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Tree spacing along the Kalahari transect in southern Africa

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Spatial pattern in tree distribution is examined at 10 sites along the IGBP Kalahari Transect in southern Africa in order to examine the patterns of community structure across a large average annual rainfall gradient. Analysis indicates aggregation among all individuals in the vegetation communities at most sites, with no occurrence of aggregation in individuals at the most southern arid site. The spatial distribution for the largest 25% of individuals is predominantly random. Uniform pattern is only observed in the distribution of canopy dominants at one site. A comparison between expected and observed densities of understory vegetation beneath large trees shows significant patterns at six of ten sites, with lower than expected values at both the northern and southernmost sites in the transect, and significantly higher than expected values at intermediate sites. Variation in the spatial distribution of understory individuals with respect to larger canopy individuals suggests that distribution of suitable regeneration sites and subsequent patterns of establishment may be critical phenomena in determining the spatial pattern of vegetation.

Keywords: spatial pattern°, savanna°, rainfall gradient°, Ripley's K°, Monte Carlo

Introduction

Pattern and process in savanna communities

The idea that ecological processes are evident in vegetation patterns, first formalized by Watt (1947), has been used to investigate the nature of competition, disturbance and resource heterogeneity across a range of ecosystems. The classification of spatial pattern can be thought of as a continuum moving from highly aggregated communities to regularly spaced or hyper-dispersed communities, with random distribution patterns occupying the middle of the continuum (i.e. showing no effect of either pattern). The presence of a particular pattern is often associated with the operation of ecosystem-specific processes that serve to structure the community in a non-random manner (Dale, 1999).

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The presence of hyper-dispersed community patterns has been explained as the result of density-dependent mortality associated with competition for a homogeneously distributed resource (Beals, 1968). In contrast, the observation of clumping in savanna ecosystems has been associated with high rates of disturbance or the presence of nurse sites for seedling establishment (Raffaele & Veblen, 1998). In particular, it has been hypothesized that clumping in savanna communities is a response to high fire disturbance, as vegetation in the centers of clumps tends to persist after a fire (Gignoux *et al.*, 1995). It is important to realize that regardless of the particular pattern found, the observation of pattern itself cannot elucidate the process of cause without appropriate experimental manipulation of the community under investigation (Cale *et al.*, 1989). Regardless, the observation of a particular pattern serves to establish the presence of non-random structuring mechanisms within a community and to indicate the direction in which experimental investigations should proceed.

Previous work

The low density and seemingly uniform spacing of woody vegetation in many arid systems has fostered the hypothesis that individuals in savanna communities exhibit a high degree of competitive exclusion. Consequently, there have been a variety of studies investigating the spatial pattern of woody vegetation, many of these focusing on the interaction between species pairs using nearest-neighbor techniques (Pielou, 1962). Work in the Mojave and Sonoran deserts (Yeaton & Cody, 1976; Yeaton *et al.*, 1977) shows size-dependent species dispersion patterns between *Yucca schidigera, Opuntia acanthocarpa* and *O. ramosissima.* Cody (1986) found that levels of positive and negative associations in nearest-neighbor distance were species dependent for a range of woody shrubs in a diverse Mojave Desert community. These patterns were attributed to differences in root system structure and germination requirements. In southern Africa, Smith & Goodman (1987) explored spacing relationships between *Acacia nilotica* and *Euclea divinorum* in the Mkuzi Game Reserve (27°30′–27°45′S, 32°05′–32°25′E), South Africa. Their work showed a clear size-dependent nearest-neighbor exclusion pattern in mature *Acacia* individuals and understory *Euclea*, supporting the hypothesis of density-dependent spatial regulation of water-limited savanna systems.

In addition to nearest-neighbor analysis, the spatial pattern of a community can be examined across a range of spatial scales, and therefore provide a more comprehensive picture of vegetation pattern at a site (Clark & Evans, 1954; Ripley, 1977). In their work, Phillips & MacMahon (1981) found numerous instances of aggregated dispersion patterns for saplings of 11 different species in nine different sites across the same region, with little tendency for larger individuals to form aggregated dispersion patterns. The tendency for individuals to change from aggregated to random and occasionally uniform distributions with increasing size (and decreasing density) was taken as evidence of density-dependent mortality associated with the homogeneous distribution of soil moisture in a moisture-limited environment. Skarpe (1991) investigated the dispersion of *A. erioloba* and *A. mellifera* in both mono-specific and mixed plots near Naojane, Botswana, and found a tendency for saplings of both species to exhibit aggregated distributions. Mature individuals in her plots exhibited a random spatial distribution. More recently, Jeltsch *et al.* (1999) used aerial photography to examine vegetation patterns in the Kalahari Gemsbok Park in southern Botswana. They found patterns that were generally aggregated at four out of six study sites, and random at the other two. Both Skarpe and Jeltsch's sites were located in the southern portion of the Kalahari desert. This study builds on these results by examining community-level spatial patterns in the context of a large annual rainfall gradient. Using a series of ten sites occurring on Kalahari sands from western Zambia to South Africa, the spatial pattern of vegetation communities is examined across a wide range in mean annual rainfall.

Kalahari Transect description

The distribution of Kalahari sands occupies a third of southern Africa (Scholes & Parsons, 1997). Fig. 1 indicates the extent of Kalahari sands in the region, as well as the location of the research sites included in this study. These sites are located within the Kalahari Transect, one of a number of IGBP transects designated throughout the

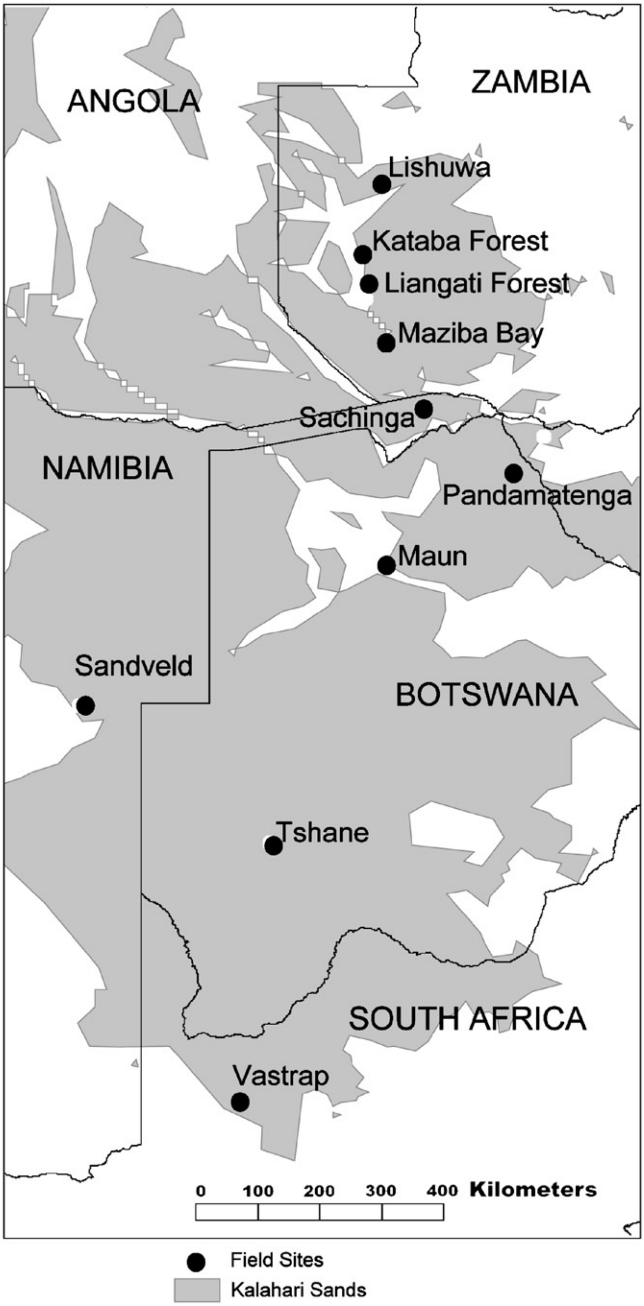

Figure 1. Location of research sites included in the study.

Table 1. *Basic site information for research sites along the Kalahari Transect. See Scholes et al. (in press) for detailed site descriptions and vegetation type classifications*

Site	Latitude	Longitude	Vegetation type	Annual Precip(mm)[*]	Coeff. of variability in annual precip[†]	Tree density (ind/ha)[‡]	Canopy height (m)[§]	% Cover	Plot dimensions
Lishuwa Communal Forest Lukulu, Zambia	14·42S	23·52E	Evergreen woodland	970	0·18	2284	9·9	84·4	50 m × 50 m
Kataba Forest Reserve Mongu, Zambia	15·44S	23·25E	Kalahari woodland	879	0·18	972	11·7	64·8	50 m × 50 m
Liangati Forest Reserve Senanga, Zambia	15·86S	23·34E	Kalahari woodland	811	0·16	460	18·0	53·7	50 m × 100 m
Maziba Bay Forest Sioma, Zambia	16·75S	23·61E	Dry Kalahari woodland	737	0·18	843	15·0	61·0	100 m × 100 m
Sachinga Agricultural Station Katima Mulilo, Namibia	17·70S	24·08E	Combretum woodland	707	0·21	169	13·8	29·9	100 m × 100 m
Pandamatenga Agricultural Station Pandamatenga, Botswana	18·66S	25·50E	Schinziophyton, Baikiaea, Burkea woodland	698	0·23	434	11·8	32·3	50 m × 100 m

Harry Oppenheimer Okavango Research Centre Maun, Botswana	19·93S	23·59E	Mopane woodland	460	0·29	968	7·6	36·1	50 m × 50 m
Sandveld Research Station Gobabis, Namibia	22·02S	19·17E	Acacia-Terminalia woodland	409	0·35	975	5·2	19·1	100 m × 100 m
Tshane Tshane, Botswana	24·17S	21·89E	Open Acacia savanna	365	0·20	181	7·0	13·8	100 m × 100 m
Vastrap Weapons Range Upington, South Africa	27·75S	21·42E	Open Acacia shrubland	216	0·43	287	2·0	5·8	100 m × 100 m

[*] Annual precipitation derived from station data. Station information provided in Scholes *et al.* (in press).

[†] Coefficient of variability in annual precipitation determined using long-term data reported in New *et al.* (1999).

[‡] Tree density scaled to individuals/ha dependent on plot size.

[§] Canopy height taken as average height of tallest 10% woody individuals at each site.

world (Koch *et al.*, 1995). The transect covers a latitudinal rainfall gradient varying from 250 mm year^{-1} in the south to 1000 mm year^{-1} in the north. Although low-frequency periodicities in annual rainfall have been observed for most of southern Africa (Tyson, 1986), rainfall events in the Kalahari are largely convective, and locations throughout the Kalahari Transect experience large variability in inter-annual rainfall amounts. The coefficient of variability in annual rainfall for the 20th century ranges from a minimum of 16% in the north to over 40% at the transect's southern extreme (Table 1). The large gradient in both the mean and variation of annual rainfall results in dramatic changes in vegetation structure along the transect. Vegetation type ranges from partially closed woodlands in the north to open shrub land in the south (Table 1). Throughout the transect, the mixed life-form composition characteristic of savanna communities is maintained. The consistency in geomorphology over the entire region (primarily deep Kalahari sands) allows for an analysis of vegetation structure and ecosystem processes independent of soil type (Thomas & Shaw, 1991). Sand depth varies widely across the extent of the Kalahari sand sheet, from 10 to 100+ m (Thomas & Shaw, 1991), and depth to bedrock has been shown to play an important role in controlling species distribution and vegetation structure (Moore & Attwell, 1999). In order to take these considerations into account, site locations were chosen to be in areas without access to shallow water tables or near-surface bedrock, making ground-water availability of secondary importance to rainfall when considering vegetation structure. An important exception to the geologic uniformity of the region is the area around the Okavango Delta, where the occurrence of near-surface impermeable zones associated with duplex soils causes dramatically different drainage properties (Cole & Brown, 1976). This area is notable for the dominance of *Colophospermum mopane*, which forms nearly mono-specific stands where these impermeable layers are extensive (Timberlake, 1995).

Methods

Data collection

Stem maps were generated at ten sites along the Kalahari Transect. Site locations and summaries are provided in Table 1. Detailed methodology, site descriptions and criterion for site selection are provided in Scholes *et al.* (in press). A belt-transect approach was used for stem mapping, with belt width determined by stem density within a plot. Plot dimensions and stem densities are provided in Table 1. Tree location, species, diameter, height and major and minor axis of crown dimensions were measured for each individual taller than 1·5 m. At the southernmost site, the height limit on sampling was relaxed and all woody vegetation was included in the stem map. For multi-stemmed individuals, the diameter of each stem was recorded separately. Individual locations were determined to be the center of the main stem, or the estimated center when multiple-stemmed individuals were sampled. Canopy area was calculated to be an ellipse defined by the two major axes of measurement. Canopy height was estimated using a clinometer.

Canopy spatial pattern

The interpretation of spatial pattern in a particular vegetation community necessarily depends on an understanding of how the observed pattern differs from the null hypothesis of complete spatial randomness. For a given number of isotropic events (i.e. individual plants) n within a region D containing an area of a, the first moment—λ, or intensity of individuals is estimated as

$$\lambda = \frac{n}{a} \qquad \text{(Eqn.1)}$$

The second moment is defined as the number of expected individuals within some distance t of a particular point, given by $\lambda K(t)$. It can be shown that the expected number of individuals within some length scale distributed according to a Poisson process of complete spatial randomness is determined by the following function:

$$K(t) = \pi t^2 \qquad \text{(Eqn. 2)}$$

Equation (2) is known as the uni-variate Ripley's K-function (Ripley, 1977). To facilitate the interpretation of these data, Eqn (1) is transformed into the following function:

$$L(t) = \sqrt{\frac{K(t)}{\pi}} - t \qquad \text{(Eqn. 3)}$$

Equation (3) is known as the L-function and has a distribution such that under conditions of complete spatial randomness $L(t) = 0$ for all length scales. Since Eqn (3) is only valid for individuals distributed under an ideal Poisson process, it is necessary to compare results at each field site with the results of multiple simulated calculations using the same density of individuals distributed randomly in an identically sized sample area. Equation (2) is solved for a particular set of actual data by summing all neighbors within radius t of each individual. Since there will be unobserved neighbors at some search distance that lie outside the sample area, an edge correction strategy is necessary. A number of edge-correction algorithms have been developed to allow unbiased estimates of $K(t)$ for individuals near plot boundaries (Haase, 1995). Here we use the weighted edge correction technique described in Ripley (1977). If a portion of the circle defined by radius t is outside the plot, the fraction $p(x,y)$ of the circle within the plot is used to weight the count of events. Therefore, the true count of each sampled point within the search radius is $1/p(x,y)$, a method that accounts for points contained outside the plot while still maintaining the spatial pattern observed within the plot. This algorithm allows unbiased estimates of Eq (2) up to one-half the minor axis of the plot dimensions. For this analysis, the length scale varied from 25 to 50 m, depending on plot size (Table 1). The average edge-corrected value for all points at each distance scale t is taken as the estimated K-function, $\overline{K}(t)$:

$$\overline{K}(t) = \frac{a}{n^2} \sum_{x \varepsilon D, d(x,y) \leqslant} \frac{1}{p(x,y)} \qquad \text{(Eqn. 4)}$$

Equation (4) can be transformed according to Eqn (3), defining $\overline{L}(t)$:

$$\overline{L}(t) = \sqrt{\frac{\overline{K}(t)}{\pi}} - t \qquad \text{(Eqn. 5)}$$

Equation (5) allows the generation of calculated $L(t)$ values at every distance t for a set of n simulated points distributed in a region of known area. The use of sufficient simulations allows for minimum ($L_{\mathrm{MIN}}(t)$) and maximum ($L_{\mathrm{MAX}}(t)$) thresholds to be put on the expected values of Eqn (3) for any distance within the plot. Values of $L(t)$ calculated for the actual distribution of individuals sampled in the field plot ($L_{\mathrm{OBS}}(t)$) can then be compared to these thresholds to determine the significance of observed distribution patterns in the sampled data. Since the L-function is essentially a measure of the deviation between the number of observed events and the expected deviation under complete spatial randomness, values of $L_{\mathrm{OBS}}(t)$ greater than $L_{\mathrm{MAX}}(t)$ indicate significantly clumped or aggregated patterns within the plot, and values of $L_{\mathrm{OBS}}(t)$ less than $L_{\mathrm{MIN}}(t)$ indicate significantly uniform or hyper-dispersed patterns. Values of L_{OBS} falling between $L_{\mathrm{MAX}}(t)$ and $L_{\mathrm{MIN}}(t)$ indicate random distributions. The interpretation of $L_{\mathrm{OBS}}(t)$ is summarized in Table 2.

Table 2. *Summary of spatial patterns derived from L-function analysis*

Condition	Spatial pattern
$L_{\mathrm{OBS}}(t) > L_{\mathrm{MAX}}(t)$	Aggregated, clumped
$L_{\mathrm{MAX}}(t) < L_{\mathrm{OBS}}(t) > L_{\mathrm{MIN}}(t)$	Random
$L_{\mathrm{OBS}}(t) < L_{\mathrm{MIN}}(t)$	Uniform, hyper-dispersed

Using this technique, it is possible to determine the character of spatial pattern within each site. Furthermore, subsets of community data based on vegetation characteristics can be analysed to examine the distribution patterns peculiar to that population. Care should be taken when forming these subsets, as pattern may be the result of interactions between events not contained within the subset itself. For example, in this study $L(t)$ functions are not determined for small-size classes of individuals (e.g. saplings and seedlings), due to the high possibility of asymmetric effects between large and small individuals, which cannot be detected using a univariate K-function operating on small individuals' distribution only (Keddy, 1989). In this analysis, L-functions are derived for both the entire community and the largest 25% of trees with respect to crown area. The 25% threshold is adopted to provide a consistent methodology for determining dominant status across a wide range of individual canopy sizes between sites. L-functions derived from field data are compared to 1000 random distributions for each plot. Actual $L(t)$ values are compared to 95% confidence intervals for maximum and minimum $L(t)$ derived from the simulations in order to test for significant departures in dispersion patterns.

Understory distribution

A series of Monte Carlo simulations are conducted in order to investigate the effect of large trees on the clumping behavior of sub-dominant trees along the transect. At each site, we determine the region delineated by the crowns of the largest 25% trees with respect to canopy cover. The number of trees found within the total projected area of canopy dominants is determined for each site. Overlap between adjoining dominant trees is not considered when counting sub-canopy trees, so trees found under the canopies of multiple dominants are only summed once. The expected distribution of sub-canopy trees with respect to dominant tree crowns is calculated using 4000 Monte Carlo simulations of tree distribution at each site. The observed value of site level sub-canopy density is compared to this distribution to test for the significance of the observed pattern in tree distribution at each site (Fig. 2). Observed values less than the Monte Carlo mean indicate a lower number of trees under large trees than expected by chance. Values larger than the Monte Carlo mean indicate higher numbers of sub-canopy trees under large canopy trees than expected by chance. The significance of departure from the expected value is determined using the mean and standard deviation in simulated under-story density, and the normal distribution function.

Results

Canopy spatial pattern

All individuals

Figure 3 depicts the L-functions for the ten sites along the transect. When considering the spatial distribution of all individuals, all ten of the plots exhibited significantly

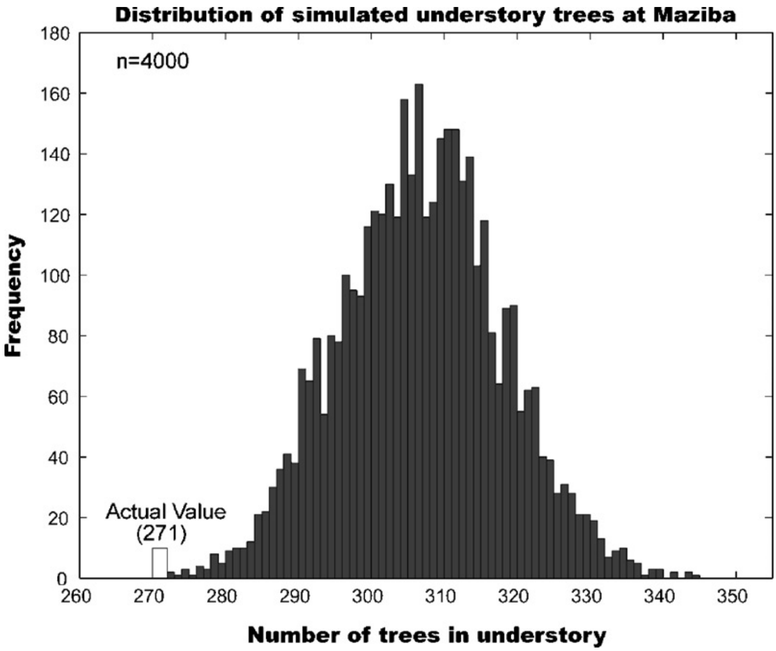

Figure 2. Simulated distribution of understory trees, and actual number observed at Maziba ($n = 4000$, $\mu = 307$, $\sigma = 11{\cdot}0$, $p < 0{\cdot}001$).

non-random distribution patterns at some distance scale. At five of the ten sites, these patterns were persistent across all distances. Aggregated patterns were found at all sites except the southernmost (Vastrap), with five sites (Lishuwa, Maziba, Pandamatenga, Maun and Sandveld) showing significantly aggregated distributions at almost all spatial scales. Uniform patterns at the community level were not observed at any sites (Fig. 4).

Canopy dominant individuals

Figure 5 depicts the L-functions for the largest 25% individuals with respect to canopy area at the ten sites along the transect. The pattern of canopy-dominant trees was predominately random at all sites except Pandamatenga and Sandveld where aggregated patterns were observed at many spatial scales. In contrast to the analysis using all individuals, uniform patterns were observed at some spatial scales for canopy-dominant individuals at Maun (Fig. 6).

Understory distribution

The distribution of understory trees in relation to the projected area of canopy dominant trees was significantly different than the expected density in six of ten plots along the transect (Fig. 7). At the wetter northern end of the transect, understory trees were under-represented beneath large canopy trees. Of the northern five sites, three—Kataba, Liangati and Maziba—exhibited a highly significant negative deviation in number of understory trees ($\mu = 131$, $\sigma = 3{\cdot}9$, $p < 0{\cdot}001$; $\mu = 78$, $\sigma = 7{\cdot}0$, $p < {\cdot}05$; $\mu = 307$, $\sigma = 11{\cdot}0$, $p < 0{\cdot}001$, respectively). Significantly lower understory

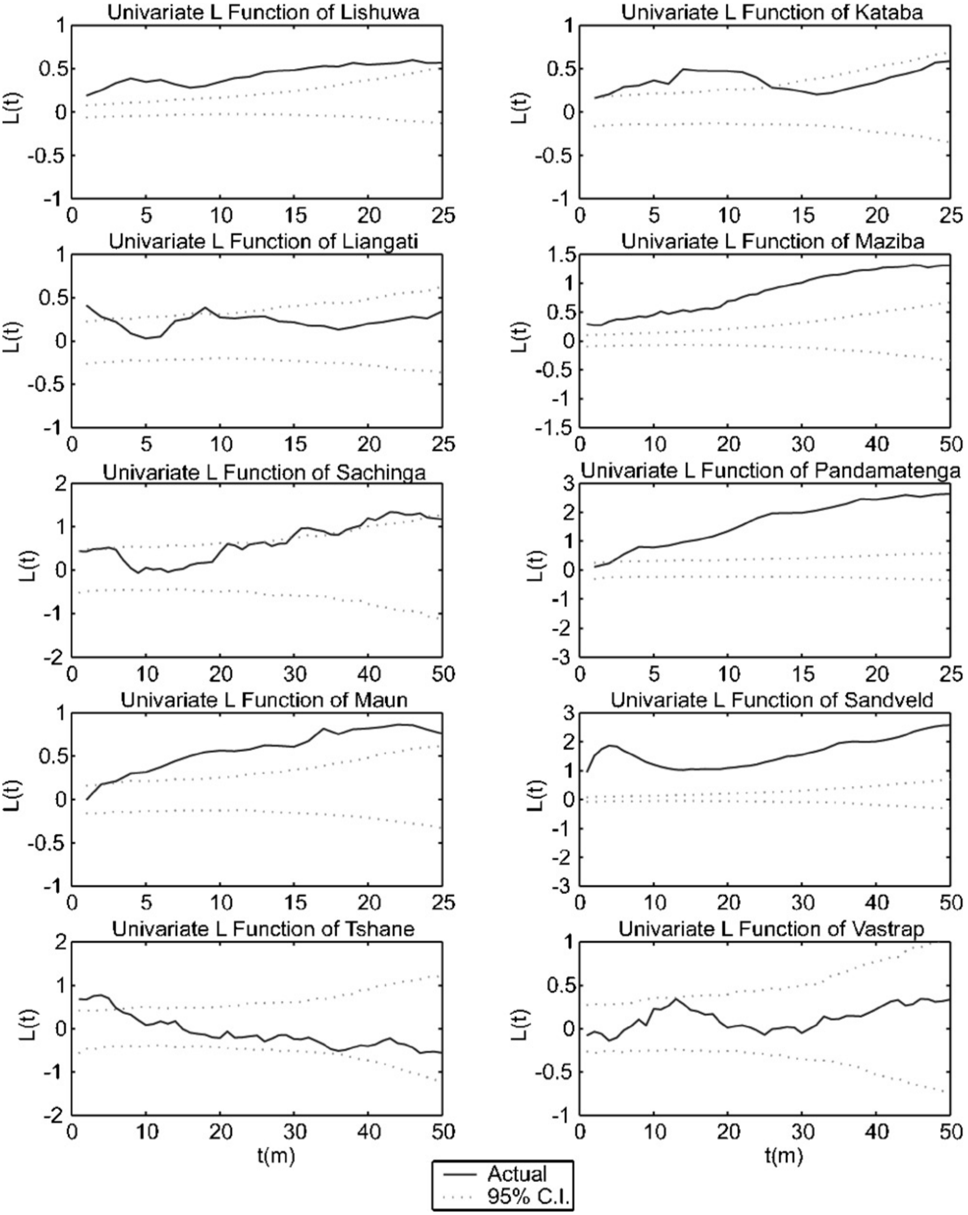

Figure 3. Community-wide spatial pattern for all research sites. Values larger than L_{MAX} indicate significant aggregation and values smaller than L_{MIN} represent significantly uniform distributions at each length scale.

density was also found at the extreme dry end of the transect at Vastrap ($\mu = 7{\cdot}3$, $\sigma = 2{\cdot}6$, $p < 0{\cdot}05$). In contrast, intermediate sites (Pandamatenga, Maun, Sandveld and Tshane) exhibited clumping of understory individuals beneath the canopy of dominant trees, with significant patterns observed at both Sandveld and Tshane ($\mu = 94$, $\sigma = 8{\cdot}7$, $p < 0{\cdot}001$; $\mu = 8$, $\sigma = 2{\cdot}6$, $p < 0{\cdot}01$, respectively). Taken as a whole, the results demonstrate clear shifts in the locations of understory individuals with respect to canopy individuals at sites across the rainfall gradient. The possible mechanisms leading to these patterns are discussed below.

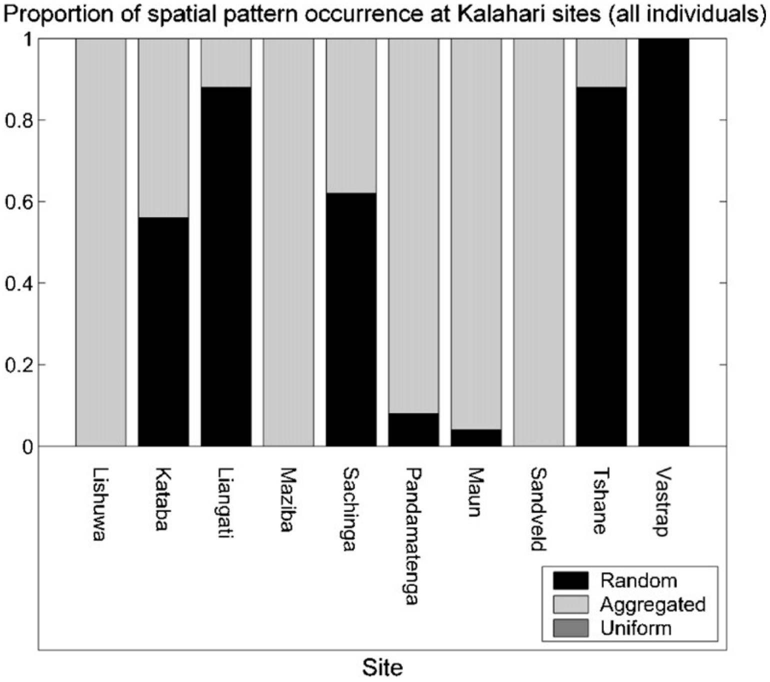

Figure 4. Summary of community-wide spatial pattern occurrence for all sites.

Discussion

From the preceding analysis, it is apparent that uniform vegetation patterns occur very rarely in the Kalahari transect sites (Fig. 4), and there is no clear tendency for larger individuals to form uniformly distributed patterns, except at the Maun site (Fig. 6). Instead, large individuals exhibit a generally random distribution, while the community as a whole tends towards an aggregated distribution. This pattern would suggest that small individuals are more aggregated than large individuals across all sites along the transect. These findings are in general agreement with that of Jeltsch in the Kalahari-Gemsbok National Park in southern Botswana (Jeltsch *et al.*, 1999), and Skarpe in the Naojane region (Skarpe, 1991).

The patterns observed in previous analyses of spatial pattern in arid communities of southern Africa are the same as the results of the current study—community patterns are often aggregated for small individuals and often random for large individuals. In the interpretation of these patterns, it is critical to consider that the detection of a random pattern in large individuals does not indicate a tendency towards becoming uniform any more than it indicates a tendency towards becoming clumped. Therefore, it is our opinion that the observation of uniform spacing patterns in savannas is a much mentioned but rarely observed phenomenon—and we believe that this observation must cast doubt on the premise that density-dependent effects are the dominant structuring mechanisms in the spatial pattern of savanna communities.

The random distribution of large trees in the present study provides evidence for strong competitive effects between large trees at only the Maun site, a mono-specific stand of *Colophospermum mopane*. In light of these findings, we believe that the aggregation of small individuals and the random distribution of large individuals is a pattern consistent with the hypothesis that competition for regeneration sites is an

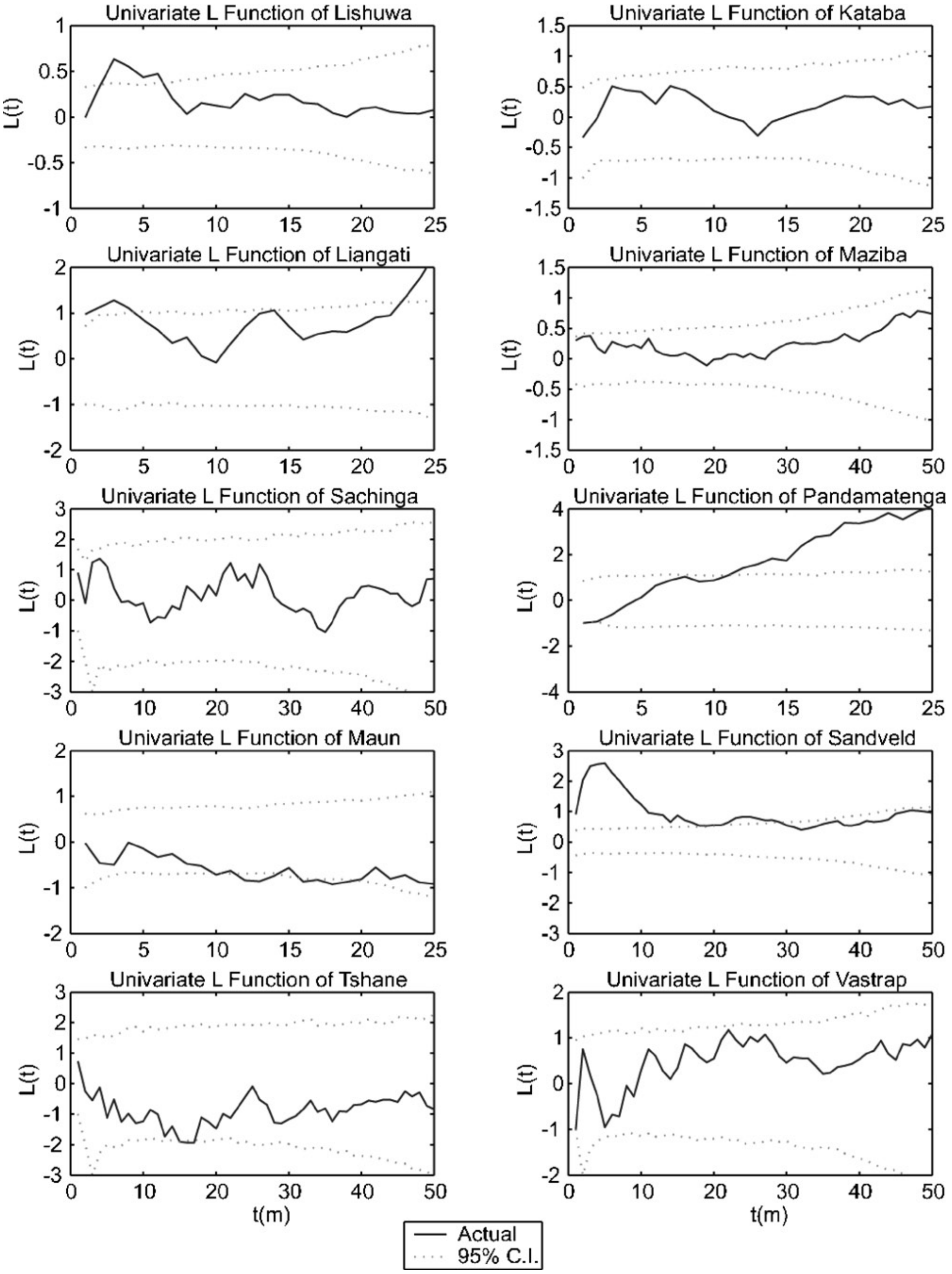

Figure 5. Spatial pattern for individuals with top 25% canopy area for all research sites. Values larger than L_{MAX} indicate significant aggregation and values smaller than L_{MIN} represent significantly uniform distributions at each length scale.

important process in savanna systems. Under such a model of spatial dynamics, clumping of small individuals will occur where sites are optimal for regeneration. Establishment of individuals into larger size classes will then be a spatially random process that arises out of the distribution of regeneration sites.

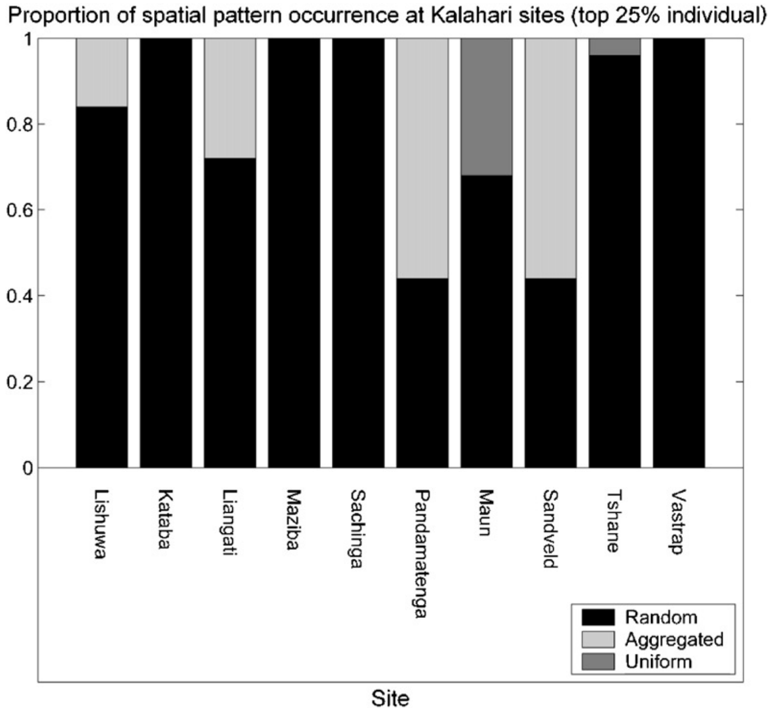

Figure 6. Summary of spatial pattern for dominant individuals (top 25% with respect to canopy area) for all sites.

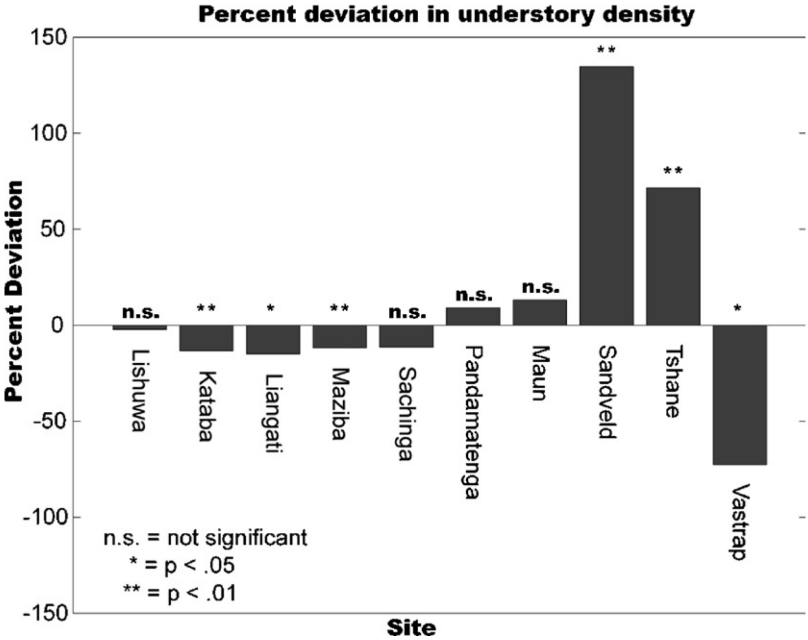

Figure 7. Deviation between expected number of understory individuals and observed number of understory individuals for each site. Negative values indicate less small tress under dominant (top 25% with respect to area) individuals than expected, positive values indicate more small trees under dominant individuals than expected.

The distribution of understory trees provides a glimpse into the changing nature of regeneration and establishment along the transect. A variety of mechanisms could explain the tendency for small individuals to exhibit non-random distributions with respect to large canopies across sites. Disturbance history (Adamoli *et al.*, 1990), herbivory (Janzen, 1970), nutrient availability (Belsky *et al.*, 1989; Blackmore *et al.*, 1990) and the particular species community (Smith & Goodman, 1987) could all be factors in determining the strong patterns exhibited. In addition, although the transect represents a physical gradient of water availability, there is also a strong gradient in canopy coverage (Table 1), and therefore changes in the light environment for understory plants along the transect. Increased rainfall at northern sites may be sufficient to provide a more stable moisture supply from year to year, as greater levels of residual soil moisture remains in the soil column at depth. This may explain the tendency for smaller individuals to be dispersed away from large canopies in the northern sites, where rainfall and soil moisture are less limiting to plant function, but canopy coverage is higher and sub-canopy light availability lower. Conversely, at the southernmost end, the lack of smaller individuals under canopy dominants is probably a result of limited water supply forcing individuals to disperse away from each other, and of the generally lower densities of individuals observed in these sites. In contrast to northern sites with greater canopy density, and the southernmost site which has extremely sparse vegetation, sites in the central Kalahari (Maun, Sandveld and Tshane) retain an intermediate canopy cover of 14–36% (Table 1) despite highly variable annual rainfall in the range 360–460 mm. In these patchy but structured canopies, large shade trees may represent an environment in which the improved water relations associated with reduced evaporative demand may offset the increased competition for existing resources and reduced light levels, particularly during periods of moisture stress (Belsky, 1994).

Although the spatial patterns of vegetation structure showed no clear trend with either rainfall or canopy coverage along the transect, it is clear that they are important factors affecting the structure of these communities. The snapshots obtained through field data collection must be supplemented by historical information regarding land tenure, disturbance and recent climatic variation. Even then, it is likely that the particular processes that govern pattern will vary along the transect, making a comprehensive assessment of pattern and process difficult over this gradient. The lack of uniform spacing in dominant individuals across the range of sites calls into question the idea of density-dependent processes as a means for determining vegetation structure in these systems. Indeed, the high degree of significant variation in the spatial distribution of small individuals with respect to large canopy individuals suggests that distribution of suitable regeneration sites and subsequent patterns of establishment may be critical phenomena in determining the spatial pattern of vegetation, and could provide new models for the dynamics of vegetation structure and pattern in the Kalahari region of southern Africa.

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