Acta Limnologica Brasiliensia

Publication of the
Brazilian Association of
Limnology

Thematic Section: Upper Paraná River Floodplain

Acta Limnologica Brasiliensia, 2017, vol. 29, e118
http://dx.doi.org/10.1590/S2179-975X7617
ISSN 2179-975X on-line version

Differences in environmental heterogeneity promote the nestedness of Chironomidae metacommunity in Neotropical floodplain lakes

Diferenças na heterogeneidade ambiental promove o aninhamento da metacomunidade de Chironomidae em lagoas de inundação neotropicais

---

Gisele Daiane Pinha[1]*, Rafael Prandini Tramonte[1], Camila Gentilin Bilia[2] and Alice Michiyo Takeda[1]

[1]Programa de Pós-graduação em Ecologia de Ambientes Aquáticos Continentais, Universidade Estadual de Maringá – UEM, Av. Colombo, 5790, CEP 87020-900, Maringá, PR, Brazil

[2]Programa de Pós-graduação em Biologia Comparada, Universidade Estadual de Maringá – UEM, Av. Colombo, 5790, CEP 87020-900, Maringá, PR, Brazil

*e-mail: pinhagisele@hotmail.com

Cite as: Pinha, G.D. et al. Differences in environmental heterogeneity promote the nestedness of Chironomidae metacommunity in Neotropical floodplain lakes. *Acta Limnologica Brasiliensia*, 2017, vol. 29, e118.

Abstract: Aim: Gradients of environmental heterogeneity perform a strong influence on the distribution of organisms and determine differences in composition, where more physically complex habitats harbor greater species richness than those simpler. We took as assumptions that differences in environmental requirements of taxa promote distinct distribution patterns which are carried through to community nestedness. Therefore, we hypothesized that more heterogeneous sites hold more nested, richer and abundant communities than those less heterogeneous ones. **Methods:** We analyzed Chironomidae occurrence of 29 floodplain lakes, through one-year-surveys. Analyses of variance were performed to test differences among data. To test our hypothesis, we calculated correlations between the gradients of environmental heterogeneity and Chironomidae metacommunity. **Results:** Highest values in all Chironomidae attributes were recorded in general to the floodplain lakes from Paraná System, mainly in September. Positive correlation between all Chironomidae attributes (i.e, richness, density, Biodiversity score and NODF index) both with PCA scores and variation coefficient values supported our initial hypothesis about the importance of environmental heterogeneity in metacommunity assembly. **Conclusions:** We have demonstrated how differences in environmental heterogeneity promote the nestedness in floodplain lakes and the importance of more heterogeneous places in supporting richer and more abundant communities in species. Such results contribute to future studies on composition and richness of Chironomidae community in other kind of environments. Nested distribution suggests that, despite the existence of floodplain lakes including most of the Chironomidae richness, considering the dispersal ability of species and environmental requirements, there is a strong interaction between all environments of the area. Therefore, areas that have locations with different patterns of richness and composition are critical to maintaining the diversity of the group at the landscape level.

Keywords: biodiversity; distribution models; floodplain; dispersion; richness.

Resumo: Objetivo: Os gradientes de heterogeneidade ambiental exercem uma forte influência na distribuição de organismos e determinam diferenças na composição, onde habitats fisicamente mais complexos possuem maior riqueza de espécies do que aqueles mais simples. Tomamos como pressupostos que as diferenças nos requisitos ambientais dos taxa promovem padrões de distribuição distintos, que contribuem para o aninhamento da comunidade. Portanto, levantamos a hipótese de que locais mais heterogêneos mantenham comunidades mais aninhadas, mais ricas e abundantes do que locais menos heterogêneos. **Métodos:** Analisamos a ocorrência de Chironomidae de 29 lagoas de uma planície de inundações, ao longo de um ano de amostragens. Foram realizadas análises de variância para testar diferenças entre dados. Para testar nossa hipótese, calculamos as correlações entre os gradientes de heterogeneidade ambiental e a comunidade Chironomidae. **Resultados:** Os valores mais altos de todos os atributos de Chironomidae foram registrados em geral para as lagoas de inundação do Sistema Paraná, principalmente em setembro. A correlação positiva entre todos os atributos de Chironomidae (ou seja, riqueza, densidade, escore de Biodiversidade e índice de NODF), tanto com os escores PCA quanto com os valores do coeficiente de variação, corroboram à nossa hipótese inicial sobre a importância da heterogeneidade ambiental na montagem das metacomunidades. **Conclusões:** Nós demonstramos como as diferenças na heterogeneidade ambiental promovem o aninhamento nas lagoas de planícies de inundação e a importância de lugares mais heterogêneos para apoiar comunidades mais ricas e mais abundantes em espécies. Tais resultados contribuem para futuros estudos sobre composição e riqueza da comunidade de Chironomidae em outros tipos de ambientes. A distribuição aninhada sugere que, apesar da existência de lagoas de inundação que incluem a maior parte da riqueza de Chironomidae, considerando a capacidade de dispersão das espécies e os requisitos ambientais, há uma forte interação entre todos os ambientes da área. Portanto, áreas que possuem locais com diferentes padrões de riqueza e composição são fundamentais para manter a diversidade do grupo ao nível da paisagem.

Palavras-chave: biodiversidade; modelos de distribuição; planície de inundação; dispersão; riqueza.

1. Introduction

Some of the goals of community studies have been the search for both the distribution patterns in biological communities and the mechanisms that promote changes in species richness and composition of a given area (Leibold et al., 2004; Velho et al., 2004; Cadotte et al., 2006; Moore & Swihart, 2007). In this context, arises a new approach, which considers as a set of local communities that are linked by dispersal of multiple potentially interacting species (Gilpin & Hanski, 1991; Wilson, 1992). This concept, known as Metacommunity theory, describes processes that occur at the various scales and suggests novel ways of thinking about both interaction and dispersion of species (Leibold et al., 2004; Cadotte et al., 2006; Presley et al., 2011).

Nestedness is one of the most studied and important distribution pattern in metacommunities. Nestedness pattern is found when sites with lower species richness tend to harbor proper subsets of those, richer (Patterson & Atmar, 1986; Atmar & Patterson, 1993). In a perfectly nested system, any species present in a given site will be found in all sites with equal or greater species richness, and any species absent from a site will be absent from all less rich sites as well (Moore & Swihart, 2007). Therefore, nestedness requires a gradient in richness, and nestedness among assemblages with identical richness should not exist (Almeida-Neto et al., 2008).

Nested distribution of organisms can arises from differences in the attributes of the species (Kodric-Brown & Brown, 1993), such as area requested, abundance and tolerance to abiotic variables (Cook & Quinn, 1998; Almeida-Neto et al., 2008) that result in selective extinction (Patterson & Atmar, 1986) or differential colonization (Cook & Quinn, 1995) among species, or yet, by differences in environmental variables such as isolation, size, quality, and habitat nestedness (Almeida-Neto et al., 2008). In this case, both heterogeneity habitat composition and structure (Worthen, 1996; Tolonen et al., 2001; Downes et al., 2000) perform a strong influence on the distribution of organisms and determine differences in composition, where more physically complex habitats harbor greater species richness than those simpler (Bell et al., 1991; Downes et al., 2000; Shostell & Williams, 2007). Although many studies have just explored whether a community displays the pattern nested or not and which metric should be used (e.g., Cook & Quinn, 1995; Wright et al., 1997; Almeida-Neto et al., 2008; Rashleigh 2008; Ulrich et al., 2009), few of them have evaluated the relationship between such pattern and the environmental characteristics (e.g., Petsch et al., 2015).

Floodplains, like the Upper Paraná River, are considered as holders of high environmental heterogeneity (Thomaz et al., 2007; Lansac-Tôha et al., 2009), formed by a mosaic of aquatic habitats, terrestrial and transition (Thomaz et al., 2007) where are found several floodplain lakes (Souza Filho & Stevaux, 2004). According to Worthen et al. (1998), Fernández-Juricic (2002) and Bloch et al. (2007) in sites like these, different architectures can be determinant for success or not of the establishment of a species, in accordance both with its environmental requirements and its dispersion ability.

Variability in richness and environmental requirements of each species make Chironomidae a useful group for exploring distribution patterns in the Paraná River Floodplain (Rosin et al., 2009, 2010; Petsch et al., 2015). Furthermore, this group is important from the standpoint of environmental conservation and management (Morais et al., 2010; Roque et al., 2010), because if there is a nestedness of species in a region, the areas with high taxa harbor the majority diversity, encompassing both taxa over generalists, as those rarer, or more specialists in a certain resource (Melo et al., 2014).

Relationships between attributes of richness, density and Biodiversity scores with environmental characteristics were accessed for comparing the occurrence of Chironomidae morphospecies in 29 floodplain lakes. We took as assumptions that differences in environmental requirements of taxa promote distinct distribution patterns which are carried through to community nestedness. Therefore, we hypothesized that more heterogeneous sites hold communities which are more nested, richer and abundant than less heterogeneous sites. Thus, we expect that the greater environmental similarity between two environments, greater number of species shared between them.

2. Material and Methods

2.1. Study area

The Upper Paraná River floodplain (located between the geographical coordinates: 22°40'S; 53°10'W and 22°60'S; 53°40'W) is characterized by an extensive wetland with about 230 Km, and located 18 Km downstream from the Dam of Engenheiro Sérgio Motta, approximately 200 Km from Itaipu Reservoir (Orfeo & Stevaux, 2002). The climate of the region, according to the Köppen system, is classified as Cfa (tropical-subtropical), with an average annual temperature of 22 °C and average annual rainfall of 1500 mm (Eletrosul, 1986).

We performed sampling at 29 floodplain lakes of three different systems of the upper Paraná River floodplain, named according to the principal channel that each lake is related: *i)* floodplain lakes from Baía River; *ii)* floodplain lakes from Ivinhema River; *iii)* floodplain lakes from Paraná River (Figure 1). Lakes differ regarding variations in physical and chemical characteristics of water (Roberto et al., 2009), besides differences in habitat structure, area, depth, height of the dike marginal distance of the channels, macrophyte composition, riparian vegetation cover on the water body.

2.2. Biological and abiotic data sampling

To study the distribution pattern of Chironomidae we performed sampling quarterly from March to December 2010, entered the Long Term Ecological Program (PELD/CNPq). At each station, we took samples at three sites along transects: two close to the shores and one in the central region of the water body. At each site, four samples were taken with a modified Petersen grab: three for biological analysis and one for sedimentological estimating the organic matter content.

Concomitants the biological samplings we surveyed data of water temperature, dissolved oxygen, pH, turbidity and conductivity. The chlorophyll-*a* ($\mu g\ L^{-1}$), Nitrate ($NO_3\ \mu g\ L^{-1}$) e Orthophosphate ($PO_4\ \mu g\ L^{-1}$) we determined from an aliquot of 500 ml of water sample stored in a polyethylene bottle and cooled to -20 °C by methods proposed by Golterman et al. (1978), Zagatto et al. (1982) and Mackereth et al. (1978), respectively.

The sediment was washed in 2.0, 1.0 and 0.2 mm sequential sieves. The sediment retained by the last sieve was fixed in 70% alcohol, and was sorted using a stereo-microscope. Chironomidae larvae were dissected and mounted on slides with Hoyer, according to methodology proposed by Trivinho-Strixino & Strixino (1995). The larvae were identified to the lowest possible taxonomic level using the identification keys of Trivinho-Strixino (2011) and Epler (1995). The slides are stored in the Zoobentos Laboratory (NUPELIA/UEM), Maringá, Brazil.

We determined the riparian vegetation cover over each lake from a gridded mirror, where counted the number of squares filled, according to the Equation 1:

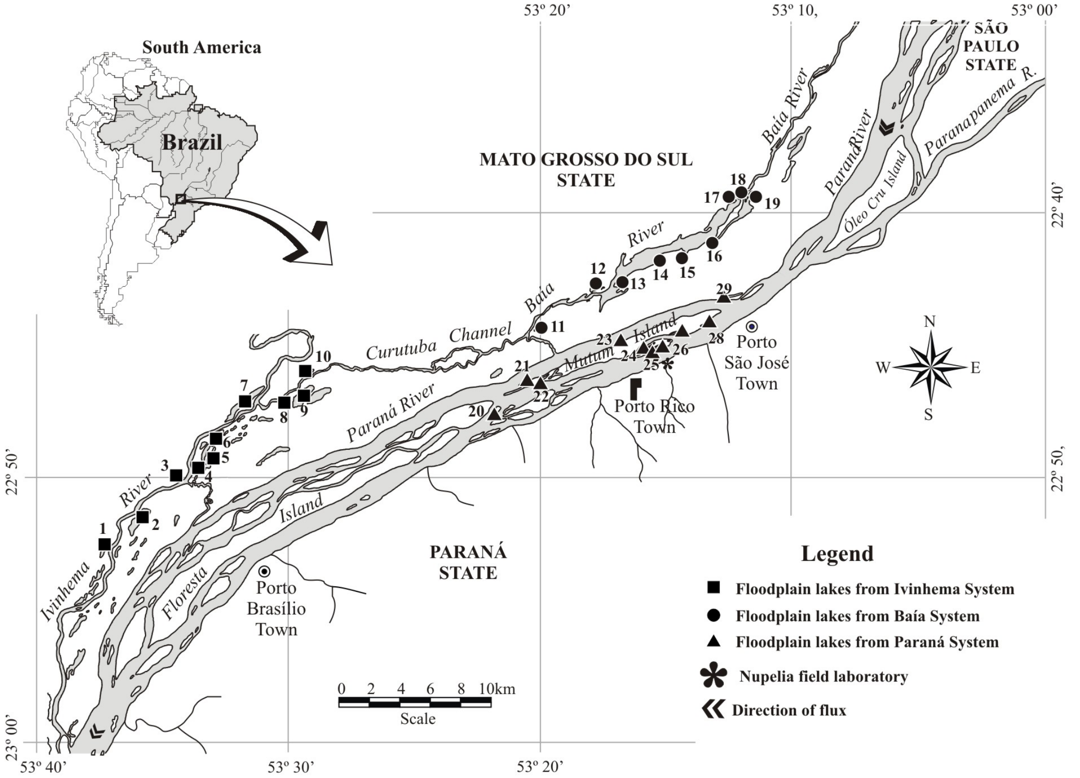

Figure 1. Map of the Upper Paraná River Floodplain with the localization of the sampled lakes. *Ivinhema System*: (**1**) Peroba = Per; (**2**) Ventura = Ven; (**3**) Zé do Paco = ZPa; (**4**) Boca Ipoitã = BIp; (**5**) Patos = Pat; (**6**) Capivara = Cap; (**7**) Finado Raimundo = FRa; (**8**) Jacaré = Jac; (**9**) Sumida = Sum; (**10**) Cervo = Cer. *Baía System*: (**11**) Traíra = Tra; (**12**) Guaraná = Gua; (**13**) Fechada = Fec; (**14**) Pousada Garças = PGa; (**15**) Porcos = Por; (**16**) Aurélio = Aur; (**17**) Maria Luiza = MLu; (**18**) Gavião = Gav; (**19**) Onça = Onc. *Paraná System*: (**20**) Pombas = Pom; (**21**) Manezinho = Man; (**22**) Osmar = Osm; (**23**) Bilé = Bil; (**24**) Leopoldo = Leo; (**25**) Genipapo = Gen; (**26**) Clara = Cla; (**27**) Pau Véio = PVe; (**28**) Pousada = Pou; (**29**) Garças = Gar.

$$\mathrm{RVC} = \left(\frac{\sum_{i=1}^{n} \mathrm{Fq}}{n} \right) * 100 \qquad (1)$$

where the percentage of tree cover (*TC*) was done by sum of the filled squares (*Fq*) divided by total of squares (*n*) multiplied by 100.

We determined the granulometric texture using methodology modified of Wentworth (1922). Organic matter content was obtained from by burning 10 g sediment at furnace (560 °C) for four hours.

2.3. Data analysis

To access some gradient in environmental data we also performed a Principal Components Analysis (PCA; Gauch, 1986). This analysis reduces the dimensionality of the data, thus facilitating the interpretation of results and identification of spatial patterns. We used ANOVA to test the significance of the axes generated by PCA, and we represent the results graphically. PCA analysis was performed PC-Ord 5.0 software (McCune & Mefford, 1999), the generated axes were tested by ANOVA and the graphics made by the software Statistica 7.1 (StatSoft, 2005). To access the environmental heterogeneity, we calculated the coefficient of variation for each lake. For the environmental heterogeneity index, we considered the physical (temperature, structure of the substrate and the environment, the influence of the channel); chemical (concentrations of oxygen, nitrate, ammonium and phosphate) and biological characteristics (riparian vegetation cover and chlorophyll-*a*) of each environment.

Biodiversity Score (BS; Ranta et al., 1999) was achieved by summing the morphotypes Rarity Index i_1, i_2, i_3,..., i_n from the environments *j*, using the Equation 2:

$$BS_j = \sum_{i=1}^{n} RI \qquad (2)$$

where BS_j is the Biodiversity Score for each environment *j*; and *RI* is the Rarity Index for each species *i* which was accessed by Equation 3:

$$RI = \frac{1}{\sum_i O_i} \qquad (3)$$

(with $O_i < RI > 0$ *e* $1 \le i \le n$), where ΣO_i is the sum of the environments in which there was found the morphotype incidence *i*, among the total of studied environments. The rarer the occurrence of a species in an environment, the higher will be its index (varying from $0 < RI \le 1$).

Higher *BS* values suggest a greater incidence of rare taxa in the analyzed environment *j*. Because *BS* varies both with number of taxa found and with number of sampled environments, we made a correction for their values, using the Equation 4. Thus, relationships between environmental scores are retained and our results can be compared with other works.

$$EB(\%) = \left(\frac{EB_j}{N}\right) * 100 \qquad (4)$$

where *EB(%)* is the Biodiversity Score percentage of environment *j*, according to the total number of taxa included in the study (*N*).

To detect the level of nestedness between Chironomidae communities considering the variations of each floodplain lake along the sampled periods, we performed nestedness analyses, according to the NODF index ("Nestedness metric based on Overlap and Decreasing Fill"). The NODF index was proposed by Almeida-Neto et al. (2008) and is based on a comparison of pairs of rows using properties associated with nestedness in an incidence matrix. We built an incidence matrix based on the ordering of environments into columns according to their environmental "status", with species richness arranged in rows from the most frequent to the rarest. We performed nestedness analysis through the *vegan* package in the free software R (R Development Core Team, 2011).

To identify patterns for the gradient of environmental heterogeneity (i.e., eigenvectors of the first PCA axis and variation coefficient) and biological attributes (i.e, species richness, biodiversity index, density and NODF index) we performed analyses of variance (one-way ANOVA) considering both spatial (among lakes) and temporal (among periods) variations. Relationships between the gradient of environmental heterogeneity and the attributes of Chironomidae communities were accessed by Spearman's correlations. The analysis and graphics were performed in the software Statistica 7.1 (Statsoft, 2005). All associations were inferred with significant values for $\alpha \le 0.05$.

3. Results

Principal Components Analysis (PCA) was significant for the first two axes even when considered variations among floodplain lakes systems (Axis 1: $F_{(2,113)} = 35.50$; p<0.01; Axis 2: $F_{(2,113)} = 10.59$; p<0.01) or among lakes (Axis 1: $F_{(27,88)} = 13.69$; p<0.01; Axis 2: $F_{(27,88)} = 3.51$; p<0.01), which summarized 33.92% of data variance. The distinction of the floodplain lakes in relation to both physical and chemical variables of the water, as the characteristics of the surroundings and granulometric texture was essential for the grouping of the floodplain lakes between the axes and highlight the spatial separation of the lakes sampled Paraná River in relation to other environments. Axis 1 was positively influenced by high values of conductivity, vegetation cover and granules, while high values of phosphorus, medium sand and chlorophyll-a influenced the negative quadrant of this axis (Figure 2). On the other hand, high values of course and fine sands influenced negatively the axis 2 while high concentrations of mud influenced positively such axis.

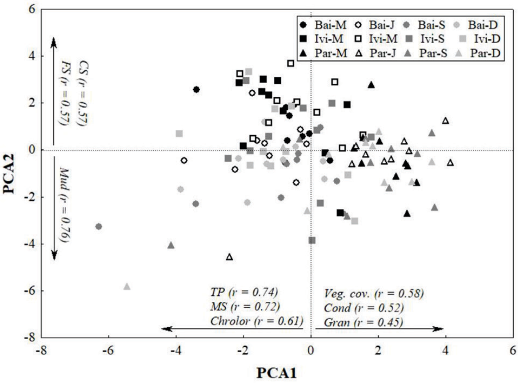

Figure 2. Principal Component Analysis Ordination showing the eigenvectors of environmental variables that most influenced axes 1 and 2. Legend: Bai = floodplain lakes system of Baía River; Ivi = floodplain lakes system of Ivinhema River; Par = floodplain lakes system of Paraná River; M = March; J = June; S = September; D = December. Inside of the graph: Cond. = conductivity; Chloro. = chlorophyll-a; gran. = Granules; CS = coarse sands; MS = medium sands; FS. = fine sands; Veg. cov. = vegetation cover; TP = total Phosphorus.

There were no differences in coefficient of variation in relation to floodplain lakes values (Figure 3A), but we found high values of this index for Ivinhema and Paraná systems than for Baía system (Figure 3B) and a tendency to increasing values through the sampled period (Figure 3C)

We recorded a total of 9098 Chironomidae larvae, identified in 104 morphospecies. Chironominae subfamily was the most representative (75 morphospecies), followed by Tanypodinae (25 morphoespecies) and Orthocladiinae (4 morphospecies).

Highest values of all Chironomidae attributes were recorded in general to the floodplain lakes from Paraná System (Figures 4 and 5), mainly in September (Figure 6). However, within each system were observed some environments richer than others: Maria Luíza to Baía sytem; Cervo, Patos and Ventura in Ivinhema River system and Bilé, Genipapo, Clara and Garças in Paraná River system (Figures 4A-D).

Correlations between the gradients of environmental and Chironomidae community attributes were all positive and significant (Table 1).

4. Discussion

Positive correlation between all Chironomidae attributes (i.e, richness, density, Biodiversity score and NODF index) both with PCA scores and coefficient of variation values supported our initial hypothesis about the importance of environmental heterogeneity in metacommunity assembly. We know for long time that heterogeneous environments can support more species, and there must be a positive relationship between the species diversity and structural complexity of the environment (Cornell & Lawton, 1992; Bell et al., 1991). The correlations between the gradients of environmental heterogeneity and biotic environment agree with these authors, suggesting that the more dissimilar are the environmental characteristics of two floodplain lakes, smaller than number of species shared between them.

From the Principal Component Analysis, we observe a clustering between floodplain lakes sampled the Paraná River, distinguishing them from others. The environments in this area are particularly interesting because the small size of their water bodies as well as the historical processes of their formation,

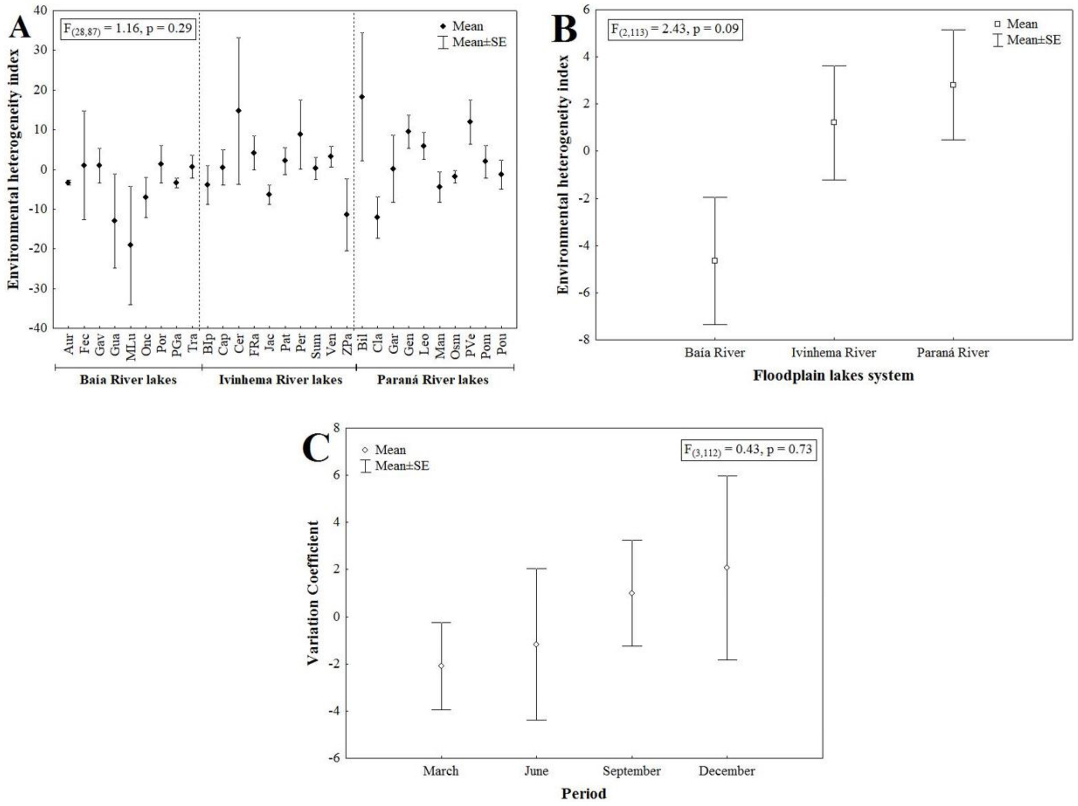

Figure 3. Coefficient of variation values according to the mean and standard error (SE) of (A) each floodplain lakes; (B) floodplain lakes system; and (C) periods. Please vide Figure 1 for lakes name abbreviation.

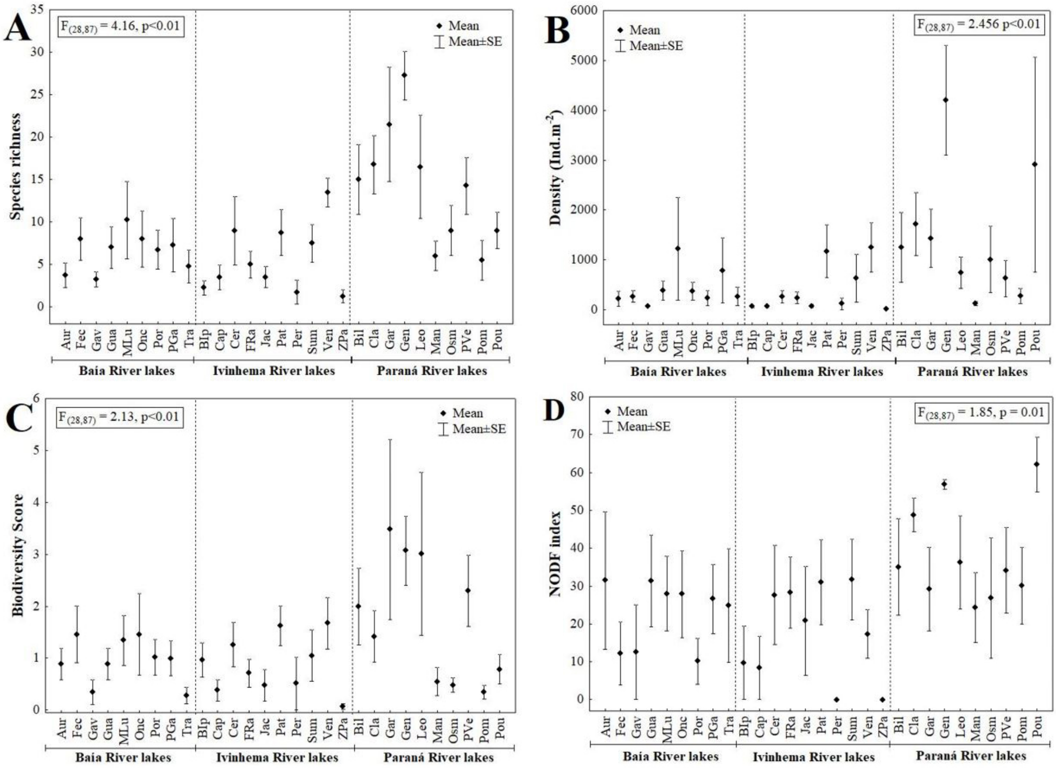

Figure 4. Variations in Chironomidae community in each floodplain lake according to the mean and standard error (SE) of (A) species richness; (B) density; (C) Biodiversity score; and (D) NODF index. Please vide Figure 1 for lakes name abbreviation.

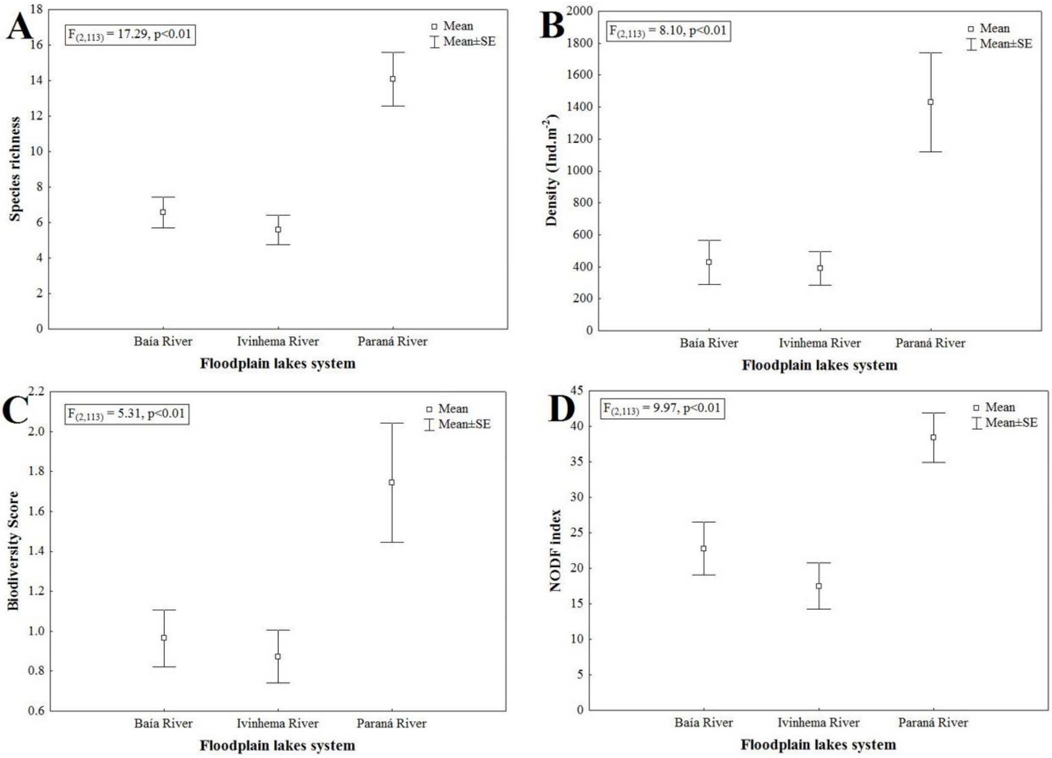

Figure 5. Variations in Chironomidae community in each floodplain lake system according to the mean and standard error (SE) of (A) species richness; (B) density; (C) Biodiversity score; and (D) NODF index.

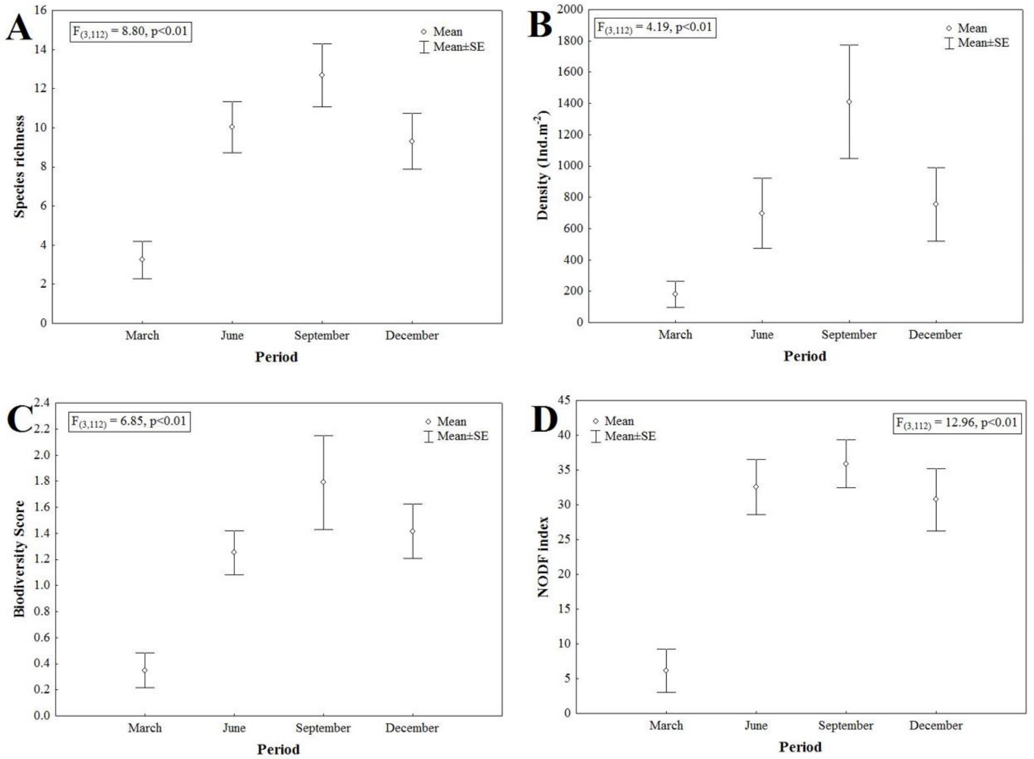

Figure 6. Variations in Chironomidae community in each sampled period according to the mean and standard error (SE) of (A) species richness; (B) density; (C) Biodiversity score; and (D) NODF index.

Table 1. Results of Spearman's correlation between the gradients of environmental heterogeneity with Chironomidae community attributes.

	Correl. (ρ)	$T_{(2,113)}$	p
PCA1 * S	0.268	2.969	0.004
CV * S	0.200	2.176	0.032
PCA1 * Density	0.183	1.985	0.050
CV * Density	0.216	2.364	0.020
PCA1 * BS	0.190	2.067	0.041
CV * BS	0.199	2.170	0.032
PCA1 * NODF	0.208	2.266	0.025
CV * NODF	0.192	2.090	0.039

PCA1 = Axis 1 scores of PCA; CV = coefficient of variation; S = species richness; BS = Biodiversity scores.

promote the presence of dense tree vegetation and well preserved in its banks, which promote similar limnological characteristics. Such results summed with the high values of coefficient of variation found for lakes of Paraná system may have influenced the high values found for attributes of species richness, density and Biodiversity score and suggest that these environments are more heterogeneous than those of other systems.

The presence of riparian vegetation cover on the banks of the lakes from Paraná System, may indicate a greater input of litter and branches the sediment in these bodies of water, which, according Sanseverino & Nessimian (2008), provides shelter and food source for the larvae of many genera of this group. Likewise, Callisto et al. (2002) and Kleine & Trivinho-Strixino (2005) emphasize the positive relationship between the presence of riparian vegetation with the abundance both Chironomidae as other invertebrates. This fact, summed of all other environmental characteristics of these water bodies are strengthened by habitat selection theory, which predicts that both spread and colonization of areas that provide a better fitness than species are highly nonrandom (Van Baalen & Hochberg, 2001; Morris, 2003).

Temporal variation of data was also significant in our study both for gradients of environmental heterogeneity and Chironomidae community attributes. According to Pinha et al. (2016), periods with high environmental heterogeneity (i.e., drought periods represented by September) can support more taxa in relation to sites or periods with low environmental heterogeneity (i.e., flood periods represented by March) and facilitate the formation of a nested distribution.

Nestedness analysis has been widely used to measure the structure of a biological community

(Fleishman & Murphy, 1999; Hylander et al., 2005; Meyer & Kalko, 2008) including lentic freshwater (Baber et al., 2004; Angeler et al., 2008; Wissinger et al., 2009), but few studies have explored the factors leading to this pattern (Florencio et al., 2011). Therefore, correlations between the attributes of species communities with characteristics of the environment are important to understand the processes that drive the biological communities of an area.

Although historical extinctions were originally assumed to be the main causes of nestedness of a region (Atmar & Patterson, 1993), local migrations, through differential dispersal abilities of the species may also be very important in generation of nestedness (Cook & Quinn, 1995), and allied to the requirements of each species to colonize or not an environment may have been the main cause of nestedness Chironomidae community of floodplain lakes. Despite Chironomidae being winged organisms when adults (Armitage et al., 1995), their dispersal ability, when we consider only one reproductive cycle, is limited, which makes the richest lakes important dispersers community to adjacent areas (*mass effect*; Gonzalez, 2009), where the colonization of species will depend both on their environmental requirements (*species sorting*; Gonzalez, 2009) and the environmental characteristics.

The nested pattern Chironomidae community observed here agrees with Cook et al. (2004), which considers the nestedness as the result of the set of species throughout the region being filtered by specific environmental restrictions of each. Thus, the distribution of each taxon between the floodplain lakes is determined by their ability to overcome environmental limitations. Based on these assumptions and on our results, a nested pattern will develop if there is a hierarchical relationship between (1) the species - in their sensitivity limiting factors; and (2) locations - if they are capable or not of supporting the species.

Correlations between Chironomidae community attributes and gradients of environmental heterogeneity are important for studies on conservation and ecosystem management. According Summerville et al. (2003), there is a tendency to change the focus of conservation biology: the preservation of a single rare species within a given habitat for the preservation of whole communities within larger regions requiring that more attention be given to the composition of Biodiversity and the way species interact spatially. This change is due in part to the fact that models based on patterns between species and habitat are rarely valid for all species within a community (Nally & Fleishman, 2004). Therefore, the ability to detect communities that include most of the species richness of site makes the nestedness analysis an important tool in the search for distribution patterns of a biological community and has been widely used in the studies about conservation and management of biodiversity of it given area.

Our understanding about conservation status of both species and ecosystem is poor worldwide (Nally & Fleishman, 2004). Thus, to assess their current state and estimating how environmental characteristics may affect their future condition are vital measures for making decisions that maximize protection of biodiversity and the services provided by the ecosystem. As we have demonstrated from the environmental characteristics we can predict how an environment will be rich in number of taxa of Chironomidae, thus contributing to future studies on composition and richness of this community.

Nested distribution suggests that, despite the existence of floodplain lakes including most of the Chironomidae richness, considering the dispersal ability of species and environmental requirements, there must be a strong interaction between all environments of the area. Therefore, areas that have locations with different patterns of richness and composition are critical to maintaining the diversity of the group at the landscape level.

Acknowledgements

We would like to thank the Long-Term Ecological Research (LTER/CNPq) program for the opportunity to develop this study, the Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura of the Universidade Estadual de Maringá (Nupelia/UEM) for logistical support and CAPES for the postgraduate scholarship. We are also thankful to two anonymous reviewers for their valuable comments about the manuscript. We also would like to thank the Basic Limnology Laboratory/Nupelia for providing abiotic variables data.

References

ALMEIDA-NETO, M., GIMARÃES, P., GUIMARÃES JUNIOR, P.R., LOYOLA, R.D. and ULRICH, W. A consistent metric for nestedness analysis in ecological systems: reconciling concept and quantification. *Oikos*, 2008, 117(8), 1227-1239. http://dx.doi.org/10.1111/j.0030-1299.2008.16644.x.

ANGELER, D.G., VIEDMA, O., CIRUJANO, S., ALVAREZ-COBELAS, M. and SÁNCHEZ-CARRILLO, S. Microinvertebrate and plant beta diversity in dry soils of a semiarid agricultural wetland complex. *Marine & Freshwater Research*, 2008, 59(5), 418-428. http://dx.doi.org/10.1071/MF07206.

ARMITAGE, P.D., PINDER, L.C. and CRANSTON, P. *The Chironomidae: the biology and ecology of non-biting midges*. London: Chapman & Hall, 1995.

ATMAR, W. and PATTERSON, B.D. The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia*, 1993, 96(3), 373-382. PMid:28313653. http://dx.doi.org/10.1007/BF00317508.

BABER, M.J., FLEISHMAN, E., BABBITT, K.J. and TARR, T.L. The relationship between wetland hydroperiod and nestedness patterns in assemblages of larval amphibians and predatory macroinvertebrates. *Oikos*, 2004, 107(1), 16-27. http://dx.doi.org/10.1111/j.0030-1299.2004.12968.x.

BELL, S.S., MCCOY, E.D. and MUSHINSKY, H.R. *Habitat structure: the physical arrangement of objects in space*. London: Chapman & Hall, 1991.

BLOCH, C.P., HIGGINS, C.L. and WILLIG, M.R. Effects of large-scale disturbance on metacommunity structure of terrestrial gastropods: temporal trends in nestedness. *Oikos*, 2007, 116(3), 395-406. http://dx.doi.org/10.1111/j.0030-1299.2007.15391.x.

CADOTTE, M.W., FORTNER, A.M. and FUKAMI, T. The effects of resource enrichment, dispersal, and predation on local and metacommunity structure. *Oecologia*, 2006, 149(1), 150-157. PMid:16639564. http://dx.doi.org/10.1007/s00442-006-0426-z.

CALLISTO, M., BARBOSA, F.A.R. and MORENO, P. The influence of eucalyptus plantations on the macrofauna associated with *Salvinia auriculata* in southeast Brazil. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, 2002, 62(1), 63-68. PMid:12185924. http://dx.doi.org/10.1590/S1519-69842002000100008.

COOK, R.R. and QUINN, J.F. The influence of colonization in nested species subsets. *Oecologia*, 1995, 102(4), 413-424. PMid:28306884. http://dx.doi.org/10.1007/BF00341353.

COOK, R.R. and QUINN, J.F. An evaluation of randomization models for nested species subsets analysis. *Oecologia*, 1998, 113(4), 584-592. PMid:28308039. http://dx.doi.org/10.1007/s004420050412.

COOK, R.R., ANGERMEIER, P.L., FINN, D.L., POFF, N.L. and KRUEGER, K.L. Geographic variation in patterns of nestedness among local stream fish assemblages in Virginia. *Oecologia*, 2004, 140(4), 639-649. PMid:15278423. http://dx.doi.org/10.1007/s00442-004-1618-z.

CORNELL, H.V. and LAWTON, J.H. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology*, 1992, 61(1), 1-12. http://dx.doi.org/10.2307/5503.

DOWNES, B.J., LAKE, P.S., SCHREIBER, E.S.G. and GLAISTER, A. Habitat structure, resources and diversity: the separate effects of surface roughness and macroalgae on stream invertebrates. *Oecologia*, 2000, 123(4), 569-581. PMid:28308766. http://dx.doi.org/10.1007/PL00008862.

ELETROSUL. *Ilha Grande: a vegetação da área de influência do reservatório da usina hidrelétrica de Ilha Grande (PR/MS)*. Florianópolis, 1986, 52 p.

EPLER, J.H. *Identification manual for the larval Chironomidae (Diptera) of Florida*. Florida: Department of Environmental Protection, 1995.

FERNÁNDEZ-JURICIC, E. Can human disturbance promote nestedness? A case study with breeding birds in urban habitat fragments. *Oecologia*, 2002, 131(2), 269-278. PMid:28547695. http://dx.doi.org/10.1007/s00442-002-0883-y.

FLEISHMAN, E. and MURPHY, D.D. Patterns and processes of nestedness in a Great Basin butterfly community. *Oecologia*, 1999, 119(1), 133-139. PMid:28308153. http://dx.doi.org/10.1007/s004420050769.

FLORENCIO, M., DÍAZ-PANIAGUA, C., SERRANO, L. and BILTON, D.T. Spatio-temporal nested patterns in macroinvertebrate assemblages across a pond network with a wide hydroperiod range. *Oecologia*, 2011, 166(2), 469-483. PMid:21120669. http://dx.doi.org/10.1007/s00442-010-1847-2.

GAUCH, J.R. *Multivariate analysis in community ecology*. Cambridge: Cambridge University Press, 1986.

GILPIN, M.E. and HANSKI, I.A. *Metapopulation dynamics: empiricaland theoretical investigations*. London: Academic Press, 1991.

GOLTERMAN, H.L., CLYMO, R.S. and OHNSTADT, M.A.M. *Methods for physical and chemical analysis of freshwaters*. Oxford: Blackwell Scientific, 1978.

GONZALEZ, A. Metacommunities: spatial community ecology. In: Wiley, ed. *Encyclopedia of Life Sciences (ELS)*. Chichester: John Wiley & Sons, 2009.

HYLANDER, K., NILSSON, C., JONSSON, B.G. and GÖTHNER, T. Differences in habitat quality explain nestedness in a land snail meta-community. *Oikos*, 2005, 108(2), 351-361. http://dx.doi.org/10.1111/j.0030-1299.2005.13400.x.

KLEINE, P. and TRIVINHO-STRIXINO, S. Chironomidae and other aquatic macroinvertebrates of a first order stream: community response after habitat fragmentation. *Acta Limnologica Brasiliensia*, 2005, 17(1), 81-90.

KODRIC-BROWN, A. and BROWN, J.H. Highly structured fish communities in Australian desert springs. *Ecology*, 1993, 74(6), 1847-1855. http://dx.doi.org/10.2307/1939942.

LANSAC-TÔHA, F.A., BONECKER, C.C., VELHO, L.F.M., SIMÕES, N.R., DIAS, J.D., ALVES, G.M. and TAKAHASHI, E.M. Biodiversity of zooplankton communities in the Upper Paraná River floodplain: interannual variation from long-term studies. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, 2009, 69(2), 539-549, Supplement. PMid:19738961. http://dx.doi.org/10.1590/S1519-69842009000300009.

LEIBOLD, M.A., HOLYOAK, M., MOUQUET, N., AMARASEKARE, P., CHASE, J.M., HOOPES, M.F., HOLT, R.D., SHURIN, J.B., LAW, R., TILMAN, D., LOREAU, M. and GONZALEZ, A. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, 2004, 7(7), 601-613. http://dx.doi.org/10.1111/j.1461-0248.2004.00608.x.

MACKERETH, F.J.H., HERON, J. and TALLING, J.F. *Water analysis some revised methods for limnologist*. Ambleside: Freshwater Biological Association. Scientific Publication, 1978.

MCCUNE, B. and MEFFORD, M.J. *PC-ORD: multivariate analysis of ecological data, version 4* [software]. Gleneden Beach: MjM Software Design, 1999.

MELO, A.S., CIANCIARUSO, M.V. and ALMEIDA-NETO, M. treeNODF: nestedness to phylogenetic, functional and other tree-based diversity metrics. *Methods in Ecology and Evolution*, 2014, 5(6), 563-572. http://dx.doi.org/10.1111/2041-210X.12185.

MEYER, C.F.J. and KALKO, E.K.V. Bat assemblages on Neotropical land-bridge islands: nested subsets and null model analyses of species co-occurrence patterns. *Diversity & Distributions*, 2008, 14(4), 644-654. http://dx.doi.org/10.1111/j.1472-4642.2007.00462.x.

MOORE, J.E. and SWIHART, R.K. Toward ecologically explicit null models of nestedness. *Oecologia*, 2007, 152(4), 763-777. PMid:17370091. http://dx.doi.org/10.1007/s00442-007-0696-0.

MORAIS, S.S., MOLOZZI, J., VIANA, A.L., VIANA, T.H. and CALLISTO, M. Diversity of larvae of littoral Chironomidae (Diptera: Insecta) and their role as bioindicators in urban reservoirs of different trophic levels. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, 2010, 70(4), 995-1004. PMid:21180904. http://dx.doi.org/10.1590/S1519-69842010000500011.

MORRIS, D.W. Toward an ecological synthesis: a case for habitat selection. *Oecologia*, 2003, 136(1), 1-13. PMid:12690550. http://dx.doi.org/10.1007/s00442-003-1241-4.

NALLY, R.M. and FLEISHMAN, E. A successful predictive model of species richness based on indicator species. *Conservation Biology*, 2004, 18(3), 646-654. http://dx.doi.org/10.1111/j.1523-1739.2004.00328_18_3.x.

ORFEO, O. and STEVAUX, J. Hydraulic and morphological characteristics of middle and upper reaches of the Paraná River (Argentina and Brazil). *Geomorphology*, 2002, 44(3-4), 309-322. http://dx.doi.org/10.1016/S0169-555X(01)00180-5.

PATTERSON, B.D. and ATMAR, W. Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biological Journal of the Linnean Society*, 1986, 28(1-2), 65-82. http://dx.doi.org/10.1111/j.1095-8312.1986.tb01749.x.

PETSCH, D.K., PINHA, G.D., DIAS, J.D. and TAKEDA, A.M. Temporal nestedness in Chironomidae and the importance of environmental and spatial factors in species rarity. *Hydrobiologia*, 2015, 745(1), 181-193. http://dx.doi.org/10.1007/s10750-014-2105-0.

PINHA, G.D., PETSCH, D.K., RAGONHA, F.H., GUGLIELMETTI, R.S., BILIA, C.G., TRAMONTE, R.P. and TAKEDA, A.M. Benthic invertebrates nestedness in flood and drought periods in a Neotropical floodplain: looking for the richest environments. *Acta Limnologica Brasiliensia*, 2016, 28(e8). http://dx.doi.org/10.1590/S2179-975X1316.

PRESLEY, J.S., WILLIG, M.R., BLOCH, C.P., CASTRO-ARELLANO, I., HIGGINS, C.L. and KLINGBEIL, B.T. A complex metacommunity structure for gastropods along an elevational gradient. *Biotropica*, 2011, 43(4), 480-488. http://dx.doi.org/10.1111/j.1744-7429.2010.00727.x.

R DEVELOPMENT CORE TEAM. *R: a language and environment for statistical computing* [software]. Vienna: R Foundation for Statistical Computing, 2011 [viewed 15 June 2017]. Available from: http://www.R-project.org

RANTA, P., TANSKANEN, A., NIEMELÄ, J. and KURTTO, A. Selection of islands for conservation in the urban archipelago of Helsinki, Finland. *Conservation Biology*, 1999, 13(6), 1293-1300. http://dx.doi.org/10.1046/j.1523-1739.1999.98290.x.

RASHLEIGH, B. Nestedness in riverine mussel communities: patterns across sites and fish hosts. *Ecography*, 2008, 31(5), 612-619. http://dx.doi.org/10.1111/j.0906-7590.2008.05300.x.

ROBERTO, M.C., SANTANA, N.F. and THOMAZ, S.M. Limnology in the Upper Paraná River floodplain: large-scale spatial and temporal patterns, and the influence of reservoirs. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, 2009, 69(2), 717-725, Supplement. PMid:19738977. http://dx.doi.org/10.1590/S1519-69842009000300025.

ROQUE, F.O., SIQUEIRA, T., BINI, L.M., RIBEIRO, M.C., TAMBOSI, L.R., CIOCHETI, G. and

TRIVINHO-STRIXINO, S. Untangling associations between chironomid taxa in Neotropical streams using local and landscape filters. *Freshwater Biology*, 2010, 55(4), 847-865. http://dx.doi.org/10.1111/j.1365-2427.2009.02314.x.

ROSIN, G.C., MANGAROTTI, D.P.O. and TAKEDA, A.M. Chironomidae (Diptera) community structure in two subsystems with different states of conservation in a floodplain of southern Brazil. *Acta Limnologica Brasiliensia*, 2010, 22(3), 276-286. http://dx.doi.org/10.4322/actalb.02203004.

ROSIN, G.C., OLIVEIRA-MANGAROTTI, D.P., TAKEDA, A.M. and BUTAKKA, C.M. Consequences of a dam construction upstream from the Upper Paraná River floodplain (Brazil): temporal analysis of the Chironomidae community over an eight-year period. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, 2009, 69(2), 591-608, Supplement. PMid:19738966. http://dx.doi.org/10.1590/S1519-69842009000300014.

SANSEVERINO, A.M. and NESSIMIAN, J.L. Larvas de Chironomidae (Diptera) em depósitos de folhiço submerso em um riacho de primeira ordem da Mata Atlântica (Rio de Janeiro, Brasil). *Revista Brasileira de Entomologia*, 2008, 52(1), 95-104. http://dx.doi.org/10.1590/S0085-56262008000100017.

SHOSTELL, J.M. and WILLIAMS, B.S. Habitat complexity as a determinate of benthic macroinvertebrate community structure in cypress tree reservoirs. *Hydrobiologia*, 2007, 575(1), 389-399. http://dx.doi.org/10.1007/s10750-006-0385-8.

SOUZA-FILHO, E. and STEVAUX, J.C. Geomorphology of the Paraná River in the reach between the Paranapanema and Ivaí Rivers. In: A.A. AGOSTINHO, L. RODRIGUES, L.C. GOMES, S.M. THOMAZ and L.E. MIRANDA, eds. *Structure and functioning of the Paraná River and its floodplain*. Maringá: Eduem, 2004, pp. 8-13.

STATSOFT. *Statistica: data analysis software system, version 7.1* [software]. Tulsa: StatSoft, 2005 [viewed 15 June 2017]. Available from: www.statsoft.inc

SUMMERVILLE, K.S., BOULWARE, M.J., VEECH, J.A. and CRIST, T.O. Spatial Variation in Species Diversity and Composition of Forest Lepidoptera in Eastern Deciduous Forests of North America. *Conservation Biology*, 2003, 17(4), 1045-1057. http://dx.doi.org/10.1046/j.1523-1739.2003.02059.x.

THOMAZ, , S.M., BINI, L.M. and BOZELLI, R.L. Floods increase similarity among aquatic habitats in river-floodplains systems. *Hydrobiologia*, 2007, 579(1), 1-13. http://dx.doi.org/10.1007/s10750-006-0285-y.

TOLONEN, K.T., HÄMÄLÄINEN, H., HOLOPAINEN, I.J. and KARJALAINEN, J. Influences of habitat type and environmental variables on littoral macroinvertebrate communities in a large lake system. *Archiv für Hydrobiologie*, 2001, 152(1), 39-67. http://dx.doi.org/10.1127/archiv-hydrobiol/152/2001/39.

TRIVINHO-STRIXINO, S. *Larvas de Chironomidae: guia de identificação*. São Carlos: Laboratorio de Entomologia, Departamento de Hidrobiologia, Universidade Federal de São Carlos, 2011.

TRIVINHO-STRIXINO, S. and STRIXINO, G. *Larvas de Chironomidae (Diptera) do Estado de São Paulo: guia de identificação e diagnose dos gêneros*. São Carlos: Universidade Federal de São Carlos, 1995, 229 p.

ULRICH, W., ALMEIDA NETO, M. and GOTELLI, N.J. A consumer's guide to nestedness analysis. *Oikos*, 2009, 118(1), 3-17. http://dx.doi.org/10.1111/j.1600-0706.2008.17053.x.

VAN BAALEN, M. and HOCHBERG, M.E. Dispersal in antagonistic interactions. In: J. CLOBERT, M., BAGUETTE, T.G. BENTON and J.M. BULLOCK, eds. *Dispersal*. New York: Oxford University Press, 2001, pp. 299-310.

VELHO, L.F.M., BINI, L.M. and LANSAC-TÔHA, F.A. Testate amoeba (Rhizopoda) diversity in plankton of the Upper Paraná River floodplain, Brazil. *Hydrobiologia*, 2004, 523(1), 103-111. http://dx.doi.org/10.1023/B:HYDR.0000033098.46753.9f.

WENTWORTH, C.K. A scale of grade and class terms for clastic sediments. *The Journal of Geology*, 1922, 30(5), 377-392. http://dx.doi.org/10.1086/622910.

WILSON, D.S. Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. *Ecology*, 1992, 73(6), 1984-2000. http://dx.doi.org/10.2307/1941449.

WISSINGER, S.A., GREIG, H. and MCINTOSH, A. Absence of species replacements between permanent and temporary lentic communities in New Zealand. *Journal of the North American Benthological Society*, 2009, 28(1), 12-23. http://dx.doi.org/10.1899/08-007.1.

WORTHEN, W.B. Community composition and nested-subset analyses: basic descriptors for community ecology. *Oikos*, 1996, 76(3), 417-426. http://dx.doi.org/10.2307/3546335.

WORTHEN, W.B., JONES, M.T. and JETTON, R.M. Community structure and environmental stress: desiccation promotes nestedness in mycophagous fly communities. *Oikos*, 1998, 81(1), 45-54. http://dx.doi.org/10.2307/3546466.

WRIGHT, D.H., PATTERSON, B.D., MIKKELSON, G.M., CUTLER, A. and ATMAR, A. A comparative analysis of nested subset patterns of species composition. *Oecologia*, 1997, 113(1), 1-20. PMid:28307284. http://dx.doi.org/10.1007/s004420050348.

ZAGATTO, E.A.G., JACINTHO, A.O., REIS, B.F., KRUG, F.J., BERGAMIN, H., PESSENDA, L.C.R., MORTATTI, J. and GINÉ, M.F. *Manual de análises de plantas empregando sistemas de 1982*. Piracicaba: CENA, 1982.

Received: 15 June 2017
Accepted: 08 November 2017