



Spatial heterogeneity in the herbaceous layer of a semi-arid savanna ecosystem

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Abstract

Despite increasing recognition of the role spatial pattern can play in ecosystem function, few studies have quantified spatial heterogeneity in savanna ecosystems. The spatial distribution of herbaceous biomass and species composition was measured across three scales in a semi-arid savanna in central Kenya, and patterns were related to environmental variables at different scales. Herbaceous biomass declined across a rainfall gradient and from upper to lower topographic positions, but variation within a site (across 5–50 m) was similar in magnitude to among-site variation associated with rainfall and topography. Geostatistical analyses showed that patchiness at scales of 5–25 m explained 20% of total variation in herbaceous biomass. This pattern arose from the presence of both 5–10-m diameter patches containing high herbaceous biomass ($> 170 \text{ g m}^{-2}$) and 5–10-m diameter patches characterized by nearly bare soil surfaces ($< 40 \text{ g m}^{-2}$). Patch structure was contingent on topography, with larger bare patches at ridgeline and upper hillslope positions. Grass species distributions showed the greatest degree of patch structure and species turnover across distances of 5–45 m. Additional community variation was associated with topography, with minimal variation in species composition across the rainfall gradient. Pattern diversity significantly exceeded levels reported for four other grassland ecosystems, suggesting fundamental differences in local processes generating spatial pattern. It is hypothesized that heterogeneously distributed grazing pressure, interacting with the distribution of shrub canopies, is an important factor generating such high levels of small-scale patch structure in this savanna.

Introduction

Factors generating spatial patterns in plant communities have received increasing attention from ecologists. In grasslands, abiotic influences such as topographic variation and disturbance impart spatial patterns to plant communities at varying scales through their effects on soil moisture, nutrient availability, temperature, and removal of dominant species (Schimel et al. 1985; Glenn et al. 1992; Collins 1992; Frank et al. 1994; Fisk et al. 1998). Biotic factors can also generate and maintain vegetation patches independent of topographic or pedologic boundaries. Potential mechanisms of patch formation include localized competitive interactions between individuals

coupled with dispersal (Frelich et al. 1993; Pacala and Levin 1997), feedbacks between soil nutrient availability and litter quality of plant species (Wedin and Tilman 1990), and localized trophic feedbacks between soils, plants, and herbivores (Schlesinger et al. 1990; Pastor et al. 1998; Gabriela et al. 2000).

Distinct spatial patterns consisting of vegetated patches alternating with areas of bare soil have been described for semi-arid grasslands and savanna ecosystems worldwide (Aguiar and Sala 1999; Tongway et al. 2001). These alternating patches are often observed across distances of 10–100 m and have been attributed to interactions between highly variable rainfall in time and space, soils prone to surface runoff, and aggregation of plant individuals that trap run-

off. Hence, patches of bare soil and grass cover in these systems are largely an expression of abiotic controls on moisture availability, possibly augmented by positive local interactions among closely-spaced individuals which more effectively hold soil moisture.

A separate vein of research in semi-arid ecosystems has focused on the interaction between a key biotic factor, grazing by large herbivores, and rainfall, in determining the prevalence of degraded bare soil and the abundance of annual and perennial grass communities. For example, Le Houerou (1989:84) reported that in regions of Burkina-Faso and Mali, high stocking rates during years following drought created "large extents of permanently bare ground with a sealed surface," and Kelly and Walker (1976) documented dramatically higher cover of bare soil and annual grasses at intensively grazed sites compared to moderately grazed, perennial-dominated sites. Recent theoretical analyses mechanistically explain how increased grazing intensity can lead to the formation of two alternate stable states, a 'bare-soil' state or a 'vegetated' state, due to a positive feedback between water infiltration or nutrient retention and plant cover (Rietkerk and van de Koppel 1997; Rietkerk et al. 1997). In essence, these models predict that if increases in grazing intensity reduce plant cover beyond a threshold, then feedbacks between plants and the soil can create a stable, degraded bare state which can not be reversed simply by reducing grazing pressure. Rietkerk and van de Koppel (1997) suggest that their model predictions might explain the type of two-phase patch mosaics documented at 10–100 m scales in many semi-arid ecosystems. However, the spatial scale at which these processes may operate, and the spatial patterns that may occur in intensively grazed landscapes, have received limited empirical attention.

In addition to local spatial patterning associated with alternation of bare and vegetated areas, small-scale patch structure is often observed in the distribution of plant species. For grasslands, McNaughton (1983) was one of the first to quantify and emphasize the potential functional importance of this 'pattern diversity' in the distribution of grass species, where pattern diversity is a measure of dissimilarity in species composition of plots within the same sward. More recent studies have shown that fire and grazing, two of the primary determinants of savanna dynamics, have strong and opposing effects on pattern diversity in tallgrass prairie (Collins 1992; Knapp et al. 1999). In savannas and grasslands, pattern diversity may also improve the foraging environment for na-

tive herbivores and impart stability to grass – grazer interactions (McNaughton 1994; Knapp et al. 1999). However, few studies have quantified spatial patterns in savanna ecosystems at different scales (Rietkerk et al. 2000) or compared measures of local spatial heterogeneity among savannas (Aguiar and Sala 1999).

The objectives of this study were therefore (1) to quantify the spatial distribution of herbaceous communities and bare soil at local (0–50 m), landscape (1–5 km), and regional (10–25 km) scales within a semi-arid savanna ecosystem in central Kenya; (2) to relate the distribution of communities to topographic variation, which occurs at the landscape scale, and a rainfall gradient, which operates at the regional scale; and (3) to examine variation in the contribution of pattern diversity, or small-scale patch structure in the distribution of plant species, to overall sward diversity among different ecosystems.

Study area

Plant community patterns were evaluated during 1998 at the Mpala Research Centre and associated Mpala ranch which encompasses some 190 km² of semi-arid savanna within the Laikipia district of central Kenya (36°53' E, 0°20' N). The landscape is underlain by well drained, friable sandy loams developed from metamorphic basement rocks (Ahn and Geiger 1987). A region of 'black cotton' soils developed from volcanic rocks also occurs in southwestern Mpala (Ahn and Geiger 1987), but this area was excluded to focus on plant community heterogeneity within a geologically uniform landscape. The study area encompassed a north – south rainfall gradient. Mean annual rainfall during 1989–1993 was 239 mm in the northern study area, 350 mm in the central study area, and 430 mm in the southern area. These averages reflect a relatively dry series of years, and the long-term (1972–1995) annual mean, available for the southern study area only, was 501 mm (CV = 0.35). Rainfall in the south was 888 mm in 1998, the year of sampling, due to the influence of an El Niño Southern Oscillation. Topography in all three study areas consisted of gently rolling hills and occasional granitic inselbergs. Inselbergs are a unique and rare component of the landscape, and were not sampled. Woody vegetation is dominated by *Acacia brevispica*, *A. mellifera*, and *A. etbaica* and underlain by a discontinuous herbaceous layer (Young et al. 1995). *Euphorbia nyikae* is common in the north, but absent in the cen-

tral and southern region of Mpala. Young et al. (1995) previously described a two-phase mosaic at Mpala consisting of long-term glades (short-grass lawns lacking woody vegetation; 1% of the landscape) and *Acacia*-dominated bushland (99% of the landscape). This study focuses on herb-layer patterns within the *Acacia*-dominated bushland. Fire may previously have been an important component of Laikipia's savannas, but has been actively suppressed by ranch managers since European settlement. No large-scale fires are known to have affected the study areas in recent decades. All fires occurring in response to the accumulation of standing dead biomass following high rainfall in 1998 were quickly extinguished. Mpala is currently managed for livestock production using traditional Maasai herding methods. During 1998–99, cattle stocking rate at Mpala averaged 16 animals km⁻² or 4,750 kg km⁻², calculated on the basis of herd age structure and weight variations among calves, heifers, steers, cows and bulls. The most common native grazers and mixed-feeders are impala (*Aepyceros melampus*), zebra (*Equus burchellii*), waterbuck (*Kobus ellipsiprymnus*), buffalo (*Syncerus caffer*) and eland (*Taurotragus oryx*).

Methods

Field sampling

A stratified, nested sampling design (Gross et al. 1995) was used to quantify plant community composition and heterogeneity across three spatial scales. At the local scale, herb-layer vegetation was sampled 10 times along a 50-m transect oriented north-south with plots sampled at 5-m intervals. Transects were distributed in systematic grids with 1-km spacing between transects. Across Mpala, three grids of transects were sampled corresponding to the rainfall gradient: one grid in the northern study area (low rainfall, 16 transects), one grid in the central study area (intermediate rainfall, 18 transects), and one in the south (high rainfall, 12 transects). This sampling design was used to evaluate plant community patterns within a 50-m transect, within topographically variable landscapes (1–5 km), and across the rainfall gradient (up to 23 km).

Herb-layer vegetation was sampled at 5-m intervals along each transect by canopy interception (Frank and McNaughton 1990) with a 10-point pin frame that held pins at a 45° angle. Previous grass-

land sampling showed measurements of plot diversity (H') and percent similarity among plots (1-PS) reached an asymptote with the use of 10 pins (McNaughton 1983) such that sampling intensity was sufficient for this study's objectives. Herbaceous biomass was calculated using regression equations derived from clipped plots, with separate equations derived for stoloniferous grasses ($y = 36.32 \times x_1 + 172.44 \times x_2$; $r^2 = 0.87$, $F_{2,34} = 538$, $P < 0.0001$), bunchgrasses ($y = 41.66 \times x$; $r^2 = 0.89$, $F_{1,8} = 62.4$, $P < 0.0001$), thin-leaved grasses ($y = 26.46 \times x$; $r^2 = 0.91$, $F_{1,11} = 115$, $P < 0.0001$), and forbs ($y = 51.88 \times x$; $r^2 = 0.96$, $F_{1,16} = 433$, $P < 0.0001$), where $y = g \cdot m^{-2}$, $x = \text{mean contacts per pin}$, $x_1 = \text{mean leaf contacts per pin}$, and $x_2 = \text{mean stem contacts per pin}$. At each pin-frame position (plot), cover of shrub species was estimated visually to the nearest 10%. All sampling was conducted during December, 1998, which corresponded to late wet-season conditions following El Niño rains when grass species set seed and could be identified reliably. Nomenclature followed Polhill (1972–1982). Because the focus was on grasses, which dominate the understorey, forbs were recorded as a single group. At each transect, the topographic position was also recorded (ridge = 1, upper hillslope = 2, lower hillslope = 3, or lowland = 4), and a single soil core was collected from the plot located at 25 m. At six transects (two in each grid) a soil core was collected from all 10 plots along the transect.

Analyses of spatial patterns

Spatial patterns in herbaceous biomass at local scales were examined with geostatistics (Robertson and Gross 1994; Goovaerts 1998) which quantify the size and degree of patchiness in the distribution of a given variable. Semivariance across distances of 5–40 m was calculated with GS+ (Gamma Design Software 1998). Exponential, spherical and linear models were fitted to the pattern of semivariance versus distance separating sampling points using unweighted least-squares analyses, and the best-fit model was selected using the Akaike Information Criterion (Webster and McBratney 1989). The number of pairs of plots used to construct the semivariogram ranged from 414 at the 5 m separation distance to a minimum of 184 at the 30 m separation distance. Parameters derived from the best-fit model quantified two key aspects of patchiness in a variate's distribution. First, the proportion of sample variance explained by patchiness at

scales of 5–40 m (i.e. the degree to which patches were differentiated from the surrounding area by their distinct, within-patch homogeneity) is reflected in the difference between the sill (asymptote) and the nugget (y-intercept) of the variogram. Second, the mean diameter of those patches is estimated by the range, or separation distance where the variogram reaches an asymptote. Because patches could arise from aggregation of low-biomass or high-biomass plots (or both), further analyses of local patch structure were conducted following community classifications (see below). Standard analysis of variance was used to compare mean cover of herb-layer biomass for transects at different topographic positions and across the rainfall gradient.

Three different approaches were used to analyze the spatial distribution of plant species and communities. The first two methods involved spatially-explicit analysis of community distributions. In these two analyses, percent cover of bare soil was included along with percent cover of grass species and forbs because many plots were only bare soil and this clearly was an important component of spatial pattern. The third method evaluated species diversity patterns, and was based only on cover of grass species and forbs.

The first method examined (1) the number of communities occurring within a given transect, and (2) the number of transitions between community types that occurred along a transect. To define community types, a hierarchical, agglomerative, numerical clustering analysis based on Euclidean distances and Ward's method for determination of group linkages was used (McCune and Mefford 1999). The clustering analysis was applied to individual plots so that community definition was not constrained to spatial scales larger than the transect. Clustering was terminated when 75% of the total information in the species-by-plot matrix remained, where Wishart (1969) objective function was used to define information lost as agglomeration proceeded (McCune and Mefford 1999). At this level of information remaining, the relationship between information lost versus number of communities reached an asymptote, indicating a useful compromise between number of communities identified and information retained. The number of community transitions along a transect was calculated as the number of times the community type changed between two adjacent plots anywhere along the transect. For example, a string of plots identified as communities ABBCD would yield four communities and three

transitions. Following community classification, the aggregation of extremely low-biomass communities (dominated by bare soil and annual grasses; containing $< 40 \text{ g m}^{-2}$) within transects, and the aggregation of high-biomass communities ($> 170 \text{ g m}^{-2}$) within transects were analyzed.

The second method examined changes in proportional similarity (PS; Beals (1969)) among plots as a function of the distance separating those plots, where PS_{ij} is the sum of species abundances which plots i and j have in common, and PS for a given distance class is calculated as the mean PS of all plot pairs within the data set separated by that distance. For example, PS at a distance of 5 m was calculated as the mean PS of all plots within the data set separated by 5 m (in this case $46 \times 9 = 414$ pairs). This index varies from 0, if plot pairs have no species in common, to 1, if all plot pairs have identical species composition. PS at scales greater than 1 km was calculated using the species composition of the plot located at 25 m on each transect, and comparing this to the plot located at 25 m on other transects within the same grid (separation distances of 1–5 km) or in other grids (separation distances > 5 km). This method provides a single metric of similarity among plots in species composition which can be evaluated across all three spatial scales sampled in this study, and has been used recently to evaluate spatial patterns in the species diversity of tropical forests (Condit et al. 2002).

The third method examined the degree to which overall species diversity within a transect, measured as $H' = -\sum p_i \ln p_i$ (Whittaker 1972), was related to pattern diversity. Pattern diversity quantifies the magnitude of species turnover among plots within a sward, and is measured as $1 - PS$ (see definition of PS above). When evaluated at the level of a transect, $1-PS$ equals 1 if each of the 10 plots within the transect contain a completely different set of species, and 0 when the relative abundance of species is the same for all plots. In addition to conducting this analysis for Mpala, the same statistics were obtained for six other grasslands and savannas worldwide. Data were obtained from the literature for the Serengeti (McNaughton 1983), California grasslands (McNaughton 1968, 1983), and Cantabrian Mountains grasslands (Rodriguez and Gomez-Sal 1994). For these latter two sites, the correlation statistics were available, but not individual site means. Data for Yellowstone National Park grasslands were provided by D. A. Frank (pers. com.), and sampling methods were described by Frank and McNaughton (1991). Data for

Table 1. Means and coefficients of variation (CV) for herbaceous biomass at Mpala, Kenya. Within-transect CV was based on variation among the 10 plots within each transect, averaged across all 46 transects. Among-transect CV refers to variation in mean biomass among each of the 46 transects.

	Mean biomass (g m ⁻²)	CV
Within transects	109.6	0.869
Among transects	109.6	0.866
Mean and variation among transects within regions		
South (high rainfall)	171.2	0.482
Central (intermediate rainfall)	101.3	0.653
North (low rainfall)	72.6	0.261
Mean and variation among transects within topographic positions		
Ridge/upper hillslope	89.3	0.806
Lower hillslope/lowlands	141.1	0.695

Konza prairie were obtained from the LTER web site (<http://climate.konza.ksu.edu>) and all statistics reported here are for the 18 transects sampled during July, 1990, following methods described by Collins (1992). Data for grasslands in the Western Ghats of India were provided by M. Sankaran (pers. com.) following methods described by Sankaran (2001).

Soil analyses

All soil cores were oven dried at 60–80 °C for 36 h and passed through a 2-mm sieve prior to analysis. Water holding capacity of each core was determined for a 25-g subsample by adding 25 ml water and recording the percent drained by gravity after 30 min. Percent sand was measured for each core gravimetrically by sieving. A subsample of each core was returned to Syracuse University, oven-dried, and analyzed for total C and N by Dumas combustion with a Carlo-Erba Model 1500 (Carlo Erba Instruments, Milan, Italy).

Results

Herbaceous biomass and species composition

Mean herbaceous biomass declined from the mesic southern study area to the arid north ($F_{2,40} = 10.17$, $P = 0.0003$; Table 1). Biomass was also lower along upper hillslopes and ridgelines relative to lower hillslopes and lowlands ($F_{1,40} = 4.00$, $P = 0.05$; Table 1), with no interaction between topography and location along the rainfall gradient ($F_{2,40} = 2.42$, $P = 0.10$).

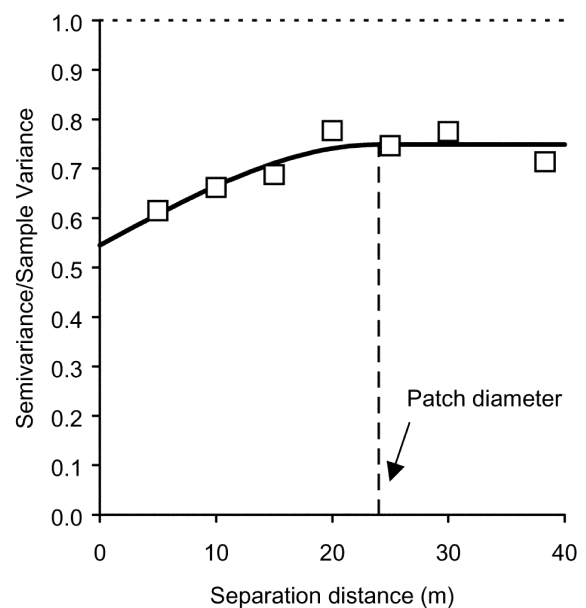


Figure 1. Semivariogram quantifying patchiness in the distribution of herbaceous biomass within transects at Mpala, Kenya. Semivariance reaches an asymptote, or sill, at 75% of sample variance with a mean patch diameter, or range, of 24.0 m.

However, variation in herbaceous biomass was as great within as among transects (Table 1). Variation among transects was lower when evaluated within upper vs. lower topographic positions and even lower for each of the three regions along the rainfall gradient, i.e. variation in biomass among transects was primarily associated with rainfall, and to a lesser degree with topography. Geostatistical analysis of biomass variation across scales of 5–40 m showed that semivariance is best fit by a spherical model, indicating that biomass is spatially structured at a scale of 5–25 m (Figure 1). Semivariance reached an asymptote or sill at 75% of total sample variance. Approximately 20% of total sample variation (sill – y-intercept = $0.75 - 0.55 = 0.20$) was explained by the presence of patches with a diameter of 24 m (Figure 1). The y-intercept indicates 55% of variation in biomass occurs at scales < 5 m and/or due to measurement error. The asymptote of 0.75 indicates that 25% of sample variance occurs at scales > 40 m, consistent with the significant landscape-scale variation across the rainfall gradient (Table 1).

Five perennial grass species and forbs dominated the understory layer (Table 2). Numerical clustering of all 460 plots identified 14 communities (Figure 2, Table 2). Six communities were dominated by a single perennial grass species (*Pennisetum stramineum*,

Pennisetum mezianum, *Cynodon dactylon*, *Enteropogon macrostachyus*, *Themeda triandra*, or *Chloris roxburghiana*) and one was dominated by herbaceous dicots. Plots dominated by the most common grass, *Digitaria milaniana*, were resolved into two clusters, one with high *Digitaria milaniana* abundance and the other with moderate *Digitaria milaniana* cover. One community was a mixture of perennial grasses including *Cymbopogon pospischilii*, *Harpachne schimperii*, *Eragrostis superba*, *Cenchrus ciliaris*, and *Bothriochloa insculpta*. One community consisted almost entirely of bare soil (proportional cover = 0.93), and three communities contained $\geq 25\%$ bare soil with either annual grasses (*Eragrostis papposa* or *Aristida* spp.) or a low-biomass mixture of dicots and grasses. Complete bare soil plots comprised 11.5% of the total sample, moderate bare soil plots 13.5%, and low-biomass annual communities 8.9% (33.9% combined), such that perennial grass cover is lacking from a significant portion of the landscape.

Spatial distribution of communities

A primary goal was to quantify the spatial heterogeneity of plant communities and bare soil across scales of 5 m–25 km. At scales of 5–45 m, the following were examined: (1) size of patches consisting of high and low biomass communities, and (2) local turnover of all communities within transects. Four communities identified in the clustering analysis were characterized by high cover (25–100%) of bare soil and extremely low herbaceous biomass ($< 40 \text{ g m}^{-2}$; Tables 2 and 3). Whenever these communities occurred within a transect, the mean number of adjacent bare-soil plots (separated by 5 m) was 2.0, i.e. mean patch size was $> 5 \text{ m}$ but $< 10 \text{ m}$. Bare-soil communities occurred more frequently and in larger patches at upper topographic positions (mean number of adjacent plots = 2.2) than lower topographic positions (mean = 1.8; $t_{44} = 2.21$, $P = 0.03$). Four high-biomass communities, all averaging $> 170 \text{ g m}^{-2}$ (Table 3), were identified in the clustering analysis. These communities were also aggregated within transects, with mean number of adjacent high-biomass plots equal to 2.0. No difference in mean patch size of high-biomass communities was observed at upper versus lower topographic positions ($t_{44} = 1.45$, $P = 0.15$). In other words, the landscape consisted of a discontinuous herbaceous layer, with high- and low-biomass communities aggregated in 5–10 m patches. Both patch

types contribute to the spatial structure identified by the geostatistical analysis (Figure 1).

Inspection of the distribution of all communities within transects showed extremely high local heterogeneity: the median number of communities per transect was five (out of a possible 10 if every plot was a different community in every transect), and ranged from two to eight. Furthermore, the median number of transitions from one community type to the next along a 50-m transect was seven (range two – nine). Thus, no transect consisted of a single community, and most transects encompassed significant local turnover in the dominant grass species. At the landscape scale, 12 of 14 communities were represented in the southern area, all 14 communities in the central area, and 13 of 14 communities in the north.

The analysis of proportional similarity among plots as a function of separation distance (Figure 3) clearly showed that most variation in species composition across the entire study area occurs within transects (5 – 45 m). Proportional similarity declined rapidly across separation distances of 5 – 45 m ($r^2 = 0.87$, $F_{1,7} = 45.2$, $P = 0.0002$), declined minimally across distances of 45 m–5 km ($r^2 = 0.59$, $F_{1,4} = 5.7$, $P = 0.07$), and then even increased slightly across distances of 5–23 km ($r^2 = 0.62$, $F_{1,4} = 6.59$, $P = 0.06$; Figure 3).

Analysis of factors contributing to variation in species diversity among transects also emphasized the importance of local patchiness in species distributions. Overall species diversity of a sward (H') was most highly correlated with pattern diversity ($r = 0.79$, $df = 44$, $P < 0.001$; Figure 4). H' was also correlated to a lesser degree with mean point richness of the 10 plots within each transect ($r = 0.62$, $df = 44$, $P < 0.001$). Furthermore, pattern diversity and point richness did not covary ($r = 0.19$, $df = 44$, $P = 0.20$) suggesting that both contributed independently to H' .

Mean pattern diversity was far greater at Mpala compared to four other savanna ecosystems for which similar measurements were available (Figure 5; $F_{4,215} = 23.63$, $P < 0.0001$ for one-way ANOVA; $P < 0.0001$ for all comparisons between Mpala and other systems by Tukey's honest significant difference, HSD). Konza prairie, Serengeti, and Yellowstone grasslands all showed similar levels of pattern diversity to one another (Tukey HSD, $P > 0.25$ for pairwise comparisons) and grasslands of the Western Ghats exhibited slightly lower pattern diversity than those of the Serengeti (Tukey HSD, $P = 0.018$).

Table 3. Mean topographic position, biomass, soil characteristics, and shrub cover for 14 communities at Mpala, Kenya, defined by numerical clustering analysis. Mean topographic position could potentially range from 1.0, for communities that occurred only along ridgelines, to 4.0 for communities that occurred exclusively at lowland positions. See Methods for further description of topographic position scores. WHC is water-holding capacity.

	Mean topographic position	Biomass (g m ⁻²)	Total soil N (%)	WHC (%)	Sand (%)	Shrub Cover (%)
Grand Mean		110	0.098	41.9	75.8	28
Community type						
<i>Aristida</i> – bare soil	2.0	36	0.067	34.7	77.6	20
<i>Cynodon</i>	2.1	172	0.077	39.5	73.9	19
<i>Eragrostis</i> – bare soil	2.2	27	0.088	39.5	72.4	20
Bare soil – complete	2.2	4	0.073	37.3	73.6	14
Bare soil – moderate	2.3	30	0.090	39.8	76.2	22
<i>Digitaria</i> – bare soil	2.3	114	0.095	41.0	76.9	44
<i>Themeda</i>	2.5	135	0.114	44.4	72.2	28
<i>Chloris</i>	2.5	45	ns ^a	ns	ns	20
Dicots – <i>Digitaria</i>	2.6	91	0.125	45.2	79.2	35
Mixed perennials	2.6	92	0.087	40.2	79.0	33
<i>Pennisetum stramineum</i>	2.6	248	0.123	49.6	73.2	36
<i>Enteropogon</i>	2.8	90	0.112	41.3	76.9	57
<i>Digitaria</i>	2.8	175	0.094	43.7	75.6	29
<i>Pennisetum mezianum</i>	3.5	296	0.196	54.1	75.2	27

^aNot sampled

Is the high contribution of within-sward spatial heterogeneity (pattern diversity) to overall sward diversity (H') at Mpala a consistent feature of savannas? Relationships among species diversity (H'), pattern diversity (1-PS), and point richness for seven grassland and savanna ecosystems worldwide indicate that it is not (Table 4). For Mpala, Konza and Serengeti, species diversity was more strongly correlated with pattern diversity than point richness. The opposite relationship was observed for grasslands in California and Spain, where species diversity was primarily associated with point richness (Table 4). Grasslands from the Western Ghats and Yellowstone fell between these two extremes: species diversity was nearly equally correlated with both pattern diversity and point richness.

Environmental correlates of community composition

All communities occurred at both upper and lower topographic positions, but communities dominated by annuals, bare soil and *Cynodon dactylon* were more frequent along ridgelines and upper hillslopes and were associated with lower water-holding capacity (WHC) and lower soil N (Table 3). Grasses occurring more frequently at lower topographic positions, especially *Pennisetum mezianum* but also *Digitaria milaniana* and *Enteropogon macrostachyus*, were associ-

ated with higher soil N and WHC. Soil texture, position along the rainfall gradient (metres north), and shrub cover were not correlated with topography, soil N, or WHC (Table 5). Total soil N closely reflected total soil C (soil C = $11.36 \times \text{soil N} + 0.014$; $r^2 = 0.96$ $F_{1,45} = 1181$, $P < 0.001$), reflecting a nearly constant C:N ratio across topographic positions. Despite the low covariance between shrub cover and soil N in terms of community means, there was a positive correlation between soil N and shrub cover of the plot where the core was collected ($r^2 = 0.15$, $F_{1,44} = 7.76$, $P = 0.008$) where mean predicted soil N was 0.086% for plots with no cover and 0.133% for plots with 100% cover. Plots dominated by *Enteropogon macrostachyus* were associated with high cover of shrub canopies compared with all other communities, while bare soil patches and annual grasses were associated with low shrub cover (Table 3).

Discussion

Distinct spatial patterns in savannas have been documented with aerial photographs or satellite imagery (Tongway et al. 2001), but few studies have quantified spatial heterogeneity across scales in terms of biomass or species composition (Collins 1992; Rietkirk et al. 2000). The combined analyses presented

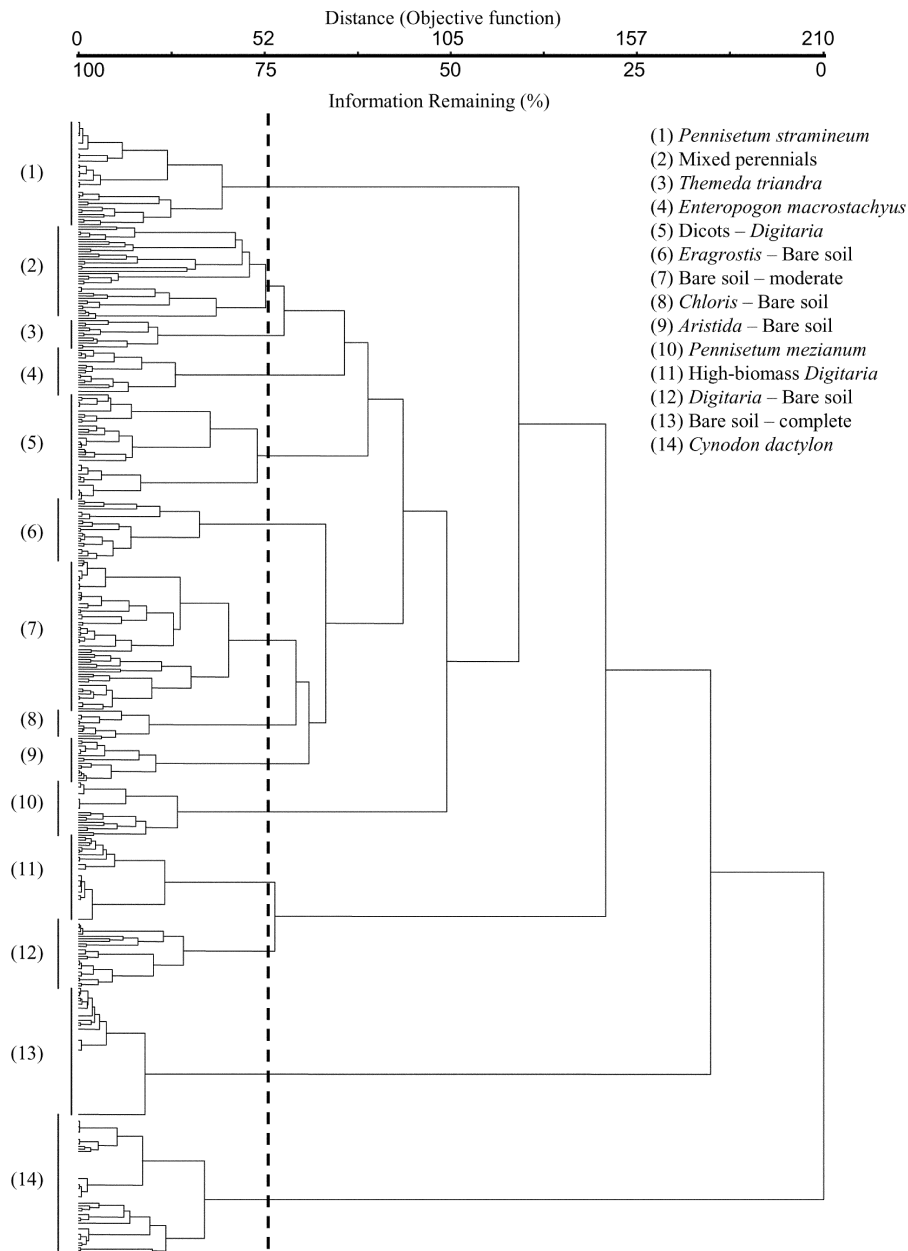


Figure 2. Dendrogram of 14 communities identified by a cluster analysis (Wishart's information measure) of all 460 plots sampled at Mpala, Kenya.

here lead to three general conclusions concerning spatial heterogeneity at Mpala. First, spatial variation in the distribution of both bare soil and grass species is greatest across scales of 5–45 m (Figures 1, 3 and 4). The herbaceous layer is a discontinuous mosaic characterized by 5–10 m diameter patches of high ($> 170 \text{ g m}^{-2}$) herbaceous biomass and 5–10 m diameter patches of bare soil, and the distribution of dominant

grass species is extremely variable across distances of only 5–45 m (Figures 3 and 4). Second, the distribution of bare soil and herb communities is associated to a lesser degree with topography, which in turn is correlated with soil N and water-holding capacity (Tables 3 and 5), demonstrating a second hierarchical level of spatial variation. Third, the least degree of variation in species composition was associated with

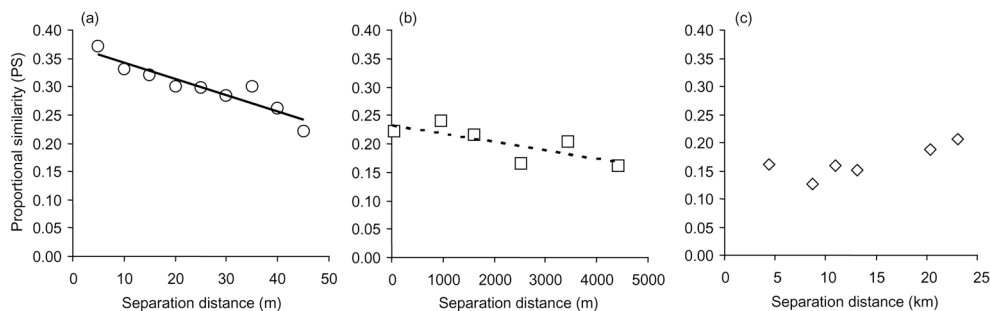


Figure 3. Changes in proportional similarity (PS) in species composition among plots as a function of the distance separating plots at Mpala, Kenya. Relationships are evaluated across separation distances of (a) 5–45 m, derived from variation among plots within transects, (b) distances of 45–5000 m, derived from variation among plots within regions, and (c) distances of 5–23 km, derived from variation among regions of Mpala.

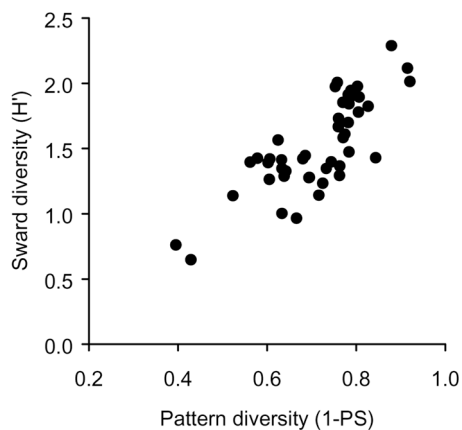


Figure 4. Relationship between sward diversity (H' , calculated from the species abundance values averaged across the 10 plots in each transect) versus pattern diversity (1-PS, calculated as the mean for all pairs of plots within each transect) at Mpala, Kenya ($n = 46$ transects).

the rainfall gradient, i.e. patterns in the local and topographic distribution of grass species and bare soil are repeated across the gradient.

The strong correlation between sward diversity and pattern diversity (Figure 4) demonstrates that patchiness within a sward and variation in species composition among patches, rather than diversity within plots, is a central feature of the herbaceous layer at Mpala. Pattern diversity was also the primary factor underlying sward diversity in Serengeti grasslands and Konza tallgrass prairie (Table 4). In sharp contrast, sward diversity in grasslands of California and the Cantabrian Mountains was correlated only with species richness within plots. These differences show that pattern diversity is not necessarily a determinant of sward diversity, and that within-sward patch structure varies greatly among sites. Pattern diversity at Mpala is also far higher than levels ob-

served in other savannas (Figure 5), reflecting the lack of evenly-distributed dominant grass species. Further comparison with community structure at Konza emphasizes this point: while each of the 18 swards at Konza contained one or more grass species that was present in all subplots per transect (Collins and Glenn 1990), not even one of the 46 transects measured at Mpala contained a species that was present in all subplots. These comparisons among systems spanning four continents and both tropical and temperate climates indicate that Mpala represents an extreme case of locally-structured heterogeneity. Clearly, identification of the factors responsible for such major differences in spatial structure among these savannas is necessary to understand their functional organization.

Potential determinants of spatial heterogeneity

Banded vegetation patterns have been documented in semi-arid regions worldwide, typically on gentle slopes where bare strips, which generate runoff as overland sheetflow, alternate with vegetated strips, which capture runoff (Tongway et al. 2001). Bare and vegetated strips are typically each 10–100 m in width (D'Herbes et al. 2001). Recent simulation analyses confirm that interactions between runoff, plant cover, and water infiltration are indeed capable of generating the conspicuous striped patterns observed in these systems (Klausmeier 1999).

The herbaceous mosaic documented at Mpala is irregular, containing bare patches within a highly heterogeneous background of grass species but no clearly banded pattern. Although runoff – runoff exchange between bare and vegetated patches may certainly play a role in the organization and maintenance

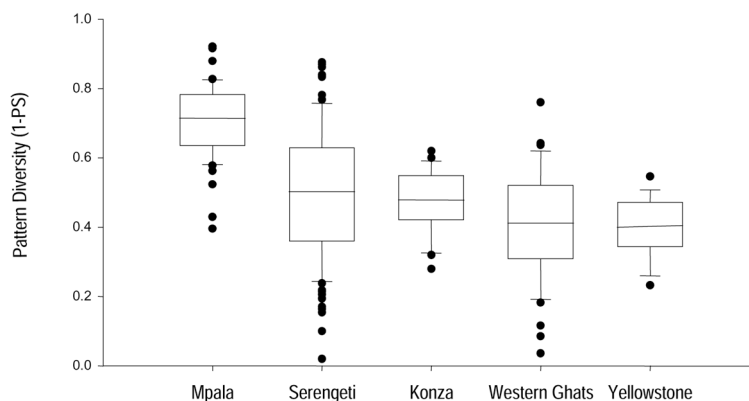


Figure 5. Boxplots of pattern diversity (1-PS) measured for Mpala, Kenya, and four other savannas for comparison, ordered by decreasing mean pattern diversity. Boxes show the mean and 25th and 75th percentiles, error bars show the 10th and 90th percentiles, and solid circles show outliers exceeding the 10th and 90th percentiles. Sample sizes are given in Table 4.

Table 4. Correlations between sward diversity (H'), pattern diversity (1-PS) and point richness (mean number of species per plot within a site) for 7 savanna and grassland sites. See text for data sources for each site.

Site	Country	Sample size (n)	H' vs (1-PS)		H' vs Point Richness	
			r	P	r	P
Mpala	Kenya	46	0.79	0.001	0.62	0.001
Konza prairie	USA	18	0.91	0.001	0.60	0.009
Serengeti	Tanzania	105	0.73	0.001	0.58	0.001
Western Ghats	India	40	0.73	0.001	0.80	0.001
Yellowstone	USA	11	0.77	0.006	0.87	0.001
Cantabrian Mtns	Spain	20	0.40	0.063	0.71	0.001
California	USA	6	NS	0.747	0.84	0.05

Table 5. Correlations (r) among environmental factors measured for each community type at Mpala, Kenya (see Table 4). WHC is water-holding capacity and 'metres north' is a measure of a plot's location along the rainfall gradient. Significant correlations at the $P \leq 0.05$ level are shown in boldface ($n = 46$).

	Topographic Position	Total Soil N (%)	WHC	Sand (%)	Shrub cover (%)
Metres north	-0.35	-0.26	-0.49	0.41	-0.28
Shrub cover (%)	0.41	0.30	0.28	0.40	
Sand (%)	0.12	-0.03	-0.15		
WHC	0.85	0.93			
Soil N (%)	0.89				

of the current landscape, it is hypothesized that other localized factors generate such a high degree of small-scale patch structure. Two factors which could strongly affect local patchiness in herb-layer communities are grazing by large herbivores (Bakker et al. 1983; Gibson 1988; Hiernaux 1998; Knapp et al. 1999; Gabriela et al. 2000) and shrub canopies (Georgiadis 1989; Belsky et al. 1989; Schlesinger et al. 1996; Reid et al. 1999), particularly if their influences interact. Work by Rietkirk et al. (2000) in a West African savanna documented 5–10 m diameter bare

patches, similar to those documented in this study, at intermediate levels of grazing impact, while fine-grained (0.5–2.8 m scale) patchiness occurred at low and high grazing impact. Large grazers forage heterogeneously at local scales, due to variation in the spatial distribution of forage quality and quantity and to feedbacks among animal behaviour, stocking rates, and forage regrowth patterns (Weber et al. 1998; Gabriela et al. 2000). Spatially variable grazing can reduce competitive interactions in grasslands (McNaughton 1983; Belsky 1992; Edwards et al. 2000;

van der Waal et al. 2000), and potentially prevent the expression of plant distribution patterns related to edaphic factors operating at larger spatial scales (Sala et al. 1986; Fuhlendorf and Smiens 1998). Ongoing studies show that grazing has a major influence on herbaceous biomass and productivity at Mpala (D.J. Augustine, unpubl. data) but long-term and large-scale studies are needed to address effects on spatial patterns.

In addition, shrubs cover more than a quarter of Mpala and clusters of small shrubs create patches of dense thorn cover that prevent grazing for several years until crown height increases. Patches of thorn cover are also commonly created when elephants feed from large shrubs, leaving broken stems strewn across the ground. Adler et al. (2001) outlined how patch grazing, which can be induced by shrub cover and other local deterrents to grazing, can amplify spatial heterogeneity in grasslands. Experiments are needed to confirm whether local grazing heterogeneity is indeed an important force underlying the high degree of small-scale patchiness documented for the herb layer.

Results from Mpala indicate that factors creating local patchiness also depend on topography. Grass species could obviously respond directly to changes in soil characteristics along topographic gradients (Schimel et al. 1985). However, topography could also indirectly mediate interactions at local scales, for example if lower water-holding capacity and soil N increases the susceptibility of ridgetop communities to grazing, or if grazing intensity varies with topography. This latter interpretation is consistent with the larger aggregation of bare soil and annual communities at upper compared to lower topographic positions.

If grazing can indeed play an important role in the spatial organization of savannas, why is pattern diversity lower in Serengeti, Konza, Yellowstone and the Western Ghats, all of which support significant populations of large grazers? Comparisons among systems suggest no simple correlate with pattern diversity. In Serengeti and Yellowstone, herbivore migrations lead to intense but short (pulsed) episodes of grazing on relatively nutrient-rich grasslands (Frank et al. 1998), which contrasts with the year-round grazing pressure at Mpala, Konza and the Western Ghats. In addition to grazing, fire is an important force at Konza Prairie and in the Western Ghats. At Konza, frequent fires reduce pattern diversity (Collins 1992), counteracting the positive effects of grazers on pattern diversity

(Knapp et al. 1999). In contrast, Mpala is underlain by nutrient-poor soils, the region is intensively grazed by resident herbivores, and fires are actively suppressed. These ecosystem-level differences suggest complex relationships among soils, grazing patterns, and fire could be related to the high level of pattern diversity and small-scale patch structure documented at Mpala. This hypothesis is consistent with studies from semi-arid landscapes in the southwestern US, where year-round grazing in the absence of fire has increased the spatial heterogeneity of soil resources and plant communities (Schlesinger et al. 1990, 1996).

Clearly, experimental studies are needed to test the relative importance of soils, runoff, plants, grazing pressure and fire in regulating the spatial structure of semi-arid landscapes, particularly where livestock grazing pressure is intense. At Mpala, one third of the landscape is composed of bare soil patches and annual communities with extremely low herb biomass and almost no useable forage for livestock or native grazers. At best, these areas represent a source of runoff to downslope grass patches that require runoff subsidies (Aguiar and Sala 1999). At worst, these areas could support productive perennial communities, but have been driven to an alternate stable state by grazing and the consequent loss of plant cover, organic inputs to the soil, and water infiltration capabilities (Rietkerk and van de Koppel 1997; Rietkerk et al. 1997). Greater understanding of factors responsible for the small-scale patch structure documented at Mpala will improve the ability of managers to influence the retention of surface runoff and nutrients within the vegetation (Ludwig and Tongway 1995; Reid et al. 1999), the resilience of ecosystems during drought (Rodriguez and Gomez-Sal 1994), and the productivity of rangelands for native and domestic herbivores.

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