



## Partitioning beta diversity of aquatic Oligochaeta in different environments of a Neotropical floodplain

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**ABSTRACT.** We tested the hypothesis that the contribution of the nestedness component is higher in environments with more similar features (lentic or lotic), whereas the contribution of the turnover component is higher in environments with more dissimilar features (lotic *vs.* lentic). To this end, we partitioned beta diversity of the Oligochaeta community into 12 environments of the Upper Paraná River floodplain. We recorded 986 individuals of 17 taxa. Through Redundancy Analysis, we observed a differentiation between lentic and lotic habitats both by environmental features as species composition. Our hypothesis was partially supported, because in environments with more similar hydrological characteristics, we observed a greater contribution of the nestedness component only in lentic environments, whereas in lotic environments, the turnover component showed a higher value. Moreover, when analyzed the different environments (lentic *vs.* lotic), we noticed a very similar contribution of both components. Some species were more frequent, as *A. pigueti* and *P. americana*, while others were exclusive to some environments (*N. bonettoi* and *H. aedeochaeta*). We evidenced the importance of each component in structuring Oligochaeta community, nonetheless, in a different way between environments with more similar (nestedness to lentic and turnover to lotic) or dissimilar (almost the same contribution of both) features.

**Keywords:** turnover, nestedness, lentic, lotic, richness.

## Partição da diversidade beta de Oligochaeta aquático em diferentes ambientes de uma planície de inundação neotropical

**RESUMO.** Nós testamos a hipótese de que a contribuição do componente aninhamento é maior em ambientes com características hidrológicas semelhantes (lênticos ou lóticos), enquanto o componente *turnover* é maior em ambientes com características mais diferentes (lótico *vs.* lêntico). Para tal, particionamos a diversidade beta da comunidade de Oligochaeta entre 12 ambientes da planície de inundação do alto rio Paraná. Registramos 986 indivíduos, consistindo em 17 táxons. Por meio da Análise de Redundância, observamos uma diferenciação entre ambientes lênticos e lóticos, tanto pelos fatores ambientais como também pelas espécies. Nossa hipótese foi parcialmente corroborada uma vez que em relação aos ambientes com características mais similares, observamos maior contribuição do componente aninhamento apenas nos ambientes lênticos, enquanto nos ambientes lóticos, o componente *turnover* foi maior. Ainda, ao analisarmos os ambientes mais diferentes, notamos uma contribuição muito semelhante de ambos os componentes. Algumas espécies foram mais frequentes, como *A. pigueti* e *P. americana*, enquanto outras foram exclusivas de alguns ambientes (*N. bonettoi* e *H. aedeochaeta*). Nós evidenciamos a importância de cada componente na estruturação da comunidade de Oligochaeta, no entanto, de uma forma diferente entre os ambientes com características mais semelhantes (aninhamento para lênticos e *turnover* para lóticos) ou diferentes (contribuição semelhante de ambos).

**Palavras-chave:** *turnover*, aninhamento, lêntico, lótico, riqueza.

### Introdução

The concept of beta diversity is not new, and the first suggestions for its use were made by Koch (1957) and Whittaker (1960). According to Anderson et al. (2006), beta diversity can be measured

as the variability in species composition among sampling units for a given area at a certain spatial scale. The concept has been used in many studies and for different biological groups, as invertebrates (ALDEA et al., 2009; BRAULT et al., 2013). Thus,

the increasing interest of ecologists, concomitantly with the development of new methods of study, has made the subject a popular topic in ecology (MELO et al., 2011).

Beta diversity may reflect two different phenomena: nestedness and spatial turnover (HARRISON et al., 1992; BASELGA, 2010). Nestedness is found when sites with lower species richness tend to be subsets of those species present in richer sites (DARLINGTON, 1957; ATMAR; PATTERSON, 1993). Unlike nestedness, spatial turnover implies the replacement of some species by others as a consequence of environmental sorting or spatial and historical constraints (QIAN et al., 2005). In this way, according to Baselga (2010), all situations where communities are not identical can be described by only these two main patterns (turnover and nestedness) or combinations of both, since the only processes required to generate all the possible patterns are species replacement and loss or gain of species.

Riverine floodplains are among the most biologically diverse ecosystems in the world (TOCKNER; STANFORD, 2002). In pristine condition, they encompass a variety of lotic and lentic sites, such as pools, lakes, rivers and channels (WARD; TOCKNER, 2001). In these systems, some environments are more similar, such as those with more lentic (lakes and some channels) or more lotic characteristics (rivers and most of the channels). The Upper Paraná River floodplain is an ecologically important area, because it provides a mosaic of aquatic, terrestrial and transition habitats, where physical and chemical differences produce a high heterogeneity (THOMAZ et al., 2007) and support a high biological diversity (AGOSTINHO et al., 2004). This environmental heterogeneity favors studies of beta diversity in this floodplain, as those performed by Bonecker et al. (2013), Lansac-Tôha et al. (2009) and Thomaz et al. (2003, 2009). However, these studies did not evaluate the importance of turnover and nestedness components. Actually, since this is a recent approach, few studies have partitioned the beta diversity.

Oligochaeta is an important group of the benthic community and commonly found in water bodies (BRINKHURST; JAMIESON, 1971; TIMM; VELDHUIJZEN VAN ZANTEN, 2002). Most are benthic deposit feeders and burrow in the sediment (MARTIN et al., 2008), therefore, very related to the environment in which they live and used as a biological indicator in many freshwater environments (TAKEDA, 1999). Some studies were carried out on the spatial distribution and ecology of this group in the Upper Paraná River floodplain (BEHREND et al., 2009; TAKEDA, 1999;

TAKEDA et al., 2004), but, using a completely different approach. In agreement with Christoffersen (2010), little is known about the aquatic oligochaetes of South America, therefore much research remains to be done regarding these invertebrates.

Thus, this study aimed to analyze the Oligochaeta community structure through beta diversity partitioning in the Upper Paraná River floodplain (Brazil). We hypothesized that the importance of nestedness and turnover components of Oligochaeta community can be different according to the types of environments of this floodplain. Based on this hypothesis, we tested the predictions that the contribution of the nestedness component is higher in environments with more similar characteristics (lentic or lotic), while the contribution of the turnover component is higher in environments with more dissimilar characteristics (lotic vs. lentic).

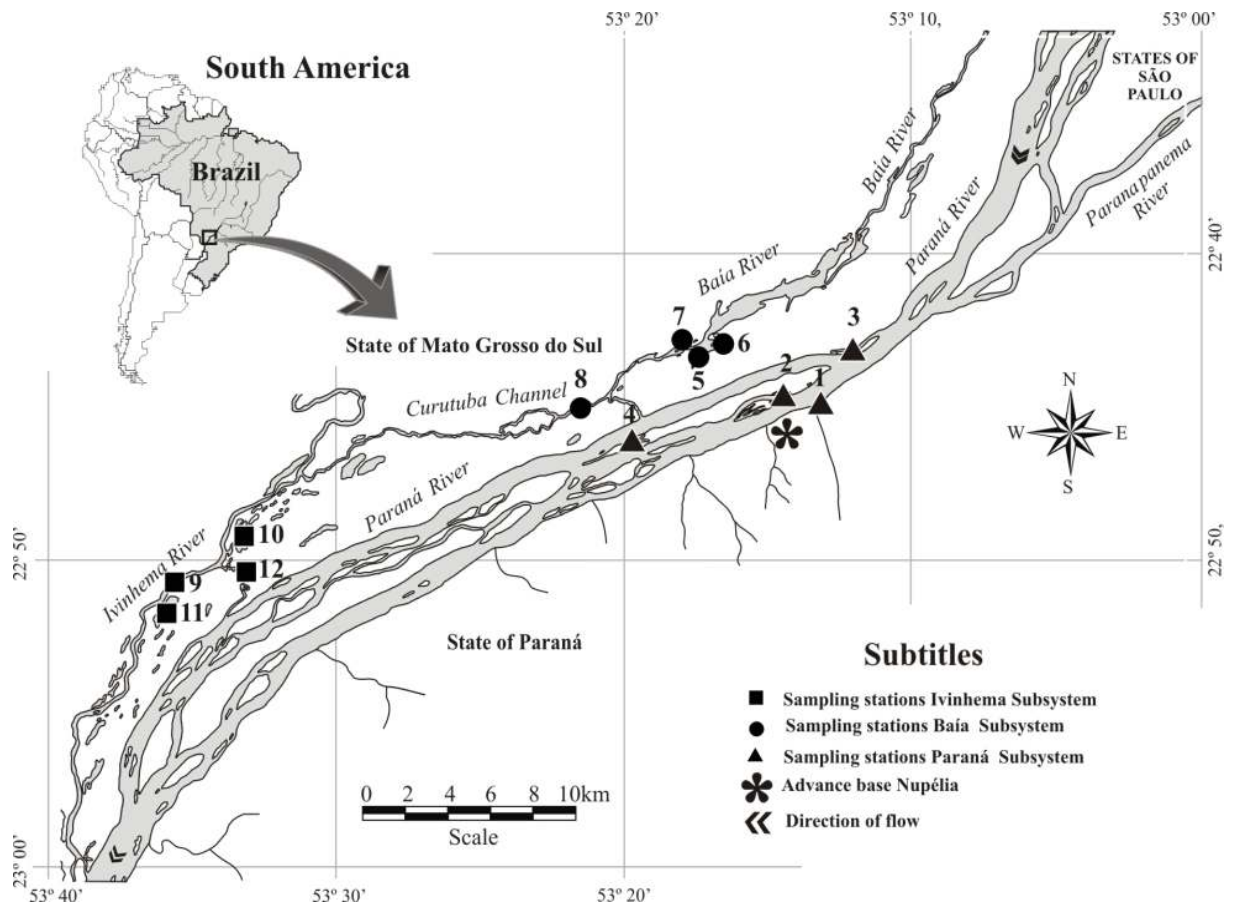
## Material and methods

### Study area

The Upper Paraná River is characterized by an extensive floodplain that was originally 480 km in length. However, after the construction of the Engenheiro Sérgio Motta Dam in 1998, its extent was reduced to 230 km, between this dam and Itaipu Reservoir (AGOSTINHO et al., 2008). We developed this study in the Upper Paraná River floodplain, in 12 different environments (lotic and lentic) inserted in the Long Term Ecological Research (LTER) site 6 (Figure 1). The selected environments included the Baía River (because semilentic conditions, as reduced flow and high organic matter), Osmar, Garças, Guaraná, Fechada, Ventura and Patos lakes as the lentic environments, while Ivinhema and Paraná rivers and Ipoitã and Curutuba channels as lotic environments.

### Data collection

We collected zoobenthos samples on March, June, September and December 2009 at 12 sites using a modified Petersen grab (0.0345m<sup>2</sup>). In each environment, benthic samples were taken from the center, right and left margins, three samples for biological analysis and one for particle size analysis. We washed the samples collected for biological analysis through a set of sieves (2.0, 1.0 and 0.2 mm). The material retained on the last sieve was fixed in 80% alcohol and sorted under a stereomicroscope. We identified Oligochaeta species to the lowest taxonomic level according to Brinkhurst and Marchese (1991).



**Figure 1.** Location of sampling stations. 1- Paraná River; 2- Pau Veio Backwater; 3- Garças Lake; 4- Osmar Lake; 5- Baía River; 6- Fechada Lake; 7- Guaraná Lake; 8- Curutuba Channel; 9- Ivinhema River; 10- Patos Lake; 11- Ventura Lake; 12- Ipoitã Channel.

Particle size analysis was determined using the methodology of Wentworth (1922) and organic matter content was estimated from 20 g sediment incinerated at 560°C four hours. The Limnology Laboratory team (Nupelia /UEM) measured, concomitant to biological samplings, the following abiotic variables: pH, temperature (°C), conductivity ( $\mu\text{S cm}^{-1}$ ), dissolved oxygen ( $\text{mg L}^{-1}$ ) and depth (m).

### Data analysis

The beta diversity provides dissimilarity measures between environments analyzed, but, according to Baselga (2010), to evaluate the influential factors on the results, we partitioned the total dissimilarity (Sorensen dissimilarity -  $\beta_{\text{sor}}$ ) into the following two components: spatial turnover ( $\beta_{\text{sim}}$ ) and nestedness ( $\beta_{\text{nes}}$ ). Thus, we can evaluate if the total dissimilarity is more related to the species replacement between sites (turnover) or species loss from site to site (nestedness), in lentic and lotic environments. These calculations were made from a routine work executed on R program, with the *vegan* package, according to Baselga (2010).

The partition of beta diversity was calculated pairwise between each environment, where the mean of total dissimilarity ( $\beta_{\text{sor}}$ ) and of each component ( $\beta_{\text{sim}}$  and  $\beta_{\text{nes}}$ ) was measured for lentic *vs.* lentic (lentic), lotic *vs.* lotic (lotic) and lotic *vs.* lentic environments. Then, from the mean, we calculated the proportion of each component in relation to the total dissimilarity, in order to make the data more comparable (Equation 1). We made the graphs using Statistica software (STATSOFT, 2005).

$$\beta_{\text{COMP.L}} (\%) = (\beta_{\text{sor.L}} / \beta_{\text{COMP.L}}) * 100 \quad (\text{Equation 1})$$

where  $_{\text{COMP}}$  = beta diversity component ( $\beta_{\text{sim}}$  or  $\beta_{\text{nes}}$ );  $_{\text{L}}$  = environment (lentic, lotic and lotic *vs.* lentic). In this way,  $\beta_{\text{COMP.L}} (\%)$  is the proportion of the total dissimilarity, which is explained by a given component ( $\beta_{\text{sim}}$  or  $\beta_{\text{nes}}$ ) to a given environment ( $_{\text{L}}$ ),  $\beta_{\text{sor.L}}$  is the Sorensen dissimilarity of a given environment ( $_{\text{L}}$ ), whereas  $\beta_{\text{COMP.L}}$  is the mean dissimilarity of this component.

We used Redundancy Analysis (RDA) to measure the main environmental variables involved in the Oligochaeta community structure.

This is a method that combines Regression and Principal Component Analysis (PCA), being a direct extension of the Regression Analysis to model multivariate data (LEGENDRE; LEGENDRE, 1998). Once our study did not aim to evidence temporal differences, the four samples were treated as replicates and we performed only one redundancy analysis. We use the *permutest* function to assess the significance of the analysis explanation. We used a species abundance matrix and another with environmental variables (depth, temperature, conductivity, pH, dissolved oxygen, pebbles, granules, very coarse sand, coarse sand, medium sand, fine sand, very fine sand, mud and organic matter). This analysis was run using the R Core Team (2013), through *vegan* package.

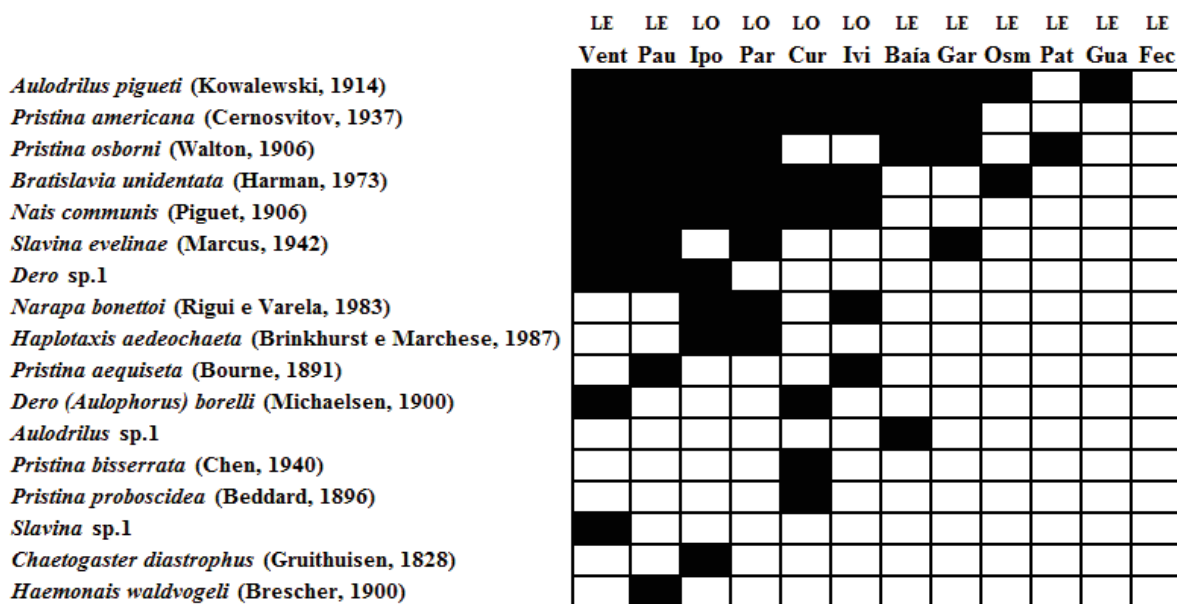
## Results

We recorded 986 individuals of Oligochaeta, belonging to 17 taxa distributed into three families: Naididae, Narapidae and Haplotaxidae. Naididae was the most representative family, with 15 taxa, followed by Narapidae, one species (*Narapa bonettoi*) and Haplotaxidae, one species (*Haplotaxis aedeochaeta*). In the family Naididae, Naidinae had higher richness, but Tubificinae, despite the low richness (only *Aulodrilus pigueti* and *Aulodrilus* sp.1), was also representative due to the predominance of *Aulodrilus pigueti* in most

environments. Species ordered on the top of the matrix, such as *A. pigueti*, *Pristina americana*, *Pristina orborni*, *Nais communis* and *Bratislavia unidentata*, were the most frequent species, occurring in many environments. On the other hand, species that were in the end of matrix represent the rarest, with low occurrence. We observed more rare species than common (Figure 2).

Considering this presence/absence matrix of Oligochaeta (Figure 2), we also observed that Ventura and Pau Vêio (lentic environments) and the four lotic environments were the richest ones, whereas Guaraná and Patos lakes have low richness (with the occurrence of a single species). In Fechada Lake, we observed no Oligochaeta.

In lentic environments, the nestedness component ( $\beta_{nes}$ ) had a greater contribution to the total dissimilarity, different from that observed in lotic environments, where the turnover component ( $\beta_{sim}$ ) showed a higher value (Table 2). Differences between components  $\beta_{sim}$  and  $\beta_{nes}$  were verified for lentic and lotic environments (Figure 3A e Figure 3B). By analyzing the beta diversity between different environments (lotic *vs.* lentic), we noticed a very similar contribution of nestedness and turnover components, so that the percentage values of the two components were very close (Figure 4).

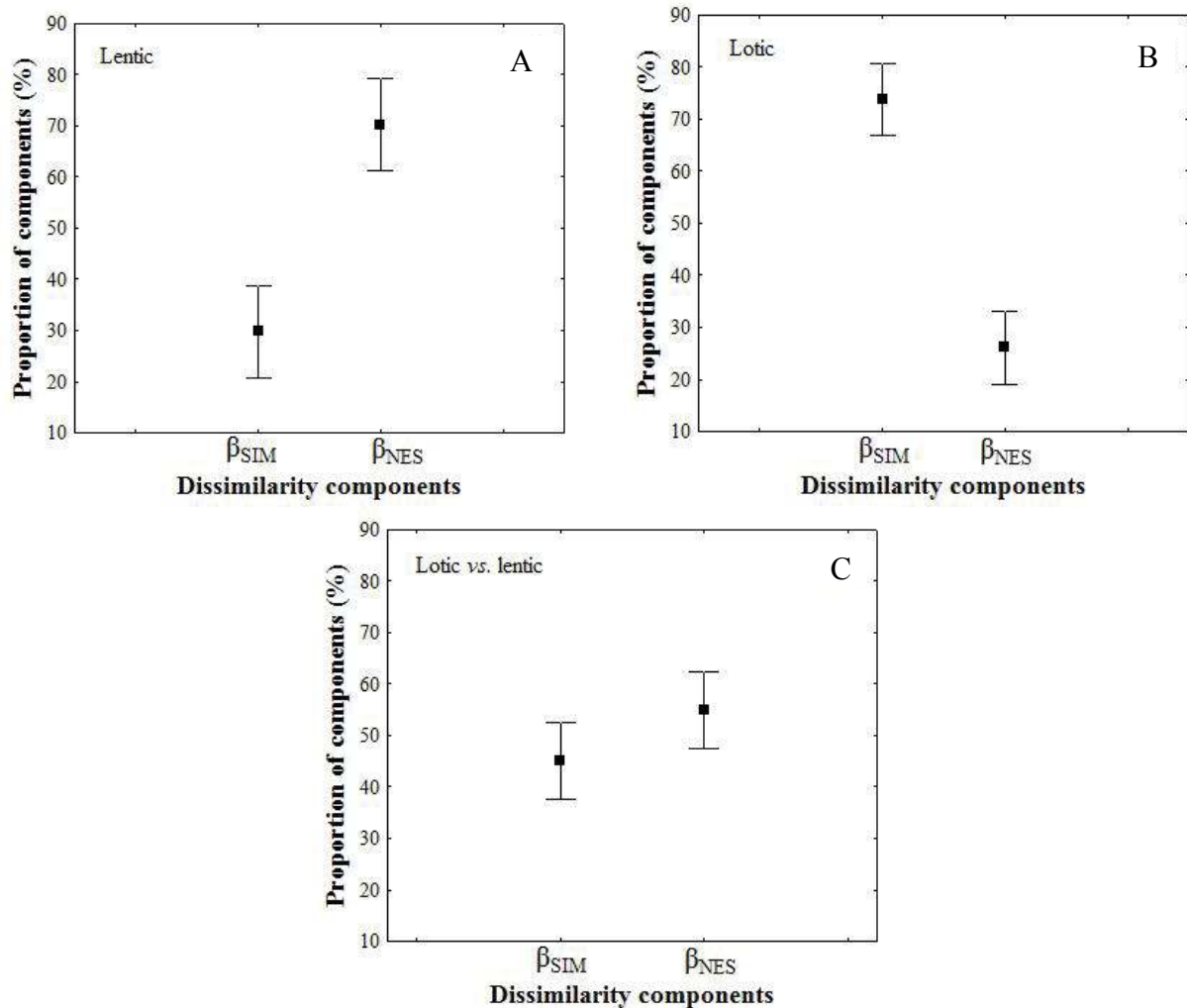


**Figure 2.** Presence (black square) and absence (white square) of Oligochaeta taxa in different environments in the Upper Paraná River floodplain. LE= lentic features; LO= lotic features; Vent= Ventura Lake; Pau= Pau Vêio Backwater; Ipo= Ipoitã Channel; Cur= Curutuba Channell; Ivi= Ivinhema River; Baía= Baía River; Gar= Garças Lake; Osm= Osmar Lake; Pat= Patos Lake; Gua= Guaraná Lake; Fec= Fechada Lake.

**Table 2.** Partition of beta diversity (Sorensen dissimilarity -  $\beta_{sor}$ ) in two components: spatial turnover ( $\beta_{sim}$ ) and nestedness ( $\beta_{nes}$ ). Partition of dissimilarity in mean and percentage according to Sorensen dissimilarity.

| Partition of $\beta$ diversity | $\beta_{SIM}$ |       |                  | $\beta_{NES}$ |       |                  | $\beta_{SOR}$ |       |                  |
|--------------------------------|---------------|-------|------------------|---------------|-------|------------------|---------------|-------|------------------|
|                                | Lentic        | Lotic | Lotic vs. Lentic | Lentic        | Lotic | Lotic vs. Lentic | Lentic        | Lotic | Lotic vs. Lentic |
| Mean                           | 0.19          | 0.27  | 0.25             | 0.43          | 0.08  | 0.33             | 0.62          | 0.36  | 0.58             |
| Proportion                     | 30.46         | 76.80 | 42.69            | 69.54         | 23.20 | 57.31            |               |       |                  |

LE= lentic features; LO= lotic features; Vent= Ventura Lake; Pau= Pau Véio Backwater; Ipo= Ipoitã Channel; Cur= Curutuba Channell; Ivi= Ivinhema River; Baía= Baía River; Gar= Garças Lake; Osm= Osmar Lake; Pat= Patos Lake; Gua= Guaraná Lake; Fec= Fechada Lake.



**Figure 3.** Partitioning of beta diversity in spatial turnover ( $\beta_{sim}$ ) and nestedness ( $\beta_{nes}$ ) from environments with lentic features (A), lotic features (B) and lotic vs. lentic features (C). Symbols= mean; bars = standard error.

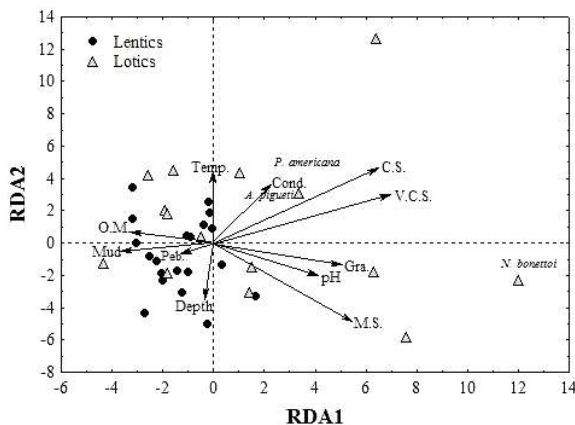
The results of Redundancy Analysis (RDA) explained 60% of the total data variance data ( $p < 0.05$ ) and  $R^2$  adjusted= 0.33. We observed, in general, a separation between lentic and lotic environments, where higher values of medium sand, granules, pH, coarse sand and very coarse sand were observed in lotic environments and higher values of organic matter, mud, pebbles and temperature in lentic environments. For the species, only *N. bonettoi* was strongly correlated

with lotic environments. In addition, lentic environments were more similar each other than lotic ones (Figure 3).

**Discussion**

In nature, the replacement and loss (or gain) of species are combined in an infinite number of ways, leading to complex patterns of community dissimilarity (CARVALHO et al., 2013). In our study, the hypothesis was partially supported,

because between environments with more similar hydrological characteristics, only in the lentic the nestedness component was higher, while in more different environments, both the turnover and nestedness components had a very similar contribution to the total dissimilarity found. Our results highlight the complexity of biological communities, where many patterns can be registered according to different environments analyzed.



**Figure 4.** Redundancy Analysis for Oligochaeta community and abiotic variables in lentic and lotic environments in the Upper Paraná River floodplain (OM= organic matter; Peb= pebbles; Temp= temperature; Cond= conductivity; CS= coarse sand; VCS= very coarse sand; Gra= granules; MS = medium sand).

In lotic environments, the turnover component was more important to the total dissimilarity. This is related to the fact that, among the considered lotic environments, we have two large rivers (Paraná and Ivinhema) and two secondary channels (Curutuba and Ipoitã) with very different characteristics. That could make these environments more dissimilar from lentic (environments with a reduced flow and high organic matter) and, therefore, with a higher turnover of species between them. The Curutuba channel differs from the other lotic environments because it consists mainly of pebbly substrate and has slower flow (ROCHA; SOUZA FILHO, 2008), which consequently leads to an increase in the amount of organic matter. Species such as *Dero (Aulophorus) borelli*, *Pristina bisserrata* and *Pristina proboscidea* occurred, among lotic environments, exclusively in the Curutuba Channel, which may suggest that these species should occur in local with these characteristics, and then, contributed to the turnover in lotic environments.

On the other hand, *Narapa bonettoi* and *Haplotaxis aedeochaeta* are found in velocity conditions and sandy sediments (MONTANHOLI-MARTINS; TAKEDA, 2001; BLETTLER et al., 2008;

MARCHESE et al., 2008), characteristics of Paraná and Ivinhema rivers and Ipoitã Channel (ROCHA; SOUZA FILHO, 2005; CORRADINI et al., 2008), where they occurred. The species of occurrence restricted to some environments demonstrated more contribution to beta diversity through turnover components. In this context, Pandit and Kolasa (2012) observed that the turnover increased with environmental variability among specialists but this relationship dissolved with generalist species.

Nestedness component was more important in lentic environments, which indicates that there was a higher loss than turnover of species among sites studied. This may have occurred because, except for the Baía, these environments are lakes, and in spite of having some particularities, share important common characteristics, such as reduced flow and higher organic matter content and lower dissolved oxygen. RDA demonstrated it, because all the lentic environments were more similar than lotic ones, and were related to higher levels of mud and organic matter. These features may be decisive to the occurrence of Oligochaeta, and then, only the species adapted to these conditions could establish, making environments with lentic characteristics more similar to each other than those with lotic characteristics.

Differences in habitat characteristics such as isolation, size, quality and nested habitats or in species attributes, such as area requirements, abundance and tolerance to abiotic factors are the major explanations for the emergence of nestedness in communities (DARLINGTON, 1957; ATMAR; PATTERSON, 1993; WRIGHT et al., 1998; HIGGINS et al., 2006; HYLANDER et al., 2005). Some of these factors, such as habitat quality and tolerance to abiotic factors, may have favored the establishment of species between lentic environments, so, the sites with more suitable conditions could sustain a higher number of species. Therefore, we observed a lower turnover and increased nestedness, where the environments which have fewer species became merely a subset of the richest environments. Moreover, only the most common species, such as *P. americana* and *A. pigueti*, related to high values of organic matter, mud and low dissolved oxygen (MONTANHOLI-MARTINS; TAKEDA, 1999) were successful in poor environments, whereas the less common occurred mainly, or exclusively, in rich environments.

When analyzed environments with more different characteristics, that is, lentic *vs.* lotic, we observed a very similar contribution of both components. Some sites (poorer in relation to the

number of species) were subsets of those richer in species. This can be observed through the high contribution of the nestedness component to the total dissimilarity. Nevertheless, other sites showed a completely different species composition, also indicating a significant contribution of the turnover component for the total dissimilarity. This is related to the recognition of the Upper Paraná River floodplain as having a high environmental heterogeneity (THOMAZ et al., 2004), therefore, able to support a high number of species (AGOSTINHO et al., 2004), which contribute to a high beta diversity.

### Conclusion

Although our hypothesis was partially confirmed, we found interesting results from the partitioning of beta diversity for Oligochaeta, where it was possible to evidence that its components, nestedness and turnover, were important in structuring this community. Nonetheless, in a different way between environments with more similar (nestedness for lentic and turnover for lotic) or dissimilar (almost the same contribution of both) characteristics. Moreover, the relationship between these findings and environmental factors allow us to know a little more about ecology and distribution of this group. Therefore, we consider the partitioning of beta diversity an important tool for a better understanding of the factors that influence richness, composition and distribution of biological communities.

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