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SPATIAL SIGNATURE OF ENVIRONMENTAL HETEROGENEITY, DISPERSAL, AND COMPETITION IN SUCCESSIONAL GRASSLANDS

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Abstract. The fate of individual plants is strongly influenced by their spatial context (e.g., their location relative to competitors or environmental gradients). Recent theoretical developments indicate that spatial structure in plant communities arises as an outcome of environmental heterogeneity, intra- and interspecific competition, and localized dispersal. Furthermore, each of these forces is predicted to leave a signature on the spatial and temporal pattern within the community. We track the development of spatial structure in successional grasslands in southern California for five years, using a series of large-scale field experiments. We compare the observed changes in spatial structure to the predictions of a spatially explicit model of plant competition in heterogeneous landscapes. We conclude that environmental heterogeneity led to the development of aggregation in the first year at scales of 1–2 m. Over time, aggregation was detectable at distances greater than 4 m, and species become segregated as a result of competition and localized dispersal. Large-scale disturbances (fire) homogenized the community by decreasing the level of aggregation and segregation. In contrast, disturbance by pocket gophers and ground squirrels increased local-scale heterogeneity by creating annual-dominated aggregates. The speed with which spatial structure develops in seemingly homogeneous environments illustrates the importance of incorporating spatial context in empirical studies and models of plant community dynamics.

Key words: annual vs. perennial grasses; community ecology; competition; dispersal; environmental heterogeneity; grassland; invasions; southern California (USA); spatial correlation; spatial model.

INTRODUCTION

Spatial context has long been recognized as a key factor determining competitive interactions in plant communities (Godwin 1923, Watt 1947, Harper 1961, van Andel and Dueck 1982, Mithen et al. 1984, Czárán and Bartha 1989, Marshall 1990, Thórhallsdóttir 1990, Rees et al. 1996). The study of the role of spatial patterns in plant community dynamics has developed rapidly as a result of major advances in the development of statistical tools for the description of spatial pattern (Dale 2000, Bjørnstad and Falck 2001, Purves and Law 2002, Wagner 2003). There has been a concomitant development of theory exploring the effect of spatial context on population and community dynamics (Levins and Culver 1971, Armstrong 1976, Hastings 1980, Pacala 1986, Silvertown et al. 1992, Pacala and Rees 1998, Bolker and Pacala 1999). Recent theoretical work shows how the spatial correlations within and among species are shaped by localized competitive interactions and dispersal (Bolker and Pacala 1999), possibly as affected by environmental heterogeneity (Bolker 2003, Snyder and Chesson 2003). Spatial correlation functions appear to provide a natural meeting point for theoretical models and statistical analyses of data.

Motivated by the theoretical link between biological mechanism and spatial correlation, we provide a detailed empirical investigation of spatial pattern formation in experimental grasslands shown to be influenced by competitive interactions (Seabloom et al. 2003). Specifically, we estimate the spatial correlation functions within and among species in these grasslands through the course of a succession. In replicate plots, we initiated succession experimentally with spatially random seeding, such that any subsequent nonrandom patterns would emerge as a result of ecological interactions rather than from spatially variable initial propagule densities. We discuss how the experiment relates to current theory and how it provides insights into the roles of environmental heterogeneity, competition, and dispersal in the dynamics of California grasslands.

Most grasslands are characterized by small-statured plants, such that fairly small-scaled experimental replicates contain large numbers of individuals (10^2–10^4/m^2). Grasslands also have been the focus of a great deal of experimental and theoretical work on community dynamics and function (e.g., Platt and Weiss

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TABLE 1. Population parameter values used to generate the spatial correlation functions in Fig. 1.

Term	Parameter	Global value	Species 1	Species 2
Global parameters				
$\bar{e}$	mean establishment probability	0.8		
σ_e^2	variance in establishment	0.01		
m_E	environmental scale	4.0		
Species-specific parameters†				
r_i	intrinsic rate of increase		87.88	1
R_i	reproductive output		88.88	2
K_i	nonspatial carrying capacity		5.49	1.25
m_{Di}	dispersal scale		67	10
m_{Ui}	competition scale		2	2
β_{ij}	interspecific competition coefficient‡			
β_{12}			1.25	
β_{21}				0.088

† Species 1 has a long dispersal distance and high reproductive output but is a weak competitor; species 2 has a short dispersal distance and low reproductive output but is a strong competitor.

‡ The population-level parameter β_{ij} is related to the individual-level, per capita competitive effect of species i on species j through the relationship $\beta_{ij} = (\alpha_{ij}/\alpha_{ii})(K_j/K_i)$; see Appendix A. If $\beta_{ij} > 1$, species i cannot invade a monoculture of species j. Here, species 1 cannot invade a nonspatial monoculture of species 2, but species 2 can invade a nonspatial monoculture of species 1.

1977, Moloney and Levin 1992, Wedin and Tilman 1993, Hector et al. 1999, Turnbull et al. 1999, Naeem et al. 2000). In addition, California grasslands are sites of one of the most dramatic plant invasions worldwide (Mooney et al. 1986, D'Antonio and Vitousek 1992). During the latter part of the 19th century, nearly all of the native perennial grass flora (in 9.2×10^6 ha) was displaced by a suite of exotic annual grasses and forbs from southern Europe along the Mediterranean (Heady 1977, Jackson 1985). The relative roles of environmental (abiotic) and competitive effects in this transition are yet to be determined.

Spatial pattern formation in plant communities results from spatial variability in individual rates of establishment, fecundity, and mortality. These demographic rates are determined by environmental heterogeneities and by the spatial distribution of intra- and interspecific competitors, possibly as modulated by biotic (e.g., herbivores and pathogens) or abiotic (e.g., fire) disturbance regimes. Thus spatial patterns and successional changes in spatial patterns may contain a signature of the underlying ecological mechanisms that govern the dynamics.

Recent theoretical work suggests that these issues may be approached by considering spatial correlation and cross-correlation functions (Bolker and Pacala 1999, Bolker 2003, Snyder and Chesson 2003). Accordingly, a primary focus of this paper is to study the spatial correlation functions in replicate experimental grasslands. However, in order to interpret the analyses, we need qualitative theoretical predictions about the correlation functions that result from the actions of local dispersal and competitive interactions combined with (1) demographic stochasticity, (2) interspecific interactions, and (3) environmental heterogeneity. The moment equations and resultant correlation functions for (1) and (2) were developed by Bolker and Pacala (1999), for (2) and (3) by Snyder and Chesson (2003), and for (1) and (3) by Bolker (2003). We compare our empirical results to a model that incorporates (1), (2), and (3). As this model is a combination of previously published models (Bolker and Pacala 1999, Bolker 2003), we present a brief overview of the model here and reserve the full model derivation for the Appendix. We use the predictions of this model to interpret the pattern in the data. We focus on the overall shape of the (cross-) correlation functions; local aggregation of conspecifics (which we refer to as ''aggregation''); interspecific segregation; and, finally, the temporal persistence of aggregates (measured by space–time correlations and referred to as ''persistence''). Note that we have intentionally kept the formulation of this model general, as our intention is to explore the general effects of spatial processes on the development of spatial structure in plant communities, not to fit a model to this specific grassland system.

Conceptual framework

We base our theoretical predictions on a continuous-space, continuous-time model in which the plant life cycle consists of recruitment, reproduction, and death (Bolker and Pacala 1999, Bolker 2003). All notation follows Bolker and Pacala (1999) and parameters are defined in Table 1. Fecundity decreases linearly with density until a cut-off at zero: our analysis is based on an expansion around the average or equilibrium conditions, so the cut-off does not affect our (approximate) results.

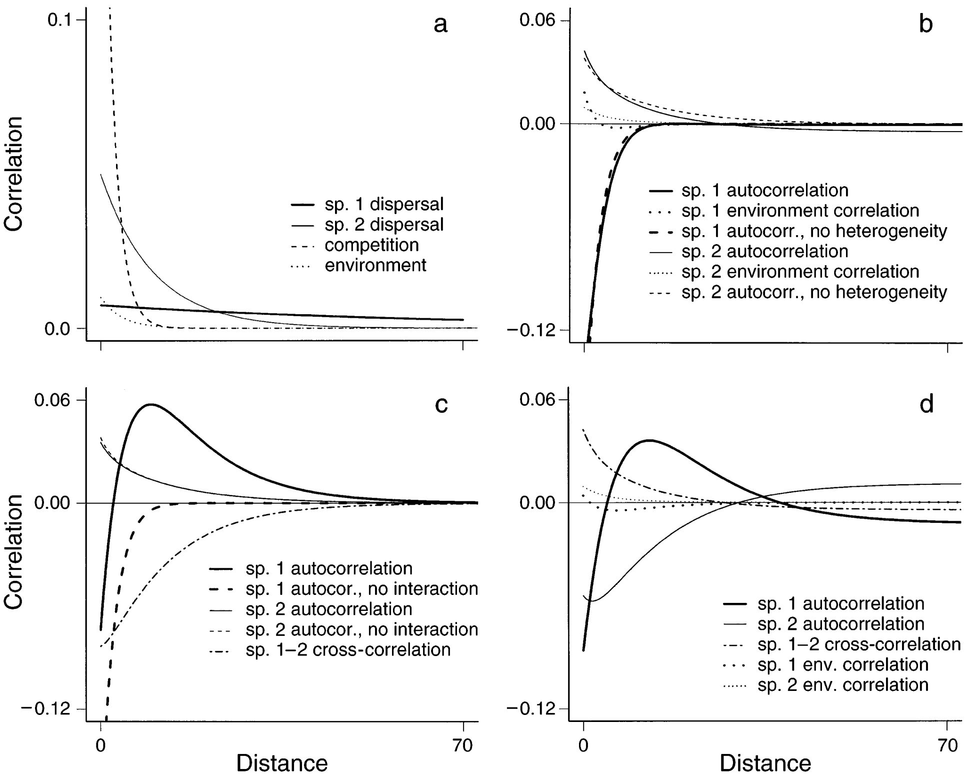

FIG. 1. Effect of environmental heterogeneity (b), competition (c), and the interaction between environmental heterogeneity and competition (d) on the spatial correlation of two competing plant species as predicted from the moment equations. Species 1 (thick lines) is a fugitive species that disperses widely but is a weak competitor. Species 2 (thin lines) is a strong competitor with localized dispersal. (a) Graphical illustration of the spatial kernels (dispersal kernels, scaled competition kernels, and the correlation function in the environment) for a given set of parameters (Table 1). (b) Autocorrelation of species 1 and 2 in a homogeneous environment in the absence of competition (dashed lines) and in a heterogeneous environment (solid lines). Dotted lines show the cross-correlation between each species and the environment. (c) Autocorrelation of species 1 and 2 in a homogeneous environment in the absence of competition (dashed lines, identical to panel b) and with competition (solid lines). The dot-dash line shows the among-species cross correlation. (d) Autocorrelation of species 1 and 2 with in a heterogeneous environment with competition (solid lines). Dotted lines show the cross-correlation between each species and the environment. The dot-dash line shows the between-species cross correlation.

The total effect of intraspecific competition experienced by an individual at any location is the per capita intraspecific competition coefficient (α_{ii}) weighted by the distance to each conspecific individual. In the model, competitive effects decay exponentially with distance as described by the competition kernel (U_{ii}). Similarly, interspecific competitive effects are a function of the interspecific competition coefficient (α_{ij}) weighted by the distance to each competitor. Seed dispersal is described as an exponential kernel (D_i). Environmental heterogeneity affects recruitment probability and is assumed to be static in space, as would be the case for abiotic factors such as soil depth or microtopography. This is in contrast to environmental gradients that may shift spatially, such as water levels along the margins of seasonal wetlands. In this model, we focus on the case in which competing species respond similarly to the environment, although we discuss the cases in which species have different responses to environmental gradients. The spatial structure of the environmental variability affecting recruitment probability is described by its overall mean, variance, and spatial correlation.

We use this model to study the effects of environmental heterogeneity, localized dispersal, and interspecific competition on spatial structure in a simple two-species community. In these simulations, we assume that one species (Sp1) has longer range dispersal than than the other (Sp2) (Fig. 1a). In addition, we assume that the better disperser (Sp1) is the inferior competitor so as to mimic a competition–dispersal trade-off ($\alpha_{12} > \alpha_{21}$). Here α_{ij} denotes the decrease in per capita fecundity of species i per unit increase in local density of species j. The population-level equivalent is $\beta_{ij} = (\alpha_{ij}/\alpha_{ii})(K_j/K_i)$, which accounts for differences in carrying capacity and self-competition, and determines coexistence and exclusion in the analogous nonspatial model (Appendix) (Bolker and Pacala 1999).

TABLE 2. Effects of environmental heterogeneity, local dispersal, and local competition on spatial structure of plant communities.

Process	Time scale	Aggregation	Segregation	Persistence
Environmental heterogeneity	0	↑	↑↓†	↑
Local dispersal	1+	↑	−‡	↑
Local competition	1+	↑↓§	↑	↓

Note: Time scale indicates the minimum number of reproductive events necessary for a given process to effect spatial structure in a successional community initiated with random seed distribution.

† The effects of environmental heterogeneity will depend on whether the species have a preference for the same habitat type. If species have similar habitat preferences, environmental heterogeneity should decrease segregation.

‡ Local dispersal is necessary, but not sufficient, for segregation to occur.

§ In a homogeneous, single-species setting, local competition always reduces aggregation, but interactions among local intra- and interspecific competition and environmental heterogeneity can also lead to increased aggregation.

The spatial scales of competition, dispersal, and environmental heterogeneity for these cases are illustrated in Fig. 1. Parameter values are presented in Table 1.

We illustrate the spatial patterns formed at equilibrium by two species competing in a heterogeneous environment, using a hierarchy of model complexities (Fig. 1b–d). The first model has neither interspecific competition nor heterogeneity ($\alpha_{ij} = \alpha_{ji} = 0$, $\sigma_e^2 = 0$); the next has interspecific competition but no environmental heterogeneity (α_{ij}, $\alpha_{ji} \neq 0$, $\sigma_e^2 = 0$); the third has environmental heterogeneity but no interspecific competition ($\alpha_{ij} = \alpha_{ji} = 0$, $\sigma_e^2 > 0$); and the final model represents the full heterogeneous competitive system (α_{ij}, $\alpha_{ji} \neq 0$, $\sigma_e^2 > 0$). Throughout, we assume that favorable locations have enhanced recruitment rates for both species. The alternative assumption of different responses to the environment by each species (e.g., Snyder and Chesson 2003) would result in spatial segregation that would appear immediately after random seeding, before any ecological interactions have taken place.

Homogeneous environment, no interspecific competition.—In the absence of interspecific competition and environmental heterogeneity, individuals of the long-dispersing species (Sp1) will be regularly spaced (the correlation function will be negative at short distances), because local intraspecific competition inhibits nearby conspecifics. This intraspecific competition is a form of self-thinning. In contrast, the distribution of short-dispersing Sp2 is a balance between self-thinning and spatial aggregation caused by local dispersal. The resultant correlation function can be locally positive (Fig. 1b) or close to zero, depending on the relative strength of clustering and thinning. For reference, these two no-competition/no-heterogeneity correlation functions are shown as dashed lines in Fig. 1b–c. The cross-correlation function between the two species (not shown) is zero at all distances, because the species neither interact directly through competition nor indirectly through common responses to environmental heterogeneities.

Heterogeneous environment.—In the absence of interspecific competition, both the short- and long-dispersing species aggregate on the good habitat because of the enhanced recruitment rates in these areas. This results in positive cross-correlation between habitat quality and both species' distribution (dotted cross-correlation functions in Fig. 1b). The positive autocorrelation of the environment enhances the aggregation of each species (solid lines in Fig. 1b). As in the homogeneous environment, however, intraspecific competition leads to self-thinning and thus inhibits local aggregation (most strongly in the widely dispersing species, where local dispersal cannot enhance aggregation). Given strong intraspecific competition, autocorrelation may remain negative up to intermediate spatial scales (not shown). In such a case, the individuals will be found in aggregates restricted to the good habitat. Thus, positive association with good habitat may indirectly induce a positive association between the two species.

Interspecific competition.—When both species compete in a homogeneous environment (Fig. 1c), the two species will weakly segregate in space because the stronger competitor (Sp2) displaces the weaker competitor (Sp1). The exclusion of Sp1 leads to negative cross-correlation between the two species (Fig. 1c). As in the non-interactive case, local dispersal enhances aggregation of Sp2. Competitive exclusion may also induce aggregation at intermediate scales, as the fugitive species (Sp1) becomes restricted to open spaces between the aggregates of the competitive dominant (Sp2) (Fig. 1c, solid lines).

Heterogeneous competitive landscapes.—The combined effects of heterogeneity and interspecific competition lead to complicated, but explicable, patterns. The short-dispersing competitor (Sp2) shows patterns similar to those in the heterogeneous and non-interactive case (Fig. 1b); individuals are found in aggregates on the good habitat (leading to positive local correlation among individuals and positive cross-correlation between the species and the habitat). Interspe-

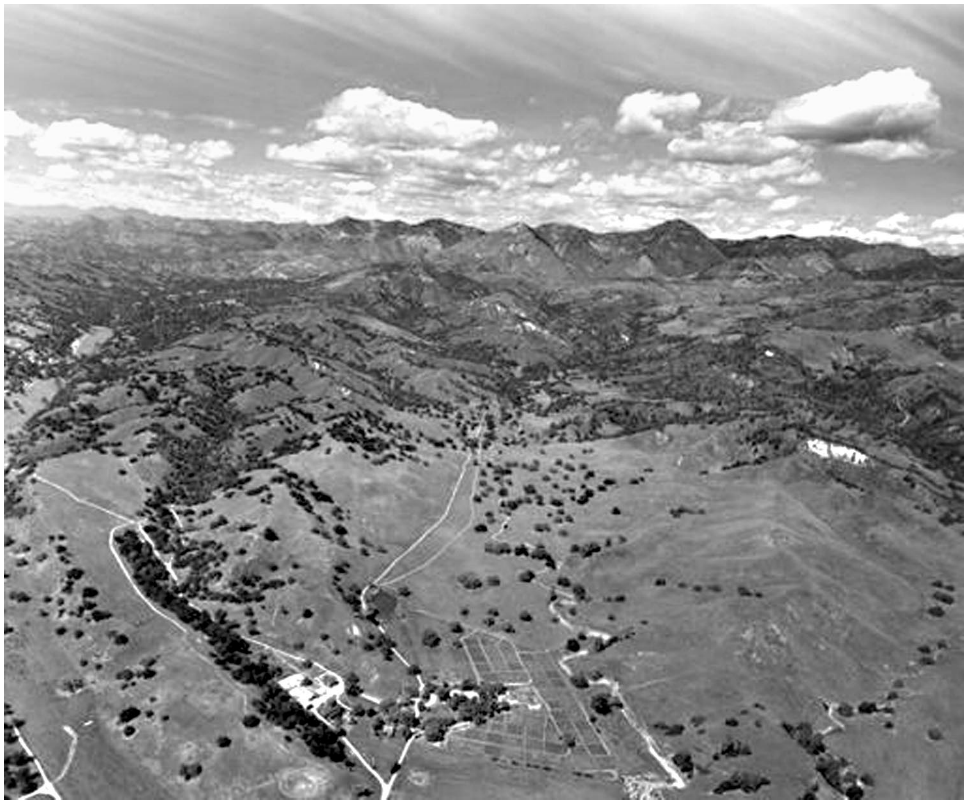

PLATE. 1. Field experiment at Sedgwick Natural Reserve in March 2003. Large square plots in the center of the photo are the 20 × 20 m replicates of the Successional Experiment. Photo credit: Pacific Western Aerial Surveys.

cific competition leads to exclusion of the fugitive (Sp1) from the good habitat, causing a zero or slightly negative cross-correlation with habitat quality. Furthermore, the combination of environmental heterogeneity and competition may induce aggregation in the weak competitor (Sp1) at intermediate scales.

Disturbance and spatial structure.—Mortality-inducing disturbance can change the spatial distribution of recruitment through the creation of empty microsites. Generally, either fine-scale (relative to the size of individual plants) or global (plot-wide) disturbances will simply lower the mean density and erode spatial pattern. In contrast, intermediate-scale disturbances will have more interesting effects on spatial structure in the community (Moloney and Levin 1996). Acting alone, disturbance will induce spatial correlation as a function of distance proportional to the probability that two individuals a given distance apart will both experience the same disturbance (B. M. Bolker, *unpublished data*). In combination with the other processes included in the model, patchy disturbance should both decrease the role of competition at short distances and allow for patchy opportunities for local dispersal, both tending to increase aggregation.

In summary (see Table 2), localized dispersal increases aggregation within a species (i.e., high spatial correlation at short distances), but it does not directly affect the degree of spatial segregation among species, although some degree of local dispersal is necessary for spatial segregation. In contrast, local competition may either increase or decrease aggregation within a species, and increases segregation among species. Environmental heterogeneity increases aggregation and may increase or decrease segregation, depending on the strength of competition between the two species. Unlike dispersal and competitive interactions that are independent of location, the environmental heterogeneity in this model is linked to specific spatial locations (simulating factors such as microtopography or variation in soil fertility). As a consequence, spatial structures generated by environmental heterogeneity will be temporally persistent, whereas those generated by endogenous factors (dispersal and intra- and interspecific competition) should ‘‘wander,’’ possibly slowly, around the fields.

In the case of secondary succession, environmental heterogeneity differs from competition and dispersal in that it acts prior to the first reproductive event by acting directly on the recruitment and establishment of randomly seeded, pre-reproductive individuals. Thus we can attribute any spatial structure prior to reproduction (year 1) to the effects of environmental heterogeneity on establishment, as long as the initial distribution of seed is random.

Implications for the field experiment

Based on the model, we predict that environmental heterogeneity, local dispersal, and competition should leave distinct signatures on the spatial and temporal correlation structure of successional grasslands. Specifically: (1) *environmental heterogeneity* should create aggregation in year 1 prior to the first round of reproduction and seed dispersal, and the locations of aggregates should remain relatively fixed through time; (2) *local dispersal* should increase aggregation after year 1, but the location of the aggregates may be spatially persistent or transient, depending on the level of environmental heterogeneity; (3) *competition* should lower aggregation and increase segregation after year 1, and (as with dispersal) the location of spatial aggregates may be spatially persistent (again depending on the level of environmental heterogeneity); and (4) *disturbance* at large scales (e.g., burning of an entire plot) should lower the effects of competition and thus decrease segregation. Smaller scale disturbances (e.g., gopher mounds) should act in a manner similar to environmental heterogeneity to increase aggregation.

METHODS

Study system

We conducted the research for this project at the Sedgwick Natural Reserve, a 2382-ha reserve that lies ~50 km northeast of Santa Barbara, California, USA (see Plate 1). The area has a mediterranean climate with hot, dry summers and cool, wet winters. Mean rainfall is ~380 mm/yr. The study was conducted on a floodplain terrace that was actively farmed until the start of the experiment. The soils are a sandy, clay loam and are lower in C (1.97%) and N (0.18%) concentrations than adjacent stands of native perennial grasses (C, 3.37%; N, 0.30%; Seabloom et al. 2003).

In January of 1998, we added seeds (500 live seeds/m^2 per species) of five native perennial grass species (*Bromus carinatus*, *Elymus glaucus*, *Nassella cernua*, *Nassella pulchra*, and *Poa secunda*) to newly plowed fields. These species are typical of relict stands of native grasses present on the reserve. The seeds were purchased from a local grower (S&S Seeds, Carpinteria, California, USA) and represent collections from a wide area in California that were grown in mixed stands at a nursery located a few kilometers from the study site.

We focus our analyses on the competitive interactions between four groups of species: native long-lived perennial grasses, native short-lived perennial grasses, exotic annual grasses, and a suite of native and exotic forbs. *N. pulchra* and *N. cernua* are long-lived (>100 yr; Hamilton 1997) native grasses that often dominate relict native grasslands on the reserve. *B. carinatus* and *E. glaucus* are short-lived (5–10 yr) native grasses that are found in sites of higher fertility, such as under oak canopies. The exotic annual grasses are among the most widespread and abundant species in California grasslands (Heady 1977). The most common annual grasses in our experiments (in order of abundance) are *B. hordeaceus*, *B. diandris*, *B. madritensis*, *Hordeum murinum*, and *Vulpia myuros*. The annual forbs are mix of native (e.g., *Amsinkia menziesii*) and exotic species (e.g., *Brassica nigra*, *Erodium cicutarium*, and *Medicago polymorpha*).

We have selected these groupings because of apparent functional similarity in their responses to our experimental treatments (Fig. 2). We recalculated all analyses on the basis of the dominant species in each group and found no qualitative effects on the results (not shown).

Experimental design

We discuss the results of two experiments, one (''successional experiment'') of greater spatial and temporal extent (400-m^2 plots monitored for five years) and one (''establishment experiment'') in smaller plots (20 m^2) in which we track the short-term changes in established grasslands (4-yr-old mix of annual and perennial species) and early-successional grasslands (1-yr-old mix of annual and perennial species).

Successional experiment.—The successional experiment took place in 36 20 × 20 m plots surrounded by a buried fence (1.5 m below ground and 0.5 m above ground) to exclude or contain pocket gophers (*Thomomys bottae*), an abundant subterranean herbivore. We added four pocket gophers to half of the 400 m^2 plots in the winter of 2000, creating a density typical of natural populations of *T. bottae* (Seabloom and Reichman 2001). The pocket gopher treatment was crossed with one of three other treatments (Control, Burn, or Nitrogen addition) for a total of six treatment combinations. Each treatment was replicated six times in a completely randomized block design. The burn was conducted in the summer of 2000. The nitrogen addition consisted of quarterly additions of NH_4NO_3 for an annual rate of 4 g $N \cdot m^{-2} \cdot yr^{-1}$, a rate typical of urbanized areas in southern California. Native ground squirrels (*Spermophilus beecheyi*) colonized the plots naturally.

We collected 364 spatially indexed presence–absence surveys in each plot. At each point, we recorded every species that touched a vertical wire suspended at the point. We also recorded the presence of litter, bare ground, and pocket gopher or ground squirrel soil disturbance. These presence–absence samples were distributed in grids at two spatial scales. At the largest scale, samples were collected in an 8 × 8 array of points every 2 m. At the smaller scale, we established three randomly located 1-m^2 subplots for finer scale sampling. Each subplot was composed of a 10 × 10 array of points located at 0.1 m centers. No samples were collected within 2 m of the plot boundary to minimize edge effects. Censuses were conducted at peak biomass in the spring prior to seedfall (April or May) in 1999–

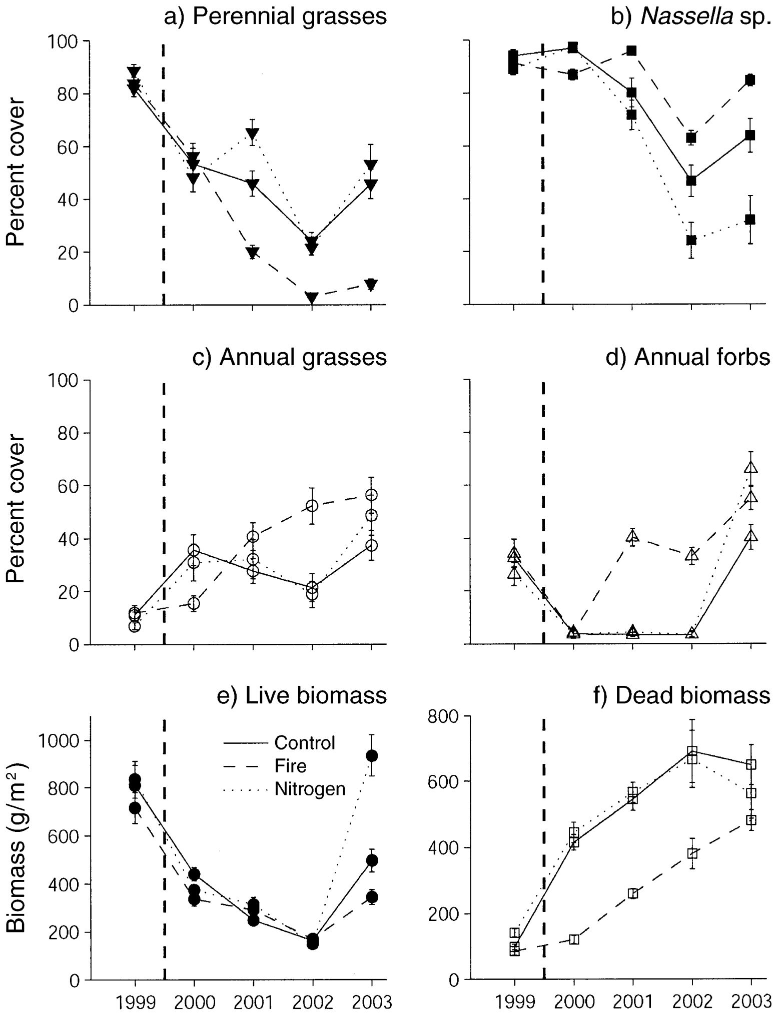

FIG. 2. (a) Short-lived perennial grasses (*Bromus carinatus* and *Elymus glaucus*) declined in abundance over time and were virtually eliminated from plots burned prior to the 2000 growing season. (b) *Nassella* had the opposite response, with its highest abundance in the burned plots and lowest in the nitrogen addition plots. (c,d) Burning also increased annual grass and forb abundance. The overall decline in cover reflects (e) the fivefold decrease in aboveground production and (f) the corresponding fivefold increase in dead biomass over the course of the experiment. Vertical dotted lines represent the time at which the summer burn and the first nitrogen application occurred. Error bars represent ±1 SEM ($N = 12$).

2003. At the same time as the presence–absence surveys, we collected all aboveground biomass from two 0.1×1 m strips adjacent to each of the three 1-m^2 subplots, sorted the live and dead material, dried the samples to a constant mass, and weighed the material to the nearest 0.1 g.

Establishment experiment.—The goal of the establishment experiment was to supplement the results of the successional experiment in two important ways. First, we sampled the spatial structure of the establishment experiment in the first season after planting prior to reproduction. As noted in *Implications for the field experiment*, the spatial structure prior to reproduction provides important insight into the role of environmental heterogeneity. Second, in the establishment experiment, we randomly sowed both exotic annual and native perennial seeds. In the successional experiment, we only seeded native perennial species, assuming that decades of plowing had homogenized the annual seed bank. By sowing both sets of species randomly, we tested the validity of the assumption that the patterns observed in the successional experiment were not the result of pre-existing spatial structure in the exotic annual seed bank.

The establishment experiment took place in 16 4×5 m plots. The plots were assigned one of two community composition treatments: established mixed grasslands (4-yr-old community) or mixed successional (1-yr-old community). Half of the plots were burned in the summer of 2000 prior to seed addition, for a total of four treatment combinations (two community types crossed with two levels of burning). The experiment had four replicates of all four treatments in a randomized-block design.

The established mixed-grassland plots were composed of the communities that resulted from the original sowing of perennial grasses in 1997 that, at the time of first data collection (2001), had undergone four years of succession. These plots were the same age as the plots in the successional experiment in 2001. To establish the mixed-successional communities, we used a broad-spectrum, short-duration herbicide (Roundup) early in the growing season of 2000 to kill all perennial grasses. After the 2000 growing season, we added annual and perennial seeds to establish the mixed-successional plots. Seeding rates were established by collecting all seed produced by nearby annual and perennial stands of area equal to the experimental plots. Due to the high seeding rates, we believe that the successional plots were not seed limited (i.e., there were no empty microsites). Note that annual plants colonized the herbicide-treated plots during the 2000 growing season, so the annual seed addition should be viewed as seed augmentation.

We collected 200 spatially indexed presence–absence surveys in each established experiment plot. These samples were distributed in two subplots of 100 samples each (10 × 10 array at 0.1 m centers) as previously described. No samples were collected within 1 m of the plot boundaries to minimize edge effects. Samples were collected in 2001 prior to any reproduction and seed dispersal (i.e., species distributions were the outcome of a single recruitment event), and in 2002 after two rounds of recruitment and one round of reproduction and dispersal. We collected biomass samples adjacent to each of the subplots as described for the successional experiment.

Plant sizes.—Plant species always will be segregated at the scale of the individual because two individuals cannot occupy exactly the same location. To control for this trivial source of ‘‘segregation,’’ we need to compare the scale of aggregation to the size of individual plants. To do this, we measured the basal radius and maximum radius of two of the most common annual grasses (*B. madritensis* and *B. hordeaceus*), both short-lived perennial grasses (*B. carinatus* and *E. glaucus*), and the long-lived perennial (*Nassella pulchra*). We made measurements on five individuals of each species in two 2-yr-old monoculture stands of each species and five individuals from a 5-yr-old mixed stand.

Statistical analyses

We estimated the spatial correlation functions for each functional group from the spatially indexed presence–absence surveys using the spline correlogram (with df = 7; Bjørnstad and Falck 2001). Conceptually, we consider the presence–absence grid to constitute a Bernoulli random field for which the spline correlogram allows a nonparametric estimate of the underlying spatial correlation function. In this context, ‘‘nonparametric’’ means that the method does not require assumptions about the form of the correlational function (such as exponential or Gaussian functions). We used the replicated plots to quantify the uncertainty in the functions and present error envelopes that represent point-wise standard errors. We also used bootstrapping of individual replicates to estimate uncertainty in the individual spatial correlation functions (Bjørnstad and Falck 2001). We do not present the latter, as the among-replicate error provides a more robust measure of uncertainty than the bootstrapping algorithm used for unreplicated data. The conclusions presented are not qualitatively altered if error envelopes are estimated using bootstrapping. We estimated the cross-correlation functions for each pair of guilds nonparametrically using a spline cross-correlogram (with df = 7).

The derivation of the spline cross-correlogram follows naturally from Hall and Patil (1994), Bjørnstad and Falck (2001), and Bjørnstad and Bascompte (2001). Let z_i be the Bernoulli variable indicating the presence–absence of species A at location x, and w_j be the corresponding variable for species B at location y. Denote their respective spatial mean and spatial variance by μ_z, σ_z^2, μ_w, and σ_w^2. Let further ρ_{ij} be the distance between the two locations.

The pairwise cross-correlation of the two species at the two locations is then given by:

$$C(\rho_{ij}) = (z_i - \mu_z)(w_j - \mu_w)/(\sigma_z \sigma_w). \tag{1}$$

Define the kernel estimator

$$\tilde{\xi}(\rho) = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} \kappa(\rho_{ij}/h) C(\rho_{ij})}{\sum_{i=1}^{n} \sum_{j=1}^{n} \kappa(\rho_{ij}/h)} \tag{2}$$

where κ is a kernel function with bandwidth h. As a direct extension of theorem 3.1 in Hall and Patil (1994), $\tilde{\xi}(\rho)$ will be a consistent and nonparametric estimator of the underlying cross-correlation function of the Bernoulli random field. We use a cubic B-spline as an equivalent kernel function (Nychka 1995), because this adapts better to irregularly spaced data (Jones et al. 1994). The R library used to calculate the spline (cross-)correlograms is included as a digital supplement.

Our model predicts that spatial correlation and cross-correlation may take a variety of forms in the face of competition. Fig. 1 suggests three important summary statistics: (1) the level of local aggregation, which can be measured by the value of the spatial correlation function at distance zero; (2) the level of local segregation, which can be measured by the value of the cross-correlation function at distance zero (note that this value can be positive for species that aggregate in a common preferred environment); and finally (3) the range of spatial dependence. We measure this as the distance at which the function crosses $y = 0$, a measure variously known as the *x*-intercept, or the L_0 correlation length (Bjørnstad and Falck 2001). The submitted R library explicitly calculates these measures (see the Supplement).

RESULTS

Compositional changes

The experimental grasslands in the successional experiment showed strong compositional changes through the course of succession (Fig. 2). Short-lived native perennial grasses declined in cover in the unburned plots and were nearly extirpated in the burned plots. The opposite pattern was true for annual forbs, which were almost completely displaced in the control plots after three growing seasons. A single summer burn increased their areal cover from 3% to 40%. The burning also increased the abundance of exotic annual grasses from 21% to 53%. Note that the overall decline in total cover in the control plots corresponds to a fivefold decline in aboveground production from 1999 to 2002, driven by a corresponding fivefold increase in dead biomass over the same time period. As a result, total standing crop remained relatively constant at 779 ± 42 g/m^2 (mean ± 1 SE). The decline in cover of perennial grasses from 2001 to 2002 is largely due to the low rainfall in the 2001–2002 growing season (263 mm) which falls in the lowest 10% of the long-term precipitation in this region (Michaelsen et al. 1987). Perennial grasses in irrigated plots in a different study maintained similar cover over this period (E. W. Seabloom, *unpublished data*).

Spatial structure

We calculated the spatial (cross-)correlation within and among the four functional groups after a single year of growth (prior to reproduction and dispersal), following random seeding in the establishment experiment. We also calculated the spatial structure in years 2–5 for the data from the successional experiment.

After a single year of growth, following random seeding of annuals and perennials (establishment experiment), all taxa were significantly spatially aggregated at scales of ~1.0–1.5 m (not shown). Note that we did not measure the spatial aggregation of the newly emerged seedlings, and this first measurement reflects all processes that occurred during the first growing season. There was little evidence of spatial segregation in these incipient grasslands, except in the case of the short-lived perennials and annual forbs that had a negative cross-correlation at scales of up to 1.0 m. These patterns were very similar in year 2 (successional experiment) after a single dispersal event and two seasonal cycles of growth and mortality. In Fig. 3, we depict this pattern in the successional experiment because of its larger spatial extent. Note that the similarity in spatial structure between the successional experiment and the establishment experiment indicates that the annual seed bank in the successional experiment was sufficiently well-mixed to mimic the random seeding of annuals in the establishment experiment.

The degree of aggregation increased over time, such that the range of spatial aggregation in the 4-yr-old grasslands (establishment and successional experiment) was 2–4 m (Fig. 4). The annual forbs were an exception, exhibiting aggregation out to only ~1.5 m. In addition to the increased aggregation, these older grasslands also showed clear evidence of spatial segregation. Short-lived perennial grasses were strongly segregated from *Nassella* (to 1.5 m) and annual grasses (to 2.5 m). Annual grasses and forbs were positively correlated at scales out to ~1 m. We only show the patterns from year 4; the spatial structure was similar through years 3–5.

The summer burn increased the abundance of annual species, probably by removing litter and creating more competition-free sites for seedling recruitment (Fig. 2). The spatial structure of this recruitment-dominated system (Fig. 5) was similar to the structure in the 1-yr-old grasslands (establishment experiment) and 2-yr-old grasslands (successional experiment) (Fig. 3); aggregation occurred at shorter spatial scales and with little between-species segregation.

Disturbance resulting from pocket gopher and squirrel burrowing affected the spatial structure of the grassland communities, albeit at a smaller scale than burning. The disturbances themselves were spatially aggregated at the <2 m scale as a result of central-place (squirrel) and area-restricted (gopher) foraging behaviors (Klaas et al. 2000, Seabloom and Reichman 2001). The native short-lived and long-lived perennial grasses were negatively correlated with the disturbances. The annual grasses and forbs, in contrast, were positively correlated with the disturbance (Fig. 6). The disturbance-induced association and segregation exhibited by the different groups are, thus, as predicted by competition–disturbance theory.

Despite the comparable levels of aggregation, annual grasses and forbs differed strongly in their spatiotemporal persistence. The presence of all grasses was positively correlated with their presence four years (or more) into the past (Fig. 7). In contrast, the annual forbs were very weakly correlated across years, indicating that their spatial location varied, although their levels of spatial clustering remained constant. The annual forbs were the species that increased in abundance most strongly in response to disturbance (Fig. 2). Their lack of spatiotemporal persistence may reflect the fugitive nature of their life histories.

A trivial source of local-scale aggregation and segregation occurs at the scale of individual plants: species become segregated because two individuals cannot occupy the same spatial location. In our experiments, the scale of aggregation is many times larger than the size of individual plants. The mean radius of an annual grass was 7.5 cm, the mean radius of a short-lived perennial

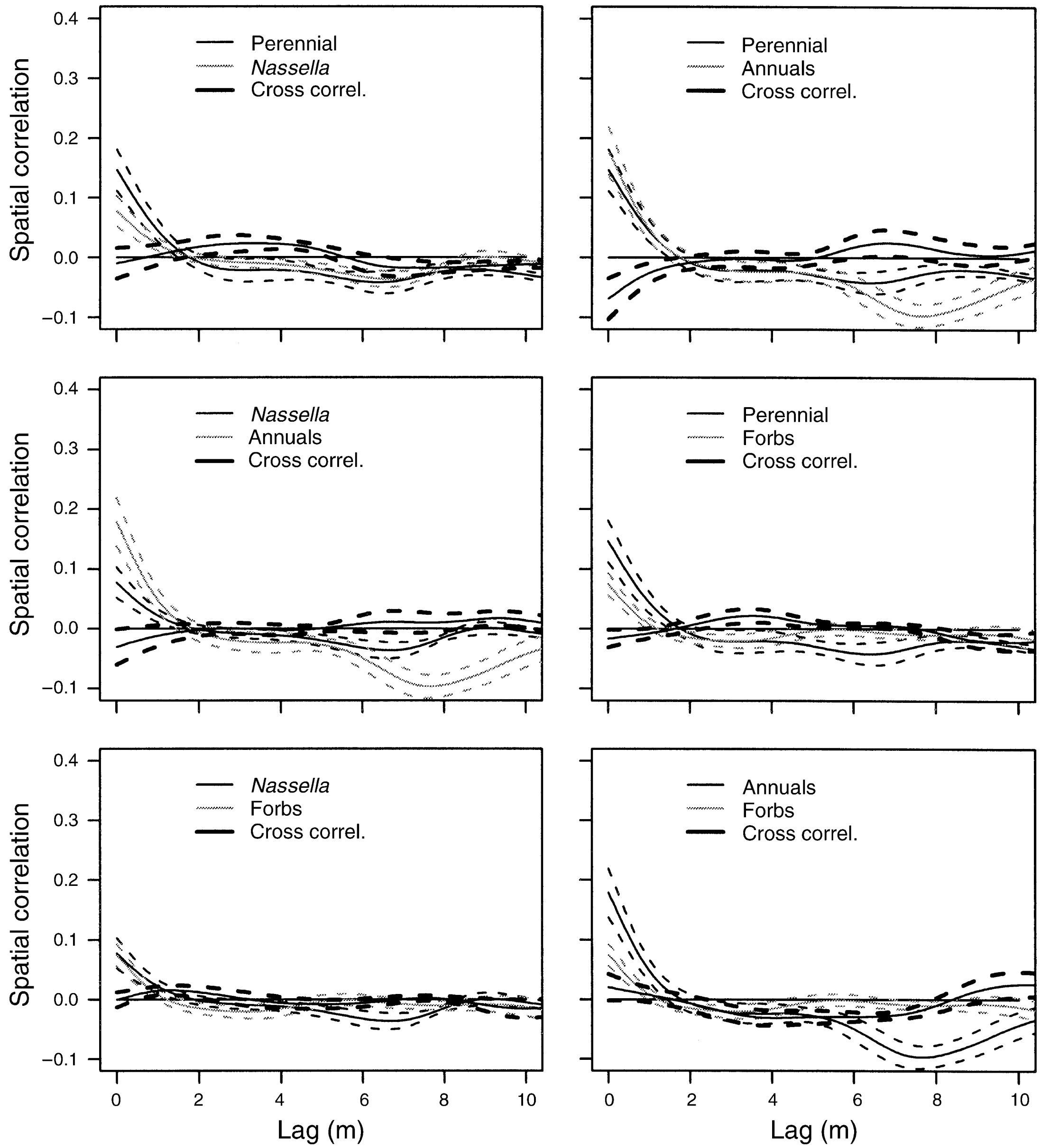

FIG. 3. Correlation functions after one year of growth and reproduction following random seeding. Aggregation can be detected at scales up to 2 m, a distance significantly larger than the size of a single plant. There was little evidence for segregation in these incipient communities; cross correlations were not different from 0 except for a single case. Short-lived perennial and annual grasses were somewhat segregated. Error envelopes (dashed lines) represent ±1 SEM ($N = 12$). The mean (and 1 SD) percent cover values of the different groups in the plots were: short-lived perennial grasses 82% (11%), *Nassella* 94% (8%), annual grasses 27% (10%), and annual forbs 15% (17%).

grass was 18.9 cm, and *Nassella pulchra* had a mean radius of 12.1 cm (Table 3), whereas aggregation occurs at the scale of multiple meters.

DISCUSSION

We found that spatial structure arises early during experimental-grassland succession and increases over time. In our experiments, we started with a dense, random distribution of seeds, such that there were few potential empty microsites and no spatial correlation in seeding. Furthermore, our study site was flat and composed of soils that were homogenized by decades of plowing, atypically homogeneous initial conditions. Nevertheless, after the first growing season and prior to reproduction and seed dispersal, significant spatial aggregation was evident at the 1–2 m scale. During subsequent years, most taxa were aggregated at >4 m, and there was clear spatial segregation at smaller spatial scales. The spatial organization of the community was strongly affected by disturbance. Burning eroded

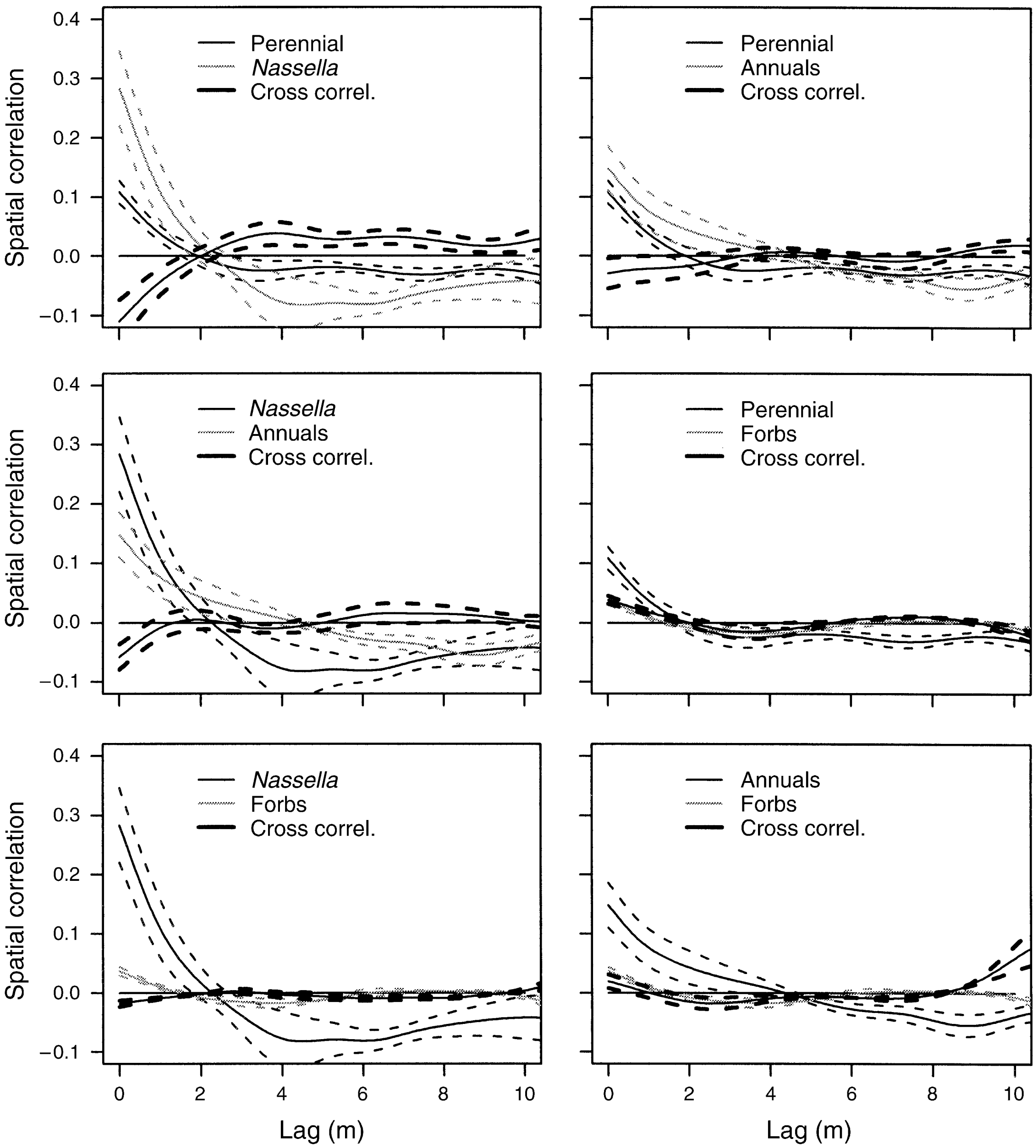

FIG. 4. Correlation functions in four-year-old grasslands. Aggregation can be detected at scales up to 2–4 m. In addition, there is significant segregation between *Nassella* and the other grasses, and a weak segregation between annual and short-lived perennial grasses. There is a tendency toward spatial association between annual grasses and forbs. Error envelopes (dashed lines) represent ±1 SEM (N = 12). The mean (1 SD) cover values of the different groups in the plots were: short-lived grasses 24% (11%), *Nassella* 45% (20%), annual grasses 23% (18%), and annual forbs 0.2% (0.4%).

spatial structure in the communities, whereas animal disturbances enhanced local-scale differentiation.

Prior to the first reproductive event, we found strong aggregation at the local scales (1–2 m) in all groups of species. Although this was fairly small scaled, the aggregation occurred at scales of tens to hundreds of individuals. The structure was therefore not due to the extent of single individuals. The most plausible explanation of this initial spatial structuring is the presence of underlying environmental heterogeneities that affect germination and/or establishment (Fig. 1b).

Aggregation increased over time in the successional grasslands due to local dispersal and probably due to continued influences of environmental heterogeneities. In addition, segregation among groups increased. In particular, short-lived perennial grasses became spatially segregated from the long-lived perennial grass (*Nassella*) and the exotic annual grasses. In contrast, annual grasses and forbs were positively correlated with one another, presumably due, in part, to their preference for disturbed habitats. The enhanced segregation is likely to be a testimony to the increasing importance

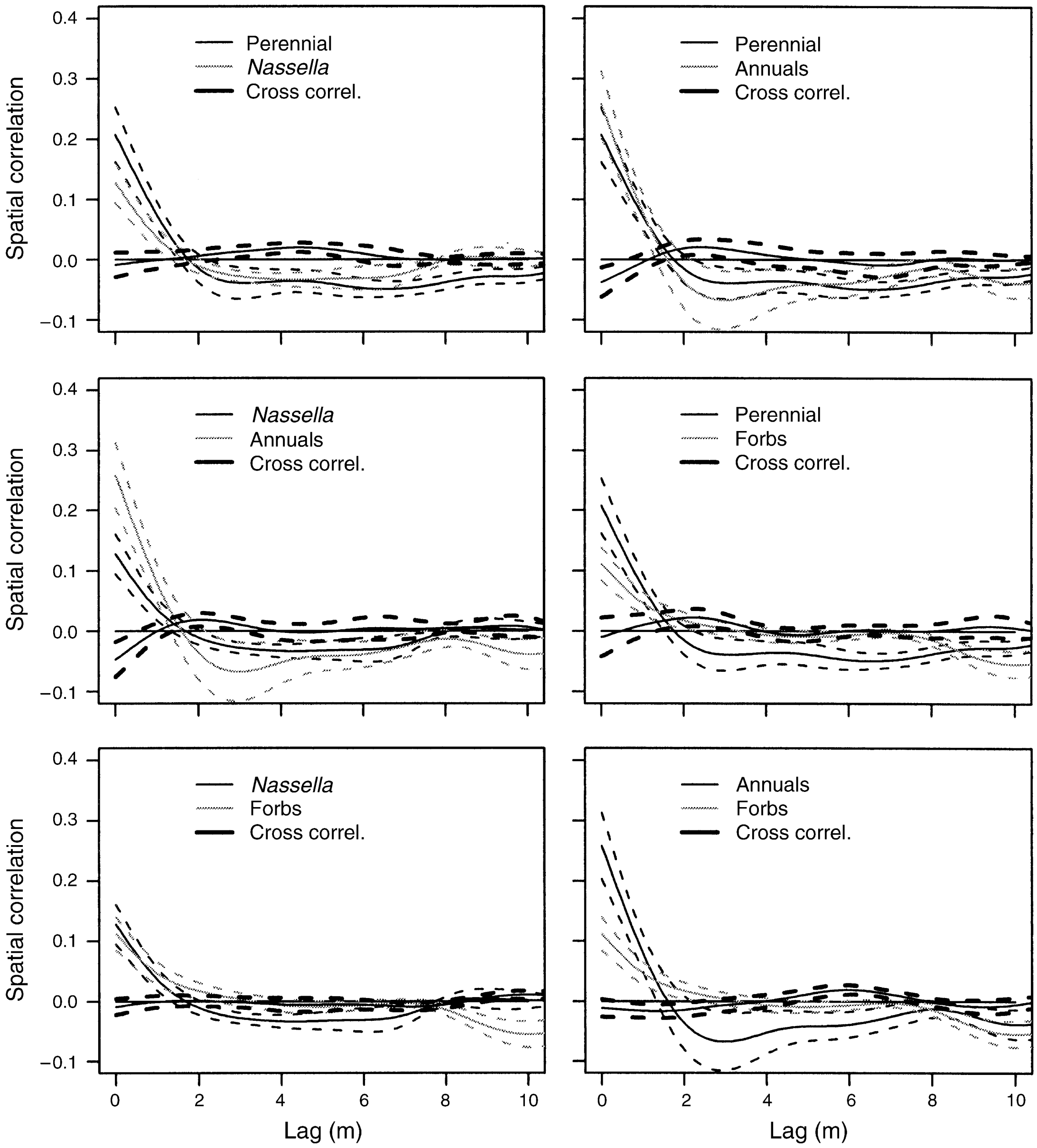

FIG. 5. Correlation functions in four-year-old grasslands approximately two growing seasons after a summer burn (2001). Aggregations can be detected up to the 1–2 m range. There is no significant segregation between species. Error envelopes (dashed lines) represent ±1 SEM ($N = 12$). The mean (1 SD) cover values of the different groups in the plots were: short-lived grasses 3% (3%), *Nassella* 59% (13%), annual grasses 68% (15%), and annual forbs 2% (3%).

of competition (Table 2). Werner and Platt (1976) also found evidence that species segregation increased over the course of segregation in grassland systems in their study of the distribution of *Solidago* sp. (Asteraceae) in two midwestern grasslands.

We suspect that much of the larger scale (>5 m) spatial structure in the annual forbs is due to localized dispersal, because the aggregates of these species do not occur in the same place over time. It is possible that ideal environmental conditions switch from year to year, but this seems unlikely in a flat site in which the soils have been homogenized by decades of plowing. It is conceivable that shifting environmental heterogeneities would erode spatial persistence. For example, in wetland systems where water level is the primary determinant of species composition, fluctuating water levels drive spatial changes the dynamic environmental gradient to which plants have to adjust (Seabloom et al. 2001).

Disturbance has strong effects on the composition of grassland communities (Cooper 1926, Watt 1947, Platt and Weiss 1985, Collins 1987), and theory suggests

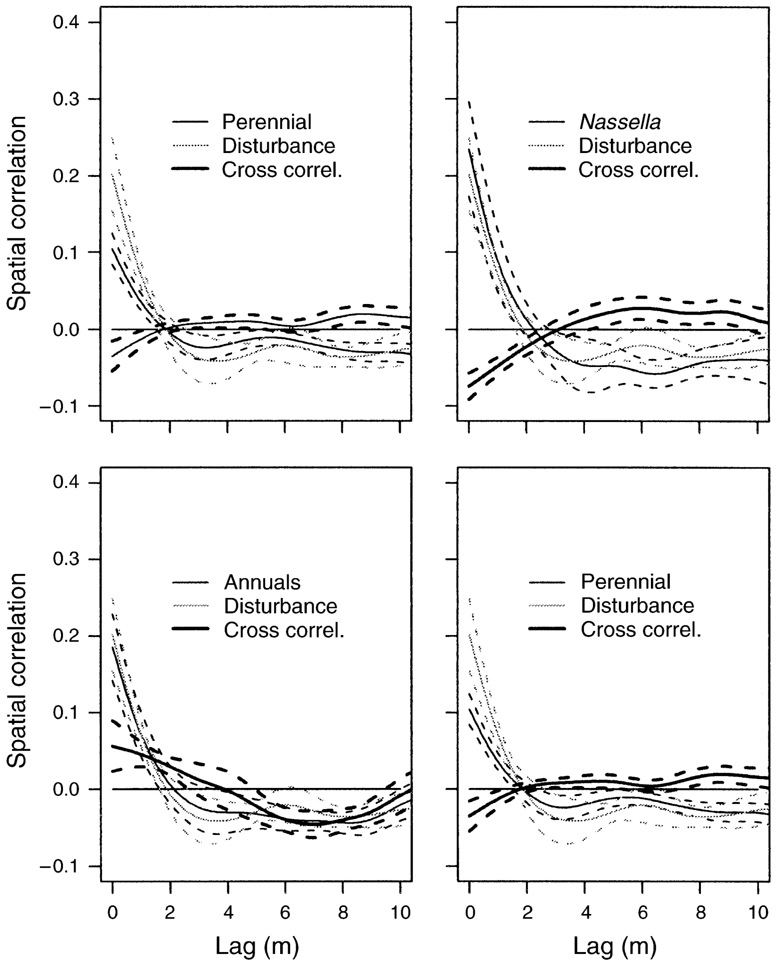

FIG. 6. Pocket gopher and squirrel disturbances are aggregated out to scales of ~2–3 m. *Nassella* is negatively correlated with animal disturbance at scales of up to 1 m, and annual grasses and forbs are positively correlated with animal disturbance at scales of up to 0.5 m. Confidence envelopes (dashed lines) represent ±1 SEM ($N = 12$).

that disturbance should further affect the spatial structure of communities (Moloney and Levin 1996, Wiegand et al. 1998, Seabloom and Richards 2003). We have shown empirically that two common disturbances in grasslands had strong effects on spatial structuring, and that their effects on community heterogeneity were scale dependent. Burning decreased aggregation and segregation, whereas animal disturbance (digging by pocket gophers and squirrels) increased species segregation at local scales (<2 m).

We can make a preliminary, qualitative interpretation of the spatial patterns on the basis of our mechanistic plant competition model. As Fig. 1 suggests, the exact patterns of spatial correlation depend delicately on the balance of strength and scale of dispersal, within-and between-species competition, and environmental heterogeneity. Interpreted in the light of the moment equations, the early aggregation in all species is consistent with the presence of underlying environmental heterogeneities. The gradual build-up of negative cross-correlations among species (Fig. 4), particularly among the grasses, is as expected from significant interspecific competition. Burning appears to erode these features and illustrates how disturbance can counteract the spatial self-organization that results from interspecific interactions (Fig. 5). The forbs, which become increasingly rare through the succession, appear to play a fugitive role, with little temporal pattern to their spatial distribution. The positive cross-correlation between annuals and forbs is consistent with low interspecific competition and aggregation on patches of favorable habitat (Fig. 1b). This is supported by the analysis of disturbances (Fig. 6), showing how both annuals and forbs aggregate on disturbed patches (in ''competition-free'' habitat).

The traditional way to estimate spatial interactions (using the parameters of a spatial competition model) is to observe the demographic and spatial processes (fecundity, mortality, germination) and their dependence on distance and local density directly, using

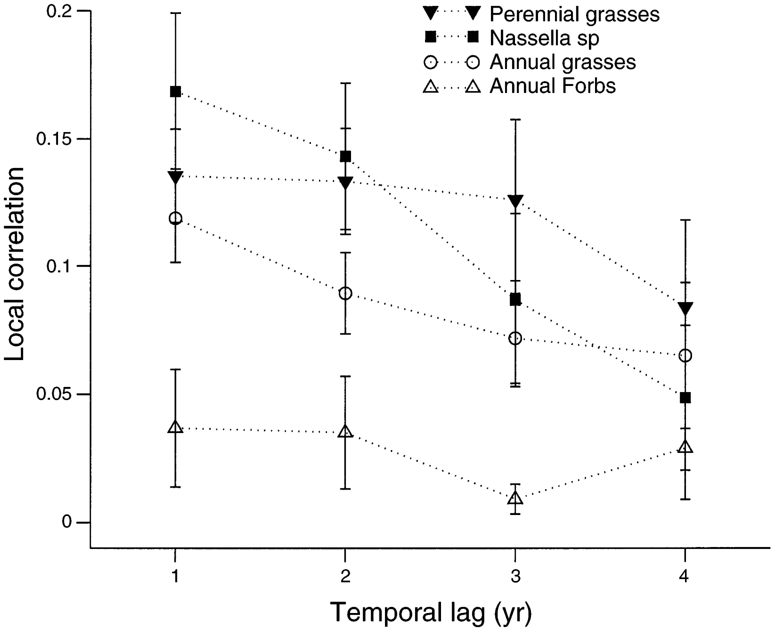

FIG. 7. All grass species are significantly positively correlated at temporal lags of at least four years. In contrast, annual forbs show little temporal correlation. Local correlation is estimated using the mean intercept of the spline correlograms. Error bars represent ±1 SEM ($N = 12$).

neighborhood models based on maximum likelihood (Pacala and Silander 1987, Pacala et al. 1993), or to use the range of statistical approaches to infer dispersal from the relationships between seed or seedling distribution and locations of adults (Ribbens et al. 1994, Clark et al. 1999, Nathan and Muller-Landau 2000). These approaches are straightforward, but are also highly labor-intensive, system-specific, and largely fail to account for spatial environmental variation (but see Hubbell et al. [2001], as a beginning in this direction). Another approach under construction is the work by Chesson and co-workers to quantify the components of the variation-dependent coexistence mechanisms (storage effect, nonlinear competition, and growth-habitat covariances; Chesson 2000) in natural communities. In contrast to our approach, this work aims to quantify the spatial and/or temporal covariances between density and population growth, rather than to identify the specific spatial interactions that give rise to these patterns.

To complement these approaches, we are currently developing tools that are more complete, but less specific, to link pattern and process in competitive grassland communities (B. M. Bolker, O. N. Bjørnstad, E. W. Seabloom, *unpublished manuscript*). In this work, we hope to link the models and data quantitatively by inferring the scale and shape of both competition and dispersal kernels in successive spatial snapshots. To do this, we use *spatial spectra* to subtract (deconvolve) the influence of correlated environmental variables from observed population patterns. This approach extends a variety of other research endeavors that, like ours, have studied how spatial interactions and environmental variation combine to produce population patterns. The novelty of our work lies in moving beyond qualitative descriptions to rigorous parameter estimation tools based on spatial correlations (Roughgarden 1977, Moloney and Levin 1996, Lande et al. 1999).

We have shown that there are distinctive signals embedded in the spatial structure of grasslands that reflect the importance of environmental heterogeneity, dispersal, and competition in determining community dynamics. Environmental heterogeneity creates aggre-

TABLE 3. Average size of common annual and perennial grass species in restored experimental grasslands.

Life span	Species	Basal radius (cm) Mean ± 1 SEM	Maximum radius (cm) Mean ± 1 SEM
Annual	*Bromus hordeaceus*	0.83 ± 0.10	6.23 ± 0.71
Annual	*Bromus madritiensis*	1.40 ± 0.21	9.20 ± 2.51
Perennial	*Elymus glaucus*	1.41 ± 0.22	9.37 ± 1.53
Perennial	*Bromus carinatus*	1.77 ± 0.09	14.77 ± 2.69
Perennial	*Nassella pulchra*	2.19 ± 0.06	18.87 ± 1.65

gation in the first year of succession. Over time, species become increasingly spatially segregated due to the combined effects of environmental heterogeneity, competition, and dispersal. In contrast, disturbances such as fires homogenize the community by decreasing aggregation and segregation. We also have demonstrated that complex patterns of aggregation and segregation emerge rapidly in grassland plant communities, even in the absence of obvious abiotic gradients or variability in propagule supply. Given the well-documented effects of local density of neighbors on plant vital rates (Mithen et al. 1984, Pacala 1986), our study further illustrates the importance of the spatial dimension to plant community dynamics.

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APPENDIX

A derivation of the spatial model is available in ESA's Electronic Data Archive: *Ecological Archives* M075-008-A1.

SUPPLEMENT

An R library to calculate the spline correlogram and cross-correlogram is available in ESA's Electronic Data Archive: *Ecological Archives* M075-008-S1.