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Effects of human disturbance and riparian conditions on Odonata (Insecta) assemblages in eastern Amazon basin streams

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ABSTRACT

Riparian vegetation is an important determinant of the physical, chemical, and biological condition of streams, and odonates are useful indicators of riparian condition. To identify environmental factors that structure Odonata assemblages in tropical forest streams, we collected adult odonate specimens and habitat data from 50 stream sites located in the Brazilian municipality of Paragominas (Pará state). We collected 1769 specimens representing 11 families, 41 genera, and 97 species. Of these species, 56 were Zygoptera, and 41 were Anisoptera. Improved environmental condition was reflected in increased Zygoptera species richness and reduced Anisoptera species richness. Channel shading was strongly and positively related to Zygoptera richness, and negatively to Anisoptera richness. Zygoptera species richness, but not Anisoptera species richness, was related positively to bank angle, quantity of wood in the stream bed, electrical conductivity, and decreased water temperature. Altered riparian vegetation structure was the principal determinant of odonate assemblage structure. Our results indicate that maintaining intact riparian vegetation is fundamental for conserving or re-establishing aquatic odonate assemblage structure.

1. Introduction

Factors that vary at different spatial and temporal scales, such as environmental condition (Weigel et al., 2003; Ligeiro et al., 2010), water quality (Larsen et al., 1988; Oliveira et al., 2011), and human activities (Ometo et al., 2000; Allan, 2004) are important determinants of stream community structure. As a consequence, the environmental heterogeneity of aquatic systems will be directly linked to alteration in these factors (Grinnell, 1917). We consider environmental heterogeneity as an umbrella term for all factors relating to spatial complexity, diversity, or structure in the environment (Stein et al., 2014).

In general species persist within a limited range of environmental conditions and resources that constrain their distribution. Species can be excluded from local assemblages because they are not adjusted to the

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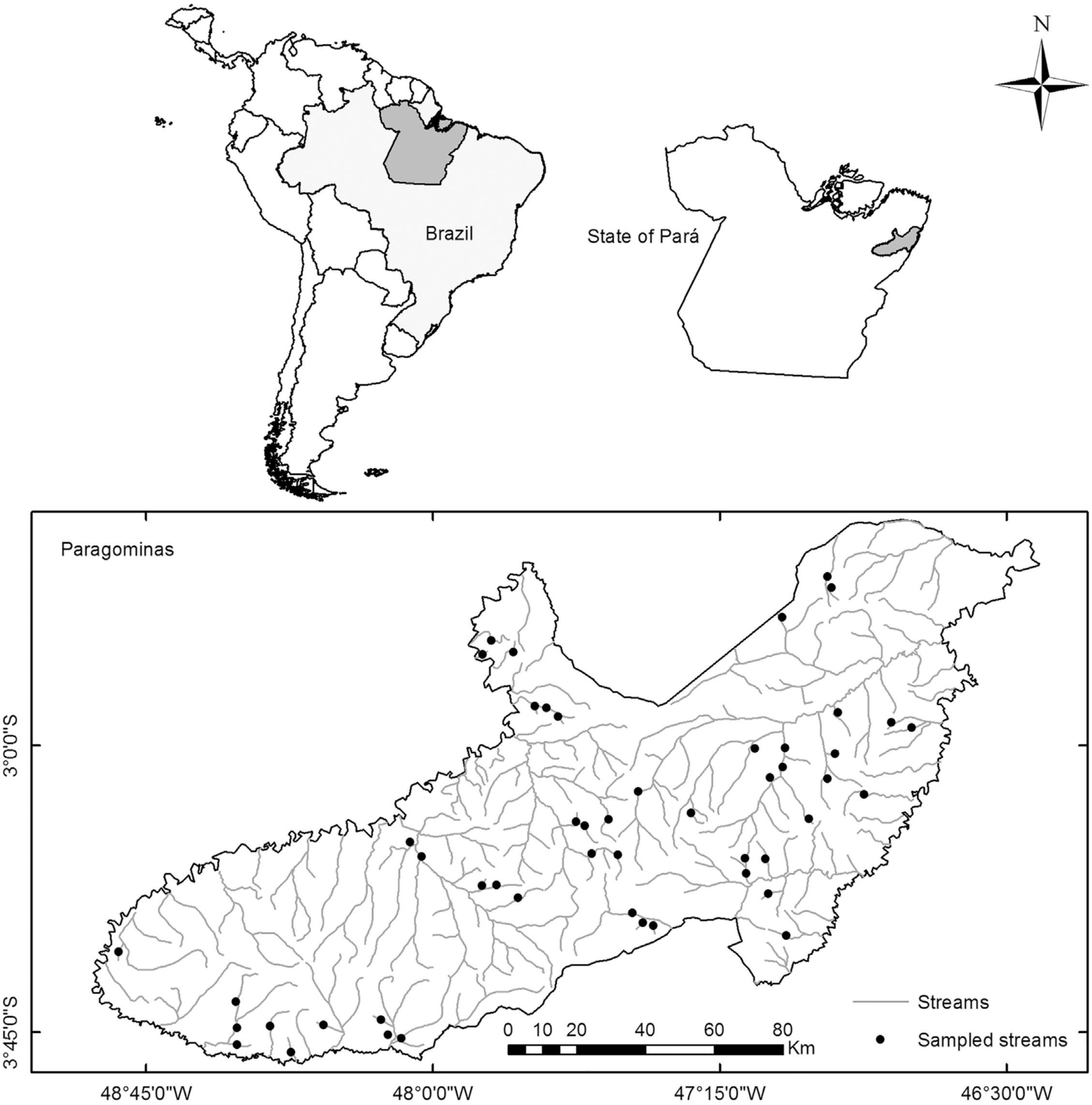

Fig. 1. Drainage network of the municipality of Paragominas (Pará, Brazil) in the eastern Amazon basin, and the distribution of the 50 sites surveyed in 2011.

abiotic conditions at a given site (Kraft et al., 2015), or because of the combined effects of both abiotic and biotic factors (Jackson et al., 2001). Species thus will be expected to be most closely associated with the habitat conditions to which they are best adapted. In this case, habitats characterized by a greater variety of microhabitats would be expected to have greater species richness, by allowing the occurrence of a range of species with different habitat requirements (González-Megías et al., 2007).

Riparian vegetation is a principal factor influencing the heterogeneity of aquatic environments (Gregory et al., 1991; Tews et al., 2004). This influence is especially important in headwater streams, which are relatively small in size and highly dependent on the structure and productivity of adjacent forests. Wood of different sizes that is deposited into the stream from the riparian zone may increase the retention of organic material and influence stream flow patterns, as well as provide habitats, substrates, and feeding resources for aquatic insects and other invertebrates (Gregory et al., 1991). Anthropogenic disturbances in the landscape surrounding these aquatic environments may modify all these variables, reducing environmental condition and altering the diversity and composition of the aquatic fauna (Juen et al., 2007; Oertli, 2008; Silva-Pinto et al., 2012; Rodrigues et al., 2016).

The Odonata (dragonflies and damselflies) represent a particularly useful assemblage for detecting the effects of habitat disturbance, given that their distribution, species composition, and richness tend to be closely related to the conditions of the physical environment (Williams et al., 2004; Monteiro-Júnior et al., 2013). In addition, these insects have a long life cycle, are widely-distributed in aquatic systems (Corbet, 1983), and have an aquatic larval stage and terrestrial/aerial adults (Oertli, 2008), which makes them good indicators of the quality of both aquatic and terrestrial systems (Briers and Biggs, 2003).

The variable ecophysiological requirements of these insects (e.g. flying behavior and thermoregulation capacity) help us understand species responses to environmental changes, which act as filters of their distributions (Corbet, 1999). In dense canopy forests, for example, the tree crowns intercept most of the solar radiation and heat, restricting the presence of species that require access to these conditions (Théry, 2001). Given their ecophysiological demands, a number of studies have investigated how odonate diversity is affected by riparian vegetation modifications (Samways and Steytler, 1996), water body conservation status (Stewart and Samways, 1998), physical and chemical habitat variables (Jacob et al., 1984; Oliveira-Junior et al., 2013), and anthropogenic disturbances (Oertli, 2008; Silva et al., 2010; Carvalho et al., 2013; Monteiro-Júnior et al., 2013, Rodrigues et al., 2016). Based on the interaction of thermoregulation, body size, and the degree of sunlight availability in small streams, De Marco et al. (2015) created the ecophysiological hypothesis. That hypothesis predicts greater Zygoptera species richness in more shaded streams and less richness in less shaded streams. The opposite pattern is expected for Anisoptera.

Therefore, the objective of this paper was to evaluate the relationship between environmental condition and multiple physical and chemical stream habitat characteristics on adult odonate assemblages in the eastern Amazon basin. Given the different ecological requirements of the two odonate suborders in terms of thermoregulation, dispersal capacity, and environmental sensitivity (May, 1991; McCauley, 2007) and considering the predictions of the ecophysiological hypothesis (De Marco et al., 2015), they were predicted to respond differently to variations in the condition of the riparian vegetation, and stream physical and chemical characteristics. Based on the thermoregulatory characteristics of the two suborders, riparian vegetation condition was expected to be the primary factor affecting the distribution and richness of odonate species. Specifically, a reduction in Zygoptera species richness, and an increase in Anisoptera species richness was expected along a gradient of increasing stream canopy openness (Samways and Steytler, 1996).

2. Material and methods

2.1. Study area

We studied 50 Amazonian stream sites in the municipality of Paragominas, located in the northeast of the Brazilian state of Pará (Fig. 1). The sampled streams ranged from 1st to 3rd order at 1:100,000 scale, following Strahler (1957), and they varied in conservation status and riparian vegetation cover. The region's climate is predominantly humid tropical with a short, well-defined dry season (Köppen category Af; Peel et al., 2007). Mean annual precipitation is 200 cm and the dry season is between June and December. Mean annual temperature is 27.2 °C and the relative humidity is 81% (Gardner et al., 2013).

The natural vegetation of the study area is dense rainforest, mixed open rainforest with lianas and palms, and dense alluvial rainforest (Gardner et al., 2013). Large tracts of pristine forest habitat represent the region's original climax vegetation (Putz and Redford, 2010; Gardner et al., 2013; Moura et al., 2013). Land uses range from new secondary forest, plantations of eucalyptus (*Eucalyptus* sp.), teak (*Tectona grandis*) and Brazilian firetree (*Schizolobium parahyba* var. *amazonicum*), cattle pasture, small farms, and large mechanized farms that typically produce rice and soybeans.

2.2. Data collection

2.2.1. Collection of specimens and laboratory procedures

Sampling was performed by a single collector in all study sites to avoid problems of skew in the data. Data were collected during the dry season (June–August 2011) along a disturbance gradient. We chose this period because the intensity of precipitation during the rainy season hinders site access and data collection for many variables, including odonate collection, given their ecophysiological demands (see May, 1976, 1991; Corbet, 1999). Studies have also shown that a greater abundance and species richness of adult and larval odonates can be found during the dry season (Baptista et al., 2001; Fulan and Henry, 2007).

A 150 m site on each stream was subdivided into 10 sections, each 15 m long and separated by 11 transects, which were used for collecting physical habitat at the site. Adult odonates were collected in the first two 5-m segments of each section, with a total of 20 segments being sampled per site. These segments were grouped into a single sample unit for data analysis. Odonate adults were sampled by using an entomological net (diameter: 40 cm, depth: 65 cm) attached to a 90-cm-long aluminium handle. Each site was sampled by a single collector for 1 h, with approximately 3 min in each segment (Oliveira-Junior et al., 2015). This approach has been used successfully in previous studies (Juen and De Marco, 2012; Calvão et al., 2013; Carvalho et al., 2013; Oliveira-Junior et al., 2013, 2015), and has proven to be an effective rapid sampling technique.

The temperature and relative humidity of the air were measured in a shady location, between 10:00 h and 14:00 h, when the sun's rays reached the surface of the stream. This prerequisite is essential to ensure that all the different groups of odonates (conformers, heliotherms, and endotherms) are active at the time of specimen collection (De Marco and Resende, 2002). The specimens were prepared following the protocol described by Lencioni (2005), and were identified using taxonomic keys (Borror, 1945; Belle, 1988; Garrison, 1990; Belle, 1996; Lencioni, 2005, 2006; Garrison et al., 2006, 2010), as well as comparing with voucher specimens available in entomological collections. Voucher specimens were deposited in the zoological collection of the Federal University of Pará in Belém, Pará (Brazil).

2.2.2. Analysis of stream physical habitat

We applied a Habitat Integrity Index, (HII; Nessimian et al., 2008) and a set of quantitative physical habitat measures from Peck et al. (2006) to assess environmental conditions. The HII includes 12 qualitative metrics: riparian land use; extent and condition of the riparian forest; channel sediment type and retention mechanisms; bank structure and erosion; stream bed substrate; presence of aquatic vegetation and detritus; and the distribution of riffles, pools, and meanders. Each item is scored between four and six. These scores are summed and ranked in relation to habitat integrity, with potential values ranging from 0 (least integrity) to 1 (most integrity).

Peck et al. (2006) described how to quantify riparian vegetation, anthropogenic impacts related to the vegetation, and stream structure variables. Mean channel shading was estimated using a convex densiometer at the central point of the channel, where four measurements were taken, upstream, downstream, left, and right banks. An assessment of the riparian zone was conducted in a 10 m^2 quadrat located at each margin of the stream at each transect, based on a visual estimate of the proportion of the canopy consisting of large trees (Diameter at Breast Height-DBH > 30 cm), shrubs (height < 0.5 m), exposed soil, and mean total canopy cover (> 75%). Anthropogenic impacts, including the proximity of buildings, roads, rubbish, agriculture, and other activities, were also assessed. To characterize stream channel structure and morphology we measured a number of variables in each transect and/or sector: depth, wetted width, bankfull height, bank angle, quantity of medium-large (> 60 cm in diameter and 5 m in length) wood, overhanging vegetation within 1 m of the water surface, macrophyte cover, and substrate embeddedness. Discharge, channel slope, and sinuosity of each site were also measured (Peck et al., 2006).

2.2.3. Water quality

We used a multiparameter Horiba U-51 probe to measure four physical-chemical characteristics of the water at each site: electrical conductivity (µS/cm), pH, dissolved oxygen (mg/L), and temperature (°C).

2.3. Data analysis

The sampling efficiency for odonates was tested with sample-based species accumulation curves and with species-area rarefaction by the MaoTau method, using the same estimator with 1000 randomizations based on an increasing number of segments (1–20 segments per stream) (Colwell et al., 2004).

To compare species composition among the stream sites, we conducted a Principal Coordinates Analysis (PCoA) and used bubble-plots of the PCoA results to represent the environmental gradient with HII. The dissimilarity measure in the PCoA was the Bray-Curtis index (Legendre and Legendre, 1998). We assessed the relationship of Odonata species composition and channel shading by ranking the relative abundance of all species (except those represented by fewer than three specimens or present at only one site) and compared this ranking with the percentage of channel shading for the stream sites.

To avoid multi-colinearity problems, a Pearson correlation matrix was constructed with the values for all the variables. When a correlation of 0.7 or more was found between two variables, we selected the one known to have a systematic influence on the occurrence of odonates (Ferreira et al., 2014). A forward stepwise procedure was used to select the environmental variables model that best explained the variation observed in the odonate assemblage composition. We used simple regressions to evaluate the relationship between the HII and species richness, and multiple regressions (Zar, 1999) to test the response of species richness to the different metric scores. To test if the regression models were spatially autocorrelated, we assessed the Moran I values of the residuals of all regressions, and considered Moran $I > 0.2$ as autocorrelated.

All analyses were performed by separate suborders (Anisoptera and Zygoptera) and run in the R vegan package (R Development Core Team, 2011). The spatial analyses were conducted in SAM (Spatial Analysis in Macroecology) software (Rangel et al., 2010).

3. Results

3.1. Odonate assemblages, accumulation curves, and site environmental quality

We collected 1769 odonate specimens, representing 97 species, 41 genera, and 11 families. Just over half [961] of the specimens were Zygoptera, representing eight families (Calopterygidae, Coenagrionidae, Dicteriadidae, Megapodagrionidae, Perilestidae, Polythoridae, Protoneuridae, and Pseudostigmatidae), 19 genera, and 56 species. The other 808 specimens were Anisoptera, representing 41 species, 22 genera, and three families (Aeshnidae, Gomphidae and Libellulidae).

None of the species accumulation curves (Jackknife 1) or species-area rarefaction curves (Mao Tau) reached an asymptote (Fig. 2). However, sampling efficiency was 79% (observed richness/estimated richness) (Jackknife 1) and 78% (Mao Tau).

The HII ranged from 0.28 to 0.96, representing a wide gradient of environmental conditions. The condition of the sites had a significant, and contrasting, effect on the species richness of the two odonate suborders. We found a significant negative relationship ($r^2 = 0.411$, $p < 0.001$) between HII and Anisoptera species richness (Fig. 3A). On the other hand, Zygoptera species richness increased significantly ($r^2 = 0.310$, $p < 0.001$) with increasing HII values (Fig. 3B). A reduction of 10% in environmental condition of streams (a difference of 0.10 in the value of HII) was related to a mean decrease of 11 Anisoptera species and a mean increase of 13 Zygoptera species (Fig. 3).

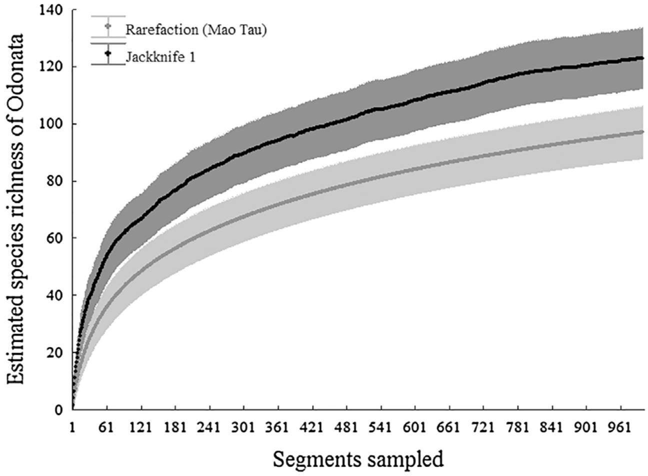

Fig. 2. Species accumulation curve for odonates (first-order Jackknife and Mao Tau; average ± confidence interval) in Paragominas.

3.2. Effect of anthropogenic disturbance and riparian conditions on odonata species composition

None of the Moran I values exceeded 0.2, indicating that the models were spatially unbiased (Supplement 1). Only the first axis of the PCoA was analyzed, because the value observed for the second axis was not greater than that estimated by the broken-stick model. The first axis alone (representing the site HII scores) accounted for 33% of the variation in Anisoptera species composition among sites and 20% for Zygoptera. The sites differed in species composition for both Anisoptera (Fig. 4A) and Zygoptera (Fig. 4B). The different locations and sizes of the bubbles indicate a wide variation in species composition along the HII gradient (larger bubbles represent sites with greater integrity).

We found no significant relationship between odonate species richness and riparian vegetation ($R^2 = 0.040$, $p = 0.871$). Nevertheless, riparian vegetation affected species richness at the suborder level (Anisoptera: $R^2 = 0.390$, $p < 0.001$; Zygoptera: $R^2 = 0.300$, $p = 0.006$). Reduced stream canopy cover generated an increase in Anisoptera species richness (curve slope = -0.567, $p < 0.001$), and a decrease in Zygoptera species richness (curve slope = 0.405, $p = 0.006$; Table 1). Species composition also varied systematically with degree of channel shading, indicating a remarkable degree of species substitution as percent of channel shading changed (Fig. 5). The relative abundance of Anisoptera species was higher with less channel shading (Fig. 5A); however, species density of Zygoptera increased with increased channel shading (Fig. 5B).

The variables related to anthropogenic impacts did not affect odonate species richness ($R^2 = 0.128$, $p = 0.408$). Similar results were obtained when the data were analyzed by suborder (Anisoptera: $R^2 = 0.178$, $p = 0.184$; Zygoptera: $R^2 = 0.138$, $p = 0.353$), indicating that these variables did not account for the differences in the species richness of the two groups (Table 2). However, increased incidence of rubbish was associated with increased Anisoptera richness.

Variation in stream physical habitat structure did not explain total odonate species richness ($R^2 = 0.326$, $p = 0.312$) nor that of Anisoptera ($R^2 = 0.402$, $p = 0.105$). Those variables only affected Zygoptera species richness ($R^2 = 0.440$, $p = 0.043$), which increased with bank angle (curve slope = 0.353, $p = 0.048$) and the quantity of wood in the stream bed (curve slope = 0.325, $p = 0.026$; Table 3).

Water quality did not affect odonate species richness significantly ($R^2 = 0.143$, $p = 0.131$) nor that of the Anisoptera ($R^2 = 0.120$, $p = 0.208$); however, those variables did affect Zygoptera species richness ($R^2 = 0.263$, $p = 0.007$). Zygoptera species richness increased with increasing conductivity (curve slope = 0.279, $p = 0.039$), but decreased with increasing water temperature (curve slope = -0.457, $p < 0.001$; Table 4).

3.3. Factors affecting odonate assemblage structure

In general, riparian vegetation was the principal factor explaining Anisoptera and Zygoptera species richness at the study sites, although several other factors related to the site physical structure and water quality also affected Zygoptera assemblages. Based on these results, we developed a conceptual model, which summarizes the principal factors that may influence the characteristics of odonate assemblages in Amazonian streams (Fig. 6). Our model indicates that riparian vegetation is the principal factor structuring Anisoptera and Zygoptera assemblages, and that variable also influences other factors related significantly to the assemblages of these two suborders. Greater channel shading, bank angle, wood, electrical conductivity, and water temperature all contribute to increased Zygoptera species richness. On the other hand, increased canopy openness and rubbish were associated

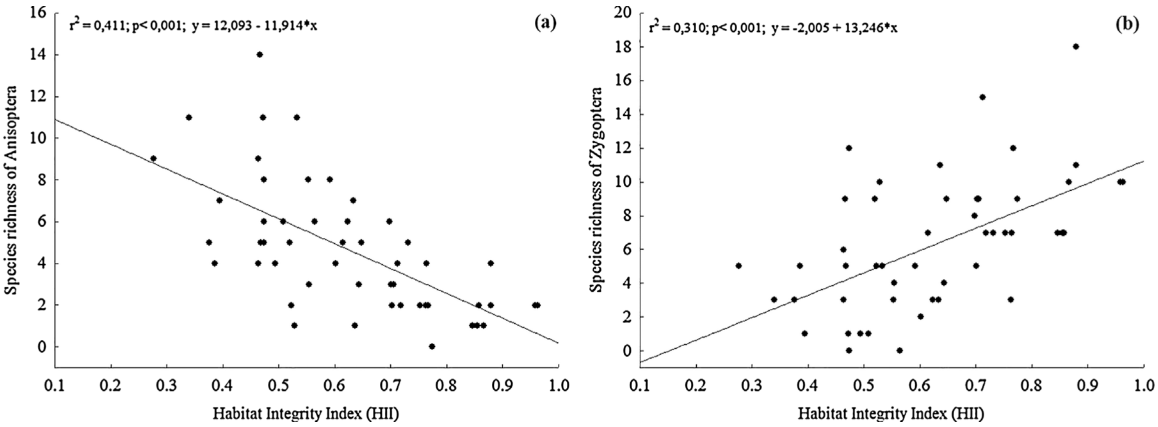

Fig. 3. Relationships between the habitat integrity index (HII) and the species richness of (a) Anisoptera and (b) Zygoptera in Paragominas stream sites.

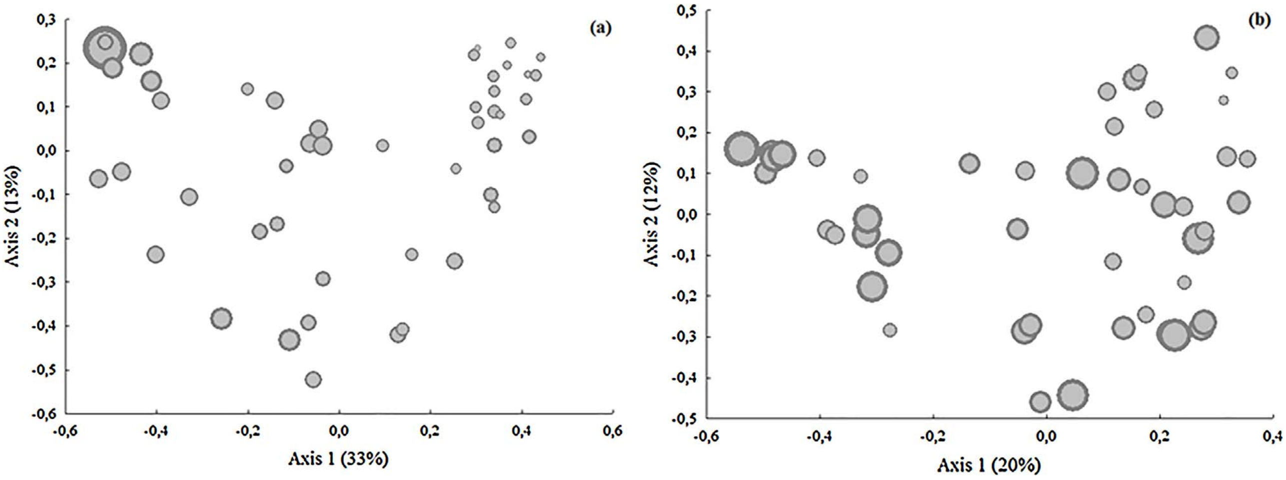

Fig. 4. Ordination of sampled stream sites based on the assemblage composition of (a) Anisoptera and (b) Zygoptera in Paragominas. Bubble locations and sizes represent the environmental gradient measured by the Habitat Integrity Index (PCoA axis 1).

with increased Anisoptera species richness (Fig. 6).

4. Discussion

Riparian vegetation was the principal factor related to the environmental condition of our study sites and had a strong effect on odonate assemblages. The removal of this vegetation had a negative effect on Zygoptera composition and species richness. Most of the species of this suborder are highly dependent on areas with dense vegetation. As damselflies are small and have thin bodies (and thus a high surface area to volume ratio), it seems likely that they are more vulnerable to overheating and desiccation, and are thus more sensitive to environmental variation due to ecophysiological restrictions (Corbet, 1999; Corbet and May, 2008). These species are expected to be limited to shaded environments with greater densities of riparian vegetation, that is, better preserved environments (Juen and De Marco, 2011).

Because most Anisoptera are heliothermic, they are generally highly dependent on access to solar radiation (Remsburg et al., 2008), needing to heat themselves up prior to activity (Corbet and May, 2008; Resende, 2010). This was the case of *Erythrodiplax fusca* (Rambur, 1842) and *Orthemis discolor* (Burmeister, 1839) sampled in this study, which normally avoid shady areas (Samways et al., 2005; Ward and Mill, 2005; Remsburg et al., 2008). As demonstrated by Carvalho et al. (2013), generalist species adapted for lentic environments, including most Anisoptera, would be expected in altered habitats, which provide such conditions for their migrations and establishment (Solimini et al., 1997).

Differences in Odonata species composition among sites with different levels of conservation was due to their different environmental requirements. In general, species with more exacting requirements

Table 1
Results of multiple regression analysis for Anisoptera and Zygoptera species richness relative to site riparian vegetation of stream sites. SE = Standard Error. Values in bold type are significant at $p < 0.05$.

Variable (riparian vegetation)	Anisoptera				Zygoptera			
	β	SE	t[44]	P	β	SE	t[44]	P
Channel shading	**−0.567**	**0.132**	**−4.302**	**< 0.001**	**0.405**	**0.141**	**2.867**	**0.006**
Large trees	−0.078	0.207	0.377	0.708	0.126	0.221	0.570	0.572
Shrubs	0.078	0.160	0.487	0.628	−0.098	0.172	−0.573	0.570
Exposed soil	0.125	0.141	0.887	0.380	−0.274	0.151	−1.819	0.076
Total cover	−0.016	0.194	−0.081	0.936	0.037	0.207	0.178	0.859

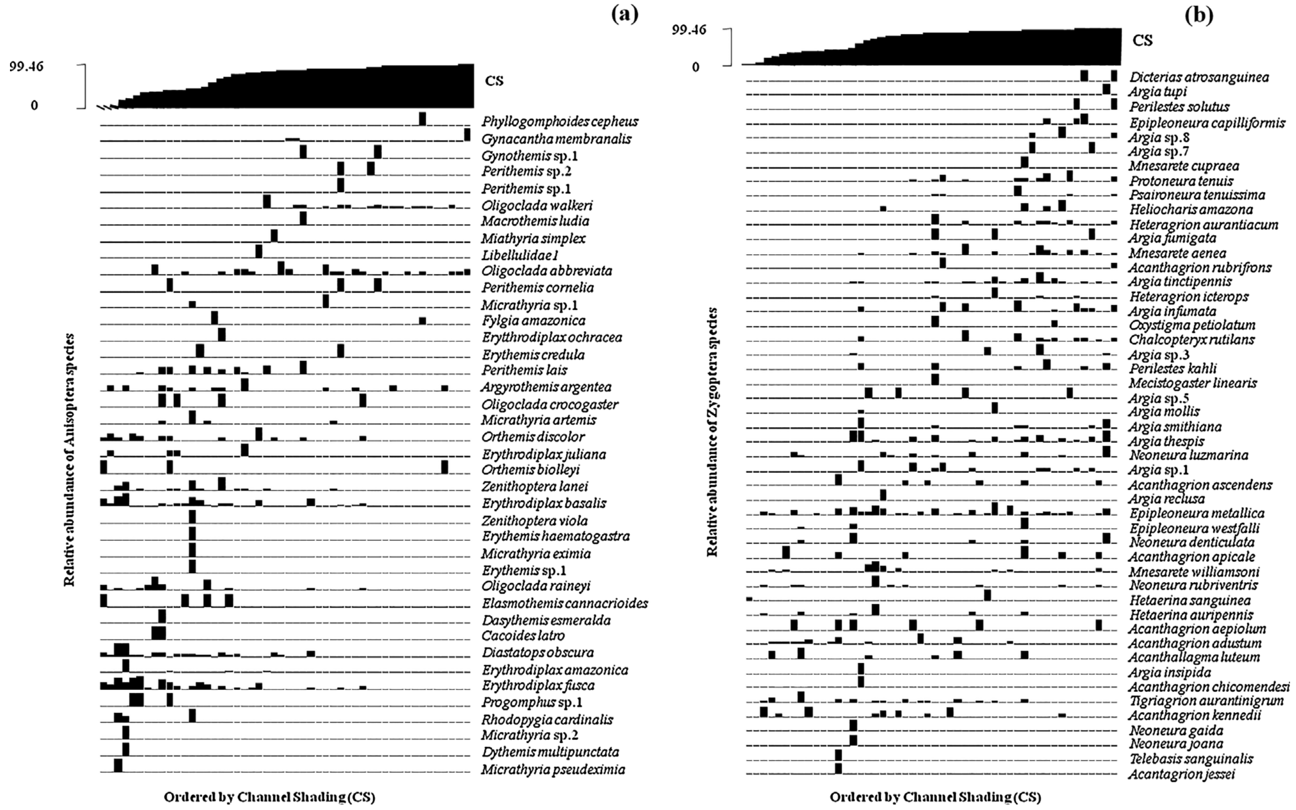

Fig. 5. Direct ordination of the relative abundance of the odonate species found in Paragominas stream sites, ranked by channel shading (CS). Species are ranked along the y axis by the mean reciprocal, weighted by the channel shading: (a) Anisoptera; (b) Zygoptera.

(most of the Zygoptera), with narrow niches and restricted ranges in temperature and insolation, are associated with densely vegetated streams. However, species with wider niches (e.g., most of the Anisoptera) can inhabit more exposed environments (Carvalho et al., 2013; Monteiro-Júnior et al., 2013). Thus, changes in air temperatures above small Amazonian streams affect the physiological processes of odonata species, leading to a change in the composition of species in such environments. These contrasting responses of the two Odonata suborders, their composition related to the environmental gradient, provide a reliable tool for assessing aquatic habitat changes (Monteiro-Júnior et al., 2014). It is well documented that aquatic habitats that suffer anthropogenic impacts tend change in species composition, with assemblages generally dominated by species with wide geographic ranges (Tokeshi and Townsend, 1987), such as the larger bodied Anisoptera. These species have greater dispersal capacities and are better in moving between environments (Monteiro-Júnior et al., 2014).

In aquatic systems, as we found in our results, species richness tends to increase in more heterogeneous and less disturbed environments, which favor the coexistence of species with different ecophyisological requirements (Williams et al., 2004; Dias-Silva et al., 2010). In this case, environmental condition will be an important factor in the structuring of aquatic assemblages. In a study of adult odonates, Suh and Samways (2005) emphasized the importance of having multiple biotopes and microhabitat conditions to ensure high species richness or the conservation of rare species. This diversity will only be guaranteed if the natural heterogeneity of existing water courses is maintained.

Our results are consistent with those of Carvalho et al. (2013) and Foote and Hornung (2005), indicating that riparian vegetation is a more important determinant of odonate assemblage structure than water quality. Others also have shown that odonates are not normally affected by subtle variations in water quality (Takamura et al., 1991; Hardersen, 2000; Woodcock and Huryn, 2007). Nevertheless these organisms are excellent indicators of anthropogenic impacts and modifications in the chemical structure of the watercourse (Samways and Steytler, 1996), such as dissolved oxygen (Courtney and Clements, 1998), pH (Jacob et al., 1984), and concentrations of pollutants (Couceiro et al., 2007).

Although physical-chemical variables are considered important determinants of the distribution patterns of many aquatic insects

Table 2
Results of multiple regression analysis for Anisoptera and Zygoptera species richness relative to human impacts on Paragominas stream sites. SE = Standard Error. Values in bold type are significant at $p < 0.05$.

Variable (human impact)	Anisoptera				Zygoptera			
	β	SE	t[44]	P	β	SE	t[44]	P
Proximity to:								
Buildings	−0.060	0.177	−0.342	0.734	−0.101	0.181	−0.561	0.578
Roads	−0.035	0.141	−0.249	0.805	−0.127	0.145	−0.881	0.383
Rubbish	**0.376**	**0.163**	**2.309**	**0.026**	−0.067	0.167	−0.405	0.688
Agriculture	−0.257	0.161	−1.597	0.118	−0.153	0.165	−0.932	0.356
Silviculture	−0.101	0.140	−0.720	0.476	0.072	0.144	0.499	0.620
Total impact	0.222	0.183	1.214	0.231	−0.146	0.188	−0.780	0.439

Table 3
Results of multiple regression analysis for Anisoptera and Zygoptera species richness relative to stream channel physical habitat structure. SE = Standard Error. Values in bold type are significant at $p < 0.05$.

Variable (channel structure)	Anisoptera				Zygoptera			
	β	SE	t[44]	P	β	SE	t[44]	P
Channel width	0.311	0.194	1.603	0.118	−0.057	0.188	−0.302	0.764
Bankfull height	−0.180	0.147	−1.227	0.228	−0.141	0.142	−0.991	0.328
Bank angle	−0.573	0.178	−3.218	0.003	**0.353**	**0.172**	**2.047**	**0.048**
Macrophytes	−0.003	0.164	−0.017	0.987	−0.123	0.158	−0.777	0.442
All wood (size class 1) in the stream bed	−0.135	0.194	−0.693	0.493	−0.202	0.188	−1.075	0.290
Large wood (size class 4) in the stream bed	−0.036	0.144	−0.253	0.802	**0.325**	**0.140**	**2.326**	**0.026**
Overhanging vegetation	−0.012	0.169	−0.071	0.944	−0.176	0.164	−1.074	0.290
Channel embeddedness	−0.096	0.141	−0.685	0.498	−0.036	0.136	−0.261	0.795
Channel slope	−0.004	0.190	−0.023	0.982	−0.155	0.184	−0.842	0.405
Channel sinuosity	0.098	0.159	0.621	0.539	−0.050	0.153	−0.324	0.748
Channel mean depth	0.121	0.169	0.712	0.481	−0.045	0.164	−0.277	0.784
Discharge	−0.042	0.193	−0.218	0.829	−0.028	0.187	−0.148	0.883

(Zamora-Muñoz et al., 1993), water quality was only relevant to Zygoptera species richness in our study. A similar situation was reported by Oliveira-Junior et al. (2013) in a transition area between the Amazon rainforest and the Cerrado (savanna) in central Brazil. Zygoptera species richness was correlated with increased electrical conductivity, and decreased water temperature. Electrical conductivity stimulates increased production of algae and macroinvertebrates in nutrient-poor Amazon streams, thereby increasing food availability for predators, such as Zygoptera larvae (Ribeiro et al., 1998). Absence of riparian vegetation, which stabilizes the temperature of aquatic habitats by shading them (Fritzsons et al., 2005), is a surrogate for increased water temperature. The decline in Zygoptera species richness in warmer waters thus may also reflect the removal of riparian vegetation from these sites.

The reduced dispersal capacity of smaller-bodied species, including most Zygoptera, makes them more dependent on local conditions, such as local habitat structure (Tscharntke et al., 2002). By contrast, larger-bodied species, which include most of the Anisoptera, have a greater capacity for thermoregulation (endothermic) and dispersal (Corbet, 1999). These species are more capable of colonizing new areas with altered ecological conditions, reinforcing their adaptability to novel conditions, such as the physical-chemical parameters evaluated in our study.

The quantity of wood in the stream beds also influenced Zygoptera species richness, probably because these species oviposit epiphytically or endophytically (Fulan and Henry, 2007). The twigs and branches in the stream beds, derived from riparian vegetation, are typical of the substrates in which the species of this suborder deposit their fertilized eggs (Foote and Hornung, 2005) and provide ideal conditions for larval development.

Other anthropogenic impacts measured in our study (not related to riparian vegetation) did not affect odonate species richness. This is likely because the majority of the metrics developed from Peck et al. (2006) did not vary enough to affect the odonate assemblages at our sites, given that such variables as the presence of sewage, buildings, walls, and channel dredging, were absent from the study sites. It is nevertheless important to note that anthropogenic impacts can influence odonate assemblage structure (Buss et al., 2002; Suh and Samways, 2005; Monteiro-Júnior et al., 2013), especially in relation to the HII (Nessimian et al., 2008).

Environmental condition and riparian vegetation structure had a significant effect on odonate assemblages in the study area. Reduced environmental condition of streams led to reduced Zygoptera species richness and increased Anisoptera species richness. The presence or absence of riparian vegetation likely affected other factors, such as water temperature and substrate quantity/quality, and can thus be considered a principal determinant of adult odonate assemblage structure as seen in other studies (Carvalho et al., 2013; Monteiro-Júnior et al., 2013; Rodrigues et al., 2016). Based on these results, the maintenance of riparian vegetation appears to be a fundamental requirement for conserving the Zygoptera fauna in aquatic environments. The loss of Zygoptera species may alter predator-prey relationships especially for smaller-bodied organisms in the ecosystem, leading to a disequilibrium in important prey such as Diptera, Ephemeroptera, and Trichoptera, or even vertebrate predators like fishes, amphibians, and birds.

Overall, our study provides guidelines for predicting the effects of modifications in the environmental variables we measured. This reinforces the conclusion that associations of different odonate taxa with specific habitat types can be a useful tool for evaluating odonate responses to environmental modifications.

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Table 4
Results of multiple regression analysis for Anisoptera and Zygoptera species richness relative to water quality of Paragominas sites. SE = Standard Error. Values in bold type are significant at $p < 0.05$.

Physical-chemical characteristic of the water	Anisoptera				Zygoptera			
	β	SE	t[44]	P	β	SE	t[44]	P
Temperature	0.280	0.143	1.962	0.056	**−0.457**	**0.131**	**−3.495**	**< 0.001**
Dissolved oxygen	−0.234	0.146	−1.608	0.115	−0.047	0.133	−0.354	0.725
pH	−0.129	0.147	−0.880	0.383	0.200	0.134	1.487	0.144
Electrical conductivity	−0.025	0.143	−0.173	0.864	**0.279**	**0.131**	**2.131**	**0.039**

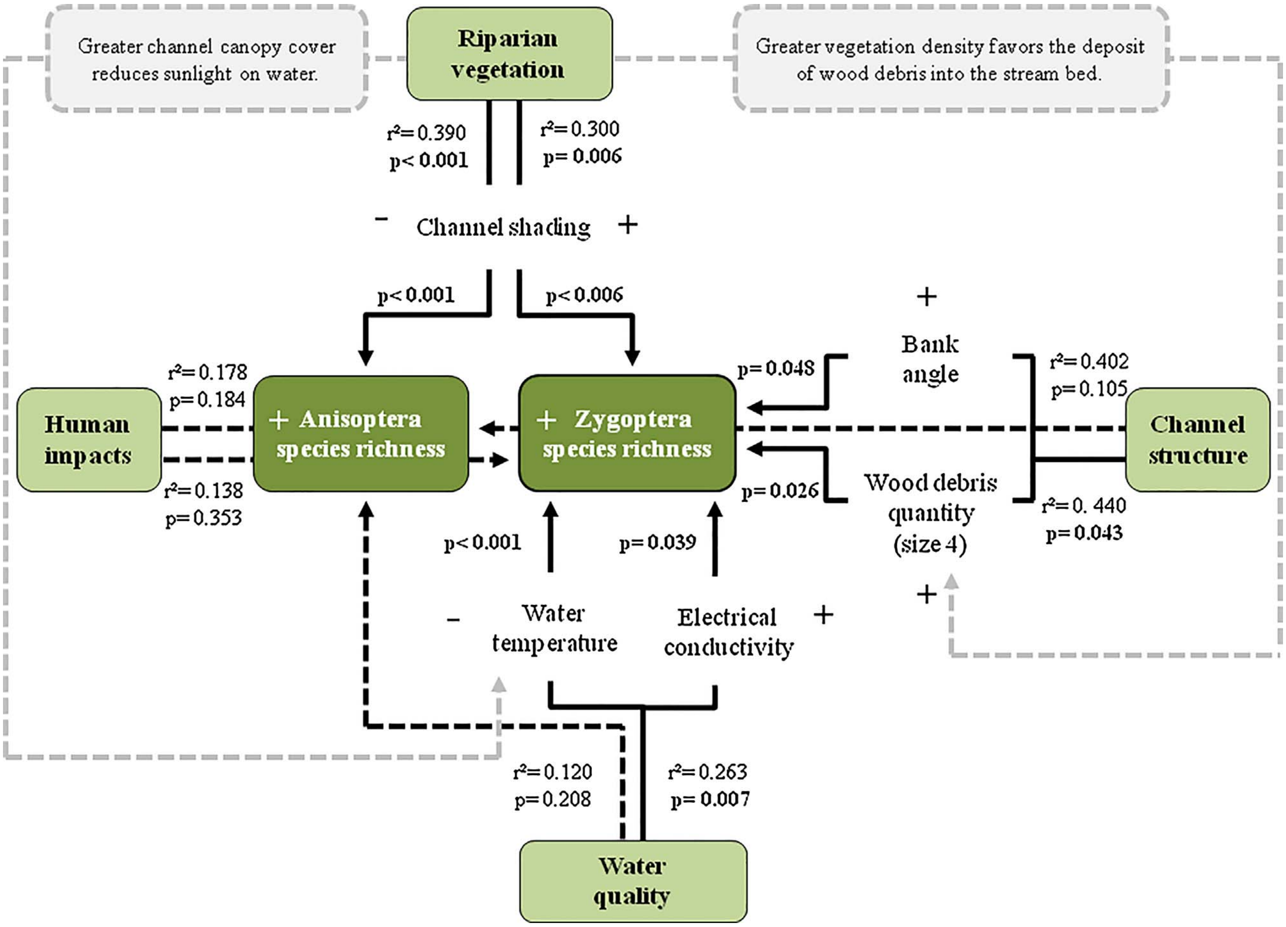

Fig. 6. Conceptual model representing the effects of environmental variables on Anisoptera and Zygoptera species richness. The solid black lines and p values in bold type represent significant relationships, whereas the dotted black lines refer to non-significant relationships. Positive (+) signs represent an increase, while negative (−) ones, a decrease. The gray dotted lines show the relationships between variables.

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