Diversity and distribution of oligochaetes in tropical forested streams, southeastern Brazil

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ABSTRACT

The distribution and beta diversity of oligochaete assemblages were investigated in different spatial scales to verify the influence of environmental factors and geographic distance on their structure. Two types of mesohabitats (riffles and pools) were sampled in eight first-order streams located in four preservation areas (Poço D'Anta Municipal Biological Reserve, Santa Cândida Municipal Biological Reserve, Ibitipoca State Park and a private farm called Fazenda Floresta) and two Atlantic Forest phytophysiognomies (Seasonal Semideciduous Forest and Rocky Field). Variations in the taxon richness, abundance and composition of the oligochaete assemblages occurred between streams and phytophysiognomies, but not between riffles and pools in the same stream. Low beta diversity values were found and both turnover and nestedness contributed similarly in the environments studied, which could have occurred because of the high capability of oligochaetes to adapt to different environmental conditions. Although the canonical correspondence analysis explained 85.5% of the data (first three axes), the partial Mantel test showed greater influence of geographic distance on the faunal composition than the environmental variables measured. Simple linear regression confirmed this result and showed that the decay of similarity increased with distance between streams. The information from this study sheds light on how environmental and spatial factors determine the variation in the distribution and diversity of oligochaetes in forested low-order streams.

Key words: Beta diversity, habitat heterogeneity, mesohabitats, distance, preserved areas, lotic environments.

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INTRODUCTION

Aquatic Oligochaeta (Annelida, Clitellata) is a diverse and abundant group, which occur in a diversity of waterbodies, with important participation in nutrient cycling and energy flow processes (Pelegri and Blackburn, 1995; Vorobyev *et al.*, 2010). Besides this, some species are sensitive to changes in the water chemistry (Yap *et al.*, 2006) and are often used in biomonitoring studies (Kazanci and Girgin, 1998; Ferreira *et al.*, 2011).

The distribution of oligochaetes and other invertebrates in forested streams is influenced by the entry of leaves, twigs, branches and other plant components, which accumulate in streambeds forming litter patches (Allan, 1995). Many aquatic oligochaete species feed on detritus and periphyton (Smith and Kaster, 1986), so litter is a rich food source. Additionally, the litter patches serve as refuge against predators and increase the bottom area that can be colonized.

Variations in water speed contribute to the spatial heterogeneity of streams, through the formation of erosional and depositional areas (Beisel *et al.*, 1998) and can also influence the distribution and the abundance of

oligochaetes in streams (Verdonschot, 2001). The characteristics of these areas influence the distribution of food and the availability of dissolved oxygen, and hence on the composition and the distribution of invertebrates (Allan, 1995). However, while the effect of physical differences between riffle and pool mesohabitats, such as water speed, depth and substrate particle size, are well known for many invertebrates in streams, especially insects (Logan and Brooker, 1983; Vinson and Hawkins, 1998; Baptista et al., 2001; Rosa et al., 2011), the influences on the structure and distribution of oligochaetes are still little known. Besides local characteristics, factors related to the broader spatial scale (landscape) can influence the environmental characteristics on the smaller scale of the habitat (such as habitat patches), resulting in a hierarchical relationship of the environmental variables on multiple spatial scales (Heino, 2009). This pattern, together with the dispersal capacity of the species (Timm, 1980; Milbrink, 1999) and types of resources used by them (Ragonha and Takeda, 2014), determines how the composition of assemblages varies between habitats and landscapes. Therefore, environmental factors related to differences in altitude, geo-





graphic distance and vegetation, for example, should influence the environmental characteristics of small streams and the composition of aquatic oligochaetes (Prenda and Gallardo, 1992). Species with high dispersal ability may be present in all places and greater similarity in community composition is expected (Thompson and Townsend, 2006). Although many species of aquatic oligochaetes present a wide geographic distribution (Martin *et al.*, 2008), they do not have a good ability of disperse, (compared to aquatic insects, for example), so differences in their richness and composition can be related to the distance between sites, besides smaller scale environmental characteristics such as substrate types and water flow variations (Verdonschot, 1999, 2001; Alves *et al.*, 2008).

Because of the lack of studies about the ecological processes responsible for the diversity and distribution of aquatic oligochaetes considering different habitat spatial scales, our objective in this study was to verify how different mesohabitats (litter in riffles and in pools), geographic distance between streams and type of phytophysognomy (seasonal semideciduous forest and rocky field), as well as their interaction, can influence variations in the composition (beta diversity) and structure of the assemblage of oligochaetes in low-order streams. We expected to find greater variation in the fauna composition (beta diversity) between streams located farther apart and in different phytophysiognomies. We also expected to find greater similarity in the fauna structure between the same type of habitat (riffles or pools) in different streams than between different habitats (riffles and pools) of a single stream.

METHODS

Study area

The study was carried out in four forested areas in southeastern Brazil, inserted in the Atlantic Forest biome considered a hotspot: Particular area- Fazenda Floresta (21°43' to 21°44'S and 43°16' to 43°17'W); Poço D'Anta Municipal Biological Reserve (21°44' to 21°45'S and 43°18' to 43°19'W); Santa Cândida Municipal Biological Reserve (21°41' to 21°42'S and 43°20' to 43°21'W) and Ibitipoca State Park (21°40' to 21°43'S and 43°52' to 43°54' W). The first two areas are connected to a forested corridor and are about 10 km from the Santa Cândida Municipal Biological Reserve, all located in area of the Seasonal Semideciduous Forest phytophysognomy and located in the Paraíba do Sul river basin. The Ibitipoca State Park, about 60 km away from the other three preserved areas, lies in an area with high altitude (more than 1250m above the ocean level) that is a water divisor between two important water basin from Brazilian southeast (Rio Grande and Paraíba do Sul river basins). It has predominance of Rocky Fields and some Seasonal Semideciduous Forest areas (IBGE, 1991; Salimena-Pires, 1997). Eight first-order streams were sampled, all with well-preserved riparian vegetation (for the characteristics of each stream see Rodrigues *et al.*, 2013).

Sampling

The streams were sampled during the dry season, in May, June, July and September 2010 and June 2011. We choose this period due to the greater spatial separation of the riffles and pools because of the smaller water flow, facilitating the visualization of the mesohabitats during the sampling. Along each stream we obtained samples of the submerged litter from 10 riffles and 10 pools with a Surber sampler (area of 0.04 m², mesh of 0.21 mm). The litter collected was fixed in a 4% formaldehyde solution and sorted under a stereoscopic microscope. After drying the litter, its components (whole leaves, leaf fragments, trunks, branches and seeds/fruits) were separated and weighed on a precision scale (0.1 mg).

The list of all oligochaete species collected was published in a previous work (Rodrigues et al., 2013). In the present work we excluded the Megadrili from the analysis since it is a nomen nudum; Pristina minuta is a synonymy of Pristina osborni and Aulophorus, subgenus of Dero, is now considered genus. The organisms were identified to different taxonomic levels, so in the statistical analyses we used the Operational Taxonomic Units (OTU) system, which considers different organisms as belonging to a single taxon, independent of the level of identification (family, genus or species) (Silveira et al., 2003). In each stream, three measurements of the abiotic variables were carried out longitudinally along the collection segment. The variables measured were water temperature, dissolved oxygen, pH and electrical conductivity, with a Horiba U-10 multiparameter meter. Water samples were also obtained from all the sites and taken to the laboratory for analysis of total nitrogen and total phosphorous (Valderrama, 1981). Three sediment samples were obtained randomly from each stream segment for characterization of granulometry and organic matter content according to NBR 7181/84 and NBR 13600/96 (ABNT, 1984, 1996). We collected only three samples because the sediment was very homogeneous along the stretch. The depth and the width were measured with graduated ruler, the water flow was calculated by the float method (Martinelli and Krusche, 2007) and the geographic coordinates were obtained with a GPS Garmin MAP 76CSX.

Data analysis

After checking the data for normality and homogeneity (Levene test, P>0.05), analysis of variance (factorial ANOVA) was applied to test the effect of the mesohabitats, streams and phytophysognomy, as well as the effect

of the interactions of these factors, on the abundance, richness and alpha and beta diversity, using the Statistica 7 program (Statsoft, 2004). Analysis of similarity (Anosim) was used to check differences in species composition between the two mesohabitats as well as to verify differences in the litter composition between riffles and pools, considering the weight of each plant components. This analysis was carried out with the Vegan (Oksanen *et al.*, 2011) package of the R program (R Development Core Team, 2011).

The Sorensen index (βsor) was employed to analyze the beta diversity between streams, mesohabitats and phytophysiognomies, based on the species abundance data. This index helps understand the influence of ecological processes (turnover and nestedness) related to spatial variation on the composition of the species at the sites studied. The index is partitioned into two additive components: spatial turnover, measured by the Simpson index (βsim), and nestedness (\(\beta \)nes), measured by the difference between the Sorensen and Simpson indices (Baselga, 2010). Turnover is a measure of the substitution of species between sites as a consequence of the effect of spatial or environmental factors and historic processes (Qian et al., 2005), while nestedness occurs when communities in places with a lower number of species correspond to subsets of species in places with greater richness, reflecting a process of losing or gaining species (Ulrich and Gotelli, 2007). For this analysis, we used the Betapart (Baselga et al., 2013) package of the R program (R Development Core Team, 2011). Finally, we compared the values generated for turnover and nestedness by simple analysis of variance (ANOVA) to check which of the two components contributed most to the variation in the composition of oligochaetes between the streams, mesohabitats and phytophysiognomies.

The association of the taxa with the environmental variables of the streams was investigated by canonical correspondence analysis (CCA) using the Monte Carlo test to establish the significance of the axes (999 permutations). For this analysis, the abundance data from the principal matrix were log-transformed $[\log (x+1)]$ and the matrix of environmental data was adjusted by the standard deviation. The variables used in the CCA were those that presented factor loading greater than 0.7 in the principal component analysis (PCA), carried out previously with all the physical and chemical variables, granulometry, organic matter and litter components. This analysis was performed with the PC-Ord 5.10 program (McCune and Mefford, 2006). The partial Mantel test was used to discover which factor (environmental variables or geographic distance, calculated from the geographic coordinates in UTM) had the strongest influence on the fauna. Linear regression analysis was used to test whether higher beta diversity values could be found with increasing geographic distance between the streams. For this analysis, we used the beta diversity values for each stream based on the quantitative Chao index (Chao *et al.*, 2005). This index is relatively independent of the richness and is accurate even with a small number of samples (Soininen *et al.*, 2007). The beta diversity from the Chao index and the distance matrix were calculated with the Vegan (Oksanen *et al.*, 2011) package of the R program (R Development Core Team, 2011) and the regression was performed with the Statistica 7 program (Statsoft, 2004).

RESULTS

All the streams had high oxygen content, low conductivity and alkaline pH. The lowest organic matter levels were found, in streams II and III of Floresta and streams I and II of Ibitipoca State Park. The temperature (F=49.550; P<0.01), oxygen (F=4.907; P=0.004) and pH (F=3.351; P=0.021) were different among the streams (Tab. 1). With respect to the litter composition (Tab. 2), the analysis of similarity showed a tiny difference (low value of R) between riffles and pools of the following streams: Floresta I (Anosim R=0.207, P=0.011); Santa Cândida (Anosim R=0.210, P=0.012); and Ibitipoca I (Anosim R=0.269, P=0.008). All told we collected 4310 specimens, belonging to the families Naididae (subfamilies Naidinae, Pristininae, Tubificinae and Rhyacodrilinae) and Enchytraeidae. Pristina biserrata was found only in riffles from the stream Floresta II and while Aulophorus furcatus and Dero (Dero) sp. were found only in pools from the same stream, all with low abundance (Tab. 3). The highest abundances were found in Santa Cândida and Floresta III streams, due mainly the high abundance of Nais variabilis and Enchytraeidae in Santa Cândida and of Nais communis in Floresta III. The highest richness was found in Floresta II stream, which, along with Floresta I stream, presented the highest alpha diversity values (Tab. 4).

Unlike our hypothesis that the structure of oligochaetes would differ between riffles and pools of a single stream, the abundance, richness and alpha diversity did not differ between the two mesohabitats. Besides this, the ANOVA results did not show any effect of the interaction between mesohabitat and stream and between mesohabitat and phytophysognomy on the variables described above. The analysis of similarity showed that the composition of oligochaetes was slightly different only the mesohabitats from Santa Cândida stream (Anosim R=0.175; P=0.003), probably due the high abundance of N. variabilis and Enchytraeidae found in riffles compared with that found in pools. However, differences between streams and phytophysiognomies were observed, along with the effect of the interaction between these two factors on the abundance, the richness and the alpha diversity (Tab. 5). Considering the beta diversity, the Sorensen index values did

Tab. 1. Mean and standard deviation of limnological variables, granulometric fractions and organic matter percentage of the streams in Fazenda Floresta, Poço D'Anta Municipal Biological Reserve, Santa Cândida Municipal Biological Reserve and Ibitipoca State Park.

	Water temperature	Oxygen	Hd	Conductivity	Total nitrogen	Total phosphorous % Coarse	% Coarse	% Medium	% Medium % Fine sand % Silt		% Organic
				(µScm ⁻¹)	$(\mu { m gL}^{-1})$						matter
Floresta I	18.5 ± 0.10^{a}	10.8 ± 0.90^{a}	10.8 ± 0.90^{a} 8.23 ± 0.57^{ab}	21.16 ± 7.59^{a}	373.53 ± 135.67^{a}	37.58 ± 22.4^{a}	$43.13{\pm}11.95^a$	44.45 ± 10.99^a 11.46 ± 3.46^a 0.95 ± 0.15^a 17.73 ± 5.04^{ab}	11.46 ± 3.46^{a}	0.95 ± 0.15^{a}	17.73 ± 5.04^{ab}
Floresta II	18.3 ± 0.26^{ab}	11.07 ± 0.66^{a}	8.12 ± 0.52^{ab}	16.60 ± 1.60^{a}	341.60 ± 102.36^{a}	93.05 ± 47.14^{a}	54.03 ± 1.11^{ab}	40.02 ± 1.22^{ab}	5.02 ± 1.23^{ab}	0.92 ± 0.10^a 3.29 ± 0.38^b	$3.29{\pm}0.38^b$
Floresta III	18.16 ± 0.35^{ab}	10.80±0.90a 8.20±0.57ab	8.20±0.57ab	21.40±7.25 ^a	338.71 ± 84.59^a	33.96 ± 13.81^{a}	46.68±7.04ª	$46.68 \pm 7.04^{a} \qquad 38.89 \pm 5.56^{ab} \qquad 12.95 \pm 4.16^{a} \qquad 1.46 \pm 0.50^{a} \qquad 2.94 \pm 1.52^{b}$	12.95 ± 4.16^{a}	1.46 ± 0.50^{a}	2.94±1.52 ^b
Poço D'Anta	$17.03\pm0.56^{\rm b}$	9.50±1.12a,b 8.49±0.03ab	8.49 ± 0.03^{ab}	19.70±2.19 ^a	736.40 ± 198.84^{a}	$80.89{\pm}18.08^{a}$	43.11 ± 9.86^{a}	44.12 ± 5.89^{ab}	44.12 ± 5.89^{ab} 11.32 ± 5.15^{a} 1.42 ± 0.32^{a} 14.38 ± 6.61^{ab}	1.42 ± 0.32^{a}	14.38 ± 6.61^{ab}
Santa Cândida	la 17.96±0.49ªb	8.43 ± 0.15^{b}	8.85 ± 0.57^{a}	19.43 ± 3.06^{a}	871.41 ± 365.06^{a}	42.77 ± 9.16^{a}	$57.18{\pm}20.30^{ab}$	$57.18\pm20.30^{ab} 33.67\pm17.18^{abc} 7.20\pm3.22^{ab} 1.65\pm0.88^{a} 18.11\pm5.15^{ab}$	$7.20{\pm}3.22^{ab}$	1.65 ± 0.88^{a}	$18.11{\pm}5.15^{ab}$
Ibitipoca I	14.4±0.17 [∞]	10.83 ± 0.05^{a}	7.60 ± 0.26^{b}	11.1 ± 0.96^{a}	505.98±296.54a	49.12 ± 7.51^a	$88.0 \ 3\pm 12.01^{\circ}$	$88.0\ 3\pm12.01^{\circ} 10.77\pm11.78^{\circ} 0.84\pm0.27^{b} 0.31\pm0.13^{a} 1.17\pm0.69^{b}$	0.84±0.27 ^b	0.31 ± 0.13^{a}	$1.17{\pm}0.69^{b}$
Ibitipoca II	$13.1{\pm}0.60^{\mathrm{d}}$	10.8 ± 0.40^{a} 7.70 ± 0.10^{b}	7.70 ± 0.10^{b}	18.73 ± 2.20^{a}	414.6 ± 215.70^{a}	60.89 ± 39.70^{a}	78.15 ± 5.21^{bc}	$21.47\pm5.26^{\rm abc}$ $0.30\pm0.07^{\rm b}$ $0.04\pm0.00^{\rm a}$	0.30 ± 0.07^{b}	0.04 ± 0.00^{a}	2.52 ± 1.00^{b}
Ibitipoca III	$15.2\pm1.00^{\circ}$	11.06 ± 0.90^{a} 7.66 ± 0.30^{b}	7.66±0.30b	16.63 ± 5.60^{a}	304.39±73.40a	198.52±182.3 ^a	78.08±1.07bc	78.08±1.07bc 18.53±3.91bc	2.25±1.40 ^b 1.10±1.44 ^a 47.1±36.24 ^a	1.10 ± 1.44^{a}	$47.1 {\pm} 36.24^{a}$
		,	,								

 a^{-d} Different letters in the columns means that the values are significantly different (P<0.05).

Tab. 2. Mean and standard deviation of litter components (%) in riffles and pools of the streams sampled in Fazenda Floresta, Poço D'Anta Municipal Biological Reserve, Santa Cândida Municipal Biological Reserve and Ibitipoca State Park.

			Fragmen	ıt leaf	Sticks/wood				Particulate material	material
	Riffle	Pool	Riffle	Pool	Riffle	Pool	Riffle	Pool	Riffle	Pool
Floresta I	10.47±12.57	11.77±15.36	29.15±20.35	60.83±24.65	35±22.79	21.92±20.97	1.577±4.99	070	24.21±30.15	5.46±10.31
Floresta II	3.64 ± 5.26	10.43 ± 19.30	47.04±23.85	42.1 ± 23.66	48.89±22.3	41.3±23.82	0.4 ± 1.29	1.16 ± 2.86	0∓0	4.98±13.27
	11.61 ± 14.26	20.68 ± 16.49	37.29±18.79	31.63±25.68	23.48 ± 16.34	22.83 ± 19.47	6.92 ± 10.33	5.02±9.67	20.68±23.74	19.82 ± 30.06
Poço D'Anta	13.23±9.79	15.77±15.97	52.58±22.82	45.98 ± 16.09	30.36 ± 19.48	37.09±21.72	0=0	0=0	3.81 ± 12.06	1.15 ± 2.46
-	17.5±12.58	22.37±16.64	18.5 ± 13.34	55.11±17.45	19.5±12.87	11.86 ± 11.31	20.5 ± 2.06	0=0	21.5±15.71	10.63 ± 12.27
Ibitipoca I	17.67 ± 10.70	6.3±8.76	64.44 ± 15.60	63.67±18.87	17.88 ± 10.78	16.8 ± 16.13	0=0	0=0	0∓0	13.21 ± 11.68
Ibitipoca II 2	25.44±15.84	10.43 ± 19.30	46.57±16.83	42.1 ± 23.66	23.46±21.66	41.3±23.82	0=0	1.16 ± 2.86	4.52±7.29	4.98±13.27
Ibitipoca III	10.89±7.54	14.52±10.51	46.81±22.56	36.66±20.35	30.03 ± 20.38	23.15±17.11	0.49 ± 1.58	0=0	11.75±16.36	25.65±25.43

vary significantly only between riffles and pools, in a single stream, only in Santa Cândida and Ibitipoca III, and no significant variation was observed in the others streams. Contrary to our expectation, significant variations did occur between the same mesohabitat of different streams, as can be seen in Fig. 1. The turnover and nestedness components contributed similarly to the beta diversity found for the mesohabitats of the majority of the streams (six of the eight streams studied), but there was a greater tendency for turnover of the oligochaete species between riffles and pools of Floresta III stream (F=21.003, df=2, P<0.01), while nestedness had the greatest influence on the variation of the species composition between riffles and pools of Ibitipoca III stream (F=34.354, df=2, P<0.01). Low beta

diversity values for the streams were generated by the Sorensen index. The contribution of the turnover and nest-edness components was similar, with the exception of Ibitipoca III stream, in which the variation in the composition of oligochaetes was more strongly influenced by the nestedness of species (F=12.076, df=7, P<0.01) (Fig. 2). No differences in beta diversity were detected between the phytophysiognomies. The composition of oligochaetes was influenced both by the turnover and nestedness of species (Fig. 3). The first three axes of the CCA explained 43.0% (axis 1), 22.3% (axis 2) and 20.2% (axis 3) of the total variance of the data (cumulative total=85.5%). The environmental variables most strongly related to axis 1 were the granulometric fraction, temperature and altitude,

Tab. 3. Numerical abundance of the taxa collected in riffle (R) and pool (P) mesohabitats in each stream.

	Flor		Flor		Flo	resta	Po				Ibitij		Ibitip			
						П	D'A								11	
							R									
NAIDIDAE																
Naidinae																
Chaetogaster diastrophus (Gruithuisen 1828)	40	59	22	32	22	38	42	39	4	16	-	1	-	-	10	30
Aulophorus furcatus (Oken 1815)	-	-	-	4	\- (<i>J</i> -	-	-	-	-	-	-	-	-	-	-
Dero (Dero) sp.	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Nais communis Piguet 1906	85	33	-	(-)	333	242	10	-	-	-	-	-	-	-	-	-
Nais variabilis Piguet 1906	-	-	-0	2	-	-	-	1	452	89	-	-	-	-	-	3
Pristininae																
Pristina (Pristina) longiseta leidyi Smith 1896	5	44	5	1	21	22	-	-	1	1	-	2	-	3	1	-
Pristina (Pristina) proboscidea Beddard 1896	9	12	14	9	17	9	1	-	-	-	1	1	-	2	-	-
Pristina (Pristina) aequiseta Bourne 1891	8	1	5	2	2	1	1	-	1	9	-	-	-	-	-	1
Pristina (Pristina) biserrata Chen, 1940	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-
Pristina (Pristinella) osborni (Walton 1906)	24	17	6	1	26	38	8	5	28	22	2	9	-	6	2	13
Pristina (Pristinella) sima (Marcus 1944)	-	-	-	-	4	7	9	10	-	-	-	-	-	-	-	1
Pristina (Pristinella) jenkinae (Stephenson 1932)	30	4	124	10	48	24	1	-	13	6	-	-	2	-	1	2
Pristina (Pristinella) sp.1	83	67	23	57	44	17	4	16	2	1	-	-	-	-	2	2
Pristina (Pristinella) sp.2	-	-	-	-	-	-	-	-	6	1	41	23	55	9	-	-
Rhyachodrilinae																
Bothrioneurum Stolc 1886	-	-	1	3	-	1	-	-	1	1	1	12	-	1	-	-
Tubificinae																
Immature Tubificinae	-	8	1	23	4	7	-	-	8	40	-	86	1	8	-	1
ENCHYTRAEIDAE	37	23	27	14	95	40	14	23	510	119	172	38	54	46	56	51

Tab. 4. Total abundance, total richness and alpha diversity (Shannon) in each stream and in each mesohabitat.

		Abundance			Richness		A	Alpha diversity				
		Riffle	Pool		Riffle	Pool		Riffle	Pool			
Floresta I	589	321	268	10	9	10	2.001	1.883	1.947			
Floresta II	392	233	159	14	11	13	1.937	1.594	1.894			
Floresta III	1062	616	446	12	11	12	1.611	1.559	1.634			
Poço D'Anta	184	90	94	10	9	6	1.618	1.623	1.454			
Santa Cândida	1331	1026	305	11	11	11	1.185	0.984	1.594			
Ibitipoca I	389	217	172	8	5	8	1.247	0.591	1.401			
Ibitipoca II	187	112	75	8	4	7	1.149	0.815	1.278			
Ibitipoca III	176	72	104	10	6	9	1.191	0.787	1.356			

in that order. Dissolved oxygen and organic matter were correlated with axis 3 and no environmental variables were correlated with axis 2. Therefore, we plotted the graph in function of axes 1 and 3.

The ordering showed that the taxa Pristina sp2, Bothrioneurum and immature Tubificinae were most closely related to the streams Ibitipoca I and II, at higher altitudes, predominance of coarse substrate and low quantity of organic matter. The presence of Enchytraeidae was not related specifically to any stream - specimens were abundant in all of them. However, this family had a stronger association with coarse sand and lower water temperature values. The other species were associated with streams with a higher quantity of medium and fine sand, higher water temperature and greater organic matter quantity. Only one specimen each of the species P. biserrata, A. furcatus and Dero sp. was found, making it impossible to associate them with any variable or stream (Fig. 4). According to the partial Mantel test, the geographic distance had a greater influence on the composition of oligochaete assemblages (r=0.4886; P=0.0252) than the local environmental vari-

Tab. 5. Effect and interaction of mesohabitats, streams and phytophysiognomies on the abundance, richness and alpha diversity.

		•	•
	GL		P
Abundance			
Mesohabitat	1	0.0154	0.8979
Stream	7	3.7207	0.014
Phytophysiognomie	1	25.605	0.0002
Mesohabitat x stream	7	0.9434	0.5295
Mesohabitat x phytophysiognomie	1	0.6998	0.5652
Stream x phytophysiognomie	7	4.4147	0.0348
Richness			
Mesohabitat	1	1.3538	0.2574
Stream	7	34.3993	< 0.0001
Phytophysiognomie	1	58.9711	< 0.0001
Mesohabitat x stream	7	0.3198	0.9219
Mesohabitat x phytophysiognomie	1	0.0283	0.865
Stream x phytophysiognomie	7	53.6316	0.0001
Alpha diversity			
Mesohabitat	1	2.0172	0.168
Stream	7	22.0302	< 0.0001
Phytophysiognomie	12	42.7079	< 0.0001
Mesohabitat x stream	7	1.056	0.4724
Mesohabitat x phytophysiognomie	1	0.7481	0.5803
Stream x phytophysiognomie	7	7.3103	0.0096

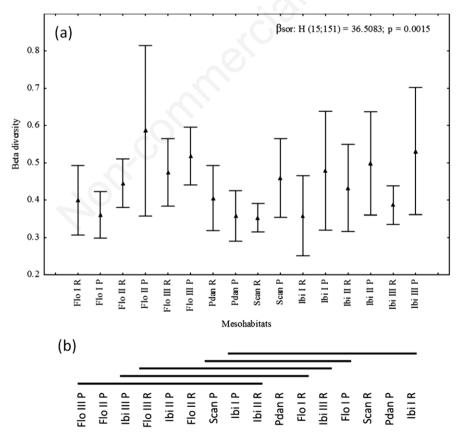


Fig. 1. a) Beta diversity of Sorensen (βsor) of riffles (R) and pools (P) of the streams sampled in Fazenda Floresta (Flo), Poço D'Anta Municipal Biological Reserve (Pdan), Santa Cândida Municipal Biological Reserve (Scan) and Ibitipoca State Park (Ibi); bars represent the 95% confidence interval. b) Statistical comparison of the values of beta diversity of Sorensen between the mesohabitats; sites linked by the same bar does not show significant difference (P>0.05).

ables (r=0.1346; P=0.2236), but the relation between distance and beta diversity was low, as shown by the regression analysis (Fig. 5).

DISCUSSION

One of our hypothesis was that we would found greater similarity in the fauna structure between the same type of habitat (riffles or pools) in different streams than between different habitats of a single stream, however, the fauna structure of riffles and pools of a single stream was similar. Previous studies have demonstrated that the richness and distribution of oligochaetes could be influenced by the substrate composition and heterogeneity (Dumnicka, 1994; Martínez-Ansemil and Collado, 1996; Schenková and Helešic, 2006; Gorni and Alves, 2012), the quality and availability of food (Learner et al., 1978; Collado and Schmelz, 2001) as well by the water flow, although there isn't a clear relation between the last variable and their distribution. (Verdonschot, 2001). In the present study, the litter composition between riffles and pools was similar in all streams and differences in the abundance

were more significative. Probably the slow water speed of the riffles (±0.30 ms⁻¹) was not a limiting factor for the distribution of the oligochaetes in these habitats. Furthermore the similarity of the litter composition probably created similar conditions between mesohabitats of the same stream, resulting in a structure similar fauna. According Syrovátka et al. (2009) the flow conditions were less important in explaining the distribution of oligochaetes than the differences in the amount of organic matter and roughness of the substrate. On the other hand, according to the CCA results, the dissimilarity of the oligochaete assemblages between the streams was associated with the distinct environmental characteristics. The type de phytophysiognomies resulted in greater similarity of streams I and II of Ibitipoca park (flowing through rocky fields), which stood apart from stream III of this park (seasonal semideciduous forest). The streams in rocky fields have beds made up predominantly of rocks and coarse sand, with low organic matter percentage, in contrast to stream III, with more organic matter. The other streams differed from Ibitipoca streams in function of the greater

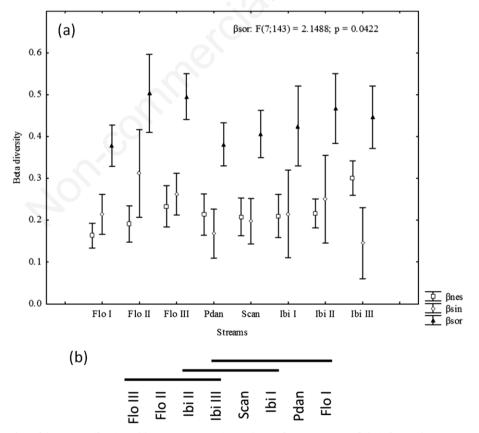


Fig. 2. a) Beta diversity of Sorensen (βsor) and its components (nestedness, βnes; turnover, βsim) for each stream sample in Fazenda Floresta (Flo), Poço D'Anta Municipal Biological Reserve (Pdan), Santa Cândida Municipal Biological Reserve (Sca) and Ibitipoca State Park (Ibi); bars represent the 95% confidence interval. b) Statistical comparison of the values of beta diversity of Sorensen among the streams; sites linked by the same bar does not show significant difference (P>0.05).

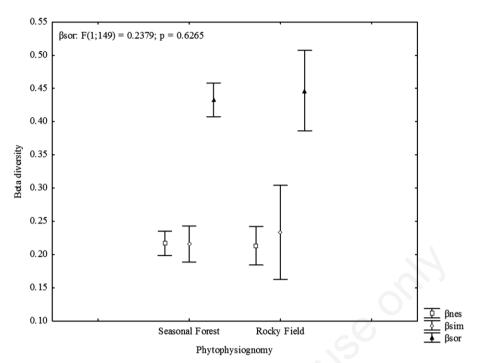


Fig. 3. Beta diversity of Sorensen (β sor) and its components (nestedness, β nes; turnover, β sim) for the two phytophysiognomies studied. The bars represent the 95% confidence interval.

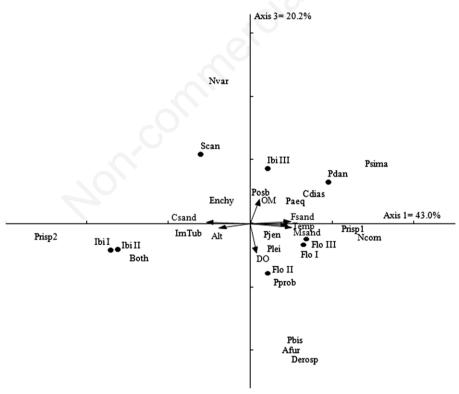


Fig. 4. Canonical correspondence analysis of the oligochaete species and environmental variables in streams of Fazenda Floresta (Flo), Poço D'Anta Municipal Biological Reserve (Pdan), Santa Cândida Municipal Biological Reserve (Sca) and Ibitipoca State Park (Ibi). Nvar, Nais variabilis; Enchy, Enchytraeidae; Posb, Pristina osborni; Paeq, Pristina aequiseta; Cdias, Chaetogaster diastrophus; Psima, Pristina sima; Pjenk, Pristina jenkinae; Plei, Pristina leidyi; Prisp1, Pristina sp1; Ncom, Nais communis; Pprob, Pristina proboscidea; ImTub, imature tubificinae; Both, Bothrioneurum; Prisp2, Pristina sp2; Pbis, Pristina biserrata; Afur, Aulophorus furcatus; Derosp, Dero (Dero) sp.; Csand, corse sand; Msand, medium sand; Fsand, fine sand; OM, organic matter; Temp, temperature; DO, dissolved oxygen; Alt, altitude.

quantity of medium and fine sediment fractions and higher water temperature. In these streams, the species *N. communis*, *Pristina* sp1, *P. jenkinae*, *P. leidyi* and *P. proboscidea* were more abundant.

Streams that were located the furthest apart (60 km) did not present the highest beta diversity values. This result can possibly be explained by the weak relation found between the increase in distance and the beta diversity of oligochaetes. Both the turnover and nestedness contributed to the variations in composition, except for Ibitipoca III stream, in which the species composition was only significantly influenced by nestedness.

According to Thompson and Townsend (2006), if the dissimilarity in the species composition is influenced by limitations of dispersion, then higher species turnover than nestedness should be expected between sites. In this case, the increase in dissimilarity will have a positive relation with the distance between the sites sampled (Stevens *et al.*, 2007). On the other hand, if the dissimilarity between sites results from selection of habitats, causing the presence or absence of species, there will be a positive correlation between the increase in dissimilarity of fauna and environmental differences between the sites, with a stronger contribution of nestedness than turnover. Probably the dispersion limitations of oligochaetes did not constitute a barrier to the species, nor did the differences in environmental variables between streams, as shown by the partial Mantel

analysis. This explains the low beta diversity values found for the streams and the similar contribution of turnover and nestedness, with the exception of Ibitipoca III stream, whose environmental differences probably were a determining factor for the process of habitat selection to act on the species composition. Although the CCA grouped Floresta I, II and III streams in function of similarities of some environmental variables, Floresta III stream presented higher beta diversity than Floresta I and II streams, located in the same forest fragment, followed by Poço D'Anta stream, which is located in a nearby area, connected by a forest corridor to Fazenda Floresta. Possibly other factors not measured in this study, such as interactions of species, might have generated greater dissimilarities in the fauna of these streams. According to Chust et al. (2004), animals with low mobility normally respond more strongly to small variations in the environment, so they tend to be structured by species turnover in the landscape. Many oligochaete species are adapted to pronounced changes in environmental conditions (Gnaiger and Staudigl, 1987; Montalto and Marchese, 2005), enabling these invertebrates to colonize a wide range of environments (Prenda and Gallardo, 1992). Therefore, the high adaptive capability of oligochaetes to different environmental conditions can help explain the low beta diversity in the environments studied, considering that the taxa found in the present study have wide distribution.

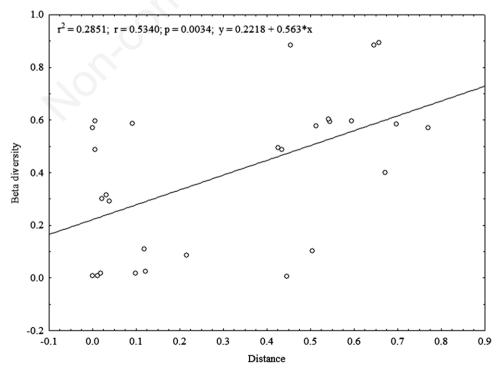


Fig. 5. Relation between beta diversity and distance of the streams studied.

Studies analyzing the effect of environmental variables and spatial scale on the variation of the structure and distribution of benthic invertebrate species are necessary to understand the ecological processes that determine the patterns of diversity in streams. According to Nijboer *et al.* (2004), it is important to sample different mesohabitats within a single stream to obtain a good understanding of the distribution and true diversity of oligochaetes in these settings. Besides this, ecological studies to investigate the assemblages of invertebrates of streams in nearby and distant areas help to understand what scale best determines variations in the diversity of these organisms.

CONCLUSIONS

In this study, variations in the richness of taxa, abundance and composition of oligochaete assemblages occurred between streams but not between riffles and pools of any single stream, demonstrating a weaker effect of the mesohabitat compared to the effect of geographic distance and of phytophysognomy on the variation of the structure of the oligochaete assemblages. With respect to the beta diversity, no pattern was found, since this varied between the mesohabitats of some streams and among the streams, regardless of the differences in the phytophysiognomies and in the geographic distances between the environments.

Although the relation between similarity in the composition of invertebrate assemblages and geographic distance has been better investigated in recent years, this relation is still little known for oligochaetes. Therefore, the information in this study should help understand how environmental and spatial factors determine the variation of the richness and diversity of oligochaetes in low-order forested streams.

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