Species richness and beta-diversity of aquatic macrophytes assemblages in three floodplain tropical lagoons: evaluating the effects of sampling size and depth gradients

by

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Abstract

Using aquatic macrophyte data gathered in three lagoons of the Paraná River floodplain we showed a strong effect of sample size on species richness. Incidence-based species richness estimators (Chao 2, jackknife 1, jackknife 2, incidence-based coverage estimator and bootstrap) were compared to evaluate their performance in estimating the species richness throughout transect sampling method. Our results suggest that the best estimate of the species richness was gave by jackknife 2 estimator. Nevertheless, the transect sampling design was considered inappropriate to estimate aquatic macrophytes species richness. Depth gradient was not a good predictor of the species richness and species turnover (beta diversity). The dynamics of these environments, subject to high water-level fluctuation prevents the formation and permanence of a clear floristic depth-related gradient.

Keywords: **species richness, beta diversity, plant zonation, aquatic macrophytes, floodplain, Paraná River**.

Resumo

Utilizando dados da assembléia de macrófitas aquáticas coletados em três lagoas da planície de inundação do Alto Rio Paraná, nós evidenciamos um forte efeito do tamanho da amostra sobre a estimativa da riqueza de espécies. Estimadores da riqueza de espécies baseados em dados de presença/ausência (Chao 2, jackknife 1, jackknife 2, "incidence-based coverage estimator" e bootstrap) foram comparados com o objetivo de avaliar suas performances em estimativas utilizando dados obtidos através de transecções. Nossos resultados sugerem que as melhores estimativas foram fornecidas pelo estimador jackknife 2. No entanto, o método das transecções foi considerado inadequado para estimar a riqueza de espécies de macrófitas. O gradiente de profundidade não foi um bom preditor da riqueza de espécies e das alterações na composição de espécies (diversidade beta). A dinâmica desses ambientes, sujeitos a grande flutuação dos níveis de água, restringem a formação de um claro gradiente florístico relacionado com a profundidade.

Introduction

Aquatic macrophyte assemblages are important elements within the spatial structuring and dynamics of shallow tropical floodplain lagoons, where they may occupy large areas (JUNK 1986; ESTEVES 1998). Most of the studies undertaken to date in such floodplains have concentrated on describing species assemblages and evaluating functional properties, such as primary production (JUNK & PIEDADE 1993) and decomposition (PAGIORO & THOMAZ 1999) of a few species. However, aquatic vegetation assemblages can also be successfully used to test general hypotheses about community ecology, in part due to the clear environmental gradients, like water depth (and its related variables), which fluctuates considerably in floodplain lagoons (NEIFF 1978, 1986; POTT et al. 1989, 1992). An important objective of plant ecology is to predict the spatial and temporal patterns in species richness, composition and abundance (NILSSON & KEDDY 1988; WEITHER & KEDDY 1995).

The number of species surveyed in a sample taken from a system is always lower then the true species richness (GASTON 1996). However, ecologists have rarely quantified the magnitude of this underestimation in diversity assessment studies. Thus, the sample size is a key aspect that should be evaluated to verify the reliability of observed species richness (HURLBERT 1971; PEET 1974; GASTON 1996). For aquatic macrophytes assemblages, transects along water depth gradients, a systematic sampling designs, are frequently used (POTT et al. 1989, 1992). Nevertheless, it is unknown their efficiency in species richness assessments.

On the other hand, it is likely that water depth gradients affect not only species richness (alpha diversity) but also species turnover (beta diversity). In these cases, transects are used successfully to evaluate patterns in plant zonation.

In this paper, we evaluated the effect of sample size and transect sampling design on the estimation of aquatic macrophyte species richness in three lagoons located in the Upper Paraná River floodplain, Brazil. We also tested the effect of water depth on species richness, beta diversity indices, and the occurrence and cover of species with different life forms.

Methods

The fieldwork was carried out in three floodplain lagoons of the Upper Paraná River. Seasonal water level variation in this stretch of the floodplain is about 2.5 meters. Clara and Garças are permanent lagoons, the latter being always connected to main channel of the Paraná River. Canal do Meio is a temporary lagoon (Fig. 1) that connects with Paraná River only during the floods. A detailed limnological characterization of Clara, Canal do Meio and Garças lagoons can be found in PAGIORO et al. (1997) and PAES DA SILVA & THOMAZ (1997). Table 1 summarizes the results of these studies and provides a brief general description of the lagoons studied.

The aquatic macrophytes were sampled during the low water period (August 1998), when it would be expected the higher diversity and dissimilarities between the lagoons (NEIFF 1978).

In each lagoon, intensive surveys were carried out to determine the total number of species ("true" species richness). During these surveys, the entire lagoon shoreline was prospected using a boat or walking in the littoral regions. Grapnels were used when necessary to sample submerged vegetation.

After intensive surveys, transects (two for Clara Lagoon and one for Canal do Meio and Garças lagoons) were used to register aquatic macrophyte presence. In addition, plant species found within the quadrats were visually scored on a DOMIN-KRAJINA cover scale (1 = <20; 2 = 21-40; 3 = 31-60; 4 = 61-80; 5 = 81-100% cover).

The number of quadrats within each transect was dependent on aquatic macrophyte stand size. Our sampling unit was a 0.5 x 0.5 m² wood quadrat allocated every 2 m along the transect. Depth was measured within each quadrat. The distances from the shoreline to the quadrats were registered using a tape labeled every 0.5 meters. These data (distance and depth) were used to estimate the slope (depth gradient) of each transect. Table 1 shows the minimum and maximum values of water depth and the number of quadrats in each lagoon.

Data analysis

To estimate the species richness of aquatic macrophytes in each lagoon, we used nonparametric extrapolating indices. These indices are based on incidence (presence/-absence) data (CHAZDON et al. 1998). For all estimates, quadrats were considered sampling units. These were done using the EstiMateS program (COLWELL, 1997).

The Chao 2 ($S_{Chao\,2}$) (CHAO 1987) is given by:

$$S_{Chao2} = S_{obs} + \frac{Q_1^2}{2Q_2}$$

where, S_{obs} is the total number of species observed in all quadrats in each lagoon, Q_1 is the number of species found in only one quadrat (uniques) and Q_2 is the number of species found in exactly two quadrats (duplicates).

The second estimator, the Incidence-based Coverage Estimator (S_{ice}), is based on species found in 10 or fewer quadrats (LEE & CHAO 1994; CHAZDON et al. 1998). S_{ice} is:

$$S_{ice} = S_{freq} + \frac{S_{inf}}{C_{ice}} + \frac{Q_1}{C_{ice}} \gamma_{ice}^2$$

where, S_{freq} is the number of frequent species (each found in more than 10 quadrats), S_{inf} is the number of infrequent species (each found in 10 or less quadrats); C_{ice} is given by

$$C_{ice} = 1 - \frac{Q_1}{N_{inf}}$$

where

$$N_{inf} = \sum_{j=1}^{10} j Q_j$$

The coefficient of variation of the Q_j's (γ_{ice}^2) is

where m_{inf} is the number of quadrats that have at least one infrequent species.

$$\gamma_{ice}^2 = \max \left\{ \frac{S_{inf} \, m_{inf} \sum_{j=1}^{10} j(j-1) Q_j}{C_{ice} \, m_{inf} - 1 \, (N_{inf})^2} - 1 \right\}$$

The third estimator was the first-order jackknife (S_{jack1}) estimator of species richness (BURNHAM & OVERTON 1978, 1979; HELTSHE & FORRESTER 1983) that is given by

$$S_{jach1} = S_{obs} + Q_1 \left(\frac{m-1}{m} \right)$$

where m is the total number of quadrats .

The second-order jackknife estimator (S_{jack2}) of species richness (incidence-based) (SMITH & VAN BELLE 1984) was calculated as

$$S_{jack2} = S_{obs} + \left[\frac{Q_1(2m-3)}{m} - \frac{Q_2(m-2)^2}{m(m-1)} \right]$$

Finally, the bootstrap estimator of species richness (S_{boot}; incidence-based) (SMITH & VAN BELLE 1984) was found using the following equation

$$S_{boot} = S_{obs} + \sum_{k=1}^{S_{obs}} (1 - P_k)^m$$

where p_k is the proportion of samples that contain k species.

The "true" species richness for each lagoon was considered to be all the species recorded in these lagoons during intensive surveys. The species richness found in these surveys was compared to the number of species found in transects using the five non-parametric estimators.

The effect of sample size (number of quadrats sampled) on observed and estimated species richness was evaluated by comparing species-accumulation curves.

Beta diversity indices were applied to quantify turnover in species composition. These indices measured how species composition changes within transects in each lagoon (WHITTAKER 1960; WILSON & SHMIDA 1984; HARRISON et al. 1992; BLACKBURN & GASTON 1996). The first one, β-1, allows the direct comparison among transects taking into account unequal number of quadrats. Formally, β-1 = $[(R/\alpha)-1]/[N-1]$ where R is the regional diversity (the number of species recorded in each transect), α and N are the mean alpha diversity and the number of quadrats

within a transect, respectively.

The second index, β-2, measures the amount by which regional diversity exceeds the maximum diversity attained by a quadrat. It is given by β-2 = $[(R/\alpha_{max})-1]/[N-1]$ where α_{max} is the maximum value of alpha diversity in the collection of N quadrats in each transect.

The relationship between beta diversity indices and littoral slope and the relationship between total species richness of a transect (square root transformed) and littoral slope were tested using the PEARSON correlation coefficient.

We modeled the pattern of occurrence (presence/absence data) of the most frequent species (> 25 %) using logistic regression (VAN DEN BERG et al. 1999). SPEARMAN correlations were used to assess the strength of the relationship between life forms (emergent, free-floating and submerged plants) cover and depth. The probability levels of these tests are approximate since observations may not be independent, given that our observations can be spatially autocorrelated.

Results

A total of 28 species were recorded in the three lagoons as a result of intensive surveys. The total species richness, for each lagoon, was 22 for Clara, 18 for Garças lagoon and 13 for Canal do Meio lagoon. From the total (28 species), 20 species were recorded in our transects. The most frequent species were *Salvinia auriculata* AUBLET (61% of the quadrats), *Eichhornia azurea* (SWARTZ) KUNTH (57 %), *Ricciocarpus* sp. (32 %), *Nymphaea amazonum* MART. (15 %) and *Cabomba* sp. (10 %). The other species occurred in less than 10 % of the quadrats sampled.

Even using the maximum sample size in each lagoon, all estimators underestimated the total ("true") number of species, i.e., the number of species recorded in the intensive surveys in each lagoon. For Clara lagoon, the estimated species richness varied from 16.1 (bootstrap) to 20.9 (jackknife 2); for Garças from 9.1 (jackknife 2) to 12.5 (bootstrap), and for Canal do Meio from 10.9 (bootstrap) to 12.8 (jackknife 2). Jackknife 2, ICE and Chao 2 estimators approached an asymptote faster than jackknife 1 and bootstrap estimators (Fig. 2).

There was a positive relationship between β-1 and β-2 (Fig. 3A). Species turnover did not differ among lagoons. Nevertheless, it is noticeable that some transects of Clara lagoon were highly heterogeneous as can be seen by the high β-1 and β-2 values (Fig. 3A).

Littoral slope was not correlated with either β diversity indices (for β-2, $r = 0.045$; $P = 0.855$ and for β-1, $r = 0.256$; $P = 0.290$; Fig. 3B) or total species richness ($r = -0.45$; $P = 0.052$; $n = 19$; Fig. 3C). However, the relationship between species richness and slope became significant ($r = -0.61$; $P = 0.007$) after excluding an outlier registered in Clara lagoon (Fig. 3C).

Beta diversity indices and species richness were also not correlated with the coefficient of variation of depth, a measure of transect heterogeneity ($r = 0.33$; $P = 0.162$ for β-1 and $r = 0.204$; $P = 0.402$ for β-2; $n = 19$).

As shown above, *S. auriculata* (free-floating), *E. azurea* (emergent) and *Ricciocarpus* sp. (free-floating) were the three most frequent species. Water depth was positively related to the occurrence and cover of *E. azurea* and *Ricciocarpus* sp. (Table 2). Using these models, 76 % of quadrats with *E. azurea* and 7 % with *Ricciocarpus* sp. were predicted correctly. The occurrence and cover of *N. amazonum* and emergent species

(*Cyperus* sp., *Polygonum punctatum* ELL., *P. ferrugineum* WEDD, *P. hidropiperoides* MICHX., *Althernantera phylloxiroides* (MART.) GRISEB., *Paspalum repens* BERG, *Myriophylum* sp., *Commelina* sp., *Ludwigia* sp. and Poaceae) were negatively correlated with depth. Nevertheless, the small number of quadrats sampled at higher depths and the decrease in the frequency of *N. amazonum* and *Ricciocarpus* sp prevents good predictions of their occurrence at such depths. The occurrence and cover of *S. auriculata* and other free-floating species were not correlated with depth according to both SPEARMAN correlation and logistic regression (Tab.1).

Discussion

Estimating species richness

The estimators and species-accumulation curves used in our study are important tools to show the sufficiency of the sampling method and sample size. Even a large number of quadrats (91 in Clara lagoon) was insufficient to estimate the "true" number of species. Thus, we strongly advise that the assessment of aquatic macrophyte species richness of floodplain lagoons should not be restricted to transects, a systematic sample method. Other studies have also pointed out that systematic sampling designs are not suitable to furnish independent data points, but they can be adequate in detecting spatial patterns (LEGENDRE & FORTIN 1989; FORTIN et al. 1989). Transects were not adequate to estimate the species richness in four lagoons located in the Pantanal, a Paraguay River floodplain (POTT et al. 1989, 1992). In all cases, the number of species recorded in transects was lower than the "true" richness determined by intensive surveys. We suggest that aquatic macrophyte richness in lagoons is best estimated using intensive surveys which take into account some other measure of the sampling effort (e. g., time spent, perimeter of shoreline investigated or total area surveyed). This procedure is necessary for comparison purposes since species richness estimates are dependent on sampling effort (see Fig. 2).

According to CHAZDON et al. (1998) the independence of the sample size beyond some minimum threshold is one feature that can be used to evaluate the performance of species richness estimators. Our results show that S_{ice} and S_{Chao2} approached an asymptotic species number first. Using this criterion, it seems that these estimators are appropriate for estimating the richness of aquatic macrophyte assemblages.

The best performance by the species richness estimations was by bootstrap and jackknife 2, since they approached more the real number of species. Nevertheless, these estimators had this performance only considering the maximum sample size. Thus we advise that studies of aquatic macrophyte species richness should be based on all adequate estimators.

Plant zonation patterns

In this study, our expectations were the following: -(1) species richness should be related to water depth and slope. In deeper and steeply sloped littorals aquatic macrophyte growth can be light-limited. In addition, steeply sloped littorals are areas of erosion and transport, subject to high sediment instability. Thus just few species could tolerate such environmental conditions. -(2) Beta diversity (species turnover) should increase with the environmental dissimilarity, as measured by differences in depths, among quadrats. -(3) Finally, frequency of species with particular life forms (mainly emergent and submerged) should be predicated by depth.

Plant zonation patterns that occur on lakeshores (SPENCE 1982; SCULTHORPE 1985; POTT et al. 1989, 1992; NILSSON & WILSON 1991 and references therein) and mountain sites (NILSSON & WILSON 1991) have been frequently studied. The detection and explanation of such patterns are a common goal in plant ecology studies. In aquatic ecosystems, most researches demonstrate a significant effect of some environmental factor (depth, substrate slope, organic matter and nutrients) on some community structure property, like species richness and biomass (DUARTE & KALFF 1986; DUARTE et al. 1986; BAILEY 1988; NILSSON & WILSON 1991). So, it seems that these depth-related environmental gradients play a predominant role in aquatic macrophyte ecology.

Our results, however, contradict the generality of these effects. Among the community properties analyzed (species richness, beta diversity, species composition, and occurrence/cover of dominant species/life forms), only the occurrence of three species (the free-floating *Ricciocarpus* sp., the emergent *E. azurea* and the floating-leaved *Nymphaea amazonum*) and of emergent species was satisfactorily predicted by water depth. The absence of clear relationships between community properties and depth-related environmental gradients cannot be inferred from the results presented, but the data suggest some probable explanations. Littoral slope values observed for the floodplain lagoons sampled did not reach a threshold value. In other words, only after some critical value this variable becomes an important predictor of aquatic macrophyte community properties (HÅKANSON 1977; DUARTE & KALFF 1986). CANFIELD & DUARTE (1988) suggest that the influence of littoral slope on the abundance of aquatic macrophytes needs additional research before improved empirical models can be developed for lakes located in limited geographical regions. Although this statement was made with regard to abundance, we believe that it is valid for other community properties like the ones studied here.

Also, both the shallowness of floodplain lagoons and the flood pulse (JUNK et al. 1989) are likely controlling factors of aquatic plant community in these ecosystems. The "assembly rule" (in the sense of DIAMOND 1975) that we suggest is as follows. First, floods prevent the formation of a stable plant zonation (ZUTSHI & GOPAL 1990) and bring seeds and other vegetative propagules from the species pool, which can colonize most of the areas in the lagoons. Depth will be an important controlling factor only after a maximum and a minimum threshold (SPENCE 1982). Second, the occurrence of species in a determined place along the depth gradient will be a function of which ones arrive first ("pre-emption of space hypothesis"; BEGON et al. 1996). The assembly model that we suggest can be tested using experiments. As an example, during low water period, species occurrence, species richness or any other community property should be measured along depth gradients; after this, all possible vegetation should be removed. After floods, the same variables should be continuously obtained. If our model holds, there will be no relationship (i) between the depth-related variables and community properties (before and after the floods) and (ii) mainly, there will be no relationship between the species orders of occurrence along the depth gradient, obtained before and after the flood. The next step of our research program on aquatic macrophyte ecology will be to test the validity of this model.

The occurrence of the groups of emergents, along depth gradients, in lentic water bodies of the Upper Paraná River floodplain, is highly predictable. Nevertheless, the precise identity of the species belonging to this group, except in the case of *E. azurea*,

can not be predicted by using depth as the unique predictor variable.

In short, we suggest that the spatial distribution of aquatic macrophytes in floodplain lagoons is strongly controlled by stochastic processes mainly related to dispersion and colonization.

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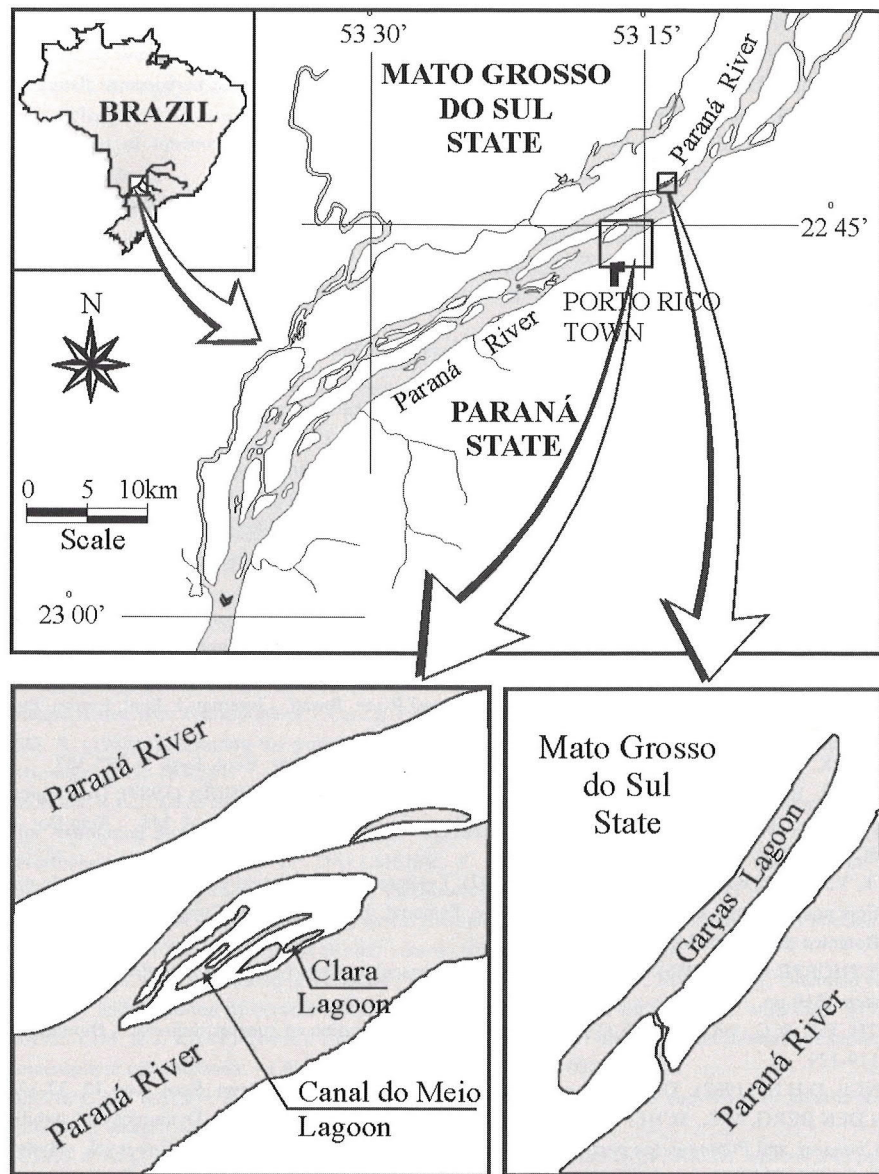
Fig. 1:
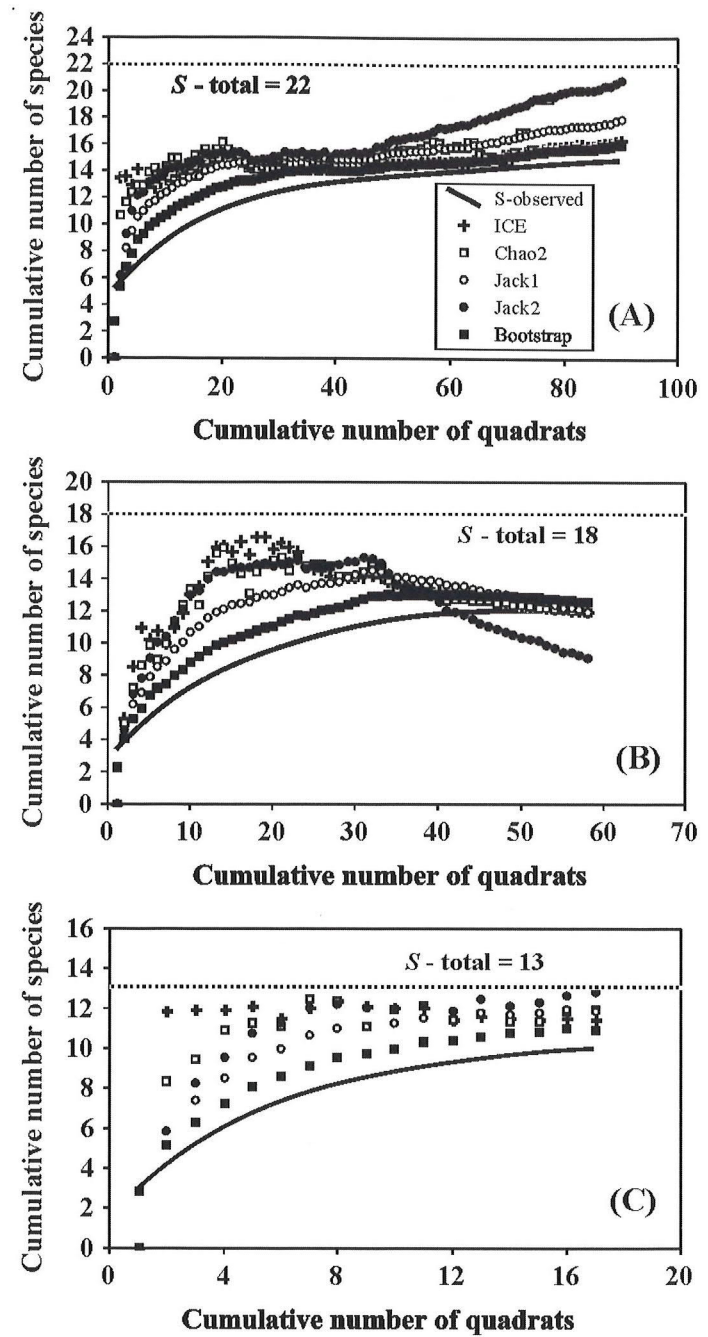Location of the floodplain lagoons where the samples were taken.

Fig. 2:
Cumulative number of species of aquatic macrophytes observed and using incidence based estimators at Clara (A), Garças (B) and Canal do Meio (C) lagoons. S-total indicates the number of species registered in intensive surveys in each lagoon (approximately the "true" number of species).
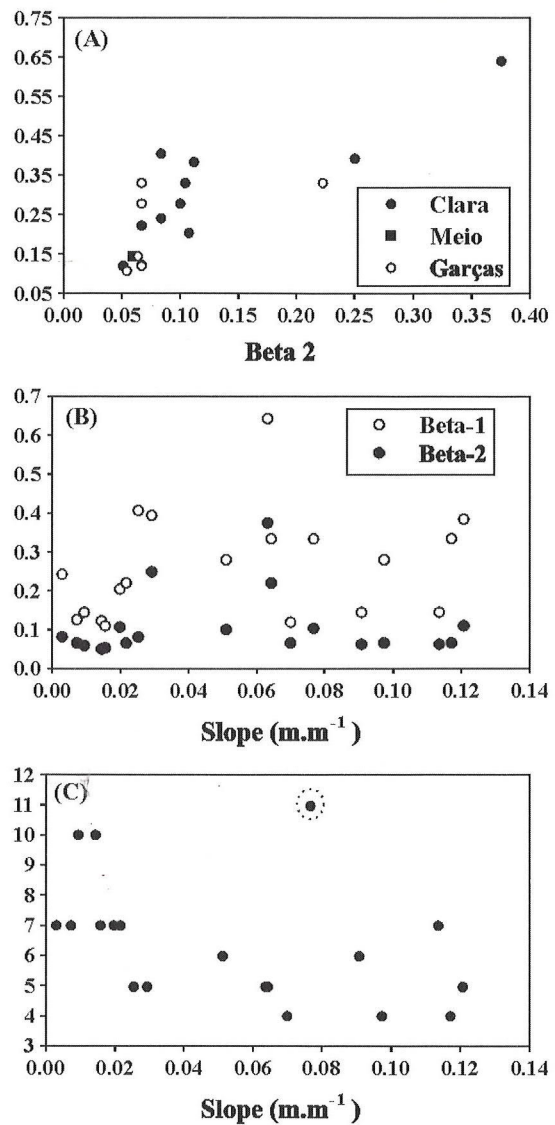
Fig. 3:
Relationships between beta-1 and beta-2 indices (A), between the slope and beta diversity indices (B) and between the slope and the aquatic macrophytes species richness (C). The observation circulated in (C) was considered an outlier.

Table 1: Number of quadrats, sampling depths and basic limnological characteristics in the lagoons. Data from PAGIORO et al. (1997), PAES DA SILVA & THOMAZ (1997) and R. R A. Rocha (unpubl. data).

	Clara	Canal do Meio	Garças
Number of quadrats	91	59	18
Depth amplitude (cm)	5 - 155	5 - 120	5 - 260
pH	5.4 - 7.0	5.1 - 6.5	6.26 - 7.02
Alkalinity (mEq/l)	0.35 – 0.7	0.05 – 0.85	0.23 - 0.62
Secchi disk (m)	0.10 - 1.2	0.05 - 1.6	0.50 - 0.80
Electrical conductivity (μS/cm)	50 - 93	23 - 134	46 - 62.7

Table 2: Statistical results evaluating the relationship between species/life forms cover/occurrence and depth. For cover data SPEARMAN correlation was used and for occurrence data logistic regression. BONFERRONI criterion was used to correct for multiple tests of significance. Thus. statistic (R or t) was considered significant if $P < 0.004$.

Species/life forms	Spearman's results		logistic regression	
	r	P	t	P
E. azurea	0.56	0.0000	4.78	0.0000
Ricciocarpus sp.	0.26	0.0009	2.65	0.0089
S. auriculata	-0.10	0.2100	-1.34	0.1832
N. amazonum	-0.28	0.0004	-3.19	0.0017
Emergent	-0.54	0.0000	-5.67	0.0000
Free-floating	0.00	0.9843	-1.57	0.1193
Submerged	-0.02	0.7807	-0.59	0.5555