

Spatial pattern analysis in Namaqualand desert plant communities: evidence for general positive interactions

N. S. Eccles, K. J. Esler, & R. M. Cowling

Abstract

This paper investigates the spatial arrangement of individual plants in mapped plots in two desert communities in the winter rainfall region of South Africa. In both communities there was a very strong tendency towards clumped patterns when all plants were considered together. There was also a predominance of clumped patterns when the most abundant species in both communities were considered individually. When the arrangement of the most abundant species was considered relative to the arrangement of all other individuals at the within-clump scale, there was a high frequency of positive associations in both communities (62% and 65%). We speculate that these patterns represent a combination of seed dispersal strategies that favour clumped patterns and a predominance of positive interactions between plants in both of the communities. When specific pairwise associations between the most abundant species were considered at the within-clump scale, differences were apparent between the two communities. In the short strandveld community neutral associations predominated, while in the medium strandveld, neutral and positive association accounted for equal proportions of the associations. This between-plot difference was also apparent when the volumes of plants were related to an index of neighbourhood competitiveness. In the short strandveld there were no significant relationships while in the medium strandveld there were some weak (but significant) relationships. These differences were not altogether unexpected. If we assume that plants in the medium strandveld are generally longer-lived, then interactions between plants are likely to develop over a longer time and, therefore, are likely to be stronger.

Keywords: Coexistence, Diversity, Mutualism, Winter rainfall deserts

Introduction

The winter-rainfall Succulent Karoo of southern Africa is an unusual desert ecosystem. Local and regional species richness levels are higher than any other desert system with as many as four times the number of species as equivalent sized areas of North American winter rainfall deserts (Cowling et al. 1998). It is estimated that there are some 4489 species in an area of 112 000 km², with about 40% of these species being endemic to the biome (Hilton-Taylor 1996). It is also unusual in terms of the growth forms that dominate the system. Short- to medium-lived succulents (and in particular leaf succulents) predominate and the geophyte flora is unusually rich. In contrast, there is a comparative lack of grasses and large shrubs (Milton et al. 1997). Despite the unusual structural composition of these communities, the ratio of functional diversity to species diversity is relatively low, suggesting a great deal of niche overlap and species redundancy (Cowling et al. 1994). This poses the question: how is this diversity, with its apparent redundancy, maintained in the system? The answer to this is particularly elusive in the context of communities occurring on the coastal sand plains where small-scale heterogeneity is very limited and as such, the potential for diverse 'habitat niches' (Hubbell & Foster 1990) is also limited.

Since habitat niches cannot be invoked as the sole stabilizer of diversity, we need to look to biotic interactions and stochasticity (Shmida & Ellner 1984). Studies from the eastern transitional region of the Succulent Karoo (in the Southern Karoo Domain (Jürgens 1991)) have suggested cyclical succession as a good general model for within-community behaviour (Yeaton & Esler 1990). According to this model, several species of small-seeded Mesembryanthemaceae (the dominant leaf succulent shrubs) germinate and establish in open areas between established plants. This guild of pioneers then act as seed traps for wind-dispersed seeds and serve as facilitators during the establishment phase of the secondary colonizers. Once established, the colonizers out-compete the pioneer succulents and persist until they die. This type of behaviour is not unique to this desert system (e.g., Valiente-Banuet & Ezcurra 1991) and is essentially analogous to an assembly of loose or facultative host-parasitoid like relationships (Wilson & Nisbet 1997). Given this analogy it is possible to borrow (at least conceptually) the theoretical work described in Hassel et al. (1991) in order to explain the stability of the two guilds in such systems. These authors suggest that spatial heterogeneity in the distributions of the interacting species is a key stabilizing factor. While this explains the stable coexistence of the two guilds (the pioneer guild and the successor guild) within these systems, it does not explain the stable coexistence of several species within each guild. This is perhaps reflected in the simulation model of this cyclical succession dynamic in the eastern succulent karoo region proposed by Wiegand et al. (1995) which relies on the inclusion of small-scale disturbances in order to achieve coexistence of the five main species.

The Southern Karoo Domain is, however, characterized by far greater structural and functional diversity than the strictly winter rainfall Namaqualand-Namib Domain (Cowling et al. 1994; Milton et al. 1997). In addition, evidence for the competitive interactions which are crucial to this cyclical succession model, and which abound in the form of simple nearest neighbour relationships in the Southern Karoo Domain (e.g., Esler & Cowling 1993) are not a common feature in the Namaqualand-Namib Domain (R. M. Cowling & J. J. Midgley unpublished data). It would thus seem that there is an additional dimension to plant interaction (or stochasticity) which is important in the dynamics of these Namaqualand communities.

Therefore, our objectives in this study were: firstly, to generate hypotheses or predictions about the behaviour of individuals and species in two communities in the strongly winter-rainfall succulent vegetation of Namaqualand; and secondly, to speculate on how these could contribute to the maintenance of diversity in communities. To do this in a rigorous and quantitative manner we used an analysis of the spatial arrangement of individuals within the communities.

Materials and methods

Nomenclature

Nomenclature used was according to Arnold & DeWet (1993) for all taxa except the Mesembryanthemaceae (Mesembryanthema, Aizoaceae *sensu* Bittrich & Hartmann 1988) where it was according to the Bolus Herbarium (BOL). Families and authors for all species mentioned are listed in Table 2.

The study area is located near the mouth of the Groen River on the west coast of South Africa (30°51¹ S 17°34¹ E). The area receives predominantly winter rainfall with an estimated annual average of 140 mm. Fog and dew are a regular occurrence and may contribute significantly to the total precipitation. It is, however, unclear whether this additional precipitation can be used by plants (von Willert et al. 1992). Temperatures in the area are generally moderate. The average maximum temperature in January (the hottest month) is around 20 °C while the average minimum temperature in June (the coolest month) is around 9 °C. Frosts do not occur. Wind is a very important feature of the climatic regime (Desmet & Cowling 1998). Wind results in high evaporative demands (particularly during hot berg-wind events); it may result in physical damage to plants through sand blasting; and may have profound effects on dispersal phases (particularly seeds) in plant life cycles. The soils in the area are characterized by a shallow sandy orthic A horizon; a red apedal B horizon of variable depth (20–150 cm); and an underlying duripan or 'dorbank' subsoil. The combination of a B horizon of variable depth and an impenetrable subsoil result in a range of effective plant rooting depths. This appears to be correlated with the occurrence of the two characteristic plant communities in the area: the short strandveld occurring on shallower soils and the medium strandveld occurring on deeper soils. The short strandveld is dominated by plants which are structurally small (usually less than 50 cm tall) and often relatively short-lived. The most abundant species in this community are *Didelta carnosa* var. *tomentosa* (an annual or biennial), *Arctotis merxmulleri* (a geophyte), *Cephalophyllum spongiosum*, (a sprawling leaf succulent) and *Pteronia onobromoides*, (an evergreen, non-succulent shrub). Plants in the medium strandveld are generally much larger (up to 2 m tall). The most abundant species are *Pteronia onobromoides* and *Tetragonia fruticosa* (a semi-deciduous, fleshy-leaved shrub). Even species which are common to both communities (e.g., *Pteronia onobromoides* and *Othonna cylindrica*) are larger in the medium strandveld than in the short strandveld.

Table 1. Summary of pairwise associations between individuals of species with more than 40 individuals in the short strandveld plot. The codes used are: De – dead plants; Cs – *Cephalophyllum spongiosum*; Po – *Pteronia onobromoides*; Dc – *Didelta carnos* var. *tomentos*; Oo – *Osteospermum oppositifolium*; Ht – *Helichrysum trichostatum*; Rf – *Ruschia fugitans*; Oc – *Othonna cylindrica*; Eb – *Euphorbia burmannii*; Gc – *Galenia crystallina*; Zs – *Zygophyllum spinosum*; Am – *Arctotis merxmuelleri*; Vs – *Vanzijlia annulata*.

	De	Cs	Po	Dc	Oo	Ht	Rf	Oc	Eb	Gc	Zs	Am	Vs
De	0	0	0	+	+	0	0	0	+	0	0	0	0
Cs		0	+	+	0	0	0	0	0	0	0	0	0
Po			0	+	0	0	+	0	+	–	+	+	+
Dc				0	0	0	0	+	0	0	0	+	0
Oo					0	+	0	0	0	0	0	+	0
Ht						0	0	0	0	0	0	0	0
Rf							0	0	0	–	0	0	0
Oc								0	+	0	0	0	+
Eb									0	0	0	0	0
Gc										0	–	–	0
Zs											0	+	0
Am												0	–
Vs													0

Community analysis

A 12.5 × 25 m plot was laid out in the short strandveld community and another of 30 × 50 m was laid out in the medium strandveld. In each of these, the location, size (height and two crown diameters) and species of individuals with at least one dimension greater than 10 cm were recorded. In addition, the location and size of dead individuals were recorded. In the short strandveld plot, 1567 individuals representing 40 species were mapped while in the medium strandveld, 1534 individuals representing 36 species were mapped. These data were used to investigate several aspects of spatial pattern in each community. Firstly, we investigated the overall dispersion of individuals ignoring species. Secondly, we investigated the point patterns for individual species with more than 40 individuals. Thirdly, we considered all pairwise relationships between the species in this restricted subset of the data. Finally, we considered the distributions with each species with more than 10 individuals relative to all the other individuals in the community (Figure 1). These four aspects of pattern were investigated using the density functions of point-to-point distances for appropriate subsets of data. Ripley's univariate and bivariate K -functions were used for this (Diggle 1983; Ripley 1987). A weighting approach was used to correct for edge effects (Diggle 1983). This approach yields unbiased results for distances up to half the shortest side of the plot (Haase 1995). In order to make interpretation easier, the K -functions were transformed to $L(t)$ -functions (Prentice & Werger 1985; Rebertus et al. 1989). This transformation has the effect of stabilizing the variance and under complete spatial randomness the expectation for $L(t)$ is zero. For the univariate cases, 95% confidence limits of the $L(t)$ -functions for complete spatial randomness were estimated using random permutations of the plants in the plots. These were based on 100 simulations each. Departures of the empirical function below the lower confidence limit indicate significant regularity while positive values above the upper confidence limit indicate aggregation (Prentice & Werger 1985). For the bivariate analyses, confidence intervals were once again estimated using a randomization approach. In this case, however, the primary structure of each of the individual point patterns was retained and only their relative locations were randomized using toroidal shifts. Positive values above the confidence limits indicate significant 'attraction' between the subsets of points while negative values below the confidence limits indicate significant 'repulsion'.

In the case of the pairwise species comparisons where positive interactions were suggested, we calculated an index of asymmetry. In order to do this we defined a C-function for each species in the pair:-

where n_1 and n_2 are the number of individuals in each of the two subsets being compared; t is the distance from the focal individual which defines the scale at which pattern is being considered; A is the area of the plot; u_{ij} is the distance between the i th and the j th plants; $I_t(u)$ is defined to be 1 if $t \geq u$ or 0 otherwise (i.e. a counter variable); and w_{ij} is the weighting factor to correct for edge effects (the proportion of the circumference of the circle with radius u_{ij} and centered on the point i and passing through j that lies within the plot boundaries). Unlike the K -functions which are in essence the average of the density functions for all individuals in a population (and therefore symmetrical), the C -function is based on the coefficient of variation between density distribution for the individuals in each of the populations. For a species that is obligately associated with another, the variation should be low since all the individuals will be closely associated with the other species. In contrast, where the species is less obligately dependent on the association, the values for C will be greater since individuals will not always be associated with the other species. The index of asymmetry (cv ratio) between two species is then simply the ratio of the C -functions for each of the species.

Table 2. Summary of the associations between species with more than 10 individuals and all the other individuals in the two communities.

Species	SSV	MSV	Family
Dead	0	+	
<i>Cephalophyllum spongiosum</i> (L.Bolus) L.Bolus	+		Mesembryanthemaceae
<i>Pteronia onobromooides</i> DC.	+	+	Asteraceae
<i>Didelta carnosus</i> (L.f.) Aiton var.	+		Asteraceae
<i>tomentosa</i> (Less.) Roessler			
<i>Osteospermum oppositifolium</i> (Ait.) T.Norl.	+	+	Asteraceae Asteraceae
<i>Helichrysum trichostatum</i> (Thunb.) Less.	+		
<i>Ruschia fugitans</i> L.Bolus	0		Mesembryanthemaceae
<i>Othonna cylindrica</i> (Lam.) DC.	0	+	Asteraceae
<i>Euphorbia burmannii</i> E.Mey. ex Boiss.	+		Euphorbiaceae
<i>Galenia crystallina</i> (Eckl. & Zeyh.) Fenzl.	—		Aizoaceae
<i>Zygophyllum spinosum</i> L.	+		Zygophyllaceae
<i>Arctotis merxmuelleri</i> (Harv.) P.Beauv.	+	0	Asteraceae
<i>Vanzijlia annulata</i> (Aberger) L.Bolus	+		Mesembryanthemaceae
<i>Hermannia amoena</i> Dinter ex Friedr.-Holzh.	+		Sterculiaceae
<i>Asparagus capensis</i> L.	0	0	Asparagaceae
<i>Ficinia nigrescens</i> (Schrud.) J.Raynal	+		Cyperaceae Fabaceae
<i>Lessertia rigida</i> E.Mey	+		
<i>Limonium perigrinum</i> (P.J.Bergius) R.A.Dyer	+		Plumbaginaceae
<i>Hermannia cuneifolia</i> Jacq.	0		Sterculiaceae
<i>Ehrharta calycina</i> J.E.Sm.	—		Poaceae
<i>Crassula subaphylla</i> L.	+		Crassulaceae
<i>Trachyandra falcata</i> (L.f.) Kunth	—		Liliaceae
<i>Lampranthus multiseriatus</i> (L.Bolus) N.E.Br.	0		Mesembryanthemaceae
<i>Lycium ferocissimum</i> Meirs	0	0	Solanaceae
<i>Zygophyllum morsana</i> L.	+	+	Zygophyllaceae
<i>Eriochepalus africanus</i> L.	—	+	Asteraceae
<i>Stoeberia utilis</i> (L.Bolus) Van Jaarsv.		+	Mesembryanthemaceae
<i>Chrysanthemoides incana</i> Burn.f.) Norl.		+	Asteraceae
<i>Pharnaceum lanatum</i> Berl.	+	—	Aizoaceae
<i>Tetragonia fruticosa</i> L.	+	+	Aizoaceae
<i>Manochlamys albicans</i> (Aiton) Aellen		0	Chenopodiaceae
<i>Ruschia</i> sp.		0	Mesembryanthemaceae
<i>Pteronia divaricata</i> (P.J.Bergius) Less.		0	Asteraceae
<i>Euphorbia mauritanica</i> L.		+	Euphorbiaceae
<i>Asparagus lignosis</i> Burm.f.		+	Asparagaceae
<i>Senecio</i> cf. <i>Pinguifolius</i> (DC.) Sch.Bip.		+	Asteraceae
<i>Salvia lanceolata</i> Lam.		+	Lamiaceae

$$100.A. \frac{\sqrt{\left(\sum_{i=1}^{n_1} \left(\sum_{j=1}^{n_2} w_{ij}^{-1} I_t(u_{ij}) \right)^2 - \left(\sum_{i=1}^{n_1} \sum_{j=1}^{n_2} w_{ij}^{-1} I_t(u_{ij}) \right)^2 / n_1 \right)}}{n_2}$$

Table 3. Summary of pairwise associations between individuals of species with more than 40 individuals in the medium strandveld plot. The codes used are: De – dead plants; Zm – *Zygophyllum morganiana*; Po – *Pteronia onobromoides*; Ea – *Eriocephalus africanus*; Oo – *Osteospermum oppositifolium*; Oc – *Othonna cylindrica*; Am – *Arctotis merxmulleri*; Su – *Stoeberia utilis*; Ci – *Chrysanthemoides incana*; Pl – *Pharnaceum lanatum*; Tf – *Tetragonia fruticosa*.

	De	Zm	Po	Ea	Oo	Oc	Am	Su	Ci	Pl	Tf
De	0	+	+	-	+	0	0	+	+	0	+
Zm		0	+	0	+	0	0	0	+	+	+
Po			0	+	+	+	0	0	+	-	+
Ea				0	0	0	0	0	0	-	-
Oo					0	0	0	0	+	-	+
Oc						0	0	0	0	0	0
Am							0	0	+	0	0
Su								0	-	0	+
Ci									0	0	+
Pl										0	-
Tf											0

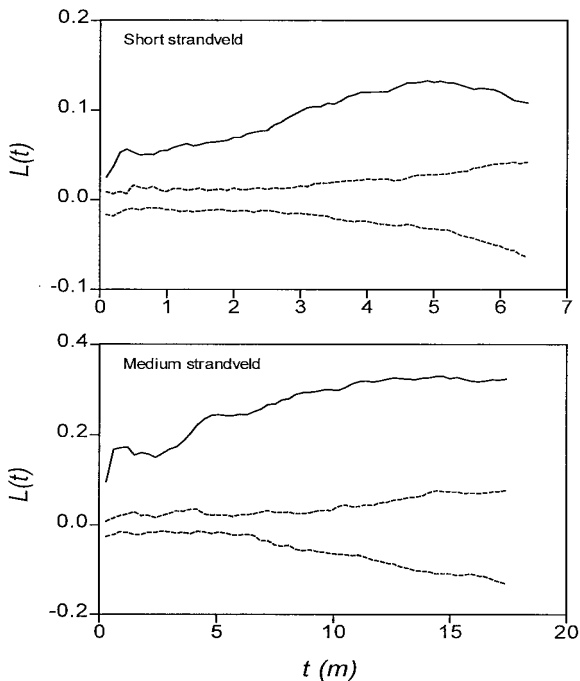


Figure 1. The overall dispersion patterns of individuals in two Namaqualand communities. The solid line represents the actual calculated L values while the broken lines represent the 95% confidence limits

When this index is close to one, the relationship can be said to be symmetrical. As it moves away from one (either greater or less than one), the symmetry becomes weaker. Whether the index becomes less than one or greater depends on which of the two species is less obligately dependent on the association. The

interpretation of these asymmetry indices is not without difficulties. From a purely statistical point of view, nothing is known about the sampling distribution of this statistic and it is even difficult to conceive of randomization approaches that might resolve this. For this reason we made no attempt to perform any significance tests on the values calculated. From a biological perspective, asymmetry may reflect an interaction that is tending towards commensalism (+/0) or it may simply be a result of demographic imbalances where one of the species is much less abundant than the other and its mutualism potential therefore becomes 'saturated'. Nonetheless, we felt that calculating this index was a valuable exercise since it provided a means for detecting any 'extreme' deviation from symmetry which might suggest that the observed positive interaction is in fact commensal (+/0) or even a +/- exploitation interaction.

Finally, in the absence of any time series data for mortality we were forced to make use of an indirect approach to assess the likelihood that thinning was an important aspect of within-clump dynamics. We assumed that if thinning were occurring, there should be a significant relationship between the size of individuals and an index of their neighbourhood 'competitiveness'. As an index of neighbourhood competitiveness, we used angular competition index described in Randall & Rejmánek (1993). This involves the calculation of the sum of the angles subtended by the crowns of competitors within a certain radius of the focal individual. The relationship between this index and the focal plant volumes was then investigated by means of regression. This analysis was carried out on the entire communities regardless of species as well as on the subsets of species that had more than 40 individuals. It is important to emphasize that pattern analysis is an explicitly inductive tool (Silvertown & Wilson 1994). Much of the criticism of pattern analysis protocols (e.g., Cale et al. 1989) stems from their use to detect particular processes (such as competition) which is a deductive rather than an inductive exercise. The basic logic behind the approach is that certain patterns can be linked with likely processes and these likely processes should form the basis for more deductive inquiry (Ludwig & Reynolds 1988; Silvertown & Wilson 1994). In general, more than one process can be invoked to explain any particular pattern. In such cases, the most parsimonious explanation for the patterns should be tested first. In addition, this analysis is based on static patterns. The results are therefore tentative and may well change after a second census of the communities as has been the experience in other similar studies conducted in tropical forests (Hubbell & Foster 1992).

Results

Community 1 – the short strandveld. When all individuals in this community were considered together the overwhelming pattern was significant clumping apparent at all scales up to 6 m (Figure 1). The majority of plants occur in dense clumps with a mean diameter of 2.5 m (sem=0.11 based on a subsample of 20 clumps), and which are surrounded by open ground. A greater diversity of patterns emerged when species with more than 40 individuals were considered on their own (Figure 2). In the case of dead plants, as well as *Cephalophyllum spongiosum* individuals, the distributions were clearly random over the entire range of scales investigated. The remainder of species all showed some degree of intraspecific clumping at assorted scales. For example, *Arctotis merxmulleri* and *Vanzijlia annulata* showed clumping at almost all scales except less than about 0.5 m where they did not depart significantly from complete spatial randomness. In contrast, clumping in *Galenia crystallina* and *Euphorbia burmannii* was restricted to less than 2 m and less than 0.5 m, respectively. Significant clumping at intermediate scales was evident in the case of *Ruschia fugitans* and *Othonna cylindrica*. Significant regularity was noticeably absent in all instances. In order to

simplify the interpretation of the pair-wise patterns, we made use of the observed strong first order clumping and restricted our attention to within-clump patterns (i.e. patterns which were apparent at scales less than a maximum of 4.0 m). Clumps were defined on the basis of the maximum clump size (4.0 m) rather than the mean of 2.5 m. At this scale, 71% of the interactions were not significantly different from randomness, 23% were positive and only 6% were negative (Table 1). This general trend of random interactions being most abundant followed by positive interactions and with negative interactions being the least abundant was consistent in all but two species. In the case of *Galenia crystallina*, negative associations accounted for 33% of the total while there were no positive interactions recorded. In *Pteronia onobromoides*, seven out of the 12 interactions were positive, four were random and one was negative. For the 18 positive interactions, the indices of asymmetry suggested that, in general, asymmetry was weak (Figure 3). In no instances were there any order of magnitude differences (i.e., cv ratios less than 0.1 or greater than 10). Where asymmetry was apparent, this was usually associated with large differences in the number of individuals in the two populations. In contrast to the dominance of neutral associations within-clumps when specific species pairs were considered, pairwise analyses between individual species and the rest of the community were characterized by a predominance of positive associations (62%) over either random (22%) or negative (15%) associations (Table 2). Finally, there were no significant relationships between the size of individuals and the competition index within-clumps at the 5% level.

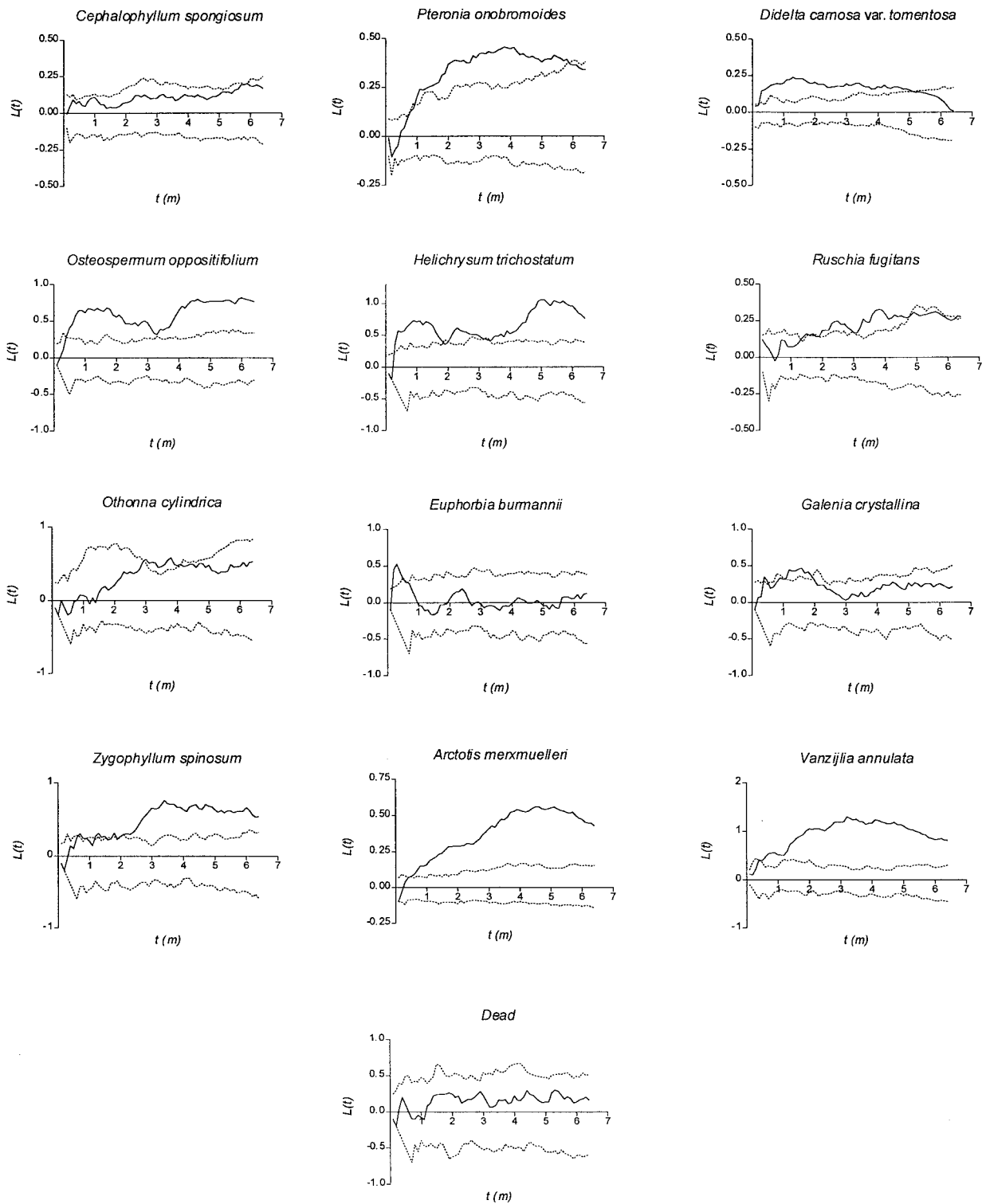


Figure 2. Dispersion patterns for species with more than 40 individuals in the short strandveld community. The solid line represents the actual calculated L values while the broken lines represent the 95% confidence limits.

Community 2 – the medium strandveld. As with the short strandveld, the overall pattern of dispersion in this community was towards clumping at all scales considered (Figure 1). In this case, the clumps tended to be larger than in the short strandveld (mean=5.17 m, sem=0.34, $n = 20$) which is not surprising given the larger overall size of the individuals. In terms of the patterns in univariate density functions for the 11 species which had more than 40 individuals (Figure 4), there were no species that were completely randomly distributed over the entire range of scales investigated. Only *Othonna cylindrica* showed any significant regularity and the rest of the species showed significant aggregation at some spatial

scale, although this was fairly 'weak' in the case of the dead plants and *Zygophyllum morganiana*. For the bivariate patterns, we once again restricted our attention to within-clump patterns, in this case patterns which were apparent at scales less than 7 m (Table 3). In this community, a much lower percentage of the interactions were random (49% as opposed to 71%). Positive interactions accounted for 38% of the remaining interactions while negative interactions made up 13%. The higher percentage of negative interactions in this community can largely be attributed to one species (*Pharnaceum lanatum*) which accounted for 55% of the negative interactions (7% of the total).

Removing this species from the calculation yielded 49% random interactions, 44% positive interactions and 7% negative interactions. Once again, there were generally no extreme asymmetries detected at the within-clump scale (Figure 5). In terms of the pairwise analyses between individual species and the rest of the individuals in the community, the ratios were similar to those in the short strandveld. Positive associations dominated (65%), followed by neutral associations (30%) while there was only one species (5%) which was negatively associated with all the rest (Table 2).

In the regression analyses of the relationship between individual volumes and their associated competition indices there was overall a statistically significant relationship at the 5% level. However, the biological significance of this is difficult to assess. The regression only accounted for 0.7% of the variation and no clear trend is evident from the scatter plot (Figure 6). In addition to this, overall 'trend', there were statistically significant relationships in *Eriocephalus africanus* and *Osteospermum oppositifolium* (F. prob=0.002 and 0.01 respectively). In the case of *Osteospermum oppositifolium*, the biological significance of this relationship was dubious as the variance accounted for by the regression was very low (4%). In *Eriocephalus africanus* the relationship was more meaningful with nearly 16% of the variance accounted for by the regression. In addition, the biological significance of this relationship is supported by the fact that *E. africanus* is negatively associated with *Tetragonia fruticosa* (Table 3). Despite the general weakness of these relationships, there are additional lines of evidence which suggest that competition may play a larger role in this community than in the short strandveld. The most important of these is the fairly high frequency of positive associations between dead plants and selected species (60%, Table 3). One possible explanation for this difference between the two communities is that plants in this medium strandveld community may be generally longer lived. If this difference in longevity can be assumed, it seems reasonable to hypothesize that the medium strandveld community should be the more 'structured' of the two communities. Because individuals are more persistent, it is likely that certain interactions (particularly competition) will have longer to develop and should therefore be more apparent.

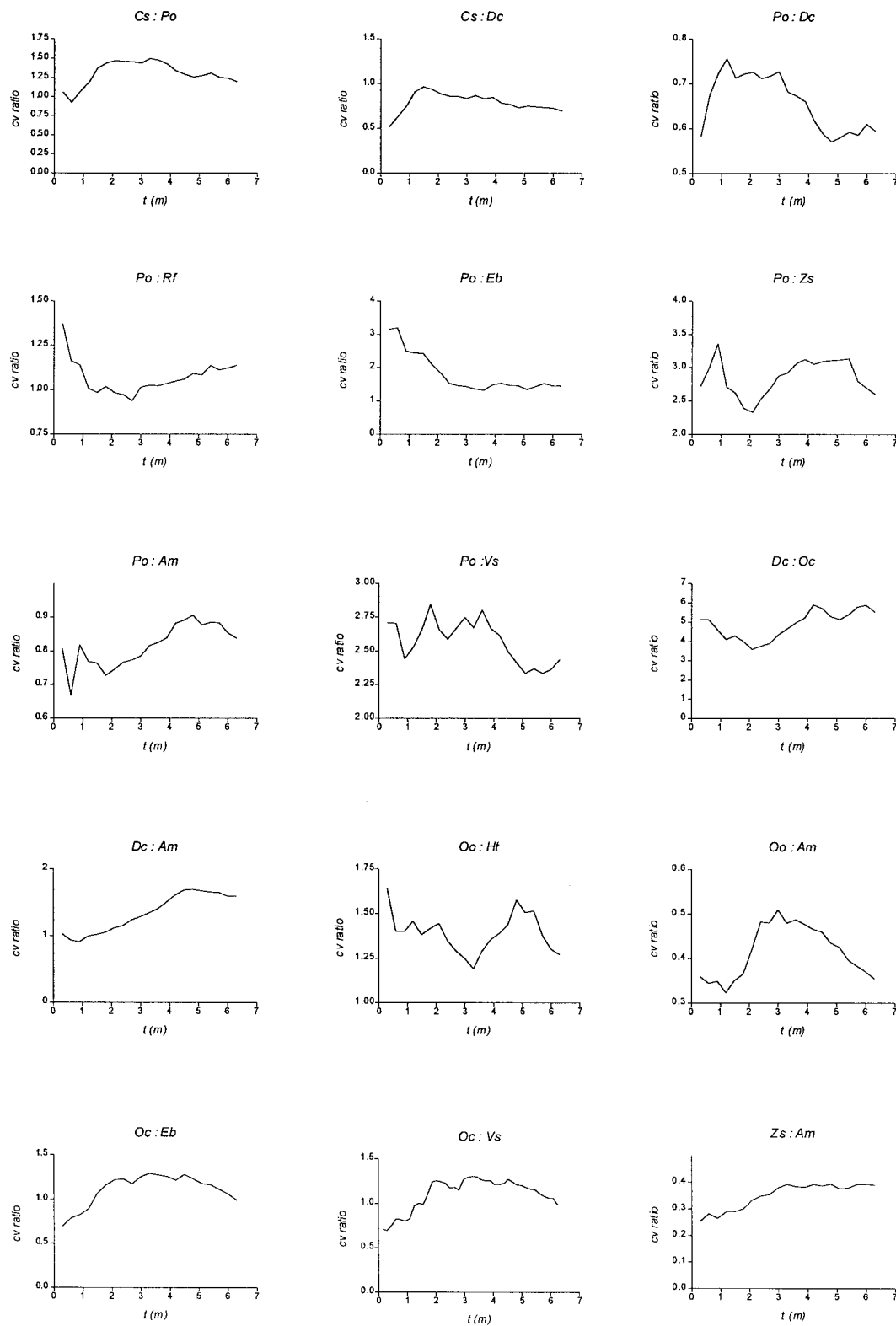


Figure 3. Asymmetry indices (cv ratio) for positive pairwise associations in the short strandveld community. Species codes are: Cs – *Cephalophyllum spongiosum*; Po – *Pteronia onobromoides*; Dc – *Didelta carnosa* var. *tomentosae*; Rf – *Ruschia fugitans*; Eb – *Euphorbia burmanii*; Zs – *Zygophyllum spinosum*; Am – *Arctotis merxmulleri*; Vs – *Vanzijlia annulata*; Oc – *Othonna cylindrica*; Oo – *Osteospermum oppositifolium*.

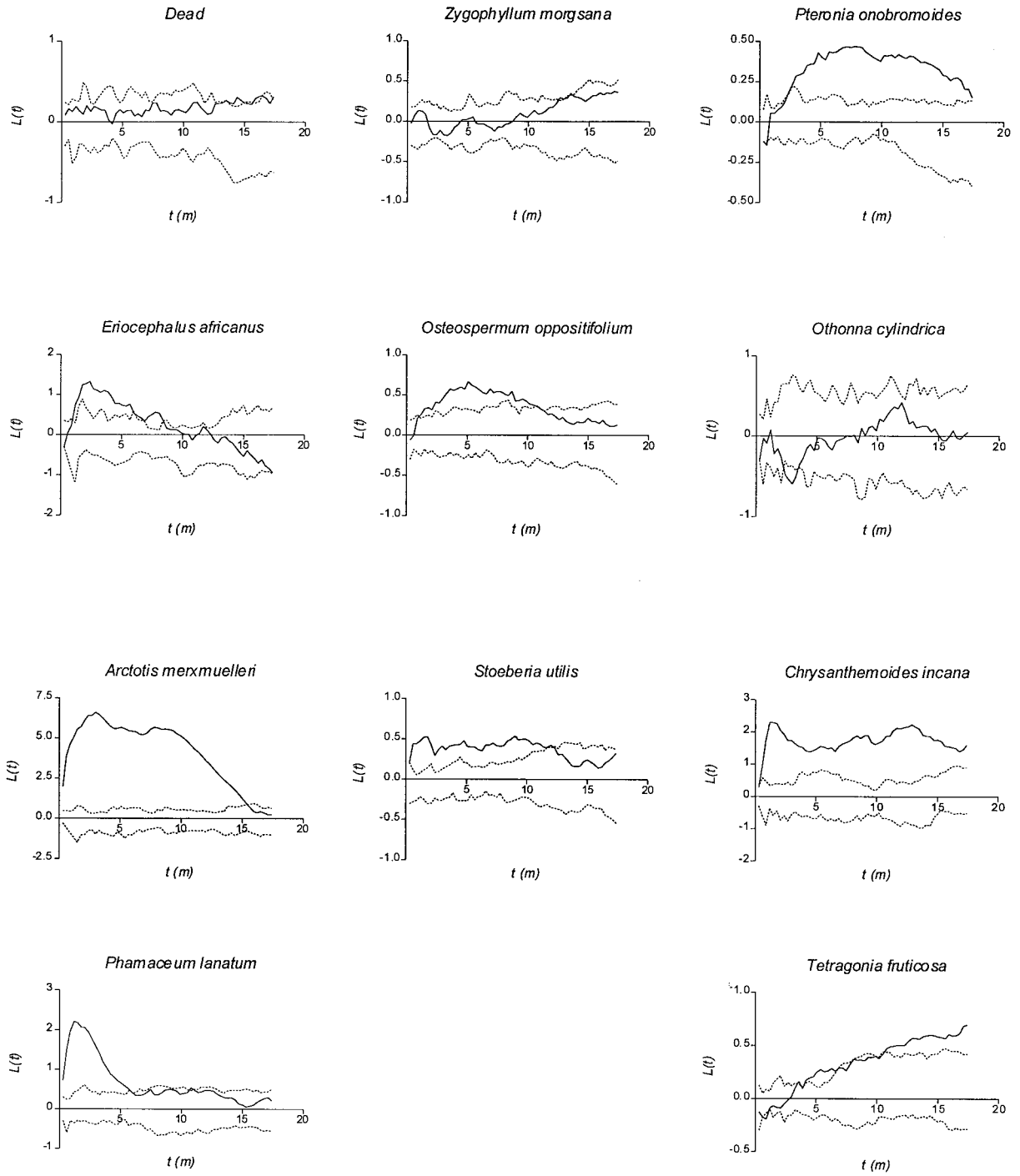


Figure 4. Dispersion patterns for species with more than 40 individuals in the medium strandveld community. The solid line represents the actual calculated L values while the broken lines represent the 95% confidence limits.

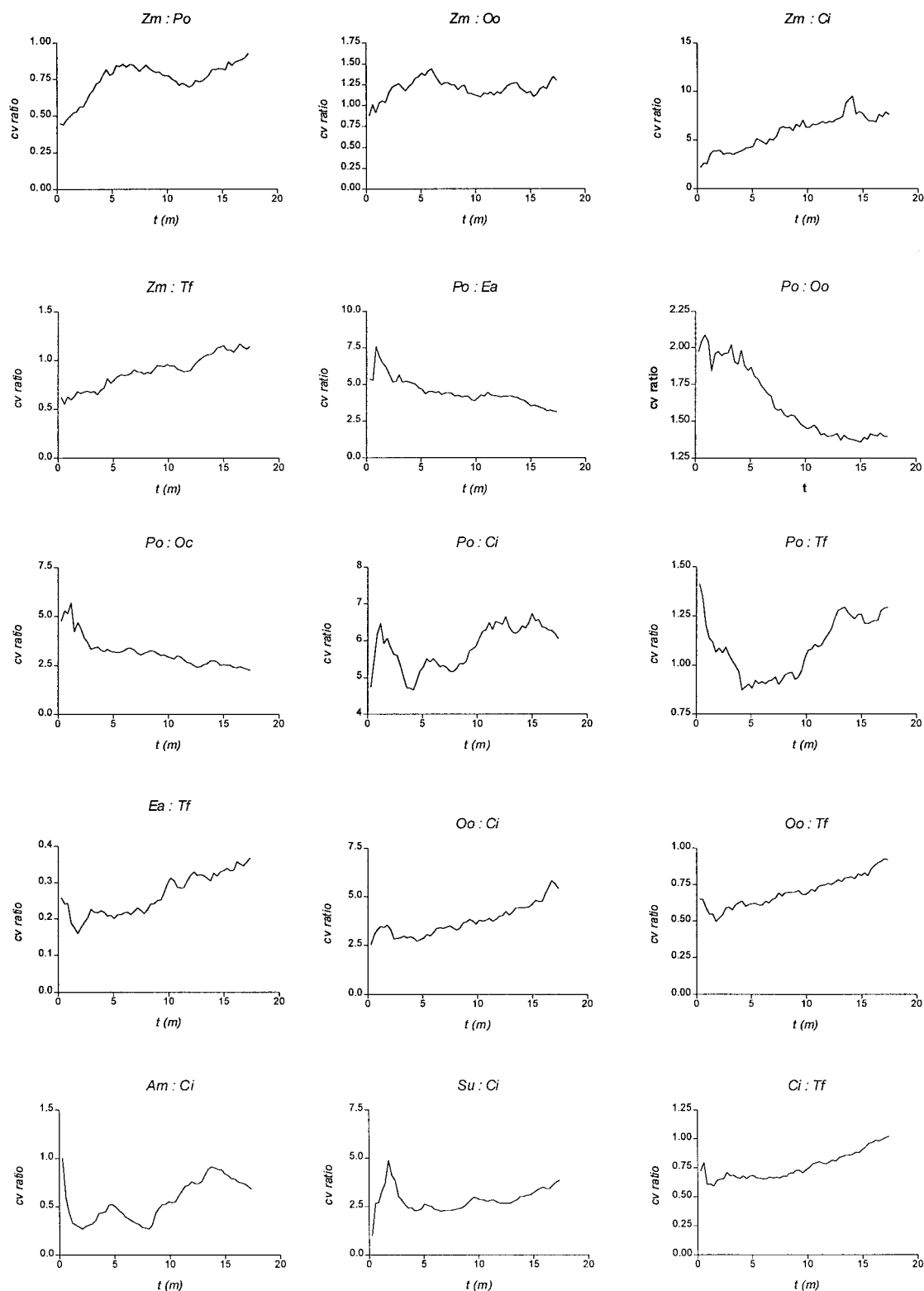


Figure 5. Asymmetry indices (cv ratio) for positive pairwise associations in the medium strandveld community. Species codes are: Zm – *Zygophyllum morganii*; Po – *Pteronia onobromoides*; Oo – *Osteospermum oppositifolium*; Ci – *Chrysanthemoides incana*; Tf – *Tetragonia fruticosa*; Ea – *Eriochepalus africanus*; Oc – *Othonna cylindrica*; Am – *Arctotis merxmuelleri*; Su – *Stoeberia utilis*.

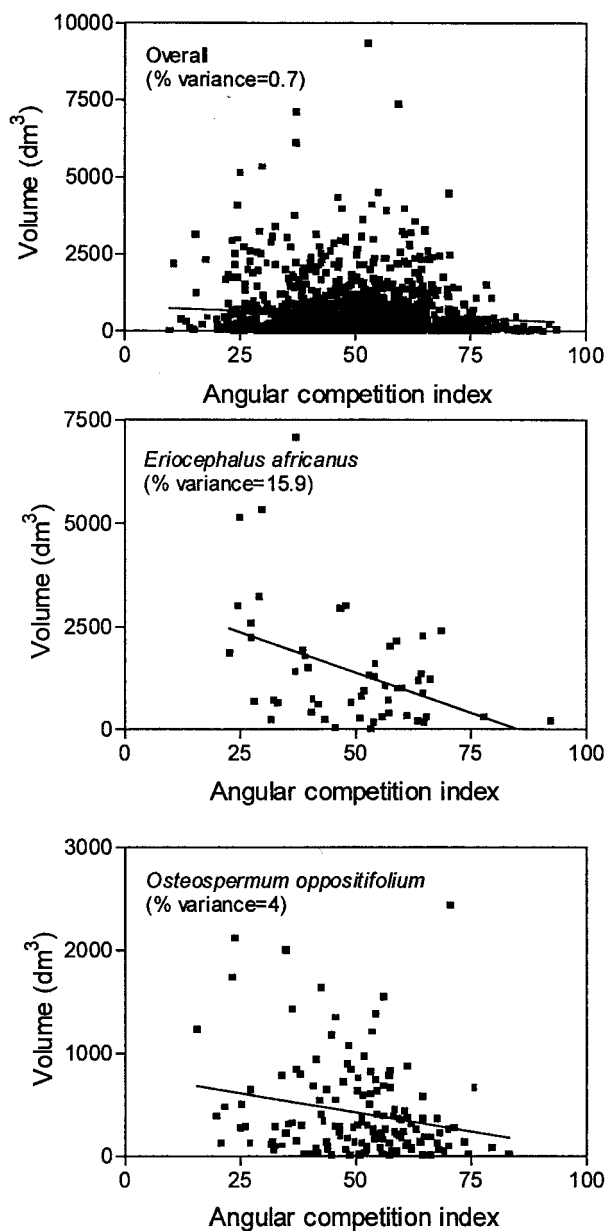


Figure 6. Scatter plots for the statistically significant regressions of plant volume against the angular competition index.

Discussion

The general patterns that emerge from this study are very provocative. This is not because they are necessarily unusual, but rather because they are probably fairly common (e.g., Prentice & Werger 1985; Couteron & Kokou 1997), and we feel that they have been frequently misinterpreted. We argue that the most parsimonious interpretation of the cosmopolitan clumping that characterizes both communities, is that a dominant form of interaction between individuals is direct facultative mutualism (Boucher et al. 1982). Clearly, this is not the only possible explanation. For one, clumping in communities could result from a patchy physical environment (Ludwig & Reynolds 1988; Couteron & Kokou 1997). In the case of this system, however, this does not seem to be the most likely possibility. There is no obvious macroscopic heterogeneity that corresponds with the vegetation clumps: there are no rocks which force pattern; no dramatic soil differences that correspond with the vegetation clumps; and very little topographic variation.

Since it seems unlikely that the observed patterns can be attributed to abiotic heterogeneity, it is necessary to consider potential biotic causes. One possibility is that the patterns are a result of contagious biotic process such as vegetative reproduction or limited seed dispersal (Ludwig & Reynolds 1988). And in this system where wind plays a key role in seed dispersal of many species (Milton et al. 1997), there can be no doubt that the seed trapping effect of existing vegetation does play a role in the maintenance of the clumped structure. In other species, seed dispersal is very limited and seeds simply fall below the parent plant where they germinate and grow. Both of these common seed dispersal patterns would promote clumps. However, are they enough to explain the clumping observed and what are the implications of these clumps in terms of plant interactions?

When considering plant interactions, it is useful to distinguish between immediate and net interactions (Callaway & Walker 1997; Holmgren et al. 1997). Three net behavioural models have been invoked in the literature on desert vegetation to explain clumped patterns. The first is the process of maturation thinning (Phillips & MacMahon 1981; Prentice & Werger 1985). According to this model, seedlings and small individuals tend to be highly clumped as a result of dispersal characteristics. However, as the individuals mature, competition occurs, and with it thinning occurs. There is, therefore, a trend in patterns of dispersion from clumped through random and finally, if the system is left for long enough, to regularity (Phillips & MacMahon 1981). Here the clumping structure apparent in spatial analyses is largely an artifact of contagious dispersal phenomena already described, along with the demographic patterns in populations. In short, if large numbers of seedlings and juveniles occur in clumps, these will create a statistical critical mass that will confer an overall clumped pattern to the population. Such sequences have commonly been used as a *post hoc* explanation for why static patterns of individual dispersion do not unequivocally suggest competition i.e. for why plants are not regularly dispersed (e.g. Phillips & MacMahon 1981; Prentice & Werger 1985). They have also been used as a basis for a critique of classical nearest neighbour analyses (Wright & Howe 1987). However, in terms of our analysis, the important feature of such behaviour is that there should be evidence of competition within-clumps. The lack of any statistically significant relationships between the volumes of individuals and their within clump angular competition indices in the short strandveld plot, and the general lack of any biologically interpretable relationships (with one exception) in the medium strandveld plot, make this possibility an unlikely general model.

The second behavioural category commonly described in desert systems and which could in theory produce clumped patterns is cyclical succession (Yeaton & Manzanares 1986; Yeaton & Esler 1990; Valiente-Banuet & Ezcurra 1991). As already mentioned in the introduction, cyclical succession is a net +/- interaction that is analogous to a host-parasitoid type relationship. Once again, this proposed behavioural model poses a serious challenge to pattern analysis, in this case because it is very difficult to resolve asymmetric interactions, let alone interactions which are completely opposite. However, we can break down the cyclical succession model into immediate interactions and by doing this it is clear that competition is again a very important sub-model (as found by Yeaton & Esler 1990 and Esler & Cowling 1993). There should, once again, be evidence for competition within-clumps and as we have already discussed this does not appear to be the case. In addition, the asymmetry indices which we calculated do not suggest any extreme asymmetries in the interactions tested. However, the high frequency of positive

associations between dead plants and various species in the medium strandveld could well indicate that cyclical succession is occurring.

The third common behavioural category reported in desert systems is the nurse-plant effect (Silvertown & Wilson 1994). This behavioural pattern is often used synonymously with the cyclical succession (e.g., Valiente-Banuet & Ezcurra 1991). However, we prefer to treat the two as separate models. According to our definition, the nurse-plant effect relies on the structural differentiation of the members of the association into different niches throughout their lives. The relationship is therefore not a +/- pseudo host-parasitoid relationship but rather a +/- commensal relationship. Species which become nurse plants are usually structurally large and long lived. We feel that this behaviour is unlikely to play a dominant role in the communities that we investigated since it relies on structural diversity that does not exist. In addition, it is difficult to identify consistent clump dominants particularly in the short strandveld community (although we present no data or rigorous analysis to demonstrate this observation). Such systems should also be characterized by a great deal of asymmetry in terms of the positive interactions. As mentioned, this is not apparent from the asymmetry indices that we calculated. Finally, there should also be traces of competition at spatial scales greater than the primary clumping as a result of competition between-clump dominants (Silvertown & Wilson 1994). However, the low frequency of negative interactions within species (univariate patterns) and the lack of evidence for negative interactions at between-clump spatial scales suggests that this is not the case.

Having identified possible inconsistencies between the patterns that we observed and the three most commonly invoked models of desert community behaviour, we return now to our initial speculation that interactions between plants in these communities are dominated by direct facultative mutualisms. This has important implications. Clearly, the first implication is that this hypothesis must be tested. Also, the nature of the mutualisms, if they in fact exist, should be characterized. There are several possible mechanisms which could lead to positive interactions (Callaway 1995). Occurrence in clumps may favourably modify the water relations of members of the clump through mutual shading or through boundary layer changes (Monteith & Unsworth 1990). It may also afford protection against grazing or trampling. Finally, there may be a certain amount of soil enrichment with organic carbon and nutrients immediately under plant canopies (but see Stock et al. 1999). These mechanisms all fall within the 'ecosystem engineer' concept coined by Jones et al. (1997). An 'ecosystem engineer' is defined as an organism which physically modifies, maintains and creates habitats. This proposed model is almost the exact opposite of the situation in the neotropical forest plots described by Hubbell & Foster (1990) where the matrix of unfavorable conditions is maintained by the presence of vegetation producing 'diffuse competition'.

In terms of community processes, it is important to establish that these interactions can in fact be stable. Early theoretical models suggested that mutualisms should be inherently unstable (May 1982). However, more recent work has suggested that the juxtaposition of positive and negative interactions is important in constraining these mutualisms, and in this way stabilizing them. Once again, the concept of 'net' interaction is relevant and the balance between positive and negative interactions will dictate the stability of interactions (Callaway & Walker 1997; Holmgren et al. 1997). It will also play a central role in determining

the spatial patterns which emerge in communities. Dominance of positive interactions would result in clumping structure being favoured even though this would, in theory, increase the potential for competition. Positive and negative interactions may be separated spatially (e.g., above and below ground – Bertness & Leonard 1997) or they may be separated temporally. The latter case can be viewed as an extension of the thesis proposed by Goldberg and Novoplansky (1997) for competitive interactions.

Finally, we return to the second question that we set out to address: how the proposed interactions could contribute to the maintenance of the species diversity in these systems. Until recently, the conclusion that any community was dominated by mutualisms would necessarily have been interpreted as suggesting that the system should be unstable (May 1982). However, it has recently been suggested that mutualisms may in fact stabilize diversity, not only between different trophic levels (as suggested by Levine 1980), but also within a trophic level. Hacker & Gaines (1997) proposed a graphical extension of the ‘intermediate disturbance’ hypothesis to demonstrate how positive interactions could significantly contribute to maintenance of diversity in physically harsh environments. Wilson & Nisbet (1997) used a spatially explicit cellular automata model to investigate the effect of ‘cooperation’ (positive interactions) between species in defining boundaries between these species distributions. Their simulations showed that increased cooperation resulted in more gradual boundaries (i.e., coexistence) between species. In conclusion, the two strandveld communities which we investigated both represent assemblages of vegetation clumps or micro-communities. We speculate that this clumping is the product of a positive feedback between substantial physical benefits associated mutual shading and microhabitat modification (‘ecosystem engineering’) and the dominant seed dispersal strategies.

Acknowledgements

We thank William Bond, Phil Desmet, Pat Holmes and two anonymous referees for their valuable comments on a draft manuscript. In addition, Jess Kemper, Angela Mbathe and Terry Wilson helped out with field work. This work was funded by the Foundation for Research Development.

- Arnold, T. H. & DeWet, B. C. 1993. Plants of southern Africa: names and distribution. *Mem. Bot. Surv. S. A.* 62: 1–825.
- Bertness, M. D. & Leonard, G. H. 1997. The role of positive interactions in communities: lessons from intertidal habitats. *Ecology* 78(7): 1976–1989.
- Bittrich, V. & Hartmann, H. 1988. The Aizoaceae – a new approach. *Bot. J. Lin. Soc.* 97: 239–254.
- Boucher, D. H., James, S. & Keeler, K. H. 1982. The ecology of mutualisms. *Ann. Rev. Ecol. Syst.* 13: 315–347.
- Cale, W. G., Henebry, G. M. & Yeakley, J. A. 1989. Inferring process from pattern in natural communities. Can we understand what we see? *Bioscience* 39(9): 600–605.
- Callaway, R. M. 1995. Positive interactions among plants. *Bot. Rev.* 61(4): 306–348
- Callaway, R. M. & Walker, L. R. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78(7): 1958–1965.
- Couteron, P. & Kokou, K. 1997. Woody vegetation spatial patterns in a semi-arid savanna of Burkina Faso, West Africa. *Pl. Ecol.* 132: 211–227.
- Cowling, R. M., Esler, K. J., Midgley, G. F. & Honig, M. A. 1994. Plant functional diversity, species diversity and climate in arid and semi-arid southern Africa. *J. Arid Environ* 27: 141–158.
- Cowling, R. M., Rundel, P. W., Desmet, P. G. & Esler, K. J. 1998. Extraordinarily high regional-scale plant diversity in southern African arid lands: subcontinental and global comparisons. *Bio-div. Let.* (in press).
- Desmet, P. G. & Cowling, R. M. 1998. Climate of the karoo: A functional approach. In: Dean, R. & Milton, S. J. (Eds), *The Karoo: ecology patterns and Processes*. Cambridge University Press, Cambridge (in press).
- Diggle, P. J. 1983. *Statistical Analysis of Spatial Point Patterns*. Academic Press, London.
- Esler, K. J. & Cowling, R. M. 1993. Edaphic factors and competition as determinants of pattern in South African karoo vegetation. *S. A. J. Bot.* 58: 461–468.
- Goldberg, D. & Novoplansky, A. 1997. On the relative importance of competition in unproductive environments. *J. Ecol.* 85: 409–418.
- 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.
- Hacker, S. D. & Gaines, S. D. 1997. Some implications of direct positive interactions for community species diversity. *Ecology* 78(7): 1990–2003.
- Hassell, M. P., May, R. M., Pacala, S. W. & Chesson, P. L. 1991. The persistence of host-parasitoid associations in patchy environments. I. A general criterion. *Am. Nat.* 138(3): 568–583.
- Hilton-Taylor, C. 1996. Patterns and characteristics of the flora of the Succulent Karoo Biome, southern Africa. Pp. 58–72. In: van der Maesen, L. J. E., van der Burgt, X. M. & van Medenbach de Rooy, J. M. (eds), *The Biodiversity of African Plants*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Holmgren, M., Scheffer, M. & Huston, M. A. 1997. The interplay of facilitation and competition in plant communities. *Ecology* 78(7): 1966–1975.

- Hubbell, S. P. & Foster, R. B. 1990. The fate of juvenile trees in a neotropical forest: implications for the natural maintenance of tropical tree diversity. Pp. 325–349 In: Bawa, K. S. & Hadley, M. (eds), Reproductive Ecology of Tropical Forest Plants. UNESCO/International Union of Biological Sciences, Paris.
- Hubbell, S. P. & Foster, R. B. 1992. Short-term dynamics of a neotropical forest: why ecological research matters to tropical conservation and management. *Oikos* 63(1): 48–61.
- Jones, C. G., Lawton, J. H. & Shachak, M. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78(7): 1946–1957.
- Jürgens, N. 1991. A new approach to the Namib Region. I: Phytogeographic subdivision. *Vegetatio* 97: 21–38.
- Levine, S. 1980. Indirect mutualism: Variations on a theme. *Am. Nat.* 116: 441–448.
- Ludwig, J. A. & Reynolds, J. F. 1988. *Statistical Ecology. A Primer on Methods and Computing*. John Wiley & Sons, New York.
- May, R. M. 1982. Mutualistic interactions among species. *Nature* 296: 803–804.
- Milton, S. J., Yeaton, R. I., Dean, W. R. J. and Vlok, J. H. J. 1997. Succulent Karoo. pp. 131–166. In: Cowling, R. M., Richardson, D. M. & Pierce, S. M. (eds), *Vegetation of Southern Africa*. Cambridge University Press, Cambridge.
- Monteith, J. L. & Unsworth, M. H. 1990. *Principles of Environmental Physics*. 2nd Ed. Edward Arnold, London.
- Prentice, I. C. & Werger, M. J. A. 1985. Clump spacing in a dwarf desert shrub community. *Vegetatio* 63: 133–139.
- Phillips, D. L. & MacMahon, J. A. 1981. Competition and spacing patterns in desert shrubs. *J. Ecol.* 69: 97–115.
- Randall, J. M. & Rejmánek, M. 1993. Interference of bull thistle (*Cirsium vulgare*) with growth of ponderosa pine (*Pinus ponderosa*) seedlings in a forest plantation. *Can. J. For. Res.* 23: 1507–1513.
- Rebertus, A. J., Williamson, G. B. & Moser, E. B. 1989. Fire induces changes in *Quercus laevis* spatial pattern in Florida sandhills. *J. Ecol.* 77: 638–650.
- Ripley, B. D. 1987. Spatial point pattern analysis in ecology. Pp. 407–431. In: Legendre, P. & Legendre, L. (eds), *Developments in Numerical Ecology*. Springer-Verlag, Berlin.
- Shmida, A. & Ellner, S. 1984. Coexistence of plant species with similar niches. *Vegetatio* 58: 29–55.
- Silvertown, J. & Wilson, J. B. 1994. Community structure in a desert perennial community. *Ecology* 75(2): 409–417.
- Stock, W. D., Dlamini, T. & Cowling, R. M. 1999. Plant-induced fertile islands as possible indicators of desertification in a succulent desert ecosystem in northern Namaqualand, South Africa. *Plant Ecol.* 142: 161–167 (this issue).
- Valiente-Banuet, A. & Ezcurra, E. 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacán valley, Mexico. *J. Ecol.* 79: 961–971.
- Von Willert, D. J., Eller, B. M., Werger, M. J. A., Brinckmann, & Ihlenfeldt, H-D. 1992. *Life Strategies of Succulents in Deserts with Special Reference to the Namib Desert*. Cambridge University Press, Cambridge.
- Wiegand, T., Milton, S. J. & Wissel, C. 1995. A simulation model for a shrub ecosystem in the semiarid karoo, South Africa. *Ecology* 76(7): 2205–2221.

Wilson, W. G. & Nisbet, R. M. 1997. Cooperation and competition along smooth environmental gradients. *Ecology* 78(7): 2004–2017. 20

Wright, S. J. & Howe, H. F. 1987. Pattern and mortality in Colorado Desert plants. *Oecologia* 73: 543–552.

Yeaton, R. I. & Esler, K. J. 1990. The dynamics of a succulent karoo vegetation. A study of species association and recruitment. *Vegetatio* 88: 103–113.

Yeaton, R. I. & Manzanares, A. R. 1986. Organization of vegetation mosaics in the *Acacia schaffneri* – *Opuntia streptacantha* association, southern Chihuahuan Desert, Mexico. *J. Ecol.* 74: 211–217.