

Effect of environmental filters on Chironomidae (Insecta: Diptera) assemblages of neotropical watersheds

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ABSTRACT

Effect of environmental filters on Chironomidae (Insecta: Diptera) assemblages of neotropical watersheds

Environmental filters act at different spatial scales, selecting species with characteristics that allow them to successfully establish and survive under local environmental conditions. We sought to evaluate how environmental filters (physical/chemical, habitat composition, and landscape) and different levels of anthropogenic disturbances affect the abundance of Chironomidae in neotropical semi-arid watersheds. Chironomidae larvae were sampled in six reservoirs (112 sites) in the Piranhas-Assu and Paraíba watersheds (NE Brazil) during the dry season. The distribution of Chironomidae larvae was best explained in Least Disturbed sites, with 82.1 % of the total explained variance in the Piranhas-Assu watershed and 64.2 % in the Paraíba watershed. The interactions of filters (physical/chemical, habitat composition, and landscape) best explained the abundance distributions of Chironomidae larvae in the watersheds and sites subjected to different levels of anthropogenic disturbances. The physical/chemical conditions of the water as well as habitat composition depend on landscape characteristics, because anthropogenic activities in watersheds increase nutrient concentrations in the water, promoting the increase of the trophic state of the environment as well as habitat homogenization. This study showed that, independent of the anthropogenic disturbance level, interactions of environmental factors act as strong environmental filters on the distributions of local communities, such as Chironomidae assemblages.

Key words: environmental degradation, benthic macroinvertebrates, species selection, reservoirs, semi-arid

RESUMO

Efeitos dos filtros ambientais sobre as assembleias de Chironomidae (Insecta: Diptera) em bacias hidrográficas neotropical

Os filtros ambientais atuam em diferentes escalas espaciais selecionando espécies com características adequadas capazes de sobreviver e se estabelecer sob condições ambientais específicas. Procuramos avaliar como os filtros ambientais (físico/químico, composição do habitat e paisagem) e os diferentes níveis de distúrbios antropogênicos afetam a abundância de Chironomi-

dae em bacias hidrográficas no semiárido neotropical. As larvas de Chironomidae foram amostradas em seis reservatórios (112 locais) nas bacias hidrográficas do rio Piranhas-Assu e do rio Paraíba (NE Brasil) durante a estação seca. A distribuição das larvas de Chironomidae foi melhor explicada nos locais menos perturbados, com 82.1 % da variação total explicada para a bacia hidrográfica do rio Piranhas-Assu e 64.2 % para a bacia hidrográfica do rio Paraíba. As interações entre os filtros (físico/químico, composição do habitat e paisagem) explicaram melhor a distribuição da abundância das larvas de Chironomidae nas bacias hidrográficas e locais sujeitos a diferentes níveis de distúrbio antropogênico. As condições físicas e químicas da água e a composição do habitat dependem das características da paisagem, pois as atividades antrópicas desenvolvidas nas bacias hidrográficas aumentam as concentrações de nutrientes na água, promovendo o aumento do estado trófico do ambiente e a homogeneização dos habitats. Este estudo, mostrou que, independente do nível de distúrbio antropogênico, as interações entre os fatores ambientais atuam como fortes filtros ambientais na distribuição das comunidades locais, a exemplo, das assembléias de Chironomidae.

Palavras chave: *degradação ambiental, macroinvertebrados bentônicos, seleção de espécies, reservatórios, semi-árido*

INTRODUCTION

Ecologists seek to understand the processes involved in the selection of species that constitute communities (Diamond, 1975; Berryman & Millstein, 1989; Hubbell, 2001). Studies investigating the factors that could operate on species selection (also known as “assembly rules”) initially focused on competitive relationships (Diamond, 1975; Holt, 1977), although later studies suggested that community compositions could reflect species combinations responding to different environmental filters (Keddy, 1992; Poff, 1997). Environmental filters can be classified as phylogeographic (speciation histories, extinctions, and migrations) or ecological (interactions of biotic and abiotic factors) (Keddy, 1992; Vergnon *et al.*, 2009; Götzenberger *et al.*, 2012).

Environmental filters act at different spatial scales to select species capable of becoming established in any given locality (Keddy, 1992; Poff, 1997; Götzenberger *et al.*, 2012). That selection process acts on intrinsic characteristics of the species, so that only species with the best combinations of characteristics for a specific local environment will become successfully established (Poff, 1997; Heino *et al.*, 2007; Bedoya *et al.*, 2011). In spite of the effects of environmental filters on species selection, dispersal potential allows some species to exist in inadequate habitats even though they cannot establish viable populations (Leibold *et al.*, 2004; Winegardner *et al.*, 2012).

The main filters that select species in aquatic ecosystems are the physical/chemical conditions

of the water, habitat characteristics, and biological interactions (Poff, 1997). Anthropogenic disturbances also are considered filters of local species selection (Heino *et al.*, 2013), and when occurring at watersheds scales they can exert severe pressure on aquatic ecosystems and promote changes on small spatial scales (Allan, 2004). Those anthropogenic modifications result in the deterioration of the physical habitat and water quality, affect the natural dynamics of communities, and increase the interactional complexity between the factors that govern local species assemblage compositions (Bruno *et al.*, 2014; Azevêdo *et al.*, 2017). Sites with lower levels of anthropogenic disturbance, on the other hand, tend to present more diversified habitats, better physical/chemical water conditions, and increased abundances of species sensitive to anthropogenic impacts (Molozzi *et al.*, 2013). The effects of disturbances on local assemblages will also depend on disturbance frequencies and intensities, initial ecological conditions, and species' sensitivities (Hawkins *et al.*, 2015).

We selected the Chironomidae family (Insecta: Diptera) for this study due to its high abundance and wide sensitivity range to the environmental qualities of freshwater ecosystems (Serra *et al.*, 2016; 2017a,b), especially reservoirs (e.g., Zhang *et al.*, 2010; Magbanua *et al.*, 2015; Beghelli *et al.*, 2016; Azevêdo *et al.*, 2017). Chironomidae tolerance of wide ecological amplitudes allows them to inhabit sites experiencing different levels of anthropogenic impacts, and where members of other invertebrate groups (such as Ephemeroptera, Plecoptera, and Trichoptera) are rare (Odume &

Muller, 2011, Serra *et al.*, 2017a). Our main objective was to evaluate how different levels of anthropogenic disturbances and environmental filters (physical and chemical, habitat composition, and landscape) affect Chironomidae abundance in neotropical semiarid watersheds by: i) classifying sites using anthropogenic impact levels as Least Disturbed sites, Intermediate Disturbed sites, and Severely Disturbed sites; ii) determining which

filters (physical/chemical, habitat composition, and landscape) most influence Chironomidae abundance in those three site categories. We tested the hypothesis that the interactions between environmental filters exert a strong influence on the abundance of Chironomidae in sites subjected to different levels of anthropogenic disturbances, due to the interdependence between environmental factors acting on multiple spatial scales.



Figure 1. Location of reservoirs and respective sampling sites. Sabugí, Passagem das Traíras, and Cruzeta reservoirs located in the Piranhas-Assu watershed, Rio Grande do Norte and Poções, Sumé, and Cordeiro reservoirs located in the Paraíba watershed, Paraíba, Northeastern of Brazil. Figure in Jovem-Azevêdo *et al.* (2019). *Localização dos reservatórios e respectivos locais de amostragem. Os reservatórios Sabugí, Passagem das Traíras e Cruzeta, localizados na bacia hidrográfica do rio Piranhas-Assu, Rio Grande do Norte e os reservatórios Poções, Sumé e Cordeiro, localizados na bacia hidrográfica do rio Paraíba, Paraíba, Nordeste do Brasil. Figura em Jovem-Azevêdo et al. (2019).*

MATERIALS AND METHODS

Study area and sampling sites

We selected six reservoirs in two watersheds in northeastern Brazil for study: three reservoirs in the Piranhas-Assu watershed in Rio Grande do Norte State, and three in the Paraíba watershed in Paraíba State (Fig. 1). The predominant climate in that region is hot semiarid (BSh, following the Köppen–Geiger classification), with a 9 to 10 month-long dry season, and a mean annual rainfall of approximately 800 mm in Rio Grande do Norte and 400 mm in Paraíba (Alvares *et al.*, 2013). Reservoirs located in the Brazilian semiarid region experience anthropic impacts of many types, including from agriculture, ranching, and domestic sewage disposal – uses that, together with high reservoir water residence times, contribute to high total nitrogen and total phosphorus levels (Santos & Eskinazi-Sant’Anna, 2010; Barbosa *et al.*, 2012; Azevêdo *et al.*, 2017).

We sampled 52 sites distributed among the Cruzeta (12 sites), Passagem das Traíras (10), and Sabugi (30) reservoirs in the Piranhas-Assu watershed, as well as 60 sites distributed among the Poçoões (20 sites), Cordeiro (20), and Sumé (20) reservoirs in the Paraíba watershed (Fig. 1, supplementary material- Table S1 (available at <http://www.limnetica.net/en/limnetica>)). Those sites were known from previous studies to demonstrate different levels of anthropic disturbances (Gomes *et al.*, 2018). All of the sampling sites were located in the littoral region of the reservoirs (at an average depth of 60 centimeters), because those areas are strongly influenced by the riparian zone and normally harbor the greatest species richness and abundances of benthic macroinvertebrates (Magbanua *et al.*, 2015). The sites were sampled on two occasions, one in June and one in September 2014, during the dry season.

Filter characterizations

Physical/chemical filters

The physical/chemical filters considered were based on the parameters of the water sampled at

each site. Dissolved oxygen (DO mg/L) and total dissolved solids (TDS g/L) were measured with a multiparameter probe (Horiba U-50); water transparency was determined using a Secchi disk. We sampled a liter of sub-surface water (maximum depth of 0.6 m) to determine: total phosphorus concentrations (TP µg/L), using the ascorbic acid method after digestion with persulfate; reactive soluble phosphate (PO₄- µg/L), using the ascorbic acid method; and total nitrogen (TN µg/L), using the oxidative method. All analyses were performed according to the “Standard Methods for the Examination of Water and Waste Water” (APHA, 2005). We estimated chlorophyll-*a* concentrations (Chlo-*a* µg/L) by extraction in 90 % acetone, according to the methodology described by Lorenzen (1967).

We based the trophic classification of each site on the Trophic State Index (TSI) proposed by Carlson (1977) and modified by Toledo *et al.* (1983). That index is calculated based on water transparency (m), total phosphorus concentrations (µg/L), reactive soluble phosphate (µg/L), and chlorophyll-*a* concentration (µg/L). Values from 0 to 44 correspond to oligotrophic conditions, values from 45 to 54 to mesotrophic conditions, and > 54 to eutrophic conditions.

Habitat composition filters

The habitats were characterized according to the granulometric compositions of their sediments. We collected sediment samples at each site using an Eckman-Birge dredge (area 0.225 m²) and determined their granulometric compositions following the methodology described by Suguio (1973) and modified by Callisto & Esteves (1996), as recommended in other studies (e.g., Molozzi *et al.* (2013), Azevêdo *et al.* (2017), and Gomes *et al.* (2018)). We dried the sediment samples at 60 °C for 72 hours and mechanically separated the fractions by mechanical agitation through a series of sieves. The particles were subsequently classified into six categories: gravel (> 1 mm); coarse sand (500 - 1000 µm); middle sand (250 - 500 µm); fine sand (125 - 250 µm); silt (63 - 125 µm); and mud (< 63 µm).

Landscape filters

We used the River Habitat Survey protocol, 2003 version, modified by Rowan *et al.* (2006) for lentic water bodies to characterize landscape components. We evaluated land use at each sampling site to a distance of 50 m from the littoral region to the riparian margin, to both the left and the right of the sampling point, noting: urbanization (the presence or absence of human residences) and agricultural areas (the presence or absence of pastures or agricultural areas).

Chironomidae assemblages

We collected Chironomidae larvae along the littoral region of the reservoirs (at an average depth of 60 centimeters) using an Eckman-Birge dredger (area 0.225 m²), subsequently fixing them *in situ* in 10 % formaldehyde. The samples were washed in the laboratory using 0.50 mm sieves and the chironomids identified to the genus level based on specialized identification keys (Trivinho-Strixino & Strixino, 1995; Trivinho-Strixino, 2011).

Data Analysis

Sampling site classifications

Before performing the statistical analyses, we analyzed auto-correlations among the environmental variables using the inflation factor (VIF). As no highly correlated values were identified, all of the previously selected variables were maintained. To test for significant differences in environmental characteristics between watersheds, we performed Permutational Multivariate Analysis of Variance (PerMANOVA, 9999 permutations; $\alpha \leq 0.05$). Significant differences were observed in the environmental characteristics among watersheds (PerMANOVA: Pseudo-F_{1,223} = 8.359; $p = 0.001$).

Principal Components Analysis (PCA, bi-dimensional plot) was used to discriminate the sites in terms of their levels of anthropogenic disturbance based on environmental parameters, following the approach proposed by Molozzi *et al.* (2013), Azevêdo *et al.* (2017), and Gomes *et al.*

(2018) (supplementary material- Table S2, available at <http://www.limnetica.net/en/limnetica>). Different from what we had predicted, PCA showed the formation of only two groups: sites with the lowest levels of anthropogenic disturbance were considered Least Disturbed sites (LD); sites with the highest levels of anthropogenic disturbance were considered Severely Disturbed sites (SD). Subsequent analyses were performed based on the formation of two groups showing different disturbance levels. We subsequently performed Permutational Multivariate Analysis of Variance (PerMANOVA, 9999 permutations; $\alpha \leq 0.05$) to confirm that the differences between these two groups were significant.

Chironomidae assemblages and environmental filters

To evaluate which environmental filter had the greatest influence on the distribution of Chironomidae larvae (transformed by $\log x+1$), and to explain the independent and shared effects (interactions) of the data set, we used the canonical variance partitioning as proposed by Borcard *et al.* (1992), and adapted by Cushman & McGarigal (2002). A series of Canonical Correspondence Analysis (CCA) and Partial Canonical Correspondence Analysis (pCCAs) was used to partition data variance (Cushman & McGarigal, 2002). Six combinations of environmental matrices were used to obtain the total inertia values and the variance explained, being: a = physical/chemical; b = habitat; c = landscape; d = physical/chemical + landscape; e = physical/chemical + habitat; f = habitat + landscape. The percentages of independent and shared explanations were calculated using simple mathematical equations. Those analyses were performed separately for Least Disturbed sites (LD) and Severely Disturbed sites (SD), in each watershed. In a preliminary Detrended Correspondence Analysis (DCA), our biological data exhibited a relatively long gradient (DCA axis 1 SD > 2), and species responses were primarily unimodal, implying that CCA is suitable for analyzing the data (Heino & Mykrä, 2008). The statistical significances of those analyses were obtained using Monte Carlo tests with 1000

permutations of all canonic axes. All of the analyses were conducted using R software, version 3.2.2 (R Core Development Team, 2017), with the *vegan* package.

RESULTS

Sampling site classifications

The PCA of the Piranhas-Assu watershed showed two groups of sites with different levels of anthropogenic disturbance: 21 LD and 31 SD sites (Fig. 2A). The first and second axes of the

PCA explained 40.02 % and 17.58 % of the data variability, respectively, and were correlated mainly with silt (0.80) and gravel (0.85) (supplementary material- Table S3, available at <http://www.limnetica.net/en/limnetica>); the LD and SD groups were significantly different (PerMANOVA: Pseudo- $F_{1,51} = 16.157$; $p = 0.001$). The PCA of the Paraíba watershed sites showed two groups with different levels of anthropogenic disturbance: 20 LD sites and 40 SD sites (Fig. 2B). The first and second axes of the PCA explained 35.80 % and 17.85 % of the data variability, respectively, being correlated mainly with

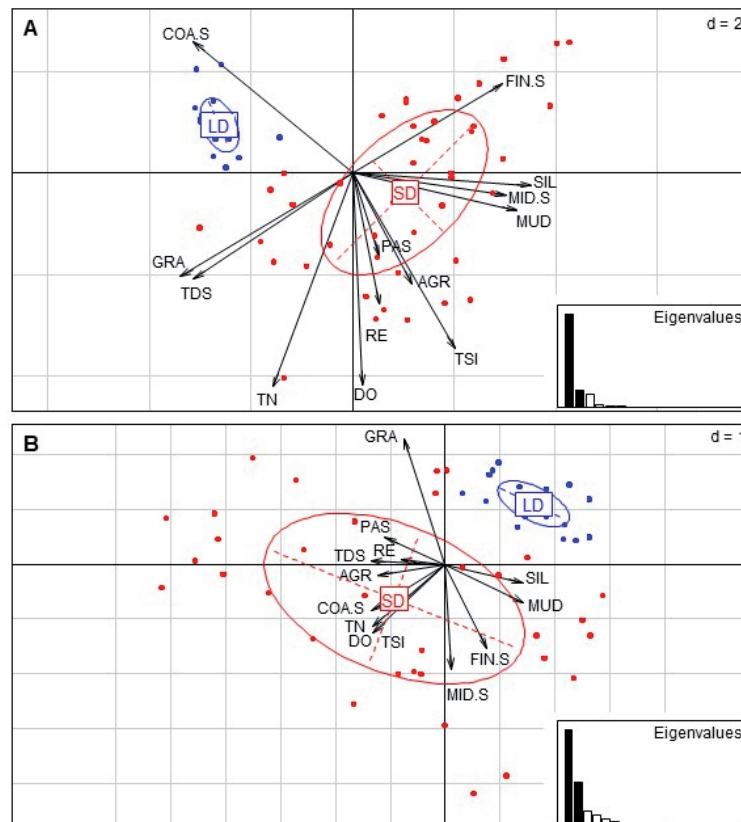


Figure 2. Results of PCA performed on the variables indicative of anthropogenic disturbance collected in the Piranhas-Assu watershed (A) and in Paraíba watershed (B) in Northeastern Brazil. Where: LD = Least Disturbed sites; SD = Severely disturbed sites; OD = Dissolved oxygen; TDS = Total dissolved solids; NT = Total nitrogen; TSI = Trophic State Index; OM = Organic matter; GRA = Gravel; COA.S = Coarse sand; MID.S = Middle sand; FIN.S = Fine sand; SIL = Silt; MU = Mud; RE = Presence of residence; PAS = Pasture area; AGR = Presence of agriculture. *Resultados da ACP realizadas com base nas variáveis indicadoras de impacto antrópico coletadas na bacia hidrográfica do rio Piranhas-Assu (A) e na bacia hidrográfica do rio Paraíba (B) Nordeste do Brasil. Onde: LD = Locais menos perturbados; SD = Locais severamente perturbados; DO = oxigênio dissolvido; TDS = Total de sólidos dissolvidos; NT = nitrogênio total; TSI = índice de estado trófico; OM = matéria orgânica; GRA = cascalho; COA.S = areia grossa; MIDS = areia média; FIN.S = areia fina; SIL = Silte; MU = argila; RE = Presença de residência; PAS = Área de pastagem; AGR = Presença de agricultura.*

silt (0.85) and dissolved oxygen (-0.71) (supplementary material- Table S3, available at <http://www.limnetica.net/en/limnetica>); the LD and SD groups were significantly different (PerMANOVA: Pseudo- $F_{1,59} = 8.214$; $p = 0.001$).

Chironomidae assemblages and environmental filters

A total of 11 214 Chironomidae larvae were collected, distributed among 22 genera (supplementary material- Table S4, available at <http://www.limnetica.net/en/limnetica>). The most abun-

dant taxa in the LD and SD sites in the Piranhas-Assu watershed were *Goeldichironomus* (Fittkau, 1965) (2218 and 1708 individuals respectively) and *Tanytarsus* (Van der Wulp, 1874) (1306 and 975 individuals respectively). The LD sites in the Paraíba watershed showed a dominance of *Coelotanypus* (Kieffer, 1913) (200 individuals), while the dominant taxa in the SD sites were *Aedokritus* (Roback, 1958) (231 individuals) and *Polypedilum* (Kieffer, 1912) (197 individuals).

Variance partitioning of the Piranhas-Assu watershed showed that Chironomidae abun-

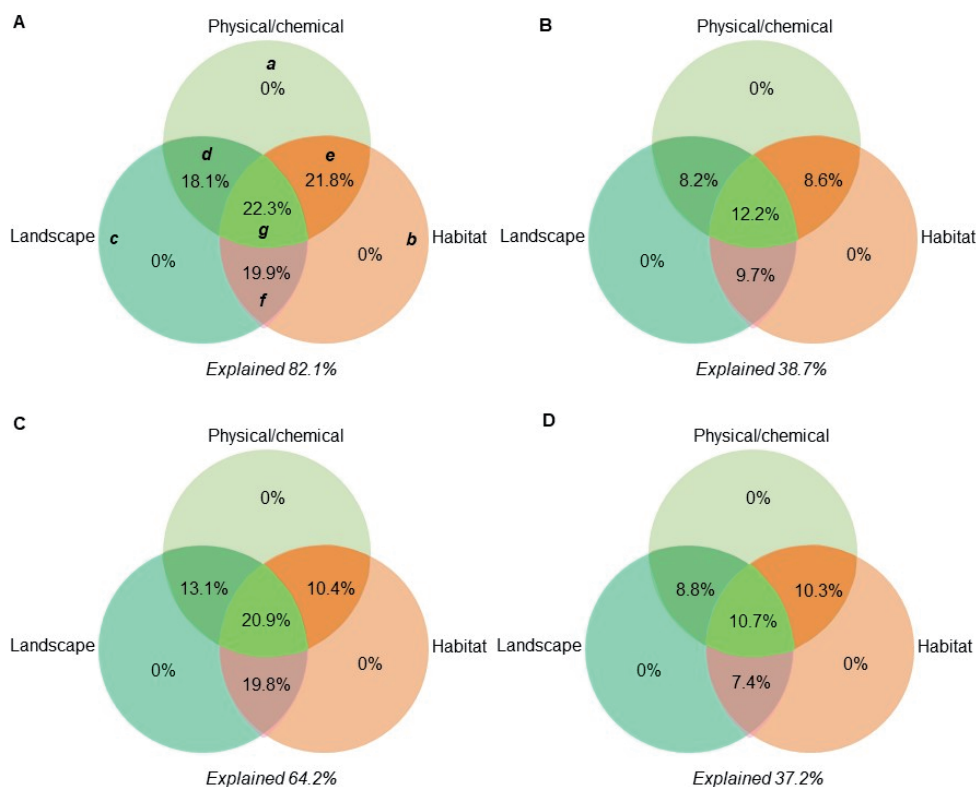


Figure 3. Percentages of independent and shared explanations by environmental filters (physical/chemical, composition of the habitat, and landscape) obtained by a series of CCAs and pCCAs for the selection of Chironomidae larvae. Where: A = Least Disturbed sites in Piranhas-Assu watershed, B = Severely disturbed sites in Piranhas-Assu watershed, C = Least Disturbed sites in Paraíba watershed, and D = Severely disturbed sites in Paraíba watershed. Results obtained by subtracting of the values of variance explained (Table 1), where: $g = [f] + ([a] - [d]) + ([a] - [e]) - [a]$; $d = [a] - [e] - (g)$; $e = [a] - [d] - (g)$; $f = [b] - [c] - (g)$. *Porcentagens de explicações independentes e compartilhadas dos filtros ambientais (físicos e químicos, composição do habitat e paisagem) obtidos por uma série de CCAs e pCCAs sobre a seleção de larvas de Chironomidae.* Onde: A = Locais menos perturbados na bacia hidrográfica de Piranhas-Assu, B = Locais severamente perturbado na bacia hidrográfica de Piranhas-Assu, C = Locais menos perturbado na bacia hidrográfica do rio Paraíba e D = Locais severamente perturbados na bacia hidrográfica do rio Paraíba. Resultados obtidos pela subtração dos valores de variância explicada (Tabela 1).

dance explained 82.1 % of the total variance in LD sites and 38.7 % of the total variance in SD sites. Chironomidae abundance in the Paraíba watershed, explained 64.2 % of the total variance in LD sites and 37.2 % in SD sites. Variance partitioning indicated that the interactions of the physical/chemical, habitat composition, and landscape filters (shared roles) best

explained Chironomidae abundance distributions in the watersheds (Fig. 3). Those same interactions in the Piranhas-Assu watershed explained 22.3 % of the total variance in LD sites and 12.2 % in SD sites (Fig. 3 A, B), and 20.9 % of the total variance in the Paraíba watershed in LD sites and 10.7 % in SD sites (Fig. 3 C, D).

Table 1. Results of the "Canonical Correspondence Analysis" (CCAs) and (pCCAs) used for the partition of canonical variance of the abundance of Chironomidae in the light of environmental filters (physical/chemical, habitat composition, and landscape), measured at Piranhas-Assu watershed, Rio Grande do Norte and Paraíba watershed, Paraíba Northeastern Brazil. Where: LD= Least Disturbed sites; SD= Severely disturbed sites. *Resultados das "Análises de Correspondência Canônica" (CCAs) e (pCCAs) utilizados para a partição da variância canônica da abundância de Chironomidae à luz de filtros ambientais (físicos e químicos, composição do habitat e paisagem), medidos nas bacias hidrográficas do rio Piranhas-Assu, Rio Grande do Norte e do rio Paraíba, Paraíba, Nordeste do Brasil. Onde: LD = Locais menos perturbados; SD = Locais severamente perturbados.*

Data set	Sum of canonical values	Variance explained	P (perm)
<i>LD- Piranhas-Assu watershed</i>			
Abundance of Chironomidae, total inertia = 0.99			
Physical/chemical	0.2858	28.74	0.0019
Habitat	0.0878	8.83	0.0899
Landscape	0.0643	6.47	0.0019
Physical/chemical + landscape	0.2627	28.24	
Physical/chemical + habitat	0.2572	32.90	
Habitat + landscape	0.078	10.06	
<i>SD- Piranhas-Assu watershed</i>			
Abundance of Chironomidae, total inertia = 0.76			
Physical/chemical	0.1296	16.86	0.0009
Habitat	0.0637	8.31	0.0049
Landscape	0.0448	5.85	0.0009
Physical/chemical + landscape	0.1183	17.21	
Physical/chemical + habitat	0.1213	20.84	
Habitat + landscape	0.0521	8.95	
<i>LD- Paraíba watershed</i>			
Abundance of Chironomidae, total inertia = 1.80			
Physical/chemical	0.5414	30.01	0.0009
Habitat	0.3663	20.31	0.0178
Landscape	0.3456	19.15	0.0679
Physical/chemical + landscape	0.5184	40.52	
Physical/chemical + habitat	0.4138	37.87	
Habitat + landscape	0.2995	27.41	
<i>SD- Paraíba watershed</i>			
Abundance of Chironomidae, total inertia = 3.07			
Physical/chemical	0.4194	13.63	0.0009
Habitat	0.2127	6.91	0.0019
Landscape	0.1123	3.65	0.0009
Physical/chemical + landscape	0.3996	14.01	
Physical/chemical + habitat	0.4001	15.48	
Habitat + landscape	0.1335	5.16	

DISCUSSION

Our results showed that Chironomidae assemblage distributions in watersheds are mainly affected by the interactions of filters physical/chemical, habitat composition, and landscape, confirming our hypothesis. Anthropogenic activities in watersheds (e.g., agriculture, urbanization) frequently increase nutrient concentrations in their waters, which increase the trophic state of the environments and promote habitat homogenization (Allan, 2004; Karaouzas & Plóciennik, 2015; Azevêdo *et al.*, 2017). The effects of larger-scale anthropogenic activities interact with local factors and influence the compositions and distributions of local communities (Pavlin *et al.*, 2011; Karaouzas & Plóciennik, 2015).

Although the least disturbed and severely disturbed sites exhibited different environmental characteristics, the filters that exerted the greatest influence on the selection of Chironomidae larvae did not vary between them, differing only in terms of the percentages of variation explained. This can be due to the fact that recently modified habitats tend to be occupied by species that evolved under similar environmental conditions and that show wide ecological plasticity (Heino *et al.*, 2013). The most representative organisms in the assemblages studied here were generalists – organisms that can be found under varied environmental conditions, have high reproductive rates in numerous habitats, and therefore exhibit wide distributions and dense populations (Odum & Muller, 2011; Gates *et al.*, 2015; Karaouzas & Plóciennik, 2015).

In addition to the generalist behaviors of some chironomids (e.g., *Goldichironomus*, *Tanytarsus*, and *Coelotanypus*), the high dispersal capacity of the group could also have influenced our results, as many chironomids are active dispersers and ours sites nearby (Heino & Mykrä, 2008; Horsák *et al.*, 2015). Our results can be viewed from a metacommunity perspective, especially the "species sorting" or "mass effect" models, where islands with different environmental characteristics are connected through species' dispersals (Leibold *et al.*, 2004; Winegardner *et al.*, 2012). Although high dispersal capacities can allow species to occur in inadequate habitats, that

mechanism does not allow the establishment of large populations under adverse environmental conditions due to selection by environmental filters (Braga *et al.*, 2017).

The highest percentages of total variance explained by filters acting on the Chironomidae assemblages were observed in the least disturbed sites because those populations are exposed to a series of, fluctuating but predictable and more stable conditions (Scheffer & Carpenter, 2003) as compared to severely disturbed sites. Severely disturbed sites, on the other hand, are often subjected to a spectrum of fluctuating disturbances (Feio *et al.*, 2014; Gomes *et al.*, 2018) that cause abrupt environmental changes and complex nonlinear population responses that make their identification and interpretation more difficult (Berryman & Millstein, 1989; Andersen *et al.*, 2009).

Although the interactions between environmental filters showed high percentages of explanation, other mechanisms, such as biotic interactions, may also play important roles in the abundance and composition of Chironomidae assemblages. Numerous studies have shown that biotic interactions can be extremely important factors in structuring local assemblies, and that those interactions can be intensified under degraded conditions due to increased competition (Connell *et al.*, 2004; Chase *et al.*, 2009; Boersma *et al.*, 2014).

This study showed that, independent of the anthropogenic disturbance level, interactions of environmental factors act as strong environmental filters on the distributions of local communities, such as Chironomidae assemblages. We therefore emphasize the importance of evaluating the independent and shared effects of data sets in light of the complexity of environmental factors that simultaneously affect the aquatic biota. Future studies that consider different seasonal periods may confirm that the patterns observed here during the dry season also occur during the rainy season.

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