the absence of herbivores. We then consider a very simple scenario where there are no fitness consequences of random foraging or random juvenile dispersal. We then examine the case where the value of a patch depends on its state, and hence there are fitness consequences for feeding on different types of vegetation and the mode of juvenile dispersal. Finally, we examine the effect of plant successional rate. Unless noted otherwise, herbivore mortality probabilities, reproduction probabilities, and foraging preferences are given by the parameter values presented in Table 1.

Plant succession in the absence of herbivores

In this paper, we assume that foragers cause disturbances that reduce patches to the bare-dominated state. If a territory is initially entirely in the bare-dominated state and there is no subsequent herbivory, the most likely pattern of succession is bare patches becoming dominated by annuals and then perennials. However, it is possible that by chance a patch never experiences the annual state and moves directly from the bare state to perennial state. In this paper, we consider three rates of succession: low (L), where $a_g = 0.05$, $a_1 = 0$, $p_g = 0.005$, and $p_1 = 0.0005$; moderate (M), where $a_g = 0.1$, $a_1 = 0$, $p_g = 0.01$, and $p_1 = 0.001$; and high (H), where

TABLE 1. Description of model parameters and their base-line value.

Parameter	Description	Value
N	patches per territory	20
a_g	global contribution to annual colonization each time step	0.1
a_l	local contribution to annual colonization each time step	0
p_g	global contribution to perennial colonization each time step	0.01
p_l	local contribution to perennial colonization each time step	0.001
w_b	weighting for bare patch encounters	1
w_a	weighting for annual patch encounters	16
w_p	weighting for perennial patch encounters	4
m_b	probability of mortality after attacking a bare patch	0.1
m_a	probability of mortality after attacking an annual patch	0.05
m_p	probability of mortality after attacking a perennial patch	0.075
r_b	probability of giving birth after attacking a bare patch	0
r_a	probability of giving birth after attacking an annual patch	0.3
r_p	probability of giving birth after attacking a perennial patch	0.15

$a_g = 0.2$, $a_l = 0$, $p_g = 0.02$, and $p_l = 0.002$. An example of successional dynamics when rates are low is presented in Fig. 4. We assume the dispersal of annuals is global, whereas the dispersal of perennials is more local. These parameter choices reflect a trade-off between dispersal and competitive ability (see review in Bolker and Pacala 1999). In this scenario, the entire habitat becomes dominated by perennial patches in the absence of herbivores.

Forager fitness is independent of successional state

Suppose herbivore demographic rates are constant across patches (i.e., $m_b = m_a = m_p = m$ and $r_b = r_a = r_p = r$), which implies that herbivore fitness is independent of the state of the patches it encounters when foraging. If m is sufficiently low and r is sufficiently high, the foragers will persist and the system will approach a unique steady-state probability distribution (see Appendix). If foragers go extinct, the entire landscape becomes dominated by perennials. However, if foragers persist, the plant community will be composed of annuals and perennials, assuming territories are open to colonization by annuals and perennials. In this case, the model predicts that the system will approach a steady state where a constant fraction of territories are occupied (see Appendix). Moreover, because all patches always have equal quality, the model predicts that in the long-term all territories will be used equally. In this case, the state of a territory, whether currently occupied or unoccupied, changes frequently, and hence MSE will not occur at any spatial scale when measured across a sufficiently long time scale.

Forager fitness depends on successional state

Suppose there are fitness consequences when feeding in the different patch types. Specifically, it is more profitable for herbivores to forage in annual patches and least profitable to forage in recently foraged bare patches (i.e., $m_a < m_p < m_b$ and $r_a > r_p > r_b$). Thus, herbivores should favor territories in an early successional state. Herbivores respond to fitness consequences by exhibiting feeding preferences, modeled by set-

ting $w_a > w_p > w_b$. The disparity between these preference weightings indicates how well herbivores can identify the state of their territory and feed in their preferred patches. We now consider the case where herbivores live ~ 10 – 20 time steps, herbivores do not give birth when feeding on bare dominated patches, and the population has a small but negative growth rate if individuals feed solely on perennial patches (see Table 1 and Appendix). Thus, for herbivores to persist they must generate conditions favorable for annuals.

Fig. 3a and b show the steady-state probability distribution for occupied and unoccupied territories when offspring disperse to randomly chosen territories. In this case, 45.4% of territories are predicted to be occupied at steady state. This equilibrium is observed for all initial conditions we investigated. For example, when low or high densities of herbivores are introduced, and when herbivores are introduced into habitat dominated by early or late successional territories. Because of the stochastic nature of plant succession, herbivory, herbivore mortality, and offspring dispersal, occupied and unoccupied territories are likely to be in a variety of vegetational states, and there is a large region of overlap between the occupied and unoccupied territories (Fig. 3a and b). Occupied territories are most likely to be in state $(b_p, a_p, p_i) = (6, 4, 10)$, and unoccupied territories in state $(b_p, a_p, p_i) = (0, 4, 16)$. As in the previous example, all territories constantly change their state and hence the model does not predict MSE when the system is measured across long time scales at any spatial scale.

Juveniles settle in high quality territories

The model predicts that, if juveniles are selective about where they settle, then equilibrium herbivore population size increases. In this scenario 53.0% of patches are occupied at steady state as compared to 45.4% with random dispersal. Occupied territories still exhibit a range of states, with state $(8, 6, 6)$ now most likely (Fig. 3c and d). Herbivores that are selective during dispersal achieve a higher equilibrium because their territories contain more of their preferred food.

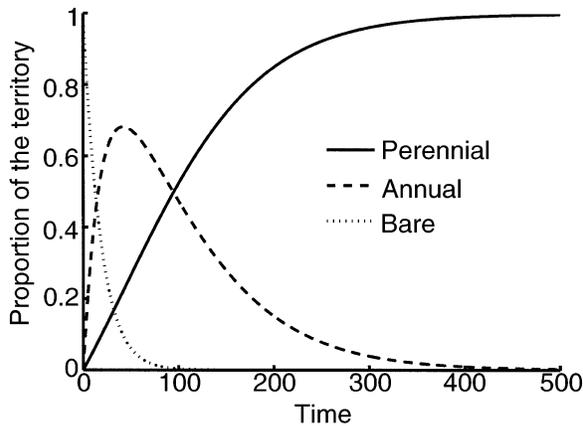


FIG. 4. An example of patch succession described by Eqs. 6–11. At time $t = 0$ the territory is assumed to be entirely in the bare-dominated state. The curves show the expected proportion of patches in the bare, annual, and perennial state through time ($N = 20$).

More interestingly, the state of occupied and unoccupied territories become radically different. Unoccupied patches are now nearly exclusively in the perennial-dominated state because territories vacated due to herbivore death typically have higher quality than perennial-dominated unoccupied patches. At equilibrium, births equal deaths, and offspring nearly always quickly recolonize recently emptied patches.

At steady state, only a subset of territories are typically used by herbivores creating a long-term stable pattern at the landscape scale. The specific territories that are occupied depends on which initial colonization events were successful (i.e., history matters). Although occupied territories change their state frequently because of foraging and succession, the region of the landscape occupied by herbivores remains stable, even though each territory is intrinsically identical. Thus, when juveniles are selective during dispersal the plant community that develops may be thought of as exhibiting MSE (i.e., unoccupied territories are nearly entirely dominated by perennials and occupied territories have a diverse blend of bare, annual, and perennial dominated areas). Model simulations show that long-term stable patterns of territory use is typical for a wide range of parameter values, provided herbivores prefer annuals over perennials. In *Discussion*, we address further the robustness of our general results.

Effects of successional rate

In this section we examine the effect of plant successional rate for the cases when herbivores are selective when dispersing. When successional rates are low (L), herbivores heavily exploit their territory, reducing much of it to the bare-dominated state (Fig. 5a). When successional rate is higher (M and H), many patches in occupied territories escape to the perennial-dominated state (Fig. 5b and c). The greatest expected num-

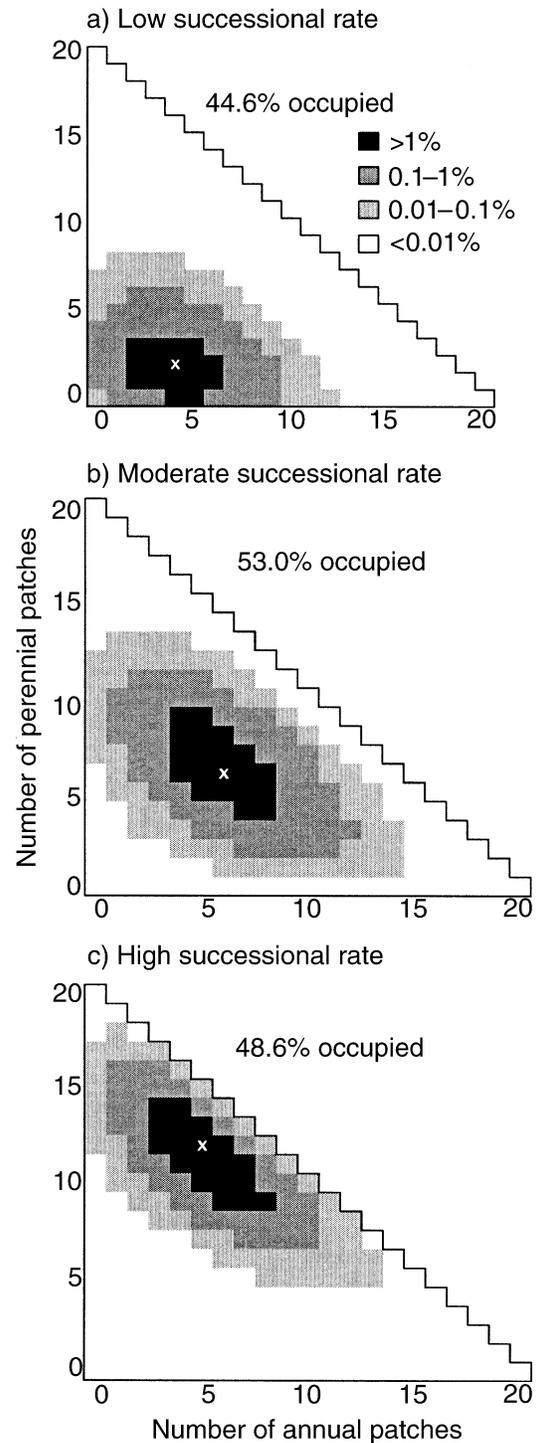


FIG. 5. Steady-state probabilities for occupied territories when offspring disperse to the higher quality territories. The examples differ in the rate of succession: (a) low, (b) moderate, and (c) high. Unoccupied territories at equilibrium are nearly always in the perennial-dominated state (see Fig. 3d) and thus are not plotted. Fractions of territories occupied at equilibrium are 44.6%, 53.0%, and 48.6% for the low, moderate, and high cases, respectively. The gray scale shows the percentage of territories in each vegetative state, and the white \times shows the most common state.

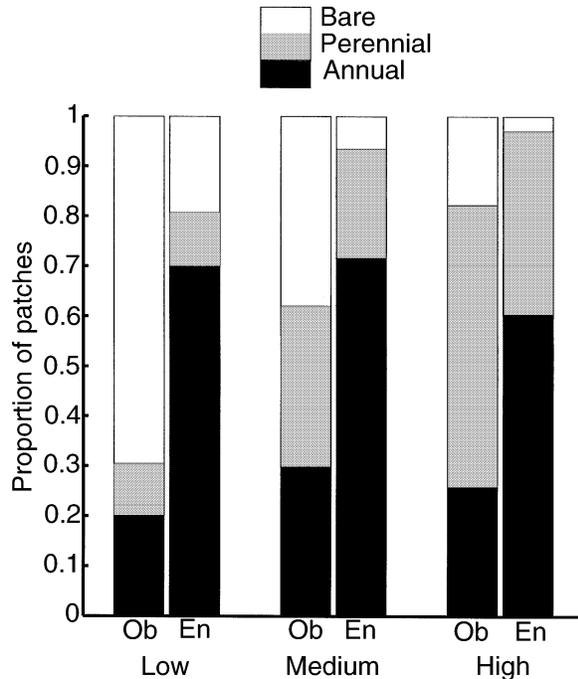


FIG. 6. Composition of occupied territories and the types of patches encountered by foraging herbivores at equilibrium under three rates of plant succession (low, medium, and high). For each successional rate, the proportion of bare, annual, and perennial patches present (or observed) by the animal in the territory (Ob) is shown adjacent to what the animal actually encounters when foraging (En).

ber of annual patches in an occupied territory occurs at intermediate successional rates. The increased density of annuals results in lower herbivore mortality and higher herbivore fecundity. As a result, highest herbivore densities (i.e., the highest proportion of occupied territories) occur at intermediate rates. If successional rate is very low or territory size is very small, herbivores may be driven to extinction. In these extreme cases, it may be that recently used territories become so dominated by bare patches that their quality is less than longer-term abandoned patches, and as a result, herbivores should try to use all of the landscape.

A measure of within-territory patch use is the mean time required for an herbivore to return to a perennial patch. If foraging is random, the expected return time is $N = 20$ time steps. When herbivores exhibit foraging preferences (Table 1) the low, moderate, and high rates of succession lead to expected return times to perennial patches of 21.5, 32, and 32.75 time steps, respectively. Fig. 6 shows the equilibrium abundance of patch states within occupied territories and the distribution of patch states herbivores encounter when foraging. The observed distribution may not accurately reflect what herbivores encounter when foraging (Possingham 1989). Surprisingly, the number of preferred annual patches observed and encountered remains relatively constant across successional rates; however, the number of bare

and perennial patches varies considerably. These results show that when successional rates are low herbivores use much of their territory; however, as rates increase herbivores may reduce the number of patches they use. If successional rates are sufficiently high, herbivores may restrict their foraging to certain patches and, as a result, their territories may become spatially structured into perennial and nonperennial regions. Depending on how well herbivores can locate their preferred food within their territory and successional rate, spatial structure within a territory may persist over time scales longer than an herbivore generation. For example, when herbivores are extremely selective ($w_b = 1$, $w_a = 10000$, $w_p = 100$) and successional rate is moderate, the return time to a perennial patch is of the order 1000 time steps (not shown), indicating very long-term abandonment of part of a territory. As with selective dispersal, extremely selective foraging can generate MSE within individual territories (i.e., abandoned portions of an occupied territory are entirely dominated by perennials while other areas are heavily used and are often in a bare or annual dominated state).

DISCUSSION

As suggested by previous experiments (see review in Seabloom and Reichman 2001), we found positive feedbacks between pocket gopher foraging and the dominance of annual plants. Pocket gopher disturbance increased the abundance of their preferred food (annual plants). In addition, pocket gopher activity is more intense in areas dominated by annual plants. Furthermore, our modeling results suggest that these positive feedbacks have the potential to create complex spatial patterns in the overlying plant community.

We have demonstrated that herbivore dispersal, social, and foraging behavior have the potential to structure plant communities over a wide range of spatial and temporal scales. In particular, we have shown that a territorial herbivore can generate distinct and highly persistent plant communities at spatial scales that are at least the size of a territory, provided herbivores target early successional species and their offspring disperse to higher quality habitat. In this case, some regions are rarely occupied by herbivores and thus become perennial dominated; whereas, other regions are nearly always occupied and consist of a mixture of annuals and perennials with species dominance related to successional rate. Herbivores may also structure plant communities at the within territory scale. Foraging preferences may cause herbivores to concentrate their foraging activities on a subset of their territory and keep it in an early successional state. As a result, a portion of their territory may escape foraging disturbances for long periods of time and become dominated by perennials.

Our model is stochastic, and hence it does not generate MSE in the strict sense because chance events can always perturb a plant community, irrespective of

its state. However, such perturbations may be extremely rare in some cases and thus plant community patterns may remain spatially stable for long periods. For example, when juvenile herbivores are good at finding high quality territories when dispersing, part of the landscape may be avoided by herbivores over many herbivore generations. However, by chance, a juvenile may choose to settle in a long-abandoned perennial-dominated territory. If this occurs, and by chance the juvenile survives the initially nonfavorable conditions, then it may eventually change the plant community in the territory. As juveniles become less able to identify high-quality territories, the average time it takes a territory to switch between distinct plant communities decreases. In contrast, a strict definition of MSE requires a permanent change in territory state. It is unlikely that a natural system could ever meet these criteria due to natural stochasticity. For this reason, we feel that our stochastic modeling approach is a more realistic representation of MSE that could be tested empirically.

An important component of our model is that herbivore disturbances are explicitly modeled as spatially discrete events. At the scale of a patch, the state of a patch changes slowly due to succession but may change rapidly after a herbivore attack. Extreme selectivity during foraging can lead to persistent spatial structure within an occupied territory as a result of the long-term abandonment of portions of the territory. These abandoned areas remain in a perennial dominated state, while more heavily used areas are often bare- or annual-dominated. This is an example of MSE at the patch scale, because all patches are intrinsically identical before the territory is colonized.

At the scale of a territory, the number of patches in each of the three successional states may vary and the degree of variation among occupied territories depends on successional rate, foraging rate, and foraging preference. Although the state of occupied territories varied, their state may always remain very distinct from unoccupied territories (Fig. 3c and d). If this distinction persists for long periods (i.e., across many herbivore generations), which is the case when juveniles are selective when dispersing, then persistent spatial structure in the plant community emerges. Because the landscape is intrinsically identical, when persistent spatial structure emerges we say the system exhibits MSE.

The formation of territories by herbivores is a key component of our model. We assume only a single individual can forage in a patch during a time step, and social interactions precludes other herbivores from using the remaining $N - 1$ patches that comprise its territory. Only rarely have models incorporated the effects of social behavior on herbivore distributions and dynamics (but see Seabloom and Reichman 2001). However, territoriality is a common social behavior that can have large impacts on the distribution of herbivores and their prey by creating refuges along the peripheries

of adjacent territories (Mech 1977, Robertson 1989). In addition, by creating a zone of repulsion around each animal, territorial behavior lowers the maximum density of animals that can coexist (Vaughan 1967, Nevo 1979, Seabloom and Reichman 2001), and hence the maximum disturbance rate. Furthermore, the presence of buffer zones between territories can create a complex disturbance regime, where disturbances aggregate at spatial scales less than individual territories but have an even distribution at scales larger than individual territories (Klaas et al. 2000, Seabloom and Reichman 2001, Reichman and Seabloom 2002). In the future, we plan to incorporate these effects and use the model to identify optimal territory size.

We have investigated robustness of our results by exploring a wide range of parameter space and found that it was difficult to identify situations in which herbivore persistence depended on initial conditions; that is, on the initial number of herbivores or configuration of the plant community. This may be surprising since herbivores encountering bare-dominated habitat (e.g., shortly after a large-scale fire) may do well because such patches quickly become colonized by high quality annuals. On the other hand, perennial-dominated patches were assumed to be associated with negative herbivore growth rates. We found that populations either nearly always went to extinction or eventually reached a unique nontrivial steady state distribution. The insensitivity of this model to initial conditions results from our explicit treatment of resource heterogeneity and our assumption that system size is large and dynamics are probabilistic. Even if initial conditions are nonfavorable (e.g., perennial dominated), some individuals may survive, reproduce, and eventually generate conditions that give the population a positive growth rate. The model did show sensitivity to initial conditions if herbivore fitness on perennials was extremely low, in which case sometimes it required a threshold density of herbivores to invade a perennial dominated habitat.

Nisbet et al. (1997) and Schwinning and Parsons (1999) also found MSE to be difficult to achieve in their models of consumer–resource dynamics when they explicitly accounted for resource heterogeneity. In contrast, MSE are much easier to generate using models that assume herbivore dynamics are only related to mean resource abundance and herbivores exhibit a nonlinear functional response (Noy-Meir 1975, van De Koppel et al. 1996). In our model, we assume a linear functional response (i.e., patches are attacked at a fixed rate irrespective of their state), and we found that the crucial component for generating MSE was foraging behavior (i.e., whether or not offspring settled in favorable habitat, and whether herbivores exhibited a strong feeding preference for early successional species).

In this paper, we focused on the situation where occupancy of a territory typically makes the value of the territory higher for future residents when compared

with long-abandoned territories. This can occur if vegetation becomes less palatable through the course of succession (Bakker et al. 1983, Bazely and Jefferies 1986, Huntly and Inouye 1988) or so dense that it inhibits foraging efficiency by obstructing forager movement (van De Koppel et al. 1996) or ability to see predators (Underwood 1982, Lagory 1986, Loughry 1993). The numerous empirical examples in which herbivory rates decrease in late successional vegetation suggest that this is a common pattern (Stobbs 1973, Ludlow et al. 1982, Coughenour 1991, Fryxell 1991, Laca et al. 1992, Wilmschurst et al. 1995, van De Koppel et al. 1996, Gibb et al. 1997, Schwinning and Parsons 1999).

On the other hand, there are many empirical examples in which herbivores continually decrease the quality of their territory by depleting the abundance of their preferred prey species (Covich 1976). For example, rabbits (Farrow 1917), woodchucks (Merriam and Merriam 1965), prairie dogs (Osborn and Allan 1949, King 1955, Koford 1958), kangaroo rats (Best 1972, Rosenzweig 1974, Schroder and Geluso 1975) and beavers (Hall 1960, Aleksziuk 1970, Jenkins 1975, Donkor and Fryxell 1999, 2000) deplete the forage quality near their den sites. If herbivores have a preference for late-successional species, then we would predict that herbivores may benefit by using the entire habitat in the long-term and hence would not generate MSE at the territory scale.

In our model dispersing animals preferentially colonize recently vacated territories because of the favorable state of their vegetation. However, recently abandoned territories may be favorable because of other properties (e.g., the presence of tunnels or dens). For example, in the gopher system it is costly to establish and maintain tunnels (Vleck 1981), and abandoned tunnels are often recolonized in hours or days by neighboring animals (Reichman et al. 1982, Zinnel and Tester 1994). Beavers are an interesting case because their foraging depletes the availability of their preferred species near their ponds (Donkor and Fryxell 1999, 2000); however setting up territories (dams) is extremely costly. In this case, they have to evaluate the benefits of using established dams vs. the costs that such dams may be associated with poor resource quality because of recent exploitation. In the future, we will incorporate such costs into models of foraging and identify their effects. We will also relax the assumptions that foragers remain in territories for their entire lives and that all foragers have equal competitive ability (Sutherland 1996).

In our simulations we have only explored the effects of biotic disturbance. Instead, suppose no herbivores are present and all disturbances are generated from abiotic sources. In the case of exogenously controlled abiotic disturbances, their duration, timing, and location will often be only loosely correlated, if at all, with the state of the plant community (e.g., flooding and hur-

ricanes). In this case, patches of annuals may be expected to be more randomly distributed in space. In other cases, abiotic disturbances may be related to plant community structure, and their patterns may be more predictable. For example, wildfire may be unlikely to affect regions recently burned because of reduced fuel levels (Mutch 1970, Johnson and Gutsell 1994).

There can be interesting interactions between abiotic and biotic disturbances. Empirical studies have found that abiotic disturbances such as fire can facilitate the colonization by herbivores that subsequently function to maintain a system in an early successional state. For example, Dublin (1990) found that browsing by elephants and antelope in the Serengeti could not lead to the observed decline in woodlands. However, the herbivores are capable of preventing woodland regeneration in a recently burned area. In this case, the interaction between abiotic and biotic disturbance creates two stable states. Although not presented here, we have added abiotic disturbances to our model. Specifically, we introduced randomly distributed disturbances that reduced patches to the bare dominated state. We found that when disturbances were relatively rare and small (patch scale) our general predictions are unchanged. However, when disturbance size is larger (territory scale) a disturbance can change a perennial dominated abandoned territory to one that becomes favorable for herbivores and thus switches its state to one where herbivores, annuals, and perennials persist. In addition, we found that herbivore population size is greatest at intermediate rates of abiotic disturbance.

Here, we have used a spatially implicit model to make predictions about spatial structure. If detailed information on local foraging movements and dispersal are known then a spatially explicit model may be appropriate. For example, Seabloom and Reichman (2001) used a spatially explicit simulation model to explore the effects of within territory foraging behavior and social behavior on the spatial structure of pocket gopher disturbances. They found that the spatial components of foraging and social behavior of pocket gophers altered the density and foraging efficiency of pocket gophers and the composition of the overlying plant community. Animals using area-restricted searching generated more compact territories that allowed the persistence of higher population densities of pocket gophers and a larger density of annual plants. Conversely, the creation of territorial buffers along the edges of territories lowered the maximum pocket gopher density and increased perennial abundance.

Our model has highlighted how incorporating herbivore behavior into a model can dramatically alter predictions of plant community structure. The complex positive feedbacks that arise even in the simple scenario considered here demonstrates that biotically-generated disturbances have the potential to generate spatially and temporally complex patterns of disturbance

that shape plant–herbivore communities in ways that may be very distinct from abiotic disturbances.

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APPENDIX

A description of the conditions promoting herbivore persistence is provided in ESA's Electronic Data Archive: *Ecological Archives* E084-076-A1.