UNIVERSIDADE FEDERALDO ESTADO DO RIO DE JANEIRO

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Viviane Bielinski Skinner

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Viviane Bielinski Skinner

Dissertação apresentada ao curso de Pós-Graduação em Biodiversidade Neotropical da Universidade Federal do Estado do Rio de Janeiro como requisito parcial para a obtenção do Grau de Mestre em Ciências Biológicas

Orientador: Prof. Dr. Ricardo Silva Cardoso

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DEDICATÓRIA

Dedico esta dissertação ao meu pai,
Marcelo Skinner (*In memoriam*),
com todo meu amor e gratidão.

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APRESENTAÇÃO

Esta dissertação apresentada como requisito para obtenção do grau de Mestre em Ciências Biológicas é um manuscrito e, portanto, encontra-se no formato do periódico Diversity and Distribution à que será submetido.

A distribuição de abundância das espécies (SAD) é um dos descritores de comunidades mais simples e informativos (McGill *et al*., 2007) e por isso vem tendo destaque no estudo da ecologia. Resumidamente, a SAD é uma representação de um padrão amplamente conhecido em ecologia, na qual as comunidades possuem poucas espécies abundantes e muitas espécies raras. A estruturação destas comunidades deve-se a repartição dos recursos ambientais, tais como luz, temperatura, umidade e nutrientes, que variam como um mosaico determinado por variações espaciais e temporais (Whittaker, 1965; Crawley, 1986; Ricklefs, 1990). Alguns modelos de distribuição foram introduzidos a fim explicar os mecanismos da curva das SADs e os padrões que determinam a estrutura e a organização das comunidades. Os modelos mais conhecidos e utilizados são o geométrico (Montomurra, 1932 *apud* Whittaker, 1965), o logseries (Fisher *et al*., 1943), lognormal (Preston, 1948) e o broken stick (MacArthur, 1957) (Figura 1).

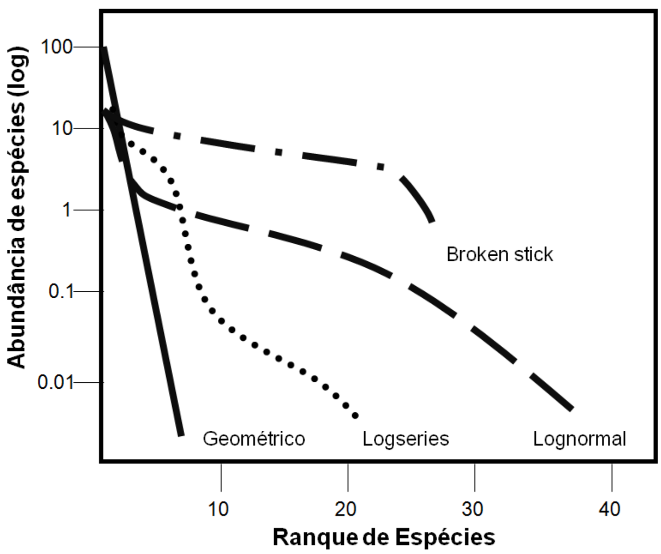

Figura 1: Representação dos modelos tradicionais de distribuição da abundância das espécies.

O modelo geométrico possui baixa equitabilidade, e uma alta abundância para apenas uma espécie, diminuído abrupta e constantemente nas demais. Em contraste o modelo broken stick prediz alta equitabilidade, dada a repartição aleatória do nicho entre as espécies. Os modelos logseries e lognormal compreendem equitabilidades intermediárias, quando comparados aos dois modelos citados anteriormente. A principal diferença entre os modelos logseries e o lognormal reside na proporção de espécies raras em cada um – sendo esta proporção alta no modelo logseries e baixa no modelo lognormal.

Ainda há muito a ser estudado sobre os padrões, mecanismos e modelos da SAD, apesar da grande quantidade de trabalhos utilizando-a com diversos enfoques. São exemplos destes enfoques a comparação dos gradientes temporal (Magurran, 2007), e espacial (Whittaker, 1965; Borda-de-Água *et al*., 2012), a análise das comunidades através dos táxons e ecossistemas (White *et al*., 2012) ou mesmo trabalhos que buscam entender o que regula a forma da curva das SADs (McGill, 2003; Magurran & Henderson, 2003). As SADs foram utilizadas em estudos nos ambientes terrestres, dulciaquícolas e marinhos (McGill *et al*., 2007). Entretanto, para praias arenosas, Dexter (1992) foi a única a associar os gráficos de abundância propostos por Whittaker (1965) com a riqueza e a diversidade da macrofauna de praias arenosas dando um enfoque macroecológico.

Neste sentido, pretende-se associar as SADs da macrofauna aos modelos de distribuição tradicionais (geométrico, lognomal, broken stick e logseries). Bem como, verificar a existência de padrões nos descritores da comunidade e nos parâmetros morfodinâmicos das praias arenosas em relação aos modelos ajustados.

Foram compilados dados de 86 praias arenosas da América Neotropical, totalizando 102 curvas de SAD. Das 86 praias, 14 foram amostradas mais de uma vez. A fim de relacionar os modelos com descritores ecológicos e parâmetros morfodinâmicos, escolhemos as seguintes variáveis: riqueza (H'); diversidade de Shannon (S); equitabilidade de Pielou (J'); abundancia total; α da logseries; declividade da praia (1/declive); tamanho do grão (mm) e Índice de Praias (BI). Todos os modelos foram testados para cada SAD, seus ajustes avaliados por máxima verossimilhança, e o melhor foi escolhido pelo Critério de Informação de Akaike (AIC). Foi realizada uma ANOVA para testar diferenças entre as variáveis e os modelos de distribuição. Para comparar a freqüência dos estados morfodinâmicos de praias entre os modelos foi utilizado o teste Qui- quadrado.

O modelo logseries apresentou os melhores ajustes para a macrofauana de praias arenosas, seguido pelos modelos: broken stick, lognomal e geométrico. Os descritores ecológicos e parâmetros morfodinâmicos apresentaram diferenças significativas entres os três modelos predominantes – logseries, broken stick e lognormal. Consequentemente foi possível averiguar que as SADs da macrofauna apresentaram diferentes modelos ao longo do gradiente morfodinâmico de praias arenosas.

ABSTRACT

Aim: To fit geometric, lognormal, broken stick and logseries models to the species abundance distributions (SADs) of sandy beaches macrofauna of South America, and compare the adjusts in order to identify patterns on sandy beach community and morphodynamic parameters for each model.

Location: Our own field data and published ones were compiled totaling 86 sandy beaches on Neotropical region, being 72 beaches from the Brazilian coast; eight from Uruguay; two from Argentina; two from Chile and two from Panama.

Methods: Species abundance distributions were fitted to the geometric, lognormal, broken stick and logseries models and evaluated by maximum-likelihood and the best model was selected by the lowest values of Akaike Information Criterion (AIC). ANOVA was used to test significant differences between the models to every ecological descriptors/environmental parameters (richness; Shannon's diversity; Pielou's evenness; global abundance; logseries α; beach face slope; grain size; Beach Index (BI)).

Results: Logseries provided better fit to most of the beach macrofaunal SADs, followed by broken-stick, lognormal and geometric series. Ecological descriptors and morphodynamic parameters showed significant difference among the three predominant models - logseries, broken stick and lognormal.

Main conclusions: The macrofaunal SADs had distinct distribution models across the sandy beaches morphodynamic gradient. Logseries model was predominant among the studied sandy beaches. Dissipative beaches were characterized by a lognormal or a logseries distribution, depending on the proportions of rare species. Intermediate sandy beaches showed a logseries distribution pattern, while reflective sandy beaches mainly had a broken stick distribution.

Key words: Species abundance distribution; sandy beaches; morphodynamic states; logseries; lognormal; broken stick; macrofauna.

RESUMO

Objetivo: Ajustar os modelos: geométrico, lognormal, broken stick e logseries às distribuições de abundância das espécies (SADs) da macrofauna das praias da região Neotropical. Comparar os ajustes e selecionar o melhor, além de identificar padrões nos descritores de comunidade e nos parâmetros morfodinâmicos em cada modelo.

Localização: Foi realizada uma compilação que inclui dados próprios e publicados de 86 praias da região Neotrpical, sendo 72 na costa brasileira, oito no Uruguai; duas na Argentina; duas no Chile e duas no Panamá.

Metodologia: As SADs foram ajustadas aos modelos: geométrico, lognomal, broken stick e logseries, e avaliados por máxima verossimilhança. O melhor ajuste foi selecionado pelo Critério de Informação de Akaike (AIC). Uma ANOVA foi realizada para testar diferenças entre os modelos e os descritores ecológicos/parâmetros morfodinâmicos (riqueza; diversidade de Shannon; equitabilidade de Pielou; abundancia total; α da logseries; declividade da praia; tamanho do grão e Índice de Praias (BI).

Resultados: O modelo logseries apresentou os melhores ajustes, seguido pelos modelos broken stick, lognomal e geométrico. Os descritores ecológicos e parâmetros morfodinâmicos apresentaram diferenças significativas entres os três modelos predominantes – logseries, broken stick e lognormal.

Principais conclusões: As SADs da macrofauna apresentaram diferentes modelos através do gradiente morfodinâmico de praias arenosas. O modelo logseries foi predominante entre as praias estudadas. Praias dissipativas foram caracterizadas pelos modelos de distribuições logseries e lognormal, dependendo da proporção de espécies raras. Praias intermediárias mostraram uma distribuição preferencialmente logseries, enquanto praias reflectivas apresentaram um padrão de distribuição broken stick.

Palavras-chave: Distribuição da abundancia das espécies; praias arenosas; estados morfodinâmicos; logseries; lognormal; broken stick; macrofauna.

INTRODUCTION

Species abundance distribution (SAD) has been playing an important role in ecology, as it details the abundance of each species within an assemblage (McGill *et al*., 2007). In short, SAD is the representation of a very well known community pattern - few species are abundant and many are rare - which are structured by the environmental resource partitioning, such as light, temperature, moisture and nourishing that change as a mosaic set by spatial and temporal variations (Whittaker, 1965; Crawley, 1986; Ricklefs, 1990). Some models were introduced to explain the mechanism of SADs hollow-curve, and the patterns assigning the structure and organization of communities. Among these models the most widely known and used are the geometric (Montomurra, 1932 *apud* Whittaker, 1965), logseries (Fisher *et al*., 1943), lognormal (Preston, 1948) and the broken stick model (MacArthur, 1957).

Accordingly these models have biological predictions behind the math, and yet a direct link with evenness (Tokeshi, 1993). The geometric model predicts mighty unequal abundances in contrast with broken stick, which predicts extremely even abundances. While lognormal and logseries models represent intermediate evenness in the communities - with distinctions about the proportions of very rare species (high in logseries, low in lognormal) (McGill *et al*., 2007). Higher richness will consequently be found on logseries and lognormal, when compared with the two extremes, – geometric and broken stick – that may not afford extremely high richness (Whittaker, 1965).

There is still much to investigate about SADs patterns and its mechanisms. Although numerous papers have been using SADs in many approaches, such as to compare gradients, as spatial (Whittaker, 1965; Borda-de-Água *et al*., 2012) and temporal gradient (Magurran, 2007), and also to analyze communities across taxa and ecosystems (White *et al*., 2012) or to understand what rule the shape of SADs, focusing on the rarity of species (McGill, 2003; Magurran & Henderson, 2003). SADs in marine environment have been largely studied by ecologists in the 70’s (McGill *et al*., 2007), who found out that SADs have a great potential as environmental indicators, which may evidence the state of health of the ecosystem (Gray *et al*., 1979), leading SADs studies towards conservation. Dexter (1992) was the unique to associate the abundance plots proposed by Whittaker (1965) with the macrofauna of sandy beaches richness and diversity with a macroecological approach.

Macrofaunal communities from exposed sandy beaches have consistent patterns towards physical factors. Morphodynamics parameters not only describe each sandy beach type, but also affect ecological descriptors as richness and diversity, namely biodiversity (Brown & McLachlan, 2006; Ortega *et al*., 2011). Many hypotheses - The *swash exclusion hypothesis* (McLachlan *et al*., 1993; the *habitat harshness hypothesis* (Defeo *et al*., 2001, 2003); the s*and and swash exclusion hypothesis* (Nel, 2001; McLachlan, 2001) - have been postulated to explain the structure of the macrofauna by morphodynamic patterns. These hypotheses assert that sandy beaches are physically controlled environments that could be harsh, or more benign environments to the macrofaunal populations. Harsh environments are the ones with great wave action, steep slopes and coarse grain size and which consequently force macrofauna to converge more energy toward pulling trough (Defeo *et al.*, 2001, 2003) - classified as reflective beaches. On the other hand sandy beaches with gentle slopes, fine grain size and dissipative wave energy may allow species to merge more energy for reproduction hence assisting the establishment of populations. Therefore the main paradigm in sandy beaches shore states that greater species richness, abundances and diversities should be found in dissipative beaches, decreasing towards reflective beaches.

Altogether the physical factors that influence the descriptors of sandy beach macrofauna are fundamental to understand the biological predictions from the models. Consequently we hypothesize that for reflective beaches a geometric or broken stick distribution will be found, whereas for intermediate and dissipative beaches we predict a logseries or lognormal distribution, depending on the proportions of rare species (McGill *et al.*, 2007; Magurran & McGill, 2011). Hence we have a threefold aim, which is (1) to fit geometric, lognormal, broken stick and logseries models to SADs of sandy beach macrofauna of South American beaches, and (2) compare the fits in order (3) to identify patterns on sandy beach community and environmental parameters for each model.

METHODS

We compiled data from 86 sandy beaches on Neotropical America, being 44 (1-44) from our own field data across Rio de Janeiro coast. The detailed description of the biological and environmental sampling of 30 (1-30) of these sandy beaches is found on Cardoso *et al.*

(2012), as well as the remaining 14 (31-44), which have their sampling methodology similar to Veloso *et al*. (2003). Besides, we collected data from published papers, which include 34 Brazilian (Borzone *et al*., 1996; Calliari *et al*., 1996; Souza & Gianuca, 1996; Veloso & Cardoso, 2001; Fernandes & Soares-Gomes, 2006; Lepka, 2008; Cardoso *et al*., 2012; Santos *et al*., 2014; Campos *et al*., 2008)(45-72), eight Uruguayan (Defeo *et al*., 1992; Barboza *et al*., 2012) (73-80), two Argentinean (Mendez *et al*., 2009)(81-82), two Chilean (Sánchez & Mena, 1982; Clarke & Peña, 1988) (83-84) and two Panamanian (Dexter, 1979) (85-86) sandy beaches. Almost 80% of the data was sampled during summer; 12 sandy beaches were sampled during summer and winter, eight during spring; and two other beaches were sampled more than once in the same season. A total of 102 species abundance distributions (SADs) were set regarding the abundance of macrofaunal organisms (Table 1). The only insect that was considered part of the macrofauna was the Coleopteran *Phaleria testacea*.

In order to relate the fitted model to community descriptors/morphodynamic parameters, we gathered the following variables: richness (H'); Shannon's diversity (S); Pielou's evenness (J'); global abundance; Logseries α; beach face slope (1/slope); grain size (mm); Beach Index (BI). Diversity and evenness were calculated using the package 'vegan' (Oksanen *et al*., 2013) in R. The beach index (BI) (McLachlan & Dorvlo 2005) was calculated for each beach, when possible, as a measure of its morphodynamic state, using the formula, BI = (mean grain size · tide) ⁄ slope). Logseries α was extracted from the results of model fitting, and was used as a biological community descriptor, being an informative and robust measure of diversity, as it represents the number of extremely rare species on the assemblage (Magurran, 2004; Magurran & McGill, 2011), even when the model fitted was not the logseries.

All SADs were fitted to the logseries, lognormal, broken stick and geometric models using the function *fitsad* in R. Adjusts were evaluated by maximum-likelihood and the best model was selected by the lowest values of Akaike Information Criterion (AIC). Every step of fitting the models and comparing adjusts were made using 'sads' R package (Prado & Miranda, 2013).

Data was tested for normality using Shapiro-Wilk test (package ´stats´ in R) and for homoscedasticity through Cochran Test. When needed data was log-transformed to fit both assumptions.

One-way ANOVA was used to test significant differences between all variables (richness; Shannon's diversity; Pielou's evenness; global abundance; Logseries α; beach face slope; grain size; and Beach Index) and the selected model for each SAD. Tukey's honest significant difference (HSD) was used *a posteriori* to assess significant differences among SADs models. ANOVA and Tukey HSD were performed using the package 'vegan' (Oksanen *et al.*, 2013) in R.

The distribution of beach morphodynamic states among the models was compared by Chi-square test (χ^2).

RESULTS

The 86 sandy beaches surveys recorded a total of 102 SADs, which showed substantial variations among ecological descriptors and morphodynamic parameters. In relation to sandy beach physical parameters, sand grain size varied between 0.13 and 1.16 mm (-0.21 to 2.94 phi) and beach face slopes between 1/4.78 and 1/66.66. The full range of morphodynamic states from reflective (BI<1.5) to dissipative (Bi>2) was registered, with the lowest and highest values of beach index being 0.98 and 2.55, respectively. Thus, 23 sandy beaches were classified as dissipative, 41 as intermediate and 27 as reflective, however 11 sandy beaches could not be classified, because there were missing values for the calculation. Concerning community descriptors, richness and global abundance showed the larger variations, ranging from two to 42 species and five to 13,099 individuals, respectively. Metrics of Shannon diversity, evenness and logseries α naturally had smaller variation. Diversity varied from 0.49 to 3.44, while evenness from 0.13 to 0.99 and logseries α from 0.54 to 6.17.

There was a significant difference on the predominant morphodynamic state for each SAD model (χ^2= 28.55; p=0.00) (Figure 1), thus establishing patterns for SADs on the sandy beach ecology.

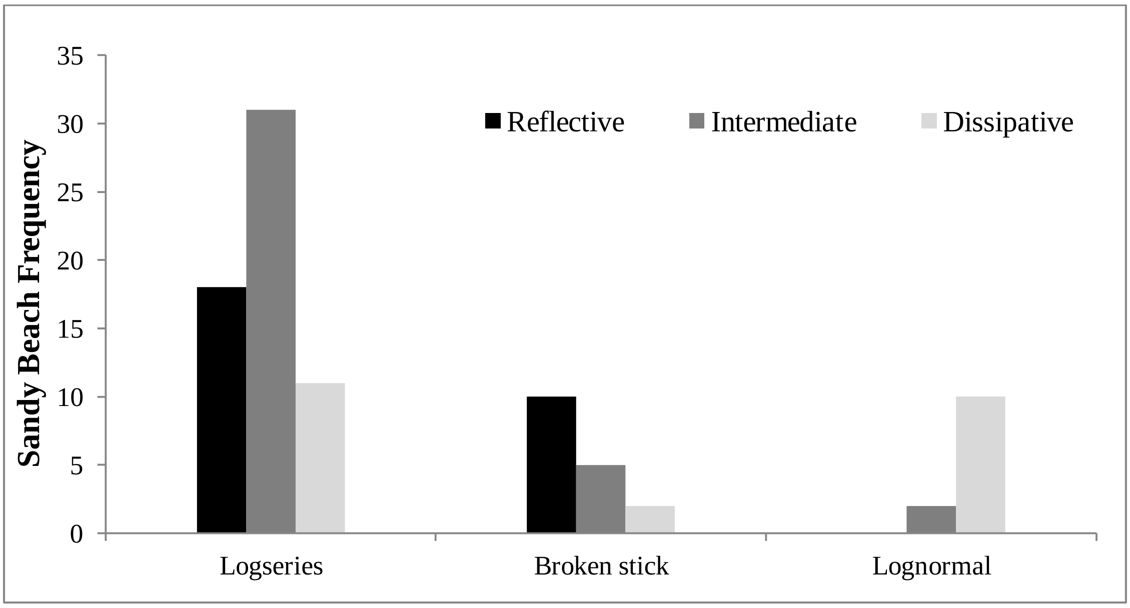

Figure 1: Distribution frequency of the morphodynamic states of sandy beaches among the distribution models

Logseries provided better fit to most of the beach macrofauna, followed by broken stick, lognormal and geometric series, according to Akaike Information Criterion (AIC) test (Table1). This indicates that most of the sandy beaches present an intermediate level of evenness with an elevated proportion of rare species, represented by logseries adjust, while some sandy beaches macrofaunal communities had an extremely even distribution of species, verified by the adjust of broken stick model. Lognormal model assumptions show that a small group of beaches report the same intermediate level of evenness seen for logseries fitted SADs, however differing on the lower proportion of rare species. Geometric model only provided better fit for two sandy beaches, when the most abundant species are excluded the shape of SAD accomplish a linear tendency. Besides, they have an intermediate morphodynamic state, and, when compared to our database it shows high richness and diversity, low abundance and an unexpectedly elevated evenness.

In spite of containing data from sandy beaches that were sampled more than once, among these, only 4 of 14 showed temporal variation in the model. From these 4 beaches 3 were sampled during summer and winter, showing seasonal differences in the model. Another beach, which was sampled monthly in the same season showed difference in one of the months.

Table 1: Goodness of fit, model selection and logseries α for each SAD. The best model according to Akaike´s Information Criterion (AIC) is highlighted in bold for each SAD. (*) sandy beaches sampled during winter; (●) sandy beaches sampled more than once in the same season; (inf) infinite values.

		AIC				
	Beach Name	**logseries**	**broken stick**	**lognormal**	**geometric**	**logseries α**
1	Antigos	32.5	**29.0**	33.3	30.7	1.60
2	Aventureiro	**63.8**	78.7	67.9	77.7	0.82
	Aventureiro*	77.8	**72.6**	76.2	74.0	1.98
3	Bananal	**77.6**	89.6	83.9	89.3	2.44
	Bananal*	36.6	**36.0**	39.7	37.1	1.88
4	Barra de Guaratiba	50.2	**43.3**	48.9	45.9	0.63
5	Brava	**30.6**	34.8	34.1	33.9	1.41
6	Camiranga	38.9	**35.4**	39.3	37.1	1.26
	Camiranga*	65.2	**64.0**	66.8	64.8	2.88
7	Caxadaço	**26.0**	28.3	29.2	27.9	1.80
8	Copacabana	34.7	**29.2**	32.4	31.3	1.55
9	Dentro da Urca	**64.0**	64.8	67.0	66.1	1.33
10	Dois Rios	**73.1**	82.1	77.7	82.0	2.19
	Dois Rios*	**106.5**	131.3	114.1	129.3	3.54
11	Feiticeira	**41.0**	50.8	44.3	47.4	0.96
	Feiticeira*	**56.9**	61.6	60.1	60.8	1.93
12	Ferradura	**83.0**	98.6	87.0	96.7	1.84
13	Fora da Urca	**57.3**	59.1	60.1	60.4	1.07
14	Forno	**90.0**	113.9	96.0	110.2	2.32
15	Forte do Imbuí	70.4	**69.4**	73.7	71.0	1.62
16	Freguesia de Santana	**83.9**	95.2	88.0	93.8	1.89
	Freguesia de Santana*	**69.3**	83.8	73.3	80.4	1.80
17	Funda	**72.3**	92.8	77.4	89.8	0.96
18	Ipanema	22.9	**18.7**	20.2	20.6	1.65
19	Itacoatiara	**35.8**	37.2	38.5	38.2	0.43
20	JoãoFernandes	8.8	**8.2**	10.8	8.7	3.00
21	Lopes Mendes	**97.8**	98.6	101.4	99.1	3.07
	Lopes Mendes*	**103.5**	119.9	111.9	119.0	3.36
22	Macumba	41.6	**39.8**	42.3	40.8	1.13
23	Meio	**26.5**	26.8	29.5	28.2	0.60
24	Palmas	**42.0**	47.1	47.1	47.5	1.93
	Palmas*	**27.6**	29.5	31.3	29.7	1.66
25	Perigoso	**62.7**	75.3	64.3	70.0	0.91
26	Pouso	**74.6**	81.8	78.9	81.8	1.77
	Pouso*	**72.9**	86.0	76.9	83.0	2.17
27	Prainha	47.7	**45.6**	48.7	47.1	1.41
28	Provetá	57.0	60.5	**56.8**	58.8	1.51
	Provetá*	**37.1**	44.7	42.3	44.5	1.51

29	São Conrado	**45.2**	45.9	47.0	45.9	1.45
30	Sono	**33.8**	42.0	37.0	39.3	0.74
31	Barra da Tijuca	**88.4**	128.1	93.9	115.9	2.59
32	Carapebus	60.1	**55.4**	60.0	57.5	1.12
33	Foguete	**102.1**	127.5	110.6	125.8	2.76
34	Formosa	**99.4**	111.0	106.1	111.6	2.70
35	Grumari	**44.6**	50.4	47.8	49.2	0.92
36	Itaipu	**53.6**	59.6	59.3	60.5	1.94
37	Itaipuaçu	25.8	**25.5**	28.9	27.1	0.63
38	Jaconé	**64.7**	82.3	66.1	74.3	0.86
39	Marambaia	**70.5**	90.5	77.8	91.9	0.94
40	Massambaba	**77.8**	113.5	83.8	105.6	1.67
41	Pecado	**53.1**	54.5	53.7	54.4	1.19
42	Peró	89.1	88.6	89.5	**83.3**	2.96
43	Tucuns	**61.8**	64.9	64.6	64.7	1.80
44	Unamar	60.7	**58.0**	61.1	59.2	1.99
45	Bessa	**33.7**	35.3	36.4	33.8	5.23
46	Cabo Branco (site1)	**34.3**	37.7	36.1	36.1	2.72
47	Cabo Branco (site1)	**74.3**	123.0	77.8	104.0	2.06
48	Sul Jaguanum	**138.0**	180.7	144.0	172.8	2.59
49	Catita	96.6	94.0	96.3	**93.6**	5.12
50	Escalhau	**84.8**	92.7	88.1	91.6	1.94
51	Estopa	**73.5**	73.6	74.4	74.3	1.17
52	Boqueirão	**70.1**	78.4	74.6	78.8	1.10
53	Costa Azul	95.4	**88.9**	92.5	inf	0.70
54	Pontal	100.3	**98.4**	98.8	inf	0.64
55	Itacuraçá (site 1)	**111.0**	142.1	116.7	139.9	1.80
	Itacuraçá (site 1)*	**92.8**	114.6	97.8	inf	1.00
56	Itacuraçá (site 2)	**102.9**	114.3	106.4	113.2	1.89
	Itacuraçá (site 2)*	**98.3**	136.2	102.6	inf	1.11
57	Armação	29.6	**25.8**	31.6	28.6	0.59
58	Matadeiro	69.5	**66.7**	71.7	68.6	1.68
59	Barrancos•	**163.1**	191.5	168.7	188.8	2.68
	Barrancos•	**123.5**	140.6	128.6	139.1	1.53
	Barrancos•	**173.6**	200.3	182.1	200.6	3.15
60	Concheiros•	19.5	13.6	**9.7**	16.7	0.48
	Concheiros•	**30.0**	38.4	33.0	35.2	0.84
	Concheiros•	**31.7**	34.3	33.7	33.7	0.89
61	Altair	**281.1**	430.8	295.1	inf	3.55
62	Querência	**241.3**	412.1	252.9	inf	3.49
63	Centro	102.2	136.9	**100.4**	inf	0.94
64	Farol	134.0	140.4	**131.7**	140.3	1.80
65	Fora Norte	160.1	168.8	**158.2**	167.5	1.76
66	Fora Sul	145.4	154.7	**142.7**	154.7	1.66

67	Fortaleza	159.1	178.3	**152.2**	inf	1.75
68	Gaivotas	**55.1**	56.6	59.5	58.0	1.12
69	Grande	181.6	189.6	**175.9**	188.2	2.38
70	Leste	121.1	152.5	**117.3**	inf	1.55
71	Ponta Sul	**150.4**	162.7	157.3	162.6	4.38
72	Ponta do Bicho	125.1	124.0	**122.1**	124.1	1.41
73	Achiras	**121.0**	135.3	125.8	135.8	1.56
74	Aguada	**156.3**	226.6	166.1	222.1	2.54
75	Arachania	**104.7**	109.5	108.8	110.8	1.29
76	Atami	170.1	178.0	**165.9**	176.7	2.23
77	Barra Del Chuy	**218.0**	267.0	227.0	inf	2.39
78	Manantiales	35.2	**28.8**	31.7	31.3	0.97
79	Punta Del Diablo	**87.6**	103.2	89.5	98.8	1.45
80	Santa Isabel	110.1	**109.7**	112.6	110.8	1.29
81	El Arco	**80.3**	127.0	87.0	112.5	4.13
82	Isla Monte León	**159.4**	182.0	167.4	181.2	3.89
83	CaletaErrazuris	**445.8**	523.5	453.5	inf	4.80
84	Morrilos	146.3	159.7	**142.8**	inf	1.37
85	Boy Scout	**291.7**	582.7	294.2	inf	6.17
86	Shimmey	**110.8**	163.5	122.3	158.3	4.05

ANOVA indicated the existence of significant differences on ecological descriptors and morphodynamic parameters among the three main models - logseries, broken stick and lognormal (Table 2). For broken stick model, richness and global abundance values of the sandy beaches are low and the evenness is elevated. This pattern corroborates with morphodynamic parameters results that establish a reflective condition for broken stick model, with low values of beach index and beach face slope. Considering that logseries and lognormal models are very similar, their results were not extremely divergent. Richness values are quite similar, and so is evenness, showing significant differences only in relation to broken stick model. Both had high values of global abundances, but lognormal exhibited the highest values. Logseries model detained the higher values of beach index and lognormal the most flat sandy beaches, contrasting with the sandy beaches patterns, where a positive relation is expected between slope and Beach Index. Although logseries α was marginally significant, we may consider this an important result, once higher values for logseries confirm the assumptions of this model, where logseries distribution has higher proportions of rare species than lognormal. Diversity and grain size were not significantly different among the distribution models.

Table 2: Analysis of variance. Relation between the descriptor of community/morphodynamic parameters and the distribution models. *p*= probability level; Results of Tukey (HSD) post-hoc test to indicate statistical significance. (*)Log-transformed values; (**) marginally significant result, but considered as important as the other variables. BS = broken stick; LS = logseries; LN = lognormal.

Variables	F	*p*	Tukey (HSD)		
			BS	LS	LN
Richness*	8.97	0.00	5.85	10.83	11.19
Global Abundance*	9.75	0.00	676.42	1230.76	2116.66
Evenness	12.02	0.00	0.75	0.51	0.54
Logseries α*	2.57	0.08**	1.51	2.02	1.77
Beach Index*	14.12	0.00	1.47	2.10	1.73
Slope (1/m)*	8.89	0.00	13.60	19.16	33.24

DISCUSSION

Macrofaunal SADs of sandy beaches had distinct distribution models over the exposure range. Logseries model was predominant among the studied sandy beaches in response to the mophodynamic states. Dissipative beaches recognized by its more benign environment achieved a lognormal or a logseries distribution. Intermediate sandy beaches are transitional environments between the extremes of sandy beach morphodynamic types (Short & Wright, 1983) and showed a logseries distribution pattern. Reflective sandy beaches, known as harsh environments, are characterized by severe physical factors as high wave action, coarse grain size and steep slope, mainly had a broken stick distribution. The geometric model had a weak fit for macrofaunal communities of sandy beach. Considering the high abundance and low richness predicted by this model, it does not attain to the macrofaunal characteristics, where low richness is always correlated with low abundances, as in reflective beaches (Defeo & McLachlan, 2005).

Sandy beach environment is physically controlled by the instability of the substratum, tides and wave action. Moreover the exposure and harshness of this habitat require essential species adaptations, such as the ability of burrowing and surfing, and a physical resistance (McLachlan & Brown, 2006). Thus reflective sandy beaches sharply affect the macrofaunal populations (the *habitat harshness hypothesis* (Defeo *et al.,* 2001, 2003); the *swash exclusion hypothesis* (McLachlan *et al*., 1993)), where harsh conditions control species richness (the *multicausal environmental severity hypothesis* (Brazeiro, 2001)), and consequently abundance and diversity too. Although for some communities a poor fit of the broken stick distribution was found (Bastow, 1991; Hirao *et al*., 2013), it is known that this model is applicable in small communities (Tokeshi, 1993), which is exactly what is seen to the macrofauna of reflective sandy beaches or pocket beaches. This distribution model is a resource-partitioning model, where the niche is divided randomly among species, and predicts extremely even abundances (Tokeshi, 1993; McGill *et al*., 2007). An example of niche partitioning is the zonation in sandy beaches. The zones have contrasting physical characteristics (Salvat, 1964), which consequently affect differently the macrofaunal composition and structure in each zone. In reflective beaches the most specialized species dominate a tidal zone where their adaptations permit them to live under those specific conditions and thus decreasing the ecological interactions among species, therefore revealing an elevated evenness. Moreover, the low richness explained by the *swash exclusion hypothesis* is here validated by the predominance of species of the supralittoral and midlittoral (i.e *Excirolana braziliensis*, *Excirolana armata* and *Atlatorchestoidea brasiliensis*), thus suggesting that species have been excluded from the swash zone.

The main paradigm of sandy beaches states that richness, abundance, biomass and diversity increase sharply from the reflective to the dissipative morphodynamic state, in response to the decrease in grain size, wave action and beach face slope (McLachlan & Dorvlo, 2005). Intermediate or dissipative beaches are more benign environments and do not force the organisms to divert excessive energy towards maintenance leading them to direct their energy to reproduction and growth, thus establishing the populations easily. Lognormal and logseries models represent better the SADs on these sandy beaches types. These models are associated to higher richness and global abundance of the macrofauna (Figure 2). The difference between these two distribution models for sandy beach SADs is defined by the rarity of species (McGill *et al*., 2007).

Several ecological descriptors affect SAD shapes. Among these, the importance of rare species in SAD shapes, and consequently on the fitted model, has been highlighted for many authors (Magurran & Henderson 2003; Magurran 2007; McGill, 2003; Ulrich & Ollik, 2004; Gray *et al*., 2005), and could be reinforced in here. The highest values of the logseries α, that characterize high proportion of rare species (Magurran, 2004), were found for the logseries distribution, and lower values for the lognormal. This pattern corroborates with Magurran & Henderson (2003) when working with fishes assemblages and with McGill (2003) when investigating the log-left-skewness of the species abundance distribution curve.

In general, apart from the taxonomic group or ecosystem, a lognormal distribution is found to most of the assemblages (May, 1975; Sugihara, 1980; Magurran & Henderson 2003, Ulrich et al., 2010). Indeed, this must be related to the global abundance, once species abundance distributions have been studied in distinct ecosystems with moderate species richness (30-300) (McGill et al., 2007), and consequently high global abundances. However, for the macrofauna studied the maximum richness was of 42 species, which is quite low when compared with birds (Mac Nally, 2007), fishes (Magurran & Henderson 2003), insects (Hirao et al., 2013), or trees (Gray et al., 2006) assemblages. This new spectrum of richness studied

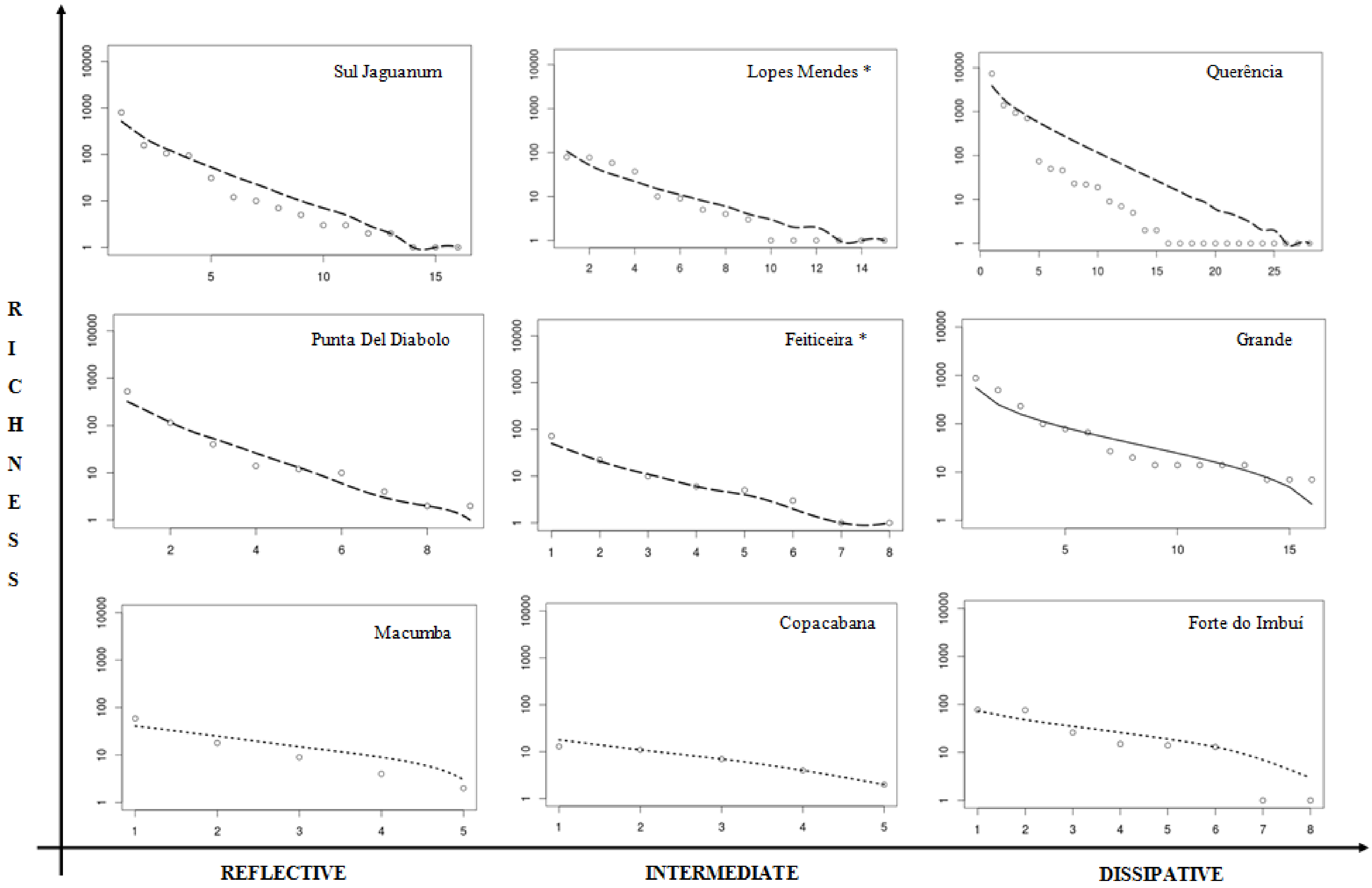

Figure 2: Patterns concerning richness and the distribution models across sandy beaches morphodynamic states. (••••••) Broken stick; (— — —) logseries; (——) lognormal;

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may inspire forward studies covering the missing gaps, on both communities and environmental parameters

Altogether, we could indicate that lower richness and higher evenness in sandy beaches macrofauna will preferentially have a broken stick distribution, while higher richness and higher global abundance of the macrofauna are represented by a logseries or lognormal distributions - depending on the proportion of rare species in the community (Figure 3).

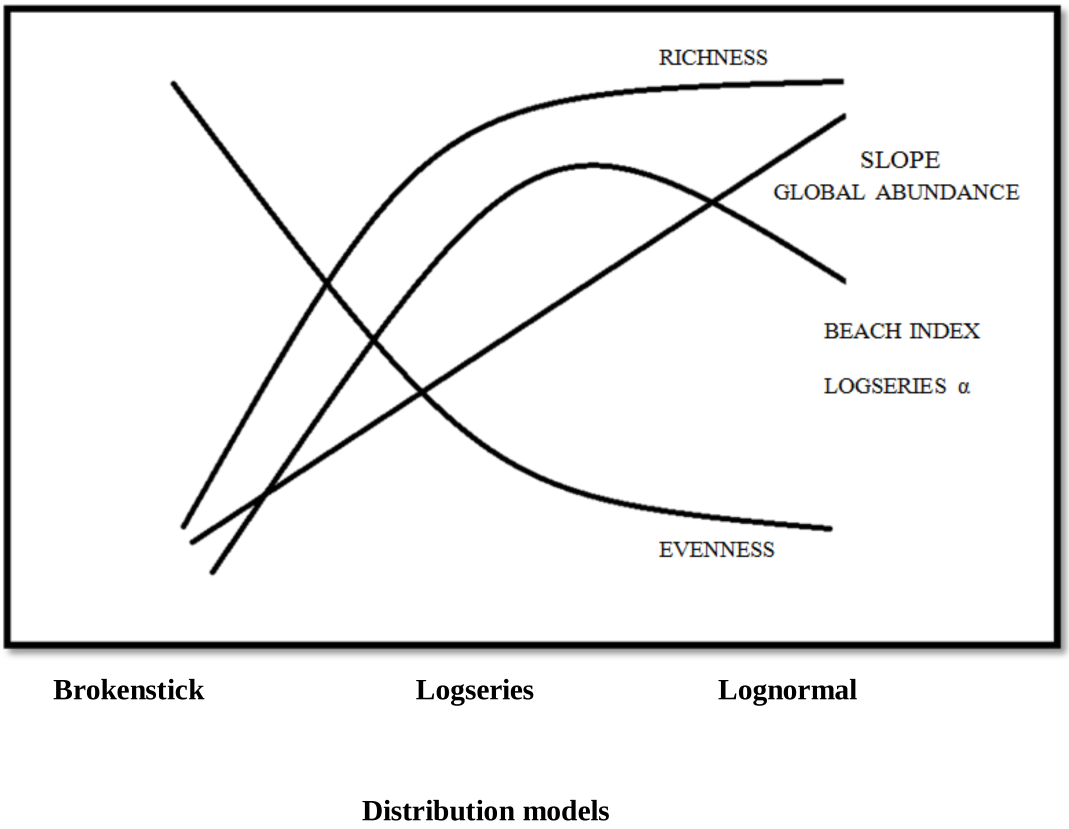

Figure 3: Patterns ecological descriptors and morphodynamic parameters in sandy beaches across the distribution models.

Future perspectives may elucidate temporal variations as suggested by Magurran (2007). This approach will drive us to understand a little more about the shape of SADs curves and the distributions models, thus helping us to elucidate the effect of commonness and the rarity on the macrofauna. Another interesting way will be to fit the data to the gambin model (Ugland, 2007; Matthews *et al.*, 2014), to compare these results (using traditional models) with a single model method, by the analysis of the single parameter – gambin α - that describes the shape of the resultant SAD curve.

CONCLUSÃO

Podemos concluir que a SADs da macrofauna se modificam através dos estados morfodinâmicos das praias arenosas, e consequentemente são representados por diferentes modelos de distribuição. Além disto, foi possível verificar que assim como a proporção de espécies raras é essencial na determinação do modelo de distribuição, a riqueza, a abundância total e a equitabilidade também são fundamentais.

Os descritores ecológicos e os parâmetros morfodinâmicos apresentam padrões entre os modelos. A riqueza e a abundancia global aumentam consideravelmente da distribuição broken stick em direção à logseries e lognormal, enquanto a equitabilidade segue um padrão inverso. O α da logseries tem seus maiores valores para a distribuição logseries, como previsto por outros trabalhos. Com relação aos parâmetros morfodinâmicos é possível averiguar que no modelo broken stick predominam praias reflectivas, para o modelo logseries praias intermediárias e para lognormal praias dissipativas.

O modelo logseries foi o mais representativo dentre as SADs da macrofauna de praias arenosas, em consequência da grande quantidade de espécies com números baixíssimos de indivíduos, ou mesmo por apenas um indivíduo, em todos os tipos morfodinâmicos de praia.

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