Does richness of Oligochaeta (Annelida) follows a linear distribution with habitat structural heterogeneity in aquatic sediments?

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ABSTRACT

Sediment of aquatic environments supports several local communities, among them aquatic invertebrates. Habitat structural heterogeneity in sediments of aquatic ecosystems is related to a number of factors, including variability in the particle size of the substrate and availability of different food resources, the two structures that comprise the aquatic sediment. These structures are necessary for the stability of zoobenthic community, including the Oligochaeta assemblage, favoring richness as habitat heterogeneity increases. To analyze the habitat structural heterogeneity, we use these following structures: granulometric composition and organic matter composition, and we tested these structures together (habitat heterogeneity) and separately (granulometric and organic matter heterogeneity). This study investigated the relationship between habitat structural heterogeneity and richness of the Oligochaeta assemblage. We hypothesized that there is a positive linear relationship between habitat structural heterogeneity and richness of Oligochaeta, and predicted that the granulometric composition is more important than organic matter composition for increasing richness. There was no linear relationship between Oligochaeta richness and habitat heterogeneity; but the analysis showed an asymmetric triangular dispersion pattern, being granulometric heterogeneity more important than organic matter heterogeneity for richness of Oligochaeta. These results indicated that habitat structural heterogeneity was beneficial for richness of Oligochaeta until certain threshold and after this, the relationship between structural heterogeneity of habitats and richness of Oligochaeta is negative with decrease of diversity due to the filling of interstitial spaces which gradually reduces the ability to colonize these habitats.

Key words: neotropical, invertebrates, asymmetrical distribution, aquatic environments, type of sediments, organic matter composition.

INTRODUCTION

Heterogeneity is defined as the complexity and/or variability of the properties of a system in space and/or time (Li and Reynolds, 1995). The term *habitat structure* refers to the physical structure and space serving as a support for the communities of plants and animals (McCoy and Bell, 1991), and these are considered important factors for ecological diversity (McArthur and McArthur, 1961). Habitat structure has an important role in determining species diversity (Bell *et al*., 1991), generally resulting in a linear relationship between species diversity and habitat structure (McArthur and McArthur, 1961; Rosenzweig and Winakur, 1969). However, some studies have found that this relationship may not always be linear for all communities (Whittaker, 1960; Magurran, 1988). In aquatic habitats the structural heterogeneity of sediments is related to a variety of factors such as variability of particle size (Brown, 2003) and availability of different food resources, as organic matter (Schwindt *et al*., 2001; Da Rocha *et al.,* 2006). Variations in both particle size and food resource are often linked to presence of other organisms associated with these habitats (Jackson *et al*., 2008; Buschbaum *et al*., 2009). Habitat heterogeneity is a key

factor enhancing the stability of communities, such as macroinvertebrates in environments exposed to great disturbances (Mykra *et al*., 2011). The importance of granulometric and organic matter compositions on benthic community is widely known in literature (Buss *et al.,* 2004; Costa and Melo, 2008; Tokeshi and Arakaki, 2011). Benthic communities often exhibit preferences for certain substrates and particle sizes (Arakaki and Tokeshi, 2005; Rae, 2004). The substrates not only represent the habitat but also food resource for many organisms, then relationship of benthic organisms with grain size of sediment can be complex. In general, high richness tends to be associated with the diversity of particle sizes (Etter and Grassle, 1992). Oligochaeta is one of the most abundant groups among benthic invertebrates (Takeda, 1999; Ezcurra de Drago *et al.,* 2005), recorded in almost all freshwater environments, and also in various neotropical floodplain environments as the Paraná River floodplain (Stevaux and Takeda, 2002; Takeda and Fujita, 2004; Behrend *et al*., 2009). Oligochaeta represent an excellent tool in studies of sediment morphological changes because the life cycle of these organisms are fully aquatic and also they have the ability to penetrate into sediments (Lafont *et al.,*

2007). Many species of Oligochaeta have direct relation with the size of the particles, thus differences in granulometric composition of sediment may influence the richness. In general, the sediments of aquatic ecosystems may be composed by pebbles, granules, very coarse sandy, coarse sandy, medium sandy, fine sand and very fine sandy accord to the habitat (Ezcurra de Drago *et al.*, 2005; Behrend *et al.*, 2009; Ragonha *et al.*, 2013). Another factor that highly influences the richness of Oligochaeta are the different compositions of organic matter that are food for these annelids, and accordance the species can feed from coarse particulate organic matter or extremely small (Marchese, 1987; Marchese *et al.*, 2002; Behrend *et al.*, 2009). Thus habitats where there are heterogeneity of both structures as particle size and organic matter the higher colonization of different species in this habitats (Rae, 2004; Arakaki and Tokeshi, 2005).

Many studies have been conducted on increasing structural variability and its relationship to biological diversity using macrophytes (Dibble *et al.*, 2006). Researchers also found that an increase in structural diversity causes also positive richness of fish (Harrel and Dibble, 2001; Agostinho *et al.*, 2007) and in invertebrates (Rennie and Jackson, 2005; Thomaz *et al.,* 2008; Mormul *et al.*, 2011). However, investigations into sediment structural variations (particle size distribution and organic matter), as structural heterogeneity, in freshwater habitats are needed, in order to determine patterns of diversity and distribution, which have not be consolidated yet.

The objective of this study was to investigate until what point the increase in structural heterogeneity in benthic habitats (granulometric composition and matter organic composition) positively influenced richness of Oligochaeta on neotropical floodplain. We tested the hypothesis that exist linear relationship between habitat structural heterogeneity and richness of Oligochaeta, and our prediction is that the granulometric composition is more important than organic matter composition for α-diversity.

METHODS

Study area

This study was conducted in the Upper Paraná River floodplain (Paraná, Brazil). The sampling area stretched from cities Três Lagoas (Mato Grosso do Sul, Brazil) to Guaíra (Paraná, Brazil), between the Porto Primavera and Itaipu dams, approximately 230 km and cover an area of 526,752 ha (Souza Filho and Stevaux, 1997). Samples were collected at 12 stations, grouped into three subsystems, the Paraná, Ivinhema and Baía (Fig. 1).

The Paraná subsystem consists of the Paraná River and associated floodplain lakes. The stretch of this river that was studied presents a braided channel, with mean current flow relatively high, varied width and extensive island

(Pauleto *et al.*, 2009). In this stretch the river has an average depth of 4.0 m and could reach 15.0 m (Thomaz *et al.*, 1992). In this subsystem, samples were collected in Paraná subsystem comprised by stations of sampling the Paraná River (22°75'68"- 53°25'31"), Pau Véio Lake (22°74'81"-53°25'62"), Garças Lake (22°72'51"- 53°21'67"), and Osmar Lake (22°77'40"- 53°33'22"). Ivinhema subsystem consists of Ivinhema River as the main channel, which is one of main tributaries situated on the right bank of the Paraná River (Pauleto *et al.*, 2009). It is connected to Paraná River through Ipoitã Channel (Thomaz *et al.,* 1992). In this subsystem, samples were collected in Ivinhema River (22°82'86"- 53°56'61"), the Ipoitã Channel (22°83'59"- 53°56'37"), Patos Lake (22°82'53"-53°55'50"), and Ventura Lake (22°85'65"- 53°60'02").

The Baía subsystem includes the Baía River and connects to Paraná River through a channel its lower stretch (Baía Channel) and connected to Ivinhema River through Curutuba Channel (Pauleto *et al.*, 2009). Baía River, a sinuous channel, with lentic characteristic, presents varied width, a mean depth of 3.2 m, low declivity and low current flow and is directly influenced by the hydrological regime of Paraná River (Thomaz *et al.*, 1992). In this subsystem, samples were collected in Baía River (22°72'31"-53°29'04"), the Curutuba Channel (22°75'32"- 53°35'85"), Guaraná Lake (22°72'12"- 53°30'31"), and Fechada Lake (22°71'19"- 53°27'85").

Sampling

Samples were collected in February, June, September and November 2008. In all environments right margin (RM), left margin (LM) and center (CE) region were sampled. At each region, four samples were taken, three for biological analysis and one for assessment of habitat structural heterogeneity (granulometric and organic matter compositions), using a Petersen grab modified (0.0345 m²).

The collected material was placed in gallons and washed through a system of screens varying in mesh size (2.0-1.0 and 0.2 mm). The material retained in the 0.2 mm screens was fixed with 80% alcohol and sorted under stereomicroscope. Oligochaeta were identified under optical microscope, in accordance with the identification keys of Brinkhurst and Jamieson (1971), Righi (1984), and Brinkhurst and Marchese (1991).

Environmental variables

The sediments were classified into different size classes using the scale of Wentworth (1922), while an estimation of organic matter was obtained by burning 20 g dry sediment in an oven at 560°C for about 4 h. Water levels of Paraná River in 2008 were provided by Research Nucleus in Limnology, Ichthyology and Aquaculture (NUPELIA). The laboratory of Basic Limnology of NU-

PELIA/UEM provided the environmental variables: depth (m), temperature (ºC), electric conductivity (ms/cm), pH, and dissolved oxygen (mg/L).

Abiotic analysis

In order to establish levels of habitat heterogeneity, values were calculated using the Shannon-Wiener index for each component of sediment (granulometric and organic matter compositions), and was verified the relationship this components together and separately. The Shannon-Wiener index was chosen as it is considered to best represent the habitats structural heterogeneity. This index takes into account the number of different sizes of particles separated by the sieves, and the equitability of different particle sizes.

To verify the influence of abiotic variables, other than granulometric and organic matter compositions, we used a principal component analysis (PCA), using PC-ORD 5.0 software (McCune and Mefford, 1999). Axes were retained for interpretations according to the broken-stick criteria. The variables used in the ordination were depth (m), pH, temperature (°C), conductivity (ms/cm), and dissolved oxygen (mg/L). We subsequently performed an analysis of variance (ANOVA), with the PCA axes scores retained for interpretation, to examine whether there were any differences between the sampling.

Biotic analysis

In our investigations, the same pattern using richness, Shannon-Wiener and Margalef indices were verified, therefore our results were not subjected to the effects of organism abundance and were chosen by richness. In
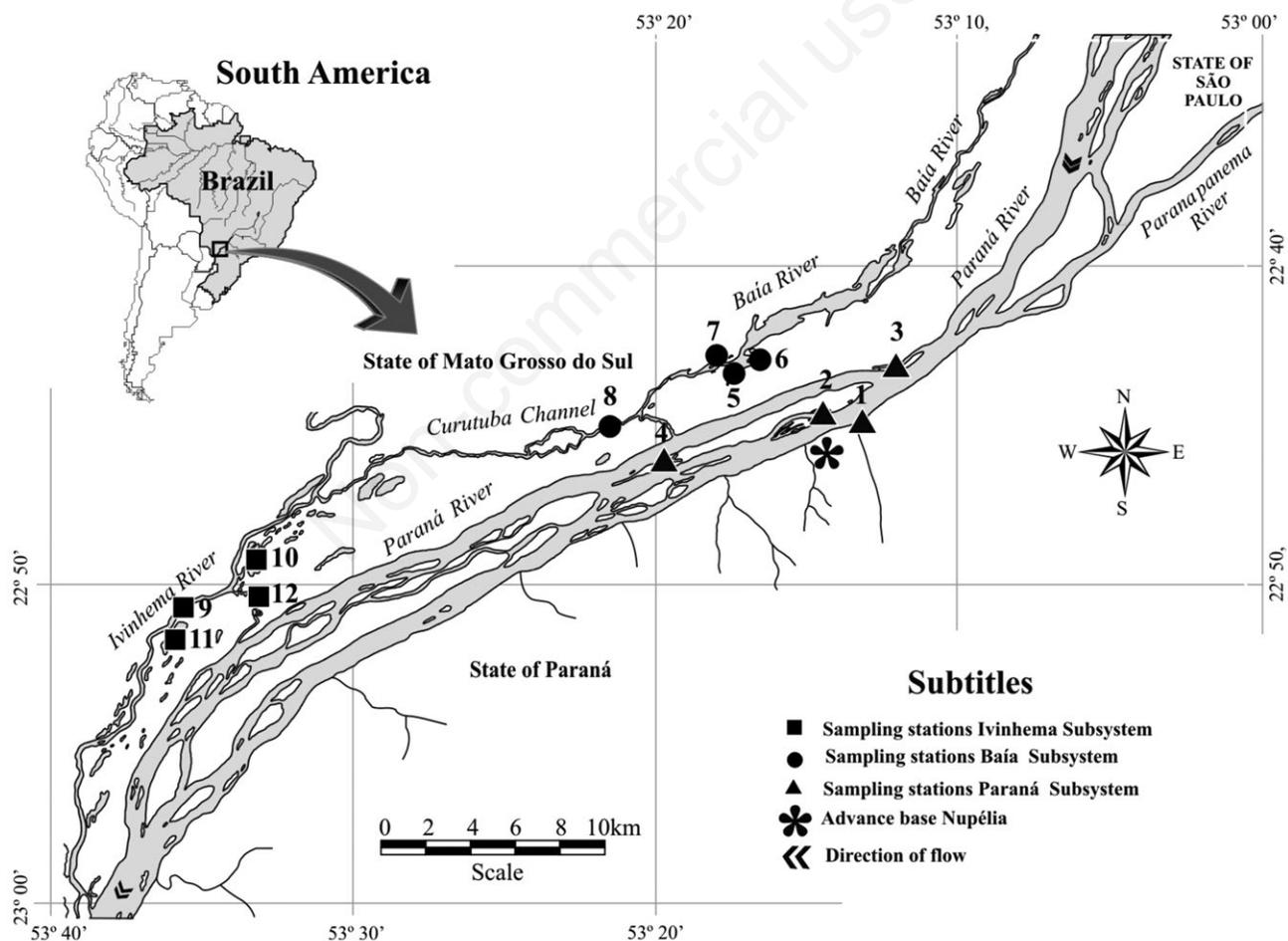

Fig. 1. Sampling stations of the Paraná River floodplain. 1, Paraná River (main channel); 2, Pau Véio Lake (lake with connection); 3, Garças Lake (lake with connection); 4, Osmar Lake (lake isolated); 5, Baía River (main channel); 6, Fechada Lake (lake isolated); 7, Guaraná Lake (lake with connection); 8, Curutuba Channel (secondary channel); 9, Ivinhema River (main channel); 10, Patos Lake (lake with connection); 11, Ventura Lake (lake isolated); 12, Ipoitã Channel (secondary channel).

order to assess the relationship between habitat structural heterogeneity and richness of Oligochaeta, we performed simple linear regression analysis, and analyzed separate structure (granulometric and organic matter compositions) to verify the affected response (richness). The analysis was performed using Statistica 7.1 software. The dominance index was calculated according to Kownacki (1971), by the given formula d= (Q.100/∑Q)*f, where Q is the mean number of specimens of species examined in the investigated series of samples; ∑Q is the sum of the mean quantities of specimens of all species and f is the frequency calculated from the ratio n/N, where n=number of samples representing the species investigated, N=number of samples in the series.

Possible patterns for relationship between richness of Oligochaeta and habitat structural heterogeneity (granulometric and organic matter compositions) were tested (structures together and separately), according to the null model, using the EcoSim v. 7.71 software (Gotelli and Entsminger, 2004) in order to test the existence of relationship in form of envelope restrictions: analysis of dispersion and triangular envelope. According to this model, the envelope constraint is defined initially by connecting the points Xmax, Ymin, and Ymax Xmedian and Xmin, Ymin, and Ymax and Xmax are only maximum for variables X and Y. Xmin is only minimum for the variables X and Y, and X median is the median of X (structural heterogeneity of habitat, respectively) (Gotelli and Entsminger, 2004). In this study, 5000 randomizations were used for this test.

RESULTS

Abiotic analyses

It was established that during all four samples periods, the level of the Paraná River was below that considered to represent floodplain high water conditions (>3.5 m) (Fig. 2). There was a flood between the first
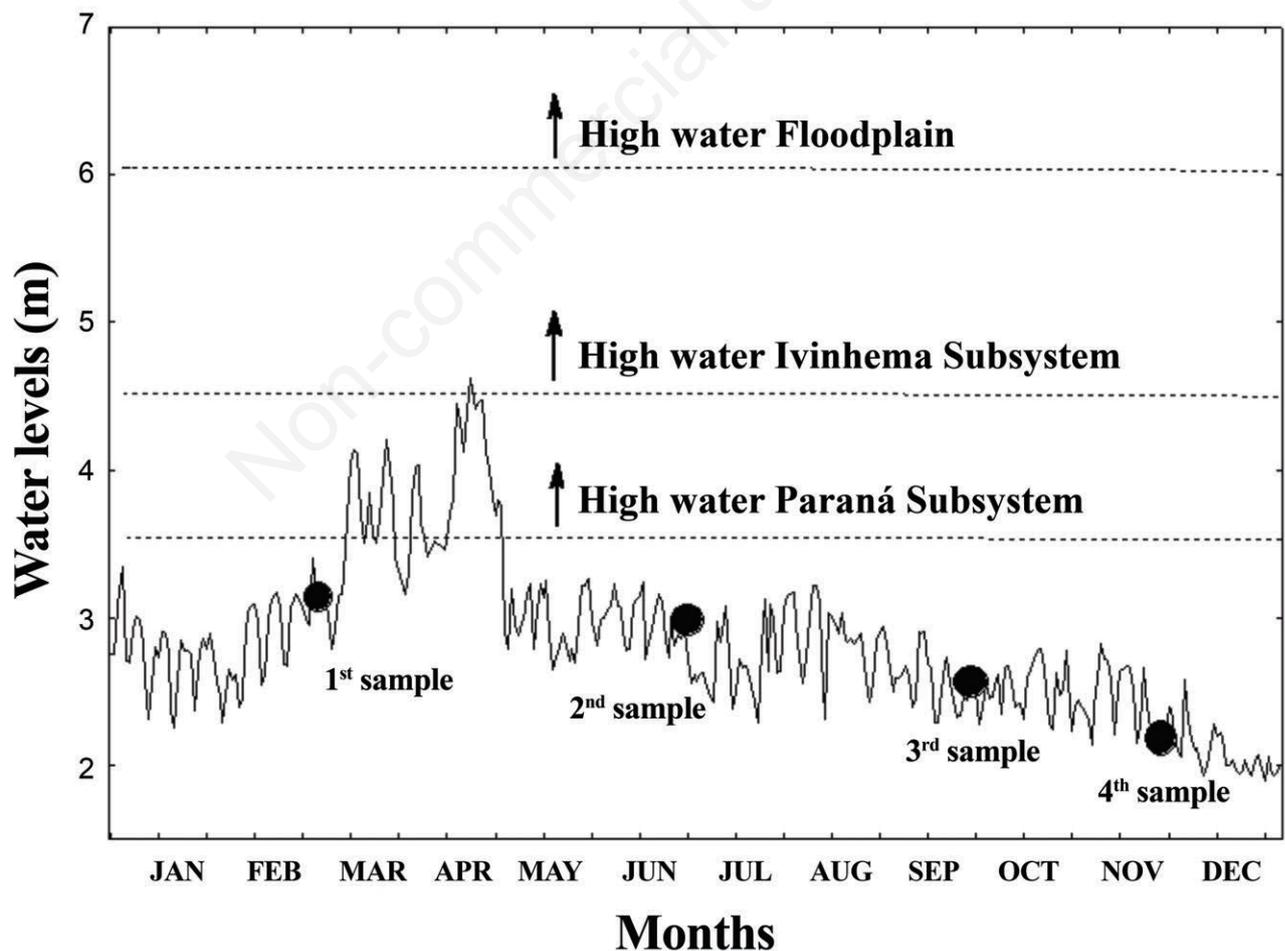

Fig. 2. Daily data of the river level of the River Paraná (m) in 2008, obtained by fluviometric station of Porto Rico-PR, the research base of the NUPELIA.

and second sampling periods, affecting not only the habitat of the Paraná subsystem (>3.5 m), but also that of the Ivinhema subsystem (>4.6 m) (Souza Filho, 2009). The second sample period were taken two months after the floodplain high water period.

Consequently, the four samples periods were accepted as replicates of floodplain low water conditions and the analysis of variance (ANOVA), using the PCA scores of abiotic factors , has confirmed the no significant for axis1 (F=1.46, P=0.23) and for axis 2 (F=0.40, P=0.75), which demonstrate that it does not have temporal variation between samples.

Biotic analyses

The species *Pristina americana* and *Aulodrilus pigueti* were dominant in almost all habitats of the three subsystems, while *Narapa bonettoi* dominated mainly lotic habitats as: Paraná River (CE), Ivinhema River (CE and RM) Ipoitã Channel (CE and RM) **(**Tab. 1).

Habitat structural heterogeneity

Simple regression analysis between habitat heterogeneity (granulometric+organic matter compositions) and richness of Oligochaeta showed no significance, with F (1.142)=3.15; P=0.07.

However, data distribution formed a triangular pattern, and the test to confirm data dispersion in envelope was significant (P (observed<expected)=0.04). The highest richness of Oligochaeta was found with index value (structural heterogeneity) of 1.98 (standard deviation =0.77) (Fig. 3).

Organic matter structural heterogeneity

Simple linear regression did not show relationship between organic matter heterogeneity and richness of Oligochaeta (F(1.142)=1.25; P=0.26). The dispersion asymmetric test between richness and organic matter heterogeneity does not have significant effect in the triangular pattern (P (observed>expected)=0.11) (Fig. 4).

Granulometric structural heterogeneity

Linear regression analysis showed significant differences (F(1.138)=6.21; P=0.01) between richness of Oligochaeta and granulometric heterogeneity. The assumption of linearity was observed in both, the intercept and in the slope, which were significant with a negative correlation between richness and granulometric heterogeneity (β= -0.63), but the explanation was only 3%. Assumptions of normality and homoscedasticity were not reached. It was verified through the scatter plot of rich-
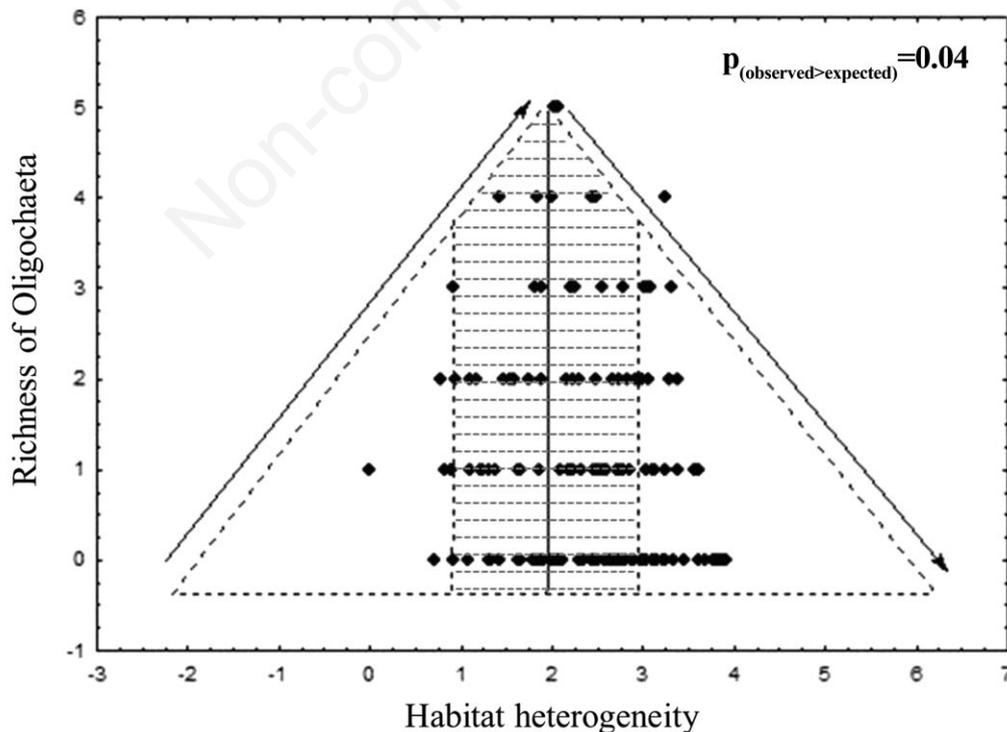

Fig. 3. The relationship between Oligochaeta richnessand habitat heterogeneity (granulometric and organic matter compositions).

ness of Oligochaeta and granulometric heterogeneity a triangular pattern. Thus, we therefore performed an asymmetric dispersion test. In a total of 5000 randomizations, only 105 habitats (a total of 144 habitats) were allocated outside the envelope restrictions, that indicates the probability of habitats being restricted to an asymmetrical triangular by chance is low (P=0.03), which states the existence of this triangular pattern. Consequently, richness of Oligochaeta is at its maximum when the granulometric heterogeneity value is 1 (standard deviation=0.40). This area encompasses about 75% of the habitats studied (Fig. 5).

DISCUSSION

The hypothesis of a linear relationship between habitat structural heterogeneity and richness of Oligochaeta was not confirmed, however a triangular pattern distribution was detected, in which there is an increase in richness until certain threshold, and after this, the richness of Oligochaeta decreases.

Studies on habitat structural heterogeneity using aquatic macrophyte have already been performed (Rennie and Jackson, 2005; Thomaz *et al.*, 2008; Mormul *et al.*, 2011), but the use of sediment (granulometric and organic matter compositions) as components of habitat structure are scarce in freshwater environments, despite

the fact that a large proportion of aquatic organisms inhabits the sediment, both for reproduction and feeding, such as the zoobenthic community. Many studies emphasized the relationship of granulometric and organic matter compositions on the Oligochaeta distribution (Takeda and Fujita, 2004; Lafont *et al.*, 2007; Behrend *et al.*, 2009) and other benthic organisms (Rae, 2004; Arakaki and Tokeshi, 2005), which demonstrates the importance of these structures of habitat for invertebrate community. Such importance is probably stronger for Oligochaeta, which commonly shows strong relationships with the structures of sediment. However in homogeneous sediments there is dominance of Oligochaeta species related to the predominant structure in this habitat.

Some few species dominated the habitats, such as *Narapa bonettoi*. This species was highly abundant in center regions of Paraná and Ivinhema Rivers, which is expected due to morphology of lotic sandy sediments (Montanholi-Martins and Takeda, 1999; Takeda *et al.*, 2004; Blettler *et al.*, 2008). *Pristina americana* is related with high values of organic matter, mud and low oxygen conditions (Montanholi-Martins and Takeda, 1999), thus explaining why this species was only recorded in lentic environments and littoral regions. The species *Aulodrilus pigueti* is generalist and adapted to a variety of environments and habitats (Behrend *et al.,* 2009; Ragonha *et al.,*
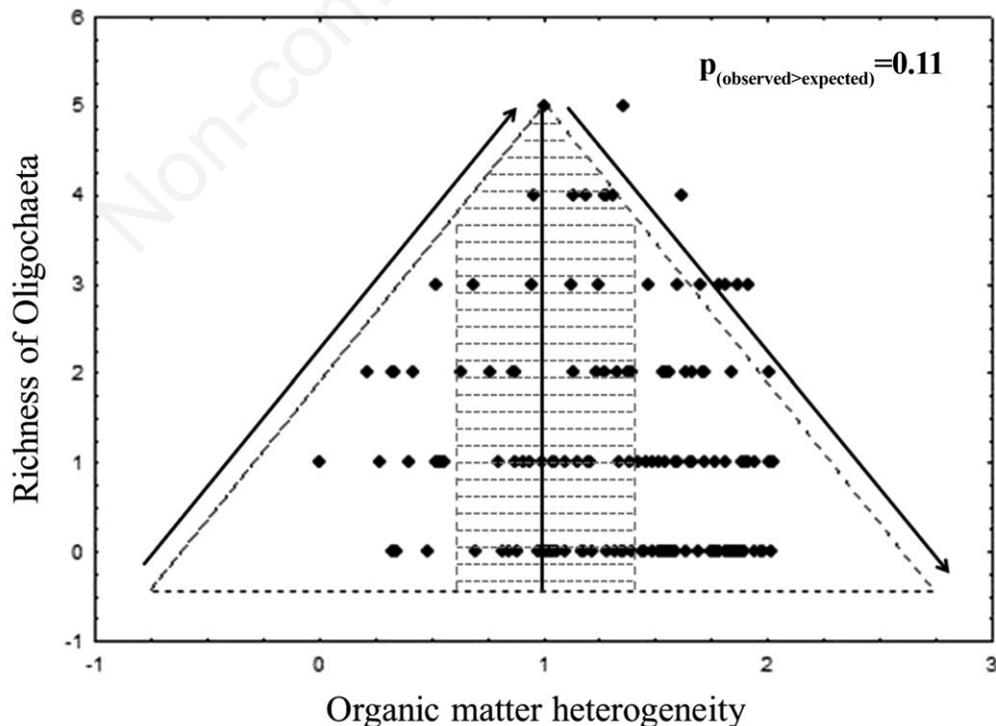

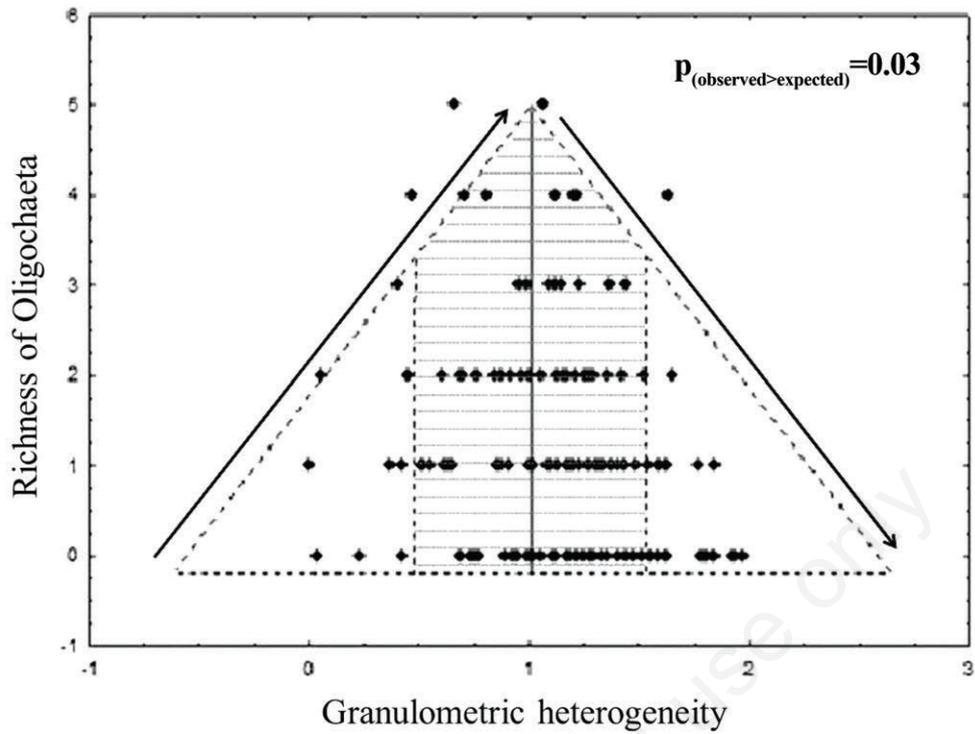**Fig. 4.** The relationship between Oligochaeta richness and organic matter heterogeneity.

Fig. 5. Relationship between Oligochaeta richness and granulometric heterogeneity.
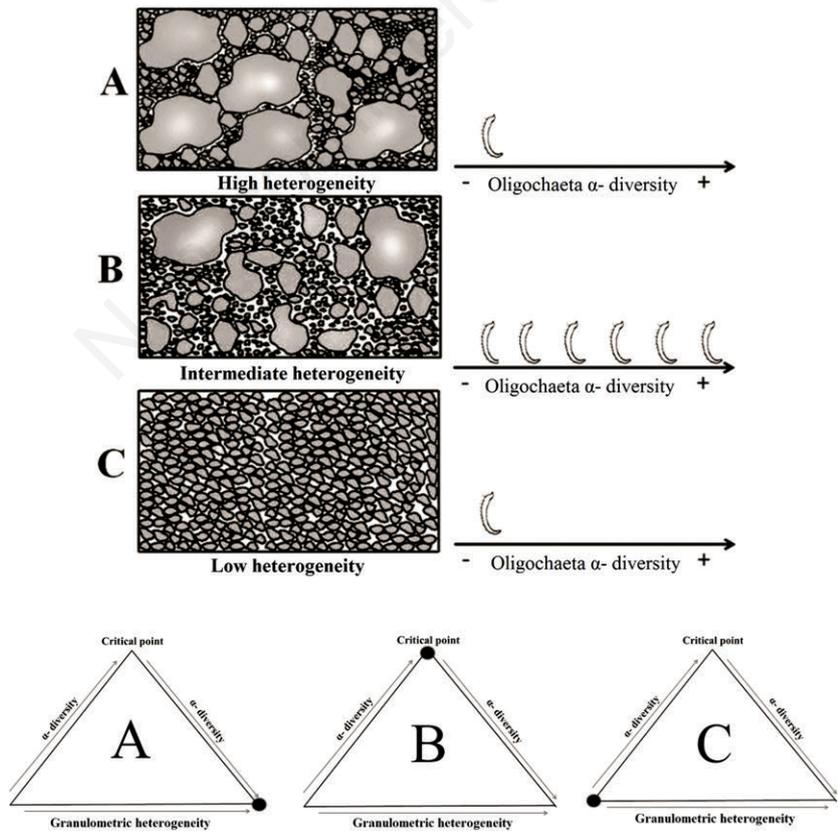

Fig. 6. Theoretical conceptual model of structural heterogeneity of granulometric composition and Oligochaeta α- diversity. A) High heterogeneity. B) Intermediate heterogeneity. C) Low heterogeneity.

Tab. 1. Index of dominance Kownacki (1971) for species of Oligochaeta sample in different *habitat* of the floodplain of the Paraná River separate for subsystems. Dominant (10-100), subdominant (1 to 9.99), non-dominant (0 to 0.99); dominant species are underlined.

Habitat subsystem Paraná

Species of Oligochaeta	Paraná CE	Paraná MD	Paraná ME	Pau Véio CE	Pau Véio MD	Pau Véio ME	Osmar CE	Osmar MD	Osmar ME	Garças CE	Garças MD	Garças ME
Haplotaxidae												
Haplotaxis aedochaeta - Brinkhurst & Marchese, 1987	1.92	-	-	-	-	-	-	-	-	-	-	-
Naididae												
Pristininae (subfamily)												
Pristina americana - Cernosvitov, 1925	-	60.41	18.18	2.58	-	0.69	-	2.77	0.30	69.30	50.00	-
P. proboscidae - Müller, 1773	-	0.52	0.56	0.51	6.00	10.41	-	-	0.92	-	-	25.00
Naidinae (subfamily)												
Bratislavia unidentata - Harman, 1973	-	7.29	-	-	-	-	-	-	0.92	-	-	-
Dero (Dero) righii - Varela, 1990	-	-	-	-	-	-	-	2.77	2.46	-	-	-
D.D. digitata - Müller, 1773	-	-	0.56	0.17	-	-	-	-	-	-	-	-
D.D. pectinata - Aiyer, 1929	-	-	-	0.17	-	-	-	-	-	-	-	-
D. (Aulophorus) furcatus - Müller, 1773	-	-	-	-	-	-	-	-	-	1.92	-	-
Haemonais waldvogeli - Brestscher, 1990	-	-	-	0.17	-	-	1.25	-	0.30	-	-	-
Nais communis - Pigueti, 1906	-	-	-	0.17	-	-	1.25	-	2.16	-	-	-
Slavina evelinae - Marcus, 1943	-	-	7.38	-	-	16.66	-	-	-	-	-	-
Tubificinae (subfamily)												
Limnodrilus hoffmeisteri - Claparede, 1862	-	-	-	-	-	-	1.25	-	-	-	-	-
Paranadrilus descolei - Gavrilov, 1955	-	9.37	-	-	-	-	20.00	-	0.30	-	-	-
Aulodrilus pigueti - Kowalewski, 1914	-	2.08	2.27	91.72	51.00	45.83	18.75	38.88	56.48	-	-	-
Narapidae												
Narapa bonettoi - Righi & Varela, 1983	92.30	-	5.11	-	-	-	-	-	-	-	-	-
Total of species	2	5	6	7	2	4	5	3	8	2	1	1

Habitat subsystem Baía

Species of Oligochaeta	Baía CE	Baía MD	Baía ME	Curutuba CE	Curutuba MD	Curutuba ME	Fechada CE	Fechada MD	Fechada ME	Guaraná CE	Guaraná MD	Guaraná ME
Naididae												
Pristinae (subfamily)												
Pristina americana - Cernosvitov, 1925	-	-	25.00	-	27.50	-	-	25.00	-	25.00	25.00	-
Naidinae (subfamily)												
D. (Aulophorus) borelli - Michaelse, 1900	-	-	-	12.50	-	-	-	-	-	-	-	-
Slavina evelinae - Marcus, 1943	-	-	-	-	0.26	2.27	-	-	-	-	-	-
Tubificinae (subfamily)												
Paranadrilus descolei - Gavrilov, 1955	-	-	-	-	27.90	-	-	-	-	-	-	-
Aulodrilus pigueti - Kowalewski, 1914	-	25.00	-	12.50	25.00	54.50	-	-	-	-	-	-
Narapidae												
Narapa bonettoi - Righi & Varela, 1983	-	-	-	-	-	9.00	-	-	-	-	-	-
Total of species	0	1	1	2	4	3	0	1	0	1	1	0

Tab. 1. Continued from previous page.

Species of Oligochaeta	*Habitat* subsystem Ivinhema											
	Ivinhema CE	Ivinhema MD	Ivinhema ME	Ipoitã CE	Ipoitã MD	Ipoitã ME	Ventura CE	Ventura MD	Ventura ME	Patos CE	Patos MD	Patos ME
Haplotaxidae												
Haplotaxis aedochaeta - Brinkhurst & Marchese, 1987	4.16	-	-	-	-	-	-	-	-	-	-	-
Naididae												
Pristina americana - Cernovitov, 1925	-	-	24.13	12.5	15.00	29.16	38.09	-	87.87	-	-	8.33
P. aequiseta - Bourne, 1891	-	-	-	-	1.25	-	-	-	-	-	-	-
P. osborni - Walton, 1906	-	-	-	-	-	1.38	-	-	-	-	-	-
Naidinae (subfamily)												
Bratislavia unidentata - Harman, 1973	-	-	-	-	-	-	-	-	0.75	-	-	-
Dero(Dero) righii - Varela, 1900	-	-	-	-	-	1.38	-	-	-	2.08	-	-
D. (D.) sawayai - Marcus, 1943	-	-	-	-	-	-	-	-	-	2.08	-	-
Dero (Aulophorus) hymanae - Müller, 1773	-	-	-	-	-	-	-	12.50	-	-	-	-
Stemphensoniana trivandrana - Cernovitov, 1983	-	-	-	-	-	5.55	2.38	-	0.75	2.08	-	-
Tubificinae (subfamily)												
Aulodrilus pigueti - Kowalewski, 1914	-	45.00	32.32	-	26.50	16.66	3.57	12.50	3.03	56.25	25.00	16.66
Narapidae												
Narapa bonettoi - Righi & Varela, 1983	20.83	20.00	2.15	12.50	10.00	1.38	-	-	-	-	-	-
Total of species	2	2	3	2	4	6	3	2	4	4	1	2

CE, center region; RM, right margin; LM, left margin.

2013) and was registered in the three subsystems and in all types of environments. Although these species dominated the referred habitats the heterogeneity in these habitats favored the colonization of other species rarely recorded, such as *Dero* (*Dero*) *digitata*, *Dero* (*Dero*) *pectinata*, *Dero* (*Dero*) *sawayai*, *Dero* (*Aulophorus*) *borelli*, *Pristina aequiseta* and *Pristina osborni* and these results corroborate with studies developed by Rae (2004) and Arakaki and Tokeshi (2005) where habitats with higher heterogeneity of sediment showed higher local diversity of zoobenthos.

Studies of aquatic invertebrate conducted by Taniguchi *et al.* (2003) and Taniguchi and Tokeshi (2004) found a positive linear correlation with habitat structural heterogeneity and higher values of richness, the same results were found in neotropical floodplains (Higuti *et al.,* 2007; Thomaz *et al.,* 2008). However, no positive linear correlations were detected between habitat structural heterogeneity and richness of Oligochaeta. This result validates those of Thistle *et al.* (2010) and Tokeshi and Arakaki (2011), in which excessive structure of habitats can result in a harmful habitat to richness. The granulometric structural heterogeneity (P<0.05) was more important than organic matter structural heterogeneity (P>0.05), as predicted, with increased of Oligochaeta richness until the index value =1.0. Above this value it was observed a progressive decrease of richness of Oligochaeta, since the interstices between larger sediment particles were filled with smaller grains that make the sediment unfavourable to the establishment of Oligochaeta. Consequently, compressed habitats make difficult the movement and colonization by other species, Tokeshi and Arakaki (2011) called it *small area of space*, which is filled with these smaller particles, and Stevaux and Takeda (2002) demonstrated that interstitial spaces for many invertebrates, especially Oligochaeta are very important, and we elaborated a theoretical conceptual model for a better understanding (Fig. 6).

CONCLUSIONS

As a result, the heterogeneity of habitat is favorable for benthic organisms until a certain threshold of structuration and after this there were a negative influence of structural heterogeneity of habitats on richness of Oligochaeta. Thus, among the structures that comprise the sediment, the granulometric composition has higher influence than organic matter composition on the richness of Oligochaeta in habitats of floodplain environments.

However, further studies examining the relationship between habitat heterogeneity and richness are needed, mainly with the zoobenthic community which includes several groups like molluscs, crustaceans, annelids and insect larvae with different life strategies.

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