Scales of spatial variation in tropical benthic assemblages and their ecological relevance: epibionts on Caribbean mangrove roots as a model system

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ABSTRACT: The analysis of spatial patterns of biodiversity remains a focal issue in ecological studies. The recognition of spatial scales at which significant differences in biodiversity are detected allows us to infer the relative importance of the ecological processes that may shape those patterns. In marine benthic studies, small-scale variability is always seen, irrespective of habitat, but little consensus exists on the relative importance of variability at intermediate and wider spatial scales, and thus the drivers acting at each of those scales. In this study, the relevance of different spatial scales for fouling assemblages on the roots of the Caribbean red mangrove *Rhizophora mangle* L. was assessed by partitioning variation in richness and species composition over 4 natural and nested spatial scales observed on 5 occasions. Spatial scales consisted of 2 marine parks (about 400 km apart), sectors representing environmental gradients (1–2 km apart), sites within each sector (50–400 m apart), and neighbouring roots (1–2 m apart). Species richness and species composition varied significantly at all spatial scales. The greatest partitioned variation for richness was among parks, followed by neighbouring roots, whereas the opposite pattern was found for species composition. The relative magnitude of sector and site variability depended on the park, for both species richness and composition. These results highlight the importance of processes that operate at the scales of 100s of kilometres and a few metres over local drivers such as environmental gradients and the dispersal abilities of larvae.

KEY WORDS: Species diversity · Spatial scales · Hierarchical design · Variance components · Caribbean Sea · *Rhizophora* mangrove roots

INTRODUCTION

After a century of ecological studies, the issue of how to describe patterns and spatial scales of variation in species diversity remains a focal point of ecological debates (Levin 1992, Lawton 1999, Chave 2013). Explicit demonstration of the existence of different scales of spatial variation may allow inference about the relative importance of the potential pro-

cesses responsible for these patterns (Allen & Starr 1982, Benedetti-Cecchi et al. 2012, Nash et al. 2014). This information is also useful for determining the spatial scales at which to focus management decisions (Underwood 1995) and in designing experiments to test the predictions of relevant theories (Simberloff 2004). Several methods and statistical procedures have been proposed to identify the relevance of different scales of spatial variation of natural

populations and assemblages (e.g. Andrew & Mapstone 1987, Underwood & Chapman 1996, 1998, Borcard et al. 2004, Josefson 2009). However, explicitly incorporating a multi-scale perspective into research and management actions remains a challenge (Fraschetti et al. 2005, Nash et al. 2014), basically because spatial scales tend to be arbitrarily defined by the observer (Levin 1992, Gaston & Blackburn 2007) and, commonly, do not match the natural scales of ecological phenomena (Huston 1999, Chase & Knight 2013).

The task of detecting temporal and/or spatial scales at which patterns occur and processes operate is particularly difficult in benthic marine studies. This issue has been discussed extensively for temperate and subtropical marine habitats (Underwood et al. 2000, Fraschetti et al. 2005, Terlizzi et al. 2007) and, to a lesser extent, for tropical habitats (but see Farnsworth & Ellison 1996, Cruz-Motta 2007, Guerra-Castro et al. 2011b, Eidens et al. 2015). One of the commonly recognized problems lies in the design of field surveys and experiments at relevant spatial scales (i.e. those at which patterns can be directly associated with processes that shape populations and communities). Marine habitats tend to be continuously heterogeneous, so the identification of natural units of observation (i.e. grain size) and the scale (i.e. extent) are hard to define (Weinberg 1978, Thrush et al. 1997). Despite these difficulties, a clear pattern has been identified by several authors for marine benthic habitats: variability in species diversity and abundances is larger at very small spatial scales of 10s to 100s of centimetres (Anderson et al. 2005a, Fraschetti et al. 2005, Chapman et al. 2010), but there is not a clear pattern in the hierarchy of variation over larger and intermediate spatial scales of 10s to 1000s of kilometres (Fraschetti et al. 2005, Chapman et al. 2010). This lack of consistency could be a consequence of the relative weight and variety of processes operating in each one of the evaluated benthic systems, but also — as suggested by Wheatley & Johnson (2009) for terrestrial systems — could be an artefact produced by the selection of arbitrary spatial scales, especially when the area being studied cannot be divided, *a priori*, into natural and discrete units (Andrew & Mapstone 1987).

However, some tropical marine coastal habitats such as mangrove islands (Simberloff 1976, Farnsworth & Ellison 1996) have proven to be suitable systems for defining natural and discrete units of observation at several spatial scales. In particular, prop roots of the Caribbean coastal mangrove *Rhizophora mangle* are fouled by numerous (>500) species of invertebrates and algae (Díaz & Rützler 2009, Diaz

2012). These substrates can be considered as ecological islands that are readily identifiable at a number of natural spatial scales (Farnsworth & Ellison 1996, Guerra-Castro et al. 2011a), including roots at the finest scale, clustered with neighbouring roots at a particular site in a mangrove cay (intermediate scale), to groups of cays or sites in a region (broader scale). At each one of these scales, potential biological and environmental factors can easily be identified, and be proposed as processes that govern the abundance and diversity of epibenthic species (Bingham 1992, Farnsworth & Ellison 1996).

A common finding of quantitative studies dealing with these assemblages is the great variability in composition of species among neighbouring roots, as well as differences in assemblage composition among nearby sites (Farnsworth & Ellison 1996, Hunting et al. 2008, Guerra-Castro et al. 2011a,b). The descriptions of these patterns have led to a general discussion about the potential ecological processes that govern the variation of diversity of species in these systems. In particular, the following ecological processes have been proposed by several authors: larval supply and dispersal limitations (Bingham 1992, Farnsworth & Ellison 1996), biological interactions such as predation (Wulff 2005), variation of chemical properties of roots (Hunting et al. 2008, 2010), and environmental conditions such as tidal amplitude, suspended sediment and salinity gradients (Álvarez 1989, Orihuela et al. 1991, Rützler 1995, Díaz et al. 2004). Nevertheless, there is no clear concept of how all these drivers interact nor how important they are in controlling the coexistence of species and the patterns of diversity in this tropical system.

To address these questions, we have described the patterns of spatial variation of assemblages associated with mangrove prop roots over 4 spatial scales and properly replicated in time. In particular, we used a nested sampling design to test the null hypothesis that spatial pattern is independent of scale, but more significantly, to estimate the relative importance of each of the scales (and potential processes), using the size and hierarchy of the components of variation as indicators (Underwood & Chapman 1996). Units of observations were: (1) 2 mangrove systems from 2 very different regions of the Venezuelan coast (separated by about 400 km), (2) sectors within each of these parks (1–2 km apart), (3) sites within each of the sectors (50–400 m apart) and (4) neighbouring roots (separated by 1–2 m). Variation at the first scale is potentially influenced by geographic processes, such as oceanic conditions, distance to sources of species, size of the regions, and

mainland and island effects (Farnsworth & Ellison 1996, Guerra-Castro et al. 2011b). Variation at the scale of sectors could potentially be associated with the effects of environmental gradients generated by local hydrographic dynamics among lagoons and channels in the mangrove system (Costanza et al. 1993, Nagelkerken et al. 2008, Díaz & Rützler 2009). This scale might also reflect the effect of dispersal limitations proposed by Bingham (1992) as a neutral model for these systems, particularly for species with non-feeding (lecithotrophic) larvae such as sponges and tunicates. Site scale differences could be associated with variation of physiographic variables among mangrove cays, such as local depth and exposure to light and shade (Rützler 1995, Glasby 1999, Glasby & Connell 2001). At the smallest scale, potential sources of variation could be related to the size of the root (Simberloff 1976) and individual successional processes, i.e. colonization and recruitment on the root, development of the assemblages and competition (Platt & Connell 2003, Underwood & Chapman 2006).

Here, all considered spatial scales contain natural and discrete units of observation. Therefore, the objective of this study was, by decomposition of variation across 4 hierarchical scales, to identify the relative importance of these natural spatial scales on fouling assemblages of mangrove prop roots. Findings are discussed to identify potential processes that could have caused the patterns at the different scales.

MATERIALS AND METHODS

Study area

Fringe mangrove forests from 2 marine reserves separated by 436 km along the Venezuelan coast were evaluated: Morrocoy National Park (MNP), western Venezuela, and La Restinga National Park (LRNP), eastern Venezuela (Fig. 1). These forests are dominated by *Rhizophora mangle*, which grows on the shore of the mainland, sand cays, or even in shallow waters where they can form mangrove cays. These marine reserves are located in areas with different oceanographic and meteorological characteristics. MNP stretches over 177 km^2 of mainland marine habitats with coral reefs, biogenic sandy bottoms, seagrass beds and

mangrove cays, of which 28 km^2 are occupied by mangroves surrounding a system of interconnected lagoons with oligotrophic waters. This marine reserve is open to the sea through several channels, but is also affected by freshwater inflow during seasonal rainfall (Bone et al. 2001, Laboy-Nieves et al. 2001) and anthropogenic pressures (García et al. 2008, 2011). In contrast, LRNP is an insular complex of hypersaline and eutrophic lagoons surrounded by well-developed mangroves that add up to an area of 30 km^2. This system is connected to the sea by a single channel that is 1.3 km long, 70 m wide and 6 m deep, and it is not under the effects of freshwater runoff, although mass mortalities have been reported as consequences of hurricane winds and increased turbidity (Orihuela et al. 1991). This mangrove system does not have coral patches, and most of the area
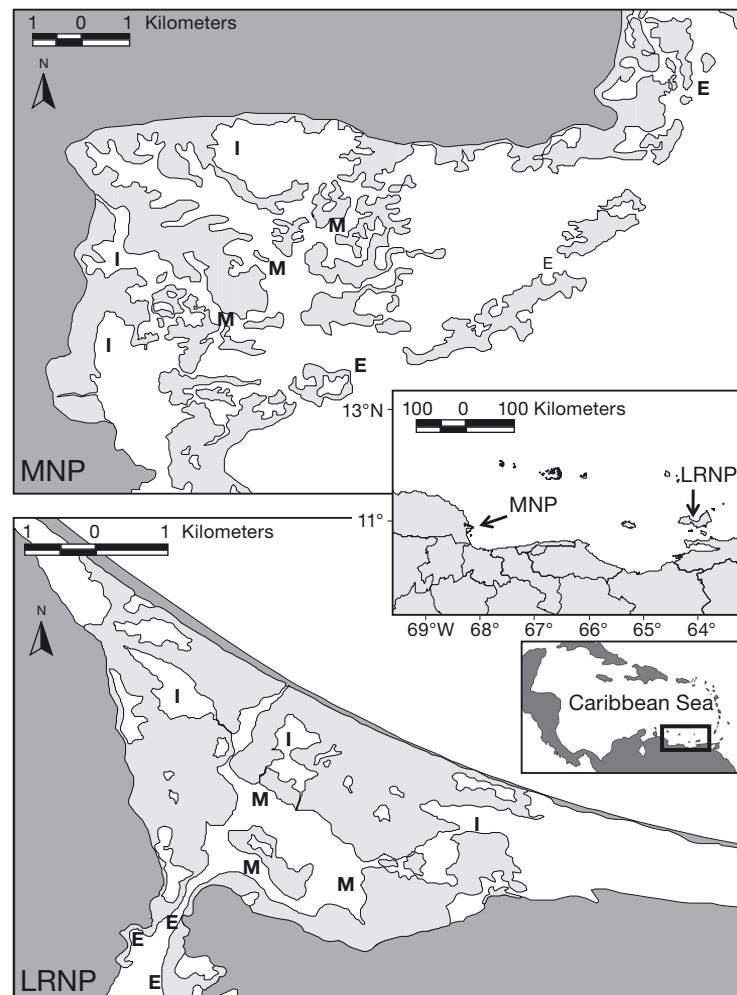

Fig. 1. Mangrove systems studied in the southeast of the Caribbean Sea at Morrocoy National Park (MNP) and La Restinga National Park (LRNP). The relative extent of each sector within each park is shown: E (external), M (intermediate) and I (internal). Light grey represents mangrove areas

consists of muddy bottoms and marginal seagrass beds. Sampling was repeated on 5 occasions, 3 to 4 mo apart, at each park, over a period of 14 mo from November 2009 to January 2011.

Hypotheses and experimental design

If geographical processes are important in maintaining levels of species diversity, we expect to find significant differences between parks. Furthermore, the direction of the differences in terms of diversity at this spatial scale would allow differentiation among competing models. In each park, 3 sectors were identified and sampled: external, i.e. mangrove zones in direct contact with the open sea; internal, i.e. mangrove lagoons isolated from the open sea but strongly influenced by in-shore processes; and intermediate, i.e. mangrove channels and lagoons where waters of external and internal sectors are mixed (Fig. 1). In this sense, if physiological tolerance or dispersal limitations of species exert important effects on species diversity, significant differences among sectors should be detected, regardless of the park under consideration.

Within each sector, 4 sites (50–400 m apart) were examined at each sampling time. Significant variation at this scale would highlight the relevance of medium-scale processes, such as variation of physiographic aspects of the local environment (e.g. exposure to light, depth, hydrodynamics) or variation of settlement strategies of species living within each sector. At each site, 8 neighbouring prop roots were evaluated to quantify variation of species diversity associated with the size of the roots and successional processes. Additionally, the length as well as the upper and apical diameters of each root were measured in the field to estimate the total area available for colonization, using the surface area equation of a truncated cone. Numbers of replicates at each site, as well as the number of sites per sector, were decided after a cost-benefit analysis from data obtained during an intensive pilot survey (Guerra-Castro et al. 2011a).

Field work and image processing

No sampled roots had contact with the bottom, and they were separated from each other by 1–2 m. Sampling was non-destructive, and species present on each root were identified *in situ* using a photographic identification guide previously prepared using local inventories (Supplement 1 at www.int-res.com/ articles/suppl/m548p097_supp.pdf). To estimate the relative abundance of each species per sample unit, several digital photographs were taken of the entire root, starting from the intertidal zone (the high tide mark) down to the tip of the root. Each root was photographed using 10 cm intervals covering the entire length and sides by means of a vertically fixed measuring tape as reference. In both parks, visibility was adequate enough to take good quality pictures. These photographs were used to estimate cover of all sessile species present (mobile fauna was not quantified), applying the point intercept technique recommended for these assemblage types (Díaz et al. 1992). All images were scaled and calibrated using the tick marks of a measuring tape to adequately estimate the length of the area photographed. A digital grid at 1 cm spacing was overlaid on each image, to yield intercept counts using Coral Point Counter v.3.6 (Kohler & Gill 2006). Using the metric references in each picture, care was taken to ensure that areas of the root that appeared in 2 images were not quantified twice. The resulting data are in the form of a species × samples matrix, with each cell containing the number of intercept points for a given species in a specified sample.

Statistical analyses

In this study, 2 components of species diversity were measured: α-diversity, as the number of species per root, and β-diversity, as the variation in species composition among roots within the study area. For this, a dissimilarity matrix was constructed using the Sørensen coefficient. This coefficient was used because (1) it excludes joint absences and can be interpreted in a probabilistic framework (Anderson et al. 2006); (2) it is one of the most widely used measures of β-diversity, allowing direct comparisons across studies (Koleff et al. 2003, Anderson et al. 2011); and (3) it equals the Bray-Curtis coefficient (see below) computed on presence/absence data (Clarke et al. 2006, Legendre & De Cáceres 2013). Simultaneously, the structure of the assemblages was compared using the Bray-Curtis coefficient of similarity (Clarke 1993) on the square-root abundances of each species. The transformation was used to downweight the dominance of highly abundant species in the calculation of similarities, relative to the less-common species. These analyses therefore examined whether the magnitudes and hierarchy of components of variation were similar when based on the presence of species (hereafter species composition)

and on their transformed abundances (hereafter assemblage structure).

Hypotheses were tested with a multifactorial linear model of mixed effects, using univariate ANOVA for α-diversity and distance-based multivariate PERMANOVA for species composition and assemblage structure. Sources of spatial variation in the model were (1) area of the root as covariate; (2) parks as 2 levels, fixed effect; (3) sectors as 3 levels, the fixed effects of internal, intermediate and external sectors; (4) sites as 4 levels, random effect; and (5) neighbouring roots as residuals. Because of the covariate, Type I sequential sums of squares were used to partition variance in the linear model. The estimates of the expected mean squares and variance components are listed in Supplement 2 at www.int-res.com/articles/suppl/m548p097_supp.pdf. Parks (P) and sectors (S) were orthogonal, and sites (Si) were nested in each combination of sector and time (T), different sites being sampled at each time. Likewise, times (5 levels, random effect) were nested in parks (as it was not possible to sample both parks at the same time), with times orthogonal to sectors. Time was used to evaluate the generality of spatial patterns, and no formal hypotheses were associated with this factor. The magnitude of these temporal changes can be statistically compared using the dispersion among centroids for each combination of S × T(P), by a PERMDISP test (Anderson 2006). The statistical significance of each term in the ANOVA and PERMANOVA were obtained using a random subset of 9999 permutations of residuals under a reduced model. It is worth highlighting that residuals in the linear model represent variation among adjacent roots. Part of this variation is due to random sampling error, but also responds to any process that operates at the smallest scale considered in this study (e.g. age of the root, history of recruitment and succession). In this analysis, however, there was no statistical test for this particular spatial scale. The hierarchy of the components of variation could be related to the ecological importance of each scale (and their processes) in sustaining the levels of α- and β-diversity, as well as in the structure of the assemblages.

Principal coordinate ordinations (PCO; Gower 1966, Anderson et al. 2008) illustrated patterns of spatial similarity in species composition and abundance structure among parks. For this, distances among centroids for the interaction term S × T(P) were calculated. Species responsible for significant differences among parks were identified with SIMPER

analysis (Clarke 1993). The abundance of the most important species across parks, sectors and sites, during all sampling times, were represented graphically using a shade plot (Clarke et al. 2014). All these analyses were carried out with the software PRIMER v.7 and PERMANOVA add-on (PRIMER-E).

RESULTS

Relevant spatial scales for α-diversity

Species richness varied significantly at all spatial scales, but the highest percentage of variation was associated with the largest spatial scale (i.e. between parks; Table 1). Species richness was higher in roots from LRNP than in those from MNP (Fig. 2). Temporal variation within each park was statistically significant (T[P]: $p < 0.05$); however, the relative component of variation associated with this source of variation was small (4% of explained variation). Similarly, differences among sectors in each park were dependent on the survey (S × T[P]: $p < 0.05$). In LRNP, internal sectors consistently had the lowest α-diversity when compared with intermediate or external sectors (pairwise t-test, $p < 0.05$; Fig. 2). In MNP, internal sectors had the lowest α-diversity, except for the last 2 sampling times (pairwise t-test, $p > 0.05$; Fig. 2). On the other hand, sectors with the highest values of diversity depended on the park and time of sampling (Fig. 2). In LRNP, α-diversity was higher in the external than in the intermediate sector only during the last 2 sampling surveys (pairwise t-test, $p < 0.05$), whereas, during the first 3 surveys, α-diversity was similar in these 2 sectors (pairwise t-test, $p > 0.05$; Fig. 2). In MNP, no significant differences were

Table 1. Permutational ANOVA of number of species per root on the basis of a mixed 4-factor linear model, with root area as a covariate. The square root of the variance components (√CV) and the relative percentages for the (non-square-rooted) variance components (%CV) are shown. P: parks; S: sectors; T: time

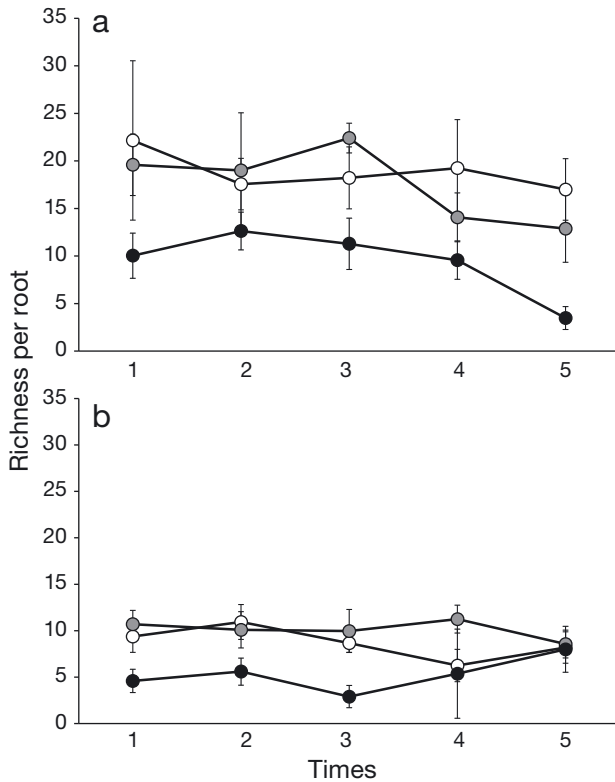| Source of variation	df	MS	F	p	√CV	%CV
Root area (covariate)	1	0.4	0.01	0.9340	0.0	0
P	1	12713.0	36.39	0.0087	5.1	36
S	2	4397.8	30.47	<0.0001	3.7	19
T(P)	8	350.2	4.44	0.0002	1.7	4
S × P	2	736.7	5.06	0.0203	1.9	5
S × T(P)	16	144.2	1.83	0.0429	1.4	3
Site = Si(S × T[P])	90	78.9	5.07	<0.0001	2.8	11
Residuals	839	15.6			3.9	22
Total	959					100

Fig. 2. Average number of epibiont species (mean ± SD) per root from the parks shown in Fig. 1, (a) LRNP and (b) MNP, during 5 sampling times (Nov 2009–Jan 2011, every 3 to 4 mo). White circles: external sectors; grey circles: intermediate; black circles: internal

detected between the external and intermediate sectors at 4 out of 5 sampling times (pairwise *t*-test, p > 0.05). However, at the fourth sampling, α-diversity in the intermediate sector duplicated that of the external sector (Fig. 2). Variability among sites within each sector was also important, as it represented

Table 2. Permutational multivariate ANOVA based on a Sørensen dissimilarity measure and a mixed 4-factor linear model, with root area as a covariate. The square root of the variance components (√CV) and the relative percentages of the (non-square-rooted) variance components (% CV) are shown. Other abbreviations as in Table 1

Source of variation	df	MS	Pseudo-*F*	p	√CV	%CV
Root area (covariate)	1	11 787	2.74	0.0003	3	0.2
P	1	470 200	24.61	0.0090	31	25
S	2	92 649	4.96	<0.0001	15	6
T(P)	8	19 146	3.22	<0.0001	12	4
S × P	2	48 685	2.58	0.0005	14	5
S × T(P)	16	18 680	3.15	<0.0001	20	10
Site = Si(S × T[P])	90	5946	4.33	<0.0001	24	15
Residuals	839	1374			37	36
Total	959					100.0

11 % of total variation, but the second highest component of variation (22 %) was associated with the residuals, i.e. variation among neighbouring roots. At this spatial scale, the area of the root did not explain any amount of variation in richness (Table 1). In general, the hierarchy of importance of spatial scales for α-diversity was:

parks > roots > sectors > sites

Relevant spatial scales for β-diversity

As for α-diversity, patterns in species composition varied significantly at all spatial scales (Table 2). The highest component of variation (36 %) was associated with the smallest spatial scale, whereas the park factor was the second most important (25 %; Table 2). Examination of the multivariate ordination plot (PCO) for centroids of the S × T(P) interaction showed that species composition in LRNP was consistently different from that in MNP (Fig. 3a). Furthermore, differences among sectors were not consistent between parks and changed among surveys (i.e. significant interactions S × P and S × T[P]; Table 2), as the PCO clearly showed that differences among sectors occurred in the same direction but at different magnitudes for each park. Differences among sectors were greater in LRNP than in MNP. These differences were seen not only in the relative position of the centroids themselves, but also in their relative dispersion, indicating that patterns of temporal variation were not the same across sectors and parks. For MNP, temporal changes in the internal sector were greater than in the intermediate sector. Similarly, temporal variation was significantly higher at sites of the intermediate sector than at sites of the external sector (PERMDISP, $F_{2,12} = 7.73$; p < 0.05). On the other hand, at LRNP, patterns of temporal variation among sectors were not statistically different when assessed with PERMDISP ($F_{2,12} = 1.71$; p > 0.05).

Dissimilarities among parks averaged 92 % (SIMPER analysis). Nevertheless, most of the recorded species were present in both parks, but the frequency of occurrence differed significantly (Table 3). As an example, *Crassostrea rhizophorae* was recorded on 72 % of the roots from LRNP, but only on 21 % of the roots from MNP (χ^2-test, p < 0.05; Table 3). Various species were found in just one of the parks. *Isognomon alatus* (bivalve), *Bostrychia tenella* (red alga), *Biemna caribea* (sponge), *Polysiphonia* sp. 1 (red algae), *Sabellastarte magnifica*
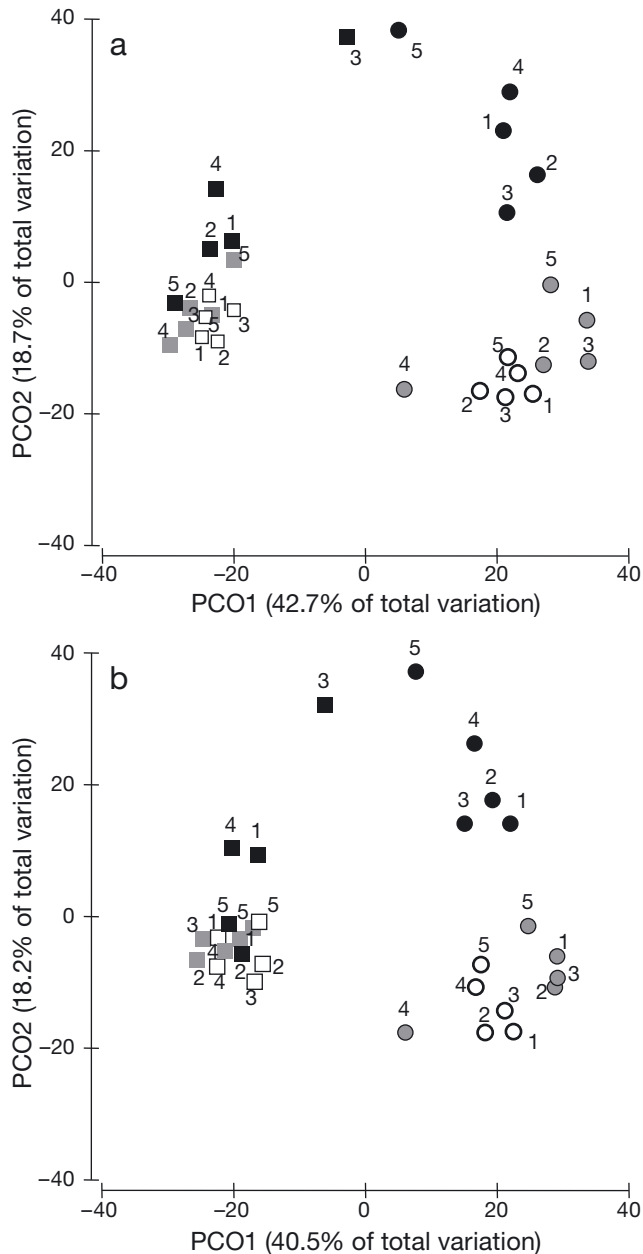
Fig. 3. Principal coordinates ordination plots (PCO) showing centroids of sites nested within the interaction term Sector × Time(Park). (a) PCO based on Sørensen dissimilarities and (b) PCO based on Bray-Curtis dissimilarities from square-rooted abundances. Squares: MNP; circles: LRNP; white: external sectors; grey: intermediate; black; internal. Numbers beside symbols indicate sampling time

(sabellid polychaete), *Lithophyllum pustulatum* (encrusting red algae), *Halimeda* sp. (green algae) and other infrequently found species were recorded exclusively in MNP. On the other hand, the sabellid polychaete *Branchiomma nigromaculatum*, the ascidians *Styela* sp. 1, *Ascidia curvata*, *Polyclinum con-*

stellatum, *Clavelina oblonga*, *C. picta*, *Distaplia bermudensis* and *Aplidium accarense*, and the sponges *Halichondria magniconulosa*, *Oceanapia nodosa* and *Haliclona twincayensis* were recorded only in LRNP.

At a lower scale, variability among sites within each sector represented around 15 % of the total variation. However, variation among sites depended on the specific park and changed significantly through time (Table 2; PERMDISP for centroids of sites nested in S × T[P]; $F_{29,90} = 5.36$; $p < 0.05$); therefore, no general hierarchical relationship among sites and sectors can be inferred. Subsequently, for each survey at each park, variation was partitioned among sectors, sites and roots. Then, the components of variation at each spatial scale were averaged, and temporal variation associated with each spatial component was estimated, and interpreted as the standard error of this spatial scale. This post hoc analysis allowed quantification of the relevance of each spatial scale for each park in sustaining β-diversity. In both cases, the highest component of variation was associated with roots. However, in LRNP, components of variation were higher among sectors than among sites (Fig. 4), whereas, in MNP, components of variation were higher among sites than among sectors (Fig. 4). Despite temporal variation, the hierarchy of spatial variation in species composition was:

$$roots > parks > sectors \neq sites$$

Relevant spatial scales for assemblage structure

When analyses were performed on the Bray-Curtis dissimilarities from square-root-transformed abundance data, the relative magnitude of the components of variation of all factors, and their hierarchical relationships, remained much the same, though with the residual variation accounting for a greater percentage of the total (Table 4). These results, taken together with the shade plot, where the most abundant species at each park are clearly identified (Fig. 5), suggest that the patterns of difference at intermediate and large spatial scales are mainly compositional and not primarily related to the abundance of species. It is also notable that differences in terms of composition and abundance of species among sectors were particularly conspicuous for LRNP, where most of the species found in external and intermediate sectors were absent in the internal sector. These differences were consistent during the first 3 sampling occasions; however, some common species (such as *C. rhizophorae*, *Botrylloides nigrum* and *Bu-*

Table 3. Species with the highest contribution to the average dissimilarity among parks (cut off for low contributions to 60% of total dissimilarity in SIMPER analysis). LRNP: La Restinga National Park; MNP: Morrocoy National Park
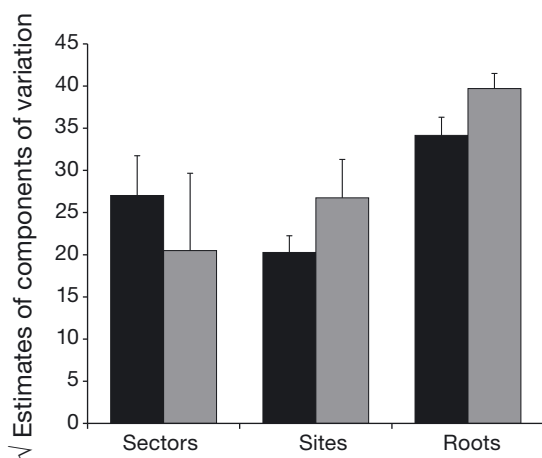
Species	Taxa type	Frequency observed	
		LRNP	MNP
Balanus sp.	Barnacle	0.40	0.15
Crassostrea rhizophorae	Bivalve mollusc	0.72	0.21
Brachidontes exustus	Bivalve mollusc	0.59	0.05
Isognomon alatus	Bivalve mollusc	0.00	0.48
Synnotum circinatum	Bryozoan	0.59	0.08
Bugula neritina	Bryozoan	0.51	0.01
Schizoporella pungens	Bryozoan	0.30	0.13
Hippopodina feegeensis	Bryozoan	0.26	0.01
Amathia sp.	Bryozoan	0.29	0.00
Scrupocellaria sp.	Bryozoan	0.01	0.25
Didemnum perlucidum	Colonial ascidian	0.34	0.14
Botrylloides nigrum	Colonial ascidian	0.32	0.08
Symplegma brakenhielmi	Colonial ascidian	0.24	0.08
Clavelina oblonga	Colonial ascidian	0.24	0.00
Symplegma rubra	Colonial ascidian	0.25	0.01
Aglaothamnion sp.	Colonial ascidian	0.04	0.18
Ecteinascidia turbinata	Colonial ascidian	0.19	0.04
Aplidium accarense	Colonial ascidian	0.23	0.00
Caulerpa verticillata	Green alga	0.05	0.46
Branchiomma nigromaculatum	Sabellid polychaete	0.55	0.00
Hydroides sp.	Serpulid polychaete	0.61	0.02
Microcosmus exasperatus	Solitary ascidian	0.53	0.16
Styela sp. 1	Solitary ascidian	0.31	0.00
Phallusia nigra	Solitary ascidian	0.26	0.08
Styela canopus	Solitary ascidian	0.28	0.04
Ascidia curvata	Solitary ascidian	0.26	0.00
Haliclona manglaris	Sponge	0.17	0.44
Mycale microsigmatosa	Sponge	0.26	0.36
Tedania ignis	Sponge	0.14	0.30
Mycale carmigropila	Sponge	0.28	0.07
Mycale magnirhaphidifera	Sponge	0.23	0.08
Dysidea etheria	Sponge	0.08	0.23
Haliclona curacaoensis	Sponge	0.28	0.02
Halisarca sp.	Sponge	0.22	0.01
Scopalina ruetzleri	Sponge	0.17	0.09

gula neritina) disappeared from intermediate and internal sectors during the fourth and fifth surveys. In contrast, differences among sectors were less obvious in MNP, with the exception of the third sampling. Some common species of internal sectors were not observed during this particular sampling time, which exacerbated differences among sectors (Fig. 5). Therefore, as in the case of β-diversity, it is clear that the structure of the assemblages varied at different spatial scales, which implies that the hierarchy between sectors and sites is dependent on the park and fluctuates over time.

DISCUSSION

Relevant scales of α-diversity, β-diversity and assemblage structure

The observed patterns of spatial variation confirmed that α- and β-diversity of mangrove root epibionts, as well as the structure of the assemblage, were dependent on processes operating at multiple spatial scales. Nevertheless, in all cases, the largest amount of variation corresponded to differences among parks and among residuals. This indicates that richness and composition of the species on roots are mainly controlled by processes operating at the broadest spatial scale of the mangrove system and the smallest spatial scale of neighbouring roots. These results are of some importance as residual variation is classically interpreted as unexplained variation (Quinn & Keough 2002); however, in this case, sampling units are whole natural units of habitat (i.e. censused, not sub-sampled),

Fig. 4. Multivariate pseudo-variance components for different spatial terms in the model of β-diversity in each of the 2 parks. Black columns: La Restinga National Park; grey columns: Morrocoy National Park. Error bars reflect the temporal variability around the averaged variance components. Note: the scale is in the same units as the Sørensen dissimilarity measure

Table 4. Estimates of components of variation (CV and $\sqrt{CV}$) and total mean squares from a 4-factor PERMANOVA analysis of Bray-Curtis dissimilarities on square-root-transformed abundance ($\sqrt{A}$), and Sørensen dissimilarities for a presence/absence analysis (β-diversity). Other abbreviations as in Table 1

Source of variation	$\sqrt{A}$			$\beta_{Sørensen}$		
	CV	$\sqrt{CV}$	Rank	CV	$\sqrt{CV}$	Rank
Root area	9	3	8	8	3	8
P	906	30	2	950	31	2
S	199	14	6	235	15	5
T(P)	150	12	7	139	12	7
S × P	216	15	5	187	14	6
S × T(P)	488	22	4	403	20	4
Site = Si(S × T[P])	721	27	3	573	24	3
Residuals	1976	44	1	1374	37	1
Total mean squares	4664			3867		

which allows estimation of natural variation at the smallest spatial scale. Consequently, it can be proposed for these assemblages that small-scale processes are as important as macro-ecological processes in driving the patterns of species diversity (Hawkins & Hartnoll 1980, Fraschetti et al. 2005, Hewitt et al. 2005, Benedetti-Cecchi et al. 2012, Thrush et al. 2013).

Furthermore, when estimates of abundance are included in the analysis, the residual component of variation appears considerably larger, in relation to total variation (or, equivalently, to that accounted for by all other factors), than it does for the analysis carried out on presence/absence data. The relationships among the other components of variation did not fundamentally change when comparing analyses on abundances with those on presence/absence data. These results suggest that neighbouring roots which share species may differ significantly in the abundances on each root, but differences among parks, sectors and/or sites are primarily due to changes in species identity rather than relative species abundances. To a lesser extent, species diversity varied also at intermediate spatial scales; in both parks, α-diversity changed along the sector's gradient, as external and middle sectors always had higher numbers of species when compared to internal sites.

Scales and processes controlling diversity of species

Species diversity and geographical processes

There are several processes that could explain differences in species diversity between parks. The first group is related to the size of the region and the proximity to sources of species. These models predict greater richness and abundance in less isolated and larger areas (MacArthur & Wilson 1967). Despite the similarity in size, mangrove islets and channels are much more complex in MNP than in LRNP, where mangrove borderlines add up to around 190 km, compared to 67 km in LRNP (Guerra-Castro 2012). In addition, MNP includes important extensions of coral reefs and seagrass beds (Bone et al. 2005), traditionally recognized as a source of species for epibenthic assemblages associated with mangrove prop roots (Rützler 1969, Diaz 2012). Consequently, patterns of differences in species richness between parks could not be explained by the 'species–area relationship' and the 'proximity to source of species' models as more species were observed in the smaller and more isolated park.

As an alternative to the island biogeography model, Wright (1983) proposed that energy availability is a better indicator of the variety of resources in a region than their relative area. Basically, if productivity is low, populations of species will be smaller, and extinction rates will be higher; a process that ultimately leads to low regional richness. Results found in this study fit the predictions of Wright's (1983) theory as LRNP, a simple mangrove system located in a eutrophic region (Gómez Gaspar 1991), had higher α-diversity than MNP, a complex mangrove system located in an oligotrophic region, surrounded by coral reefs and sea grass meadows (Bone et al. 2005).

Alternatively, historical perturbations and physiological tolerance to macro-environmental conditions may also explain differences in species diversity between parks. Basically, regions with high physiological demands will tend to have lower diversity and abundance of species than regions with less harsh environments (Hutchinson 1957, Whittaker et al. 1973). There is evidence that environmental conditions are more demanding, from a physiological perspective, at MNP than at LRNP. Rainfall tends to be heavier in the western part of Venezuela, between November and December, when severe declines in salinity for internal and intermediate sectors have been observed. These salinity falls are beyond the tolerance of most marine invertebrates, and have caused widespread mortalities (Laboy-Nieves et al. 2001, Chollett & Bone 2007). Also, pollution of water and sediments tends to be higher in MNP than in LRNP (García et al. 2008, 2011). In LRNP, on the contrary, the intensity of rainfall is usually lower; consequently, osmotic demands by freshwater runoff are rare, although mass mortalities associated with atmo-
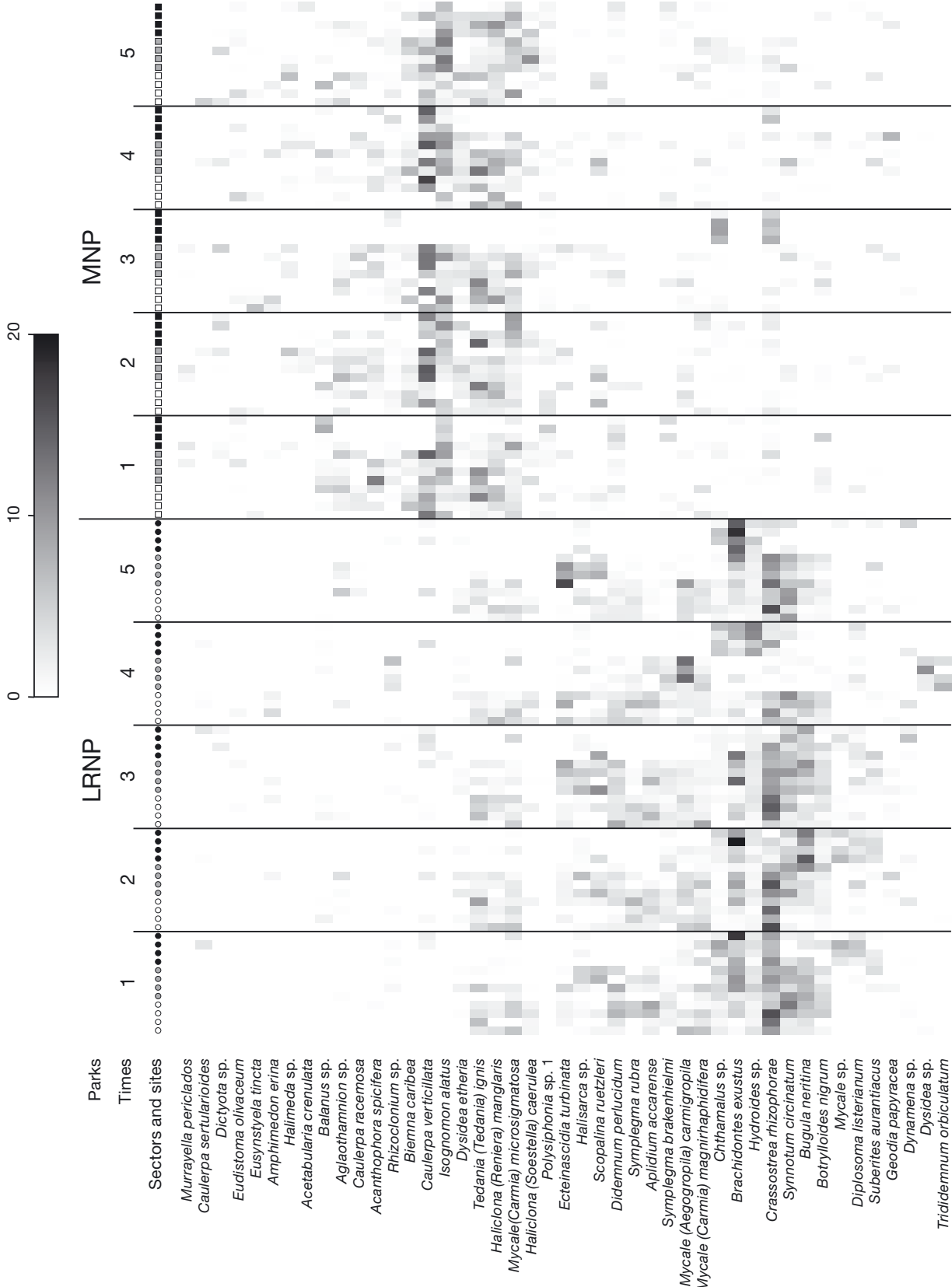
Fig. 5. Shade plot for the 4 sites of each sector (white: external; grey: intermediate; black: internal) at the 5 sampling times over Nov 2009–Jan 2011 (every 3 to 4 mo) in La Restinga National Park (LRNP, circles) and Morrocoy National Park (MNP, squares), against the 45 most abundant species, with cell shading on a linear grey scale for averaged abundance after square-root transformation (from white [absence] to dark grey [maximum matrix entry]). Sectors and sites within each time for each park are ordered left to right

spheric events have been reported (Orihuela et al. 1991). The pattern of harsher environmental conditions in the MNP region is thus consistent with the lower diversity seen there than that seen in LRNP.

In summary, 2 mechanisms might explain patterns of mangrove epibiont diversity estimated at large spatial scales: (1) local nutrient-energy supply and (2) physiological tolerance to perturbations and regular environmental conditions. However, the limitations on such an inference from a simple comparison of 2 mangrove systems are clear.

Species diversity and local processes

Explanatory models for patterns of species diversity at intermediate spatial scales fall into 2 major groups: those that evoke processes related to response of species to environmental gradients (i.e. niche view of communities; Leibold 1995, Chase 2014, Stein et al. 2014) and those related to dispersal history and stochastic distribution of species (i.e. neutral view of communities; He 2005, Hubbell 2005). Evidence in favour of the environmental control hypothesis has been offered by Inclán-Rivadeneyra (1989) for mangrove root epibionts in Bahía de la Ascension in the Yucatán Peninsula (México), by Pawlik et al. (2007) for mangroves in Key Largo (Florida) and by Díaz & Rützler (2009) for mangroves in Belize and Bocas del Toro (Panama). On the other hand, evidence for neutral mechanisms has been offered by Bingham (1992) for mangroves in the Indian River Lagoon (Florida) and by Farnsworth & Ellison (1996) for 4 mangrove cays in Belize. Unfortunately, in our study area, predictions for both models are similar because environmental harshness and source larval gradients run in the same direction. Under both models it is predicted that number of species decrease as we move from external towards internal sectors.

Under the neutral model, β-diversity could be interpreted as a rate of loss of species toward the internal zones of the mangrove systems, mainly because larvae of some species are unable to reach the internal mangrove's roots. Therefore, only species with long-lived larvae and strong swimming abilities will be able to settle and dominate internal sectors. For example, bivalves (oysters) and barnacles are the most abundant species in internal zones in both parks, which could be related to the fact that veliger larvae of bivalves, as well as the cypris larvae of barnacles, have among the longest pelagic spans of all taxa reported in this study (Svane & Young 1989, Qian

1999, Burgess et al. 2009, Page 2009). In contrast, larvae of sponges and tunicates, species characteristics of external and intermediate sectors, have short pelagic spans, favouring gregariousness of individuals of the same species in these sectors.

Turnover of species (β-diversity) as defined above could also be explained by physiological tolerance to environmental stressors, as this factor might also be the driver that controls the reduction of richness towards internal sectors. This implies that species with strong physiological tolerance to severe environmental conditions (e.g. extreme salinities, temperature) will dominate internal zones. In this case, algae, sponges and tunicates are less diverse in internal sectors mainly because spores and larvae are unable to settle and grow in roots located in these internal sectors, where salinities, temperature and other environmental conditions tend to be beyond their tolerance ranges. But given that: (1) the environmental gradient is stronger in LRNP than in MNP (Gómez Gaspar 1991, Bone et al. 2001) and (2) environmental differences correlate very well with the pattern found here (i.e. the component of variation of the factor sector was higher in LRNP than in MNP), it can be proposed that in the absence of a strong environmental gradient, neutral processes might play an important role. Furthermore, these results suggest that neutral and niche processes might be operating at the same time, but the intensity of the neutral mechanism will depend on the general environmental conditions of each park (e.g. Gravel et al. 2006, Chase 2014).

Species diversity and small-scale processes

High variability among samples has been reported extensively in studies dealing with natural (Anderson et al. 2005b, Fraschetti et al. 2005, Terlizzi et al. 2007) and artificial units of habitat (Glasby 1998, Guerra-Castro & Cruz-Motta 2014). A traditional explanation for such patterns involves a combination of spatial and biological processes, such as species–area relationships (McGuinness & Underwood 1986, Anderson 1999). These predict that larger areas will host more species, unless observed numbers of species are near the asymptote for that location, or the differences in area of the habitat units are relatively small. However, during this study, a relationship was not observed between α-diversity and root area, as the unit of habitat. Consequently, this study does not provide evidence to support species–area models as drivers of variation among roots.

An alternative proposition would be that variation among neighbouring roots reflects differing colonization times for each root and subsequent development trajectories. This model, known as supply-side ecology (Lewin 1986), has been proposed several times as a key element in understanding the structure of benthic marine communities at very small spatial scales (Underwood & Fairweather 1989, Anderson & Underwood 1994, Underwood & Chapman 2006). Essentially, the model evokes 2 processes, colonization and succession, and predicts that adjacent roots will differ in species composition due to their differing ages, with younger roots containing fewer species. However, the process of colonization in benthic marine systems is not linear (Sutherland 1974, Sutherland & Karlson 1977). The colonizing species can tolerate, induce, or inhibit the incorporation of other species in the assemblage (Connell & Slatyer 1977), so that the development of the assemblage will depend on the identity and abundance of larvae present at the moment of substrate availability and their competitive strategies with respect to later-colonizing species. Differences among neighbouring roots may thus reflect differing species presences in larval pools when the roots are available to be colonized, and, consequently, differing succession patterns.

Concluding remarks

Results of this study showed that variation at small spatial scales is as important as at geographical scales in explaining patterns of α- and β-diversity in assemblages associated with mangrove roots. This suggests that processes acting at both spatial scales are proportionally more important than processes operating at intermediate spatial scales (i.e. environmental gradients and dispersal). However, given that this is a mensurative experiment (sensu Hurlbert 1984), all tested hypotheses are necessary to support the different proposed ecological processes/explanations, but they are clearly insufficient to establish cause–effect relationships. Consequently, manipulative experiments are needed to evaluate the real impact of these processes on the patterns of species diversity of epibionts on Caribbean mangrove roots. Nonetheless, this study has detailed some interesting results about the importance of the lowest level of spatial variability in these mangrove systems. The next step should be to experimentally identify the processes that produce variation among neighbouring roots.

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