Revista Brasil. Bot., V.30, n.3, p.543-551, jul.-set. 2007

Spatial variation in the structure and floristic composition of “restinga” vegetation in southeastern Brazil[1]

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(received: January 01, 2005; accepted: September 28, 2007)

ABSTRACT – (Spatial variation in the structure and floristic composition of “restinga” vegetation in southeastern Brazil). We examined large-scale spatial variation of structural parameters and floristic composition in open *Clusia* scrub, a vegetation type of the Brazilian “restingas” (sandy coastal plain vegetation). This vegetation is organized in islands separated by sandy stretches with sparse herbaceous vegetation. We located 12 sample areas on three consecutive beach ridges, lying parallel to the coastline and at different distances from the ocean, in close proximity to two lagoons (Cabiúnas and Comprida). Each sample area was divided into three strips. We used the line intercept method to sample all woody plants ≥ 50 cm tall. We used nested ANOVA to verify structural variation between different sampling scales. TWINSPAN analysis was performed to examine the variation in floristic composition between areas. The overall diversity index was 3.07. Six species are repeatedly dominant throughout the entire sampling area. There was homogeneity in relation to diversity and species richness between beach ridges but not within beach ridges. Floristic composition and structural parameters did not vary in relation to distance from the sea but floristic composition did vary as a function of proximity to Cabiúnas or Comprida lagoon. Differences in plant cover between sample areas may be related to the paleoformation of this sandy coastal plain.

Key words **-** phytosociology, plant community, sampling scale, sandy coastal plain

RESUMO – (Variação espacial na estrutura e composição florística de uma vegetação de restinga no Sudeste brasileiro). A variação em ampla escala espacial para parâmetros estruturais e composição florística foi examinada para uma formação aberta de *Clusia*, um tipo vegetacional das restingas brasileiras. Esta vegetação é organizada em moitas separadas por areia com esparsa vegetação herbácea. Foram levantadas 12 áreas amostrais em três cordões arenosos paralelos, às margens de duas lagoas costeiras (Cabiúnas e Comprida). Estes cordões estavam dispostos a diferentes distâncias do mar. Cada área amostral foi dividida em três faixas. Usamos o método de intercepto de linha para amostrar todas as plantas lenhosas ≥ 50 cm de altura. Foi empregada ANOVA hierárquica para verificar a variação estrutural em diferentes escalas amostrais, e análise de TWINSPAN para examinar a variação na composição florística entre áreas. A diversidade total da área (*H’*) foi de 3,07. Apenas poucas espécies foram repetidamente dominantes ao longo de toda a área amostral. Houve homogeneidade em relação à diversidade e riqueza de espécies entre cordões arenosos, mas não dentro destes cordões. Composição florística e parâmetros estruturais não variaram em relação à distância do mar, mas a composição florística variou em função da lagoa que margeava. As diferenças observadas na cobertura vegetal podem estar relacionadas com a história geológica desta área de restinga.

Palavras-chave - comunidade vegetal, escala amostral, fitossociologia, restinga

Introduction

Delimitation and characterization of plant communities remains one of the main problems faced by ecologists. There is still a lack of evidence regarding the extent to which classification systems reflect the true nature of plant communities (Shrader-Frechette & McCoy 1993). In this context, problems related to sampling effort needed to produce floristic inventories that include rare species (Condit 1995, Jalonen *et al.* 1998) have been widely discussed, as has optimal sample size to detect structural variation within plant communities (Pitman *et al.* 1999). These issues are often more challenging in the tropics, where many communities have high species diversity. For instance, Campbell (1994) found that sample plots of anything less than 10 ha were insufficient to provide an accurate description of the structure of Amazon rain forests. The sampling effort needed for such a large area would not be feasible in most cases, particularly if one considers the need for replication. Since sound community ecology is one of the most important tools in biological conservation (Shrader-Frechette & McCoy 1993), this methodological difficulty must be overcome.

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[1] This paper is part of the doctoral thesis of the first author at the Graduate Program in Ecology, UFRJ.

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In Brazil, where biodiversity is probably the highest in the world (World Conservation Monitoring Center 1992), most delimitation and characterization surveys have been restricted to one-hectare plots, with a few exceptions (*e.g.*, Campbell 1994, Nascimento *et al*. 1999). This is also true for the vegetation on the Brazilian sandy coastal plains (“restingas”) where surveys often cover 1.0 hectare or less (*e.g.* Hay *et al*. 1981, Ribas *et al*. 1993, Araujo *et al*. 1998, Menezes & Araujo 1999).

Geomorphologically, “restingas” are the result of Quaternary changes in sea-level influencing the deposition of sandy marine deposits (Martin *et al*. 1993) which sometimes form broad coastal plains consisting of alternating beach ridges and swales, covered by a number of different forest, scrub and herbaceous vegetation types. These plant communities also are designated collectively as “restinga” vegetation (Araujo 1992). In prograding environments, one can assume that the age of these ridges generally increases as one goes inland (Martin *et al*. 1993) and there is a sharp gradient of abiotic factors (*e.g.*, salt spray, sand movement, soil moisture content) that decrease in intensity inland from the beach (Ehrenfeld 1990). Furthermore, in many parts of the world, species diversity and vegetation complexity increase inland from the beach (Espejel 1992, Lacerda *et al*. 1993).

Our aim was to assess the degree of floristic and phytosociological variation in the open *Clusia* scrub formation, a plant community in southeastern Brazil consisting of variously shaped thickets that are separated by sparsely vegetated areas (Araujo 1992, Araujo *et al*. 1998, 2004). This study was designed to provide answers to the following questions: (1) Is there variation in structural parameters, dominance and species composition between beach ridges in the open *Clusia* scrub?; (2) If so, is this variation a function of the distance from beach ridge to the sea?; and (3) Is there variation in structural parameters, dominance and species composition within each beach ridge?

Material and methods

Study area – “Restingas” are found all along the Brazilian coast, and differences in topography, water table level and other factors along a gradient inland from the beach create a number of different habitats and a mosaic of plant communities (Araujo 2000). “Restingas” constitute one of the biomes marginal to the Atlantic rain forest (Scarano 2002), a well-known biodiversity hotspot (Myers *et al*. 2000). In northern Rio de Janeiro state, a series of beach ridges of Pleistocene age form the broad coastal plain of the “Parque Nacional da Restinga de Jurubatiba”, 22°00’-22°23’ S, 41°15’-41°35’ W. Here, the outermost ridge, formed during the Holocene (Martin *et al*. 1993), often encloses a series of brackish or freshwater lagoons. Average annual temperature is 22.6 °C and rainfall is seasonal with a monthly maximum of 189 mm in summer (January). Average annual rainfall is *ca*. 1,200 mm; rainfall is lower from May to August and in June soils are moisture deficient.

Ten plant communities have been described for the “Parque Nacional da Restinga de Jurubatiba” and one of the most representative locally is the open *Clusia* scrub (Araujo *et al*. 1998), where the present study was carried out. This formation gets its name from *Clusia hilariana*, the most conspicuous woody plant in the landscape due to size, shape and frequency (Araujo & Scarano 2007). This dioecious, CAM (crassulacean acid metabolism; Franco *et al*. 1996) tree reaches 5-7 m in height and is the central nurse plant in most thickets (Scarano 2002, Scarano *et al*. 2004, Dias *et al*. 2005, Dias & Scarano 2007). The *Clusia* scrub formation occurs in a coastal strip from the study area, in Rio de Janeiro, to Espirito Santo and southern Bahia (Araujo 2000). The study area includes two lagoons, Cabiúnas and Comprida, and reaches the southern shore of a third, Carapebus lagoon. The open *Clusia* scrub lies on the beach ridges, at a higher level than other local vegetation types. Ground-water levels are often more than 1 m below the surface (Araujo *et al*. 1998).

Field sampling – In 7.2 ha, 12 sample areas were established in the open *Clusia* scrub – six areas near Cabiúnas lagoon and six near Comprida lagoon (figure 1). The lagoons are separated from the sea by a narrow strip of sand. The arms of the lagoons flood the swales between the beach ridges where swamp forests occur. Three sample areas were selected on each side of each lagoon. These ridges are separated from each other by approximately 100 m. On each ridge we set one sample area, so these differed in regard to distance from the sea. In each sample area, three 100 m x 20 m strips were set parallel to the shoreline, 50 m apart from one another. In each strip, ten 20 meter intercepting lines were randomly chosen. We sampled a total 7,200 meters by the line-intercept method (Brower & Zar 1984).

All woody plants over 50 cm tall were sampled. Non-woody plants over 50 cm tall that intercepted the line were recorded as herb cover. Total plant cover was calculated as total line length (7,200 m) minus line length where shrubs and non-woody plants over 50 cm tall were absent. It should be remembered that plant canopies sometimes overlap. Importance values were based only on the cover of woody plants over 50 cm tall; herb cover is dealt with in Pereira *et al*. (2004). Species were identified in the field; when this was not possible, material was dried and pressed for identification by specialists.

Data analysis – Dominance (plant cover), frequency and importance value (IV-sum of relative dominance and frequency) were calculated for each species (Müller-Dombois & Ellenberg 1974). We used the Shannon diversity index (*H’*; Magurran 1988) to calculate total species diversity and that of each sample area. Evenness also follows Magurran (1988). Diversity was calculated on the basis of plant cover data. We considered the six species with highest IV to be the dominant species and those with IV less than 1.0 to be rare species; the remaining species were designated intermediate species.

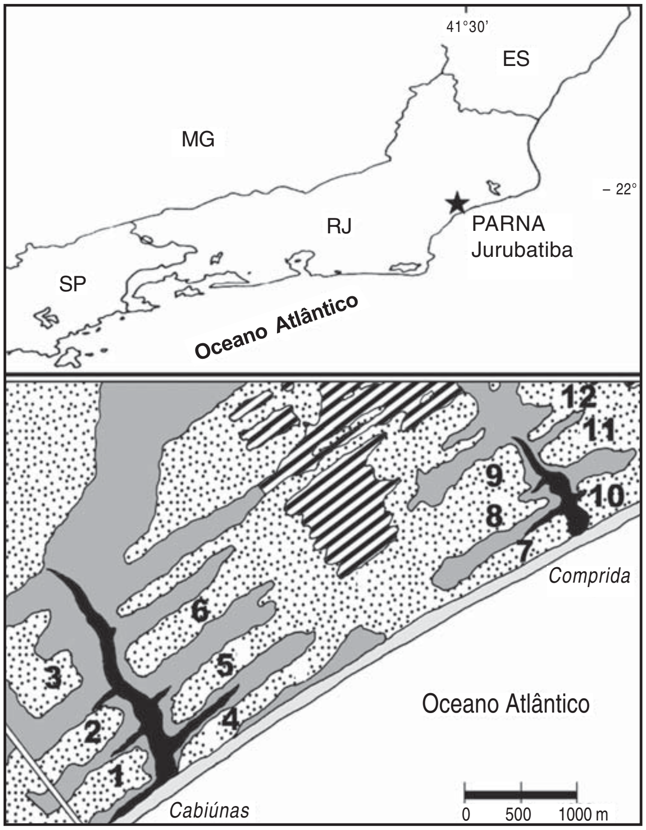

Figure 1. Study site at the "Parque Nacional da Restinga de Jurubatiba". Numbers indicate the 12 sample areas in the *Clusia* open scrub (░ = *Clusia* open scrub; ▒ = swamp forests; ▤ = periodically flooded open vegetation type ("Restinga de Ericaceae"); ■ = lagoons).

Analysis of variance for each structural parameter (diversity, species richness, vegetation cover) in the open *Clusia* scrub was carried out by means of nested ANOVA (Zar 1996). This statistical test detects differences in sampling scale (*i.e.*, strip, sample area, lagoon). The lagoons were considered to be the fixed factor and the strips the random factor. We calculated the variance percentage explained by each sampling level to verify the relative contribution of each level to the variance. We applied TWINSPAN to verify floristic composition variation between areas using species IVs. This program groups areas according to species composition and species according to area classifications. Both classifications occur at the same time and one or more species are named indicator species, that is, species that show well-defined site preference (Valentin 2000). We used PC-ORD for WINDOWS, version 3.0 (MJM Software).

Results

We sampled a total of 62 woody species from 30 families. The diversity (*H'*) and evenness indices were 3.07 and 0.74, respectively. Myrtaceae had the most species (11), followed by Leguminosae (6). The concentration of IV in a few species occurred throughout the entire study area; 42% of total IV was concentrated in the top six species (*Clusia hilariana*, *Protium icicariba*, *Myrcia lundiana*, *Erythroxylum subsessile*, *Ocotea notata* and *Myrsine parvifolia*). In relation to each individual sample area, the six species with highest IV were considered to be the dominant-species group, which coincided with the six species mentioned above in only one sample area. At the opposite extreme, in one sample area only one of the species with high IV also pertained to the group mentioned above. *Clusia hilariana* was in the dominant-species group in all 12 sample areas; *Protium icicariba* was in this group in 10 sample areas, *Myrcia lundiana* and *Erythroxylum subsessile* in seven areas, and *Ocotea notata* and *Myrsine parvifolia*, in six and four areas, respectively (table 1).

Eleven species (18%) were sparsely distributed and occurred in only one of the 12 sample areas: *Andira fraxinifolia*, *Coccoloba alnifolia*,*Croton* sp., *Cupania racemosa*, *Gomidesia fenzliana*, *Inga maritima*, *Pilocarpus spicatus*, *Schinus terebinthifolius*, *Trichilia* sp., *Vernonia rufogrisea* and *Vitex polygama* (table 1). Most of these species (nine) were found only in the Cabiúnas area while two (*Andira fraxinifolia*, *Vitex polygama*) were restricted to the Comprida area.

TWINSPAN classification of the sample areas produced three groups (table 1). Two of the groups consist of species found mainly in sample areas located near one of the two lagoons, either Cabiúnas or Comprida (Groups 1 and 3). *Vernonia crotonoides* is the indicator species that separates these two groups. This species is not restricted to Cabiúnas lagoon, but it is a first division indicator because it had high IVs near this lagoon, in contrast to the low values seen in the two sample areas where it occurs near Comprida lagoon. Group 2 is composed of species that occur indiscriminately near both lagoons; the six dominant species are in this group. Furthermore, the analysis subdivided Group 1 into Groups 1a and 1b. The former contains mostly rare or intermediate species with low IV values that are practically restricted to the area surrounding Cabiúnas lagoon. The latter has intermediate species with higher IVs and stronger presence in the area around Comprida Lagoon than those of Group 1a.

Although the groups detected by the TWINSPAN classification were related to the lagoons, nested ANOVA showed no significant variation between the two lagoons for the parameters analyzed (table 2). As a whole, only

Table 1. Species and sample area (SA) groups from TWINSPAN classification based on species IV for each sample area of the open *Clusia* scrub formation at “Parque Nacional da Restinga de Jurubatiba”. Cabiúnas (SA1-SA6) and Comprida (SA7-SA12) are the lagoons which are surrounded by the sample areas.

Species	SA2	SA3	SA5	SA6	SA1	SA4	SA8	SA9	SA11	SA12	SA7	SA10
Group 1a – Typical of Cabiúnas												
Baccharis arctostaphyloides *Baker*	–	–	1.32	–	–	0.55	–	–	–	–	–	–
Chaetocarpus myrsinites Baill.	1.63	5.78	–	–	1.01	3.84	–	–	–	–	–	–
Coccoloba alnifolia Casar.	–	–	–	–	–	0.53	–	–	–	–	–	–
Croton sp.	–	–	–	–	–	2.09	–	–	–	–	–	–
Garcinia brasiliensis Mart.	–	1.90	–	–	–	0.80	–	–	–	–	–	–
Gomidesia fenzliana O. Berg	–	–	–	–	2.00	–	–	–	–	–	–	–
Heteropterys coleoptera A. Juss.	6.44	6.45	1.45	3.77	2.78	1.14	–	–	–	0.95	–	–
Ilex integerrima (Vell.) Reissk.	–	1.68	–	11.45	–	2.20	–	–	–	–	–	–
Inga maritima Benth.	–	–	–	–	–	4.81	–	–	–	–	–	–
Pilocarpus spicatus A. St.–Hil.	–	–	–	–	–	0.73	–	–	–	–	–	–
Schinus terebinthifolius Raddi	–	–	–	–	0.87	–	–	–	–	–	–	–
Trichilia sp.	–	–	–	–	0.98	–	–	–	–	–	–	–
Vernonia crotonoides Sch. Bip ex Baker	21.25	10.04	14.70	20.43	5.96	6.28	0.80	–	1.27	–	–	–
Waltheria aspera K. Schum.	10.92	1.25	2.27	–	2.21	–	–	–	–	1.17	–	–
Amaioua pilosa K. Schum.	–	0.96	7.57	1.14	–	–	–	–	–	–	–	–
Cupania racemosa (Vell.) Radlk.	–	3.89	–	–	–	–	–	–	–	–	–	–
Eugenia ovalifolia Cambess.	1.05	2.51	2.68	–	0.96	–	–	–	4.63	–	–	–
Eugenia sulcata Spreng. ex Mart.	2.38	2.53	–	2.93	1.11	1.82	–	–	–	–	1.03	1.26
Gaylussacia brasiliensis (Spreng.) Meisn.	–	1.58	2.19	3.77	–	1.44	–	–	–	–	–	–
Gomidesia martiana O. Berg	6.92	8.97	7.49	4.98	1.91	3.67	–	–	–	1.45	–	2.78
Marlieria rubiginosa (Cambess.) Legrand	–	5.82	–	2.39	–	1.05	–	–	–	–	–	–
Pera glabrata Baill.	3.45	2.03	–	–	–	0.58	0.85	–	1.82	–	–	–
Myrsine umbellata Mart.	3.70	–	1.72	–	–	–	–	–	–	–	–	–
Vernonia rufogrisea A. St.–Hil.	–	–	–	2.63	–	–	–	–	–	–	–	–
Group 1b – Typical of Cabiúnas												
Norantea brasiliensis Choisy	0.96	0.98	1.29	–	0.15	0.89	0.76	–	–	0.95	–	–
Cupania emarginata Cambess.	–	–	–	1.29	2.11	2.80	0.76	–	–	0.92	–	1.26
Eugenia nitida Cambess.	2.73	–	3.27	11.01	1.93	1.20	0.89	6.32	–	–	3.40	–
Eugenia olivacea O. Berg	–	2.18	–	–	–	1.44	–	–	–	–	0.91	–
Ouratea cuspidata (A. St.–Hil.) Engl.	1.15	2.05	0.79	5.11	2.49	0.73	2.01	0.74	–	1.01	1.87	1.09
Tapirira guianensis Aubl.	6.59	6.54	6.15	1.17	6.57	6.30	1.67	7.38	–	5.34	–	8.92
Ternstroemia brasiliensis Cambess.	13.51	20.03	3.93	15.10	0.89	4.26	1.36	3.24	6.23	2.68	–	5.47
Group 2 – No site preference												
Allophylus puberulus Radlk.	–	–	–	–	2.67	0.56	1.78	–	–	–	2.51	–
Andira legalis (Vell.) Toledo	–	–	–	–	–	1.28	–	1.37		–		–
Byrsonima sericea DC.	4.32	0.96	–	6.61	2.83	1.84	–	0.82	5.96	11.43	–	4.92
Clusia hilariana Schltdl.	31.50	17.06	23.43	25.22	46.78	32.62	34.80	30.84	29.75	30.72	16.40	17.75
Coccoloba arborescens (Vell.) How.	6.48	11.02	–	1.83	14.00	5.08	8.97	5.38	1.02	–	2.52	9.88
Erythroxylum subsessile (Mart.) O. E. Schulz	11.03	5.58	17.24	3.42	8.66	13.73	10.79	10.32	10.79	9.39	9.22	8.83
Ocotea notata (Nees) Mez	16.86	14.84	21.49	6.91	4.38	1.84	9.41	10.63	7.14	13.31	–	3.62
Ormosia arborea (Vell.) Harms	–	–	–	–	–	0.58	0.94	–	–	–	–	–
Protium icicariba (DC.) Marchand	11.15	15.17	29.40	21.48	31.68	34.10	36.18	36.33	28.08	7.28	2.77	17.58
Myrsine parvifolia A. DC.	7.47	4.37	9.90	8.02	10.35	10.03	5.17	10.23	2.68	4.42	10.92	19.22

continue

continuation

Species	SA2	SA3	SA5	SA6	SA1	SA4	SA8	SA9	SA11	SA12	SA7	SA10
Xylopia ochrantha Mart.	3.88	3.10	3.78	1.23	1.42	–	5.78	2.15	8.52	3.07	–	–
Calyptranthes brasiliensis Spreng.	–	–	3.58	1.35	0.96	0.50	1.07	–	7.33	–	–	4.46
Capparis flexuosa (L.) L.	–	–	1.68	2.84	1.89	3.59	1.76	0.66	–	4.16	16.99	1.22
Coccoloba confusa How.	–	–	1.24	1.14	3.47	3.42	2.41	–	4.88	–	3.25	4.04
Eugenia umbelliflora O. Berg	–	3.79	8.62	2.96	6.22	13.21	2.99	5.48	1.88	1.06	22.99	13.42
Guapira opposita (Vell.) Reitz	4.35	4.35	1.79	3.32	3.33	10.52	5.69	4.73	4.30	–	16.78	17.41
Myrcia lundiana Kiarsk.	6.16	21.81	9.93	11.16	6.17	2.14	34.11	19.36	32.69	36.92	10.28	12.87
Neomitranthes obscura (DC.) Legrand	1.02	2.83	5.45	1.20	3.26	1.08	4.24	8.66	9.76	8.45	7.70	5.97
Protium heptaphyllum (Aubl.) Marchand	–	–	–	2.12	0.81	0.47	–	–	–	–	–	6.06
Senna pendula (Willd.) H. S. Irwin & R. C. Barneby	–	–	–	0.95	1.87	–	1.52	–	–	–	0.77	1.01
Tocoyena bullata Mart.	5.61	–	3.37	6.88	0.82	3.47	5.80	8.24	6.41	10.51	12.75	4.08
Group 3 – Typical of Comprida												
Erythroxylum ovalifolium Peyr.	1.63	3.38	–	1.23	4.59	4.91	4.59	7.48	5.90	3.68	20.10	13.96
Heisteria perianthomega (Vell.) Sleumer	–	–	–	1.01	2.31	1.04	1.16	–	3.51	1.89	21.74	2.27
Kielmeyera membranácea Casar.	1.20	1.33	–	–	2.58	–	2.56	3.01	7.35	9.23	2.42	1.30
Manilkara subsericea (Mart.) Dubard	4.99	–	2.25	–	0.93	1.19	4.17	4.38	–	6.65	7.73	9.34
Maytenus obtusifolia Mart.	–	–	–	–	2.67	1.62	3.39	6.65	1.37	–	4.93	–
Abarema langsdorffii (Benth.) R. C. Barneby & J. W. Grimes	–	–	–	–	–	–	–	2.72	–	12.91	–	–
Agarista revoluta (Spreng.) . J. D. Hooker ex Nied	–	3.23	–	–	–	–	0.74	2.86	1.27	2.83	–	–
Andira fraxinifolia Benth.	–	–	–	–	–	–	–	–	1.53	–	–	–
Humiria balsamifera (Aubl.) A. St.–Hil.	–	–	–	–	–	–	0.76	–	4.28	1.17	–	–
Vitex polygama Cham.	–	–	–	–	–	–	–	–	–	6.59	–	–

Table 2. Results of nested ANOVA for lagoons, sample areas nested within lagoons, strips nested within sample areas, for each factor: diversity, species richness and plant cover percentage, and the percentage of variation explained by each sampling level: lagoon, sample area and strip (*MS* = mean square; *df* = degrees of freedom; *F* = ANOVA statistic; *P* = probabilidade).

	MS	*df*	*F*	*P*	% of variation
			Diversity (*H'*)		
Lagoon	0.0760	1	0.0518	0.824	7.5
Sample area	1.468	10	1.982	0.082	22.8
Strip	0.740	24	1.993	0.0042*	69.6
			Species Richness		
Lagoon	35.85	1	0.04	0.843	7.8
Sample area	17.83	10	2.01	0.0782	23.8
Strip	8.69	24	2.05	0.003 *	68.2
			% Plant Cover		
Lagoon	3505	1	1.34	0.273	16.5
Sample area	2614.5	10	3.416	0.006 *	20.0
Strip	765.19	24	1.951	0.005 *	63.3

* indicates significant difference.

percent plant cover varied significantly between the sample areas. Nevertheless, there was significant variation in plant cover, diversity and species richness between strips within each sample area. The percentage of variation explained at each sampling level was much higher for the strips, even in relation to plant cover (table 2), therefore variation was higher within than between sample areas.

Discussion

Wiens (1989) showed the limitations of extrapolations concerning processes that occur at one sampling scale to a different scale without a correction for the sampling effort. Although large-scale sampling is important, Condit (1995) also emphasized the importance of dividing sampling effort into smaller units. In this work, we attempted to analyze variation in vegetation structure parameters for an open “restinga” at a large spatial scale, while assessing also the small-scale variation at local level within each sample area. We found that characteristics found in one sample area often could not explain those of the entire community. This clearly indicates the need for a sampling design based on a broader spatial scale as well as on different-sized sampling scales for a better assessment of floristics and vegetation structure of open “restinga” vegetation.

The first question we addressed in this paper was if there is any variation in structural parameters, dominance and species composition between beach ridges in the open *Clusia* scrub. Although we found considerable variation between sampled areas as regards species composition and structural parameters, the dominant species were the same throughout: *Clusia hilariana* and *Protium icicariba*. For instance, our large-scale study had a sample size seven times greater than that of a small-scale study (using the line intercept method within a 1 ha area) conducted previously (see Araujo *et al*. 2004), which resulted in the addition of 17 intermediate and 13 rare species in the former as compared to the latter. However, the dominant plants were the same in both studies.

Moreover, in our study, the oligarchic structure (the concentration of IV in a few species plus many species of lesser importance) found is also common in tropical forest formations, especially in disturbed or early successional communities (Keel & Prance 1979, Campbell *et al*. 1986, Pascal & Pélissier 1996), and in other open vegetation types marginal to the Atlantic rain forest (Scarano 2002). Nevertheless, diversity (*H’* = 3.07) is expectedly lower than that of Atlantic (*e.g*, Sanchez *et al*. 1999) and Amazon rain forests (*e.g*, Campbell *et al*. 1992), but surprisingly high considering the extreme environmental conditions these plants are often subjected to (*e.g.,* Scarano *et al*. 2005). This diversity is, for instance, higher than that obtained for other open woody “restinga” communities in Southeast Brazil (2.82-2.93; Pereira *et al*. 2001) sampled by the same method but with the diversity index calculations based on the number of individuals. Diversity of the shrub layer *H’* = 3.45 based on the number of individuals was even higher (Araujo *et al.* 2004). These results are due to the many species with low plant cover that occurred in only a few sample areas. These species were obviously included due to the extensive sampling scale.

The second question we addressed was as to whether this variation was a function of the distance from beach ridge to the sea. Unexpectedly, the variation in percent plant cover between the 12 sample areas was not related to distance from the sea. Thus, oceanicity effects such as those caused by wind and salt exposure, frequently found in coastal plant communities (Crawford 1998), was not responsible for the variation in several other vegetation parameters. This variation was detected in a study by Oliveira-Galvão *et al*. (1990) aimed at classifying “restinga” vegetation in this region based on remote sensing. The open *Clusia* scrub showed two different patterns, and according to the authors, the differences are in the density and size of the thickets as well as herb cover between thickets. The vegetation at points 6, 7 and 10 in our study area falls into the pattern with fewer, smaller thickets and lower herb cover between the thickets. The most conspicuous band of this open *Clusia* scrub pattern begins at the outlet of Comprida Lagoon, and extends to the northeast along the coast, to well beyond the next large lagoon, suggesting that historical factors had considerable influence in the paleo-formation of this sector of the “restinga”. Curiously, the variation in intermediate and rare species composition between sample areas detected by TWINSPAN analysis was related to lagoon proximity. The six sample areas surrounding Cabiúnas lagoon showed a tendency for higher species richness than those surrounding Comprida lagoon (54 *vs* 45 spp.). Interestingly, the richness of aquatic plants (Melo & Suzuki 1998), invertebrates (Callisto *et al*. 1998) and fish (Reis *et al*. 1998) in the lagoons is in synchrony with the results found for the vegetation. Further studies on the dynamics of the triangle terrestrial-vegetation/water-table/lagoon are needed to explain this pattern.

Thirdly, we addressed the question as to whether there was variation in structural parameters, dominance and species composition within each beach ridge. Indeed, variation in diversity, species richness and plant cover percentage within some beach ridges was higher than the variation between sampling areas. Since ridges are separated from each other by swamp forests, this internal variation could be related to local topography (see Basnet 1992) or ridge breadth and proximity to forests and other vegetation types (*e.g.*, "Restinga de Ericaceae").

In addition to the answers provided to the central questions of this paper, our results also confirmed Myrtaceae as a key family in the "restinga" flora. It had the highest number of species and two of these, *Eugenia umbelliflora* and *Myrcia lundiana*, had high importance values. High abundance and number of species of Myrtaceae has also been recorded in other "restingas" (Araujo 2000). This pattern is also found in Atlantic forest (Barroso & Peron 1994) and "cerrados" (Proença & Gibbs 1994), which further emphasizes the fact that Myrtaceae is one of the most important families of the Neotropical flora (Landrum & Kawasaki 1997). On the other hand, woody leguminous species had low importance values at this "restinga" site. Leguminosae is also one of the most frequent families at Atlantic Forest sites (Leitão-Filho 1982), including "restinga" ecosystems (Pereira & Araujo 2000), but trees and shrubs of this family are uncommon in open "restingas".

In conclusion, the large sampling scale applied in this study to investigate structural and floristic variation in open "restinga" vegetation revealed that dominant species were common throughout sampling locations although local species richness and composition varied between sites. Within-site variation was often high, which was related to the proximity of neighboring forests. Structural and floristic variation, surprisingly, were not related to the distance from the sea, but to neighboring lagoons. This study emphasizes that the understanding of plant community structure in "restinga" vegetation would benefit from the application of survey methods feasible to be carried out at spatial scales broader than the all too common one-hectare plots.

Acknowledgements – This work was supported by CNPq/PELD (LTER) program and CT-Petro/FINEP. CAPES and CNPq provided research grants. We thank the staff of NUPEM – Macaé for logistic support.

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