Spatial pattern in *Anthyllis cytisoides* shrubland on abandoned land in southeastern Spain

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Abstract. Univariate and bivariate distribution patterns of small shrubs on abandoned land in semi-arid southeastern Spain were investigated by second-order spatial analysis (Ripley's *K*-function). All shrubs (*Anthyllis cytisoides* and subdominant *Artemisia barrelieri*) were either randomly distributed or clumped at scales of 0.25 - 1.0 m. The pattern shown by *A. cytisoides* shrubs alone changed from clumped to random with decreasing density. Pattern analysis and demographic data suggest a successive replacement of *A. barrelieri*, which had high proportions (44 - 86 %) of dead shrubs, by the dominant *A. cytisoides*. In two of three plots there was a positive association between *A. cytisoides* and *A. barrelieri* at a scale of 0.25 - 0.5 m. In the third plot, believed to represent a more advanced stage of colonization, there was a negative association (repulsion) between the two species, presumably as a result of interspecific competition from *A. cytisoides*. Dead shrubs present in spring 1994 were randomly distributed in all plots. Living and dead *A. cytisoides* shrubs were positively associated at a scale of 0.5 m, suggesting that the shrubs died as a result of intraspecific competition in small clumps. The shrubland previously dominated by *A. barrelieri* is changing to *A. cytisoides* shrubland with increasing biomass and ground cover.

Keywords: *Artemisia barrelieri*; Competition; Mediterranean shrubland; Old-field succession; Second-order spatial analysis; Semi-arid.

Nomenclature: Sagredo (1987).

Introduction

Whenever an established vegetation is destroyed or disturbed, its recovery progresses through a sere of successional stages which may differ strongly in density, physiognomy and taxonomy from the original vegetation (e.g. Wood & del Moral 1988; Chapin et al. 1994). Changes in the density and physiognomy of the vegetation have strong effects on hydrology and soil erosion, particularly in arid and semi-arid environments. Here, in the usually sparse vegetation, different spatial distribution patterns of equal densities of plants can have different effects on plant water use, evapotranspiration and hydrology (Shuttleworth & Wallace 1985). Determination of the demography and patterns of sparse vegetation and the prediction of their development and possible change can therefore improve estimates of the hydrological balance of ecosystems (Wallace et al. 1990). In practice, however, such changes in the vegetative cover are rarely considered in models.

Sparse vegetation is typical of large areas of abandoned land in semi-arid southeastern Spain, which receive a mean annual rainfall of 200 - 400 mm and have up to four months of summer drought. These lands, often fields of irregular shapes and poorly defined margins depending on the local topography and soil texture, were formerly intermittently ploughed and sown with cereals. Arable cultivation ceased several decades ago and the 'fields' now support semi-natural shrublands (Puigdefábregas et al. 1996). These shrublands are presumed to represent an intermediate stage of an old-field succession. Therefore, the floristic composition, stand density and the spatial distribution patterns of the shrubs are expected to change with time which will have consequences for the hydrological balance.

As part of a wider research project (MEDALUS II - Mediterranean Desertification and Land Use) on the ecology of sparse vegetation and its effects on hydrology and soil erosion in a semi-arid environment, we investigated the trends of changes in plant density and distribution pattern. Although the land was successively abandoned and the present vegetation must therefore be a mosaic of different ages, the exact time of abandonment of particular fields is usually not known and information on the development of the vegetation must be obtained by other means. As a result of cultivation, the abandoned fields provide spatially uniform habitats which offered, in addition to material for demographic studies, the possibility for analysis and ecological interpretation of the distribution patterns and spatial relationships of perennial plants. These were investigated by second-order spatial analysis based on Ripley's *K*-function (Ripley 1976, 1981), a method which is able to detect

patterns in plant communities at different spatial scales, which are often not directly observable (e.g. Prentice & Werger 1985; Sterner et al. 1986; Skarpe 1991). We report here the demography and distribution patterns in a semi-arid shrubland with two major components, the sub-shrubs *Anthyllis cytisoides* (*Fabaceae*) and *Artemisia barrelieri* (*Asteraceae*), which were analysed in order to (1) test the null hypothesis that all perennial plants, including *A. cytisoides* and *A. barrelieri*, were randomly distributed, (2) investigate the spatial relationships between *A. cytisoides* and *A. barrelieri* and (3) determine the spatial pattern of mortality of shrubs.

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, 600 - 1000 m altitude). A detailed description of the field site is found in Puigdefábregas et al. (1996).

The climate is semi-arid; the 5-yr record for the period 1990 - 1994 gives a mean annual temperature of 15.7 °C (January 7.5 °C, August 25.4 °C) and mean annual rainfall of 259 mm (R. Lázaro unpubl. data). There is a pronounced dry season from May to September, often with practically no rainfall from June to August, and large variation both in the pattern and total amounts of rainfall from year to year.

Weathering and erosion of the mica-schist bedrock has produced extensive alluvial fan systems and colluvial deposits at the base of the mountain slopes. The deeper stony soils on these alluvial fans were used for dry-cropping with cereals following winters with sufficient rainfall. These ephemeral 'fields' have been successively abandoned since the 1960s. After cultivation ceased permanently, the lands were occupied by annual herbs and grasses, then by the dwarf-shrub *Artemisia barrelieri* and at present by the leguminous sub-shrub *Anthyllis cytisoides* with a ground cover of winter annuals (Puigdefábregas et al. 1996). Above the alluvial fans, tussock grassland of *Stipa tenacissima*, containing *A. cytisoides* as a minor component, covers the rocky mountain slopes up to the ridges at 800-1100 m. We assume that these *A. cytisoides* populations served as sources of seed for the colonization of the abandoned fields below.

Anthyllis cytisoides is a drought-deciduous subshrub which can grow to a height of 1.5 m. It is endemic to the western Mediterranean region (de Bolós & Vigo 1984). *Anthyllis cytisoides* occurs as a minor component in various types of shrubland and grassland, but it

is particularly common on disturbed sites e.g. after fires, in abandoned fields and along roadsides, where it forms low shrublands of varying density and composition. *Anthyllis cytisoides* possesses a comparatively deep root system which penetrates to a depth of ca. 5 m (Domingo et al. 1991). The young stems are green and remain photosynthetically active during the dry season when the shrubs are normally leafless. *Artemisia barrelieri* is a subshrub with small evergreen leaves and attains a height of 20 - 30 cm. It is endemic to the dry Mediterranean region of Spain (Freitag 1971). The root system only penetrates the soil to a depth of 20 - 35 cm, but is concentrated mainly in the upper 10 cm (Freitag 1971). Thus it depends on soil moisture accumulated from seasonal precipitation which is only available for a limited period each year. The species thrives particularly in sub-ruderal conditions, e.g. on fine-textured soils over alluvial sediments which are only intermittently used for agriculture (Freitag 1971). *Artemisia barrelieri* is only common in open plant communities of dry regions and is apparently a poor competitor; under more moist conditions it is replaced by other species of *Artemisia* (Freitag 1971).

Sampling method and statistical analysis

Three 10 m × 10 m plots in *A. cytisoides* shrubland were marked out in apparently homogeneous habitats (minimal relief, no rock outcrops or large stones) between October 1993 and May 1994. All plots were located on the middle parts of gently sloping alluvial fans on the western side of the Rambla Honda at 640 - 660 m a.s.l. One plot (plot 3) was extended to 20 m × 10 m because of the small number of *A. barrelieri* shrubs present. After the plots had been divided into 5 m × 5 m subplots with tape-measures, the coordinates of all perennial species, including the remains of dead shrubs, were recorded to the nearest 5 cm with a tape-measure. Basal diameter of the largest stem, shrub height, and the largest horizontal diameter of the canopy were measured, and the proportion of dead canopy was estimated. All three stands were revisited in early April 1995 to assess the extent of canopy dieback and shrub mortality after a severe drought in the summer of 1994.

All shrubs of *A. cytisoides* and *A. barrelieri* were grouped into 0.2 cm size classes based on stem diameter to give size-frequency distributions for each plot. The distribution of the shrubs was investigated by second-order spatial analysis with Ripley's *K*-function, a cumulative density function which uses the second moment, i.e. the variance of all point-to-point distances to evaluate two-dimensional distribution patterns (Ripley 1976, 1981; Diggle 1983; Upton & Fingleton 1985). A detailed description of the application of this method in

ecology has been given by Haase (1995). We started our analysis at a radius t of 0.25 m with 0.25 m increments up to 5.0 m, i.e. one half of the plot length. Edge corrections were calculated by the weighting method described by Getis & Franklin (1987) and modified by Haase (1995). The sample statistic was plotted as the derived variable

$$\sqrt{K(t)/\pi} - t \qquad (1)$$

which has zero expectation for any value of t when the pattern is Poisson random (Skarpe 1991). To evaluate statistical significance of the sample statistic, we used the values at the limit of the 2.5 % tails of 100 randomizations (mean ± 1.96 SD) for a 95% confidence interval. If the sample statistic is positive, and above the upper limit of the confidence region, i.e. significantly non-random, the sampled points have a clumped distribution at that scale, while significant negative deviation indicates a regular or uniform pattern (Diggle 1983). If the plot of the sample statistic remains within the bounds of the confidence interval for any given value of t, the null hypothesis of complete spatial randomness cannot be rejected.

The null hypothesis of spatial randomness was tested for all shrubs (*A. cytisoides*, *A. barrelieri* and other species) considered together and separately for each of the two major species, *A. cytisoides* and *A. barrelieri*. The spatial associations between *A. cytisoides* and *A. barrelieri*, and between living and dead shrubs of *A. cytisoides* were investigated with a modified procedure for analysis of bivariate distribution patterns (Diggle 1983; Upton & Fingleton 1985; Andersen 1992). Additionally, the distribution of dead shrubs was analysed to investigate a possible pattern of shrub mortality.

Results

Demography

Anthyllis cytisoides and *A. barrelieri* were the exclusive shrub species in plots 1 and 3 (Table 1). Plot 2 additionally contained one specimen of *Asparagus stipularis* and one dead *Thymus* species.

Plot 1 had similar numbers of *A. cytisoides* and *A. barrelieri* (Table 1; Fig. 1a), but the proportion of dead shrubs differed greatly between the two species (9 % and 86 %, respectively, at the first observation). Plot 2 had twice the density of *A. cytisoides*, but a similar density of *A. barrelieri* to plot 1; the proportions of dead shrubs were 23 % and 44 %, respectively. The high stand density in plot 2 was associated with a significantly ($P < 0.01$) smaller mean canopy diameter of *A. cytisoides* shrubs compared to the two other plots
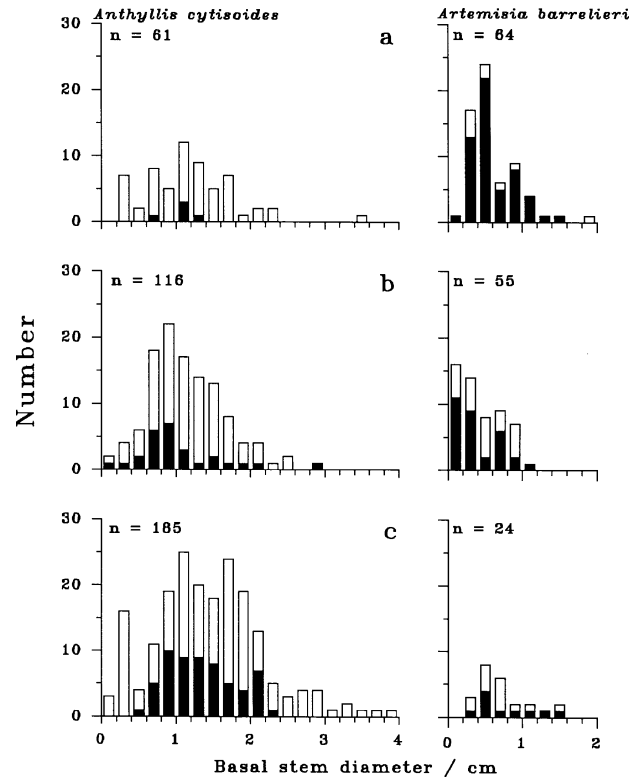

Fig. 1. Size-class distribution (basal diameter of the largest stem) of *Anthyllis cytisoides* and *Artemisia barrelieri* in three plots. Parts (**a**), (**b**) and (**c**) are for plots 1 - 3, respectively. Dead shrubs are shown in black.

(Table 2). Plots 3a and 3b had similar densities (Table 1) and proportions of dead shrubs of *A. cytisoides* (37 % and 32 %). The density of *A. barrelieri* in plot 3 was considerably lower (Table 1), while mean canopy diameter ($P < 0.05$; plot 2) and canopy height ($P < 0.001$; plot 1) of living *A. barrelieri* shrubs was significantly higher than that in plots 1 and 2 (Table 2), suggesting that these shrubs were older than those in the two other plots.

Plots 1 and 3 had irregular size-class distributions of *A. cytisoides* with comparatively high numbers of stems in the 0.2 - 0.4 cm diameter class (Fig. 1a, c), but the corresponding peak was missing in plot 2 which had a bell-shaped size-class distribution (Fig. 1b). In all three plots, dead *A. cytisoides* shrubs were restricted to the

Table 1. Number of shrubs in four 10 m × 10 m plots.

Plot	*Anthyllis*	*Artemisia*	Other	Total
1	58	64		122
2	116	55	2	173
3a	93	9		102
3b	92	15		107

Table 2. Mean diameter of the largest stem, mean horizontal canopy diameter and mean height of *Anthyllis cytisoides* and *Artemisia barrelieri* in three plots (mean ± SE; calculated for living shrubs only).

Plot	n	Stem diameter (cm)	Canopy diameter (m)	Canopy height (m)
Anthyllis				
1	52	1.30 ± 0.08	0.76 ± 0.04	0.65 ± 0.02
2	87	1.23 ± 0.05	0.63 ± 0.02	0.62 ± 0.02
3	122	1.54 ± 0.07	0.71 ± 0.03	0.69 ± 0.02
Artemisia				
1	8	0.74 ± 0.19	0.41 ± 0.08	0.23 ± 0.03
2	18	0.47 ± 0.07	0.41 ± 0.04	0.34 ± 0.03
3	14	0.73 ± 0.08	0.54 ± 0.03	0.41 ± 0.03

smaller and middle diameter-classes while dead *A. barrelieri* shrubs occurred in all size-classes (Fig. 1). The proportion of dead canopy of all living shrubs increased from 11.7 % in autumn to spring 1993/1994, when the plots were recorded, to 35.6 % in April 1995. The latter figure includes a considerable number of

shrubs (15.8 %) which had died during the summer drought of 1994 (Table 3). Overall mortality of *A. cytisoides* during the drought was much higher (17.2 %) than that of *A. barrelieri* (4.9 %).

Spatial distribution: univariate patterns

The distribution of all shrubs (*A. cytisoides* and *A. barrelieri*) was not significantly different from random in plot 3 (Fig. 2c). In plot 1 and plot 2, however, the distribution was significantly different from random at scales of 0.25 m and 0.25 - 1.0 m, respectively (Fig. 2a, b). The significant positive deviation of the sample statistic from random suggests a clumped distribution of the shrubs at these scales. In plot 2, which had a comparatively high density, clumping was particularly strong at a scale of 0.25 - 0.5 m. The distribution of *A. cytisoides* shrubs was random at all scales in plot 1, but was significantly non-random (clumped) at almost all scales in plot 2 (Fig. 3a, b). In plot 3, *A. cytisoides* shrubs were clumped at a scale of 0.5 m and at
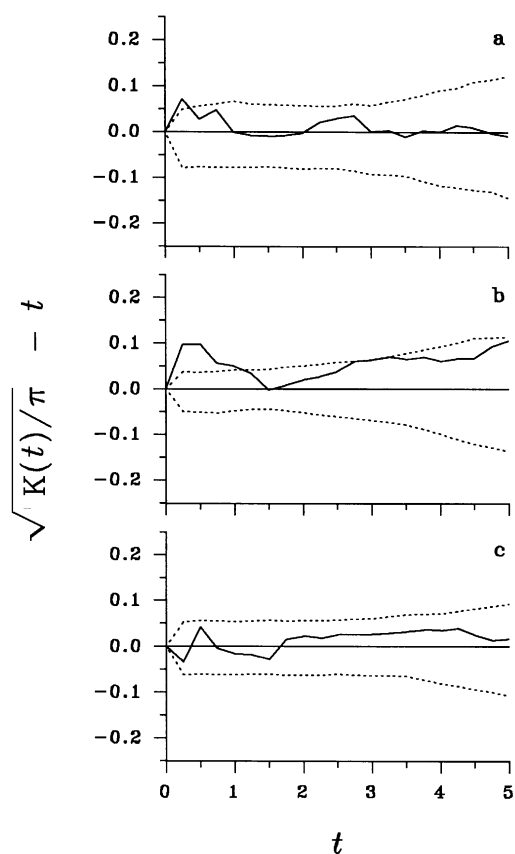

Fig. 2. Second-order spatial analysis of the distribution patterns of all shrubs in (**a**) plot 1, (**b**) plot 2, (**c**) plot 3. The dotted lines give the 95% confidence limits.
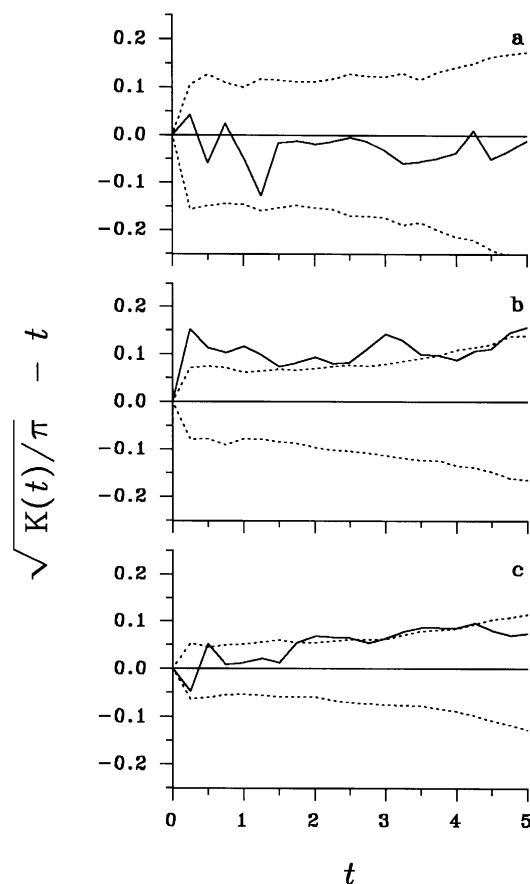

Fig. 3. Second-order spatial analysis of the distribution patterns of *Anthyllis cytisoides* shrubs in (**a**) plot 1, (**b**) plot 2, (**c**) plot 3. The dotted lines give the 95% confidence limits.
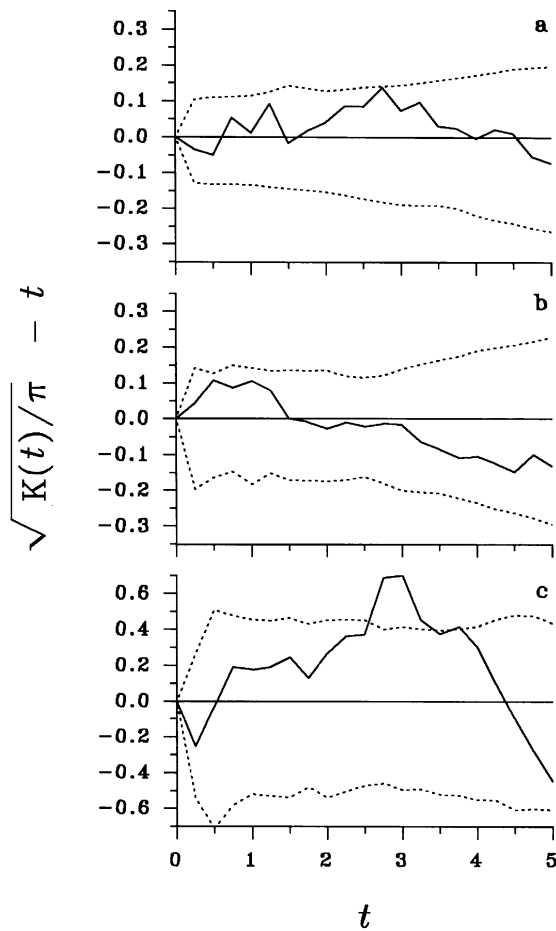
Fig. 4. Second-order spatial analysis of the distribution patterns of *Artemisia barrelieri* shrubs in (**a**) plot 1, (**b**) plot 2, (**c**) plot 3. The dotted lines give the 95% confidence limits.
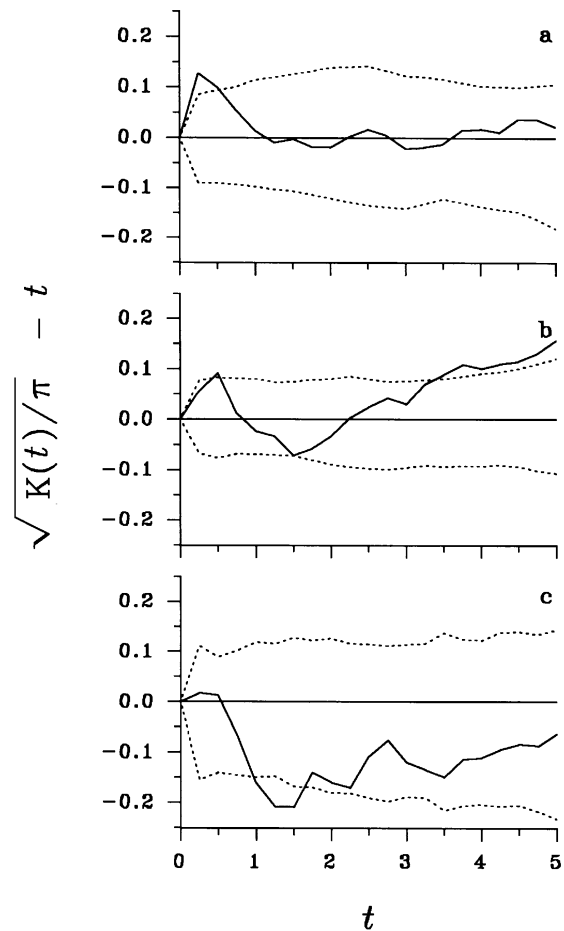
Fig. 5. Second-order spatial analysis of the bivariate distribution patterns of *Anthyllis cytisoides* and *Artemisia barrelieri* in (**a**) plot 1, (**b**) plot 2, (**c**) plot 3. The dotted lines give the 95% confidence limits.

various larger scales (Fig 3c). The distribution of *A. barrelieri* was random in plots 1 and 2 (Fig. 4a, b). The *A. barrelieri* shrubs in plot 3 were also randomly distributed at small scales but showed a clumped distribution at 2.75 - 3.75 m (Fig. 4c).

Shrubs which were dead by the spring of 1994 were randomly distributed in all plots (results not shown)

Table 3. Proportion of dead canopy of shrubs in the spring of 1994 (living shrubs only) and 1995 (including recently dead shrubs) and mortality of shrubs during the summer drought of 1994 (mean ± SE).

Plot	Dead canopy 1994 %	Dead canopy 1995 %	Number of dead shrubs	Mortality %
1	10.4 ± 3.2	44.5 ± 5.7	11	18.0
2	11.1 ± 2.3	25.6 ± 3.8	14	13.2
3	13.5 ± 2.2	36.7 ± 3.7	22*	16.2
Mean	11.7	35.6	11.8	15.8

* (3a = 6; 3b = 16)

which suggests an overall random shrub mortality irrespective of stand density.

Spatial distribution: bivariate patterns

The bivariate patterns of *A. cytisoides* and *A. barrelieri* were significantly non-random at various scales in all three plots. There was a positive association at a scale of 0.25 - 0.5 m in plot 1 and at 0.5 m and 3.5 - 5.0 m in plot 2 (Fig. 5a, b). In plot 3, however, there was a negative association (statistical repulsion) at a scale of 1.0 - 1.5 m (Fig. 5c).

Analysis of the spatial relationship between living and dead *A. cytisoides*, carried out for plots 2 and 3 only because the number of dead shrubs in plot 1 was too small, revealed that living and dead *A. cytisoides* shrubs were randomly associated and positively associated at a scale of 0.5 m, respectively (Fig. 6a, b). The overall trend was one of positive association in both plots.
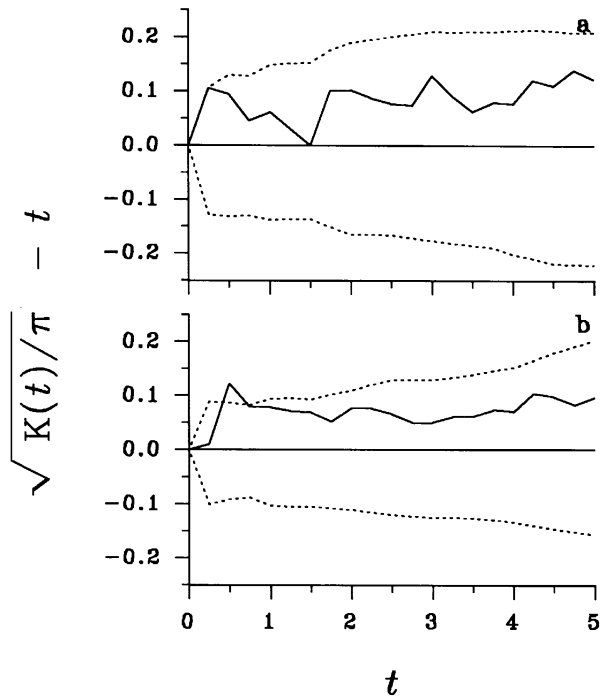
Fig. 6. Second-order spatial analysis of the bivariate distribution patterns of living and dead *Anthyllis cytisoides* in (**a**) plot 2, (**b**) plot 3. The dotted lines give the 95% confidence limits.

Discussion

Spatial patterns and spatial relationships in plant communities can reveal information on stand history, population dynamics, and intraspecific and interspecific plant-plant interactions. The distribution patterns of shrubs and trees from arid and semi-arid environments have received particular attention from plant ecologists and a general hypothesis of the development of the observed patterns has been established (Anderson 1967, 1971; Barbour 1973; King & Woodell 1973; Cox 1987). As a result of seed dispersal mechanisms and availability of seedling habitats, seedlings may initially have a clumped distribution, but density-dependent mortality can alter this pattern to a random distribution of intermediate-sized shrubs and ultimately to an overdispersed (regular) pattern of mature shrubs (Greig-Smith & Chadwick 1965; Anderson 1971; Schlesinger & Gill 1978; Phillips & MacMahon 1981; Skarpe 1991). On the other hand, Zhang & Skarpe (1995) found a continued aggregated distribution in the semi-arid subshrub *Artemisia halodendron*. A trend towards regularity in the spatial pattern is usually explained in terms of the increasing importance of competition for resources with increasing shrub size (e.g. King & Woodell 1973; Phillips & MacMahon 1981). If all species are considered together, the distribution pattern of shrubs in the analysed *Anthyllis cytisoides* shrubland shows a corresponding

trend. The clumped pattern at small scales in plots 1 and 2 changed to a random pattern in the presumably older plot 3. Pattern analysis of *A. cytisoides* alone showed a different trend, however, the pattern being random at low density (plot 1) and clumped at higher density (plot 2 and 3).

If more than one codominant species is involved, the observed distribution patterns may be additionally influenced by interactions between the different species. If interspecific competition is stronger than intraspecific competition, a negative association between two species would be expected (e.g. Kenkel 1994). This was indeed found for *A. cytisoides* and *A. barrelieri* in plot 3. It appeared, however, that this spatial relationship had developed from an initially positive association between the two species in plots 1 and 2. This is supported by the demographic results which also suggest that the three plots represent at least two different stages of colonization.

The large number of dead *A. barrelieri* in plots 1 and 2 and the small number of these shrubs left in plot 3 suggest that *A. barrelieri*, which apparently dominated an earlier stage, has been successively replaced by *A. cytisoides*. *Anthyllis cytisoides* grows to a larger size and uses more resources (Table 2), given suitable environmental conditions, which eventually leads to the decline of *A. barrelieri* which is regarded as a poor competitor (Freitag 1971). Such a successional trend has also been suggested by Puigdefábregas et al. (1996). In the Rambla Honda, only a few small patches of almost pure *A. barrelieri* stands still remain. As an alternative explanation, both species could have colonised the abandoned land at the same time and the *A. barrelieri* component is declining simply because of a shorter life-span. The relationship between the univariate and bivariate patterns, particularly in plot 1, however, appears to favour the former hypothesis. In plot 1, both single-species patterns are random but the combined pattern is clumped at a scale of 0.25 m, a distance equal to the mean crown radius of *A. barrelieri* shrubs (Table 2). The positive association at a scale of 0.25-0.5 m between *A. cytisoides* and, mostly dead, *A. barrelieri* in plots 1 and 2 suggests that the presence of an *A. barrelieri* shrub may facilitate the establishment of *A. cytisoides* seedlings nearby. Established *A. barrelieri* shrubs provide shade and locally diminish environmental extremes, but in particular, the strongly aromatic smell of its foliage may discourage browsing of this shrub and thus also protect seedlings of other species growing under or near its canopy. Similar twofold relationships have been described for other pairs of species in arid environments (see review by Fowler 1986).

As in other perennial species of dry environments, recruitment in *A. cytisoides* appears to occur only

intermittently. None of the new seedlings observed in the spring of 1994 were relocated in 1995 (Haase et al. unpubl.). The relative maxima in the 0.2 - 0.4 cm stem diameter class suggests a comparatively recent episode of recruitment of *A. cytisoides*. It is possible that because of the high shrub density, plot 2 did not provide the necessary habitats for establishment and growth of seedlings. This plot contained 107 living shrubs/100 m^2 (87 *A. cytisoides* shrubs) instead of 61 to 74 shrubs/100 m^2 (including the recruited shrubs) in the other plots. We therefore postulate that even under favourable environmental conditions, a density of approximately 1/ m^2 may constitute the maximum density of these shrublands.

The positive association of dead with living *A. cytisoides* shrubs at a scale of 0.5 m in plot 3 and the overall trend for positive association in plots 2 and 3 suggest that death of shrubs occurred as a result of unequal competition in small clumps, which probably consisted of both dominant and suppressed individuals, and eventual mortality of the smaller shrubs (e.g. Kenkel 1988). Almost all dead *A. cytisoides* had stem diameters in the smaller and middle size-classes (Fig. 1) which also suggests that the shrubs had not yet reached their maximum age and had died of causes other than senescence.

Mortality probably occurred as a result of unequal intraspecific competition for soil moisture which becomes the major limiting resource during the dry season. Even after all their above-ground parts have died, *A. cytisoides* shrubs have the ability to resprout from the rootstock in the following growing season (L. Gutiérrez pers. comm.). No resprouting of the dry shrubs was observed by April 1995, however, suggesting that the shrubs had in fact died during the previous summer drought. The observed high levels of mortality and canopy dieback after just one dry year indicates that *A. cytisoides* is not particularly drought resistant when compared with other common perennial species (Haase et al. unpubl. data), at least not in the high densities typical of present stands. The local predominance of *A. cytisoides* may be a result of temporarily favourable environmental conditions during the period following the abandonment of cultivation and of its ability to recover from browsing damage by domestic stock. Whether the dead shrubs will be replaced by seedlings of *A. cytisoides* or of other species is not known and will probably depend on the rainfall regime of subsequent years. Because of the generally highly variable rainfall, it is expected that stand density and cover of the shrubland will also be subject to considerable year-to-year variation in the future. Since *A. cytisoides* shrublands provide protection against soil erosion and are an important forage for browsing livestock, their temporary decline after prolonged periods with low rainfall would have a significant effect on local pastoralism.

References

Andersen, M. 1992. Spatial analysis of two-species interactions. *Oecologia* (*Berl.*) 91: 134-140.

Anderson, D.J. 1967. Studies on structure in plant communities V. Pattern in *Atriplex vesicaria* communities in southeastern Australia. *Austr. J. Bot.* 15: 451-458.

Anderson, D.J. 1971. Pattern in desert perennials. *J. Ecol.* 59: 555-560.

Barbour, M.G. 1973. Desert dogma re-examined: root/shoot production and plant spacing. *Am. Midl. Nat.* 89: 41-57.

Chapin, F.S. III, Walker, R.L., Fastie, C.L. & Sharman, L.C. 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecol. Monogr.* 64: 149-175.

Cox, G.W. 1987. Nearest-neighbour relationships of overlapping circles and the dispersion pattern of desert shrubs. *J. Ecol.* 75: 193-199.

de Bolós, O. & Vigo, J. 1984. *Flora dels Països Catalans.* Vol. I. Editorial Barcino, Barcelona.

Diggle, P.J. 1983. *Statistical analysis of spatial point patterns.* Academic Press, London.

Domingo, F., Puigdefábregas, J., Clark, S.C., Incoll, L.D. & Lockwood, J.G. 1991. Plant physiological behaviour in relation to water in a semiarid environment in southeast Spain. In: Kienitz, G., Milly, P.C.D., van Genuchten, M.T.H., Robsjerg, D. & Shuttleworth, W.J. (eds.) *Hydrological interactions between atmosphere, soil and vegetation*, pp. 335-343. IAHS Publication No. 204, Wallingford.

Fowler, N. 1986. The role of competition in plant communities in arid and semiarid regions. *Annu. Rev. Ecol. Syst.* 17: 89-110.

Freitag, H. 1971. Die natürliche Vegetation des südostspanischen Trockengebietes. *Bot. Jahrb.* 91: 11-310.

Getis, A. & Franklin, J. 1987. Second-order neighborhood analysis of mapped point patterns. *Ecology* 68: 473-477.

Greig-Smith, P. & Chadwick, M.J. 1965. Data on pattern within plant communities. III. *Acacia-Capparis* semi-desert scrub in the Sudan. *J. Ecol.* 53: 465-474.

Haase, P. 1995. Spatial pattern analysis in ecology based on Ripley's *K*-function: Introduction and methods of edge correction. *J. Veg. Sci.* 6: 575-582.

Kenkel, N.C. 1988. Pattern of self-thinning in jack pine: testing the random mortality hypothesis. *Ecology* 69: 1017-1024.

Kenkel, N.C. 1994. Bivariate pattern analysis of jack pine - trembling aspen interaction. *Abstr. Bot.* 18: 49-55.

King, T.J. & Woodell, S.R.J. 1973. The causes of regular pattern in desert perennials. *J. Ecol.* 61: 761-765.

Phillips, D.L. & MacMahon, J.A. 1981. Competition and spacing patterns in desert shrubs. *J. Ecol.* 69: 97-115.

Prentice, I.C. & Werger, M.J.A. 1985. Clump spacing in a desert dwarf shrub community. *Vegetatio* 63: 133-139.

Puigdefábregas, J., Alonso, J.M., Delgado, L., Domingo, F., Cueto, M., Gutiérrez, L., Lázaro, R., Nicolau, J.M., Sánchez, G., Solé, A., Torrentó, J.R., Vidal, S., Aguilera, C., Brenner, A.J., Clark, S.C. & Incoll, L.D. 1996. The Rambla Honda field site: Interactions of soil and vegetation along a catena in semi-arid SE Spain. In: Thornes, J.B. & Brandt, J. (eds.) *Mediterranean desertification and land use*, pp. 137-168. John Wiley, New York, NY.

Ripley, B.D. 1976. The second-order analysis of stationary processes. *J. Appl. Prob.* 13: 255-266.

Ripley, B.D. 1981. *Spatial statistics.* John Wiley, New York, NY.

Sagredo, R. 1987. *Flora de Almería.* Instituto de Estudios Almerienses, Almería.

Schlesinger, W.H. & Gill, D.S. 1978. Demographic studies of the chaparral shrub *Ceanothus megacarpus* in the Santa Ynez Mountains, California. *Ecology* 59: 1256-1263.

Shuttleworth, W.J. & Wallace, J.S. 1985. Evaporation from sparse crops - an energy combination theory. *Q. J. R. Meteorol. Soc.* 111: 839-855.

Skarpe, C. 1991. Spatial patterns and dynamics of woody vegetation in an arid savanna. *J. Veg. Sci.* 2: 565-572.

Sterner, R.W., Ribic, C.A. & Schatz, G.E. 1986. Testing for life historical changes in spatial patterns of four tropical tree species. *J. Ecol.* 74: 621-633.

Upton, G. & Fingleton, B. 1985. *Spatial data analysis by example. Vol. 1. Point pattern and quantitative data.* John Wiley, New York, NY.

Wallace, J.S., Roberts, J.M. & Sivakumar, M.V.K. 1990. The estimation of transpiration from sparse dryland millet using stomatal conductance and vegetation area indices. *Agric. For. Meteorol.* 51: 35-49.

Wood, D.M. & del Moral, R. 1988. Colonizing plants on the Pumice Plains, Mount St. Helens, Washington. *Am. J. Bot.* 75: 1228-1237.

Zhang Wei & Skarpe, C. 1995. Small-scale species dynamics in semi-arid steppe vegetation in Inner Mongolia. *J. Veg. Sci.* 6: 583-592.