Diversity and microdistribution of black fly (Diptera: Simuliidae) assemblages in the tropical savanna streams of the Brazilian cerrado

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We describe the abiotic factors affecting the distribution of black flies at a microhabitat scale, rather than at the regional scale usually present in the literature on the Neotropics. Black fly larvae were sampled from the Tocantins River and three tributaries, located in the Brazilian savanna (state of Tocantins, Brazil) during six bi-monthly sampling periods from October 2004-August 2005. At each sampling site, 15 random quadrats (30 x 30 cm) were sampled each period and for each quadrat were determined mean water velocity, predominant substrate type (rocks, riffle litter or riparian vegetation) and depth detrended correspondence analysis (DCA) was used to determine associations with current velocity, whereas correspondence analysis (CA) was used to estimate site specific current velocity associations. Canonical correspondence analysis (CCA) was used to identify general microhabitat associations. The CCA showed that most species had a trend towards riffle litter, except for Simulium nigrimanum *associated with rocky substrate and* Simulium cuasiexiguum *associated with riparian vegetation. The DCA showed a well defined pattern of water velocity associations. The CA revealed that the species showed different speed associations from one site to another, suggesting different competitive pressures resulting in the occurrence of different realized niches.*

Key words: Neotropical Region - microhabitat associations - diversity - species richness - water current range

Hamada et al. (2002) pointed out the relative scarcity of ecological studies on the black fly fauna of the Neotropical Region. In addition to this limited number of studies, most of the literature on this subject is restricted to a few geographical areas; in the specific case of Brazil, a large number of biomes lack ecological studies on their black fly fauna (Figueiró & Gil-Azevedo 2010), as most of the studies concentrate on the central Amazon (e.g., Hamada et al. 2002), southeastern (e.g., Araújo-Coutinho et al. 2004, Figueiró et al. 2006, Pepinelli et al. 2005) and southern (Strieder 2004, Santos et al. 2010) Mata Atlântica biomes. Another issue raised in Hamada et al. (2002) is that most of the studies on Neotropical black flies approach the ecology of the individual species population (e.g., Hamada & McCreadie 1999), rather than the whole black fly community. In recent years, some authors attempted to research the ecology of the black fly community (Hamada et al. 2002, McCreadie et al. 2004, Pepinelli et al. 2005, Figueiró et al. 2006, 2008, Landeiro et al. 2009); however, contributions to this particular field of Neotropical black fly ecology are still very limited.

The cerrado is a savanna biome characterized by low pH dystrophic soils, little availability of calcium and magnesium and high aluminium content (Furley & Ratter 1988). The typical vegetation consists of a grassland ecosystem characterized by trees that are sufficiently small or widely spaced so that the canopy does not close; this allows sufficient light to reach the ground to support an unbroken herbaceous layer consisting primarily of C4 grasses and a riparian vegetation denominated “gallery forests” along the watercourses. These gallery forests are of particular importance to the lotic systems, as they act as a physical barrier, regulating the processes between the terrestrial and the aquatic systems (Ratter et al. 1997). Several descriptive studies of a number of different cerrado regions in Brazil have been published over the years. However, most of this literature is focused mainly on the botanical aspects of this biome (Oliveira & Marquis 2002).

Black flies are one of the major components of the benthos from lotic systems; they are important at an ecosystem level as a resource for predators and as a trophic link, as they capture small organic particles. Also, due to their low digestive efficiency, their faecal pellets, which are larger than the organic matter particles ingested, make this organic matter available for organisms which are incapable of feeding on the small-sized particles on which black flies are instead able to feed (Wotton et al. 1998). Their distribution patterns may be explained by biotic factors such as trophic relationships (McIntosh & Townsend 1996), competition (Hart 1986) and food availability (Colbo & Porter 1979), as well as by abiotic factors such as distance from a lake outlet (McCreadie

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& Colbo 1993), substrate type (Ciborowski & Adler 1990, Halgos et al. 2001), water current velocity (e.g., McCreadie & Colbo 1993, Figueiró et al. 2008) and water temperature (McCreadie et al. 2005, Nascimento et al. 2007).

The present study, together with the work of Landeiro et al. (2009), stands as one of the first contributions to the literature about the ecological traits of the Brazilian cerrado black flies. Although biotic factors can influence community structure in lotic systems, abiotic factors probably play a dominant role in defining species assemblages (Allan 1995). Thus, the main objective of the present paper is to describe the abiotic factors affecting the distribution of black flies at a microhabitat scale, rather than at the regional scale usually found in the literature on the Neotropical Region. We sampled black fly assemblages in microhabitats, defined here as 30 x 30 cm areas (quadrats), at four sites and assessed abiotic factors that might facilitate coexistence of the species and contribute to the diversity of the assemblages.

Even though laboratorial studies have shown that variations in micro-scale water flow dynamics can create appropriate habitat for many specialized lotic organisms, consequently playing a pivotal role in defining the spatial distribution of the benthic community (Statzner et al. 1988), the number of field studies which actually quantified micro-velocities is extremely limited, due to the technical difficulties of such measurements (Hart et al. 1996). In this present study we employ in our analyses the local macro-velocities, that is, the velocity within each habitat patch in a water course.

MATERIALS AND METHODS

Study areas - The study areas are located in southern state of Tocantins (TO), in an area which ranges from the typical cerrado *sensu stricto*, dominated by shrubs and small trees, to the *cerradão*, composed of larger trees up to 15 m tall (Fig. 1).

Córrego do Mato (S12º39'33.0'' W48º18'27.3'') - This is a first order (Strahler 1952) tributary of the Tocantins River. It has a mean width of approximately 5 m and a 1 m mean depth. It is characterized by a dense canopy cover which provides shade for the water course and it has a predominantly rocky bed. It also features a small artificial reservoir.

Ribeirão das Lages (S12º35'7.7'' W48º2'29.2'') - This is a first order (Strahler 1952) tributary of the Paranã River, which has an average depth of 1 m and a mean width of 10 m, thus resulting in no canopy cover (there is vegetation along the water course margins, but its canopy does not provide shade for the stream) and a sandy bottom.

Piabanha (S12º45'07.8" W48º17'16.6") - This is a second order (Strahler 1952) tributary of TO, which has an average depth of 1 m and a mean width of 8 m. It is characterized by a rocky bottom and by riparian vegetation formed by 50 cm to 1 m tall small shrubs very close to the stream, which provide little shade for the margins and have partially submerged branches.

Tocantins River (12º13'05.5"S 48º25'56.7"W) - This is a river which averages 4.5 m depth and 600 m average width, shows very pronounced riparian vegetation with branches submerged in water; however, due to the great width of the river, this vegetation provide little shade.

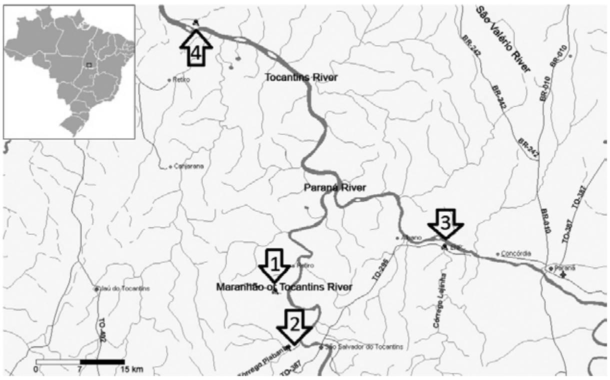

Fig. 1: map of southern state of Tocantins, Brazil, with arrows showing the four sampling sites: 1: Córrego do Mato; 2: Córrego Piabanha; 3: Ribeirão do Lages; 4: Tocantins River.

Sampling - Black fly larvae of later instars were sampled by hand during six bi-monthly sample periods, from October 2004-August 2005 (Fig. 1). At each sampling site, which consisted of a 15 m stream/river section, a random stratified sample of 15 quadrats (30 x 30 cm) was taken during each campaign. Approximately half of the quadrats in a given site was collected at the margin and the other half was collected in the middle, when this was possible (in the middle of the Tocantins River, there were no suitable substrates). In each quadrat were determined mean water velocity, depth and predominant substrate type, such as rocks, riffle litter (dead leaves trapped in the riffles) or riparian vegetation. In the tributaries, the head rod method for measuring water velocity was applied (Wilm & Storey 1944); this is a method in which the sharp edge of a ruler is placed facing upstream in order to measure the depth and then it is revolved 90 degrees, so the flat edge is opposed to the stream flow, in order to measure the increase in water elevation by looking at the impingement of water against the broad edge of the ruler. In the Tocantins River, where the application of such method was not possible, due to its depth, a flowmeter was used instead.

Larval identification - Larvae were sorted in morphotypes and their final instar specimens were dissected and identified using direct comparison with pupae collected in the sites and with the material deposited at the Laboratório de Simulídeos e Oncocercose/Instituto Oswaldo Cruz (LSO-IOC) and thanks to the aid of taxonomic bibliography (e.g., Hamada & Adler 2001, Coscarón & Coscarón-Arias 2007). The specimens are currently deposited at LSO-IOC.

Statistical methods - First, to avoid potential collecting bias, we correlated the number of larvae sampled during each sample period and at each site with the number of species identified, following Hamada et al. (2002). Secondly, to test the null hypothesis of random co-occurrence, we employed the null modelling software ECOSIM (Gotelli & Entsminger 2009) to create null models first for co-occurrence, in which we employed the C-score index (Stone & Robert 1990) with fixed sums for row and column constraints and then for niche overlap. For the niche overlap, we measured current velocity, assumed equiprobable resource states, relaxed niche breadth and retained zero states. The metrics used for quantifying niche overlap was Pianka's index.

To test the hypothesis that local black fly species richness and diversity are associated with water current variation range (the difference between the highest and lowest water current velocity found in a given site, during a given campaign) (Figueiró et al. 2008), we determined the species richness and the Shannon diversity index for each sampling site, in each sample period, as well as the water velocity range and we performed linear regressions to test whether they were related. Cook's distances were calculated in order to identify possible outliers. Species richness and Shannon diversity indices were also calculated for the assemblage of each quadrat and then, with these values, the mean diversity and species richness were calculated for each current velocity.

As our objective was to describe microhabitat associations, we opted for statistical methods that assume modal distribution to find the optimal conditions for each species. To determine general microhabitat associations, we performed a canonical correspondence analysis (CCA) using the CANOCO and PAST statistical packages. To test the significance of individual environmental variables used in the model, 5,000 Monte Carlo permutations were conducted for each of these, where only those variables with $p < 0.05$ were used in the model. Because water velocity is an extremely important niche dimension for black fly larvae, as it is directly related to food acquisition (Malmqvist & Sackmann 1996, Hart & Merz 1998, Palmer & Craig 2000), we elected to analyze this data set separately: we applied a detrended correspondence analysis (DCA) using PAST v2.10 for the whole grouped data set in order to estimate general velocity associations and correspondence analysis (CA) using Statistica v7.0 for the smaller data sets of each sampling site, to determine the site specific velocity associations. For these analyses, data was sorted in water current velocity classes.

RESULTS

A total of 2,385 larvae representing 12 species were collected (Table I). *Simulium pertinax* Kollar, 1832 and *Simulium dekeyseri* Shelley & Py-Daniel, 1981 larvae are indistinct, as *Simulium subnigrum* Lutz, 1910 and *Simulium inaequale* (Paterson & Shannon, 1927) immature larvae. When we found both species in the localities, the pairs were treated as the same entity in this work. The correlation between the number of larvae sampled and the number of species identified was not significant, so we assumed there was no sampling bias, according to the methodology described in Hamada et al. (2002).

The null model for co-occurrence found our observed index significantly above the simulated indices [observed index = 110.71, mean of simulated indices = 92.87, variance of simulated indices = 9.55, p (observed ≤ expected) = 1.00, p (observed ≥ expected) = 0.00] and in the null model for niche overlap, our mean niche overlap (Pianka index) was significantly below the simulated indices [observed mean = 0.197, mean of simulated indices = 0.345, variance of simulated indices = 0.001, p (observed ≤ expected) = 0.000, p (observed ≥ expected) = 1.000] (Fig. 2); therefore, the distributional patterns of species were not considered random.

TABLE I

Larvae sampled in the state of Tocantins, Brazil, during the study (October 2004-August 2005)

	Localities				
Species	Córrego Piabanha	Córrego do Mato	Ribeirão do Lages	Tocantins River	All sites
Simulium subpallidum Lutz, 1909	147	342	359	19	867
Simulium minusculum Lutz, 1910	4	0	0	50	54
Simulium quadrifidum Lutz, 1910	6	0	0	0	6
Simulium incrustatum Lutz, 1910	25	392	0	32	449
Simulium subnigrum Lutz, 1910/ *Simulium inaequale* (Paterson & Shannon, 1927)	89	5	0	4	98
Simulium pertinax Kollar, 1832/ *Simulium dekeyseri* Shelley & Py-Daniel, 1981	10	0	0	0	10
Simulium cuasiexiguum Shelley et al. 2001	18	0	89	132	239
Simulium nigrimanum Macquart, 1838	26	430	0	0	456
Simulium guianense Wise, 1911	0	23	0	11	34
Simulium perflavum Roubaud, 1906	0	172	0	0	172
Total larvae sampled	359	1,364	448	248	2,385

The linear regressions were significant, pointing towards a tendency for more diverse [$y = 0.9036x - 0.337$, $F = 10.74$, $p = 0.0096$, $R^2 = 0.5440$, degrees of freedom (DF) = 9, $F = 10.74$] and species rich ($y = 1.5161x + 0.8573$, $F = 7.185$, $p = 0.0252$, $R^2 = 0.4439$, DF = 9, $F = 7.185$) assemblages in streams with wider water current ranges (Fig. 3). The Cook distances were interpreted according to Cook and Weisberg (1994) and revealed no outliers.

The mean species richness of the assemblages in the current velocity gradient was a unimodal distribution skewed to the left, where the highest richness values were observed between 0.88 $m.s^{-1}$-1.17 $m.s^{-1}$. However, the average diversity of the assemblages from patches within the current velocity gradient showed a bimodal distribution, with diversity peaks at 0.76 $m.s^{-1}$ and 1.17 $m.s^{-1}$ (Fig. 4). CCA (Fig. 5) showed that riffle litter was the most frequent substrate type for most species. However, *Simulium nigrimanum* Macquart, 1838 showed an association with the rocky substrate, whereas *Simulium cuasiexiguum* Shelley et al., 2001 was strongly associated with the riparian vegetation. This analysis showed a general trend towards larvae occurrence in the middle of the streams, instead of at the margin, except for *S. nigrimanum* and *S. cuasiexiguum*.

The DCA (Fig. 6) showed three distinct groups: the first one between 0.19-0.88 $m.s^{-1}$, composed of *Simulium quadrifidum* Lutz, 1910, *S. subnigrum*/*S. inaequale*, *Simulium minusculum* Lutz, 1910, *Simulium guianense* Wise, 1911 and *Simulium perflavum* Roubaud, 1906; the second one was between 0.99-1.32 $m.s-^{-1}$, composed of *S. cuasiexiguum and S. pertinax*/*S. dekeyseri;* finally, a third group was between 1.4-1.8 $m.s^{-1}$, composed of *Simulium subpallidum* Lutz, 1910, *Simulium incrustatum* Lutz, 1910 and *S. nigrimanum*.

The CA performed for each site showed that water velocity associations for each species varied between sites (Fig. 7, Table II).

DISCUSSION

Even though several other studies, such as Horne et al. (1992) and Scheder and Waringer (2002), among others, also rely on the distributional patterns of stream macroinvertebrates to infer their microhabitat preferences, this premise can be controversial. Fonseca and Hart (2001) suggested that stream insects, such as Simuliidae, may have their ability to reach preferred microhabitats limited by dispersal constraints of drifting larvae, which means that the observed patterns would be influenced more by chance than by habitat preferences.

The null model analysis for co-occurrence indicates that the assemblages observed in the present study are not random. We employed a system that measures the tendency for species not to co-occur, so it should be expected that, in a community structured by competition, the index value would be greater than that which would be observed in a randomly assembled community. As the observed index was significantly above the simulated indices, it is likely that competition played a role in the patterns observed and that the pattern is not random. Schoener (1974) suggested that niche overlaps observed

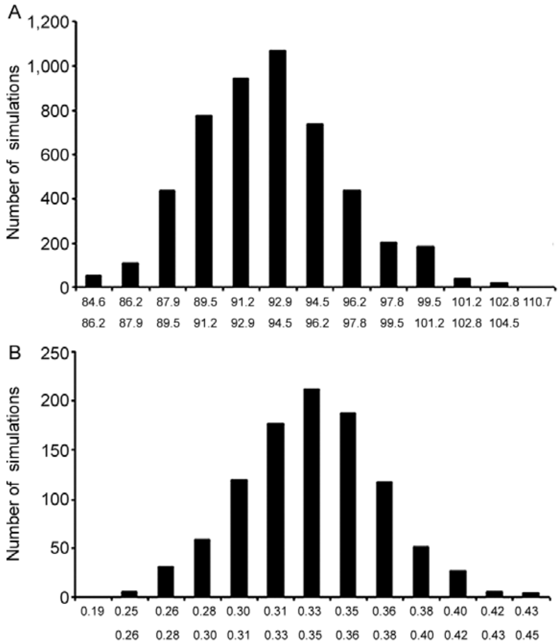

Fig. 2: null models for co-occurrence [observed index = 110.71, mean of simulated indices = 92.87, variance of simulated indices = 9.55, p (observed ≤ expected) = 1.00, p (observed ≥ expected) = 0.00] (A) and niche overlap [observed mean = 0.197, mean of simulated indices = 0.345, variance of simulated indices = 0.001, p (observed ≤ expected) = 0.000, p (observed ≥ expected) = 1.000] (B).

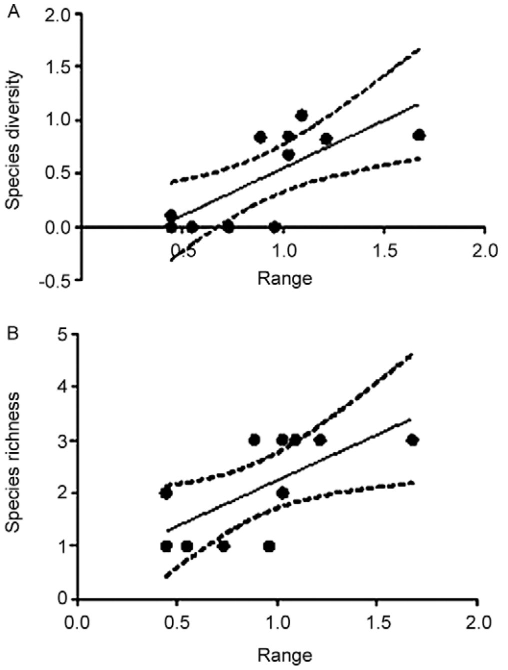

Fig. 3: linear regressions for Shannon diversity index ($y = 0.9036x - 0.337$, $F = 10.74$, $p = 0.0096$, $R^2 = 0.5440$, DF = 9, $F = 10.74$) (A) and species richness ($y = 1.5161x + 0.8573$, $F = 7.185$, $p = 0.0252$, $R^2 = 0.4439$, DF = 9, $F = 7.185$) (B) in relation to water current velocity ranges (independent variable).

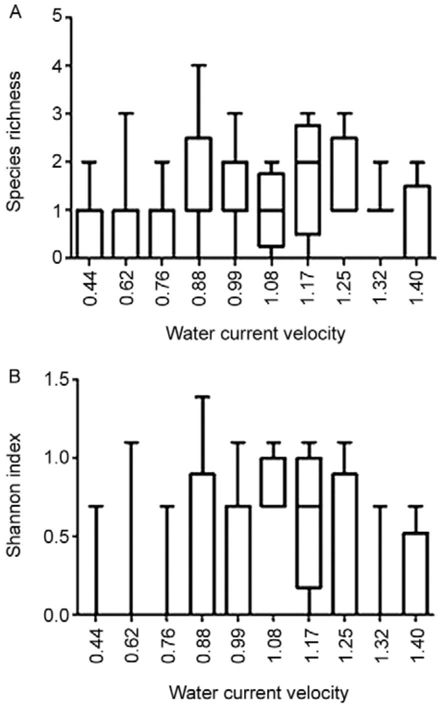

Fig. 4: box-plot graphics exhibiting the mean values for species richness (A) and Shannon diversity index of the black fly assemblages found in the water current velocity gradient (B).

in nature should happen less and be of smaller degree than what is expected to happen randomly: a significantly small observed overlap may imply interspecific competition and resource partitioning (Gotelli & Graves 1996), which was also observed in our niche overlap null model. Thus, the results from our simulations are consistent with the hypothesis that the patterns observed are not random and that the and that the community structure might be driven partially by competition and partitioning of a possible limiting resource, in this case the available space in microhabitats with suitable current velocities. The relationship between the microdistribution of black fly larvae throughout the water current gradient and their respective filter feeding is well established in the literature (McCreadie & Colbo 1993); thus, different species may present their optimal feeding rates at different water velocities. Studies have shown that other biotic factors, such as predation, may influence microdistribution, as in the case of larvae occurring in microhabitats above their optimal feeding water velocity in order to avoid natural predators (Hart & Merz 1998).

We suggest that this positive relation between water current range and local species richness and diversity proposed by Figueiró et al. (2008) can possibly be extrapolated to be applied to other filter feeding lotic macroinvertebrates, which depend on the water velocity as much as Simuliidae do.

Many studies show riffle litter association for many Neotropical black fly species (e.g., Shelley et al. 2000, Figueiró et al. 2006) as well as the association of *S. nigrimanum* to rocky substrates (Shelley et al. 2000). *S. cuasiexiguum* was probably associated with riparian vegetation because it was common to find in the Tocantins River, where the only suitable microhabitat patches for black fly immatures were riparian vegetation patches at the margin. The association of *S. minusculum* with current velocity in the larger Tocantins River confirms previous studies (Coscarón 1983, Shelley et al. 2000).

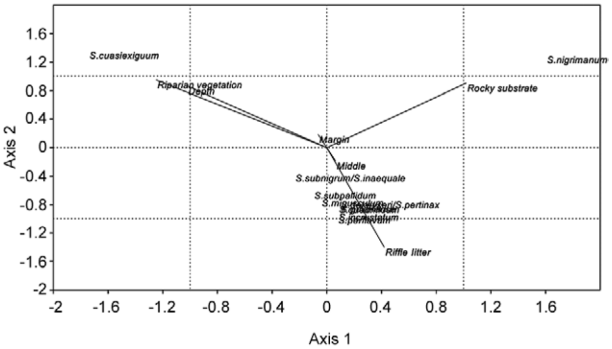

Fig. 5: ordination diagrams extracted by canonical correspondence analysis of the 12 species distribution in relation to habitat variables found significant ($p < 0.05$) under 5,000 Monte Carlo permutations (axis 1: eigenvalues = 0.64; axis 2: eigenvalues = 0.55) showing that riffle litter was the most frequent substrate type for most species and general trend towards larvae occurrence in the middle of the streams, instead of at the margin, except for *Simulium nigrimanum* and *Simulium cuasiexiguum*.

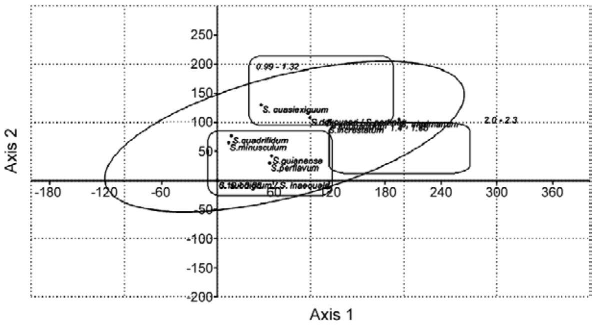

Fig. 6: detrended correspondence analysis ordination diagrams of species from the survey sites along the water current velocity gradient (axis 1: eigenvalues = 0.31; axis 2: eigenvalues = 0.031) showing three distinct groups: species associated to velocities between 0.19-0.88 $m.s^{-1}$ composed of *Simulium quadrifidum* Lutz, 1910, *Simulium subnigrum*/*Simulium inaequale*, *Simulium minusculum* Lutz, 1910, *Simulium guianense* Wise, 1911 and *Simulium perflavum* Roubaud, 1906, species associated to velocities between 0.99-1.32 $m.s^{-1}$ composed of *Simulium cuasiexiguum and Simulium pertinax*/ *Simulium dekeyseri* and species associated to velocities between 1.4-1.8 $m.s^{-1}$ composed of *Simulium subpallidum* Lutz, 1910, *Simulium incrustatum* Lutz, 1910 and *Simulium nigrimanum*.

CA revealed that the same species could show local variation of water velocity associations amongst sites, probably due to the overall differences amongst the assemblages from each site and thus to the different com-

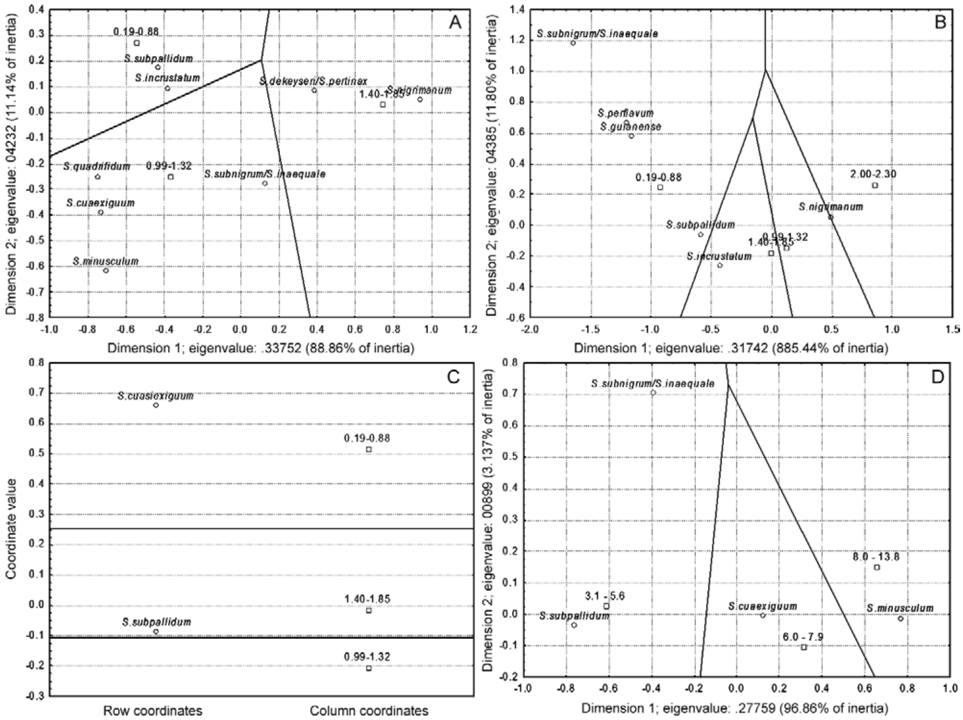

Fig. 7: ordination diagrams extracted by correspondence analyses for each sampling site showing site-specific water current velocity associations of black flies for Piabanha (A), Córrego do Mato (B), Ribeirão do Lages (C) and Tocantins River (D).

TABLE II

Water velocity ranges for the localities and its respective associated species

	0.19 m.s^{-1}-0.88 m.s^{-1}	0.99 m.s^{-1}-1.32 m.s^{-1}	1.4 m.s^{-1}-1.85 m.s^{-1}
Córrego Piabanha	*Simulium incrustatum* *Simulium subpallidum*	*Simulium minusculum* *Simulium cuasiexiguum* *Simulium quadrifidum* *Siulium subnigrum/* *Simulium inaequale*	*Simulium nigrimanum* *Simulium pertinax/* *Simulium deseykeri*
Córrego do Mato	*S. subnigrum/S. inaequale* *Simulium perflavum* *Simulium guianense* *S. subpallidum*	*S. nigrimanum*	*S. incrustatum*
Ribeirão do Lages	*S. cuasiexiguum*		*S. subpallidum*
Tocantins River	*S. subpallidum*	*S. subnigrum*	*S. cuasiexiguum* *S. minusculum*

the water velocity (m.s.) associations for each species varied amongst sites.

petitive pressures resulting in different realized niches. As we observe the two most common species, *S. subpallidum* and *S. nigrimanum*, we notice that the first one is restricted to velocities between 0.19 m.s^{-1}-0.88 m.s^{-1} when the second one is present and that in the absence of *S. nigrimanum*, *S. subpallidum* would occur at and above the velocities where the previous species is common.

Species richness variation observed along the current velocity gradient indicates that intermediate velocities support more species rich assemblages, showing a unimodal pattern which could be the reflection of these velocities, representing a transition habitat; thus, similarly to what happens with ecotones, the boundaries of several species distributions overlap in such habitats, resulting in an increased species richness. However, the diversity pattern observed along the current velocity gradient was defined by a bimodal distribution, strongly suggesting microhabitat association traits.

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