

NUMERICAL AND TAXONOMIC SCALE OF ANALYSIS IN PALEOECOLOGICAL DATA SETS: EXAMPLES FROM NEO-TROPICAL PLEISTOCENE REEF CORAL COMMUNITIES

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ABSTRACT—I investigated the degree to which the interpretation of reef coral distribution data is influenced by the numerical and taxonomic scale of analysis in Pleistocene coral communities from the Caribbean Sea. Patterns of community differentiation analyzed at both species and genus levels showed only small differences using different numerical scales (relative abundance, rank abundance and species presence and absence). Whereas some differences were observed between species and genus level patterns, they had little effect on paleoecological interpretations. The greatest differences occurred when presence and absence analyses of assemblages sampled along 40-m transects were compared with those sampled along 40-m transects augmented by a one-hour search for rare taxa. These results suggest that paleoecological interpretations of Quaternary coral communities are robust to numerical scale of analysis at the species and genus level, and to taxonomic scale between the species and genus level. However, interpretations of community structure are sensitive to sampling intensity, geographic scale, and sample size.

INTRODUCTION

COMMUNITY ECOLOGISTS generally realize that the geographic scale of a study is one of the most important factors in interpreting species distributions within and among communities (Wiens, 1989; Levin, 1992; Underwood and Chapman, 1998). But the interpretation of ecological patterns also can be strongly affected by both the numerical (relative abundance vs. rank abundance vs. presence and absence data) (Rahel, 1990), and the taxonomic (Ellis, 1985; Herman and Heip, 1988; Marchant et al., 1995; Sale and Guy, 1994; Smith and Simpsom, 1993) scale of analysis. A number of modern ecological studies address this phenomenon as it applies to marine pollution (Warwick, 1988a, 1988b, 1993), predation (He and Wright, 1992), trophic webs (Hall and Raffaelli, 1991; Martinez, 1993), and community structure in marine and aquatic habitats (Bowman and Bailey, 1997; Ferraro and Cole, 1990, 1992; Sale and Guy, 1994; Varis, 1991; Wright et al., 1995; Yant et al., 1984). Paleontologists also have long grappled with the degree to which familial and generic data reflect underlying patterns of species, especially in relation to large-scale macroevolutionary phenomena. But paleo studies conducted at the community level have generally focussed on a single taxonomic level without comparative information on either numerical or taxonomic scales of analysis.

Varying the numerical scale of analysis may alter our perception of spatial and temporal pattern and process in community structure (Rahel, 1990). For example, the presence of the same species in different communities might indicate persistence in time and space, but if the relative abundance of the component species varies widely, these same communities may be viewed as highly differentiated. However, communities that are similar in the relative abundance of their component species should also be similar in the species present within them (Rahel, 1990). Using both empirical and model communities, Rahel (1990) suggested that with decreasing scale of resolution communities tend to be less and less differentiated. He recommended either the use of several scales of analysis when interpreting species distribution patterns among different communities, or failing that, the exact scale of resolution be explicit in comparative studies of communities.

The taxonomic scale of analysis, or “taxonomic sufficiency” (Ellis, 1985), is generally selected on the basis of the question to be asked. But often the exact scale to use is open to debate, or to logistical constraints. In many studies it is impossible to identify specimens down to the species level due to lack of taxonomic

expertise, time, funding or even lack of readily identifiable characters. For example, work on marine pollution is expensive and time-consuming and relies on levels of taxonomic expertise that are not readily available. For this reason a number of studies have used comparative analysis of data from several taxonomic levels to determine the most efficient level that will still show pattern (Warwick, 1993). Of course, such a level varies with different studies, from species to phylum, but the majority of studies on living freshwater and marine communities show detectable and useful patterns above the species level (though results are poorer in more diverse communities when relative abundance data are used; Bowman and Bailey, 1997). Even phylum-level identifications have proven useful in detecting disturbance in marine benthic communities (Warwick, 1988a, 1988b). Other reasons for using taxonomic levels higher than species are more accurate identification, large time and cost savings—both in specimen and data gathering, and suiting taxonomic level to the “needs of the study” (Wright et al., 1995).

In this paper, I investigate the degree to which changing numerical and taxonomic scale affects the interpretation of community structure in Pleistocene corals from the Caribbean Sea. I address the question of how sensitive the detection of spatial distribution patterns of reef coral species are to the kinds of data we use. Specifically, do Pleistocene reef coral community data show similar patterns of differentiation at the genus level as they do at the species level? And, do relative abundance data produce the same patterns of community differentiation as rank abundance or presence and absence data? To address these questions, I focus on two data sets that represent two different spatial scales. The first data set comes from reef coral communities of the Hato Unit of the Pleistocene (125 ka) “Lower Terrace” (Herweijer and Focke, 1978) from Curaçao. These data were used previously to investigate the spatial variability of coral community structure along >40 km of coastline, and details concerning sampling, methodology, and results are presented by Pandolfi et al. (1999) and Pandolfi and Jackson (2001). The second data set is from the 125 ka terrace found along the leeward coasts of San Andrés, Curaçao, and Barbados. These data were used previously to investigate the spatial variability of coral community structure along a 2,500 km “southern Caribbean transect” (SOCA); details concerning sampling, methodology and results from this study are presented by Pandolfi and Jackson (in press).

Four numerical and two taxonomic scales of resolution are investigated. The first numerical scale is derived from the coral

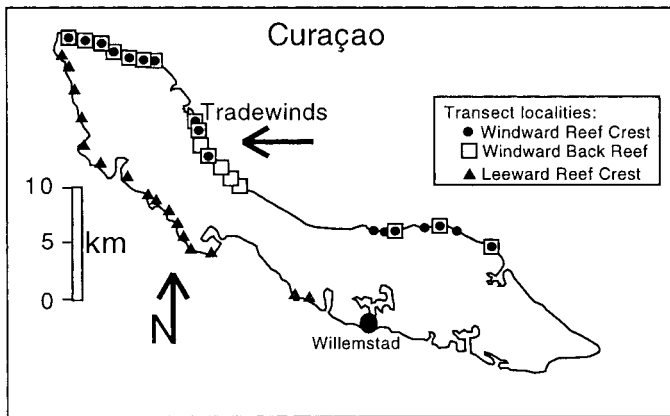


FIGURE 1—Map of Curaçao showing sampling design and location. Curaçao is located in the Netherlands Antilles about 60 km north of Venezuela. The island is oriented SE/NW and thus the entire windward coast faces northeasterly trade winds. It is subject to vigorous wind and wave conditions along its north-eastern coastline and leeward conditions on its south-western coastline. Bonaire, located about 50 km to the east reduces the fetch, and hence wind and wave energy are less severe on the south-eastern than the north-eastern windward coast. Sample transect localities are indicated for the Pleistocene Hato Member of the Lower Terrace from Curaçao, Netherlands Antilles.

abundance collected along 40-m transects only and will be referred to as the *quantitative data set*. The second is derived from the coral rank abundance of the communities surveyed along each transect and will be referred to as the *rank abundance data set*. The third is presence and absence data collected along the 40-m transects and will be referred to as the *transect binary data set*. The fourth is presence and absence data collected along these same transects plus additional taxa encountered during a 1 hour search and will be referred to as the *transect-search binary data set*. Each data set is analyzed using both species-level and generic-level data.

The results from this study show that varying the numerical and taxonomic scales of analysis generally did not alter the interpretation of coral community structure for both of the data sets. Sampling intensity played a critical role, especially when using species presence and absence data. Thus, depending on the question of interest, studies of Quaternary reefs of the Caribbean may be reliably and efficiently undertaken using presence and absence of coral genera. These results apply only to studies employing a hierarchical sampling design for capturing the maximum variability in community structure within and between coral assemblages.

METHODS

Sampling.—I compared Pleistocene distribution patterns of reef corals on Curaçao in three different environments that represent distinct wave energy regimes (Fig. 1). These environments encompass the most extreme shallow-water conditions in wave and wind energy that were likely to have occurred in the Pleistocene: a windward reef crest (WRC), a windward back reef (WBR), and a leeward reef crest (LRC). All of the data were collected from the top 2 m of the 6-m thick, 125 ka Hato Unit, of the Lower Terrace. Seven 40-m long transects were laid at each of two sites in each of the three ancient reef environments on the island. Transects were normally separated from each other by 500–1,000 m and sites varied from approximately 5 to 7 km in length. I also partially sampled a third site in each environment, where the coral assemblages were sufficiently preserved, resulting in an additional eight transects (two transects from the LRC at the southern site;

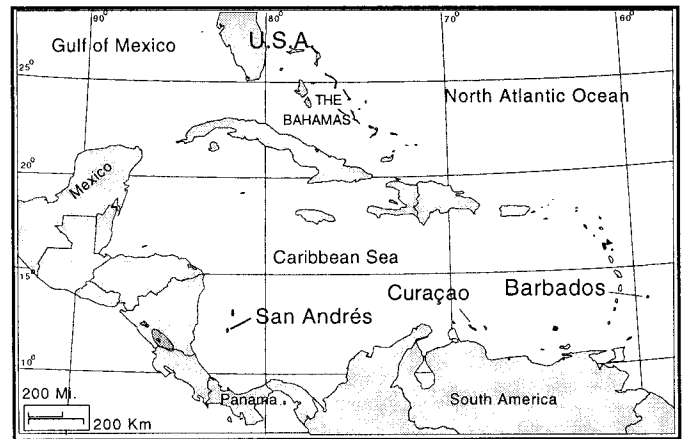


FIGURE 2—Pleistocene reef communities were sampled for >2,500 km along a southern Caribbean (SOCA) transect that included the islands of San Andrés, Curaçao, and Barbados. The Pleistocene reef crest environment from the last interglacial (around 125 ka) was sampled from the leeward coast of each of the three islands.

three transects from the WRC at the central site, and three transects from the WBR at the southern site; Fig. 1, Table 1). These eight transects were used in the ordinations but not in the analysis of similarities (ANOSIM; see below) nor ANOVA of diversity, where a more balanced experimental design was appropriate.

Where corals were encountered, their orientation and degree of fragmentation was noted where possible, and they were identified to the lowest possible taxonomic level, usually to species. The length of the transect intersected by each coral colony was recorded. Thus, the raw data for corals from each transect was the total length of transect intercepted by each coral species. After the transects were recorded, a one hour search for additional (rare) coral species not intercepted along the transect was made. Species sampling curves constructed for both transect and transect-search binary data sets showed that five to seven transects (samples) per site were sufficient to capture greater than 90 percent of the coral species richness from all three reef habitats (Pandolfi and Jackson, 2001).

For the southern Caribbean (SOCA) transect study, a similar sampling regime as Curaçao was also conducted in the Pleistocene leeward shallow reef environment on San Andrés and Barbados islands (Fig. 2). Each island was surveyed along 13 to 35 km of coastline (Table 2). I encountered 32 reef coral species from 43 transects covering 1.72 kilometers of fossil reef from the Pleistocene leeward shallow reef environment of the three islands (Table 2). Species sampling curves showed that five to seven transects (samples) were sufficient to capture greater than 90 percent of the coral species richness from San Andrés (as at Curaçao—see above); however, species richness did not level off until eight or nine transects at Barbados (Pandolfi and Jackson, in press).

Data analysis.—Comparison of taxonomic composition among all possible pairs of transects was calculated using the Bray–Curtis dissimilarity coefficient (Bray and Curtis, 1957). Dissimilarity values range from 0 (for a pair of samples with identical taxonomic composition) to 1 (for a pair of samples with no taxa in common). Abundance data were transformed to their square roots prior to the calculation to reduce the influence of occasional large abundance values for some taxa (Field et al., 1982). The transformed abundance values for each taxon were standardized by the maximum attained by that taxon. This standardization equalizes the potential contributions of taxa to the overall dissimilarity in composition. Without standardization by taxon, the Bray–Curtis

TABLE 1—Sampling protocol and coral species richness per sample for the Pleistocene Hato Unit of the Lower terrace of Curaçao (125 ka). Three environments were sampled from each of three sites along the windward (reef crest and back reef) and leeward (reef crest) coasts. Left values are for species recorded along each 40-m transect plus those encountered during a one-hour search. Right values (in parentheses) represent species richness recorded along each transect only.

Site	Windward			Site	Leeward	
	Transect	Reef crest	Back reef		Transect	Reef crest
North	1	4 (2)	9 (6)	North	1	11 (5)
	2	7 (3)	9 (5)		2	10 (5)
	3	10 (3)	12 (7)		3	14 (8)
	4	8 (3)	16 (13)		4	20 (12)
	5	8 (4)	13 (12)		5	9 (5)
	6	11 (4)	12 (9)		6	13 (7)
	7	12 (2)	11 (10)		7	10 (6)
Central	1	18 (6)	12 (6)	Central	1	12 (7)
	2	17 (3)	13 (5)		2	10 (7)
	3	13 (3)	11 (9)		3	13 (7)
	4	—	8 (8)		4	17 (8)
	5	—	12 (8)		5	9 (8)
	6	—	10 (5)		6	9 (6)
	7	—	10 (4)		7	16 (9)
South	1	18 (4)	12 (7)	South	1	12 (11)
	2	11 (3)	13 (6)		2	12 (9)
	3	10 (4)	8 (3)			
	4	21 (7)	—			
	5	11 (4)	—			
	6	13 (4)	—			
	7	9 (2)	—			
Total species diversity:		30 (15)	23 (19)			30 (21)

(BC) values are dominated by those taxa that attain high abundances (Faith et al., 1987). For the rank abundance data sets, the BC index is not appropriate because it relies on numerical values for abundance or presence and absence (Bray and Curtis, 1957). Thus, comparison of species rank abundance between all pairs of transects was calculated using Kendall's tau (τ) rank correlation coefficient (Kendall, 1962). Analysis of similarities (ANOSIM; Clarke, 1993; Clarke and Warwick, 1994) was used to determine whether assemblages from different environments and sites on Curaçao, and different islands in the Caribbean, had significantly different coral composition. I used global non-metric multidimensional scaling (GNMDS) as an ordination technique to provide a visual summary of the pattern of Bray–Curtis values and ANOSIM tests among the samples. Details of these methods can be found in Pandolfi and Minchin, 1995; Pandolfi, 1996; Jackson et al., 1996; and Pandolfi and Jackson, 2001). ANOSIM and GNMDS were performed using the PRIMER software package. Statistical significance was assessed at a probability level of 0.05.

ANOVA of species and genus diversity was conducted to determine the degree to which diversity varied with environment, site and island for both the transect-binary and transect-search data sets.

TABLE 2—Sampling data for Pleistocene coral communities from the three Caribbean islands spanning over 2,500 km. Systematic sampling in the Pleistocene covers a spatial scale that has never before been attempted on living reefs but is now being surveyed on the Great Barrier Reef (Hughes et al. 1999). Species diversity is given for transects and parenthetically for transects plus a one-hour search.

	Total number of transects	Length of island sampled (km)	Total length of transects (m)	Species diversity
San Andrés	15	13.7	600	23 (32)
Curaçao	16	35.6	640	21 (30)
Barbados	12	13.1	480	17 (22)

RESULTS

Diversity.—At Curaçao, 15 species were recorded in the windward reef crest (WRC), 19 species in the windward back reef (WBR), and 21 species in the leeward reef crest (LRC) along the transects and 30, 23, and 30 species, respectively, when the one-hour-search data were included. These translated to 9 genera in the WRC, 12 in the WBR, and 13 in the LRC along the transects (15 overall), and 15, 12, and 14 genera, respectively, when the one-hour-search data were included (17 overall). Species (S) and genus (G) richness (transect data only) showed significant differences among the three reef environments, but not among the sites within environments (Table 3). Mean transect diversity in the WRC ($S = 3.5$; $G = 3.5$) was much less than in the WBR ($S = 7.6$; $G = 5.7$) and LRC ($S = 7.1$; $G = 5.6$). Conversely, no

TABLE 3—Analysis of variance of taxonomic richness for transects from three reef zones (windward reef crest and back reef; leeward reef crest) from the 125 ka Hato Unit, Curaçao. Includes 2 sites per environment.

Source	df	SS	MS	F	P
Species richness (Transect only)					
Reef Zone	2	143.19	71.60	18.52	$\ll 0.001$
Site	1	0.857	0.857	0.22	0.641
Reef Zone \times Site	2	24.43	12.21	3.16	0.054
Error	36	139.14	3.87		
Genus richness (Transect only)					
Reef Zone	2	51.048	25.52	15.24	$\ll 0.001$
Site	1	0.024	0.024	0.01	0.9057
Reef Zone \times Site	2	7.0476	3.52	2.10	0.1367
Error	36	60.286	1.6746		
Species richness (Transect plus one-hour search)					
Reef Zone	2	15.48	7.738	0.76	0.475
Site	1	16.10	16.10	1.58	0.217
Reef Zone \times Site	2	64.33	32.17	3.16	0.054
Error	36	366.57	10.18		
Genus richness (Transect plus one-hour search)					
Reef Zone	2	17.476	8.7381	2.69	0.0814
Site	1	22.881	22.881	7.05	0.0117
Reef Zone \times Site	2	29.762	14.881	4.58	0.0168
Error	36	116.86	3.2460		

TABLE 4—Results of ANOSIM analysis for overall environment and site within environment effects for coral species composition at Curaçao. Analyses were completed on four data sets (see text) gathered from the Pleistocene Hato Unit of the Lower Terrace. WRC, windward reef crest; WBR, windward back reef; LRC, leeward reef crest. R = ANOSIM test statistic.

Main effect		Quantitative		Rank abundance		Transect binary		Transect-search binary	
		R	<i>P</i> -value	R	<i>P</i> -value	R	<i>P</i> -value	R	<i>P</i> -value
Environment	Overall	0.603	<0.0001	0.406	<0.0001	0.326	<0.0001	0.180	<0.0001
	WRC vs. WBR	0.850	<0.0001	0.468	<0.0001	0.395	<0.0001	0.148	0.001
	WRC vs. LRC	0.541	<0.0001	0.561	<0.0001	0.387	<0.0001	0.154	0.001
	WBR vs. LRC	0.419	<0.0001	0.162	0.001	0.226	<0.0001	0.241	<0.0001
Site	Within WRC	0.254	0.015	0.179	0.053	0.195	0.052	0.362	0.004
	Within WBR	0.365	0.003	0.162	0.050	0.202	0.040	0.488	0.004
	Within LRC	0.076	0.190	0.105	0.110	0.040	0.294	0.052	0.220

differences in mean transect richness were found among environments or sites when the one-hour-search data were included (WRC: $S = 10.9$; $G = 7.6$; WBR: $S = 11.3$; $G = 6.6$; LRC: $S = 12.4$; $G = 8.0$; Table 3), but genus richness had a significant site and site by environment interaction.

I found 23 species in San Andrés, 21 species in Curaçao, and 17 species in Barbados along the transects in the leeward shallow reef environment, and, 32, 30, and 22 species, respectively, when the one-hour-search data were included (Table 2). These translated to 12 genera in San Andrés, 10 in Curaçao, and nine in Barbados along the transects (14 genera overall), and 17, 14, and 12 genera, respectively, when the one-hour-search data were included (19 genera overall). Species diversity per transect was significantly different among the three islands for both the transect-binary data set ($F_{(2,42)} = 18.55$, $P < 0.00001$), with per-transect means of 10.3 for San Andrés, 7.6 for Curaçao, and 4.7 for Barbados (overall = 7.7), and the transect search data set ($F_{(2,42)} = 29.52$, $P < 0.00001$), with means of 16.9 for San Andrés, 11.6 for Curaçao, and 6.8 for Barbados (overall = 12.5).

Genus diversity per transect was also significantly different among the three islands for both the transect-binary data set ($F_{(2,42)} = 18.01$, $P < 0.00001$), with per-transect means of 5.9 for San Andrés, 4.4 for Curaçao, and 2.9 for Barbados (overall = 4.5), and the transect search data set ($F_{(2,42)} = 18.55$, $P < 0.00001$), with per-transect means of 9.1 for San Andrés, 7.1 for Curaçao, and 4.3 for Barbados (overall = 7.0).

Effects of numerical scale of analysis.—At Curaçao, ANOSIM results for the overall environment test and for pairwise comparisons of environments were essentially identical at the species level for all numerical scales of analyses (Table 4). All of the tests showed significant environmental effects. Tests between sites within each environment varied only within the WRC environment, where relative abundance and the transect-search analyses showed significant site differences (Table 4). There was no site effect within the WRC for the rank abundance and transect-binary data sets, although the *P*-values were nearly significant ($P = 0.053$ and 0.052 , respectively) (Table 4). Geographic differences in species composition were most pronounced in the WBR, where the ANOSIM statistical tests for all four data sets provided significant differences between north and central assemblages (Table 4). Conversely, the LRC showed non-significant site differences at all scales of analysis (Table 4).

In general, results of the species level GNMDS ordination among environments of the Kendall's τ correlation matrix based on the rank abundance data set, and the Bray–Curtis dissimilarity matrix based on the transect binary data set were similar to that from the B-C matrix based on the quantitative data set (Fig. 3). These three data sets showed distinct differences in taxonomic composition between the two windward reef zones, with the LRC samples falling between these. However, the ordination of the transect-search binary data set showed broad overlap among the WRC, WBR and LRC communities (Fig. 3), even though the

overall and pairwise ANOSIM statistical tests were all significant (Table 4).

Geographic differences in species composition among sites within the WRC also matched between the ANOSIM results and the GNMDS ordination plots. Both the quantitative and transect-search ordination plots show a gradient from southern to northern samples (Fig. 4) and the differences among sites were significant (Table 4). GNMDS ordinations from WBR were variable in their ability to segregate groups, with the two presence and absence data sets showing the clearest north to south gradient in species composition (Fig. 5). Most surprising is the quantitative plot that showed the highest degree of overlap between northern and central assemblages (Fig. 4) but the lowest *P*-value in the ANOSIM test (Table 4). As stated above, there were no geographic differences in species composition for any data set in the LRC (Table 4), and the corresponding ordinations showed no geographic gradients in any data set (not illustrated).

At Curaçao, ANOSIM results for the overall environment test and for pairwise comparisons of environments were essentially identical at the generic level for all numerical scales of analysis, although lower *P*-values occurred with decreasing numerical scale (Table 5). All of the tests showed significant environmental effects. ANOSIM tests between sites within each environment varied at different numerical scales for all three reef environments (Table 5). Here, only the quantitative (at WBR and LRC) and transect-search (at WRC) data sets showed significant site differences (Table 5).

Environmental differences in genus composition at Curaçao were greatest in the quantitative GNMDS ordination (Fig. 6). The ordination based on rank abundance showed clear separation of the WRC from the other two environments, which showed broad overlap. Ordinations based on the presence and absence of genera showed little distinction among Pleistocene reef environments. All of the corresponding ANOSIM tests were significant (Table 5 and Fig. 6).

Geographic differences in genus composition among sites within environments at Curaçao closely matched between the ANOSIM results and the GNMDS ordination plots for all three environments. In the WRC ordinations, quantitative, rank, and transect-binary data sets showed overlap among sites, whereas the transect-search data set showed differentiation between northern and southern sites (Fig. 7). At both WBR and LRC, only the plot based on the quantitative data showed differentiation between northern and central sites (Figs. 8 and 9, respectively).

For the three Caribbean islands in the SOCA transect, ANOSIM results for the overall island test and for pairwise island comparisons were identical at the species level for all numerical scales of analysis (Table 6). All islands were significantly different from one another in coral composition, no matter how measured. The GNMDS ordination plots also generally show distinct groupings among the three islands, with the greatest overlap occurring

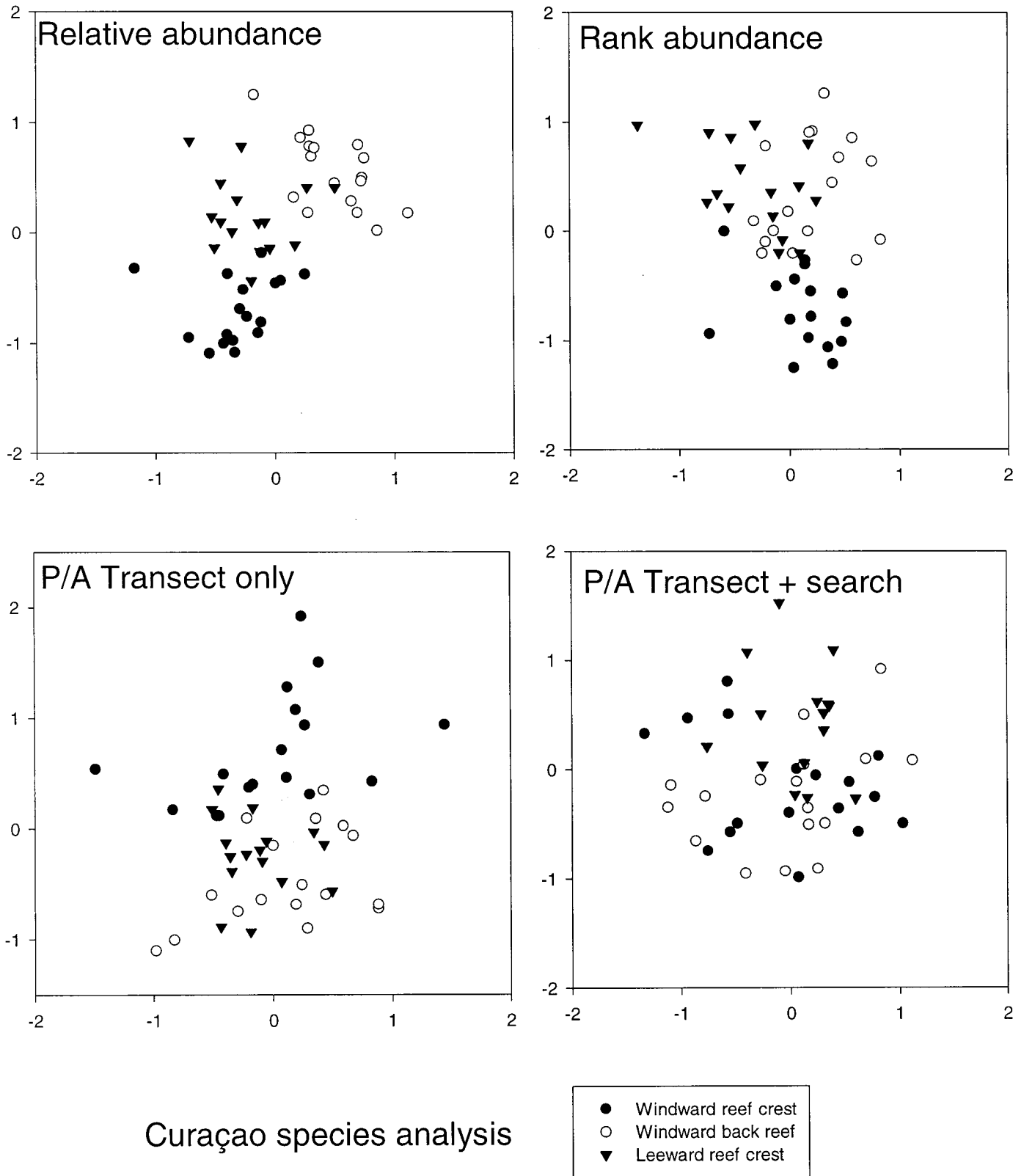


FIGURE 3—Ordination of Pleistocene species coral assemblages from Curaçao from the windward reef crest and back reef, and the leeward reef crest using quantitative, rank abundance, transect binary, and transect-search binary data sets. Quantitative, rank abundance and transect binary data sets show complete separation in reef coral community composition between the windward reef crest and back reef assemblages. The leeward reef crest shows assemblages intermediate in composition between the windward reef crest and back reef assemblages. In contrast, ordination using the transect-search data shows no clear differences in community composition among the three reef environments. Global non-metric multi-dimensional scaling (GNMDS) plots of dimension 1 and 2, from the 3-dimensional analyses. Each GNMDS was run with 20 random starting configurations, and proceeded through 400 iterations for each of 4 dimensions. The minimum stress value for the 3-dimensional analysis was 0.09 for the quantitative data set, 0.10 for the rank abundance data set, 0.14 for the transect binary data set, and 0.16 for the transect-search binary data set.

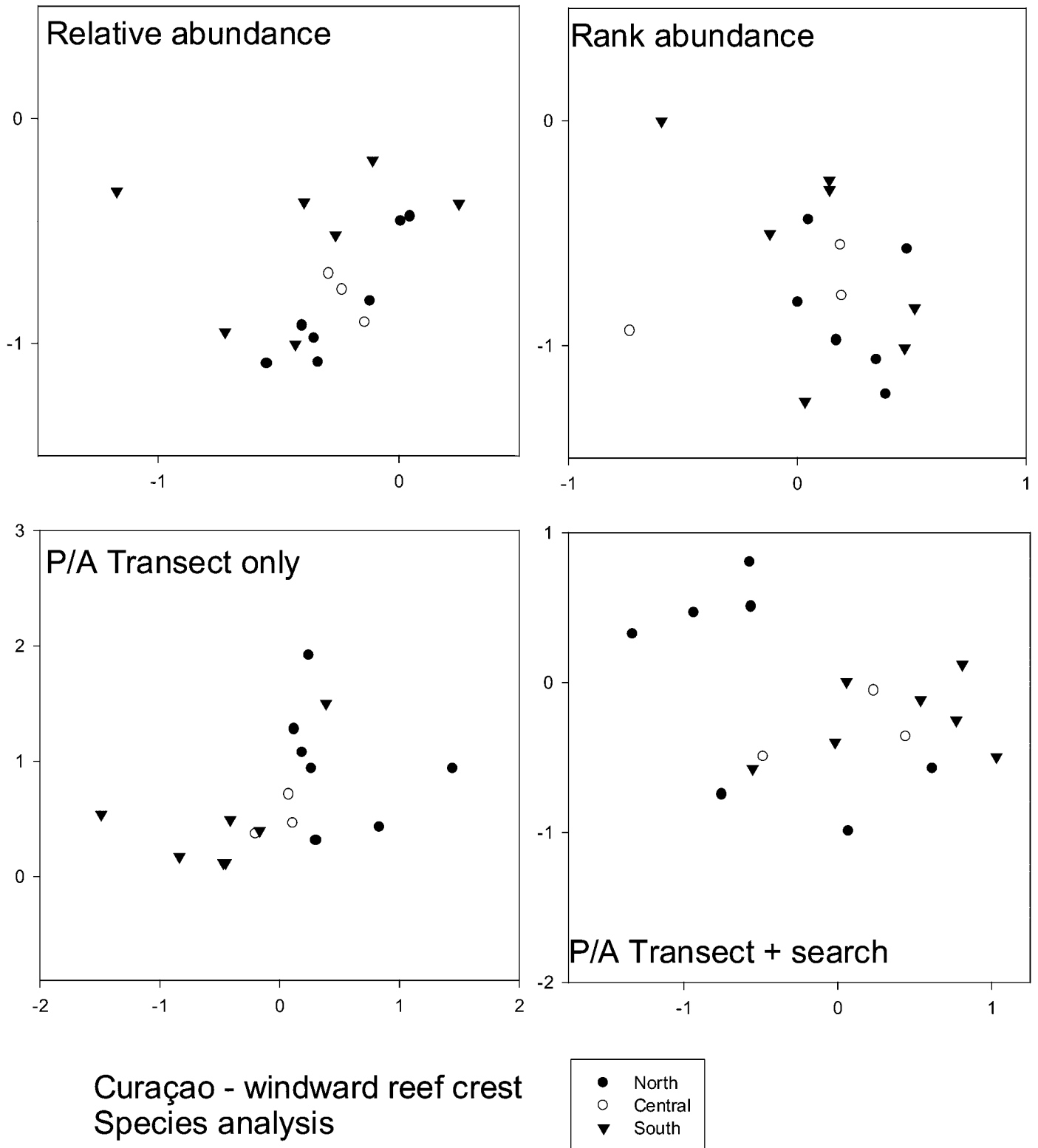


FIGURE 4—Ordination plots of Pleistocene coral species assemblages from Curaçao from the windward reef crest using quantitative, rank abundance, transect binary, and transect-search binary data sets. Geographic differences in reef coral community structure are best seen in the rank abundance and transect-search binary data sets and are absent in the transect binary data set. Seven transects were sampled from the northern and southern sites, and three transects were sampled from the central site. Same analysis as in Figure 3.

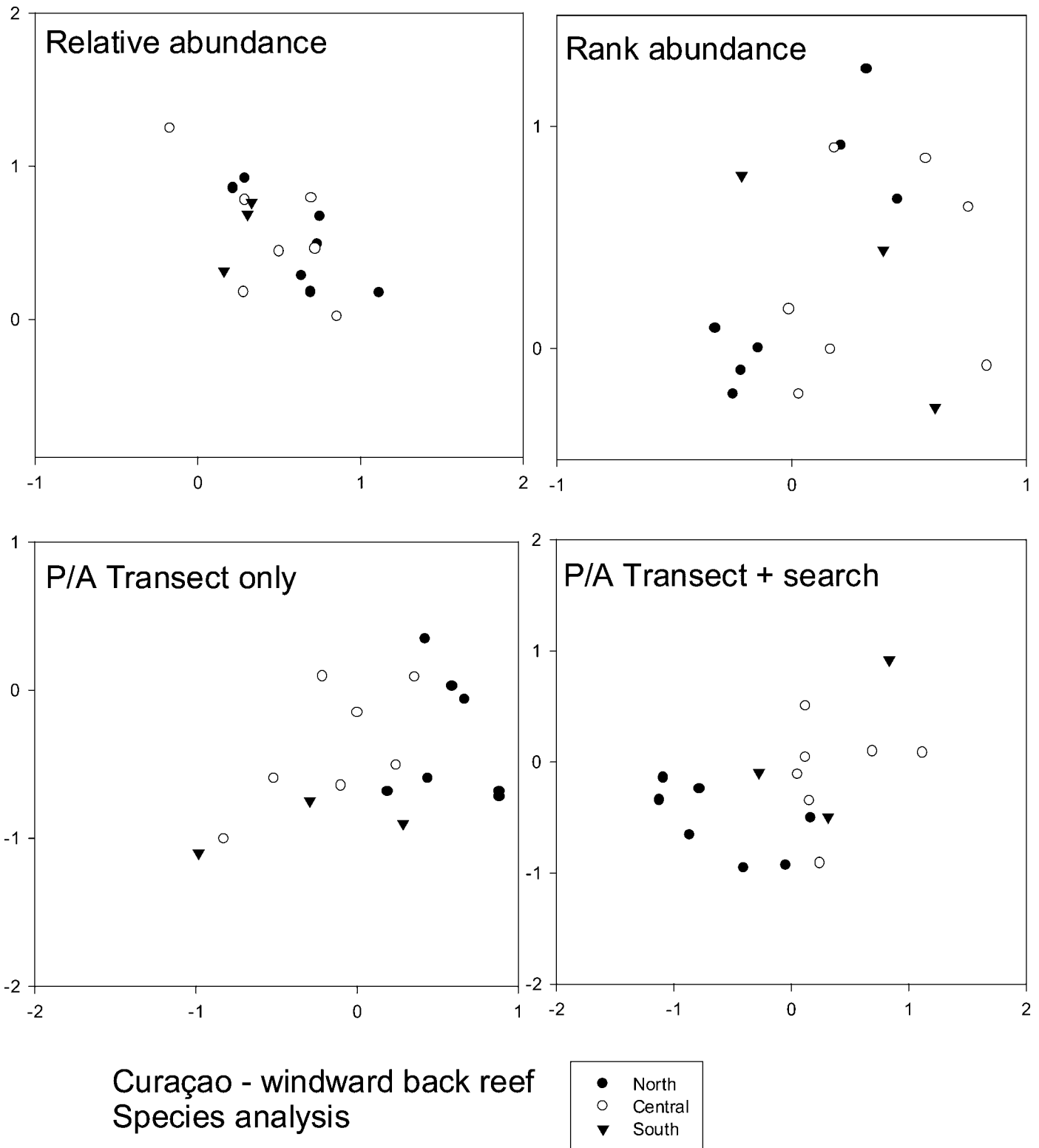


FIGURE 5—Ordination plots of Pleistocene coral species assemblages from Curaçao from the windward back reef, using quantitative, rank abundance, transect binary, and transect-search binary data sets. As in the windward reef crest, geographic differences in reef coral community structure are best seen in the rank abundance and transect-search binary data sets and are absent in the transect binary data set. Seven transects were sampled from the northern and central sites, and three transects were sampled from the southern site. Same analysis as in Figure 3.

TABLE 5—Results of ANOSIM analysis for overall environment and site within environment effects for coral genus composition at Curaçao. Analyses were completed on four data sets (see text) gathered from the Pleistocene Hato Unit of the Lower Terrace. WRC, windward reef crest; WBR, windward back reef; LRC, leeward reef crest. R = ANOSIM test statistic.

Main effect		Quantitative		Rank abundance		Transect binary		Transect-search binary	
		R	P-value	R	P-value	R	P-value	R	P-value
Environment	Overall	0.589	<0.0001	0.246	<0.0001	0.236	<0.0001	0.176	<0.0001
	WRC vs. WBR	0.876	<0.0001	0.337	<0.0001	0.309	<0.0001	0.163	0.002
	WRC vs. LRC	0.511	<0.0001	0.225	<0.0001	0.281	<0.0001	0.172	0.004
	WBR vs. LRC	0.362	<0.0001	0.177	0.001	0.106	0.012	0.186	0.003
Site	Within WRC	0.179	0.054	-0.077	0.848	-0.069	0.812	0.447	0.006
	Within WBR	0.268	0.018	0.030	0.286	0.038	0.244	0.207	0.055
	Within LRC	0.130	0.031	0.031	0.312	0.067	0.196	0.012	0.372

between San Andrés and Curaçao though the rank abundance data shows greater overlap between Barbados and Curaçao (Fig. 10).

For the three Caribbean islands in the SOCA transect, ANOSIM results for the overall island test and for pairwise island comparisons were also essentially identical at the generic level for all numerical scales of analysis, although lower *P*-values occurred with the rank abundance and transect-binary data sets (Table 7). Again, all islands were significantly different from one another in coral composition, no matter how measured. As with the species-level plots, the GNMDS ordination plots show distinct groupings among the three islands, with the greatest overlap occurring between San Andrés and Curaçao (Fig. 11).

Effects of taxonomic scale of analysis.—At Curaçao, ANOSIM results for the overall environment test and for pairwise comparisons of environments were essentially identical at the species and genus level for all numerical scales of analysis (Tables 4 and 5). However, different results among sites within environments were obtained for the quantitative, rank and transect-binary data sets. Site differences were found in the WRC and WBR environments for the species quantitative data set, but in the WBR and LRC for the genus data. Similarly, significant differences in the WBR occurred at the species level in the rank abundance and transect-binary data sets (Table 4), but not in those at the genus level (Table 5). Transect-search results among sites within environments were identical at the species and genus levels.

For the three Caribbean islands in the SOCA transect, ANOSIM results for the overall island test and for pairwise comparisons of islands were essentially identical at the species and genus level for all numerical scales of analysis (Tables 6 and 7). Lower *P*-values occurred at the rank abundance and transect-binary scales in the species level analysis (Table 6) than in the genus level analysis (Table 7). GNMDS ordination plots were also very similar between the two taxonomic levels. However, the quantitative data set at the genus level yielded an ordination plot that showed greater distinction between the San Andrés and Curaçao assemblages than did the quantitative data set at the species level (Figs. 10, 11). For the other three numerical scales of analysis, the GNMDS ordination plots showed slightly less differentiation among islands at the species level than at the genus level (Figs. 10, 11).

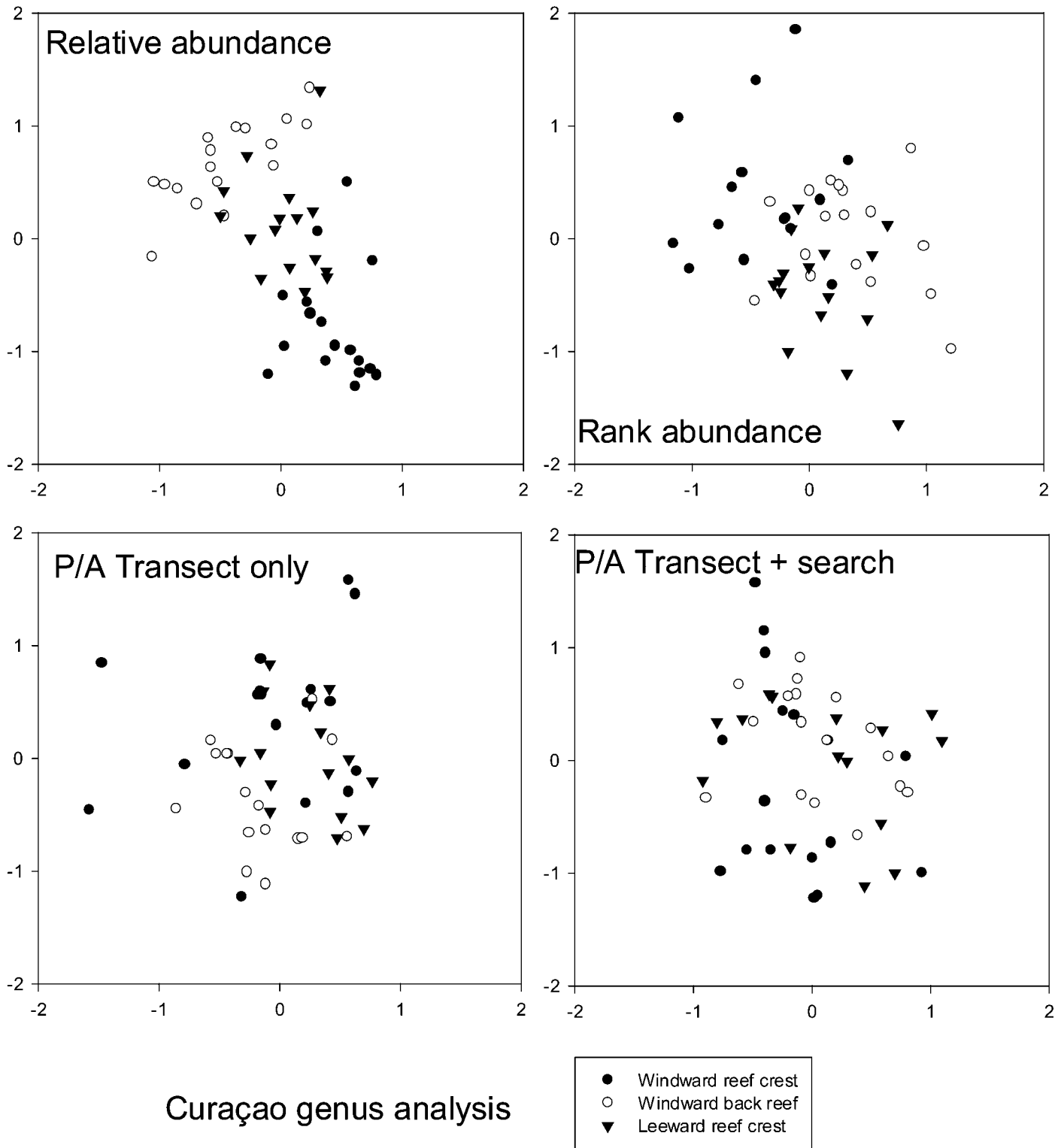
Differences in taxonomic composition.—In general, assemblages are distinguished on the basis of the relative abundance and rank order by the same five or six taxa (Pandolfi and Jackson, in press a). The abundance of dominant species such as *Acropora palmata* and the organ-pipe *Montastraea* fluctuates among environments and islands (Table 8). However, they are usually consistent among sites within environments. In contrast, less abundant taxa are much more variable in their occurrence and abundance within and among sites, environments and islands (Table 8). These results are discussed more comprehensively in a series of companion papers (Pandolfi and Jackson, 1997, 2001, in press) and will not be treated further here.

DISCUSSION

Paleontologists are frequently faced with the problem of how to most efficiently sample a given fauna or flora for the question under consideration. The two most obvious considerations are the kind of quantitative data to gather, and at what taxonomic scale to gather them. In paleoecological studies, numerical scale of analysis is often chosen without any comparative analysis, or because no choice can be made due to the nature of the data. This means that studies are not always directly comparable (e.g., presence and absence data of Pandolfi, 1996 vs. relative abundance data of Bambach and Bennington, 1996). Taxonomic scale also varies among studies for any number of reasons. On the one hand, diversity may be so high that it prohibits study of faunas or floras at lower taxonomic levels, due either to time or funding constraints (e.g., Jackson et al., 1993). On the other hand, paucity of material may mean that species are too ill defined or too low in abundance to adequately use in any quantitative analysis of distribution in space or time.

Numerical scale of analysis.—Statistical differentiation among coral communities showed little variation with increasing numerical scale of analysis. Among environments on Curaçao (Tables 4 and 5) and islands in the SOCA transect (Tables 6 and 7), ANOSIM tests showed identical results in community differentiation. Only site effects at Curaçao were different among numerical scales, and these were much more pronounced at the genus level than the species level. Thus, the species distribution patterns among environments in Pleistocene reef corals from the Caribbean are robust to the type of data collected and analyses utilized. This result supports the utility of binary data in the understanding of community structure so long as large data sets collected in a rigorous fashion are studied (Hayek and Buzas, 1997).

The results of the study mainly upheld Rahel's (1990) contrast stating that assemblages similar in taxonomic composition at a higher level of resolution (e.g., quantitative data set) are also similar at lower levels of resolution (e.g., transect binary data set), but those similar at a lower resolution are not necessarily similar at a higher level. For example, site differences at Curaçao for both the WBR and LRC at both the species and genus level showed the hierarchical pattern Rahel (1990) described (Tables 4 and 5). However, I find that this contrast may not hold when sampling intensity is increased at lower resolution relative to the data obtained at a higher resolution. In fact, the greatest differences observed in this study were those exhibited by comparison of analyses conducted on coral composition measured along the 40-m transects versus those conducted on the 40-m transects followed by a one hour search. For example, WRC communities showed significant site differences at both the species and genus level for the transect-search data set. However, the species rank abundance data set, and the generic quantitative, rank abundance, and transect-binary data sets did not show significant site differences at *P* < 0.05. Apparently, the increased sampling intensity



Curaçao genus analysis

FIGURE 6—Ordination of Pleistocene genus coral assemblages from Curaçao from the windward reef crest and back reef, and the leeward reef crest using quantitative, rank abundance, transect binary, and transect-search binary data sets. Environmental differences are greatest in the quantitative and rank abundance plots. Plots based on the presence and absence of genera show much less distinction among Pleistocene reef environments. Global non-metric multi-dimensional scaling (GNMDS) plots of dimension 1 and 2, from the 3-dimensional analyses. Each GNMDS was run with 20 random starting configurations, and proceeded through 400 iterations for each of 4 dimensions. The minimum stress value for the 3-dimensional analysis was 0.09 for the quantitative data set, 0.11 for the rank abundance data set, 0.17 for the transect binary data set, and 0.17 for the transect-search binary data set.

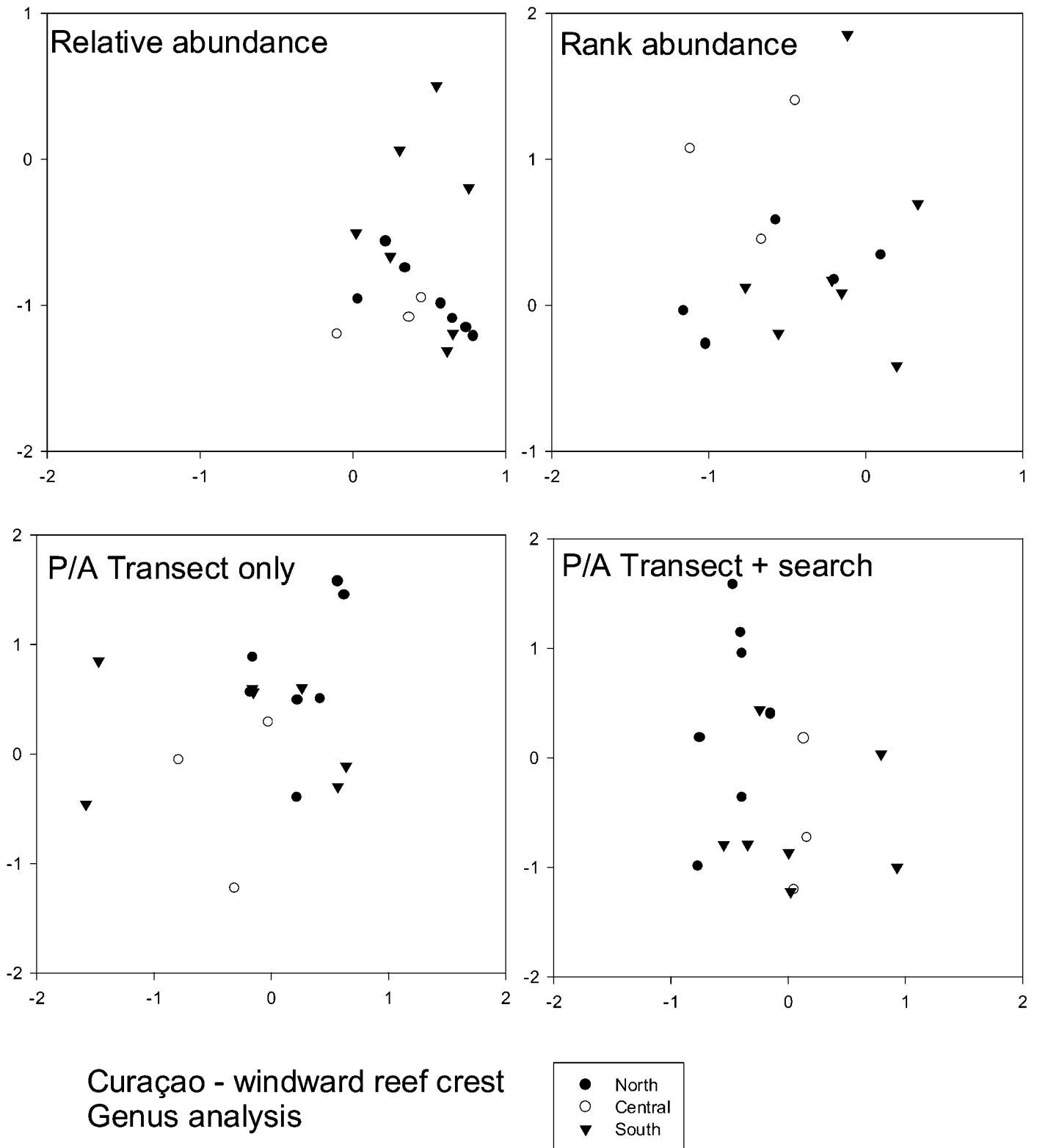


FIGURE 7—Ordination plots of Pleistocene coral genus assemblages from Curaçao from the windward reef crest environment using quantitative, rank abundance, transect binary, and transect-search binary data sets. Geographic differences in reef coral community composition are best seen in the transect-search binary data sets and are absent in the others. Seven transects were sampled from the northern and southern sites, and three transects were sampled from the central site. Same analysis as in Figure 6.

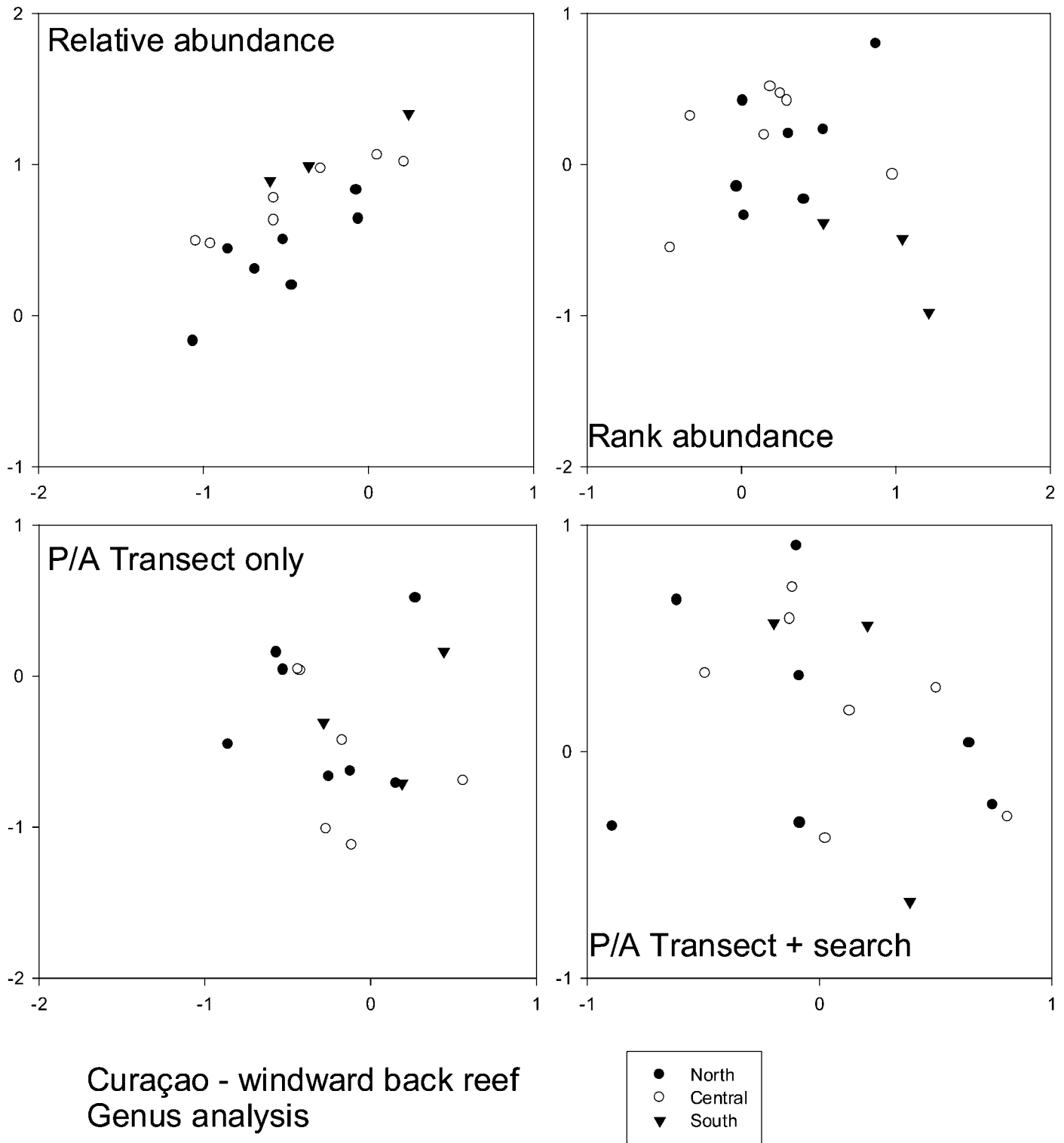


FIGURE 8—Ordination plots of Pleistocene coral genus assemblages from Curaçao from the windward back reef environment using quantitative, rank abundance, transect binary, and transect-search binary data sets. Geographic differences in reef coral community composition are best seen in the quantitative data set and are absent in the others. Seven transects were sampled from the northern and central sites, and three transects were sampled from the southern site. Same analysis as in Figure 6.

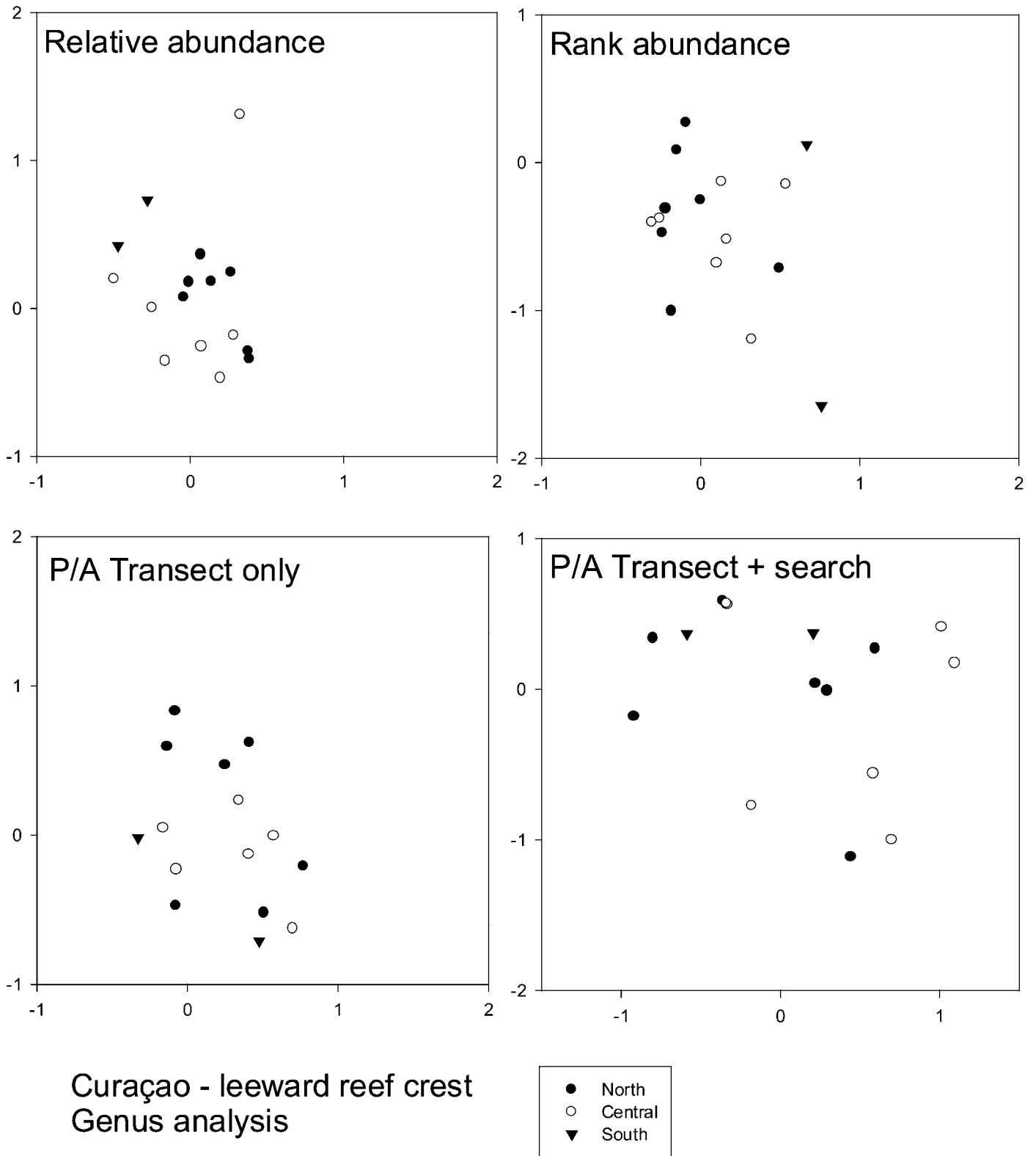


FIGURE 9—Ordination plots of Pleistocene coral genus assemblages from Curaçao from the leeward reef crest environment using quantitative, rank abundance, transect binary, and transect-search binary data sets. Geographic differences in reef coral community composition are best seen in the quantitative data set and are absent in the others. Seven transects were sampled from the northern and central sites, and two transects were sampled from the southern site. Same analysis as in Figure 6.

TABLE 6—Results of ANOSIM analysis for significant differences in Pleistocene reef coral species composition within the leeward reef crest environment among the three Caribbean islands along the SOCA transect. Analyses were completed on four data sets (see text). SA = San Andrés, CUR = Curaçao, BB = Barbados. R = ANOSIM test statistic.

Main effect		Quantitative		Rank abundance		Transect binary		Transect-search binary	
		R	P-value	R	P-value	R	P-value	R	P-value
Island	Overall	0.729	<0.0001	0.433	<0.0001	0.408	<0.0001	0.603	<0.0001
	SA vs. CUR	0.546	<0.0001	0.340	<0.0001	0.327	<0.0001	0.549	<0.0001
	SA vs. BB	0.913	<0.0001	0.669	<0.0001	0.583	<0.0001	0.728	<0.0001
	CUR vs. BB	0.719	<0.0001	0.360	<0.0001	0.385	<0.0001	0.657	<0.0001

represented by an additional hour of data gathering resulted in more community differentiation at WRC than from data gathered along the transect only. This result cautions against a simple linear relationship between numerical scale of analysis and community differentiation when sampling intensity varies across the analytical scale.

Trends from the present study suggest that when sufficient sampling intensity accompanies species presence and absence data, analyses completed at this and the quantitative analytic scale may be similar. For example, I have shown persistence in Pleistocene coral community structure through time and space in Papua New Guinea and Curaçao, respectively (Pandolfi, 1996; Pandolfi and Jackson, 2001). In the Papua New Guinea study, species presence and absence data were used, whereas in the Curaçao study, the four data sets described herein were used. The results of this study would appear to suggest that the species presence and absence trends found in Papua New Guinea might equally apply to a quantitative data set, though differences due to a markedly higher Indo-Pacific species diversity would need to be ruled out.

Finally, a note of caution when presenting ordination (and cluster) diagrams without appropriate significance testing. Ordination analyses may give patterns that appear to homogenize groups when in fact there are statistically significant differences among groups. This is best seen in the WBR ordination illustrating site differences (Fig. 5). It is recommended that paleoecological surveys not rely solely on ordination or cluster analyses for their interpretation, but include some kind of statistical analysis. Such statistical analysis relies on a rigorous sampling protocol, similar to nested sampling commonly used in ecological surveys of living systems (e.g., Underwood, 1997). Moreover, there are now a number of techniques that can be used to assess the significance of groups that are displayed on an ordination, such as ANOSIM (Clarke, 1993) and the multiresponse permutation procedure (MRPP; Zimmerman et al., 1985; McCune, 1987).

On the other hand, the absence of discrete groups in an ordination when ANOSIM shows significant differences might indicate the possibility of TYPE I error (resulting in a statistically significant difference when none actually exists) in the statistical analysis and design. Mismatches between ANOSIM and GNMDS occurred only in the Curaçao data set, at both the species [transect-search data for environments (Fig. 3); quantitative and rank abundance data for sites (Fig. 5)] and genus [both binary data sets for environment (Fig. 6)] levels. No mismatches occurred in the SOCA analysis, where the number of replicates per island (12–16) was approximately twice as large as the number of replicates per site (seven) at Curaçao. Thus, it appears that sample size needs to be greater to detect differences in taxonomic composition using GNMDS ordination than it does to detect them using ANOSIM.

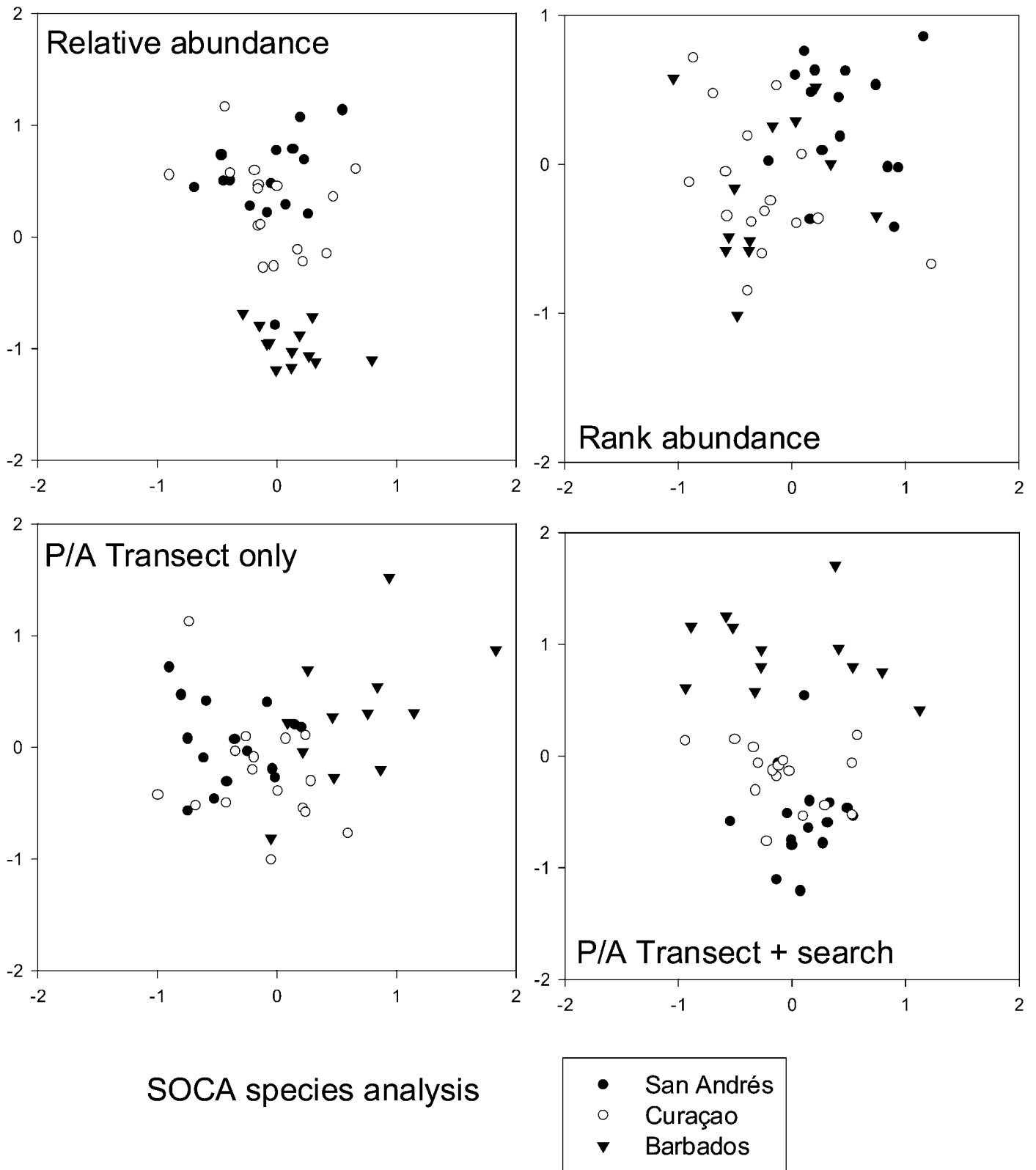
Taxonomic scale of analysis.—The results support the notion that generic-level analyses are similar to those using patterns of species distribution for Caribbean Quaternary corals at large sample size and large spatial scales. Thus, no differences in patterns between species and genus were observed among environments

at Curaçao and non-significant differences were observed among islands within the leeward reef crest environment at the scale of the SOCA transect. It appears that where species differences are greatest, so will generic differences be. The results of community differentiation among environments on Curaçao and among islands in the SOCA transect are in agreement with several studies from living marine and freshwater communities that use higher than species taxonomic levels to detect differences in community structure, usually in response to a disturbance (Ferraro and Cole, 1990; Gray et al., 1990; Herman and Heip, 1988; Warwick, 1988a, 1988b; Wright et al., 1995). Thus, broad-scale environmental and geographic studies of community structure in the fossil record are in conformance with ecological studies of living ecosystems with respect to taxonomic scale of analyses.

Wright et al. (1995) provided a series of possible reasons for obtaining similar patterns from species versus higher level data. These include: 1) species within a higher taxa are restricted in their ecological variability; 2) although species may vary ecologically among higher taxa, they do not vary more than the higher taxa do; 3) some higher taxa may be so dominated by a single species within a study area, that for these higher taxa, species and higher taxa data are essentially equivalent; 4) the analysis may be highly robust to information loss regardless of relative ecological breadth of species from the same higher taxa (Waterhouse and Farrell, 1985); and 5) redundancy in species-level data can be allowed to be maintained when they are aggregated to higher taxonomic levels, even in the absence of ecological similarities among the aggregated taxa (Herman and Heip, 1988).

For many of the coral taxa in the present study, genera are often dominated by a single species. For example, *Acropora palmata* is the ecological dominant in the WRC environment of Curaçao, and the organ-pipe *Montastraea* co-dominates with this species in the LRC environment (Pandolfi and Jackson, 2001). In these cases, the species dominance is greater than 50 percent; so generic level patterns will reflect these strong underlying species level patterns. Moreover, the ratio of species to genus in the analyzed fauna was relatively low (range: 1.58–2.14); thus genus level patterns closely follow those of their component species. It is an open question whether such patterns would be found if this ratio were higher, or if the distribution of species per genus were less uniform, as would be the case for Indo-Pacific reef corals.

However, even with the low diversity and low species to genus level ratios, substantial differences in patterns of community differentiation between the species and genus level occurred *within* environments along the Curaçao coastline. In general, more differences were shown in the species level data than in the genera level data in the WRC and WBR, although the opposite was true in the LRC (Tables 4 and 5). In these situations, sample size is more limited and geographic scale is reduced, relative to the among-environment (Curaçao) and among-island (SOCA) analyses (Tables 1 and 2). Moreover, there is probably less community differentiation to be expected using genera within than between environments at such small spatial scales, especially if individual



SOCA species analysis

- San Andrés
- Curaçao
- ▼ Barbados

FIGURE 10—Ordination of reef coral species composition from Pleistocene leeward reef crest communities along the SOCA transect at San Andrés, Curaçao, and Barbados. Note that Barbados plots well away from San Andrés and Curaçao. However, San Andrés and Curaçao are also distinct. ANOSIM statistical tests reveal that the separation of reef coral assemblages from different islands in the ordination corresponds to significant differences in species composition (Table 6). Global non-metric multi-dimensional scaling (GNMDS) plots of dimension 1 and 2 from the 3-dimensional analyses. Each GNMDS was run with 20 random starting configurations, and proceeded through 400 iterations for each of 4 dimensions. The minimum stress value for the 3-dimensional analysis was 0.08, 0.15, 0.13, and 0.12, for the quantitative, rank abundance, transect binary, and transect-search binary data set, respectively.

TABLE 7—Results of ANOSIM analysis for significant differences in Pleistocene reef coral generic composition within the leeward reef crest environment among the three Caribbean islands along the SOCA transect. Analyses were completed on four data sets (see text). SA = San Andrés, CUR = Curaçao, BB = Barbados. R = ANOSIM test statistic.

Main effect		Quantitative		Rank abundance		Transect binary		Transect-search binary	
		R	P-value	R	P-value	R	P-value	R	P-value
Island	Overall	0.612	<0.0001	0.247	<0.0001	0.247	<0.0001	0.439	<0.0001
	SA vs. CUR	0.263	<0.0001	0.098	>0.026	0.139	0.008	0.313	<0.0001
	SA vs. BB	0.845	<0.0001	0.445	<0.0001	0.421	<0.0001	0.546	<0.0001
	CUR vs. BB	0.744	<0.0001	0.260	0.001	0.237	0.001	0.531	<0.0001

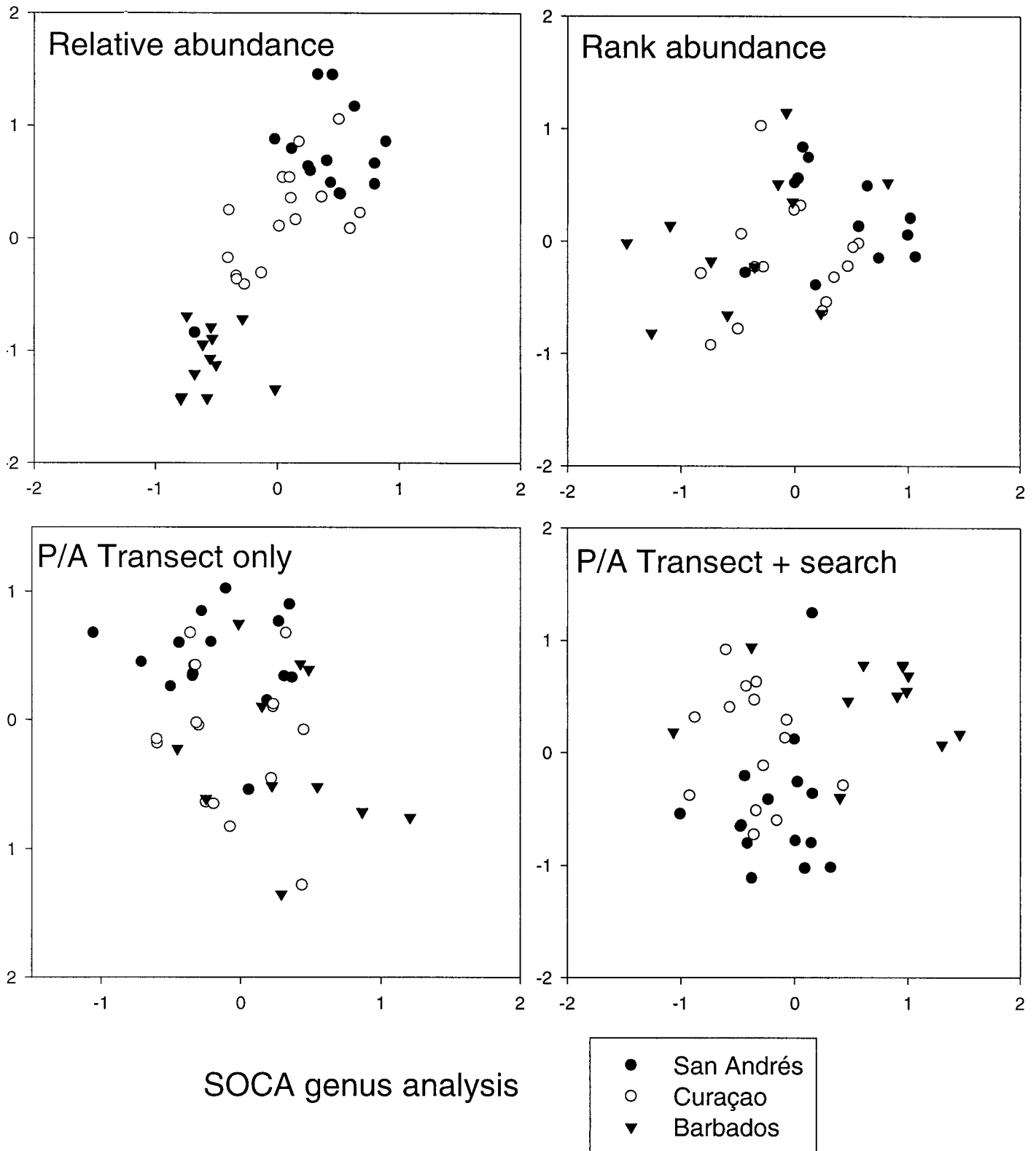
species niches vary minimally within genera. At such scales, analyses conducted at the genus level appear to be less congruent to those at the species level. Spatial scale has also been shown to be a factor in the degree to which the taxonomic scale of analysis alters interpretation of community structure in freshwater macroinvertebrate communities (Marchant et al., 1995).

How applicable are these results?—In the examples presented above where assemblages were clearly distinct high-resolution data was not necessary to test competing hypotheses of community structure. But how widely applicable are these results? Higher taxonomic and numerical scales of resolution may be necessary

to distinguish communities when there is a high degree of overlap among them. As assemblages become more similar, perhaps as geographic or environmental scope is narrowed, then more information may be needed to distinguish them. This information may be in the form of more detailed data (higher numerical scale of analysis or more intensive sampling at each locality) or increasing sampling intensity (number of localities). There is likely to be a trade-off between the ability to increase sampling intensity versus the ability to collect more intensively at each sampling locality. At what point to choose along this spectrum should probably be addressed using a pilot study before embarking on a full-fledged

TABLE 8—Mean abundance and occurrence of Pleistocene Caribbean reef coral species surveyed in this study. For Curaçao numbers represent transects pooled over the two sites with 7 replicate transects, and the total includes those two sites plus a third site with <4 transects. P = present along one-hour search only. WRC = windward reef crest; WBR = windward back reef; LRC = leeward reef crest.

Island/environment	Curaçao—WRC			Curaçao—WBR			Curaçao—LRC			SOCA—LRC		
	North 7	South 7	Total 17	North 7	Central 7	Total 17	North 7	Central 7	Total 16	San Andrés 15	Curaçao 16	Barbados 12
Species												
<i>Acropora cervicornis</i>	P	P	P	0.26	P	0.14	1.23	4.38	3.35	17.83	3.35	12.04
<i>Acropora palmata</i>	97.58	89.67	96.19	18.45	3.54	6.9	44.55	46.72	39.27	3.39	30.27	82.53
<i>Agaricia agaricites</i>	P	P	P	P	P	P	P	P	P	0.03	P	P
<i>Colpophyllia amaranthus</i>	0	0	0	0	0	0	P	P	0.01	P	0.01	0
<i>Colpophyllia breviserialis</i>	P	P	P	P	P	0.02	0	P	P	0.09	P	0
<i>Colpophyllia natans</i>	P	P	P	P	0	P	P	0	0.01	1.25	0.01	0
<i>Dendrogyra cylindricus</i>	P	P	P	P	P	0.04	P	P	P	P	P	P
<i>Dichocoenia stokesi</i>	0	0	0	0	0	0	0	0	0	0	0	P
<i>Diploria clivosa</i>	P	P	0.06	1.99	5.11	2.94	P	P	0.12	P	0.12	0
<i>Diploria labyrinthiformis</i>	P	P	P	1.27	0.18	1.1	0.07	0.87	0.65	10.16	0.65	0.3
<i>Diploria strigosa</i>	2.11	1.38	2.3	41.78	7.6	19.84	2.13	6.4	3.94	9.26	3.94	P
<i>Eusmilia fastigiata</i>	0	0	0	0	0	0	P	0	P	P	P	0
<i>Favia fragum</i>	P	P	P	P	P	P	P	P	0.01	P	0.01	P
<i>Isophyllastrea rigida</i>	0	P	P	P	P	P	0	0	0	P	0	P
<i>Isophyllia sinuosa</i>	0	P	P	0	0	0	0	0	0	P	0	0
<i>Madracis mirabilis</i>	0	0	0	0	0	0	P	0	P	P	P	0
<i>Madracis decactis</i>	0	P	P	0	0	0	0	0	0	0	0	0
<i>Manicina areolata</i>	0	0	P	0	0	0	0	0	0	0	0	0
<i>Meandrina meandrites</i>	P	P	P	0	P	P	P	P	P	0.22	P	P
<i>Millepora complanata</i>	0	0	0	0	0	0	0	P	P	0	P	0
<i>Montastraea annularis s.s.</i>	P	3.15	0.38	P	7.81	5.29	10.68	11.43	12.61	5.12	12.61	0.63
<i>Montastraea faveolata</i>	0.24	P	0.04	6.3	0.94	3.06	0.33	0.1	0.34	5.68	0.34	1.63
<i>Montastraea franksi</i>	0	0	0	0	0	0	P	0	P	0	P	0
organ-pipe <i>Montastraea</i>	P	5.73	0.92	28.27	70.89	58.05	40.96	28.24	39.12	37.93	39.12	2.16
<i>Montastraea cavernosa</i> sp. 1	P	P	P	P	P	0.02	P	P	P	0.53	P	P
<i>Montastraea cavernosa</i> sp. 2	0	0	0	P	0	P	0	0	0	0.95	0	0
<i>Montastraea cavernosa</i> sp. 3	P	P	P	0.78	P	0.18	P	P	0	P	0	0
<i>Montastraea cavernosa</i> sp. 4	0	0	P	P	P	P	0	P	P	P	P	0
<i>Mussa angulosa</i>	0	0	0	0	0	0	0	0	0	P	0	0
<i>Pocillopora cf. palmata</i>	P	P	0.06	P	0	P	P	P	P	P	P	P
<i>Porites astreoides</i>	0	0.08	0.04	0	0	0	0.04	0.31	0.23	3.48	0.23	0.64
<i>Porites divaricata</i>	0	0	0	P	0	P	0	0	0	0	0	0
<i>Porites furcata</i>	0	P	P	0	0	0	0	0	P	0.03	P	P
<i>Porites porites</i>	0	0	0	0	0	0	0	0	P	1.02	P	P
sheet <i>Montastraea</i>	P	P	P	0	0	0	P	0	0.02	P	0.02	0.08
<i>Siderastrea radians</i>	P	P	P	0.23	P	0.04	P	0	P	0.07	P	P
<i>Siderastrea siderea</i>	P	P	P	0.59	3.91	2.38	P	1.53	0.33	2.85	0.33	P
<i>Solenastrea bourini</i>	0	P	P	0	0	0	0	0	0	0	0	0
<i>Stephanocoenia intersepta</i>	0	P	P	0	0	0	0	0	0	0.07	0	P
<i>Undaria crassa</i>	0	0	0	0	0	0	P	0	P	0	P	0
<i>Undaria pusilla</i>	P	0	P	0	0	0	0	0	0	0	0	0



SOCA genus analysis

FIGURE 11—Ordination of reef coral genus composition from Pleistocene leeward reef crest communities along the SOCA transect at San Andrés, Curaçao, and Barbados. Note that Barbados plots well away from San Andrés and Curaçao. However, San Andrés and Curaçao are also distinct. ANOSIM statistical tests reveal that the separation of reef coral assemblages from different islands in the ordination corresponds to significant differences in genus composition (Table 7). Global non-metric multi-dimensional scaling (GNMDS) plots of dimension 1 and 2 from the 3-dimensional analyses. Each GNMDS was run with 20 random starting configurations, and proceeded through 400 iterations for each of 4 dimensions. The minimum stress value for the 3-dimensional analysis was 0.05, 0.10, 0.15, and 0.14, for the quantitative, rank abundance, transect binary, and transect-search binary data set, respectively.

sampling program. In many cases, it may not be feasible to present multiple scales of analysis, despite its utility in comparison among studies (Rahel, 1990).

CONCLUSIONS

1) In general, differing scales of numerical resolution did not alter the results obtained in the analysis of community structure in Pleistocene reef corals of the Caribbean. Where differences occurred they generally followed Rahel's (1990) hierarchical pattern of yielding less differentiation with decreasing numerical scale. However, altering the intensity of sampling disrupted this pattern. Thus, studies comparing numerical scales of analysis need also to assess the sampling intensity before meaningful comparisons can be made.

2) Differences in taxonomic scale did not significantly alter the interpretation of patterns of community differentiation at the scale of among environments at Curaçao nor among islands in the SOCA transect. Congruence among taxonomic levels was probably related to the limited niche differences among congeneric species of Caribbean corals, the low species to genus ratio among Caribbean corals, and the species dominance patterns that typified Pleistocene Caribbean reefs. However, greater differences between species and genus level data were observed at the smaller spatial scale (and smaller sample sizes) found within environments on Curaçao than among environments on Curaçao and among islands in the SOCA transect. Thus, sample size, range of environments, and spatial scale of study are all variables that may influence the degree to which generic and species level ecological data yield congruent results.

3) Several recommendations can be made on the basis of the results of this study. First, pilot studies to assess "taxonomic sufficiency" (Ellis, 1985; Ferraro and Cole, 1990) have been recommended in studies of living communities (Wright et al., 1995), and this recommendation applies equally to studies of community ecology in the marine fossil record. Second, Rahel's (1990) call for presentation of results from multiple numerical scales makes sense for community ecology studies in the fossil record. Lastly, some sort of appropriate statistical test, to alert others about the significance of the groupings and to help unmask trends that may not be obvious from the ordination plots, should accompany ordination of ecological data.

4) The results of this study cannot automatically be generalized to all studies of reef coral assemblages because sampling and analysis strategies will differ depending upon the question to be addressed. Other workers, especially those involved in monitoring living reef systems should guard against the design of oversimplified sampling strategies that are inadequate to detect change in living coral communities.

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ACCEPTED 15 DECEMBER 2000