Spatial patterns in species-rich sclerophyll shrublands of southwestern Australia

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Abstract

Question: The drivers of spatial patterning among plant species and the implications of those patterns for the structure and function of plant communities are of ongoing interest and debate. Here we explore the spatial patterning shown by individual species in species-rich plant communities. We (1) compare the levels of aggregation in these communities to those observed in other species-rich communities, in particular tropical rain forests, and (2) consider how abiotic conditions might influence the levels of aggregation observed.

Location: We describe the spatial structure of four species-rich Mediterranean-type shrubland communities near Eneabba, Western Australia. The four sites each contain > 10 000 plants and up to 113 species, and differ in substrate-type, species richness and composition.

Methods: We analysed the spatial patterning of all species with more than 20 individuals (233 species patterns), and used point process models for aggregated patterns to separate first-order gradient effects from second-order clustering.

Results: Aggregated distributions were most common at all sites, but especially at the site with the highest resource availability and heterogeneity and lowest species richness. A Poisson cluster process best described the majority of aggregated species, suggesting that local interactions drive fine-scale patterns in these communities.

Conclusions: As with many previous studies, we found that most species showed strong local aggregation. The proportion of species showing aggregation was less than has been described in species-rich tropical rainforests but was higher than observed in many temperate plant communities. The highest proportion of aggregated species was seen at the most resource-abundant site; this is in direct contrast to conceptual models that suggest that competition should be weakest, and aggregation most prevalent, in the most resource-limited sites.

Keywords: Aggregation; Point process model; Soil nutrients; Species richness.

Abbreviations: CAI = Community Aggregation Index; CvM = Cramer von Mises; CSR = Complete spatial randomness; HPP = Homogeneous Poisson process; IPP = Inhomogeneous Poisson process; PCF = Pair corelation function; PCP = Poisson cluster process; TRF = Tropical rain forest.

Introduction

Spatial pattern is playing an increasing role in contemporary theoretical ecology: e.g. as a determinant of competitive interactions, patterns of species diversity, and species-area relationships. Arguments drawn from observed spatial patterns are employed by both sides of the current neutral theory debate, and spatial pattern may provide empirical data relevant to its determination (Holyoak & Loreau 2006). Interest in spatial pattern in plant communities has also heightened with the development and spread of improved analytical methods of spatial analysis (Fortin & Dale 2005).

Spatial pattern in the fine-scale distribution of individuals within and among species is quantified as deviation from randomness towards aggregation or segregation (or regularity) at a given scale. Typically, plant communities include some species with distributions that are indistinguishable from random, most species are aggregated and a small minority show a regular distribution. Segregation of conspecifics has been observed for shrubs in some semi-arid and arid ecosystems (e.g. Phillips & MacMahon 1981; Schenk et al. 2003). Janzen (1970) proposed that a regular distribution of individuals facilitates species co-existence in tropical rain forest (TRF) communities, although field and experimental evidence for this is equivocal (Hyatt et al. 2003).

Observed aggregation can arise from either the first-order (gradient) or second-order (true clustering) properties of the pattern, or a combination of the two (Cressie 1993; Diggle 2003). Operationally, these two types of aggregation may be described as large and small-scale spatial trends. First-order aggregation arises from variation in the density (or intensity) of stems across the mapped community; it is essentially of abiotic origin (e.g. in response to a gradient of soil conditions) and does not imply interactions between the stems (points). Conversely, second-order aggregation results from interactions between individuals, and could be biotic (e.g. via competition

or local seed dispersal) and/or abiotic (e.g. nodes of high soil nutrients) in origin. In a given plant community both first- and second-order effects may be responsible for any spatial patterning present. Thus, what is loosely termed 'aggregation' comprises two fundamentally different patterns, which the usual null model, of complete spatial randomness (CSR) as a homogeneous Poisson process, cannot discriminate between. Statistically the distinction between first-order and second-order aggregation is even more problematic as non-homogeneous Poisson processes can mimic cluster processes. Nevertheless, ecological studies rarely use null models other than CSR to go beyond simply describing species patterns as 'aggregated' (Wiegand & Moloney 2004).

Several theoretical studies have suggested that spatial patterning can facilitate the persistence of competitively inferior species in plant communities (Amarasekare 2003); these theoretical models have recently been supported by experimental and field-based empirical studies. Stoll & Prati (2001) explored how spatial pattern mediates competitive interactions by using mixtures of four annual species. They found that survival and fecundity of weaker competitors increased in a high-density aggregated treatment relative to random mixture and low-density aggregated treatments. Building on Stoll & Prati (2001), Monzeglio & Stoll (2005) noted that spatial aggregation, which promotes intraspecific over interspecific interactions, can result in inferior competitors having higher vegetative and reproductive biomass relative to randomised patterns. Likewise, Turnbull et al. (2007) demonstrated, using neighbourhood models parameterised from field experiments, that spatial pattern can promote species coexistence as it benefits inferior competitors (especially those with small seeds). Persistence of competitively inferior species in patches where competitive intensity is low also acts to amplify aggregated patterns (Davis et al. 2005; Moeur 1993). Following on from this idea, Lehman & Tilman (1997) predict a hierarchy of aggregation reflecting the competitive hierarchy in a community. Menge & Sutherland (1987) and Collins & Khlar (1991) additionally propose that competition should be weakest, and aggregation most prevalent, in resource-limited sites, but few empirical studies have explored the relationship between spatial pattern and resource availability.

Studies comprehensively exploring fine-scale spatial pattern of many species or in species-rich communities are scarce outside of (TRF) communities. In species-rich TRF communities, almost all tree species show intense aggregation at fine scales: 99% of 1768 species were aggregated at distances of 0-10 m in six globally distributed 50-ha plots, up to 100% in one plot (Condit et al. 2000), and more than 90% of species were aggregated in communities in Central America and northeastern India (Upadhaya et al. 2003). Conversely, Armesto et al. (1986) and San José et al. (1991) found that 40-50% of species were aggregated in less species-rich temperate and savanna communities. Several studies have considered the spatial patterning of individual species (e.g. Haase et al. 1997) or a small subset of dominant species (e.g. Schurr et al. 2004) in shrubland communities. While the diversity of the shrubland systems we consider here has been compared with that of TRF in the past (Lamont et al. 1977), they differ in some important ways from TRF ecosystems. The physical factors that control the success of individual plants differ between sclerophyll shrublands, where water supply is limiting and light is abundant, and TRF, where the reverse is true. Likewise, the types of processes that may contribute to spatial patterning, such as tree-falls, fire and herbivory, also differ. Nevertheless, the fundamental biotic drivers of spatial pattern - highly-localised dispersal and intra- and inter-specific competition between plants - are likely to be the same, irrespective of the diversity of the systems being considered.

Here we describe the spatial structure of vegetation in four fire-prone, species-rich Mediterranean-climate shrubland ('kwongan') communities on low nutrient sands near Eneabba, Western Australia. We tested the following hypotheses:

1. As in other species-rich plant communities, the majority of species at each site will be aggregated, a few will follow a distribution close to CSR, and fewer still will show a regular pattern.

2. The proportion of species aggregated at each site will be predictable on the basis of that site's soil nutrient status, with less nutrient-rich sites showing higher levels of aggregation (as predicted by Collins & Klahr 1991; Menge & Sutherland 1987).

3. Since the sites were chosen for their apparent environmental uniformity, the majority of aggregated species' patterns will be explained best by a cluster rather than gradient model.

Our methodological approach also allows us to explore the efficacy of various point process models to distinguish gradient (first order) and cluster (second order) patterns of aggregation in point distribution patterns.

Methods

Vegetation

Field data were collected for four shrubland types, associated with different substrates, in kwongan near Eneabba, 270-330 km north of Perth, Western Australia (Table 1). These communities are highly diverse. Hnatiuk & Hopkins (1981) reported species richness of up to 130 species per 100 m^2 in the study area (compared with up

to 300 species per ha in some TRF communities; Lieberman & Lieberman 2007). They also described clear differences in species composition and structure for low sandy dunes and adjacent flatlands, associated with the differences in depth of unconsolidated acid sands over a less permeable lateritic substrate. Enright & Lamont (1992) showed that the absence of tall shrubs (> 1 m) and small trees (3-5 m) from the flatlands was primarily due to limited water availability in the low 'swales' over summer. These shrublands are fire-prone with a mean fire-return period of 13 years over the last 30 years (Miller et al. 2007). Many species show adaptations to cope with fire, including the ability to regrow vegetatively, and seed-based adaptations including fire-stimulated germination of soil-stored seeds and release of canopy-stored seed crops (Enright & Lamont 1989).

Sites were located in tall kwongan on deep acid sands (Crest) and calcareous sands (Limestone), and low kwongan on shallow acid sands (Swale) and on sands shallowly overlying lateritic gravels (Laterite), to provide four high-diversity data sets with contrasting community structure and composition. The sites were last burned at least 12 years prior to mapping and represented mature phase vegetation with cover > 70%. The data consisted of the species identity, x, y location and size (height, canopy diameter) for each individual of all species within the plot (excluding plants < 5 cm 'crown' diameter or height, geophytes and annuals). Due to differences in plant size and density between sites, the Swale and Laterite plots were each 30 m × 30 m, while the Crest and Limestone plots were each 40 m × 40 m. The methods used are described in more detail in Chiarucci et al. (2003). Individuals in the Myrtaceae, Proteaceae and Restionaceae dominated the four sites numerically, with the Cyperaceae, Dilleniaceae and Ericaceae (formerly Epacridaceae) also prominent; abundances of species ranged over four orders of magnitude.

Soils

Surface soil samples were collected from 90 random locations within each of the four plots to quantify soil nutrient levels and soil-stored seed (Enright et al. 2007 provide full details of the methods used). At each location a single 14 cm × 14 cm × 5 cm (depth) soil sample was removed using a custom-built sampler. Samples were dried at 40 °C for 48 h, thoroughly mixed and two 10-g sub-samples removed for analysis. One sub-sample was submitted to CSBP-Wesfarmers Pty Ltd (Perth, Australia) for standard analysis including Nitrate N, Ammonium N, available P, S and K, EC and pH. The second sub-sample was analysed at Curtin University of Technology, Perth, for exchangeable cations (Na, Ca, Mg K) using the ammonium acetate leaching method (Rayment & Higginson

1992). Following Tilman (1982), nutrient availability was quantified by using mean values and the spatial variability in nutrient availability by using the coefficient of variation (CV). We used Moran's I and Geary's C (Dale 1999) to test for spatial autocorrelation in the concentration of the soil nutrients up to distances of 10 m. Whereas the CV describes variability in the soil nutrients, the spatial autocorrelation measures quantify the extent to which this variability is spatially structured.

Spatial analysis

Measures of spatial pattern

The distribution of stems at each site was analysed (1) pooled over all species, and (2) on a species-by-species basis. We used Ripley's K-function (Diggle 2003), and the pair correlation function (PCF, $g(r)$ Stoyan & Stoyan 1994) to characterise the spatial patterns of stems at each site; note that the PCF has variously been called the neighbourhood density function (NDF - Condit et al. 2000; Perry et al. 2006) and the O-ring statistic (Wiegand & Moloney 2004). Due to its non-cumulative nature, the PCF is arguably more useful than the more commonly used K-function as it describes patterns at, rather than up to, specific distances (Perry et al. 2006). The average distance at which the PCF first suggests CSR is a measure of local patterning (cluster size). However, the K-function is useful for exploring how well a given event set conforms to a specific point process model (Stoyan & Penttinen 2000). Thus, we use the PCF to describe patterns and the K-function to explore how well alternative point-process models characterise them. We also used abundance-weighted averages of the PCF (the CAI – the community aggregation index, *sensu* Davis et al. 2005) at distances of 0.0-0.5 m and 0.0-1.0 m to provide a measure of the strength of departure from CSR for groups of species.

The K-function totals the number of points within some distance (r) of a 'focal point' (plant) and is cumulative:

$$\hat{K}(r) = A\sum_{i=1}^{n}\sum_{j=1}^{n}\frac{\omega_{ij} \cdot d_{ij}(r)}{n^2}, i \neq j \qquad (1)$$

where: $\hat{K}(r)$ = the empirical estimate of K at distance r, A = the area of the plot, n is the number of points, d_{ij} is the distance between points i and j and $d_{ij}(r) = 1$ if $d_{ij} \leq r$ and $d_{ij}(r) = 0$ if $d_{ij} > r$ and ω_{ij} is the edge-correction weighting.

We use the linearisation and variance-stabilising correction of the K-function, $L(r)$:

$$\hat{L}(r) = \sqrt{\frac{\hat{K}(r)}{\pi}} - r \qquad (2)$$

Under CSR, $L(r) \equiv 0$; aggregated patterns show $L(r) > 0$ and regular patterns $L(r) < 0$.

The PCF is similar to the K-function but uses annuli rather than closed circles (i.e. it is the derivative of the K-function), and so is non-cumulative (Stoyan & Penttinen 2000):

$$g(r) = \frac{1}{2\pi r} \cdot \frac{dK(r)}{dr} \qquad (3)$$

Following Stoyan & Stoyan (1994) we estimate $g(r)$ using an Epachenikov kernel (k) with bandwidth h:

$$k_h(x) = \frac{3}{4h} \cdot \left(1 - \frac{x^2}{h^2} 1_{(-h,h)}(x)\right) \qquad (4)$$

where: $h = \frac{0.15}{\sqrt{\lambda}}$, and λ is intensity (density).

Under CSR, $g(r) \equiv 1.0$; aggregated patterns show $g(r) > 1.0$ and regular patterns $g(r) < 1.0$.

The edge corrections described by Goreaud (1999) were used, and we calculated $L(r)$ and $g(r)$ at 0.1 m intervals up to a distance of 10 m.

Null models

To characterise the observed spatial patterns we generated simulation envelopes using three null models:

Homogeneous Poisson process (HPP; complete spatial randomness, CSR) – i.e. there is neither first-order nor second-order pattern in the distribution of stems; CSR is defined solely by λ, and λ is assumed constant (i.e. homogeneous) within the plot.

Inhomogeneous Poisson process (IPP) – first-order departure from CSR implies variation in λ across the plot, but **not** interactions between events. For each species we modelled λ as a log-quadratic function of the Cartesian coordinates (see Diggle 2003, p. 105), with parameter values estimated via maximum likelihood:

$$\log(\lambda_{x_1,x_2}) = \alpha + \beta_1 x_1 + \beta_2 x_2 + \gamma_1 x_1^2 + \gamma_2 x_2^2 + \delta x_1 x_2 \qquad (5)$$

where: x_1 and x_2 are Cartesian co-ordinates.

Poisson Cluster process (PCP) – second-order departures from CSR **do** imply interactions between points (events); i.e. the probability of a point being observed at a location is affected by the locations of other points. While there are other second-order point process models of aggregation (Diggle 2003), the PCP model has been used in ecological studies (e.g. Plotkin et al. 2000; Stamp & Lucas 1990) yielding parameters that are easily *ecologically* interpreted. In PCP models, clusters of 'offspring' events are produced using a radially symmetric Gaussian distribution (given by Eq. 6), centred on 'parent' events:

$$h(x_1, x_2) = 2(\pi\sigma^2)^{-1} \cdot \exp\left(\frac{-x_1^2 + x_2^2}{2\sigma^2}\right) \qquad (6)$$

The PCP is defined by the intensity of the parent's Poisson process (ρ) and the variance of the Gaussian distribution of parent-child distances (σ^2). The mean squared distance from 'offspring' events to their 'parents' is $2\sigma^2$; thus, ρ measures density of patches and σ patch size (note that we imply no ecological meaning by using the terms parent and offspring). When simulating the PCP we used a buffer of two SD of the patch size for the species being assessed so that parents outside the plot could contribute offspring within the plot – this represents the effects of the plot edges 'slicing through' clusters.

We fit the PCP models following the methods outlined in Diggle (2003, p. 86-87); theoretically, a PCP with given ρ and σ yields:

$$K(r)^{PCP} = \pi r^2 + \rho^{-1} \cdot \left(1 - \exp(\frac{-r^2}{4\sigma^2})\right) \qquad (7)$$

We estimated ρ and σ by minimizing $D(\theta)$:

Table 1. General properties of the four vegetation sample sites near Eneabba, Western Australia, alongside rank order of various biophysical descriptors of each site and the observed spatial patterning, from highest (1) to lowest (4). N is total number of individuals sampled, Density is mean number of individuals per m², Species is total number of species sampled [including those with $n < 20$], Sole site = number of species found only at that site (of the four surveyed), Infrequent = number of species with fewer than 20 individuals, and α is Fisher's alpha diversity (see Rosenzweig 1995).

Site	N	Density (inds.m⁻²)	Species	Sole site	Frequent ($n > 20$)	Richness rank (S)	α rank (α)	Soil nutrient resources	Water availability	Productivity	Pattern[†]
Limestone	10 674	6.7	74	45	44	4 (74)	4 (10.7)	1	2	1	1
Laterite	13 663	15.2	93	20	56	3 (93)	3 (13.6)	2	4	4	3
Crest	10 530	6.6	113	48	59	1 (113)	1 (16.8)	3.5	1	2	2
Swale	12 815	14.2	104	23	75	2 (104)	2 (15.5)	3.5	3	3	4

[†] In terms of proportion of species showing non-random distributions.

$$D(\theta) = \int_0^{r_{max}} [\{\hat{K}(r)\}^c - \{K(r)\}^c]^2 \cdot dr \qquad (8)$$

where: c is a tuning constant, for which we use a value of 0.25, as suggested by Diggle (2003) for aggregated patterns.

The parameters of the PCP model (σ and ρ) can be used to provide information about the patch structure in the sampled area (Plotkin et al. 2000; Stamp & Lucas 1990). The number of individuals present in patches of species i can be estimated from ϱ_i (the density of patches of species i) and n_i (the abundance of species i), and the mean radius of clumps of species i can be estimated from

$$\sigma_i \cdot \sqrt{(\pi / 2)} \qquad (9)$$

Assessment of significance and model fit

Simulation envelopes were calculated at $\alpha = 0.01$ on the basis of 499 Monte Carlo simulations. To assess deviation from the various null hypotheses we used the Cramer von Mises (CvM) statistic, which is the sum of the squared deviation of the observed from the expected across all distances (Perry et al. 2006); for the HPP, IPP and PCP we used the mean of the Monte Carlo simulations as the expected value. Although the theoretical value of the HPP is known (zero at all distances) we used the mean of the Monte Carlo simulations because the edge-corrected estimates of $L(r)$ are not unbiased (although we found using the theoretical estimate of $L(r)$ under CSR [zero] produced the same results in a qualitative sense). We calculated the CvM from the estimates of $L(r)$. If a species' pattern deviated significantly from CSR, as assessed on the basis of the significance of the curvewise CvM test using CSR as the null hypothesis and visual inspection, the CvM statistics of the IPP and PCP models were compared, with the lowest being deemed the 'best fit'. SpPack (Perry 2004) and the R libraries Splancs (Rowlingson & Diggle 1993) and Spatstat (Baddeley & Turner 2005) were used for all statistical analyses.

Results

Soils

There were clear differences in soil properties (Ca, Mg and K at Crest, Limestone and Swale, and total N and P at all sites) between sites. Limestone has considerably higher nutrient availability for all major plant nutrients except P, and shows greater variability in nutrient availability than the other sites. Laterite shows intermediate levels of the measured soil nutrients, while Crest and Swale show the lowest nutrient levels and spatial heterogeneity. There are significant global differences between all sites (Kruskal-Wallis tests with Bonferroni corrected p-values; $p \ll 0.01$). The general hierarchy of nutrient levels and their spatial heterogeneity can be summarised as: Limestone $\rightarrow$ Laterite $\rightarrow$ Crest $\approx$ Swale (Table 1). Spatial autocorrelation tests using Moran's I and Geary's C showed no evidence for strong or systematic spatial structuring for any of the nutrients (Ca, Mg, P, K and total N) tested at any of the sites for distances up to 10 m (Table 2).

Table 2. Summary of spatial autocorrelation analyses for Ca, Mg, P, K and total N at each of the four sites. Analyses consider distances up to 10 m using a 1-m step interval. We used $\alpha = 0.01$ and the p-values shown here are uncorrected for multiple tests; I = Moran's I ($-1 \le I \le 1$) and C = Geary's C ($0 \le C \le 2$).

Site	Nutrient	I range[†]	p-range (I)	Sign. distances (m)	C-range[†]	p-range (C)	Sign. distances (m)
Crest	Ca	–0.15 - 0.31	0.12 - 0.87	–	0.9 - 1.41	0.07 - 0.96	-
	Mg	–0.07 - 1.02	< 0.01 - 0.88	1, 8, 9	0.58 - 0.97	0.03 - 0.85	-
	K	–0.11 - 0.71	< 0.01 - 0. 95	4	0.54 - 1.11	0.02 - 0.67	-
	Total N	–0.07 - 0.37	0.03 - 0.99	–	0.58 - 1.11	0.06 - 0.88	-
	P	–0.40 - 0.21	0.05 - 0.89	–	0.60 - 1.51	0.02 - 0.92	-
Laterite	Ca	–0.33 - 0.27	< 0.01 - 0.90	4, 7	0.19 - 1.89	< 0.01 - 0.85	7, 8
	Mg	–0.04 - 0.57	0.04 - 0.78	–	0.37 - 1.09	0.03 - 0.83	-
	K	–0.16 - 0.21	0.01 - 0.85	–	0.74 - 1.20	0.10 - 0.90	-
	Total N	–0.21 - 0.48	0.13 - 0.89	–	0.79 - 1.13	0.11 - 0.75	-
	P	–0.27 - 1.12	< 0.01 - 0.87	1	0.7 - 6.0	< 0.01 - 0.81	1, 3
Limestone	Ca	–0.07 - 0.18	0.03 - 0.72	–	0.44 - 2.53	< 0.01 - 0.33	2, 3, 6, 10
	Mg	–0.04 - 0.12	0.38 - 0.98	–	0.13 - 1.99	< 0.01 - 0.54	2, 4
	K	–0.22 - 0.29	0.06 - 0.84	–	0.29 - 1.58	0.03 - 0.87	-
	Total N	–0.12 - 0.26	0.02 - 0.99	–	0.66 - 1.69	0.04 - 0.71	-
	P	–0.07 - 0.48	<0.01 - 0.84	3	0.61 - 1.09	0.02 - 0.94	-
Swale	Ca	–0.24 - 0.07	0.11 - 0.96	–	0.82 - 1.20	0.15 - 0.94	-
	Mg	–0.12 - 0.07	0.36 - 0.99	–	0.52 - 1.94	<0.01 - 0.99	2, 4
	K	–0.16 - 0.09	0.28 - 0.92	–	0.73 - 0.98	0.09 - 0.87	-
	Total N	–0.09 - 0.60	<0.01 - 0.92	7	0.81 - 1.29	0.02 - 0.98	-
	P	–0.06 - 0.31	<0.01 - 0.87	9	0.51 - 3.03	< 0.01 - 0.68	1, 8 - 10

† Note that when the number of pairs used to estimate I or C is very small ($n < \approx 15$) then the statistic can take on values outside its normal range.
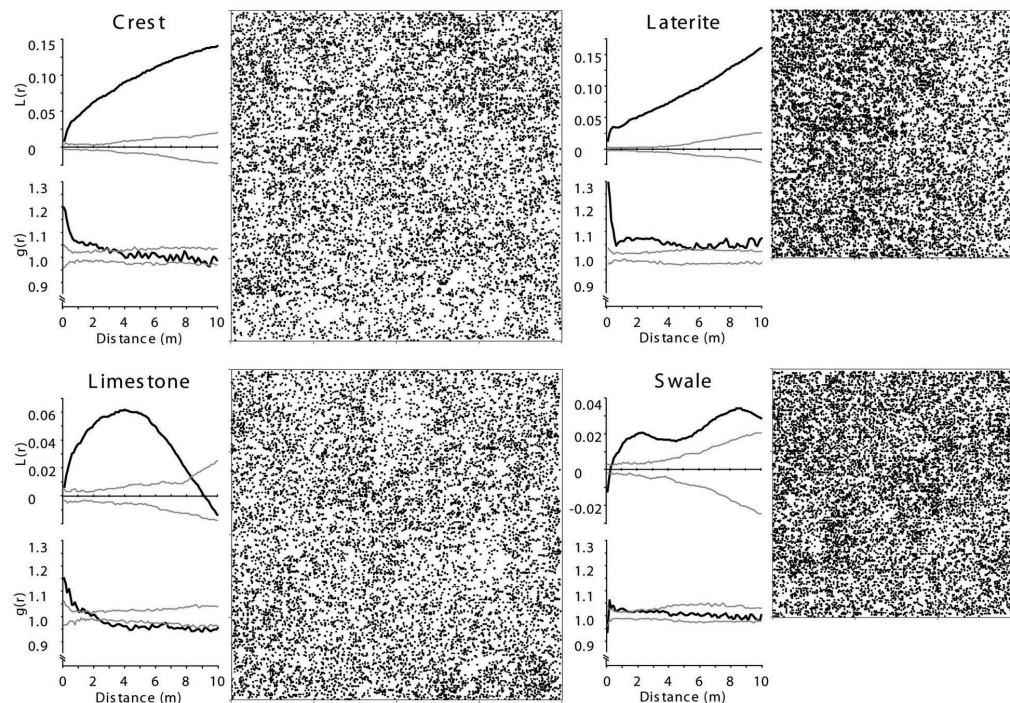
Fig. 1. Site-level patterns of stems and their corresponding *L*-functions and PCFs; confidence envelopes (grey lines) estimated at the $\alpha = 0.01$ level using a homogeneous Poisson model.

Site-level spatial patterns in the vegetation

Both the *K*-function and the PCF show strong aggregation of all stems at short distances (Fig. 1). On the basis of the PCF, plants at the Crest site are aggregated up to distances of 2 m, at the Laterite site up to 10 m, at the Limestone site up to 1.5 m before becoming regular at distances beyond 2.5 m, and at the Swale site at distances up to 2 m. At longer distances, aggregation becomes weaker for the PCF at all sites; regularity is observed at the Limestone site at distances ≈ 2.5 m for the PCF, but not for the *K*-function.

Spatial pattern of individual species

Broad description of patterns

In all, 233 species distributions were analysed. On the basis of the curvewise CvM statistic, at all sites most species were either aggregated or showed CSR (Fig. 2a). The percentage of aggregated species varied between sites, ranging between 44 and 52% (Swale) to 85 and 90% (Limestone) of all species, based on $L(r)$ and $g(r)$, respectively (Fig. 2a). Only one species showed a regular distribution at any site, *Hibbertia* aff. *hypericoides* (Dilleniaceae) at Swale (at small distances). There is a statistically significant site-by-pattern interaction ($G^2 = 23.8$ and 21.6 for
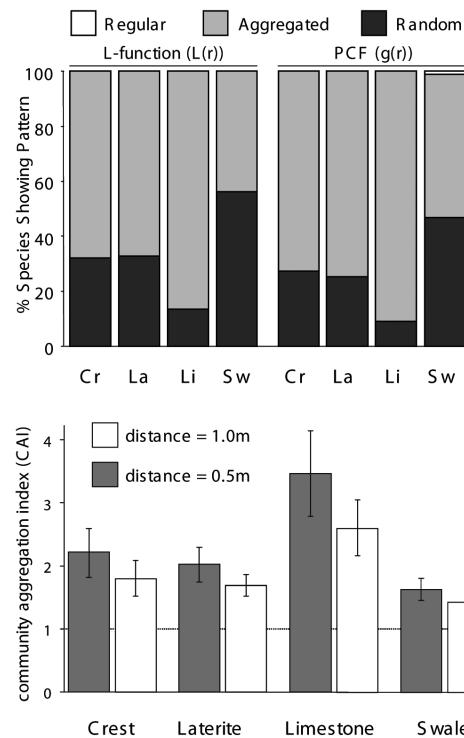

Fig. 2. a. Proportion of aggregated vs. non-aggregated (random or regular) species, based on curvewise tests, at each of the four sites; **b.** weighted average (± 1 weighted SEM) of the PCF (the community aggregation index, CAI) at 0.5 and 1.0 m for each of the four sites; dotted line indicates theoretical value under CSR.
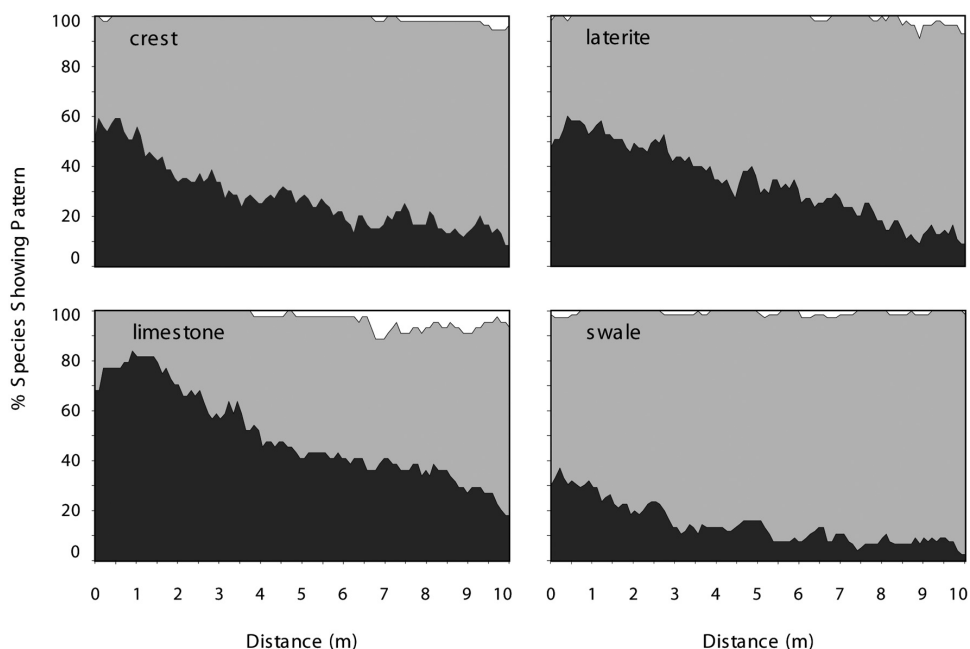
Fig. 3. Proportion of species showing different patterns by distance at each site (dark grey = aggregated, light grey = CSR, white = regular); pattern was assessed on the basis of where $g(r)$ fell in relation to the simulated confidence envelopes.

the K-function and the PCF, respectively, with $df = 3$ and $p \ll 0.0001$ for both). Limestone had the highest proportion of aggregated species, and Swale the lowest; similar trends, in terms of strength of patterning were apparent when community-wide spatial patterns (CAI) were considered (Fig. 2b).

The distances over which departure from CSR occurs also varies between sites (Fig. 3); this distance is 4.0, 2.0, 1.6 and 0.7 m at the Limestone, Laterite, Crest, and Swale, respectively, if all species are considered and 4.4, 2.6, 2.2 and 1.4 m if only aggregated species are considered. Thus, the site with the highest proportion of aggregated species (Limestone) shows local aggregation over the widest distances.

Point process models

First- (IPP) and second-order (PCP) point process models were fitted to all species that were deemed to show an aggregated pattern (i.e. significant departure from CSR; Fig. 4). For aggregated species the PCP

model provided a better fit than the IPP model, giving the best fit for 79% (30), 86% (32), 93% (37), and 91% (30) of species at Limestone, Laterite, Crest and Swale, respectively.

Based on the PCP models' parameters σ and ρ, cluster extent (spatial) and size (number of individuals) can be estimated (Table 3). Cluster extents are smallest at Limestone and largest at Crest, with Laterite and Swale approximately the same. The Laterite has the most individuals per cluster, followed by Limestone and Crest (approximately the same), and then Swale. These trends broadly reflect the aggregation patterns described above – aggregated species at Limestone are characterised by spatially small but quite dense clusters, whereas aggregated species at Swale show more spatially diffuse, lower density clusters.

Table 3. Average values for patch radius ($\sigma \cdot [\pi/2]^{1/2}$) and plants per patch for aggregated species best described by the PCP model at each of the four sites.

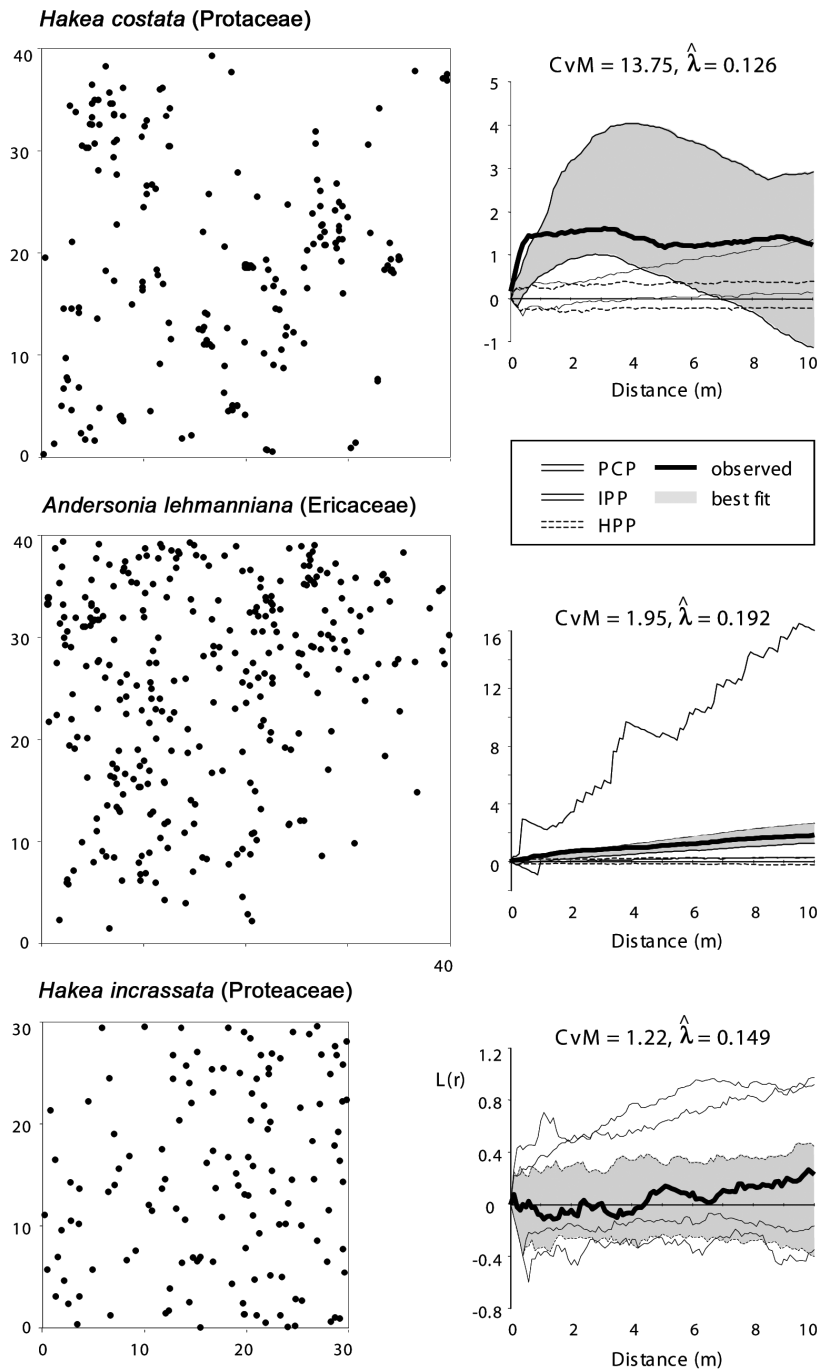| Site | n | $\sigma \cdot [\pi/2]^{1/2}$ (in metres) | | Plants / patch | |
		Mean	SD	Mean	SD
Limestone	30	2.47	2.37	11.29	13.72
Laterite	32	2.89	1.49	17.72	13.51
Crest	37	3.43	2.65	9.27	10.66
Swale	30	2.84	2.38	7.58	4.22

Fig. 4. 'Typical' examples of species fit by each of the three spatial process models: (**1**) the Poisson cluster process provides the best fit to *Hakea costata* at Limestone (**2**) the inhomogeneous Poisson process provides the best fit to *Andersonia lehmanniana* at Crest, and (**3**) the homogeneous Poisson process provides the best fit to *Hakea incrassata* at Laterite. Note that *y*-axis scaling varies on the plots of *L*(*r*).

Discussion

As with the majority of studies in species-rich ecosystems, most species in the Mediterranean-type shrublands examined here were aggregated, though the extent of aggregation ranged markedly across the four sites, from ca. 50% (Swale) to ca. 90% (Limestone) of species with $n \geq 20$. Of the remaining species, almost all showed a random (CSR) pattern, with regularity observed only once. Although at some sites the proportion of aggregated species was high, it was not as high as that reported for (TRF) communities by Hubbell (1979), Condit et al. (2000) and Upadhaya et al. (2003). The values we report are closer to, but slightly higher than, those described by Armesto et al. (1986) for temperate forest communities and San José & Fariñas (1991) for savanna forest. A possible explanation for the lower levels of aggregation (relative to TRFs) is that disturbance in kwongan predominantly occurs at the landscape level through widespread fire, whereas in TRFs, localised gap-level disturbances, with associated gap-phase dynamics, are more prevalent. Armesto et al. (1986) comment that recurrent landscape-level disturbance is likely to result in less aggregation as it reduces resource patchiness. The dominance of woody, resprouting species at these sites (55% at Limestone, 66% at Crest, 75% at Swale, 78% at Laterite; Enright et al. 2007) may also explain the relatively lower levels of aggregation compared to those observed in some TRFs. The proportion of aggregated species within sites corresponds inversely to the proportion of resprouter species within sites. Resprouter populations represent multiple establishment events, unlike fire-killed species that are represented by single-aged cohorts. Each recruitment episode represents a different configuration of environmental conditions, with fire characteristics, subsequent weather conditions, post-fire density, post-fire litter patches, and the spatial distribution of other seedlings and resprouters varying between fires and spatially within fires. As a result, the spatial patterns shown by resprouter species represent the integration of variable environmental conditions across recruitment episodes, which may act to diffuse the influence of environmental heterogeneity in spatial patterns. On the other hand, all non-sprouters are subject to the same pattern of conditions, so may respond more strongly. Finally, the size of the plots used in these studies could be significant: the large (50 ha) TRF plots encompass much more landscape heterogeneity, including multiple overlapping seed shadows and considerable within-plot topographic variation, while we consider a broader range of life forms and plant sizes.

We did not obtain support for the second of our hypotheses: aggregation is most prevalent (proportion of species) and strongest (deviation from CSR) at Limestone where resource availability is highest. This contradicts expectations from Collins & Khlar's (1991) conceptual model that attempts to link resource availability and competition to spatial patterning. The few studies that consider how resource availability affects local spatial patterning are rather ambiguous. Padien & Lajtha (1992) and Schenk et al. (2003) both found evidence for increased aggregation of individuals in more resource-rich environments. Conversely, Kikvidze et al. (2005) in a comparative study of 18 alpine grasslands, noted that aggregation was more prevalent at harsh sites, and attribute this to facilitative interactions. They also found that as species richness increased, fewer species showed random distributions. Aggregation at the sites that we consider here may indicate a competition effect, with strong competitor species tending to dominate resources and weaker ones marginalised to other microsites. This interpretation is supported by the fact that Limestone also had the lowest species richness. However, no definitive conclusion can be reached on this point given that only four sites were quantified, a common problem in studies of spatial pattern, where the effort involved in data collection usually restricts the number of sites available for analysis to one, or (rarely) a few.

Finally, we found that for aggregated species, Poisson cluster process models (PCP) better described patterns of aggregation than did inhomogeneous Poisson processes. The success of the PCP models implies that second-order effects are responsible for the observed aggregation. Interactions between individuals are a possible explanation for the second-order pattern. Such interactions could result from localised seed dispersal around parents. In these systems most recruitment occurs in the first winter following fire and there is little recruitment between fire events (Enright & Lamont 1992), so the nature of the post-fire environment would drive such patterning. A second explanation for the clustering seen in the four communities is that species are responding to local variations in environmental conditions, especially in the post-fire environment. For example, Enright & Lamont (1989) and Lamont et al. (1993) showed that litter-filled microsites play a key role in the establishment of various woody species in these systems. Quadratic trend-surfaces (IPP models) do not capture these fine-grained patterns. Nevertheless, in these landscapes there are coarser-scaled patterns related to dune crest-swale patterning – thus, it might be expected that there are gradients in species density at these broader scales. At the plot scales we consider, however, we see strong localised clustering, and it is certainly possible that the landscape comprises gradients of clusters (i.e. a combination of first-order and second-order aggregation). Plotkin et al. (2000) describe patterns of 'hierarchical aggregation' in TRF "in which the local patches are themselves clustered following a more global pattern" – such multi-scale patterning is

likely in this system, but our data are limited to local (fine) scales. Those species best described by the first-order model do not exhibit consistent spatial gradients at any of the sites; that is, the fitted gradients do not show the same orientation. This lack of consistent gradient structure suggests that the observed first-order patterns are not a response to abiotic gradients in the environment; rather they may be due to the plot edges cutting across the edges of diffuse clusters, thus resulting in apparent rather than true gradients.

Effects of sample size on pattern

It is worth commenting on the relationship between the number of events included in a specific analysis (i.e. the number of individuals representing a given species) and the outcomes of the spatial analysis. When sample sizes are small (n < ca. 20) the tests lack power because the sampling distribution has a large standard deviation and cannot be differentiated from CSR; thus we do not analyse species with fewer than 20 stems. This sample size effect may potentially account for at least part of the observed between-site differences in the proportion of aggregated species. The distribution of abundances differed between sites (Fisher's α in Table 1), and, if power increases with the abundance of a species, those with proportionally fewer infrequent species may show a higher proportion of aggregation due to this effect alone. In our analyses (Table 1) we found that the site with the highest proportion of aggregated species (Limestone) had the lowest value of Fisher's α (suggesting the most equitable distribution of abundances of the four sites). However, there was not a consistent negative relationship between α and the proportion of aggregated species (e.g. the Crest site, the site with the highest α, showed the second highest proportion of aggregated species).

Unfortunately the extent to which power (type-II error rate, β) changes with sample size (n) has been little investigated for the spatial statistics we use here. Thus, it is difficult to identify the sample size at which we can declare that we are satisfied with our type II error rate (here we have used n = 20 to ensure that a reasonable number of species is evaluated at each site). The problem is further confounded because it is possible that a species' spatial pattern is **not** independent of its abundance (e.g. see Lehman & Tilman 1997; Moeur 1993; Okuda et al. 1997). For instance, as abundance increases, competitive interactions become more likely and self-thinning processes may shift species towards more regular patterns. Alternatively, rare species may be poorer competitors and may, therefore, have enhanced survival in aggregated settings. While we do not seek to answer these difficult questions here they are worthy of future consideration.

Relation to conceptual pattern and interactions models

Enright & Lamont (1992) note the strong dominance of woody, resprouting species (> 70%) in these SW Australian shrubland ecosystems and infrequent recruitment among them (i.e. there is little or no recruitment in many resprouter species after most fires, with occasional recruitment episodes when fire and favourable post-fire environmental conditions coincide). Thus, we might expect low levels of competition within stable populations of long-lived adults (i.e. the storage effect model of Warner & Chesson 1985). Although all relatively nutrient poor, the four sites do differ in their nutrient availability, declining in the order Limestone → Laterite → Crest ~ Swale (Table 1). Clear differences are obvious in patterning (proportion of species aggregated and intensity of aggregation) across the four sites. If the models of Menge & Sutherland (1987) and Collins & Khlar (1991) hold, competition should be weakest, and aggregation most prevalent, in the most resource-limited sites. In fact, we found the opposite – the highest proportion of aggregated species was seen at the most resource-abundant site. Species richness also declined as resource availability increased, as documented in other systems (e.g. Huston 1990; Rajaniemi 2003). Although water is known to be limiting in this environment (Enright & Lamont 1992), the regular patterning seen in some arid shrublands was not observed here (e.g. cf Phillips & MacMahon 1981).

Fire and spatial heterogeneity in the post-fire environment play crucial roles in this system. Lamont et al. (1993) found that although the majority of seeds from serotinous (canopy seed storage) shrubs, many of which do not survive fires, disperse into litter-filled microsites after fires, first-year seedlings in these patches have lower survival and growth rates than those located in intervening bare areas. Further, experimental pre-summer thinning of seedlings in the litter patches increased survival of the remainder twofold and the size of the survivors by more than 30%. In the plant communities explored here, none of which have experienced fire for at least a decade, such patterning in the regeneration process may increase through time (e.g. by subsequent dispersal limitation) to produce the aggregation observed. Patchiness in the intensity of past fires may also result in aggregation (Odion & Davis 2000). In other semi-arid environments, aggregation has been interpreted as a sign of facilitation. Although we do not explore bivariate interactions here, this is certainly possible in these communities. Facilitative-type effects, both interspecific and intraspecific, may explain some of the aggregation we observed. For example, small plants may preferentially grow under the crowns of large woody individuals where soil moisture may be higher and temperatures lower. We will explore such bivariate and multivariate associations in subsequent analyses.

Conclusions

We explored spatial pattern among plant species for samples of more than 10 000 individuals from each of four plots in species-rich Mediterranean-climate shrublands in SW Australia. Although aggregation was the dominant species pattern in all four plots, it was less common than in comparable species-rich communities, such as the large TRF plots in Malaya and Panama, with many species showing CSR. This study provides tests of recent competition theory in relation to pattern: conceptual models suggest that plants at nutrient-rich sites should experience more intense competition which, in turn, results in decreased aggregation. Here, we found that the highest nutrient site had the lowest species richness and highest levels of individual species dominance, suggesting a strong competition effect, but also the highest degree of aggregation. Differences in environmental conditions between sites appear to influence levels of aggregation, with higher nutrient levels favouring dominance and aggregation, but resource variation within sites could not be related to spatial pattern at the local scale. Although we were able to discriminate between first and second-order aggregations, the prevalence of second-order aggregation awaits a satisfactory explanation.

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