

Spatial scaling and transition in pneumatophore arthropod communities

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Although most ecological variables are scale-dependent, few studies compare scale-related variation in abundance, species richness, and assemblage structure. This study considered the spatial scaling of autocorrelation and the scale of influence of specific environmental variables in mangrove pneumatophore arthropod communities (Acari, crustaceans and insects), across seven spatial scales (from 10 cm to 100 km). The objective was to determine if resource and habitat availability determine spatial patterning in the system, and to identify the scale of transition in the community. Using uni- and multivariate spatial autocorrelation methods and a non-spatial dissimilarity-ANOVA, we identified the scales at which the community significantly changes. Generally, spatial autocorrelation was found to decrease with increasing spatial scale, with notable exceptions for the larger scales. For the abundance of common species, negative spatial autocorrelation was stronger at 10 km than at 100 km, while the opposite was true for rare species. Spatial autocorrelation in species richness decreased from 1 m (strong positive autocorrelation) to 10 km (strong negative autocorrelation), but was not significant at the 100 km scale. These patterns reflect the patchy distribution of pneumatophores within mangrove forests, and that of the forests along the coast, with an additional effect attributable to poor dispersal abilities of the arthropods in a highly dynamic environment. Although the amount of resources and habitat available to arthropods exhibited a similar autocorrelation scaling pattern to that of the community, pneumatophore mass did not appear to determine the scaling of autocorrelation observed in the arthropods utilizing this habitat. Variations in the abundance of common species, as well as restricted distribution of rare species caused assemblage structure to change differently with increasing distance, from 10 cm to 100 km. The 100 km scale clearly stood out as the most distinct, indicating

biogeographical, rather than ecological, differences. Beyond these results, this study highlights the need to combine univariate and multivariate approaches, across multiple scales, when investigating scale-dependent phenomena.

Many ecological questions currently focus on quantifying spatial variability in species abundance and distributions to provide insight into the factors influencing community structure (Gascoigne et al. 2005, Crist et al. 2006, Green and Bohannan 2006, Field et al. 2008). These factors, and therefore the patterns that they generate, vary with spatial scale (i.e. extent and grain) (Levin 1992, Wu et al. 2002, Hartley et al. 2004, Cadotte and Fukami 2005, Gascoigne et al. 2005, Rahbek 2005, Procheş et al. 2008). Quantifying spatial scaling is important to understanding the spatial structure of the community, the factors driving spatial heterogeneity, and the scales at which these factors operate (Menge and Olson 1990, Ettema and Wardle 2002, Sauders et al. 2002, 2005, Urban et al. 2002, Krawchuk and Taylor 2003, Cadotte and Fukami 2005, Gascoigne et al. 2005). Furthermore, this makes it possible to identify transitions in systemic processes (Hartley et al. 2004, Quintino et al. 2006) and operational units for management (Erasmus et al. 1999, Krawchuk and Taylor 2003, Quintino et al. 2006).

Deciding on the appropriate scale to collect data without prior knowledge of the system being examined is problematic. Patterns exist at both smaller and larger scales due to the action of multiple factors that may only become apparent once sampled across scales (Krawchuk and Taylor 2003, Hartley et al. 2004, Rahbek 2005). On the one hand, the spatial extent sampled, and sampling within this extent, should be maximized to capture the full range of spatial variation and potentially structuring factors. On the other hand, the rigors of attempting this make such an endeavour rarely practicable. As a result, few habitats have been systematically surveyed to explicitly account for changes in patterns across an array of spatial scales covering a large extent (but see Farnsworth and Ellison 1996, Åberg and Pavia 1997, Procheş et al. 2008 for some examples). Furthermore, some variables show erratic scaling behaviour, while others scale predictably or in a stepwise fashion across landscapes (Wu et al. 2002; Hartley et al. 2004). This makes it difficult to generalize about the scaling behaviour of ecological variables.

Despite marine science being one of the fields where scale research has been particularly productive (e.g. Bourget et al. 1994, Saburova et al. 1995, Farnsworth and Ellison 1996, Åberg and Pavia 1997, Guichard and Bourget 1998, Eggleston et al. 1999, Fauchald et al. 2000, Gascoigne et al. 2005), it is presently difficult to draw general conclusions about the scaling behaviour of ecological variables from marine or intertidal systems (see Farnsworth

1998, Farnsworth and Ellison 1996). For example, the type of substratum, from intertidal rock and Arctic ice to estuarine or deep-sea sediment, may greatly influence the distribution patterns of marine organisms across scales. The study of mangrove-arthropod systems is no less entangled. This is partly because few mangrove systems have been surveyed simultaneously across multiple scales, and partly because the distribution and abundance of mangroves and mangrove arthropods is affected by many factors operating at different scales (Farnsworth and Ellison 1996, Farnsworth 1998, Nagelkerken et al. 2008). Although some studies have examined mangrove sediments over multiple scales, few have done so for the arthropods found on the pneumatophores of mangroves (see Nagelkerken et al. 2008). Therefore, to gain a better understanding of the spatial relationships in mangrove communities, comprehensive studies of such systems over multiple scales are required.

Here we investigate spatial and scale-related variability in an arthropod community associated with pneumatophores of the mangrove tree *Avicennia marina* (Forssk.) Vierh. (Avicenniaceae) along the eastern coast of South Africa. The mangrove pneumatophore environment is one largely belonging to the marine realm, although terrestrial and freshwater influences are also strong. Arthropod distributions in mangrove pneumatophore habitats display patchiness at three levels. Individuals may be aggregated on a pneumatophore (Procheş and Marshall 2002a), pneumatophores may be aggregated within mangrove forests (Saifullah and Elahi 1992) and the distribution of mangrove forest fragments along the coast may be patchy (Ward and Steinke 1982). The first level of patchiness is not covered by the present study, but has been partly addressed elsewhere (Procheş and Marshall 2002a), while the third level is excluded by sampling in mangrove forests only. The arthropod distributions under study are thus considered to reflect the aggregation of pneumatophores within mangrove forests at different scales (from plots to transects), across mangrove forests, and patterns of dispersal history (thus linking fundamental and realized niches, see Soberón 2007). Within mangrove forests, additional spatial variation and transitions in community structure are likely to occur beyond the vertical stratification already recorded on single pneumatophores (Procheş and Marshall 2002a).

In particular we aimed to understand the scaling behaviour of the mangrove pneumatophore arthropods, to determine if resource and habitat availability (pneumatophore mass) may spatially structure the community and to identify the scale of transition in community structure. Individual species and community variables were examined across seven spatial scales (from 10 cm to 100 km) within three mangrove forests; one of the largest orders of magnitude and number of scales considered for arthropods using a single sampling

design. Univariate comparisons were made between rare and common species, as well as multivariate comparisons between community parameters and pneumatophore mass, controlling for space. Predictions were as follows: (1) species would show positive autocorrelation across local scales, but negative at larger scales because of low dispersal abilities; (2) the scaling of autocorrelation in rare species should be shorter than common species because fewer propagules leave the natal site; (3) the community should be spatially autocorrelated at scales similar to (or smaller than) pneumatophore mass as pneumatophores are essential for the arthropods to establish.

Material and Methods

Sampling

Mangrove forests have a patchy distribution along the southern African coast, naturally occurring in open estuaries and bays (Macnae 1963). Forest patch size varies from a few square meters to hundreds of hectares, and adjacent patches are often tens of kilometers apart. The most abundant tree species in these forests is *Avicennia marina* (Forssk.) Vierh.. The pneumatophores of this species are pencil-like structures with a respiratory function (Tomlinson 1986), emerging from the sediment of the mangrove forest floor at irregular intervals. Even in stands dominated by other tree species, *Avicennia* pneumatophores are present in high numbers, due to the broad coverage of subterranean roots. Pneumatophore density is variable, reaching 1000/ m². Studies on pneumatophores have considered their size attributes, distribution (Saifullah and Elahi 1992, Beck 1998), the algal assemblages they support (for southern Africa: Phillips et al. 1994, 1996), and the spatial distribution of their sessile faunas (sponges, cnidarians etc.), including spatial scaling (Bingham 1992, Farnsworth and Ellison 1996). In southern African estuaries, the sessile communities on pneumatophores are impoverished or absent, while motile arthropod faunas dominate. The motile assemblages have been characterized both at fine (centimeters) and large (hundreds of meters – kilometers) scales (Procheş et al. 2001, Procheş and Marshall 2002b, Procheş 2004), but no cross-scale study is available.

Sampling was performed in April-August 2000, in three mangrove forests along the coast of KwaZulu-Natal (South Africa). The forest in Richards Bay covers an area of 427.5 ha and is divided by a ‘berm’ between a southern wildlife sanctuary, and a northern harbour. The forests at Beachwood (44 ha) and Bayhead (15 ha) are located within the eThekweni (Durban)

metropolitan area (Ward and Steinke 1982). One transect was set in each Richards Bay Harbour, Richards Bay Sanctuary, Beachwood and Bayhead (Fig. 1). The distance between the former two transects, as well as the distance between the latter two transects, was approximately 10 km. The distance between the Richards Bay and Durban localities (Fig. 1) was 180 km, but for simplicity this will further be referred to as the 100 km scale. Five finer scales (1 km, 100 m, 10 m, 1 m, 10 cm) were considered in each transect, following a nested design (Underwood and Chapman 1998; Fig. 1). This resulted in a total of 128 samples, allowing for comparisons between seven spatial scales. The environment within which sampling was conducted imposed some limitations on the sample layout, e.g. the distances between the sets of samples did not always represent the nominal values of their respective spatial scale. However, they did always represent between half and twice this value (e.g. double grids – nominally 100 m apart, were always between 50 and 200 m apart). The distance between the centers of the plots in a double plot, representing the 10 cm scale, was always 15 cm.

The meiofaunal arthropods on the *Avicennia* pneumatophores were collected within each of the 128 plots by cutting the pneumatophores at ground level and returning them to the laboratory, where they were extracted and counted following the method outlined by Procheş et al. (2001). Barnacles were counted separately. Pneumatophore dry mass for each sample was considered as a surrogate measure of habitat and resource availability (see Procheş and Marshall 2002a).

Taxa

The arthropods inhabiting *Avicennia* pneumatophores are characterized by their small size, generally low dispersal abilities, and high local abundance (Procheş et al. 2001). All arthropod specimens were identified to ‘morphospecies’ level, except for the harpacticoid copepods and the insect larvae, which comprised several species that were difficult to discriminate under a dissecting microscope. These two groups, representing respectively 16.86% and 10.16% of the total number of individuals, were excluded from the analyses. A total of 21 morphospecies were considered (14 Acari, 3 amphipods, 1 isopod, 1 tanaidacean, 1 barnacle, 1 collembolan; Table 1).

Single species analyses

One univariate method to study the scaling behaviour of ecological variables is to examine the spatial scaling of autocorrelation, viz. the distance at which the variable is no longer positively autocorrelated (cf. Engen et al. 2002). The scaling of autocorrelation (here identified as the x-intercept on a correlogram) is an approximation of the scaling of autocorrelation, or ‘patch size’ (Sokal and Wartenberg 1983), for that variable. This is the distance over which the measured variable remains more similar than expected by chance at sites spaced at that distance or less, than at sites located further away. This method is used to document the spatial structure of populations and assemblages, and to estimate scales of variability in biological systems (Koenig 1999, Radeloff et al. 2000, Perry et al. 2002). At local scales, where positive autocorrelation is usually observed, this may reflect the effects of biotic processes between patches such as dispersal, predation or disturbance (Legendre 1993). High levels of migration/dispersal ability are likely to increase the scaling of autocorrelation, i.e. positive autocorrelation will extend over larger distances (Engen et al. 2002), while low dispersal ability has an opposite effect.

Here, Bonferroni-corrected correlograms (with Moran’s I as an autocorrelation measure) based on log-transformed data and using SAAP (Spatial Autocorrelation Analysis Program), ver. 4.3 (Wartenberg 1989), were used to relate the autocorrelation of the variables (ordinate) against distance between samples (abscissa). A rectangular co-ordinates system was used with unequal (customized) distance classes (see Wartenberg 1989; each distance class represented one of the seven spatial scales considered). This resulted in 64, 128, 256, 512, 1024, 2048 and 4096 pairs, respectively, for the seven distance classes. According to Legendre and Fortin (1989), autocorrelation values in distance classes containing more than 1% of the total numbers of pairs can be readily interpreted. Although the lowest number of pairs, 64, approximated 1% (0.8%) of the total number (8128), we consider and interpret the results for distance class one with caution.

To compare autocorrelation values between common and rare species, common species were defined as those present in more than 10% of the samples and representing more than 1% of the total number of individuals, while species not satisfying either of these conditions were considered rare. Species present in 2-4 samples were considered, while species present in only one sample were excluded from this analysis.

To assess the spatial scaling of autocorrelation, the x-intercept on correlograms was determined for all species, community parameters, and pneumatophore mass. These are likely

to be similar if pneumatophore mass or a spatially structured variable determining pneumatophore mass is causal in structuring the species and community.

Community-level analyses

Measuring spatial variation in communities as opposed to individual species is confounded by sampling design complexity, the inability of multivariate procedures to deal with complexity and non-independence of measurements of dissimilarity (Oden and Sokal 1992, Underwood and Chapman 1998, Legendre et al. 2002, Castellano and Balleto 2002). To identify the potential causal factors determining the spatial variation in mangrove communities and the spatial scale of influence of these factors, simple and partial Mantel correlations between habitat and community dissimilarity matrices, controlling for the effect of a third matrix, such as space (Legendre and Legendre 1998, Goslee and Urban 2007) are useful. Although ranking the dissimilarity matrices may aid in linearizing non-linear relationships between variables, conventional Mantel tests assume a linear relationship between the dissimilarity matrices (see Legendre and Legendre 1998, Goslee and Urban 2007). An improvement of this technique is Goslee and Urban's (2007) recently developed the *ecodist* package for R 2.7.1 (R Development Core Team; <http://www.R-project.org>).

Ecodist computes piecewise multivariate Mantel correlation statistics and correlograms that are able to control for the effect of non-linear relationships on structure that remain hidden in traditional Mantel analyses. Spatial structure is removed separately from each distance class (i.e. the relationship need not be linear) and *ecodist* is able to approximate the nonlinear (patchy) structure within the data (Goslee and Urban 2007). The program represents a significant breakthrough in multivariate spatial analysis.

In our system, we are thus able to investigate the linear and non-linear relationships between species richness or total abundance and pneumatophore mass across the spatial scales sampled, while controlling for the effect of space. Significant correlation between the community variables and pneumatophore mass, besides common spatial structure, would be expected if habitat and resource availability (as measured by pneumatophore mass) drives community structure across spatial scales. The Mantel correlations were used to assess the contribution of the spatial relationships in community and pneumatophore mass variables (thereby accounting for the effect of pneumatophore mass on community structure versus the effect of a third, unmeasured variable on community structure). Resemblance matrices were constructed using Euclidean distances (for the matrix of geographic distances between pairs of

sampling stations) and Bray-Curtis similarities (for community variables and pneumatophore mass). A non-significant partial Mantel test (see Legendre and Legendre 1998) between community variables (species richness and total abundance) and pneumatophore mass, when controlling for the effect of space and when the remaining correlations are significant, suggests that the effect of a third spatially structured variable determines the observed spatial community structure. A non-significant partial Mantel test between community variables and a spatial matrix, controlling for pneumatophore mass, when the remaining correlations are significant, supports the hypothesis that the size of the resource available to be exploited (pneumatophore mass) controls the observed variation in community structure (see Legendre and Legendre 1998, Goslee and Urban 2007). All Mantel significance tests were performed using 10 000 randomisations.

An alternative method to overcome the problems of sampling design complexity, sampling effort and data non-independence identifies the scale of transition in community structure using Bray-Curtis similarity indices, and comparison of centroid (averaged) values across sites at a particular scale (Underwood and Chapman 1998). A nested ANOVA is then used to assess significant changes in community structure across sampling scales. The method allows the identification of the scale/s at which community structure changes, i.e. when a spatial transition in community structure occurs.

Here, Bray-Curtis dissimilarity values were calculated for pairs represented by one sample and the centroid of one set of samples it belonged to. Sets of samples were selected to represent all of the distance classes considered (a sample was compared with the centroid of the samples found in the same double plot, grid, double grid, area, transect, locality, or the centroid of all 128 samples in the study). As 21 samples contained no arthropods, the total of 107 non-empty samples were used for comparison with seven distance classes without using the same sample twice. This gave a maximum of fifteen replicate dissimilarity values for each scale, the average of which is considered to represent a typical dissimilarity value for that scale. The samples to be used for comparison at each scale were randomly chosen (Fig. 2). Bray-Curtis dissimilarity values were computed using PRIMER 5 (Plymouth Routines in Multivariate Ecological Research) on 4th root transformed data (Clarke and Warwick 1994), and then plotted against a distance axis. A one-way ANOVA, followed by a Student-Newman-Keuls test, was performed to compare the dissimilarity values for each spatial scale, using SPSS (ver. 9.0) for Windows.

Results

Univariate approaches: scaling of autocorrelation

Of the twenty-one morpho-species from three classes that were identified (Table 1), 14 species were analysed, following the rationale outlined above. The strongest positive autocorrelation was observed at the 10 cm scale for eight (4 common, 4 rare) of the 14 species, and at 1 m for the remaining six (1 common, 5 rare) species (Table 2, Fig. 3). For all species, positive autocorrelation in species abundance was characteristic of fine scales (10 cm, 1 m, 10 m, 100 m), and negative autocorrelation of large scales (10 km, 100 km). At the intermediate scale of 1 km, the abundances of some species were positively, and those of others, negatively autocorrelated. The magnitude of autocorrelation values generally decreased and became more negative with increasing distance (Table 2).

The most abundant species were often more strongly and positively autocorrelated over larger distances (up to 1 km) than less abundant species (up to 1 km, 10 m, and 1 m with a decline in abundance) (Table 2). The x-intercept on the correlogram was generally between 1 km and <10 km for the common species and between 1 m and 100 m for the rare species (Fig. 3 a,b). There was a significant relationship between the magnitude of Moran's I and species abundance in the first two distance classes (Fig. 4), although several rare species (*Agauopsis* sp., *Uroobovella* sp., Spheromatidae sp. and *Anurida maritima*) showed strong, positive autocorrelation in the 10 cm distance class (Fig. 3, Table 2).

The autocorrelation functions of community and resource measures were similar, with x-intercepts of approximately 1 km for total abundance, species richness and pneumatophore mass (Fig. 5). Positive autocorrelation was, however, strongest for abundance, followed by species richness and pneumatophore mass (Fig. 5). Total arthropod abundance closely followed the curve for the dominant species, *Tanais philetaerus* (which constituted 78% of the total arthropod abundance; Fig. 5, cf. Table 2).

Multivariate spatial approach

Although the spatial patterns of community variables and pneumatophore mass were similar (Fig. 5), the simple and partial Mantel tests revealed no significant relationships between the dissimilarity matrices of community variables and pneumatophore mass (Table 3). Therefore, the size of habitat and resource available to the arthropods utilizing the pneumatophores

played no role in structuring the community at the measured scales. Community variables and pneumatophore mass were strongly spatially structured and this structure resulted from a common spatial arrangement (Table 3). Therefore, the observed community structure largely reflects spatial structuring in an unmeasured variable that also appears to be structuring pneumatophore mass similarly. The piecewise Mantel correlograms of species richness and total abundance on pneumatophore mass, given space, clearly revealed that resource and habitat availability did not significantly influence spatial structure (results not shown).

Multivariate non-spatial approach

At all scales except 100 km, some samples were highly similar to the centroids of their respective sample sets, while others were dissimilar, causing a wide scatter of the Bray-Curtis dissimilarity values within each scale (Fig. 6). There was therefore almost as much variability in arthropod community structure at the 10 cm scale as there was at the 10 km scale. However, there were significant differences between averaged dissimilarity values, which increased with spatial scale (Table 4, Fig. 6). Three subsets of scales were significantly different; 10 cm – 1 m, 1 m – 10 km and 100 km. Maximum dissimilarity amongst samples appeared to asymptote at 1 km (Fig. 6, Table 4), whereas the range of differences between samples was narrowest at the 100 km scale (Fig. 6).

Discussion

Scaling of autocorrelation at short lags

The scaling of autocorrelation of all the species occurred at short lags of ≤ 1 km. Most marine organisms disperse as swimming larvae (Morgan 2001), and this efficient type of dispersal has been said to be one of the major differences between marine and terrestrial habitats (Ricklefs 1990; Levin 1994). Open-coast mangroves from constantly warm tropical waters are characterized by epiphytic communities where species with swimming larvae are dominant, and follow complex colonization patterns (Farnsworth and Ellison, 1996). This is not true for the strictly estuarine mangroves in southern Africa, where the localized distribution of forests makes broad-scale dispersal less advantageous, and at the same time the survival of many typically marine organisms is precluded by temporarily low salinities. Among the twenty-one species of pneumatophore arthropods considered in our study, only the barnacle, *Balanus*

amphitrite, disperses by means of swimming larvae. All the other species have crawling larvae similar to the adults, which can only disperse over limited distances (meters, tens of meters; although occasional long-distance dispersal on floating debris is possible; Ş.P., pers. obs.).

The prediction of limited dispersal ability resulting in small patch size (Engen et al. 2002) for mangrove arthropod species is supported by our results which show patches of 1m (2 species) to 10m for most species. While smaller values are common for species from other, more stable, environments (e.g. 1 m for most species in deep-sea sediment; Cosson et al. 1997), patches of 10 m lengths are considered small for the mangrove forest floor, an environment generally considered to be relatively homogeneous (see Ellison and Farnsworth 2001). A three-scale study on nematodes (which also lack swimming larvae) from mangrove sediments largely confirms our results, with most (30%) of the variation in nematode populations being accounted by the smallest (5 cm) scale, 22% by the 5 km scale, and only 5% by the 1,000 km scale (Hoda 1990). It is interesting that indeed the one species with planktonic larvae (*Balanus amphitrite*) was the only one with a second peak in autocorrelation (at the 100 m scale; see Table 2). This indicates a hierarchical patch structure, with the larger patch size probably being the effect of larval dispersal.

Although the low dispersal abilities of the species led us to believe that scaling should occur at shorter lags, the scaling of autocorrelation also clearly varied with species abundance. For the most abundant species (*Tanais philetaerus*), autocorrelation dropped substantially from 100 m to 1 km, and even more from 1 to 10 km. For the other common species, scaling/patch size was between 1 km and <10 km. For most of the rare species scaling occurred between 1 m and 100 m, while that for the two rarest species was between 10 cm and 1 m. As sample sizes were the same for the rare and common species, the observed differences in the scaling of autocorrelation for rare and common species are likely to reflect real differences between the species.

Because abundance changes faster than occupancy, i.e. a species will first increase in abundance at a site before increasing its occupancy of sites (Gaston 2003), this is likely to initially strengthen the magnitude of Moran's I at finer spatial scales and then to increase the scaling of autocorrelation, by causing positive autocorrelation in the lag above, as a species becomes more abundant. Indeed, there was a clear correlation between Moran's I and abundance in the first two distance classes – presumably indicating that nuclei of pre-dispersal population growth fit within these classes. Differences in the strength of Moran's I , and the distance at which it is highest have been shown to vary with species abundance (McGeoch and Chown 1997; Gaston 2003; McGeoch and Price 2004, Warren et al. in press). The larger

scaling observed for common species may reflect the much lower occupancy of samples for rare species, that more propagules leave the natal site of common species than for less abundant species, or that more abundant species form larger aggregations, requiring more space.

It is worth discussing the case of the few species aberrant in terms of the abundance-Moran's I relationship (outliers in Fig. 4). These are either species of (evolutionarily recent) terrestrial descent, ('secondary marine' arthropods; Procheş 2001, 2004), such as *Anurida maritima* and *Uroobovella* sp., or species that typically inhabit rocky shore/reef systems (with different habitat structure; Beck 1998, Mumby 2001), such as *Agauopsis* sp. and Spheromatidae sp. These species may display different spatial patterns of clustering depending on the abundance of the species in the observation area (see van de Koppel et al. 2008). Such alternations between dense beds of clustering and isolated clusters depending on abundance would remove the general relationship observed between I and abundance across sites, observed for most of the species examined here. On removing these species, the correlation for typically estuarine arthropods (all other species) is excellent (10 cm: $F_{1,12} = 48.12$, $r^2 = 85.78\%$, $p < 0.0001$; 1 m: $F_{1,12} = 71.93$, $r^2 = 89.99\%$, $p < 0.0001$).

Resource-consumer differences in scaling

Most of the pneumatophore arthropods feed either on the algae growing on the pneumatophores, or on organic debris trapped within the algae, the amount of which is strongly dependent on pneumatophore density and size (Procheş and Marshall 2002). In the case of predatory species (e.g. *Leioseius* sp.), pneumatophore surface area equals foraging area (Procheş and Marshall 2002), therefore the dry mass of the pneumatophores (which are regular-shaped structures) represents a reasonable surrogate for both habitat availability and resource availability.

Interestingly enough, although the magnitude of fine-scale autocorrelation was higher for biotic variables than for the mass of the pneumatophores, the scaling of autocorrelation was larger in the case of pneumatophore mass, indicating larger patch size for the resource than for that of the inhabitants/consumers. This has also been observed in more dynamic systems comprising fish and seabirds (Logerwell et al. 1998). Our results were contrary to the expectation that pneumatophore mass was the primary factor influencing community patterns. The Mantel results revealed that these reflect the spatial pattern of an unmeasured variable that structured both the community and pneumatophore mass, rather than the community being

structured by habitat and resource availability (determined from pneumatophore mass).

The distribution of populations and assemblages is generally limited to suitable patches of habitat, within which environmental variables vary to a lesser extent, as compared to the surroundings (see Legendre and Fortin 1989; Logerwell et al. 1998). At the same time, the existence of non-inhabited patches can, by mere distance effects, impose barriers resulting in local isolation. In a dynamic environment, each patch is characterized by its own processes of colonization, population growth, and extinction, leading to differences in community structure and species abundance among patches (MacArthur and Wilson 1967; Rosenzweig 1997). In the presence of an environmental gradient, these differences will tend to increase with increasing distance. Even if abiotic gradients are absent, biotic gradients derived from patch history and dispersal processes cause similar effects, particularly at fine scales (Levin 1992).

The unmeasured variable responsible for species patterns may have to do with properties of the sediment, tidal factors (in relation to elevation above/below the average water level), temperature (in turn connected with daily direct exposure to sunlight – influenced by tree shade; indeed tree shade does not extend as far as the pneumatophores), crab burrows, or other factors (see Nagelkerken et al. 2008). Since the pneumatophores themselves are not the main drivers (suggesting that pneumatophores as a resource are not limiting), the arthropod pneumatophore community structure may be structured similarly to the sediment arthropod communities (cf. Underwood and Chapman 1998).

Community structure transitions

Community structure is defined by species identity, richness and relative abundance (Clarke and Warwick, 1994), thus combining all the single factors discussed above. And indeed, community structure, similar to single-species measures, became more dissimilar with increasing spatial scale. At all scales but 100 km, there was a broad scatter of the dissimilarity values, indicating mixed (narrow and broad) variation in assemblage structure, while at the 100 km scale, variation was consistently broad (Fig. 6). These results are supported by the separate analyses of rare and common species where variations in scaling of autocorrelation were found across species.

Three subsets of distances were separated in terms of a transition in community structure by the post-hoc test following the ANOVA procedure (Table 4). Subset ‘a’ (10 cm – 1 m) corresponds to distances smaller than the patch size of most species, thus representing spatial

scales below point (or alpha) diversity (*sensu* Whittaker 1972, see Rosenzweig 1997). Subset 'c' (100 km) is clearly the most distinct, as most species (especially the rare ones) are replaced at the 100 km scale, indicating that the transition from ecological to biogeographical variation (see Cornell and Lawton 1992) happens somewhere between the 10 km and the 100 km scales. Such faunistic differences along the KwaZulu-Natal coast have been observed by Macnae (1963), who considered the mangroves in Durban to belong to a southern province, and those in Richards Bay, to a northern province (although, with a different choice of localities, more than 1,000 km could have been needed to capture an equal amount of species turnover). Subset 'b' (1 m – 10 km) comprises those scales that are probably most meaningful for community studies on pneumatophore arthropods, as ample variation is contained here, without entering the domain of geographical transitions.

If mangrove forests are in several ways intermediate between marine and terrestrial worlds, the pneumatophores themselves are unique structures, specific to this environment. Although we show here that their biomass in itself is not critical in determining the cross-scale structuring of the arthropod communities inhabiting them, these communities are nevertheless an important and distinctive constituent of mangrove ecosystems. As such, their spatial structuring needs to be considered in the conservation and management of this ecosystem. Recently, Nagelkerken et al. (2008) pointed out that “a challenge for future research is separating the roles of mangroves from those of estuaries and other shallow-water habitats, to help determine the appropriate temporal and spatial scales for habitat protection”. Indeed, human intervention affects mangrove ecosystems across several scales. In southern Africa, changes in freshwater input into estuaries are causing entire forests to disappear through estuary closure, thus causing biogeographical effects by creating gaps in dispersal. At finer scale, age-group targeted tree felling, as well as pollution, result in microenvironmental changes. This study suggests that the former are more likely to affect community structure, but the latter may be endangering the local survival of specific populations.

Pneumatophore arthropod assemblages contain species of both marine and terrestrial ancestry, and are influenced by physical factors from both environments. It is expected (Ricklefs 1990, Levin 1994) that different spatial patterns would occur between typical marine and terrestrial ecosystems, as indicated by a number of available studies (e.g. Cornell 1985; Underwood and Chapman 1996). For this system, the scaling behaviours of the community and pneumatophore mass were similar and may thus be predictable (Wu et al. 2002), however, variations in scaling were observed across species. To fully verify this and the differences/similarities between marine and terrestrial ecosystems, studies using standardized

nested hierarchical schemes, similar to the one presented here, would have to be conducted comparatively between these environments, while the present study could serve as an intermediate marine/terrestrial example.

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References

- Åberg, P. and Pavia, H. 1997. Temporal and multiple scale spatial variation in juvenile and adult abundance of the brown alga *Ascophyllum nodosum*. - Mar. Ecol. Prog. Ser. 158: 111-119
- Beck, M.W. 1998. Comparison of the measurement and effects of habitat structure on gastropods in rocky intertidal and mangrove habitats. - Mar. Ecol. Prog. Ser. 169: 165-178.
- Bingham, B.L. 1992. Life histories in an epifaunal community – coupling of adult and larval processes. - Ecology 73: 2244-2259.
- Bourget, E., Deguise J. and Daigle, G. 1994. Scales of substratum heterogeneity, structural complexity, and the early establishment of a marine epibenthic community. - J. Exp. Mar. Biol. Ecol. 181: 31-51.
- Brewer, A.M, and Gaston, K.J. 2003. The geographical range structure of the holly leaf-miner. II. Demographic rates. - J. Anim. Ecol. 72: 82-93.
- Cadotte, M.W. and Fukami, T. 2005. Dispersal, spatial scale, and species diversity in a hierarchically structured experimental landscape. - Ecol. Lett. 8: 548-557.
- Castellano, S. and Balletto, E. 2002. Is the partial Mantel test inadequate? - Evolution 56: 1871-1873.
- Clarke, K.R. and Warwick, R.M. 1994. Changes in marine communities: an approach to statistical analysis and interpretation. - Plymouth: Plymouth Marine Laboratory.
- Cornell, H.V. 1985. Local and regional richness of cynipine gall wasps on California oaks. - Ecology 64: 1247-1260.

- Cornell, H.V. and Lawton, J.H. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. - *J. Anim. Ecol.* 61: 1-12.
- Cosson, N., Sibuet, M. and Galeron, J. 1997. Community structure and spatial heterogeneity of the deep-sea macrofauna at three contrasting stations in the tropical northeast Atlantic. - *Deep-Sea Res. I - Oceanographic Res. Pap.* 44: 247-269.
- Crist, T.O., Pradhan-Devare, S.V. and Summerville, K.S. 2006. Spatial variation in insect community and species responses to habitat loss and plant community composition. - *Oecologia* 147:510-521.
- Dale, M.R.T. et al. 2002. Conceptual and mathematical relationships among methods for spatial analysis. - *Ecography* 25: 558-577.
- Eggleston, D.B. et al. 1999. Organism responses to habitat fragmentation and diversity: Habitat colonization by estuarine macrofauna. - *J. Exp. Mar. Biol. Ecol.* 236: 107-132.
- Ellison, A.M. and Farnsworth, E.J. 2001. Natural disturbance and the dynamics of marine benthic communities. - In: Bertness MD, Gaines, SD and Hay, ME (eds), *Marine community ecology*. Sunderland: Sinauer Associates, pp. 423-442.
- Engen, S. et al. 2002. Analyzing spatial structure of communities using the two-dimensional Poisson lognormal species abundance model. - *Am. Nat.* 160: 60-73.
- Erasmus, B.F.N. et al. 1999. Scale and conservation planning in the real world. - *Proc. Roy. Soc. London B* 266: 315-319.
- Ettema, C.H. and Wardle, D.A. 2002. Spatial soil ecology. - *Trends Ecol. Env.* 17: 177-183.
- Farnsworth, E.J. 1998. Issues of spatial, taxonomic and temporal scale in delineating links between mangrove diversity and ecosystem function. - *Global Ecol. Biogeogr. Lett.* 7: 15-25.
- Farnsworth, E.J. and Ellison, A.M. 1996. Scale-dependent spatial and temporal variability in biogeography of mangrove root epibiont communities. - *Ecol. Monographs* 66: 45-66.
- Fauchald, P., Erikstad, K.E. and Skarsfjord, H. 2000. Scale-dependent predator-prey interactions: The hierarchical spatial distribution of seabirds and prey. - *Ecology* 81: 773-783.
- Field R. et al. 2008. Spatial species-richness gradients across scales: a meta-analysis. - *J. Biogeogr.*, in press.
- Gascoigne, J.C. et al. 2005. Density dependence, spatial scale and patterning in sessile biota. - *Oecologia* 145: 371-381.

- Gaston, K.J. 2003. The structure and dynamics of geographic ranges. - Oxford University Press.
- Goslee, S.C. and Urban, D.L. 2007. The ecodist package for dissimilarity-based analysis of ecological data. - *J. Statist. Software* 22: 1-19.
- Green, J. and Bohannan, B.J.M. 2006. Spatial scaling of microbial biodiversity. - *Trends Ecol. Evol.* 21: 501-507.
- Guichard, F. and Bourget, E. 1998. Topographic heterogeneity, hydrodynamics, and benthic community structure: a scale-dependent cascade. - *Mar. Ecol. Prog. Ser.* 171: 59-70.
- Hartley, S. et al. 2004. Coherence and discontinuity in the scaling of species' distribution patterns. - *Proc. Roy. Soc. London B* 271: 81-88.
- Hoda, M. 1990. Variation in estuarine littoral nematode populations over three spatial scales. - *Estuarine, Coastal and Shelf Science* 30: 325-340.
- Koenig, W.D. 1999. Spatial autocorrelation of ecological phenomena. - *Trends Ecol. Evol.* 14: 22-26.
- Krawchuk, M.A. and Taylor, P.D. 2003. Changing importance of habitat structure across multiple scales for three species of insects. - *Oikos* 103: 153-161.
- Legendre P., Fortin M.-J. 1989. Spatial pattern and ecological analysis. - *Vegetatio* 80: 107-138.
- Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? - *Ecology*, 74, 1659-1673.
- Legendre, P. et al. 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. - *Ecography* 25: 601-615.
- Levin, S.A. 1992. The problem of pattern and scale in ecology. - *Ecology* 73: 1943-1967.
- Levin, S.A. 1994. Patchiness in marine and terrestrial systems - from individuals to populations. - *Phil. Trans. Roy. Soc. London B* 343: 99-103.
- Liebhold, A.M. and Gurevitch, J. 2002. Integrating the statistical analysis of spatial data in ecology. - *Ecography* 25: 553-557.
- Logerwell, E.A., Hewitt, R.P. and Demer, D.A. 1998. Scale-dependent spatial variance patterns and correlations of seabirds and prey in the southeastern Bering Sea as revealed by spectral analysis. - *Ecography* 21: 212-223.
- MacArthur, R.H. and Wilson, E.O. 1967. The theory of island biogeography. Princeton University Press, Princeton.
- Macnae, W. 1963. Mangrove swamps in South Africa. - *J. Ecol.* 51: 1-25.
- McGeoch, M.A. and Chown, S.L. 1997. The spatial variability of rare and common species in

- a gall-inhabiting Lepidoptera community. - *Ecography* 20: 123-131.
- McGeoch, M.A. and Gaston, K.J. 2002. Occupancy frequency distributions: patterns, artefacts and mechanisms. - *Biol. Rev.* 77: 311-331.
- McGeoch, M.A. and Price, W.P. 2004. Sawflies in space: abundance structure of four gall-forming species across an altitudinal gradient. - *J. Anim. Ecol.* 73: 506-516.
- Menge, B.A. and Olson, A.M. 1990. Role of scale and environmental-factors in regulation of community structure. - *Trends. Ecol. Evol.* 5: 52-57.
- Moran, P.A.P. 1950. Notes on continuous stochastic phenomena. - *Biometrika* 37: 17-23.
- Morgan, S.G. 2001. The larval ecology of marine communities. - In: Bertness MD, Gaines, SD and Hay, ME (eds), *Marine community ecology*. Sunderland: Sinauer Associates, pp. 159-182.
- Mumby, P.J. 2001. Beta and habitat diversity in marine systems: a new approach to measurement, scaling and interpretation. - *Oecologia* 128: 274-280.
- Nagelkerken, I. et al. 2008. The habitat function of mangroves for terrestrial and marine fauna: A review. - *Aq. Bot.* 89: 155-185.
- Oden, N.L. and Sokal, R.R. 1992. An investigation of three-matrix permutation tests. - *J. Classification* 9: 275-290.
- Perry, J.N. et al. 2002. Illustrations and guidelines for selecting statistical methods for quantifying spatial pattern in ecological data. - *Ecography* 25: 587-600.
- Phillips, A. et al. 1994. Horizontal zonation of epiphytic algae associated with *Avicennia marina* (Forssk.) Vierh. pneumatophores at Beachwood Mangroves Nature Reserve, Durban, South Africa. - *Botanica Marina* 37: 567-576.
- Phillips, A. et al. 1996. Vertical zonation of epiphytic algae associated with *Avicennia marina* (Forssk.) Vierh. Pneumatophores at Beachwood Mangroves Nature Sanctuary, Durban, South Africa. - *Botanica Marina* 39: 167-175.
- Procheş, Ş. 2001. Back to the sea: secondary marine organisms from a biogeographical perspective. - *Biol. J. Linn. Soc.* 74: 197-203.
- Procheş, Ş. 2004. Ecological associations between organisms of different evolutionary history: mangrove pneumatophore arthropods as a case study. - *J. Mar. Biol. Assoc. UK* 84: 341-344.
- Procheş, Ş. and Marshall, D.J. 2002a. Epiphytic algal growth and sediment deposition as determinants of arthropod distribution and abundance on mangrove pneumatophores. - *J. Mar. Biol. Assoc. UK* 82: 937-942.

- Procheş, Ş. and Marshall, D.J. 2002b. Diversity and biogeography of southern African intertidal Acari. - *J. Biogeogr* 29: 1201-1215.
- Procheş, Ş. et al. 2001. Mangrove pneumatophore arthropod assemblages and seasonality patterns. - *J. Mar. Biol. Assoc. UK* 81: 545-552.
- Procheş, Ş. et al. 2008. Dissecting the plant-insect diversity relationship in the Cape. - *Mol. Phylogenet. Evol.* doi:10.1016/j.ympev.2008.05.040.
- Quintino, V., Elliott, M. and Rodrigues, A.M. 2006. The derivation, performance and role of univariate and multivariate indicators of benthic change: Case studies at differing spatial scales. - *J. Exper. Mar. Biol. Ecol.* 330: 368–382.
- Radeloff, V.C. et al. 2000. Periodicity in spatial data and geostatistical models: autocorrelation between patches. - *Ecography* 23: 81-91.
- Rahbek, C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. - *Ecol. Lett.* 8: 224–239.
- Ricklefs, R.E. 1990. Scaling patterns and processes in marine ecosystems. - In: Sherman, K. et al. (eds), *Large marine ecosystems: patterns, processes and yields*. Washington: American Association for the Advancement of Science, pp. 169-178.
- Rosenzweig, M.L. 1997. *Species diversity in space and time* (third edition). - Cambridge University Press, Cambridge.
- Saburova, M.A., Polikarpov, I.G. and Burovsky, I.V. 1995. Spatial structure of an interstitial sandflat microphytobenthic community as related to different spatial scales. - *Mar. Ecol. Prog. Ser.* 129: 229-239.
- Saifullah, S.M. and Elahi, E. 1992. Pneumatophore density and size in mangroves of Karachi, Pakistan. - *Pakistan J. Bot.* 24: 5-10.
- Saunders, S.C. et al. 2002. The patch mosaic and ecological decomposition across spatial scales in a managed landscape of northern Wisconsin, USA. - *Basic Appl. Ecol.* 3, 49-64.
- Saunders, S.C. et al. 2005. Identifying scales of pattern in ecological data: a comparison of lacunarity, spectral and wavelet analyses. - *Ecological Complexity* 2: 87–105.
- Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. - *Ecol. Lett.* 10, 1115-1123.
- Sokal, R.R. and Oden, N.L. 1978. Spatial autocorrelation in biology. 2. Some biological implications and four applications of evolutionary and ecological interest. - *Biol. J. Linn. Soc.* 10: 229-249.

- Sokal, R.R. and Wartenberg, D.E. 1983. A test of spatial autocorrelation analysis using an isolation-by-distance model. - *Genetics* 105: 219-237.
- Tomlinson, P.B. 1986. *The botany of mangroves*. - Cambridge: Cambridge University Press.
- Underwood, A.J.U. and Chapman, M.G. 1996. Scales of spatial patterns of distribution in intertidal invertebrates. - *Oecologia* 107: 212-224.
- Underwood, A.J.U. and Chapman, M.G. 1998. A method for analysing spatial scales of variation in composition of assemblages. - *Oecologia* 117: 570-578.
- Urban, D. et al. 2002. Extending community ecology to landscapes. - *Ecoscience* 9: 200-212.
- Van de Koppel et al. 2008. Experimental evidence for spatial self-organization and its emergent effects in mussel bed ecosystems. - *Science* 322, 739-742.
- Ward, C.J. and Steinke, T.D. 1982. A note on the distribution and approximate areas of mangroves in south Africa. - *SA J. Bot.* 1: 51-53.
- Warren, M., McGeoch, M.A. and Chown, S.L. in press. The detection of spatial structure in populations and communities: an empirical case study. - *Écoscience*.
- Wartenberg, D. 1989. SAAP – A Spatial Autocorrelation Analysis Program. - Robert Wood Johnson Medical School, Piscataway, New Jersey.
- Whittaker, R.H. 1972. Evolution and the measurement of species diversity. - *Taxon* 21: 213-251.
- Wu, J. et al. 2002. Empirical patterns of the effects of changing scale on landscape metrics. - *Landscape Ecol.* 17: 761-782.

Caption to figures:

Fig. 1. Sampling design showing the 128 samples were collected from plots arranged to allow assessment of spatial patterns of species and communities at seven different spatial scales (localities 100km apart, transects 10km apart, areas 1km apart, double grids 100m apart, grids 10m apart, double plots 1 m apart, adjacent plots 10cm apart).

Fig. 2. Method for evaluating variation in community structure at different spatial scales, as developed by Underwood and Chapman (1998). Circles represent samples or centroids for subsets of 2, 4, 8, and 16 samples. Links represent randomly selected sample-centroid pairs for which dissimilarity values are calculated. A sample is always compared to the centroid of the set it belongs to, and equal numbers of dissimilarity values are calculated for sets from each spatial scale. The example in this figure illustrates how this method is applied to a set of 16 samples. In our study, the method was applied to a set of 128 samples.

Fig. 3. Bonferroni-corrected correlograms for a) common and b) rare species across seven scales. Significant I values at $p < 0.05$ are represented by closed symbols.

Fig. 4. Relationship between (log-transformed) species abundance and Moran's I in the first two distance classes; 10 cm (diamonds): $F_{1,12} = 5.0764$, $r^2=29.73\%$, $p=0.012$; 1 m (squares): $F_{1,12}=41.775$, $r^2=77.68\%$, $p=0.003$.

Fig. 5. Bonferroni-corrected correlograms for total arthropod abundance (squares), species richness (diamonds), and total pneumatophore mass (triangles) at seven scales. Significant I values at $p < 0.05$ are represented by closed symbols.

Fig. 6. The relationship between Bray-Curtis dissimilarity (among samples and sample centroids) and spatial scale. (See Materials and Methods for a full explanation.) (Likelihood Type III Test: Chi-square = 1180.05, $df=1$, $p<0.01$, Scaled deviance/ $df = 26.64$). Average values (circles) for each scale are also plotted.

Table 1. Arthropod taxa from mangrove pneumatophores.

Class/Superclass	Order/Subclass	Family	Species
Acari	Mesostigmata	Parasitidae	Parasitidae sp.
		Ascidae	<i>Leioseius</i> sp.
	Prostigmata	Uropodidae	<i>Urobovella</i> sp.
		Halacaridae	<i>Copidognathus caloglossae</i>
			<i>Acarothrix umgenica</i>
			<i>Agauopsis</i> sp.
	Oribatida	Tydeidae	Tydeidae sp.
		Tarsonemidae	Tarsonemidae sp.
		Cheyletidae	Cheyletidae sp.
		Erythraeidae	Erythraeidae sp.
Nothridae		Nothridae sp.	
Oribatulidae		Oribatulidae sp.	
Crustacea	Astigmata	Thyreophagidae	<i>Pontiobates</i> sp.
	Tanaidacea	Tanaididae	<i>Thyreophagus</i> sp.
	Isopoda	Sphaeromatidae	<i>Tanais philetaerus</i>
	Amphipoda		Sphaeromatidae sp.
			Amphipoda sp.
		Melitidae	<i>Melita zeylanica</i>
		Caprellidae	Caprellidae sp.
Collembola	Cirripedia	Balanidae	<i>Balanus amphitrite</i>
	Poduromorpha	Neanuridae	<i>Anurida maritima</i>

Table 2. Autocorrelation values (Moran's I) for arthropod species from mangrove pneumatophores at seven spatial scales. Bonferroni-corrected overall significance values are given for each correlogram. Significance: * $p < 0.050$; ** $p < 0.001$. The species are arranged in decreasing order of abundance, and species present in only one sample were excluded (total number of samples: 128).

Species	Total abundance	Samples present	10 cm	1 m	10 m	100 m	1 km	10 km	100 km	Overall significance
Common										
<i>Tanais philetaerus</i>	9362	81	0.95**	0.88**	0.79**	0.74**	0.27**	-0.53**	-0.01	0.001
<i>Copidognathus caloglossae</i>	1139	18	0.98**	0.87**	0.90**	0.11**	0.14**	-0.11**	-0.11**	0.001
<i>Balanus amphitrite</i>	772	45	0.87**	0.83**	0.20**	0.46**	-0.02	-0.24**	-0.01	0.001
<i>Leioseius</i> sp.	244	56	0.53**	0.59**	0.39**	0.03	0.22**	-0.14**	-0.05**	0.001
<i>Acarothrix umgenica</i>	144	22	0.70**	0.55**	0.11*	-0.01	0.10**	-0.04*	-0.05**	0.001
Rare										
<i>Thyreophagus</i> sp.	74	9	0.33**	0.46**	0.30**	-0.03	0.11**	-0.05**	-0.05**	0.001
<i>Melita zeylanica</i>	57	10	0.11	0.38**	-0.01	0.03	-0.06*	-0.02	-0.01	0.001
<i>Agauopsis</i> sp.	33	4	0.65**	0.41**	-0.03	0.14**	-0.03	-0.03	-0.03**	0.001
Tarsonemidae sp.	30	4	0.13*	0.22**	-0.02	-0.02	-0.02	-0.02	-0.01	0.001
<i>Uroobovella</i> sp.	25	9	0.75**	0.69**	0.74**	-0.07	-0.07*	-0.04*	-0.05**	0.001
Tydeidae sp.	16	7	-0.04	0.14*	0.08*	-0.03	0.03*	-0.02	-0.02	0.002
<i>Pontiobates</i> sp.	16	4	-0.02	0.08*	0.03	-0.02	0.01	-0.01	-0.01	0.103
Spheromatidae sp.	9	4	0.63**	-0.03	-0.03	0.01	0.08**	-0.03	-0.03**	0.001
<i>Anurida maritima</i>	4	3	0.70**	-0.02	-0.02	-0.02	-0.02	-0.02	-0.01	0.001

Table 3. Mantel analyses of the relationships between matrices representing community variables (a: species richness, b: total abundance), pneumatophore mass and space. Values above the dashes represent simple Mantel statistics, values below dashes represent partial Mantel statistics controlling for the effect of the third matrix. Results support the causal model of similar underlying spatial structure structuring the community and pneumatophore mass (see Legendre and Legendre 1998). Significance: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; tests of significance are one-tailed.

a) Species richness-mass-space relationships

	Richness	Mass	Space
Richness	-	0.06	0.05**
Mass	0.06	-	0.04**
Space	0.05***	0.04*	-

b) Total abundance-mass-space relationships

	Abundance	Mass	Space
Abundance	-	0.03	0.11***
Mass	0.03	-	0.04**
Space	0.11***	0.04*	-

Table 4. One-way ANOVA and Student-Newman-Keuls test, comparing the Bray-Curtis dissimilarity values between individual samples and the centroids of the sets they belong to, at seven scales (letters in the last row indicate significantly-different subsets, $p < 0.01$).

ANOVA	SS	df	MS	F	p
Between scales	30927.674	6	5154.612	9.168	0.001
Within scales	55097.893	98	562.223		
Total	86025.567	104			

SNK test	10 cm	1 m	10 m	100 m	1 km	10 km	100 km
Sample size	15	15	15	15	15	15	15
Minimum	1.89	11.00	10.23	13.38	22.93	16.35	57.33
Maximum	61.29	71.43	88.49	93.04	96.03	98.32	99.95
Mean	24.26	37.00	45.35	57.00	58.45	59.81	81.98
Standard error	5.08	5.39	5.96	6.89	7.59	7.14	3.98
Subset	a	ab	b	b	b	b	c

Fig. 1.

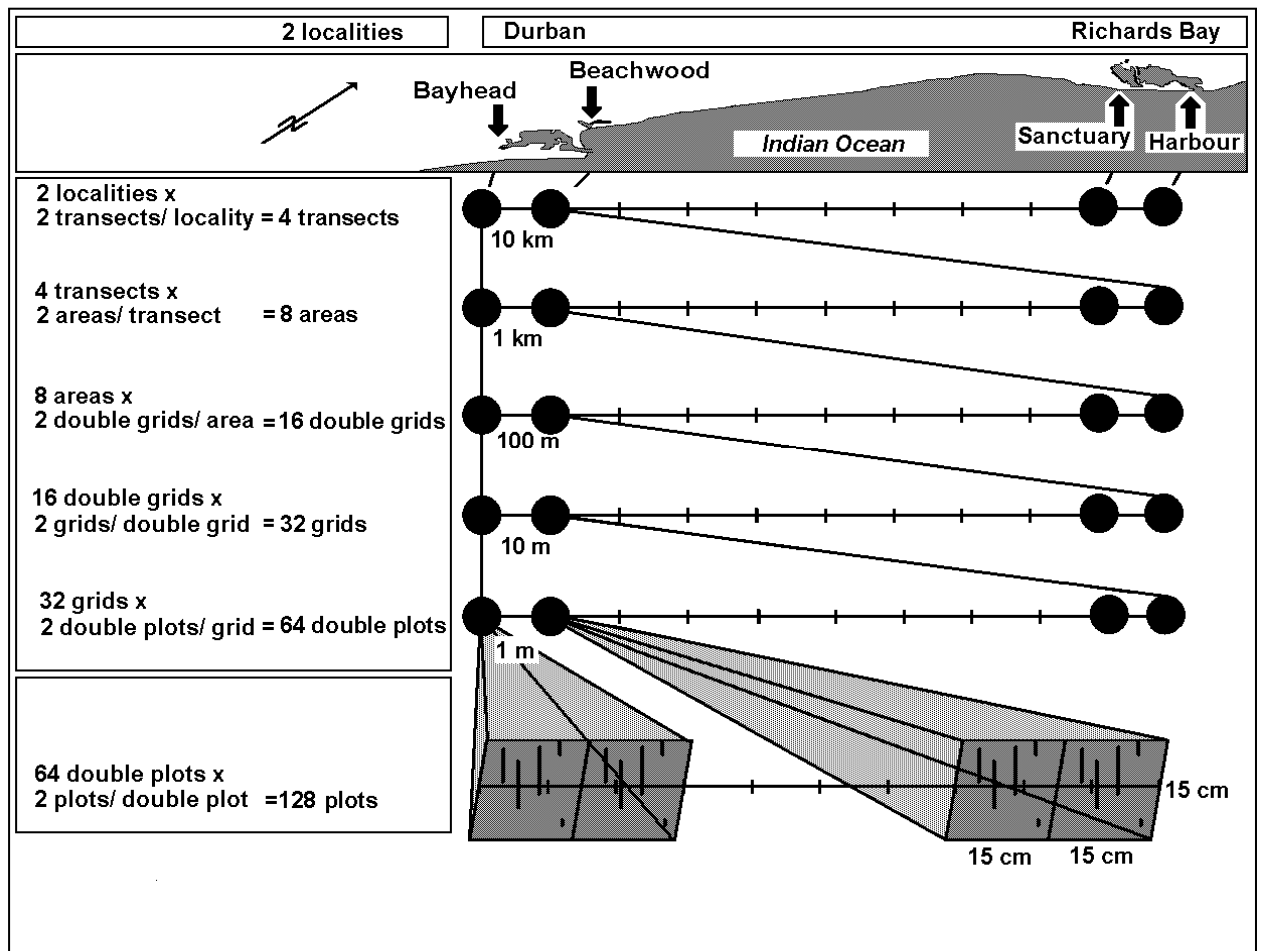


Fig. 2.

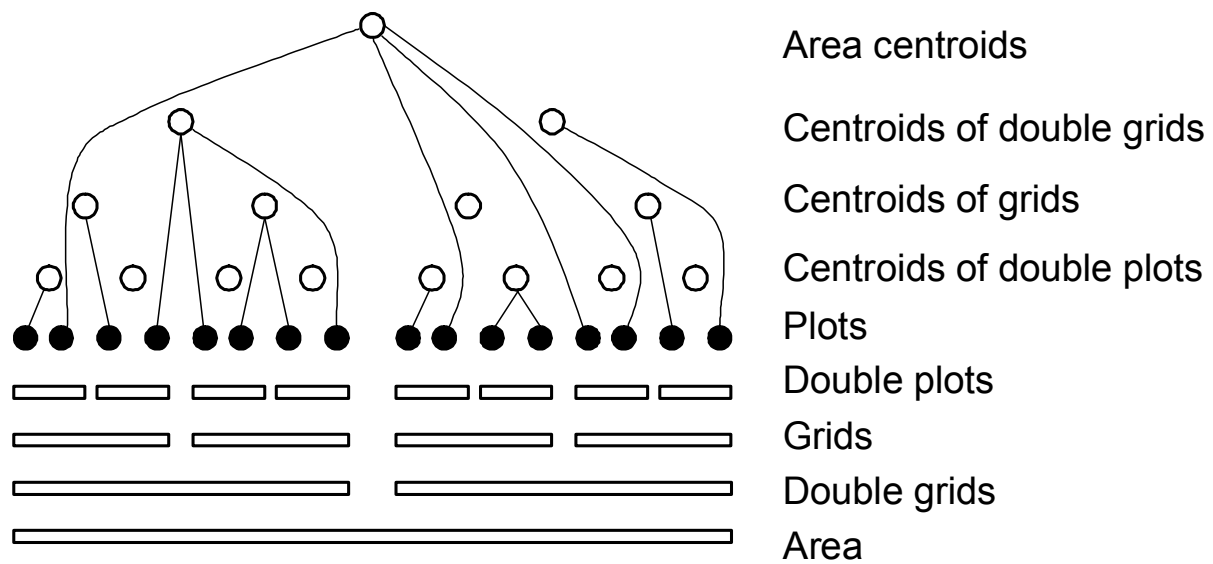


Fig. 3.

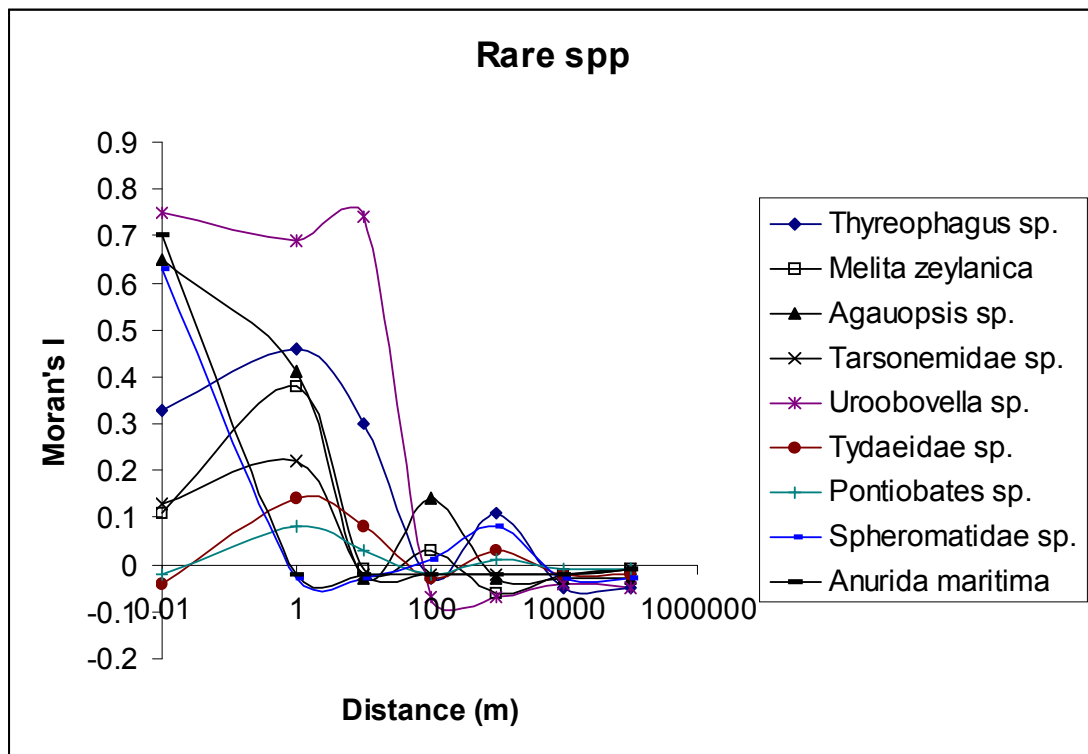
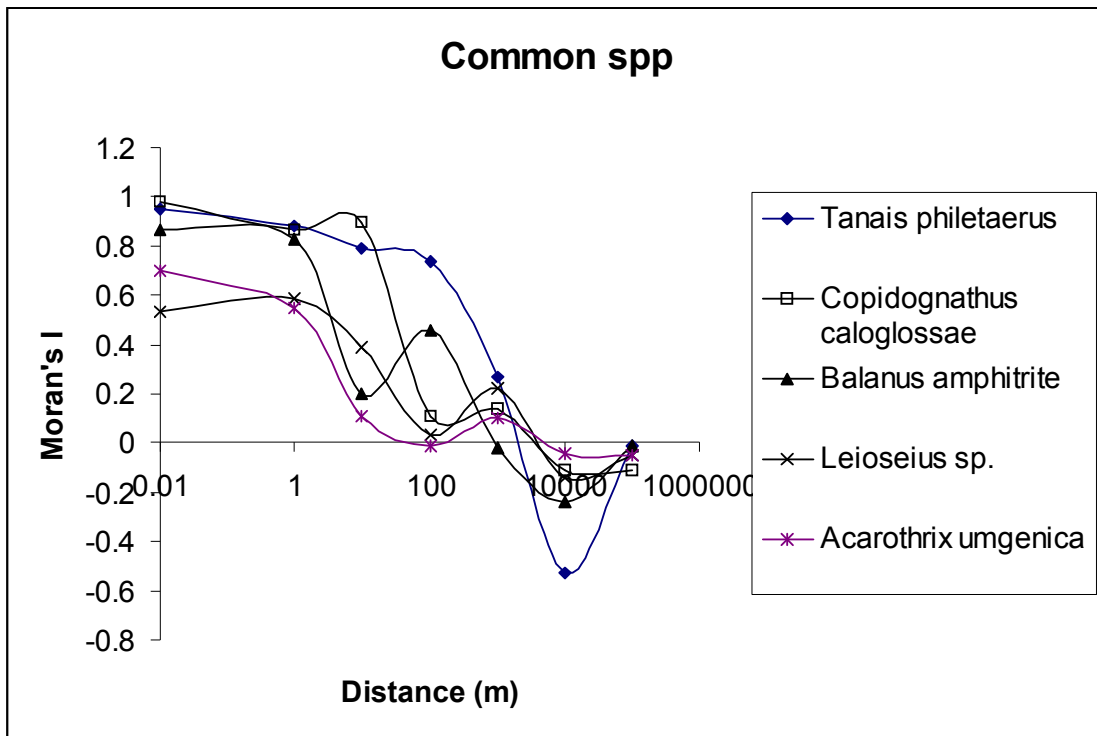


Fig. 4.

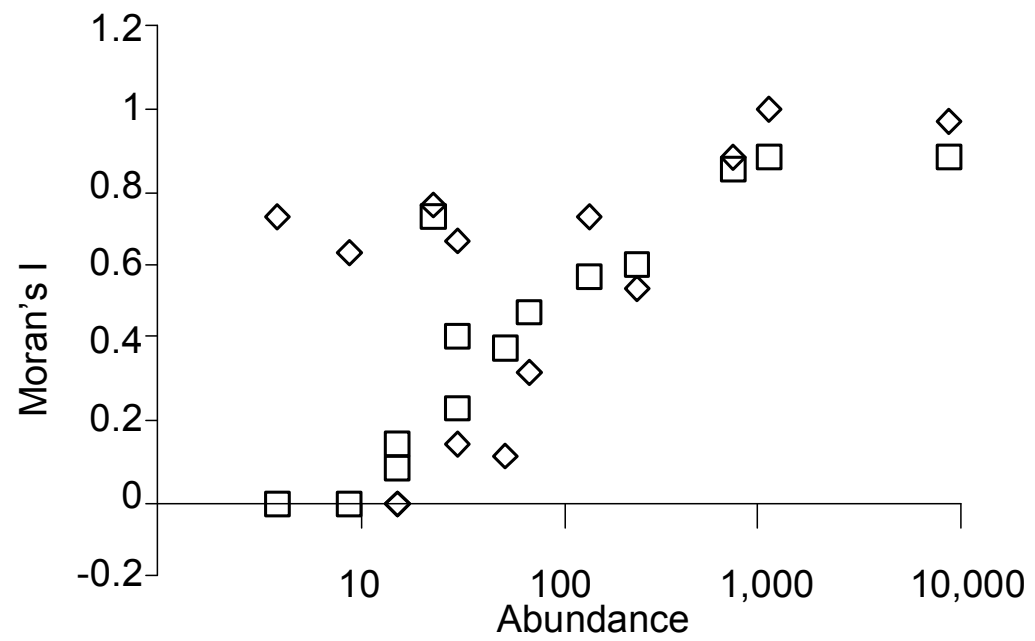


Fig. 5.

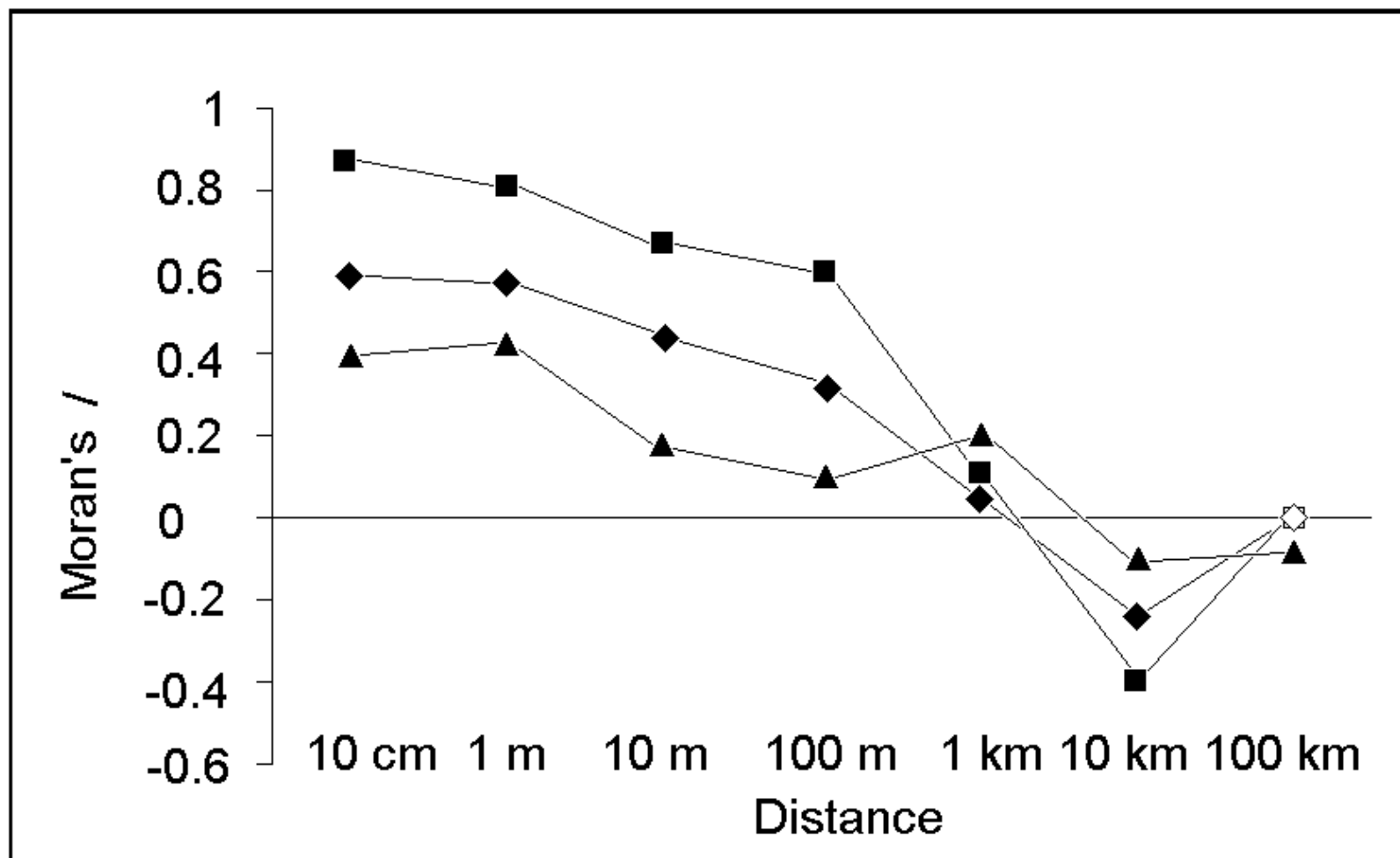


Fig. 6.

