

Spatial patterns in a two-tiered semi-arid shrubland in southeastern Spain

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Abstract. Single species and bivariate distribution patterns in a semi-arid shrubland in southeastern Spain, dominated by the tall leguminous shrub *Retama sphaerocarpa*, were investigated by second-order spatial analysis based on Ripley's *K*-function. Shrubs were significantly clumped because of a strong association of dwarf shrubs, mostly *Artemisia barrelieri*, under the canopy of *Retama*. *Retama* shrubs were randomly distributed, but when different size-classes were analysed separately, the pattern changed from significantly clumped to random and then to regular with increasing canopy diameter, suggesting increasing intraspecific competition with shrub size. *Artemisia* was significantly clumped at all scales because of aggregation under the canopy of large *Retama* shrubs. The association between the species became stronger with increasing canopy diameter of *Retama* shrubs, suggesting that facilitation prevailed over interspecific competition because of niche separation in different tiers, both above and below ground. *Retama* shrub size thus determined both the type of pattern for its own size class and tier, and the scale and intensity of the association with its understorey shrubs.

Keywords: *Artemisia barrelieri*; Competition; Facilitation; Mediterranean ecosystem; Nucleation; *Retama sphaerocarpa*; Second-order spatial analysis; Succession.

Nomenclature: Sagredo (1987).

Introduction

Two extremes of spatial distribution patterns of perennial plants have been observed in arid environments. Apparently regular patterns are thought to arise through competition for the exclusive use of soil water and nutrient resources by single individuals (e.g. King & Woodell 1973; Phillips & MacMahon 1981). On the other hand, the often extreme physical conditions can favour facilitative effects between plants, particularly during the phase of recruitment or colonisation, leading to aggregation in which neighbours buffer one another from potentially limiting physical stresses (Muller 1953; Niering et al. 1963; Franco & Nobel 1989; Franco-Pizaña et al. 1995). Patterns similar to the latter also occur in other harsh physical environments, typically

during succession in homogeneous undisturbed habitats (Yarranton & Morrison 1974; Bertness & Callaway 1994). When a community consists of different species or different size-classes of the same species, patterns usually vary with the spatial scale of the investigation (Duncan 1991; Leemans 1991; Skarpe 1991). Particularly in arid and semi-arid ecosystems, different spatial distribution patterns of the same numbers of plants have differential effects on plant water use, evaporation and hydrology (Shuttleworth & Wallace 1985). Determination of the patterns of sparse vegetation and prediction of their development and possible change can therefore improve estimates of the hydrological balance of the ecosystem (Wallace et al. 1990).

In semi-arid regions of southeastern Spain, which receive a mean annual rainfall of 200-400 mm and have up to four months of summer drought, the floodplains and lower terraces of dry valleys and river beds are often covered by open shrubland which has two major components: a scattered shrub layer composed almost exclusively of *Retama sphaerocarpa* and a dwarf shrub understorey which is often dominated by *Artemisia barrelieri*. While *Retama* is generally widely spaced with only occasional small groups of shrubs, there appears to be a particularly close spatial association of *Artemisia* and other dwarf shrubs with the latter. As part of a wider research project (MEDALUS II - Mediterranean Desertification and Land Use) on the ecology of sparse vegetation cover and its effects on hydrology and soil erosion in semi-arid environments, the distribution patterns and spatial relationships between the shrubs were investigated. Because of the apparent strong variation in the distribution pattern and spatial relationships within and between species at different spatial scales, we needed an analytical method which would be able to detect particular patterns at different scales. We chose second-order spatial analysis based on Ripley's *K*-function (Ripley 1976, 1981), which has been applied in plant ecology to analyse distribution patterns of woody plants ranging from tropical forest trees (Sternier et al. 1986) to desert shrubs (Prentice & Werger 1985; Skarpe 1991) and semi-arid steppes (Zhang & Skarpe 1995).

Material and Methods

Field site

The field site is in the Rambla Honda, a dry valley on the southern slope of the Sierra de los Filabres, ca. 40 km north of Almería, Andalucía, Spain (37° 08' N, 2° 22' W, 630 m altitude). The climate is semi-arid; at Tabernas, 10 km south of the field site, mean annual temperature is 17.9 °C and mean annual rainfall 218 mm (1965-1991; R. Lázaro unpubl.). Rainfall is highly variable between years, but a pronounced, often almost rainless dry season usually occurs from June to September.

The surrounding mountains consist of metamorphic rocks, mainly mica-schist, and there are extensive alluvial fan systems at the base of the slopes. The valley bottom is filled with deep and poorly sorted fluvial deposits, mainly sands and gravels. On the dry floodplain, soil profiles are only developed under tall shrubs; soils have low concentrations of nitrogen and organic matter (Pugnaire et al. 1996). The floodplain is covered by open shrubland with three distinct strata. The upper stratum, 1-3 m high, consists almost exclusively of *Retama*. The next layer, 0.2-0.5 m, includes dwarf shrubs, with *Artemisia* as a dominant species. The ground layer consists of conspicuous 'green islands', made up by numerous annual and perennial herbs and grasses, under the canopies of the *Retama* shrubs.

Retama sphaerocarpa is a leafless leguminous shrub, up to 4 m tall, which occurs in the Mediterranean region of northern Africa and the southern Iberian Peninsula. The roots of the shrub can penetrate to depths of >25 m (Haase et al. 1996), providing access to deep, moist soil layers. *Artemisia barrelieri* is a strongly aromatic sub-shrub, with small evergreen leaves, which attains a mean height of 20-30 cm. It is endemic to the dry Mediterranean region of Spain (Freitag 1971). The root system penetrates the soil to 20-35 cm depth, but is concentrated mainly in the upper 10 cm (Freitag 1971); thus the plants depend on moisture provided by precipitation.

Sampling method and statistical analysis

One 100 m × 20 m plot (subdivided into 20 10 m × 10 m subplots) was marked in June 1994 in *Retama* shrubland in a homogeneous area of the dry floodplain. The coordinates of the estimated centre of each woody plant were recorded to the nearest 10 cm. Basal diameter of the largest stem, canopy height, and maximum horizontal diameter of the canopy were measured for each shrub. All shrubs were grouped into size classes based on stem diameter, and size distributions were established for the two dominant species, *Retama* and

Artemisia. Small plants of *Retama* lacking woody stems were classified as juveniles.

Spatial distribution patterns were analysed by Ripley's *K*-function (Ripley 1976, 1981; Diggle 1983; Upton & Fingleton 1985; Haase 1995). A circle of radius t is centred on each point (plant) and the number of neighbours within the circle is counted. Points located near one of the borders of the sample plot require an edge correction which was calculated by the weighted method described by Getis & Franklin (1987) and modified by Haase (1995). If the distribution of the points is Poisson random, the expected value of the cumulative function $K(t)$ equals πt^2 , i.e. the area of a circle of radius t , which gives a linear plot of $\sqrt{K(t)}$ versus t . It has become common practice to plot the derived sample statistic $\sqrt{[K(t)/\pi]} - t$ because this expression has zero expectation for any value of t when the pattern is Poisson random (Skarpe 1991).

The sample statistic calculated from the data is tested against the null hypothesis of spatial randomness by randomly re-positioning all points in the plot and then analysing the generated plot as before. For statistical significance, the lowest and highest values of $\sqrt{[K(t)/\pi]} - t$ of 19 or 99 such randomizations are usually used to define the lower and upper bound of a 95% or 99% confidence interval, respectively (Haase 1995). Here, we used the values at the limit of the 2.5% tails of 100 randomizations (mean ± 1.96 SD) for a 95% confidence interval instead. If the deviation of the sample statistic from zero expectation is significantly positive, a clumped distribution of the sampled points can be assumed, while significant negative deviation suggests a regular (uniform) pattern (Diggle 1983). If the sample statistic remains within the bounds of the confidence interval at any given t , the null hypothesis of complete spatial randomness cannot be rejected.

The null hypothesis was tested for all shrubs considered together and separately for each of the two dominants, *Retama* and *Artemisia*. The spatial associations between *Retama* and understorey shrubs, and between mature shrubs and juveniles of *Retama* were investigated with a modified procedure for analysis of bivariate distribution patterns (Diggle 1983; Upton & Fingleton 1985; Andersen 1992). Changes in the spatial patterns in relation to the size of *Retama* shrubs were investigated by separate analyses which considered the *Retama* shrubs in four classes of canopy diameter: ≤ 1 m, 1-2 m, 2-3 m, and > 3 m.

Results

Size-class distribution

112 mature *Retama* shrubs (560/ha) were found in the 0.2 ha plot and 23 juveniles (115/ha), estimated to be >1 to ca. 5 yr old. The size-class distribution of *Retama* was bimodal, the smallest class (≤ 0.5 cm basal diameter) containing the largest number of shrubs (Fig. 1a). Another peak occurred in the 1.5-2.5 cm diameter class; numbers then declined continuously with increasing diameter. Most of the 186 *Artemisia* shrubs (930/ha) had stem diameters of 0.2-0.5 cm (Fig. 1b). The other understory shrubs contributed five more species with 18 individuals.

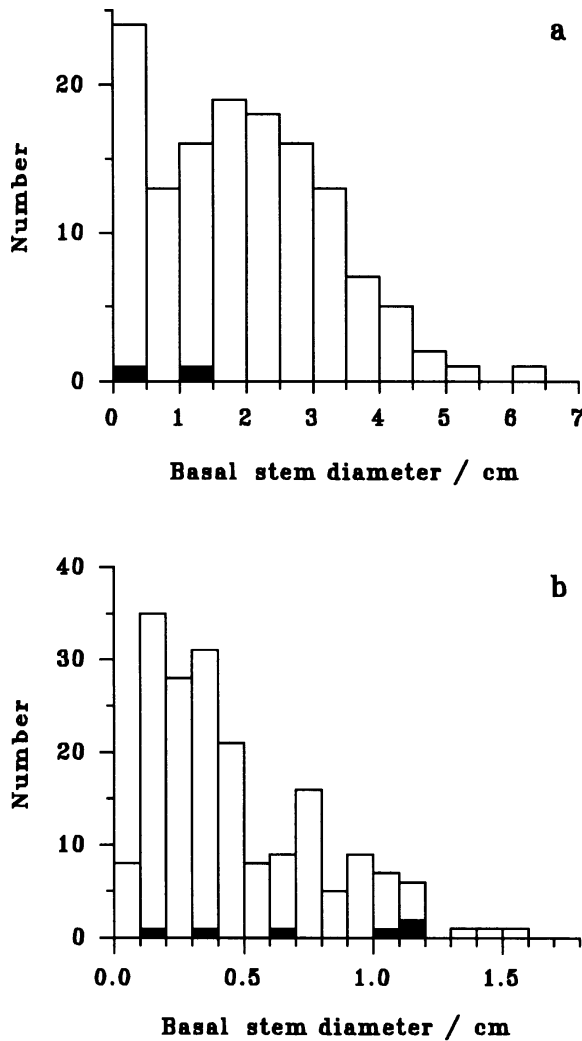


Fig. 1. Size-class distribution (basal diameter of the largest stem) of (a) *Retama sphaerocarpa* (n = 135) and (b) *Artemisia barrelieri* (n = 186) in a 100-m × 20-m plot. Dead individuals are shown in solid black.

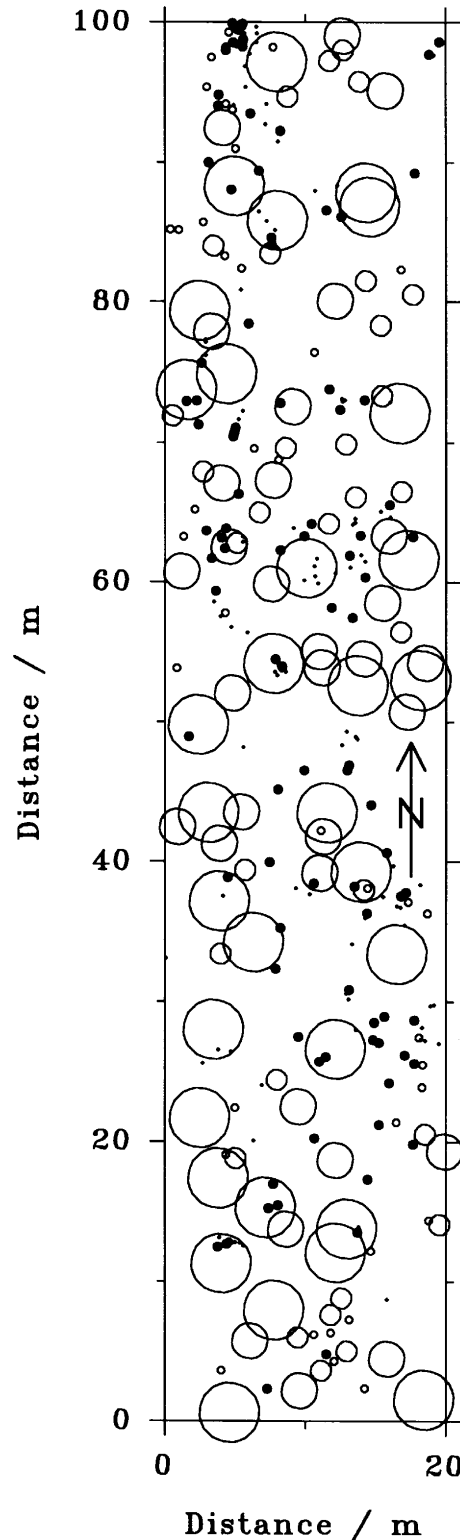


Fig. 2. Distribution map of *Retama sphaerocarpa* (open circles) and *Artemisia barrelieri* (filled circles) in the plot. Shrubs are drawn to scale according to their mean canopy diameter calculated for the size-classes ≤ 1 m, 1-2 m, 2-3 m, > 3 m for *R. sphaerocarpa* and for ≤ 0.45 m and > 0.45 m for *A. barrelieri*.

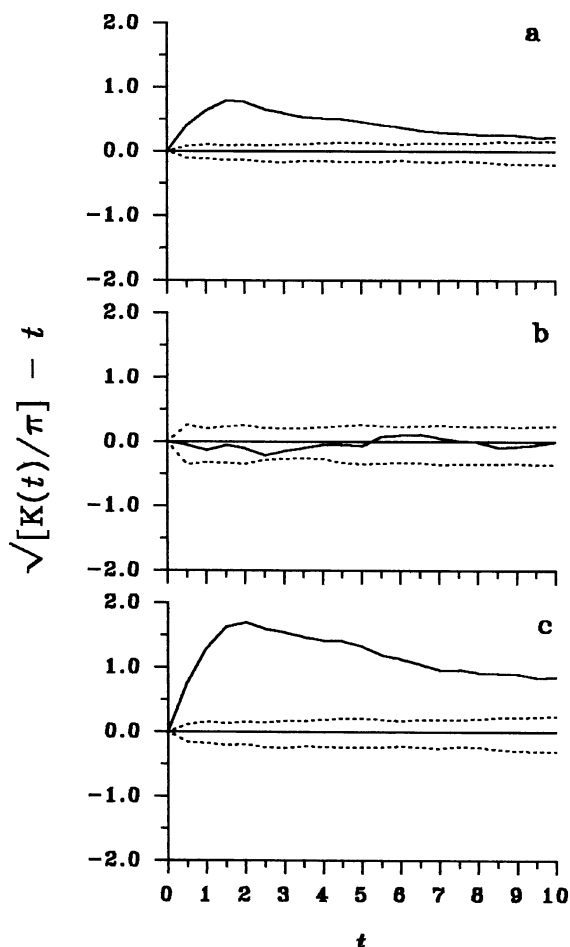


Fig. 3. Second-order spatial analysis of the distribution patterns of (a) all woody species, (b) *Retama sphaerocarpa* and (c) *Artemisia barrelieri*. Dotted lines give 95 % confidence intervals for complete spatial randomness (100 randomizations).

Single species distribution patterns

The elongated shape of the 100 m \times 20 m plot (Fig. 2) was a compromise to accommodate the plot on a stabilized part of the floodplain between recently active drainage channels. Second-order spatial analysis revealed a significantly clumped distribution of all shrubs with maximum clumping intensity at scales of 1.0–2.5 m (Fig. 3a). *Retama* shrubs alone were randomly distributed at all scales (Fig. 3b). *Artemisia* was significantly and strongly clumped at all scales with a maximum clumping intensity at 1.5–2.5 m (Fig. 3c).

When *Retama* shrubs were analyzed separately in classes of increasing canopy diameter, the spatial pattern changed from significantly clumped in the smallest size-class (Fig. 4a) to random (Fig. 4b, c), and to a pattern which was significantly regular at scales of 2.7–6.1 m (Fig. 4d).

Bivariate distribution patterns

Mature and juvenile shrubs of *Retama* showed a trend for negative association (statistical repulsion) at scales \leq 1 m (Fig. 5a). There was a significant positive association (attraction) between *Retama* and *Artemisia* at scales of up to 2.5 m (Fig. 5b). The maximum intensity at 1.0–1.5 m corresponds to the mean canopy radius of 1.25 m of the *Retama* shrubs under which *Artemisia* and other dwarf shrubs grow (Table 1). At larger scales, *Retama* and *Artemisia* were independently distributed.

The distribution of *Artemisia* was independent of that of the smallest canopy diameter class of *Retama* shrubs (Fig. 6a). There was a trend for positive association of *Artemisia* with shrubs in the 1–2 m diameter class at a scale of 0.5 m (Fig. 6b) and a significant positive association with the 2–3 m diameter class at scales of 0.5–1.2 m (Fig. 6c). The peaks at scales of 0.5 and 1.0 m, respectively, were similar to the mean horizontal canopy radius of the respective size-classes (0.75 and 1.3 m; Table 1). There was a significant positive association of *Artemisia* at scales of 0.5–3.8 m with the *Retama* shrubs in the $>$ 3 m diameter class (Fig. 6d). The association was particularly strong in the range 1.25–2.5 m with a maximum at 2 m, which again corresponds to the mean canopy radius of 2.15 m of this size-class.

Discussion

Demography

Retama sphaerocarpa often develops into a multi-stemmed shrub by resprouting from its root stock, particularly after shrubs have been burnt or severely damaged. Therefore, a size-class distribution based on the largest stem diameter can only serve as a rough approximation of age-classes of the above-ground parts of the shrubs. Approximate ageing of shrubs is possible by counting growth rings in slices from the top of the main

Table 1. Mean size of *Retama sphaerocarpa* (mature shrubs) and *Artemisia barrelieri* in a 100 m \times 20 m plot. For *R. sphaerocarpa*, data are also given for different size-classes of canopy diameter (n = number of shrubs).

Species	n	Basal \emptyset largest stem (cm)	Canopy \emptyset (m)	Canopy height (m)
<i>R. sphaerocarpa</i>				
All shrubs	112	2.34 \pm 0.11	2.51 \pm 0.13	1.97 \pm 0.09
\leq 1 m	17	0.96 \pm 0.09	0.77 \pm 0.05	0.84 \pm 0.09
1–2 m	32	1.63 \pm 0.09	1.51 \pm 0.05	1.34 \pm 0.07
2–3 m	30	2.52 \pm 0.12	2.59 \pm 0.06	2.14 \pm 0.12
$>$ 3 m	33	3.58 \pm 0.14	4.29 \pm 0.16	3.02 \pm 0.10
<i>A. barrelieri</i>	182	0.51 \pm 0.02	0.47 \pm 0.02	0.33 \pm 0.02

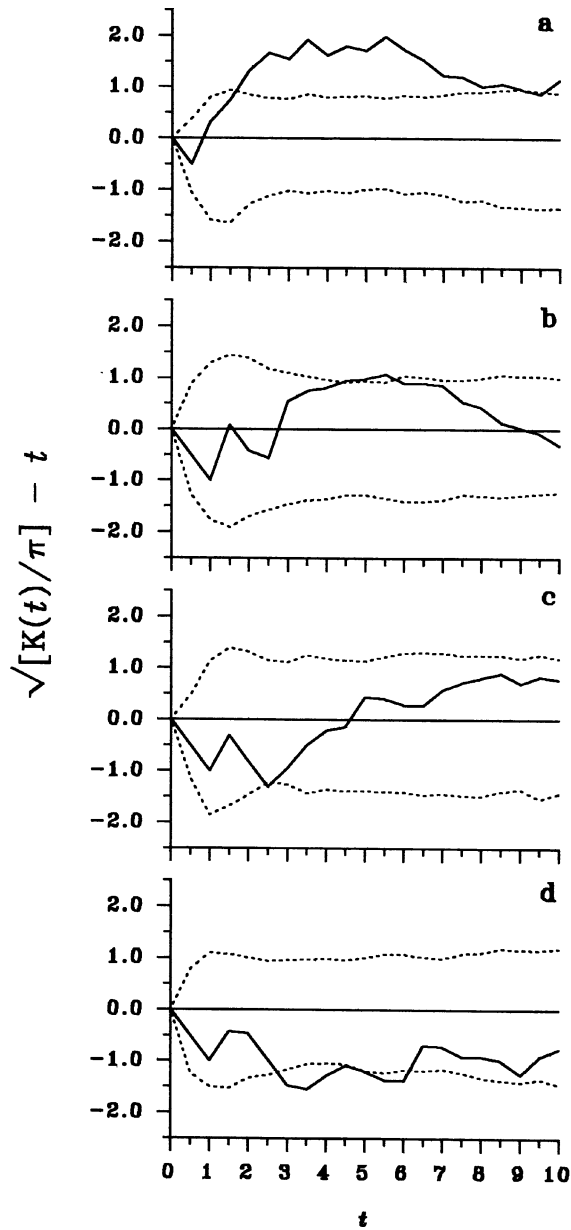


Fig. 4. Second-order spatial analysis of the distribution patterns of *Retama sphaerocarpa* in four classes of canopy diameter. (a) ≤ 1 m; (b) 1 - 2 m; (c) 2 - 3 m; (d) > 3 m.

rootstock and stem diameter - age regressions have been developed (L. Gutiérrez unpubl. data), but this method is destructive and therefore was not considered for our investigation. The size distributions of *Retama* and *Artemisia* are bimodal and irregular, respectively, and show gaps in the smaller size-classes, which is generally thought to indicate intermittent regeneration, provided that size approximates age (e.g. Keeley 1992). Size distributions with gaps in the smaller classes are com-

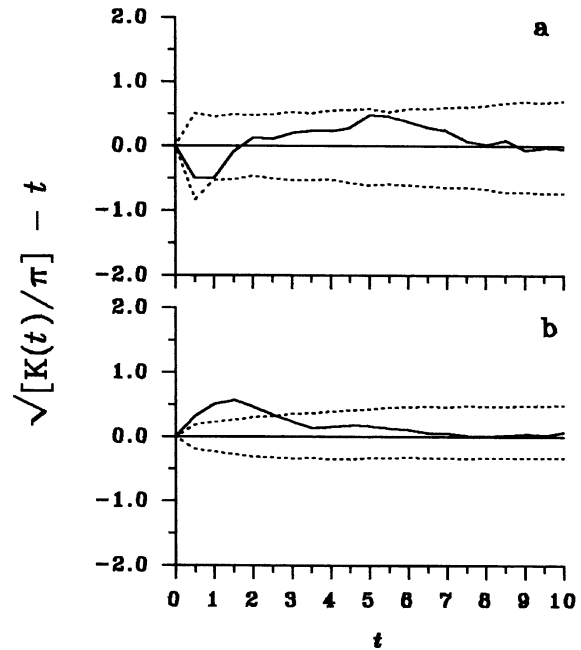


Fig. 5. Second-order spatial analysis of the bivariate distribution patterns of (a) mature and juvenile *Retama sphaerocarpa* shrubs, and (b) *Retama sphaerocarpa* (excluding juveniles) and *Artemisia barrelieri*.

monly found for perennial plants of arid and semi-arid regions (e.g. Barbour 1969; Fonteyn & Mahall 1981; Smith & Goodman 1987) as seedling survivorship and establishment become more sporadic with increasing aridity (Barbour 1969). Preliminary data on seedling survivorship suggest that this is also the case in *Retama* where total mortality in first-year seedlings was observed in 1993 and 1994 (Haase et al. unpubl. data). Mortality rates of mature shrubs are unknown. The dry floodplain was probably never used for agriculture because of the poor nutrient status of the soil and the potential danger of flash floods. Grazing by mixed flocks of sheep and goats does not affect *Retama* shrubs above seedling size. The cladodes contain alkaloids (Martín-Cordero et al. 1993) which make them unpalatable to livestock; alkaloids are also found in the leaves of the strongly aromatic *Artemisia*.

Spatial pattern

Our pattern analysis revealed that, if size-classes are ignored, *Retama* shrubs were randomly distributed at all scales. Significant clumping in the smallest size-class, however, decreased in the larger size-classes and there was an increasing trend towards regularity in the two largest classes of canopy diameter. The changing pattern is partly explained in terms of the increasing canopy diameter; shrubs in the largest diameter class had a

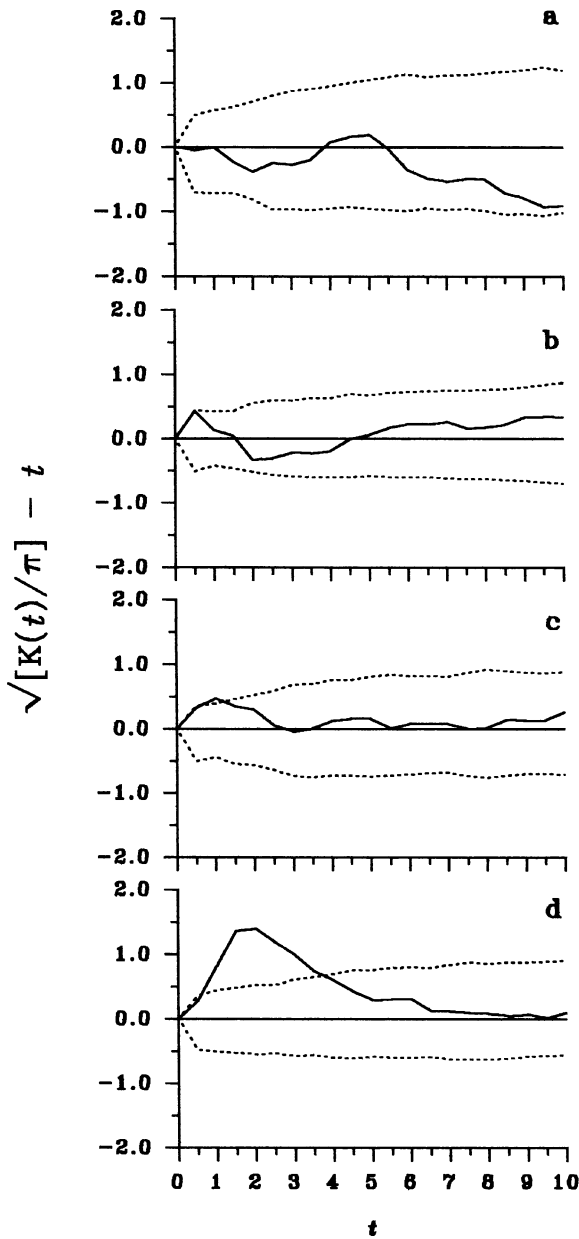


Fig. 6. Second-order spatial analysis of the bivariate distribution patterns of *Artemisia barrelieri* and *Retama sphaerocarpa* shrubs (excluding juveniles) of increasing canopy diameter. (a) ≤ 1 m, (b) 1–2 m, (c) 2–3 m, (d) > 3 m.

mean canopy diameter of 4.3 m, which probably accounts for a certain physical exclusion zone with respect to neighbouring shrubs, and may simply reflect competition for space, but not necessarily for other resources.

Clumping caused by the initial regeneration pattern which decayed slowly towards randomness as individuals matured, was also found in *Capparis decidua* in the desert scrub of the Sudan (Greig-Smith & Chadwick

1965), in desert dwarf-shrub clumps in Namaqualand, South Africa (Prentice & Werger 1985) and in mixed savanna of *Acacia erioloba* and *A. mellifera* in the Kalahari Desert (Skarpe 1991). Few of the numerous studies on spatial pattern in arid and semi-arid perennials have reported regular distribution patterns (see reviews by Barbour 1973; Fowler 1986). Random and clumped distribution patterns appear to predominate in these as in other environments (Barbour 1973). Random and clumped distribution patterns do not imply lack of competition. The concept that intraspecific competition leads from aggregation to an ultimately regular distribution of individuals was based on even-aged or even-sized populations. If a plant population consists of a mosaic of individuals of different age and size-classes, as was the case in the surveyed *Retama* shrubland, mortality as a result of competition from neighbours may not have predictable effects on the spatial pattern (Wright 1982). In such a population, competition only needs to occur between seedlings and established individuals with the result that seedlings become restricted to patches between shrubs (Wright 1982). Such a distribution pattern, and a corresponding relationship between mature and juvenile shrubs, were also found for *Retama*. *Retama sphaerocarpa* seedlings germinating under the canopy of mature shrubs normally die within days or weeks following emergence because of unsuccessful competition with annual and perennial herbs and grasses. The negative association (repulsion) of juveniles and mature shrubs at a scale of ≥ 1 to < 1.5 m must therefore be seen in relation to the mean canopy radius of 1.25 m of the *Retama* shrubs in the plot.

Overall, the shrubs in our plot showed a significantly clumped pattern which resulted from the positive spatial association between the two shrubby components. The strong positive spatial association of *Retama* and *Artemisia* suggests that interspecific competition is low, probably as a result of niche separation. The two species occupy distinct tiers of the canopy and have different root systems (Freitag 1971) and so they are likely to access different sources of water during the dry season. The close relationship between the spatial scale of the association and horizontal canopy diameter of *Retama* suggests that facilitative effects predominate. In the largest size-class, the association between the two species became much stronger and also extended some distance beyond the mean canopy radius of the *Retama* shrubs in this size-class. In these larger and probably older shrubs, the effects of litter accumulation and soil amelioration had apparently accumulated with time (Pugnaire et al. 1996) and extended beyond the horizontal projection of the canopy.

Positive spatial association between tall shrubs and smaller, shorter-lived plant species has frequently been

observed in arid and semi-arid regions (e.g. Fowler 1986). Shrubs ameliorate their sub-canopy environment, both climatically and edaphically, leading to the creation of 'fertile islands' (Garner & Steinberger 1989) that are frequently more favourable for other species than for their own seedlings. On the dry floodplains of ephemeral rivers, *Retama* shrubs initially establish on bare soil and, as they grow, intercept and accumulate windblown silt and also organic debris, in addition to their own litter, under their canopy. This improves soil texture, fertility and water holding capacity, while shading by the canopy ameliorates air and soil surface temperatures. Since light levels under the sparse canopy are rarely limiting to the growth of understory plants, the sub-canopy space becomes a favourable habitat for other plant species. Such establishment and growth of clumps of vegetation associated with persistent species, has been termed 'nucleation' and is regarded as an important process determining spatial pattern during primary succession, ideally observed in homogeneous undisturbed environments (Yarranton & Morrison 1974). Our sample plot in *Retama* shrubland was deliberately selected in an area with minimal apparent environmental variation so that distribution patterns could be interpreted on the basis of biological factors only. The pattern observed – random dispersion of mature *Retama* shrubs which act as nuclei for colonisation by many other perennial and annual species (Pugnaire et al. in press) – was similar to a pattern of nucleation characteristic of the early stages of primary succession on sand dunes, another harsh environment (Yarranton & Morrison 1974). In contrast to other examples of nucleation described in the literature (Callaway 1992, 1994), however, because of the potentially limiting water resources we do not expect this open semi-arid shrubland to develop a stand density sufficient for islands to coalesce with time.

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