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LUÍSA VICTÓRIA DA SILVA VAREIRA

**Tropical freshwater ecosystem type influences dragonfly species spatial
distribution in an estuarine island**

Belém/PA
2024

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia da Universidade Federal do Pará, como requisito parcial para obtenção do título de Mestre em Ecologia.

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia da Universidade Federal do Pará, como requisito parcial para obtenção do título de Mestre em Ecologia pela Comissão Julgadora composta pelos membros:

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O tipo de ecossistema tropical de água doce influencia a distribuição espacial de espécies de libélulas em uma ilha estuarina

RESUMO

Nós exploramos como a heterogeneidade ambiental (HA) e a conectividade entre os locais determinam a distribuição de espécies de libélulas em corpos d'água lênticos e lóticos. Esperávamos: (i) uma composição distinta de espécies e maior diversidade beta em locais lóticos; (ii) uma relação inversa dos componentes da diversidade beta (*turnover* e *nestedness*) com a HA e (iii) conectividade. Amostramos adultos de libélulas e variáveis ambientais em 23 corpos d'água lóticos e 19 lênticos em uma área protegida (APA Marajó), e medimos a conectividade dos corpos d'água usando a distância terrestre. Os corpos d'água lóticos e lênticos apresentaram condições ambientais e composição de espécies contrastantes, com várias espécies de libélulas encontradas em ambos os tipos de corpos d'água, que podem ser generalistas de habitat. A diversidade beta foi explicada principalmente pelo turnover, sendo maior nos corpos d'água lênticos. A HA e a conectividade influenciaram a diversidade beta e o turnover considerando toda a metacomunidade, mas nenhuma relação foi observada após a separação dos locais por tipo de corpo d'água. A variação ambiental dos corpos d'água sustenta uma diversidade significativa de libélulas, fornecendo caminhos de dispersão para a colonização e a ocupação de habitats adequados, aumentando a persistência das espécies. Conjuntos de diferentes ecossistemas de água doce formam redes heterogêneas que são fontes as quais compartilham organismos aquáticos, portanto, destacamos a inclusão de vários ecossistemas de água doce no planejamento de conservação de áreas protegidas ou para o monitoramento da biodiversidade.

Palavras-chave: Odonata. Águas lóticas. Águas lênticas. Heterogeneidade ambiental. Conectividade de habitat. Conservação da biodiversidade.

Tropical freshwater ecosystem type influences dragonfly species spatial distribution in an estuarine island

ABSTRACT

We examined how environmental heterogeneity (EH) and site connectivity drive dragonfly species distribution in lotic and lentic water bodies. We expected: (i) distinctive species composition and increased beta diversity in lotic sites; (ii) an inverse relationship of beta diversity components (*turnover* and *nestedness*) with EH and (iii) connectivity. We sampled dragonfly adults and environmental variables in 23 lotic and 19 lentic water bodies within a protected area (APA Marajó), using the overland distance for connectivity assessment. Lotic and lentic water bodies exhibited contrasting environmental conditions and species composition, with several dragonfly species found in both water body types, which may be habitat generalists. The beta diversity was mainly because of turnover and was higher in lentic water bodies. EH and connectivity influenced beta diversity and turnover across the entire metacommunity, but no relationships were observed after separating sites by water body type. The environmental variation of water bodies sustains significant dragonfly diversity, providing dispersal pathways for colonization and occupancy of adequate habitats, enhancing species persistence. Sets of different freshwater ecosystems form heterogeneous networks which are shared sources of aquatic organisms, therefore, we highlight the inclusion of several freshwater ecosystems in the conservation planning of protected areas or for biodiversity monitoring.

Keywords: Odonata. Lotic waters. Lentic waters. Environmental heterogeneity. Habitat connectivity. Biodiversity conservation.

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INTRODUCTION

Species distribution is a relevant biodiversity aspect for conservation which remains with information deficits caused by few resources and difficulty in accessing remote regions (Hortal et al., 2015). To fill these gaps addressing knowledge shortfalls (e.g. Hutchinsonian and Wallacean shortfalls), the species distribution patterns have been studied from a metacommunity perspective, a helpful framework to explore the ecological drivers of species distribution and variation between sites (Wilson, 1992; Leibold et al., 2004; Hortal et al., 2015). Metacommunities consist of a set of local communities that potentially exchange species by dispersion, mainly structured by local abiotic variables, biotic interactions, and stochastic factors (Wilson, 1992; Leibold et al., 2004). A metacommunity can be described by the regional diversity (gamma) constituted by local diversity (alpha diversity) and the degree to which species composition varies (beta diversity) (Whittaker, 1960; Anderson, Ellingsen & McArdle, 2006). Beta diversity, here defined as species composition dissimilarity between sites, can be decomposed in species substitution (turnover) or ordered loss of species (nestedness) (Baselga, 2010; Legendre & De Cáceres, 2013; Soininen, Heino & Wang, 2018). The evaluation of dissimilarities and beta diversity decomposition into components enables the exploration of processes and factors driving metacommunities structure (Baselga, 2010; Gianuca et al., 2017; Soininen, Heino & Wang, 2018). This is particularly interesting for understanding ecological community organization, identifying priority sites for conservation and restoration, and characterizing the effects of environmental changes (Socolar et al., 2015; Gianuca et al., 2017; Savary, Lesnard, Peres-Neto, 2023).

Beta diversity and its components vary with environmental (e.g. environmental heterogeneity) and spatial factors (e.g. connectivity between sites) which describes processes responsible for structuring metacommunities (e.g. environmental filtering, biotic interactions, dispersal, and ecological drift) (Leibold et al., 2004; Heino et al., 2015; Soininen, Heino & Wang, 2018; Chase et al., 2020). A global pattern concerning beta diversity showed that it decreases with latitude both in terms of total beta diversity and turnover, whereas nestedness increases (Soininen, Heino & Wang, 2018). Thus, a higher species turnover and total beta diversity could be expected in low latitudes, probably because of great environmental heterogeneity or dispersal limitation, the two major drivers of species turnover (Leibold et al., 2004; Heino et al., 2015; Soininen, Heino & Wang, 2018). Turnover and nestedness are independent, the former component being generally larger than nestedness and often determined by spatial extent, environmental heterogeneity, and organisms dispersal ability (Baselga, 2010, Soininen, Heino & Wang, 2018; Perez Rocha et al., 2018). A greater contribution of nestedness for beta diversity may result from loss of habitat complexity, species extinctions and recolonizations (Soininen, Heino & Wang, 2018). Therefore, the proportion of turnover and

nestedness vary according to environment type and can indicate different processes structuring metacommunities (Soininen, Heino & Wang, 2018).

Tropical regions harbor a high diversity of freshwater systems that suffer human impacts (e.g. land use changes). The impacts have been modifying habitat structure and causing idiosyncratic effects in species composition variation among local assemblages (Socolar et al., 2016). Also, in natural conditions, different freshwater ecosystems exhibit variable assemblage arrangements due to the interaction between environmental and spatial predictors (Heino et al., 2015; Ortega et al., 2021; He et al., 2023). The variation in assemblage structure can be driven by environmental filtering of species (species sorting) and dispersal, which may be limited or not depending on the distance between sites (Leibold et al., 2004; Grönroos et al., 2013; Heino et al., 2015; Chase et al., 2020). For instance, large distances among sites may result in dispersal limitation, whereas the mass effect becomes expressive with reducing distance (Leibold et al., 2004; Heino et al., 2014; Chase et al., 2020). Therefore, investigating how variation in habitat structure influences species occurrence and distribution in different scenarios (e.g. different ecosystems and human impacts) is essential for freshwater biodiversity conservation. In this sense, conservation priority is targeted at areas with high compositional variation if it helps to conserve a greater proportion of regional diversity (Maxwell et al., 2020). However, high beta diversity is not often interesting for regional diversity conservation due to the balance of local species losses (subtractive) and gains (additive) causing biotic homogenization or heterogenization (Socolar et al., 2016). Thus, to understand how environment and space shape assemblages, it is interesting to consider regions with variability of systems, for example, water bodies with contrasting environmental heterogeneity and degree of connectivity between sites (Williams et al., 2004; Heino et al., 2015; Borthagaray et al., 2023).

Freshwater ecosystems may be classified into lotic and lentic water bodies that differ in hydrology, morphology, and environmental conditions, with both harboring high biodiversity (Ribera & Vogler, 2000; Williams et al., 2004; Specziár et al., 2018). Lotic water bodies (e.g., streams and rivers) are characterized by water flow, hydrological and terrestrial connectivity because of riparian vegetation connecting habitat patches in the landscape (Ribera & Vogler, 2000; Amoros & Bornette, 2002). These water bodies characteristics contribute to high environmental heterogeneity and a great number of habitats for diverse organisms occupation (Tews et al., 2004; Stein, Gerstner, Kreft, 2015). Moreover, lotic waters are considered unstable, enabling high species substitutions because of environmental variation and connectivity, which permit active dispersion or passive ecological drift (Carrara et al., 2012; Chase et al., 2020; Ortega et al., 2021). Another important aspect is the forest cover that maintains a mild climate and acts as an allochthonous energy source, crucial to sustaining biodiversity in these sites with low autochthonous primary

productivity (Nessimian et al. 2008; De Marco, Batista & Cabette, 2015; Oliveira-Junior et al., 2017). In contrast to lotic waters, lentic water bodies (e.g. ponds, lakes, and flooded areas) have little or no water flow, because they generally are not connected to other water bodies and are found in open areas with shrubs and grasslands predominance (Ribera & Vogler, 2000; Williams, 2004; Buffagni, 2021). Therefore, compared to lotic waters these water bodies have short spatial environmental gradients, higher aquatic plant incidence, and environment stability through time, promoting its colonization by habitat generalist species with great dispersion capacity (Ribera & Vogler, 2000; Ortega et al., 2021). Recent studies showed that lentic water bodies, including the ones created by humans, provide habitats for species with ecological relevance (Simaika, Samways & Frenzel, 2016; Biggs et al., 2017; Balázs et al., 2022).

Lotic and lentic freshwater ecosystems are inhabited by Odonata, an insect group divided in two suborders Anisoptera and Zygoptera. This insects are closely related to local environmental conditions and habitat structures, thus are considered bioindicators (Oliveira-Junior et al., 2017; May, 2019; Gómez-Tolosa et al., 2021). Anisoptera species have robust bodies, generally ectothermic requiring direct sunlight for body temperature regulation; they also regulate body temperature using wing movement (Corbet & May, 2008; De Marco, Batista & Cabette, 2015). Therefore, Anisoptera species often inhabit lentic water bodies in open areas, with high solar incidence, tolerating a great variation in environmental conditions and thus are widely distributed and considered habitat generalists or open area specialists (De Marco, Batista & Cabette, 2015; Carvalho et al., 2018; Santos & Rodrigues, 2022). In contrast, the majority of Zygoptera species have thin little bodies, thermoregulating mostly with environmental temperature, and thus are considered thermal conformists (Corbet & May, 2008; De Marco, Batista & Cabette, 2015). The Zygoptera characteristics allow these insects to inhabit shaded sites, for example streams, and thus are considered forest specialists because of their narrow niches and restricted distribution (De Marco, Batista & Cabette, 2015; Carvalho et al., 2018; Santos & Rodrigues, 2022). Nevertheless, this is a generalist species classification because niche width varies within suborders and, thus, can define species occurrence. Depending on local water bodies environmental conditions and habitat structure, it is probable that will exist differences in Odonata species proportions according to niche width and specialization (habitat generalist, open area, and habitat specialists) (Carvalho et al., 2018; Buffagni, 2021; Santos & Rodrigues, 2022).

In a region composed of lotic and lentic water bodies, Odonata composition, beta diversity, and the contribution of its components will be a result of the relationship between organisms inherent characteristics, habitat structure, water quality, and the degree of water bodies connectivity (Heino et al., 2015; Johansson et al., 2019; He et al., 2023). In our study, we aimed to explore how environmental heterogeneity and connectivity between sites drive Odonata species distribution by

comparing two contrasting water body types (lotic and lentic). Thus, we expected (i) distinct specific composition between water body types and higher beta diversity in lotic water bodies compared to lentic because of differences in environmental stability and heterogeneity (Figure 1a); (ii) an inverse relationship between beta diversity components (turnover and nestedness) and environmental heterogeneity (Figure 1b); (iii) a higher nestedness contribution in connected (spatially closer) sites, whereas the less connected (spatially distant) sites will present a greater turnover contribution (Figure 1c).

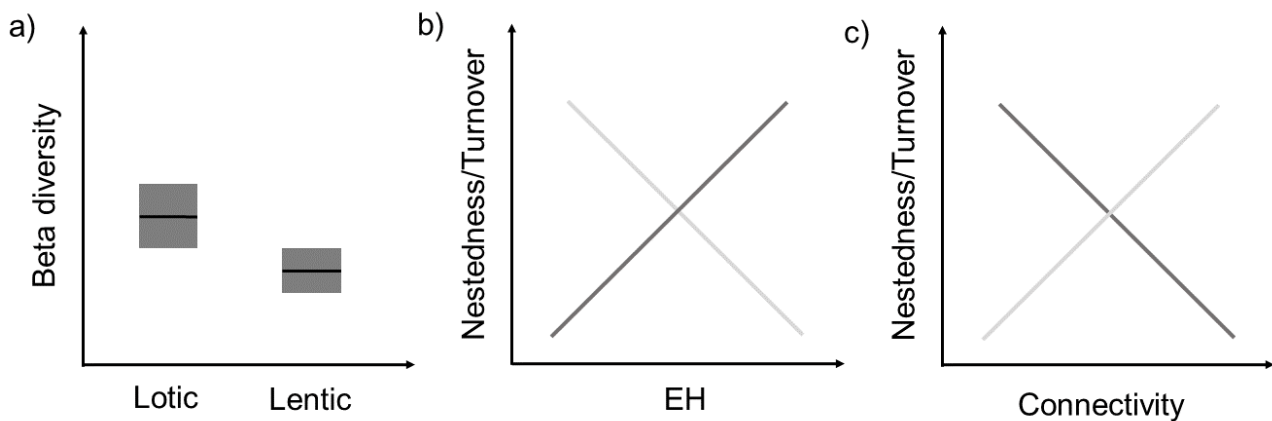


Fig 1 Scheme of the predictions assessed in this study. a) Lotic water bodies will present higher beta diversity because of forest riparian vegetation, and by presenting a higher environmental heterogeneity (EH). Lentic water bodies will present low beta diversity because these sites are generally in open areas and are considered less heterogeneous than lotic environments. b) A stronger turnover contribution (dark gray line) to beta diversity in high EH conditions (lotic water bodies) favoring distinct species colonization associated with different ecological factors. In low EH conditions (lentic water bodies), beta diversity would occur because the formation of species composition subset (nestedness - light gray line). Homogeneous environments tend to have the same species, and their compositional variation would be attributed mainly to differences in species richness. c) Connectivity enables species exchanges between sites and thus the formation of subsets (nestedness – light gray line). In less connected sites, there will be higher substitution (turnover – dark gray line) because of the limited dispersal of some species

MATERIALS AND METHODS

Study area

We carried out our study in the Área de Proteção Ambiental do Arquipélago do Marajó (APA Marajó), Pará state, Brazil, embracing Salvaterra and Cachoeira do Arari municipalities (Figure 2). The APA Marajó presents Am (tropical monsoon climate) on the east, where our sample sites are located, and Af (tropical rainforest climate) on the west according to Köppen climate classification. In Am climate, there is a less rainy season (June to November) and a rainier season (December to May) (Lima et al., 2005). The annual mean temperature is 27°C and the annual mean precipitation can be superior to 3.000 mm/year.

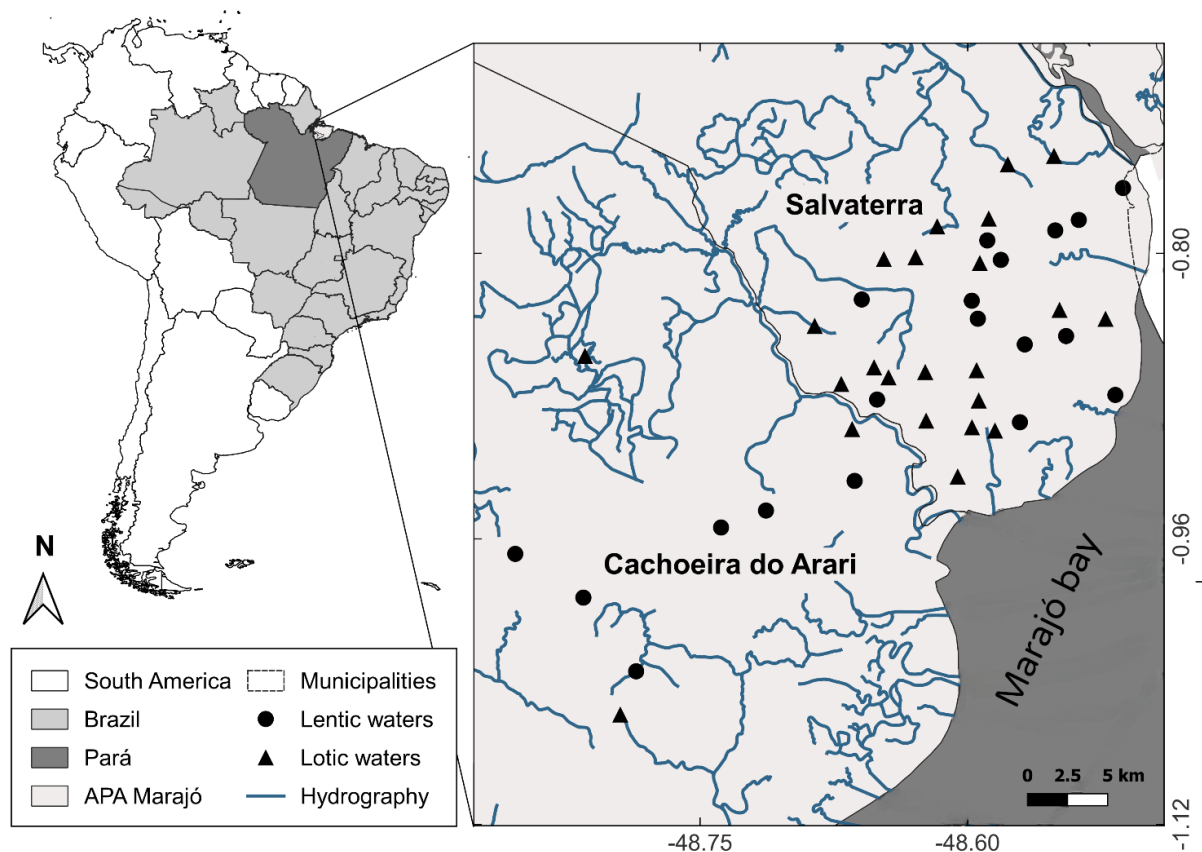


Fig 2 Sample site locations in the Área de Proteção Ambiental do Arquipélago do Marajó (APA Marajó) with lentic and lotic water bodies identified by circles and triangles, respectively (Datum Sirgas 2000)

The APA Marajó is considered the largest fluvial-estuarine island on Earth, with approximately five million hectares, influenced by seasonal inundation, winds, and tide (Lima et al., 2005). The Marajó island is located in the Amazon biome, which harbors one of the greatest hydrographic basin in the globe, including different ecosystem types covering more than 1 million km² of the basin (Nessimian et al., 2008). These characteristics make the APA Marajó a heterogeneous wetland mosaic containing lotic and lentic water bodies. Furthermore, this island stands out for being a protected area with high biodiversity. Although being a protected area, the APA Marajó suffers from land use changes because of wood exploration, agriculture, and grazing which are activities favored by the grassland predominance (Carvalho, Cruz & Calvi, 2019; Cruz & Silva, 2014).

Odonata and environmental variables sampling

We collected the dragonfly adults and environmental variables in 42 water bodies, 23 lotic (streams, locally known as *igarapés*) and 19 lentic (lakes, ponds, and flooded areas) environments. We selected streams of first to third order and lentic water bodies with similar sizes (approximately 100 m²). We sampled during the less rainy season in the region ensuring that we carried out the

samplings at a similar time of the season each year (October to November in 2022; June in 2023). We defined a 150 m stretch with 15 m longitudinal sections which were divided into three parts of 5 m each along the lotic watercourse. In the lentic water bodies, we delimited four quadrants measured from the center and divided the 150 m stretch into four parts with 37.5 m each. We collected the insects using entomological nets for about 90 minutes, during the sunlight, from 10 A.M. to 2 P.M. (Juen & De Marco, 2012). We packed each insect in an envelope for identification to species level using the keys of Lencioni (2005, 2006, 2017), Garrison et al. (2006, 2010), and specific literature for each genus. Also, we compiled information about the species conservation status (Supplementary Information - Table 2; IUCN 2024, SALVE system – De Marco et al., 2023).

We sampled environmental variables simultaneously with Odonata collection, selecting metrics that previous studies indicate as important for structuring the Odonata community (Oliveira-Júnior et al., 2017; Brasil et al., 2020). We measure lotic and lentic water quality using a multiparameter probe, including water temperature (°C), pH, electrical conductivity ($\mu\text{S}/\text{cm}$), and dissolved oxygen (%). We also measured the water bodies depth (cm) using a tape measure, and the riparian vegetation cover (%) with a densiometer. We characterized habitat structure using specific protocols for lotic and lentic water bodies. The characterization included the vegetation cover (e.g., bare ground, canopy cover and undergrowth cover), substrate type (e.g., sand, mud), and human influence (e.g., human constructions, roads) (Peck et al., 2005; Rodrigues et al., 2018). Moreover, we estimated macrophytes richness and cover using a PVC square (1 m \times 1 m) positioned randomly in macrophytes stands. We measured the percentage covered by each species (Fares et al., 2020). When macrophyte species identification was not possible during sampling, we took the biological material to the laboratory.

Data analysis

We considered each water body (lotic and lentic) as a sample, totaling 42 sampling units. Before statistical analysis, we selected our environmental variables based on previous knowledge about the group (Calvão et al., 2022) and using statistical methods. For this, we first excluded variables with more than 90% of observations equal to zero and with a coefficient of variation lower than 40%. We used Pearson correlations (r) excluding variables with $r > 0.6$ to reduce the dimension of the environmental data (Supplementary Information – Table 1). We conducted a Principal Coordinate Analysis (PCoA; Legendre & Legendre 2012) to represent and a Permutational analysis of variance (PERMANOVA; Anderson, 2001) to assess the extent of the environmental differences between the water body types (lentic and lotic). We conducted a Permutational multivariate analysis of dispersions (PERMDISP; Anderson, 2006) to analyze whether possible differences detected by the PERMANOVA are due to differences in multivariate

dispersions (environmental differences in our case; Anderson et al., 2006) (Warton, Wright & Wang, 2012). We used the standardized Euclidean distance (Legendre & Legendre, 2012) in the PCoA, PERMANOVA and PERMDISP, we represented the dissimilarities in the PCoA in two dimensions, and we assessed the statistical significance of the PERMANOVA and PERMDISP with 9999 permutations.

To evaluate differences in Odonata species composition between the two freshwater environments (expectation i; Figure 1a), we used a PERMANOVA with the water body type as explanatory variable and the composition dissimilarity summarized by Sørensen dissimilarity index (Legendre & Legendre, 2012) as a response matrix. The statistical significance of the PERMANOVA and PERMDISP were tested using 9999 permutations (Figure 3). We used the Indicator Value index (IndVal; Dufrêne & Legendre, 1997) to explore whether there were typical species of each water body type (lotic and lentic) (this analysis also refers to expectation i). The IndVal index measures the association of species with groups of sites individually and combined, with significant values indicating association with groups of sampling sites (De Cáceres, Legendre, Moretti, 2010). IndVal values result from the combination of specificity ("A" component) and fidelity or sensitivity ("B" component) indexes. The components indicate, respectively, the probability of the sampled site belonging to the group of sites where the species was collected and of finding the species at the sites belonging to the groups listed (Dufrêne & Legendre, 1997; De Cáceres & Legendre, 2009). We assessed the significance of IndVal values with 9999 permutations (Figure 3).

To assess how the beta diversity patterns of contrasting aquatic ecosystem communities are influenced by environmental heterogeneity (expectation ii; Figure 1b) and connectivity (expectation iii; Figure 1c), we calculated for each water body type the total pairwise dissimilarity (β_{sor}) by partitioning into the beta diversity components of nestedness (β_{nes}) and turnover (β_{sim}) components of beta diversity (Baselga, 2010). We calculated environmental heterogeneity as a standardized Euclidean distance matrix (Legendre & Legendre, 2012) with the environmental variables measured at each site. Finally, we used the geographic coordinates summarized in a Euclidean distance matrix to represent the spatial distance (level of connectivity between sites) (Landeiro et al., 2011). We conducted partial Mantel tests with each beta diversity [β_{sor} (total dissimilarity), β_{sim} (turnover), and β_{nes} (nestedness)] as response matrices and the environmental heterogeneity and spatial distance as explanatory matrices (Legendre & Legendre, 2012) (Figure 3). We evaluated the statistical significance of the partial Mantel tests using 9999 permutations. All statistical analyses were carried out in the R software version 4.3.2 (R Core Team, 2023) with the package "vegan" (Oksanen et al., 2022) and "betapart" (Baselga et al., 2023).

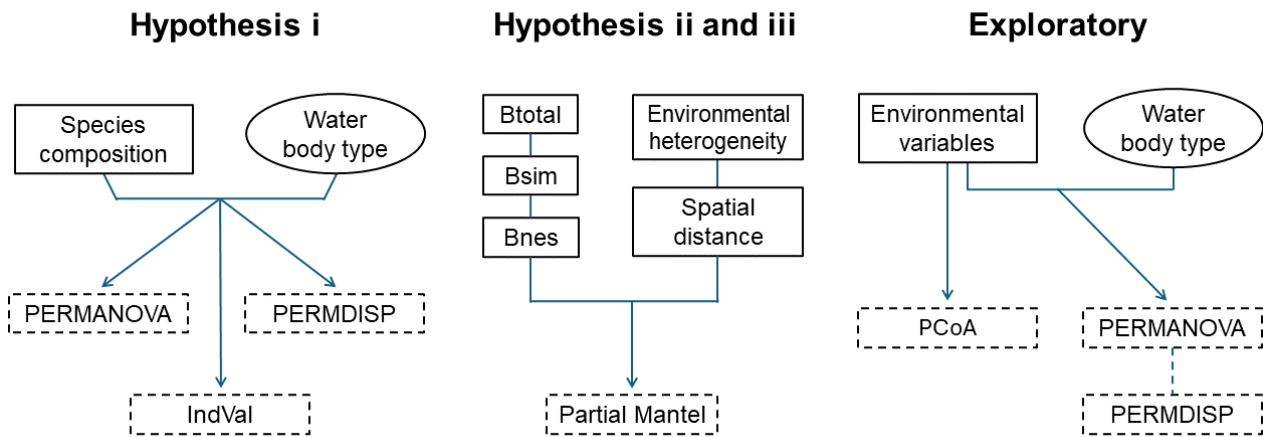


Fig 3 Data analysis scheme with rectangles representing the response and ellipses representing the predictors factor or matrices for each hypothesis predictions, arrows pointing to dashed rectangles representing statistical analysis.

RESULTS

We collected 542 individuals, distributed in 28 genera and 51 species of Anisoptera and Zygoptera suborders. In terms of total species richness and abundance, Libellulidae was the most representative family, followed by Coenagrionidae, Calopterygidae, Perilestidae, Corduliidae, and Aeshnidae (Supplementary Information – Table 2). Twenty-two species occurred in both water body types, 15 species occurred only in lotic and 13 species occurred only in lentic ecosystems. In lotic water bodies, we collected 309 individuals with the total number of individuals per site ranging from two to 34 individuals (average \pm SD: 13.43 ± 7.02). Thirty-six species were sampled in lotic water bodies, and the number of species collected per site ranged from two to 11 species (5.00 ± 2.07). In the lentic water bodies, we found 232 individuals with the total number of individuals per site ranging from eight to 26 individuals (12.21 ± 6.36). Thirty-four species were sampled in lentic water bodies, and the number of species per site ranged from two to nine species (4.68 ± 2.00).

The lentic water bodies were more than two times deeper ($81.31 \text{ cm} \pm 38.56$) than lotic ecosystems ($36.94 \text{ cm} \pm 25.75$). The mean water temperature was 29.06 ± 2.27 , the mean pH was 5.63 ± 1.02 , and mean conductivity was 20.88 ± 26.28 . Between the vegetation cover we had bare ground ($3.36\% \pm 7.89\%$), the undergrowth cover ($39.29\% \pm 24.23\%$), canopy cover ($40.28\% \pm 37.94$), and macrophyte richness (9.81 ± 5.8). The PCoA conducted with the selected environmental variables (bare ground, canopy cover, undergrowth cover, macrophyte richness, pH, temperature, and conductivity) explained 45.97% of the environmental distance variation in the two first PCoA axes (Supplementary Information – Figure 4). The two water body types tended to present different environmental conditions (Pseudo-F = 3.97; $R^2 = 0.09$; $p < 0.01$). This difference was not explained

by differences in multivariate dispersion of environmental dissimilarity (PERMDISP, Pseudo-F = 0.39; $p = 0.53$).

We found a difference in Odonata species composition among the water body type (PERMANOVA, Pseudo-F = 4.50; $R^2 = 0.10$; $p < 0.01$). Part of this difference is because of differences in multivariate dispersion of species composition dissimilarity (i.e. differences in beta diversity among water body type; PERMDISP, Pseudo-F = 6.03; $p = 0.02$). Lentic water bodies tended to present a higher beta diversity than lotic water bodies (Figure 4). The IndVal indicated that *Epipleoneura spatulatra* ($A = 0.74$; $B = 0.61$; IndVal = 0.67; $p < 0.05$), *Hetaerina sanguinea* ($A = 0.82$; $B = 0.48$; IndVal = 0.63; $p < 0.05$), and *Uracis imbuta* ($A = 1.00$; $B = 0.30$; IndVal = 0.55; $p < 0.05$) were typical species of lotic water bodies. We found that only *Erythemis vesiculosa* ($A = 1.00$; $B = 0.21$; IndVal = 0.46; $p < 0.05$) was a typical species of lentic water bodies (Supplementary Information – Table 3).

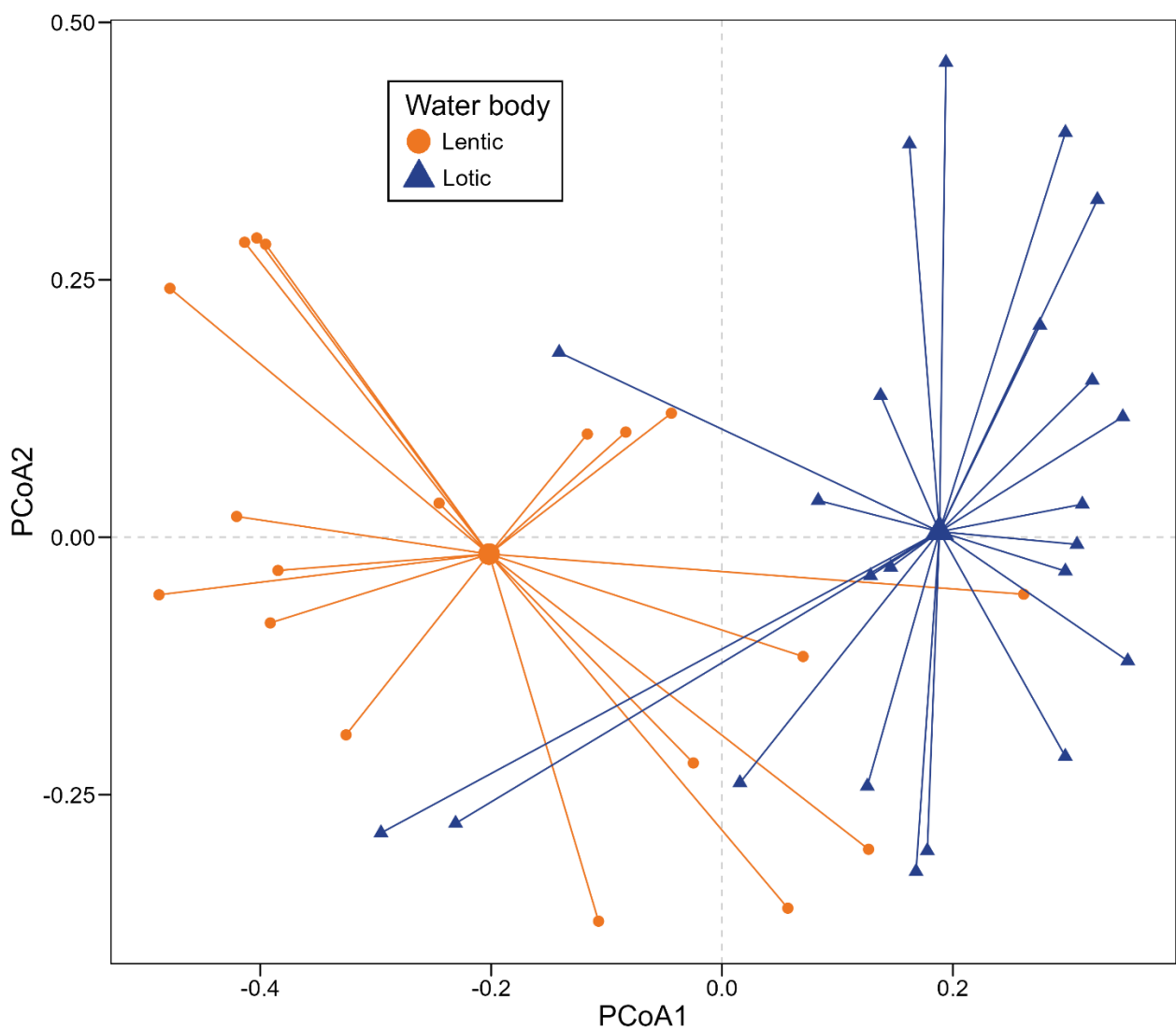


Fig 5 Dragonfly species composition variation in lentic and lotic water bodies sampled in the Área de Proteção Ambiental do Arquipélago do Marajó summarized by Principal Coordinate Analysis (PCoA) with

lentic and lotic water bodies identified by orange circles and blue triangles, respectively. The larger symbols in the middle are the centroids and the smaller symbols are our sampling units

Pairwise total beta diversity values and its components (turnover and nestedness) were different for each water body type. In lentic water bodies, the total beta diversity was greater ($\beta_{\text{sor}} = 0.85 \pm 0.16$) compared to lotics ($\beta_{\text{sor}} = 0.74 \pm 0.18$). For both water bodies, the greater contribution for beta diversity was of turnover component (lentic water bodies, $\beta_{\text{sim}} = 0.80 \pm 0.20$; lotic water bodies, $\beta_{\text{sim}} = 0.65 \pm 0.27$), and a small part of the composition variation was explained by nestedness (lentic water bodies, $\beta_{\text{nes}} = 0.05 \pm 0.07$; lotic water bodies, $\beta_{\text{nes}} = 0.09 \pm 0.13$). When we did not distinguish water body type the total beta diversity was high and mainly because explained by species turnover ($\beta_{\text{sor}} = 0.83 \pm 0.18$; $\beta_{\text{sim}} = 0.77 \pm 0.24$; $\beta_{\text{nes}} = 0.06 \pm 0.10$).

When assessing the relationship between the environment controlling for spatial distance effects across all water bodies, we found a weak but statistically significant effect over total beta diversity and turnover component (Table 4). Similarly, when assessing the effects of spatial distance controlling for distance in environmental variables, we found an effect over both total beta diversity and the turnover component. The nestedness component was not correlated with environmental or spatial distances. When we separated the water body types, we found no effects of either environmental or spatial distances on beta diversity matrices (Table 4).

Table 4 Partial Mantel tests results of the relationship between total dissimilarity (β_{sor}), turnover (β_{sim}), nestedness (β_{nes}) components and environmental distances controlling for spatial distances [$r_{\text{M}}(\text{Env} | \text{Spa})$], and spatial distances controlling for environmental distances effects [$r_{\text{M}}(\text{Spa} | \text{Env})$]. Partial Mantel correlations (r_{M}) statistically significant are in bold ($p < 0.05$)

Data	Response matrix	Environment		Space	
		$r_{\text{M}}(\text{Env} \text{Spa})$	p	$r_{\text{M}}(\text{Spa} \text{Env})$	p
Lotic and lentic waters	β_{sor}	0.13	0.02	0.18	0.01
	β_{sim}	0.14	0.02	0.16	0.01
	β_{nes}	-0.10	0.06	-0.08	0.12
Lotic waters	β_{sor}	0.10	0.17	0.15	0.11
	β_{sim}	0.12	0.13	0.12	0.16
	β_{nes}	-0.11	0.15	-0.03	0.46
Lentic waters	β_{sor}	0.15	0.06	0.22	0.39
	β_{sim}	0.14	0.08	0.04	0.30
	β_{nes}	-0.07	0.29	-0.07	0.22

DISCUSSION

In our study we explored how characteristics (environmental variables and distance between sites) of tropical lentic and lotic water bodies drive dragonflies species distribution, addressing both Hutchinsonian and Wallacean knowledge shortfalls (*sensu* Hortal et al., 2015). These knowledge shortfalls limit the effective conservation of aquatic environments and the arthropods associated (Cardoso et al., 2011; García-Gíron et al., 2023; Nori et al., 2023). According to our prediction i, we found a difference in dragonfly species composition variation when comparing lentic and lotic water bodies. But contrary to our expectations, the average beta diversity was higher in lentic water bodies. Conversely to our predictions ii and iii, we found no effect when we analyzed the influence of the environment and space after separating lentic and lotic water bodies. However, considering the overall metacommunity, we found that the environment and space influence the species composition variation (total beta diversity) and the turnover component.

Lentic and lotic species compositional variation

The distinct specific species composition between contrasting water body types we found is recurrent in the literature for several taxa (macroinvertebrate: Williams et al., 2004; Chironomidae: Specziár et al., 2018; Odonata: Balzan, 2012). The dissimilarity in species composition may occur because of environmental differences resulting in species filtering (Ribera & Vogler, 2000; Leibold et al., 2004; Perez Rocha et al., 2018). Thus, the organisms that manage to reach various habitats and pass through the filter of dispersal limitation may have niche characteristics that enable them to occupy these sites (Hutchinson, 1957; Leibold et al., 2004; Buffagni, 2020). This reasoning is further supported by the different environmental characteristics between the lotic and lentic water bodies in our study.

When analyzing the overall species distribution, few species were classified as typical of a given environment and almost half of the species were found in both water body types indicating that they may be habitat generalists. This pattern of species within an assemblage occurring in both types of water body were also observed for macroinvertebrates (Williams et al., 2004) and Odonata species elsewhere (Balzan et al., 2012). In our study region, the fluvial Marajó island, large rivers and estuaries may act as dispersal barriers, favoring the emergence of habitat generalism of Odonata species occurrence as observed in estuary regions with saline conditions (Balzan, 2012). Also, it would be relevant to include variables that may better describe species specialization, such as morphology and oviposition (e.g. endophytic laying eggs on vegetation tissues, epiphytic laying eggs on surfaces, and exophytic laying eggs directly on the water). These traits could describe species specialization considering its relationship with environmental characteristics (Corbet, 1999; McCauley, 2012; Calvão et al., 2022). Species occurring only in lentic or lotic water bodies

accounted for less than one-third of total dragonfly species, indicating the existence of fewer habitat specialists (open area and forest specialists) (Carvalho et al., 2018; Santos & Rodrigues, 2022). Agreeing with this inference, the IndVal indicated few species typical of lotic water bodies and just one for the lentic. It is important to note that using species distribution alone is a weak descriptor of specialization level, mainly for Odonata which are active dispersers with terrestrial winged insects (Grönroos et al., 2013). Thus, for a refined understanding of species specialization degree, it would be interesting to explore whether dragonfly species inhabit a site using the larvae and adult convergence (McCauley, 2012).

In the lentic water bodies we found a more variable dragonfly species composition (average of total beta diversity) which in part is because of the water bodies variety in this group (lakes, ponds, and flooded areas) (Williams et al., 2004; Specziár et al., 2018). These water bodies are relevant for sustaining dragonfly species diversity by providing habitats for their occupation and maintenance, so they need to be included in the conservation of freshwater ecosystems (Williams et al., 2004; Simaika, Samways & Frenzel, 2016; Biggs et al., 2017; Balázs et al., 2022). In the specific case of the east of APA Marajó, the conservation planning of aquatic ecosystems needs to include different environments to conserve regional biodiversity. This is because the east of Marajó island is converted into a highly connected floodplain in the rainy season allowing species dispersal to different aquatic environments (Williams et al., 2004; Socolar et al., 2016; Borthagaray et al., 2023; Savary, Lessard, Peres-Neto, 2023).

Environmental and space influence on metacommunity

For the overall metacommunity, including lentic and lotic water bodies, the environmental heterogeneity and distance between sites influenced dragonfly species compositional variation (total beta diversity) and the turnover component. The high turnover and low nestedness contributions to beta diversity are frequent patterns and may occur due to environmental variation (Williams et al., 2004; Medeiros et al., 2016; Soininen, Heino & Wang, 2018; Specziár et al., 2018). The influence of environmental and spatial distances indicates that a mass effect is responsible for metacommunity structuring owing to an excess of species dispersal for sub-optimal patches (Leibold et al., 2004; Heino et al., 2015). This result stands out from other similar studies that found environmental and dispersal effects only for streams compared to lakes (Specziár et al., 2018; He et al., 2023). We suggest that the water bodies we sampled are stepping-stone paths for species to find suitable environments because species dispersing from the continent pool first arrive at these sites and may colonize them before continuing dispersal to inner regions from the island (Borthagaray et al., 2023). Thus, these water bodies may serve as paths for dragonfly colonization and contribute to species maintenance in Marajó island.

When we analyzed the influence of environmental and spatial distances separating the data by lentic and lotic water bodies, our results did not support our expectations of an inverse relationship between beta diversity and its components with environmental heterogeneity and the influence of connectivity between sites on turnover and nestedness components. In streams of small drainage basins environmental factors structure metacommunities and spatial factors may prevail when comparing streams from different drainage basins because of dispersal limitation (Grönroos et al., 2013; Heino et al., 2015). In lentic water bodies, the factors influencing metacommunity structure vary between water body types (Heino et al., 2015). Species sorting is important for structuring metacommunities in lakes, whereas in ponds the environmental control is less definite, and we can expect an effect of dispersal limitation in isolated lakes and ponds (Heino et al., 2015). In our case, we may not have found a defined influence of environmental and spatial factors on beta diversity and its components because we included several water body types in the lentic (ponds, lakes, flooded areas) and lotic groups (streams flowing through forests, mangroves, and those under tidal influence), or because water bodies were too close to each other to hinder dispersal or to present substantial environmental differences (Heino et al., 2015; Faustino de Queiroz et al., 2022).

CONCLUSIONS

Our study is one of few attempts to explore and provide information on factors driving species distribution in two distinct water body types in a tropical estuarine region. These water bodies differ in environmental conditions enabling the occupation of a substantial dragonfly biodiversity, providing routes for them to disperse and track suitable sites to colonize, enhancing species success (Borthagaray et al., 2023). In the context of our results, it is important to highlight that to our knowledge we do not have integrative conservation of terrestrial and aquatic environments, which seems the best alternative when planning protected areas (Leal et al., 2020). Thus, considering small water bodies in conservation planning may help to achieve an integrative conservation proposal that benefits both environmental types and better protects regional diversity (Leal et al. 2020; Samways et al. 2020; Borthagaray et al., 2022).

Statements and Declarations

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Conflict of Interest

The authors state that they have no conflict of interest.

Data availability

All data supporting the findings of this study are available within the paper and its Supplementary Information.

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APÊNDICE

Supplementary Information

Tropical freshwater ecosystem type influences dragonfly species distribution in an estuarine island

Hydrobiologia

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Table 1 Environmental variables selected

Water body	Site	Bgrd (%)	Canopy (%)	Undg (%)	Macr	pH	Temp (°C)	Cond (µS)
Lentic	LMC01	0	0	28.57	7	7.5	31.8	164.1
Lentic	LMRN1	0	0	28.57	8	7.57	30.2	55.6
Lentic	LMS01	0	0	50	12	4.91	25.9	11
Lentic	LMS04	13.33	0	53.33	5	5.67	32.8	7.1
Lentic	LMS06	0	44.44	44.44	7	7.37	27.8	18.1
Lentic	MAC01	0	54.55	61.54	9	5.84	26.8	1.8
Lentic	MAC03	0	16.67	37.5	6	5.79	28.6	6.01
Lotic	PMB05	0	53.98	45.68	10	5.24	27.3	8.53
Lotic	PMB06	0	3.64	76.36	0	5.13	27.66	7.6
Lotic	PMB07	0	53.98	45.68	18	5.09	29.23	12.16
Lotic	PMB09	0	15.45	36.59	12	5.35	31.8	10.23
Lotic	PMB10	0	28.52	37.39	15	4.98	27.9	10.5
Lotic	PMB15	0	92.5	11.82	5	5.75	26.53	16.13
Lentic	PMB25	0	0	0	9	6.87	34.2	62.3
Lotic	PMB27	0	93.64	11.82	1	4.92	28.13	14.53
Lentic	PMC09	0	0	44.44	15	5.92	34.6	21.3
Lentic	PMC19	0	16.67	54.55	13	5.25	32.4	11.9
Lentic	PMR12	28.57	50	35.71	19	5.81	34.9	33.6
Lentic	PMR17	0	0	44.44	18	5.21	30.2	18
Lotic	PMRX1	14.66	18.86	11.36	19	6.46	27.4	20.6
Lotic	PMS02	0.45	83.64	53.86	18	4.5	30.03	13.03
Lotic	PMS03	0	60.68	31.14	1	4.89	25.9	24.56
Lotic	PMS10	0	62.05	64.32	10	4.25	26.96	14.36
Lotic	PMS20	0	121.36	124.32	13	5.51	28.6	17.23
Lotic	PMS24	2.27	52.39	2.05	7	6.38	30.4	4.11
Lotic	PMS26	0	85.34	19.55	8	6.15	28.1	18.1
Lotic	PMS28	4.55	9.09	20.57	21	6.48	28	20.6
Lentic	PMS30	22.22	0	22.22	6	5.69	27.3	20.2
Lentic	PMS33	0	37.5	28.57	5	3.43	31.2	18.9
Lotic	PMS34	2.73	1.36	66.48	16	8.73	29.3	18.2
Lentic	PMS36	0	16.67	44.44	9	5.9	28.5	47.3
Lentic	PMS39	0	16.67	54.55	1	4.82	29.9	11.4

Lotic	PMS40	0.23	42.73	10	13	4.62	27.3	16.4
Lotic	PMS42	0	125.45	62.5	7	4.79	27.2	10.86
Lentic	PMS43	0	37.5	50	8	6.44	27.8	44.4
Lentic	PMS44	14.29	0	50	3	6.35	28.3	16
Lotic	PMS46	1.14	64.09	7.27	11	4.65	27.4	2.38
Lotic	PMS47	0	108.18	6.82	9	5.03	28.93	9.3
Lotic	PMS48	3.64	76.02	64.66	13	6.56	29.2	17.5
Lentic	PMS49	0	44.44	58.33	20	4.93	27.4	14
Lotic	PMSN1	32.73	0.23	41.36	0	4.68	28.8	4.28
Lotic	PMSN2	0.45	103.52	7.27	5	5.2	28.01	2.78

***Variable codes:** Brgrd = bare ground; Undg = undergrowth cover; Macr = macrophyte richness; Temp = temperature; Cond = water conductivity

Table 2 Odonata species list from lotic and lentic water bodies in the APA Marajó, Pará

Táxon/autoridade	N	IUCN	SALVE	Water body	
Anisoptera					
Libellulidae					
	318			Lentic	Lotic
<i>Brachymesia herbida</i> (Gundlach, 1889)	8	LC	LC	5	3
<i>Diastatops dimidiata</i> Linnaeus, 1758	3	LC	LC	0	3
<i>Diastatops obscura</i> Fabricius, 1775	4	LC	LC	2	2
<i>Diastatops pullata</i> Burmeister, 1839	1	LC	LC	1	0
<i>Dythemis nigra</i> Martin, 1897 *	1	LC	LC	0	1
<i>Dythemis sterilis</i> Hagen, 1862	2	LC	LC	0	2
<i>Erythemis attala</i> Burmeister, 1839	1	LC	LC	1	0
<i>Erythemis credula</i> Hagen, 1861	3	LC	LC	3	0
<i>Erythemis haematogastra</i> Burmeister, 1839	1	LC	LC	1	0
<i>Erythemis peruviana</i> Rambur, 1842	8	LC	LC	7	1
<i>Erythemis vesiculosa</i> Fabricius, 1775	6	LC	LC	6	0
<i>Erythrodiplax basalis</i> (Kirby, 1897)	41	LC	LC	19	22
<i>Erythrodiplax famula</i> (Erichson, 1848)	17	LC	LC	12	5
<i>Erythrodiplax maculosa</i> (Hagen, 1861)	18	LC	LC	15	3
<i>Erythrodiplax melanica</i> Borrer, 1942	1	LC	LC	0	1
<i>Erythrodiplax umbrata</i> Linnaeus, 1758	29	LC	LC	28	1
<i>Miathyria marcella</i> Selys in Sagra, 1858	40	LC	LC	38	2

<i>Micrathyria eximia</i> Kirby, 1897	8	LC	LC	8	0
<i>Micrathyria pseudeximia</i> Westfall, 1992	2	LC	LC	2	0
<i>Micrathyria tibialis</i> Kirby, 1897	6	LC	LC	6	0
<i>Nephepeltia phryne</i> (Perty, 1834)	1	LC	LC	1	0
<i>Oligoclada abbreviata</i> (Rambur, 1842)	2	LC	LC	0	2
<i>Oligoclada walkeri</i> Geijskes, 1931	2	LC	LC	1	1
<i>Orthemis concolor</i> (Kirby, 1897)	3	LC	LC	0	3
<i>Orthemis discolor</i> (Burmeister, 1839)	7	LC	LC	4	3
<i>Orthemis sulphurata</i> Hagen, 1868	2	LC	-	1	1
<i>Pantala flavescens</i> Fabricius, 1798	2	LC	LC	2	0
<i>Perithemis lais</i> (Perty, 1834)	47	LC	LC	18	29
<i>Planiplax phoenicura</i> Ris, 1912	3	LC	LC	3	0
<i>Tauriphila argo</i> Hagen, 1869 *	1	LC	LC	1	0
<i>Uracis imbuta</i> Burmeister, 1839	21	LC	LC	0	21
<i>Zenithoptera anceps</i> Pujol-Luz, 1993	17	LC	LC	14	3
<i>Zenithoptera viola</i> Ris, 1910	9	LC	LC	8	1
Aeshnidae	1				
<i>Staurophlebia reticulata</i> Burmeister, 1839	1	LC	LC	0	1
Corduliidae	1				
<i>Aeschnosoma elegans</i> Selys, 1870	1	DD	LC	0	1
Zygoptera					
Calopterygidae	42				
<i>Hetaerina laesa</i> Hagen in Selys, 1853	1	LC	LC	0	1
<i>Hetaerina sanguinea</i> Selys, 1853 *	41	LC	LC	6	35
Coenagrionidae	228				
<i>Acanthagrion adustum</i> Williamson, 1916	37	LC	LC	10	27
<i>Acanthagrion gracile</i> (Rambur, 1842)	5	LC	LC	5	1
<i>Acanthagrion kennedii</i> Williamson, 1916	30	LC	LC	14	16
<i>Argia</i> sp. Rambur, 1842	2	LC	LC	2	0
<i>Epipleoneura metallica</i> Rácenis, 1955	13	LC	LC	0	13
<i>Epipleoneura spatulata</i> Rácenis, 1960	88	LC	LC	20	68
<i>Ischnura capreolus</i> (Hagen, 1861)	8	LC	LC	7	1
<i>Ischnura fluviatilis</i> Selys, 1876	1	LC	LC	1	0
<i>Metaleptobasis bicornis</i> (Selys, 1877)	4	DD	LC	0	4
<i>Neoneura bilinearis</i> Selys, 1860	13	LC	LC	0	13

Neoneura confundens Wasscher & van't Bosch,

2013	5	LC	LC	0	5
<i>Phoenicagrion flammeum</i> (Selys, 1876)	10	LC	LC	0	10
<i>Telebasis carminita</i> Calvert, 1909 *	12	LC	LC	12	0

Perilestidae **3**

Perilestes solutus Williamson & Williamson,

1924	3	LC	LC	0	3
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*Represents the first record of the species in Pará state. LC = Least concern; DD = data deficient.

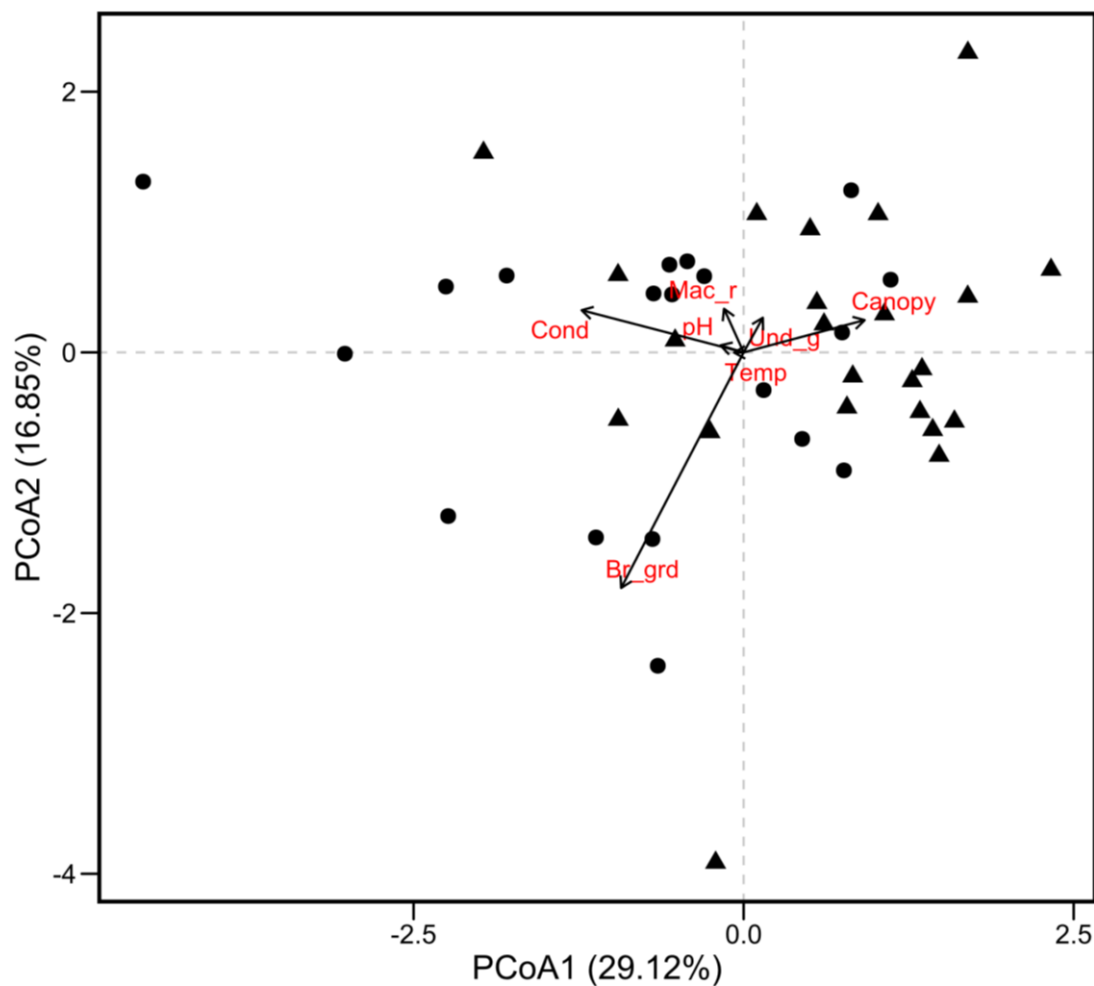


Fig 4 Ordination of lentic (circle) and lotic (triangle) water bodies by a Principal Coordinate Analysis (PCoA) conducted with environmental variables in red (Br grd = bare ground; Undg = undergrowth cover; Mac r = macrophyte richness; Temp = temperature; Cond = water conductivity)

Table 3 Species typical of lotic and lentic water bodies indicated by the Indicator Value analysis (IndVal). A = specificity; B = sensitivity. P-values < 0.05 indicate IndVal values different from those expected by chance (values in bold)

Water body type	Species	A	B	IndVal	P
Lentic	<i>Miathyria marcella</i>	0.78	0.32	0.50	0.12
	<i>Brachymesia herbida</i>	0.86	0.26	0.48	0.07
	<i>Erythrodiplax umbrata</i>	0.86	0.26	0.48	0.07
	<i>Ischnura capreolus</i>	0.86	0.26	0.48	0.08
	<i>Erythemis vesiculosa</i>	1.00	0.21	0.46	0.03
	<i>Erythemis peruviana</i>	0.83	0.21	0.42	0.16
	<i>Argia sp</i>	1.00	0.11	0.32	0.20
	<i>Micrathyria eximia</i>	1.00	0.11	0.32	0.20
	<i>Planiplax phoenicura</i>	1.00	0.11	0.32	0.20
	<i>Orthemis discolor</i>	0.71	0.11	0.27	0.58
	<i>Zenithoptera anceps</i>	0.71	0.11	0.27	0.58
	<i>Zenithoptera viola</i>	0.71	0.11	0.27	0.58
	<i>Diastatops pullata</i>	1.00	0.05	0.23	0.45
	<i>Erythemis attala</i>	1.00	0.05	0.23	0.45
	<i>Erythemis credula</i>	1.00	0.05	0.23	0.45
	<i>Erythemis haematogastra</i>	1.00	0.05	0.23	0.46
	<i>Ischnura fluviatilis</i>	1.00	0.05	0.23	0.45
	<i>Micrathyria pseudeximia</i>	1.00	0.05	0.23	0.45
	<i>Micrathyria tibialis</i>	1.00	0.05	0.23	0.45
	<i>Nephepeltia phryne</i>	1.00	0.05	0.23	0.45
<i>Pantala flavescens</i>	1.00	0.05	0.23	0.45	
<i>Tauriphila argo</i>	1.00	0.05	0.23	0.46	
<i>Telebasis carminita</i>	1.00	0.05	0.23	0.45	
Lotic	<i>Epipleoneura spatulata</i>	0.74	0.61	0.67	0.02
	<i>Hetaerina sanguinea</i>	0.82	0.48	0.63	0.02
	<i>Uracis imbuta</i>	1.00	0.30	0.55	0.01
	<i>Epipleoneura metallica</i>	1.00	0.17	0.42	0.11
	<i>Neoneura bilinearis</i>	1.00	0.17	0.42	0.12
	<i>Neoneura confundens</i>	1.00	0.13	0.36	0.24
	<i>Phoenicagrion flammeum</i>	1.00	0.13	0.36	0.24

<i>Diastatops dimidiata</i>	1.00	0.09	0.30	0.49
<i>Diastatops obscura</i>	1.00	0.09	0.30	0.50
<i>Metaleptobasis bicornis</i>	1.00	0.09	0.30	0.48
<i>Oligoclada abbreviata</i>	1.00	0.09	0.30	0.49
<i>Orthemis concolor</i>	1.00	0.09	0.30	0.50
<i>Perilestes solutus</i>	1.00	0.09	0.30	0.49
<i>Aeschnosoma elegans</i>	1.00	0.04	0.21	1.00
<i>Dythemis nigra</i>	1.00	0.04	0.21	1.00
<i>Dythemis sterilis</i>	1.00	0.04	0.21	1.00
<i>Erythrodiplax melanica</i>	1.00	0.04	0.21	1.00
<i>Hetaerina laesa</i>	1.00	0.04	0.21	1.00
<i>Staurophlebia reticulata</i>	1.00	0.04	0.21	1.00
