

R.C. Bastos^{1,2,*}, J. Brito^{1,2}, E.J. Cunha^{1,2}, G.M. Cruz², J.L.S. Pereira^{1,2}, J. Vieira³, L. Juen^{1,2}

Environmental impacts from human activities affect the diversity of the Odonata (Insecta) in the Eastern Amazon

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Abstract Land use influences the biodiversity of stream systems by changing the chemical composition of the water and the physical structure of the habitat. The present study evaluated the influence of these processes on the diversity metrics of Odonata at regional and local scales, testing the hypothesis that the two odonate suborders Anisoptera and Zygoptera will respond differently to habitat and landscape variables. The study focused on 13 sites in the municipality of Barcarena, Pará, Brazil. We found no significant impact from regional factors, although anisopterans were more affected by water temperature and Habitat Integrity Index (HII). The HII indicated that the local forest was stable, but anisopteran richness was negatively correlated with HII. It was indicating that these species favoured open areas with less riparian cover. Even though zygopterans did not exhibit a similar systematic pattern, the reduced abundance of *Chalcopteryx rutilans*, a species associated with better-preserved habitats, may indicate that some sites lack the habitat integrity necessary to establish populations of this species. These findings highlight the importance of preserving the riparian forest to maintain the health of the stream systems. We recommend more studies that focus on the broader geographic and temporal scales to account for factors such as the anthropogenic gradient and historical land use patterns.

Keywords: Freshwater systems, Anisoptera, environmental integrity, human occupation, industrial impacts, Zygoptera, Barcarena

Introduction

Human activities have modified natural environments progressively over time (Izzat-Husna & Ahmad, 2014), affecting species diversity. One common scenario is the increasing dominance of generalist species and the local extinction of more specialist species (Oliveira-Junior et al., 2015; Carvalho et al., 2018). The resulting disruption of ecological processes affects intra- and interspecific relationships, ecological services, and many other aspects of ecosystem structure and function (Chesson, 2018; Pereira et al., 2019; Bastos et al., 2021; Oliveira-Junior et al., 2021).

These activities change land use and impact biodiversity (Habel et al., 2019; Mendoza-Penagos et al., 2021). Changes in land use usually include suppression of natural vegetation and soil modification, which may have knock-on effects for adjacent freshwater systems (Bonifait & Villard, 2010). Different types of land use also affect the environment at different scales, ranging from local landscapes to regional processes, which can lead to habitat fragmentation that limits the dispersal capacity of many species (Keller & Holderegger, 2013). In landscape mosaics, habitat fragmentation may be especially restrictive for species with a reduced dispersal capacity (Keller & Holderegger, 2013). Habitat stepping stones (e.g., forest fragments) may favour dispersal, but where these features are scarce or absent, many species may become locally extinct (Oliveira-Junior et al., 2017).

One of the most impactful human activities in the Brazilian Amazon is the industrial mining of ores, which have significant environmental effects through the production of tailings and the consumption of large amounts of water (Zhou & Keeling, 2013; Žibret et al., 2018). While the impact of these ac-

1 Graduate Program in Ecology, Universidade Federal do Pará, Rua Augusto Correia, Nº 1, Bairro Guamá, CEP: 66.075-110, Belém, Pará, Brazil.

2 Laboratory of Ecology and Conservation, Universidade Federal do Pará, Rua Augusto Correia, Nº 1, Bairro Guamá, CEP: 66.075-110, Belém, Pará, Brazil.

3 ALUNORTE – Alumina do Norte do Brasil AS, Rod. PA 481, KM 12, Distrito de Murucupi, CEP: 68.447-000. Barcarena-PA.

* Corresponding Author: R.C. Bastos bastosrc.bio@gmail.com

tivities has been reduced in recent years through more effective treatment of effluents and residues (Zhou & Keeling, 2013), their impacts on local landscapes have been largely disregarded (Basu & Van Zil, 2006; Žibret et al., 2018). However, the profound impacts caused by different land uses may cause fundamental modifications in the natural dynamics of terrestrial and freshwater ecosystems. For instance, in urbanized areas, the removal of the marginal vegetation is one of the principal anthropogenic impacts on aquatic systems, which may cause siltation, homogenization of substrates, changes in the characteristics of channels, and even modifications of the natural dynamics of biological communities (Couceiro et al., 2007; Siqueira & Aprile, 2013; Monteiro-Júnior et al., 2015; Brito et al., 2021).

The freshwater environments located within land use mosaics may be affected by the disruption of environmental continuity, including impacts on the physical structure of habitats and water quality (Petersen et al., 2004; Monteiro-Júnior et al., 2015; Calvão et al., 2018). Environmental degradation can severely impact the presence and persistence of natural assemblages (Parmar et al., 2016). In particular, changes in the riparian forest cover may modify the dynamics of the entire aquatic ecosystem (Carvalho et al., 2018). The riparian vegetation functions as a buffer zone, impeding the excessive input of sediments into the stream and controlling the temperature of the air and the chemical composition of the water (Carvalho et al., 2013; Astudillo et al., 2016). The intense modification of the riparian vegetation by industrial activities or urbanization can thus have profound impacts on the assemblages of organisms that inhabit the stream. Aquatic macroinvertebrate communities may be affected by changes in environmental conditions, as well as the quantity and quality of resources, such as food and breeding sites. (O'Malley et al., 2020; Sganzerla et al., 2021; Brito et al., 2021).

The insects of the order Odonata (dragonflies and damselflies) (Corbet, 1999) are amphibiotic organisms, with a strictly aquatic larval stage and a terrestrial/flying adult stage that is associated ecologically with aquatic systems (Astudillo et al., 2016; Oliveira-Junior & Juen, 2019). Odonates may be affected either positively or negatively by environmental alterations and present specific responses to different levels of anthropogenic impact, which supports their use as bioindicators (Monteiro-Júnior et al., 2015). Even minor changes in water quality or oxygen levels may impact the populations of the more sensitive species and even cause local extinction (Astudillo et al., 2016). Many damselflies (suborder Zygoptera) the smaller odonates require highly specific conditions of water flow, oxygen, and turbidity (Corbet, 1999; Monteiro-Júnior et al., 2015; Oliveira-Junior et al., 2015). The dragonflies (suborder Anisoptera), by contrast, tend to be more tolerant, as they can survive in a broader range of environmental conditions and are often associated with more open habitats (Corbet, 1999; Carvalho et al., 2013). Given these differences, the configuration of the riparian vegetation surrounding a given body of water is likely to determine specific characteristics in the local odonate community (Astudillo et al., 2016). In this context, understanding how habitat fragmentation impacts odonate diversity will be fundamental to adequately mitigating changes caused by land development.

The Northern region of Brazil is characterized by large industrial hubs that operate in the extraction of ore. Although the population density of the Brazilian Amazon region is lower than the rest of the country, the region's larger urban centers are more prone to environmental problems (Laurance et al., 2002). For example, the municipality of Barcarena, located in the State of Pará, comprises 1,316.2 km² and is populated by approximately 127,000 inhabitants (IBGE, 2021). Even though it has a relatively low population density in comparison with the larger urban centres of the Brazilian Amazon, Barcarena is more sensitive to the environmental impacts typical of the urbanization process, including extensive land use changes and the proximity of landfills to bodies of water (Cardoso-Castro et al., 2020).

This study evaluates the effects of environmental changes at local and regional scales on the odonate community of Amazonian streams in the context of the impacts of aluminium refining and urbanization. In particular, this study identifies specific elements that could be used to evaluate impacts and monitor the quality of these Amazonian streams. We hypothesize that these activities cause changes in environmental integrity, homogenize the habitats, and decrease biodiversity. Specifically, streams closer to anthropogenic impacts will tend to have less riparian vegetation cover, more sunlight, and a greater relative abundance of generalist anisopterans (Oliveira-Junior & Juen, 2019). Conversely, streams further from human activities will tend to have more stable habitats, with greater vegetation cover, and a greater abundance of zygopterans.

Materials and Methods

Study area

The present study was carried out in the municipality of Barcarena, Pará state, Brazil. We sampled 12 streams in three field expeditions between November 2018 and May 2019 (Figure 1). The region's climate is tropical rainy, of the "Af" type in the Köppen classification system, with a mean annual precipitation of approximately 2,500 mm (Piratoba et al., 2017). The most intense rains occur between January and July, with the dry season between August and December (Teixeira et al., 2000). The region's vegetation is composed almost entirely of secondary forest at various stages of succession, reflecting different land use patterns in the area. Since the end of the 20th century, the most important economic activities have been farming and bauxite processing and shipping (Souza & Lisboa, 2006; Pereira et al., 2007; Pinto & Carvalho, 2009; CODEC, 2018).

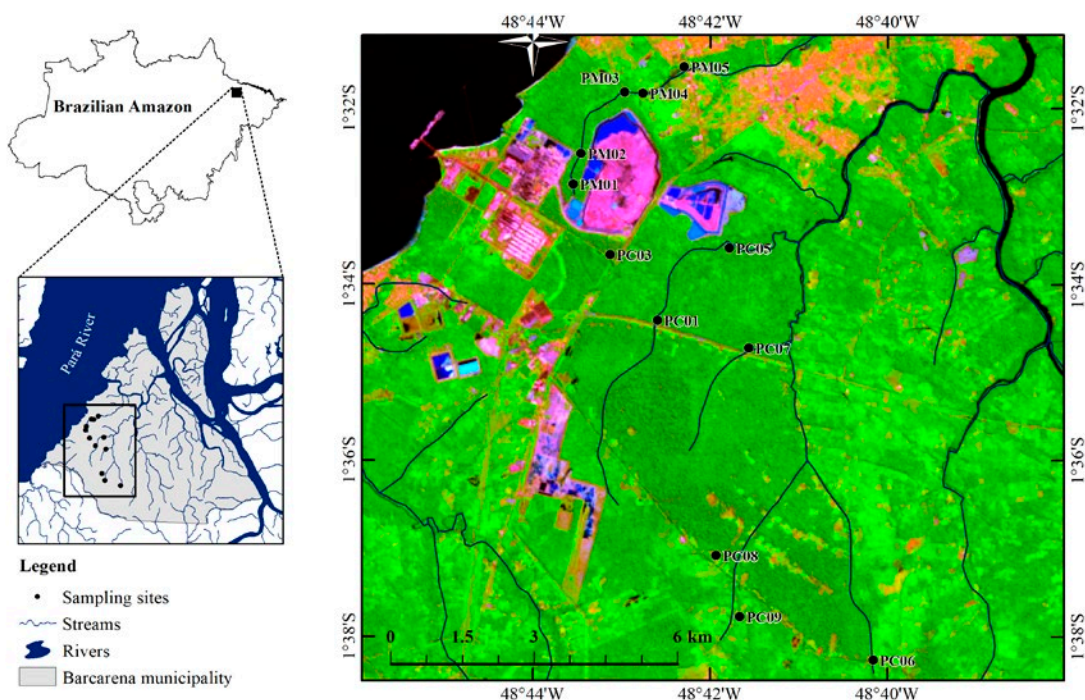


Figure 1. Landsat 8 TM false colour composite RGB (Red, Green, and Blue) image showing the study area and the location of the streams sampled in the municipality of Barcarena, Pará state, Brazil.

Biological sampling

Odonates were sampled using the fixed-area (50-meter stretch) scanning method (Calvão et al., 2016; Oliveira-Junior & Juen, 2019; Cezário et al., 2021). Collecting along stream stretches is an efficient method for rapidly describing odonate diversity (Espírito-Santo et al., 2017; Rodrigues et al., 2018; Borba et al., 2020). The adults were collected using an entomological net (40 cm in diameter and 65 cm deep, with an aluminium handle 90 cm in length), during the peak odonate activity period (10:00 to 14:00) when sunlight is most intense (Corbet, 1999). Specimens were identified to species when possible using the appropriate taxonomic keys (Lencioni, 2005; 2006; Garrison et al., 2006; Heckman, 2008; Von Ellenrieder, 2009; Pessacq, 2014). Following identification, the specimens were stored following the protocol of Lencioni (2005; 2006) and deposited in the entomological collection of the Federal University of Pará (UFPA) in Belém, Brazil. We used the Sample Coverage

Method to verify the efficiency of the sampling effort processed in the study (Chao et al., 2014). This method considers the observed abundance of species per sampled site. The higher the values observed in the analysis, the greater the probability that the sampling effort has captured the site's existing biodiversity. All sampling sites presented coverage rates equal to or greater than 50%, demonstrating a sufficient sampling effort (Supplementary I). The spatial autocorrelation among the sampled locations was assessed by the spatial vectors using the Principal Coordinates of Neighbour Matrices (PCNM) (Legendre & Anderson, 1999). This method creates spatial predictors from a distance matrix of the geographical coordinates of the sites. The spatial vectors with autocorrelation were considered significant based on the Moran Index (Dray et al., 2006; Legendre & Legendre, 2012) (Supplementary I).

Physical integrity, limnological, and landscape variables

The Habitat Integrity Index (HII) (Nessimian et al., 2008) was calculated to assess the physical conditions of the study streams and their surroundings based on 12 structural components. This index varies from impacted (0) to pristine (1) environments. Many odonate studies have successfully applied this index (Monteiro-Júnior et al., 2015; Brasil et al., 2020a). In addition to the HII, we measured three sets of environmental variables: (i) electrical conductivity (mS/cm), pH, and temperature (°C), which were measured using a Horiba U-50 multiparametric probe (<http://www.horiba.com/fileadmin/uploads/Process-Environmental/Documents/HRE1930C-U50.pdf>); (ii) environmental parameters: canopy cover (%) were measured using a spherical densiometer, and channel width (m) and depth (cm) were measured with a surveyor's tape; and (iii) parameters of water quality: phosphorus was measured in the laboratory (USEPA and Standard Method 4500-P-E) following the standard methods for the examination of water and wastewater of APHA (2017). This approach is relatively accurate and has been widely used in tropical freshwater research (Calvão et al., 2016; Oliveira-Junior et al., 2017).

To minimize the potential effects of multicollinearity, we applied Pearson's correlation, with a $r > 0.7$ threshold, and when a pair of variables passed this threshold, only one was used for further analysis (Nicacio et al., 2020). This variable was selected based on its importance for odonate ecology following the study by Brasil et al., 2020b. The multicollinearity analysis revealed a strong correlation among pH, canopy cover, and the HII. Given this, only channel width and depth, temperature, conductivity, and the HII were retained for the subsequent analyses.

Land use was measured through the processing of satellite images of the RapidEye Earth Imaging System (REIS). This system has a coverage of 72 km² per 1,500 km² and a spatial resolution of 5 m. Land use was evaluated based on 600-meter linear buffers, which varied in scale, at two levels, with radii of 30 m and 150 m. The REIS has been used in many previous studies and is known to provide an excellent baseline for the evaluating the effect of changes in landscape features on the aquatic biota (Montag et al., 2019; Leão et al., 2020; Fares et al., 2020; Adelabu et al., 2014).

Data analysis

Each site was sampled three times, and the results were pooled for each site prior to analysis. Given the physiological and ecological differences of the suborders Anisoptera and Zygoptera, their community analyses were carried out separately (Corbet & May, 2008; Oliveira-Junior & Juen, 2019). We used a Principal Components Analyses (PCA) to describe the environmental variation among the study sites and reduce these environmental dimensionalities. The environmental variables were standardized to eliminate potential differences in measurement units. The broken-stick method was used to select the number of axes to be considered, and the axes with higher eigenvalues than those predicted by the broken-stick were selected for analysis using a correlation matrix (Jackson, 1993; Legendre & Legendre, 2012). A Best Subset Regression analysis (Zhang & Cavanaugh, 2016) was applied to determine which environmental variable is more important for both odonate suborders. This method generates different combinations of the environmental predictors to model species richness and abundance. Akaike's Information Criterion (AIC), corrected for small sample sizes, eliminated all but

three variables per model. All the models with an $\Delta AICc$ lower than two ($\Delta AICc < 2$) were considered most important (Lynch et al., 2018), and the adjusted R^2 was then generated for each accepted model. A Partial Redundancy Analysis (pRDA) was applied to evaluate the relative importance of environmental (limnological and HII features) and landscape (buffers) variables for the odonate assemblage (Legendre & Legendre, 2012; Landeiro et al., 2011). In addition, the spatial filters matrix was included to analyse the possible effect of spatial autocorrelation between samples on the patterns of community structuring. The Forward Selection method (Blanchet, 2008) was used to assess the most important variables for each community. In this analysis, the dependent variable was the species composition, and the independent variables were the environmental and landscape predictors. The relationship between the composition of the odonate assemblage and the HII was also evaluated by ranking the relative abundance of the species and comparing this ranking with the HII. This approach has been used in other studies in the Amazon region (Oliveira-Junior et al., 2017; Miguel et al., 2017). All the analyses were run in the R programming environment 2019 (R Core Team, 2020) using the *adespatial* (Dray et al., 2018), *vegan* (Oksanen et al., 2013), and *ggplot2* (Wickham, 2016) packages.

Results

The streams had very similar environmental conditions. The Coefficient of Variation (CV) values ranged from 0.031 (temperature) to 1.196 (conductivity, Table 1). The mean, standard deviation (SD), and Coefficient of Variation (CV) for each parameter are given in Table 1 (Supplementary I).

Table 1. Descriptive statistics of the environmental variables of the study streams in the municipality of Barcarena, Pará state, Brazil.

| Variables | Mean | SD | CV |
|---|--------|--------|-------|
| Environmental | | | |
| Phosphor mg/L | 0.401 | 0.295 | 0.735 |
| Temperature °C | 25.512 | 0.796 | 0.031 |
| Conductivity mS/cm | 0.057 | 0.068 | 1.196 |
| Channel width (m) | 14.373 | 9.664 | 0.672 |
| Channel depth (cm) | 37.964 | 17.352 | 0.457 |
| Canopy cover (%) | 76.761 | 24.150 | 0.315 |
| HII | 0.556 | 0.206 | 0.371 |
| pH | 5.374 | 0.321 | 0.060 |
| Landscape | | | |
| Forest - 30m buffer (km ²) | 0.027 | 0.016 | 0.585 |
| Forest in regeneration - 30m buffer (km ²) | 0.010 | 0.012 | 1.176 |
| Forest - 150m buffer (km ²) | 0.168 | 0.077 | 0.459 |
| Forest in regeneration - 150m buffer (km ²) | 0.058 | 0.062 | 1.067 |

The first two PCA axes explained 69.05% of the variance found in the data, with 43.04% in the first axis and 26.01% in the second. The first axis was positively associated with channel depth and negatively associated with HII and canopy cover. The second axis was positively associated with conductivity (Table 2) (Figure 2).

Table 2. Contribution of the environmental variables to the first two axes of the Principal Components Analysis (PCA). The axes represent the environmental variables with the greatest variation, showing the correlations between environmental variables and the PCA axes.

| Environmental variables | Axis 1 | Axis 2 |
|-------------------------------|---------------|--------------|
| HIII | -0.935 | -0.114 |
| Canopy cover | -0.891 | -0.098 |
| Phosphor | 0.256 | -0.667 |
| Temperature | 0.137 | 0.681 |
| Conductivity | -0.017 | 0.774 |
| Width | 0.682 | -0.407 |
| Depth | 0.781 | -0.313 |
| Eigenvalue | 3.443 | 2.081 |
| Broken Stick | 2.718 | 1.718 |
| Explanation Proportion | 0.430 | 0.260 |

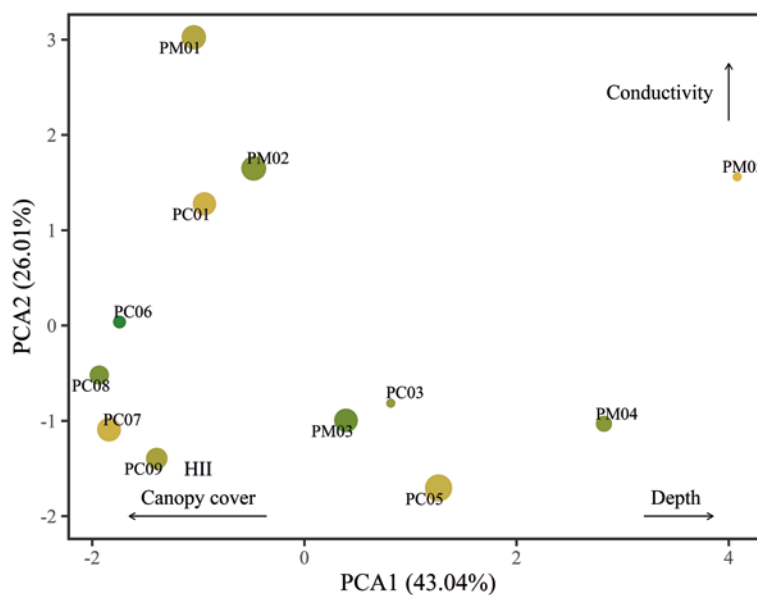


Figure 2. Principal Components Analysis of the environmental variables of the study streams in the municipality of Barcarena, Pará state, Brazil. The size of the circle representing each stream is proportional to the percentage of forest cover within a radius of 30 m, while the colour gradient represents the percentage of forest cover within a 150 m radius.

A total of 230 individuals were collected, representing 53 species. The suborder Zygoptera had higher species richness, with 31 species, representing 58.49% of the total (see Supplementary III). Eleven of the 53 odonate species registered here were recorded in the Brazilian state of Pará for the first time. The most abundant family was the Libellulidae (Anisoptera), followed by the Coenagrionidae (Zygoptera). The most abundant species were the zygopterans *Argia collata* (n=32) and *Mnesarete aenea* (n=12). None of the other species were represented by more than 10 specimens, and 13 species were represented by a single individual (Table 3). The rarer species belonged to the zygopteran families

Coenagrionidae, Calopterygidae, Protoneuridae, and Megapodagrionidae. The least abundant anisopteran species were members of the genera *Erythrodiplax* and *Erythemis*.

Table 3. Number of odonate specimens collected per species at each study stream surveyed in the municipality of Barcarena, Pará state, Brazil.

| Species/Author by suborder | Site | | | | | | | | | | | Total abundance | |
|--|------|------|------|------|------|------|------|------|------|------|------|-----------------|------|
| | PC01 | PC03 | PC05 | PC06 | PC07 | PC08 | PC09 | PM01 | PM02 | PM03 | PM04 | | PM05 |
| Anisoptera | | | | | | | | | | | | | |
| <i>Anatya guttata</i> (Erichson, 1848) * | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 5 | 0 | 1 | 8 |
| <i>Diastatops obscura</i> (Fabricius, 1775) | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 |
| <i>Dythemis multipunctata</i> (Kirby, 1894) * | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Erythemis credula</i> (Hagen, 1861) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| <i>Erythemis mithroides</i> (Therese, 1900) * | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 6 | 7 |
| <i>Erythemis peruviana</i> (Rambur, 1842) * | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| <i>Erythrodiplax</i> sp.1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Erythrodiplax basalis</i> (Kirby, 1897) | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 3 | 5 |
| <i>Erythrodiplax castanea</i> (Burmeister, 1839) | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 4 | 8 |
| <i>Erythrodiplax famula</i> (Erichson, 1848) * | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 2 |
| <i>Erythrodiplax</i> sp. | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Erythrodiplax umbrata</i> (Linnaeus, 1758) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 2 |
| <i>Fylgia amazonica</i> (Kirby, 1889) | 0 | 3 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 5 |
| <i>Micrathyria aequalis</i> (Hagen, 1861) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 2 |
| <i>Miathyria marcella</i> (Selys, 1857) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| <i>Micrathyria spinifera</i> (Calvert, 1909) | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 3 |
| <i>Oligoclada abbreviata</i> (Rambur, 1842) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 7 | 8 |
| <i>Oligoclada walkeri</i> (Geijskes, 1931) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 3 |
| <i>Orthemis attenuata</i> (Erichson, 1848) | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Orthemis biolleyi</i> (Calvert, 1906) | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Orthemis cultriformis</i> (Calvert, 1899) | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Uracis imbuta</i> (Burmeister, 1839) * | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| <i>Uracis</i> sp. | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Perithemis lais</i> (Perty, 1834) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| <i>Zenithoptera viola</i> (De Geer, 1773) | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 6 |
| Zygoptera | | | | | | | | | | | | | |
| <i>Acanthagrion adustum</i> (Williamson, 1916) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| <i>Acanthagrion kennedii</i> (Williamson, 1916) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 3 | 0 | 4 |
| <i>Acanthagrion lancea</i> (Selys, 1876) * | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 4 | 8 |
| <i>Aeolagrion dorsale</i> (Burmeister, 1839) | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 3 |

| Species/Author by suborder | Site | | | | | | | | | | | | Total abundance |
|---|------|------|------|------|------|------|------|------|------|------|------|------|-----------------|
| | PC01 | PC03 | PC05 | PC06 | PC07 | PC08 | PC09 | PM01 | PM02 | PM03 | PM04 | PM05 | |
| <i>Argia collata</i> (Selys, 1865) | 0 | 0 | 0 | 11 | 3 | 0 | 7 | 5 | 2 | 3 | 1 | 0 | 32 |
| <i>Argia fumigata</i> (Selys, 1865) | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| <i>Argia indicatrix</i> (Calvert, 1902) | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Argia infumata</i> (Selys, 1865) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| <i>Argia oculata</i> (Selys, 1865) | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 5 |
| <i>Argia</i> sp. | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 2 |
| <i>Argia</i> sp.8 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 2 |
| <i>Argia tinctipennis</i> (Selys, 1865) | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| <i>Chalcopteryx rutilans</i> (Rambur, 1842) | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Dictierias atosanguinea</i> (Selys, 1853) | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| <i>Epipleoneura metallica</i> (Rácenis, 1955) | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Hetaerina auripennis</i> (Burmeister, 1839) | 4 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 5 |
| <i>Hetaerina cruentata</i> (Rambur, 1842) * | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Hetaerina laesa</i> (Selys, 1853) | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 |
| <i>Heteragrion aurantiacum</i> (Selys, 1862) | 1 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 1 | 2 | 0 | 0 | 9 |
| <i>Heteragrion silvarum</i> (Sjöstedt, 1918) | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| <i>Heteragrion</i> sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| <i>Ischnura capreolus</i> (Hagen, 1861) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| <i>Metaleptobasis amazonica</i> (Sjöstedt, 1918) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| <i>Metaleptobasis falcifera</i> (von Ellenrieder, 2013) * | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 2 |
| <i>Mnesarete aenea</i> (Selys, 1853) | 4 | 0 | 0 | 3 | 1 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 12 |
| <i>Mnesarete williamsoni</i> (Garrison, 2006) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 |
| <i>Oxystigma petiolatum</i> (Selys, 1862) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 |
| <i>Perilestes kahli</i> (Williamson & Williamson, 1924) | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Perilestes solutus</i> (Williamson & Williamson, 1924) | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Phasmonera exigua</i> (Selys, 1886) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| <i>Protonera tenuis</i> (Selys, 1860) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| <i>Psaironeura bifurcata</i> (Sjöstedt, 1918) * | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 3 |
| <i>Psaironeura tenuissima</i> (Selys, 1886) | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 |
| <i>Telebasis vulnerata</i> (Hagen, 1861) * | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 3 |

* New record of Odonata species to Pará state.

Environmental and landscape effects on species richness

The best subset regressions indicated a positive and robust relationship between anisopteran species richness and the spatial variables, specifically with the two forest buffers (30 m and 150 m). Based on the AICc, the model that best explained anisopteran species richness was composed of the 30 m and 150 m forest buffer plus the HII (R^2 Adj. = 0.935). Considering the criteria used ($\Delta AICc < 2$), only one model was retained in this analysis (Table 4). For the Zygoptera dataset, the variables depth and HII constituted the best model for species richness (R^2 Adj. = 0.215). On the other hand, with respect to zygopteran abundance, the best model contained the variables temperature, conductivity, and a 150 m forest buffer (R^2 Adj. = 0.430) (Table 4).

Table 4. Results of the Best Subset Regression analysis for the two odonate suborders (Anisoptera and Zygoptera) and the most important environmental variables. S = species richness; N = Individual abundance; F30 = Forest (30 m buffer); F150 = Forest (150 m buffer); P = Phosphorus; HII = Habitat Integrity Index; Cond. = Conductivity; °C = air temperature; β = beta coefficient.

| Anisoptera | AIC | AICc | $\Delta AICc$ | R^2 adj. | β |
|------------------------------------|--------|--------|---------------|------------|-------------------------|
| Model (S) | | | | | |
| F30m + F150m + HII | 33.236 | 45.236 | 0 | 0.935 | -100.40; -10.12; -10.77 |
| Model (N) | | | | | |
| F30m + F150m + HII | 53.88 | 65.88 | 0 | 0.923 | -259.09; -33.48; -21.89 |
| Zygoptera | | | | | |
| Model (S) | | | | | |
| Depth + HII | 58,179 | 64,846 | 0 | 0.215 | -0.0139; 8.821 |
| HII | 58,231 | 61,659 | 0.052 | 0.159 | -7085 |
| Depth + Conductivity + HII | 58,567 | 70,567 | 0.388 | 0.225 | -0.015; -8.047; 8.345 |
| Temperature + Conductivity + F150m | 58,814 | 70,814 | 0.635 | 0.207 | -0.161; -7.336; 12.501 |
| Depth + HII + F150m | 58.888 | 70.888 | 0.709 | 0.202 | -0.015; 7.831; 12.421 |
| Model (N) | | | | | |
| Temperature + Conductivity + F150m | 71,371 | 83,371 | 0 | 0.43 | 0.922; -21.610; 43.325 |
| Conductivity + Width + F150m | 72,605 | 84,605 | 1,234 | 0.363 | -30.520; -0.337; 48.132 |
| Depth + Width + F150m | 72,966 | 84,966 | 1,595 | 0.341 | -0.021; -0.315; 55.445 |

Spatial and environmental effects on the composition of odonate assemblages

Although there were strong relationships in AICc models, the pRDA found no significant effects when all odonates were analyzed together (see Table 4 and Supplementary IV, respectively). The species composition of both suborders varied unexpectedly, with different scenarios and species of both suborders occurring in every HII gradient. However, when analyzed separately, the relative abundance of the anisopterans was greater at the sites with the lowest HII scores (Figure 3A). In particular, all the *Erythemis* species occurred in areas with low HII scores. The zygopterans observed the opposite pattern, with greater abundance at the sites with the highest HII scores (Figure 3B). The zygopteran species most dependent on high habitat integrity were *C. rutilans*, *A. indicatrix*, *A. tinctipennis*, and *H. silvarum*.

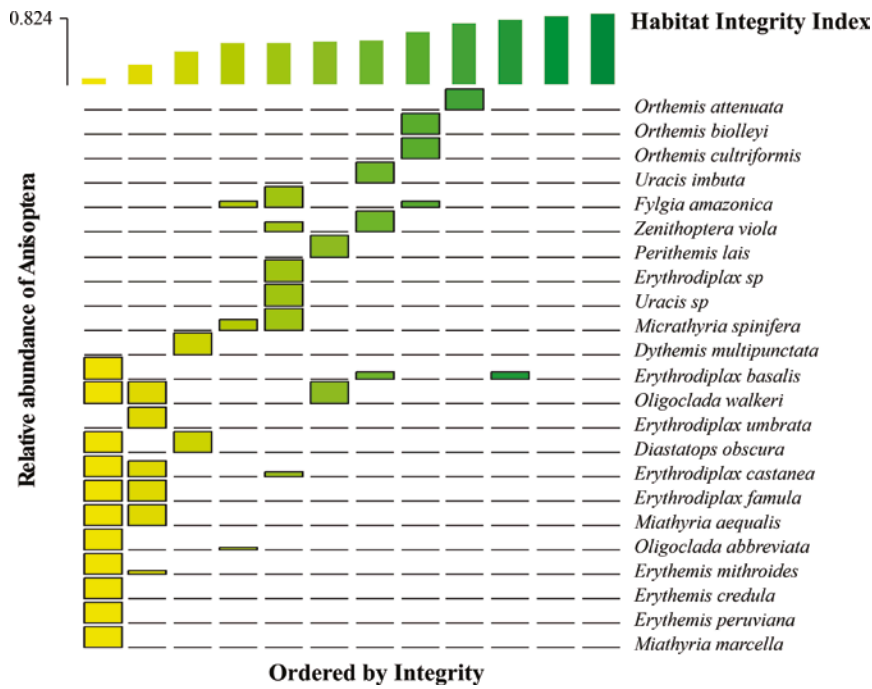


Figure 3A. Ranking of the relative abundance of anisopteran species, ranked by the HII scores of the study streams in the municipality of Barcarena, Pará state, Brazil.

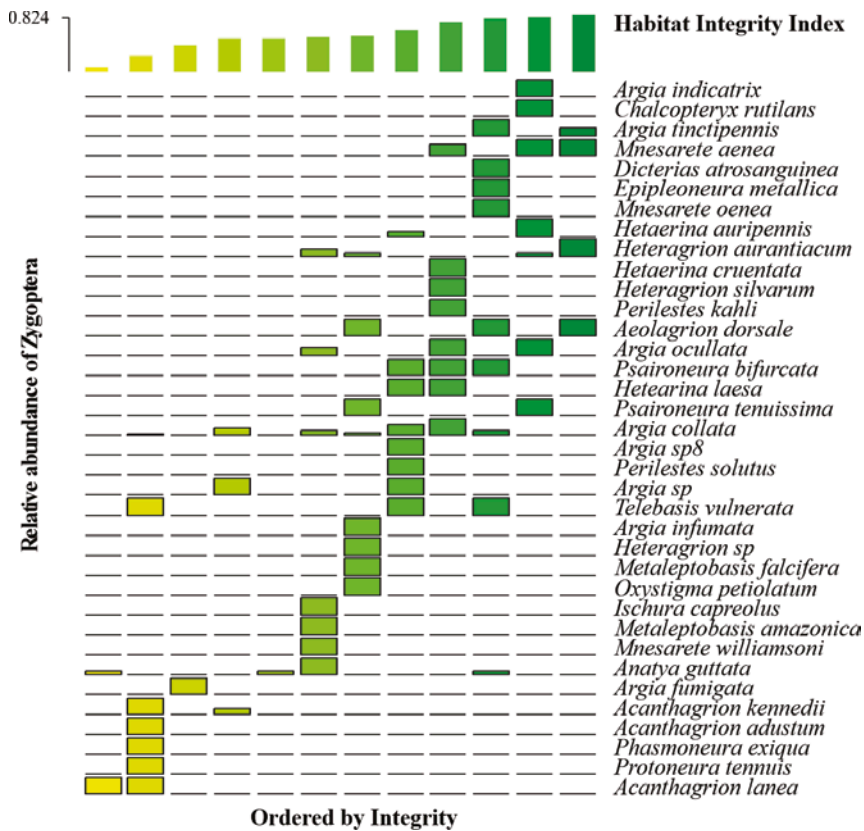


Figure 3B. Ranking of the relative abundance of zygopteran species, ranked by the HII scores of the study streams in the municipality of Barcarena, Pará state, Brazil.

Discussion

Our hypothesis was partially corroborated, given that environmental changes did affect biodiversity, although the specific patterns of variation were not predicted as completely. In particular, while environmental factors affected species abundance and richness, no effect was observed on species composition, regardless of the spatial scale analyzed. In general, anisopterans had a negative relationship with the HII and forest (30 m buffer), whereas the zygopterans were associated primarily with the physical-chemical characteristics of the water. In fact, the zygopterans were more related to the HII (positive relationship) and depth (negative relationship).

Anisoptera are typically found in more open habitats, which provide more suitable conditions for thermoregulation, breeding, and territorial behaviour (Oliveira-Junior et al., 2015; Oliveira-Junior & Juen, 2019). This pattern was confirmed in the present study, which showed that the anisopterans were associated with open areas of lower environmental integrity (Monteiro-Júnior et al., 2015). These findings reflect the more generalist traits of the anisopterans, which are more associated with impacted and urban areas than zygopteran species (Jeanmougin et al., 2014; De Marco Júnior et al., 2015).

The gradient analysis (abundance ranking) demonstrated that heliothermic genera, such as *Erythemis*, *Erythrodiplax*, *Diastatops* and *Micrathyria*, occurred in sites with low HII scores and low forest cover, which provide ideal conditions for the thermoregulatory behaviour associated with these genera (Monteiro-Júnior et al., 2015). Both predictors measure physical habitat structuring: the HII gives a local measurement; on the other hand, the buffers provide a more comprehensive range of measurements over the forest and regeneration areas. Anisoptera, which generally are more efficient dispersers, would be more likely to establish and survive in modified environments (Oliveira-Junior et al., 2015). The ranking of the relative abundance indicated that species were more closely related to specific HII scores. For example, the relative abundance of some zygopteran species, such as *A. indicatrix*, *A. tinctipennis*, *M. aenea*, and *D. atosanguinea*, was associated with high HII scores. On the other hand, the relative abundance of *A. kennedii*, *A. Adustum*, *A. fumigata*, and *A. lanea* was more related to low HII scores. These species have presented similar abundance patterns in previous studies in which other variables were used as a proxy for habitat integrity, such as the percentage of vegetation cover (Carvalho et al., 2018) and channel shading (Oliveira-Junior et al., 2019).

One potentially important factor that was not considered in the present study is that the local human population exploits most streams in the study area as a source of water for washing (clothes, dishes, etc.) and bathing. These human activities introduce a number of chemical compounds into the water, such as glycerine; sequestering and chelating materials; and surfactants, which may interfere in the aeration rates and increase the eutrophication of the streams. These activities may also result in trampling of the aquatic vegetation essential for some odonate species for perching and oviposition (Vilela et al., 2016).

Another important point in the present study is that the local landscape has been under pressure from anthropogenic impacts for a long time, and the most sensitive species may have already become locally extinct, leaving only the more resistant taxa. These taxa would be relatively less sensitive to the integrity of the environment. Miguel et al. (2017) also used the gradient approach adopted in the present study, and showed that relatively small and slender-bodied species such as those of the genus *Acanthagrion* were prevalent across the gradient, irrespective of the HII scores. Despite the slender bodies of these species and their dependence on shaded sites, they appear to colonize more open sites. This study confirms this pattern: *Acanthagrion* were relatively common at sites with low HII scores.

Environmental and landscape variables had no systematic effect on the odonate assemblage in this study. This may have been related to the limited range of variation captured by the environmental parameters, which may have been insufficient to reveal changes in the structure of the community. In particular, this lack of variation may have been influenced by the scales selected for the study, which may have been insufficient to clearly demonstrate the variation in odonate diversity. Previous studies have found significant variation at smaller scales, although the diameter of the largest buffer did not exceed 10 m (Raebel et al., 2012).

Chalcopteryx rutilans was associated with preserved sites, and is known to be an indicator of habitat integrity (Oliveira-Junior et al., 2015), and is associated with more preserved environments containing more shaded areas and allochthonous materials from the surrounding forest. These resources provide suitable ovipositing sites for this species, given that the females need woody debris and trunks for oviposition (Resende & De Marco Jr., 2010). Thus, the most preserved sites are more complex systems that support a larger number of species (Monteiro-Júnior et al., 2016) and provide more of these resources for the fauna. Other abundant species in areas of high habitat integrity were the zygopteran *M. aenea* and *A. tinctipennis*, which could be explained by the presence of allochthonous materials such as roots and woody debris, as well as tree branches, which provide the perches necessary for territorial and reproductive behaviour (von Ellenrieder, 2012; Vilela et al., 2016).

Overall, our findings indicate that the anisopteran community is affected at both spatial scales, whereas the zygopteran were influenced more by the variables at a local scale. When the suborder Anisoptera was analyzed on its own, the predicted pattern was observed, with the species in this suborder being associated with more open areas. One potentially important factor may be the historical patterns of land use in the study area. Agriculture and bauxite processing are the most important economic activities in the region and have been expanding progressively since the end of the 20th century. Future studies of the region's odonate community should thus consider a more systematic assessment of factors such as the anthropogenic gradient and historical land use patterns.

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