

Article

Odonata Species and Their Beta Diversity Patterns in Freshwater Habitats in an Atlantic Forest of Northeast Brazil

Antonio B. S. Farias ¹, Henrique Venâncio ¹, Thiago C. Gomes ¹, Kim R. Barão ², Diogo S. Vilela ³
and Jean C. Santos ^{4,*}

¹ Programa de Pós-Graduação em Ecologia e Conservação, Universidade Federal de Sergipe, São Cristóvão 49107-230, Sergipe, Brazil; antoniobrunofarias@gmail.com (A.B.S.F.); henrivens@gmail.com (H.V.); thiagonsj@gmail.com (T.C.G.)

² Laboratório de Sistemática e Diversidade de Artrópodes, Unidade Educacional Penedo, Campus Arapiraca, Universidade Federal de Alagoas, Penedo 57200-000, Alagoas, Brazil; kim.barao@penedo.ufal.br

³ Laboratory of Aquatic Insect Systematics, Federal University of Triângulo Mineiro, Uberaba 38064-200, Minas Gerais, Brazil; deeogoo@gmail.com

⁴ Departamento de Ecologia, Universidade Federal de Sergipe, São Cristóvão 49107-230, Sergipe, Brazil

* Correspondence: jcsantosbio@gmail.com

Abstract

The Atlantic Forest has undergone significant territorial reduction due to anthropogenic activities, adversely affecting its biodiversity. Consequently, it is imperative to identify the species constituting this megadiverse ecosystem, focusing on local diversity and, on a broader scale, regional diversity (beta diversity). This study inventories Odonata species and analyzes beta diversity patterns in the Atlantic Forest of Sergipe, northeastern Brazil. Sampling across the seven sites yielded 1468 specimens representing 66 species, including 14 new state records. Species richness did not differ significantly between lentic and lotic habitats; however, community composition varied markedly, primarily due to species turnover. Anisoptera were more abundant and diverse in lentic habitats, whereas Zygoptera preferred lotic environments with well-preserved riparian vegetation. High beta diversity at regional and local scales reflects strong environmental heterogeneity, with spatial and habitat factors shaping community structure. This study highlights the ecological distinctions between the two suborders, which are linked to their dispersal abilities and habitat specialisation. These findings emphasise the importance of conserving diverse aquatic habitats and riparian vegetation to maintain Odonata diversity, thereby supporting their role as bioindicators. This study fills a critical knowledge gap in northeastern Brazil and provides baseline data to guide conservation and management strategies in this threatened biome.

Keywords: Anisoptera; aquatic insects; lentic; lotic; Zygoptera



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1. Introduction

One of the primary goals of ecology is to characterise biological diversity by understanding the patterns of species abundance and distribution across space and time [1]. Species diversity can be assessed at different spatial scales, among which three are widely recognised: (a) alpha (α) diversity, or local diversity, defined as the number of species within a given site; (b) beta (β) diversity, which measures variation in species composition among communities along environmental or spatial gradients; and (c) gamma (γ) diversity, or regional diversity, representing the total number of species recorded across all sampled

habitats [2]. These metrics provide insights into the mechanisms and processes underlying community assembly and ecosystem structure, thereby improving our understanding and monitoring of biotic changes driven by natural and anthropogenic processes in terrestrial and aquatic ecosystems [3,4].

Despite recent advances in tropical community ecology, the current understanding of insect diversity patterns remains limited, largely because of the greater research focus on vertebrates [5]. This knowledge gap is partly attributed to taxonomic impediments [6,7] and incomplete species distribution data, which hinder the understanding of global biodiversity patterns and reinforce the view that tropical insects are underrepresented in conservation biology [8,9]. Insects occupy a wide range of habitats and perform essential ecological functions, including herbivory, predation, pollination, secondary seed dispersal, nutrient cycling, bioturbation, and biological control, making them fundamental to ecosystem structure and functions [10]. Consequently, they have considerable potential for use in biodiversity monitoring programs and as bioindicators of environmental quality [7]. Taxonomic groups such as the orders Coleoptera, Lepidoptera, Orthoptera, Isoptera, Hemiptera, Trichoptera, Plecoptera, and Ephemeroptera are widely used as bioindicators because of their high sensitivity to habitat degradation [7,11].

Odonata have also received increasing attention over recent decades as reliable indicators of biological integrity [7,12–16] owing to their key roles in maintaining ecosystem structure and nutrient cycling in freshwater habitats [17]. Odonates live in aquatic environments during their larval stage, making them highly sensitive to water quality changes [18,19]. In contrast, adults are strongly influenced by the riparian vegetation [20]. Moreover, the two suborders occurring in Brazil, Zygoptera and Anisoptera, differ markedly in their ecological requirements and responses to environmental disturbance owing to differences in habitat sensitivity [21–24]. Zygopteran larvae are generally less tolerant of water quality degradation, whereas adults are small-bodied, rely on riparian vegetation for perching, and exhibit limited dispersal ability. Consequently, they are primarily influenced by local environmental factors, such as physicochemical water conditions, vegetation cover, and habitat connectivity, making them more habitat-specialised [25]. In contrast, anisopteran larvae are more tolerant of environmental disturbances, and adults are medium- to large-bodied with greater dispersal ability, allowing them to exploit a wider range of habitats and making them more generalist [22]. Accordingly, anisopteran diversity is more strongly shaped by regional drivers, including climatic conditions and landscape heterogeneity [26]. Therefore, Anisoptera are expected to exhibit greater diversity in human-impacted environments and across broader spatial gradients, whereas well-preserved habitats are expected to support a higher diversity of Zygoptera [21,23].

Dragonflies and damselflies [Anisoptera and Zygoptera] (Insecta: Odonata) comprise 6496 species, 600 genera, and 39 families worldwide [27] and primarily inhabit freshwater ecosystems [28]. They are distributed across all continents except Antarctica [29,30]. The Neotropical region harbours approximately 1800 Odonata species [29]. In Brazil, the fauna comprises an estimated 910 species and 152 genera [31], including four families of anisopterans and 11 families of zygopterans [32].

Knowledge of Brazilian odonate fauna has increased substantially in recent years [33–35]. However, this knowledge remains unevenly distributed across the country's regions, likely reflecting the geographical distribution of research groups. Most studies have been conducted in the southeast, north, and central-western regions of Brazil [33]. In contrast, northeastern Brazil has a major knowledge gap regarding species richness, abundance, and distribution [34], accounting for only 9.2% of the country's Odonata scientific output [33]. Most of the available information for this region has been derived from sporadic sampling [36]. Notable studies from northeastern Brazil include Takiya et al. [37], who

investigated aquatic insect diversity in the Caatinga of two National Parks in the states of Ceará and Piauí; Santos et al. [38], who produced a rapid checklist of Odonata for the state of Sergipe; Vilela et al. [39,40], who described two new species from the northeastern Atlantic Forest; Koroiva et al. [34], who published the first checklist of dragonflies and damselflies for the state of Paraíba; and Ribeiro et al. [41,42], who compiled a checklist for the state of Bahia and evaluated both Odonata suborders as indicators of ecological change in Atlantic Forest streams. A similar pattern of knowledge asymmetry was observed in the Brazilian biomes. Most studies have focused on the Amazon, Cerrado, and Atlantic Forest, with research in the latter biome concentrated primarily in the South, Southeast, and Central-Western regions [43–50]. Despite recent advances, northeastern Brazil remains a major knowledge gap for several taxonomic groups, including odonates.

In light of the above, the objectives of this study were to (a) inventory the dragonfly and damselfly fauna and (b) analyse regional-scale variation in species distribution across the Atlantic Forest of the state of Sergipe, northeastern Brazil. This study aimed to provide baseline information on the diversity of Odonata in the northeastern Atlantic Forest and to support habitat management and conservation strategies in Sergipe. Specifically, we addressed the following questions: (a) Which Odonata species occur in the Atlantic Forest of Sergipe? (b) Are the differences in species composition among Odonata communities primarily driven by nestedness or species turnover? We tested the hypothesis that species turnover is the main mechanism explaining differences in Odonata community composition among sampling sites, between suborders (Zygoptera vs. Anisoptera), and between lotic and lentic habitats.

2. Materials and Methods

2.1. Study Area

In the state of Sergipe, the Atlantic Forest is distributed along the coastal zone and the coastal tablelands. Until 1990, the Atlantic Forest was estimated to cover approximately 41% of the state's territory [51,52]. However, extensive deforestation has reduced this cover to approximately 9% of its original extent, with the remaining forest fragments forming a strip approximately 40 km wide [52]. Several of these remnants are currently protected or are undergoing legal protection, including Serra de Itabaiana National Park, Mata do Junco Wildlife Refuge, Ibura National Forest, Santa Isabel Biological Reserve, Morro do Urubu Environmental Protection Area, South Coast Environmental Protection Area, North Coast Environmental Protection Area, and several smaller protected areas.

We selected seven sampling areas in the Atlantic Forest of Sergipe. Areas were selected based on accessibility, geographical location, water body availability, habitat diversity, and conservation importance. The main characteristics of each area are as follows.

2.1.1. Federal University of Sergipe–São Cristóvão (FUS)

The campus is located in the metropolitan region of Aracaju. Its semideciduous seasonal forest fragment covers approximately 21 ha and borders the Poxim River. The fragment is under strong anthropogenic pressure owing to urbanization and inappropriate waste disposal. The sampling point was located adjacent to a flooded area within a forest fragment (Table 1; Figure 1).

Table 1. Detailed information on the sampling areas. A—open area; B—closed area with canopy cover; C—waterfall; D—stream; E—pool; F—lentic habitat; G—lotic habitat; H—shaded environment; I—high solar incidence environment; J—small open patches with low solar incidence; K—mixed environment with both open and closed areas, partially shaded; L—anthropogenic influence; M—water abstraction system; N—flooded/wetland area; O—lake/pond; P—dam; Q—spring; R—mangrove proximity).

Sampling Area/Point	Coordinates		Sampling Date	Area	Environmental Description
Federal University of Sergipe					
P1LE	10°55'23.28" S	37°5'57.53" W	01/XII/2020	Urban	A, F, H, K, L, N
Ibura National Forest					
P2LE	10°50'35.01" S	37°8'23.61" W	02/XII/2020	Rural	A, E, F, I, L
Federal Institute of Sergipe					
P3LO	10°55'11.45" S	37°11'10.61" W	03/XII/2020	Rural	B, D, G, H
P4LO	10°55'6.03" S	37°12'15.85" W	03/XII/2020	Rural	A, D, G, I, L, P
P5LE	10°54'39.49" S	37°11'11.25" W	03/XII/2020	Rural	A, F, I, L, N, O
Crasto's Forest					
P6LE	11°22'34.18" S	37°25'9.52" W	04/XII/2020	Rural	A, F, I, L, M, O
P7LE	11°22'39.36" S	37°25'23.09" W	04/XII/2020	Rural	A, F, I, N, O, R
P8LE	11°23'24.95" S	37°24'45.16" W	04/XII/2020	Rural	A, F, I, N, O
P9LE	11°22'8.25" S	37°26'3.50" W	27/I/2021	Rural	A, F, I, N, Q
P10LE	11°22'26.40" S	37°26'2.40" W	27/I/2021	Rural	A, F, I, N, Q
P11LE	11°24'7.22" S	37°25'33.59" W	27/I/2021	Rural	A, F, I, N
P12LE	11°23'39.15" S	37°25'14.60" W	27/I/2021	Rural	A, F, I, N
P13LE	11°21'4.00" S	37°24'10.27" W	28/I/2021	Rural	A, F, I, N, R
P14LE	11°21'46.71" S	37°24'13.64" W	28/I/2021	Rural	A, F, I, N, R
P15LE	11°22'31.92" S	37°25'4.34" W	28/I/2021	Rural	A, F, I, L, M, O
P16LE	11°22'28.21" S	37°25'29.45" W	28/I/2021	Rural	A, F, I, N, O, R
Falcon Park					
P17LE	10°44'50.18" S	37°22'38.99" W	13/XII/2020	Preserved	A, E, F, I, L, O
P18LO	10°44'41.26" S	37°22'39.30" W	13/XII/2020	Preserved	B, D, G, H
Mata do Junco Wildlife Refuge					
P19LE	10°31'54.57" S	37° 3'7.65" W	14/XII/2020	Preserved	A, D, E, F, I, L, M,
P20LO	10°31'53.30" S	37° 3'10.32" W	14/XII/2020	Preserved	B, D, G, H, N
P21LO	10°32'33.72" S	37° 3'4.64" W	14/XII/2020	Preserved	B, D, G, H, J, N
P22LO	10°32'16.49" S	37° 3'32.33" W	14/XII/2020	Preserved	B, D, G, H
Serra de Itabaiana National Park					
P23LO	10°44'49.58" S	37°20'31.33" W	25/I/2021	Preserved	A, C, D, E, F, G, L
P24LO	10°44'55.03" S	37°20'20.67" W	25/I/2021	Preserved	B, D, E, F, G, H
P25LO	10°44'48.12" S	37°20'37.31" W	25/I/2021	Preserved	B, D, E, F, G, H, L
P26LO	10°45'20.48" S	37°22'6.17" W	26/I/2021	Preserved	A, E, F, I
P27LO	10°45'28.33" S	37°22'6.70" W	26/I/2021	Preserved	B, D, E, F, G, H
P28LO	10°45'20.42" S	37°20'21.43" W	26/I/2021	Preserved	B, D, E, F, G, H, J
P29LO	10°45'14.68" S	37°20'40.63" W	26/I/2021	Preserved	B, D, E, F, G, H
P30LO	10°44'51.87" S	37°20'25.16" W	01/I/2021	Preserved	D, E, F, G, K
P31LO	10°45'17.80" S	37°19'49.28" W	01/I/2021	Preserved	B, D, E, F, G, H
P32LO	10°45'21.32" S	37°19'41.82" W	01/II/2021	Preserved	B, D, E, F, G, H
P33LO	10°43'57.26" S	37°20'2.52" W	01/II/2021	Preserved	B, D, E, F, G, H, L, M
P34LO	10°44'1.79" S	37°19'48.56" W	01/II/2021	Preserved	B, D, E, F, G, H, L, M
P35LO	10°44'30.74" S	37°19'53.53" W	02/II/2021	Preserved	B, C, D, E, F, G, H, L
P36LO	10°44'22.76" S	37°19'55.04" W	02/II/2021	Preserved	B, C, D, E, F, G, H, L
P37LO	10°44'35.36" S	37°19'24.67" W	02/II/2021	Preserved	A, C, D, E, F, G, I, L, P
P38LO	10°44'43.97" S	37°19'37.21" W	02/II/2021	Preserved	B, D, E, F, G, H, L
P39LO	10°45'51.67" S	37°20'9.93" W	03/II/2021	Preserved	B, D, E, F, G, H, L

Table 1. Cont.

Sampling Area/Point	Coordinates		Sampling Date	Area	Environmental Description
P40LO	10°45'58.66" S	37°20'31.39" W	03/II/2021	Preserved	B, D, E, F, G, H, L
P41LO	10°44'49.79" S	37°20'30.92" W	07/XII/2020	Preserved	A, C, D, E, F, G, L
P42LO	10°44'48.56" S	37°20'33.06" W	07/XII/2020	Preserved	B, D, E, F, G, H
P43LO	10°45'15.98" S	37°20'31.82" W	07/XII/2020	Preserved	B, D, E, F, G, H
P44LO	10°46'0.78" S	37°20'22.22" W	07/XII/2020	Preserved	C, D, E, F, G, J, K
P45LO	10°44'51.28" S	37°20'27.41" W	13/XII/2020	Preserved	B, D, E, F, G, H, L

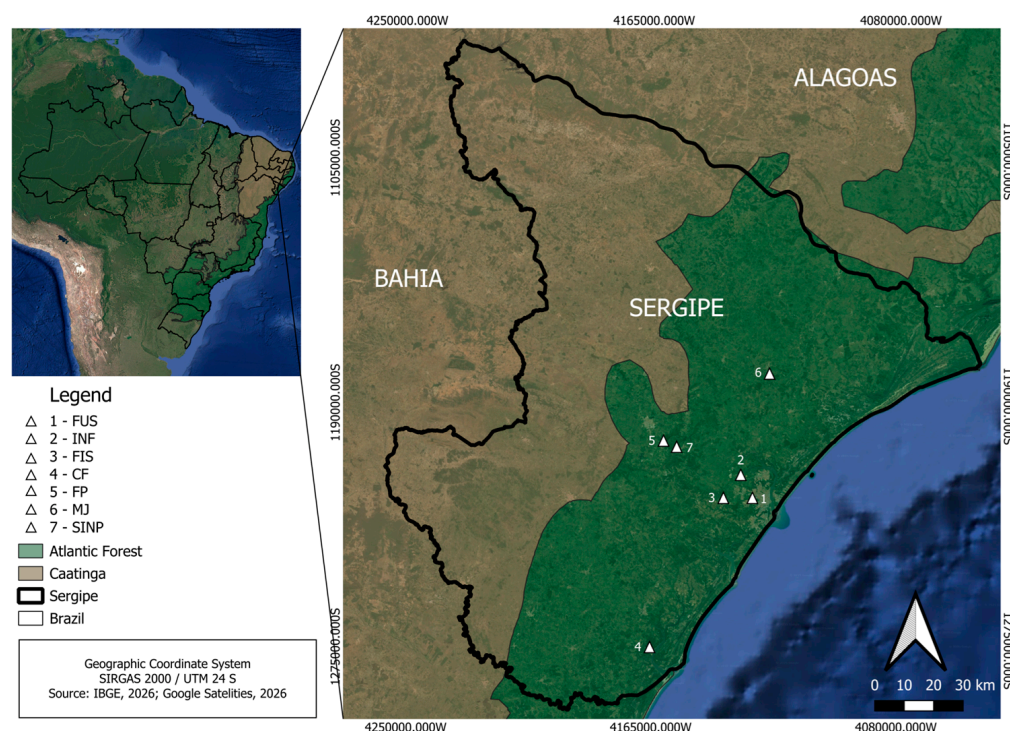


Figure 1. Odonate sampling areas (Odonata) in Sergipe, Brazil. (FUS—Federal University of Sergipe; INF—Ibura National Forest; FIS—Federal Institute of Sergipe; CF—Crasto’s Forest; FP—Falcons Park; MJ—Mata do Junco Wildlife Refuge; SINP—Serra de Itabaiana National Park). Detailed information on the sampling points is presented in Table 1.

2.1.2. Ibura National Forest (INF)

This Atlantic Forest remnant covers approximately 144.17 ha and consists of a semideciduous seasonal forest associated with mangrove vegetation. It is located in the municipality of Nossa Senhora do Socorro, over the Sapucari aquifer, and borders the mangrove areas and the Cotinguiba River to the north. Sampling was conducted in lentic habitats, including an artificial pond and a shallow water channel (Table 1; Figure 1).

2.1.3. Federal Institute of Sergipe—São Cristóvão (FIS)

Located in the metropolitan region of Aracaju, the campus is crossed by the Poxim River and borders the Poxim Reservoir. The Atlantic Forest remnants comprise approximately 400 ha of semideciduous seasonal forest at different successional stages. Three lotic sampling points were established: one with low anthropogenic disturbance, one adjacent to the reservoir dam with moderate disturbance, and one highly eutrophic site (Table 1; Figures 1 and 2A,B).

2.1.4. Crasto's Forest (CF)

Crasto's Forest is the largest and one of the most important Atlantic Forest remnants in the state of Sergipe. It is located within the South Coast Environmental Protection Area in the Crasto district of Santa Luzia do Itanhý, approximately 76 km from Aracaju. This ombrophilous forest remnant covers approximately 1000 ha and borders the Piauí River. Because the area is predominantly rural, extensive conversion to pastureland and highly eutrophic water bodies have been observed. Most of the sampling points were located in lentic habitats, predominantly associated with Juncaceae vegetation (Table 1; Figures 1 and 2G,H).

2.1.5. Falcons Park (FP)

This private reserve is located in the Gandu II district of Itabaiana, approximately 45 km from the city of Aracaju. The vegetation is characterized as a semideciduous forest. The first sampling point consisted of a small artificial pond used for duck farming, whereas the second was a stream connected to the Taboca River [53]. Signs of anthropogenic disturbance, including fencing and litter, were present but were relatively limited (Table 1; Figure 1).

2.1.6. Mata do Junco Wildlife Refuge (MJ)

This protected area is the second largest remnant of the Atlantic Forest in Sergipe, encompassing approximately 894.76 ha of semideciduous seasonal forest. It is located in the municipality of Capela, approximately 67 km from the city of Aracaju. The reserve contains 14 recorded springs that form the Lagartixo River, a tributary of the Japarutuba River Basin. The area is characterized by abundant bamboo forests. One sampling point was located at the municipal water intake, whereas the remaining three were established in lotic habitats with well-preserved riparian vegetation (Table 1; Figure 1).

2.1.7. Serra de Itabaiana National Park (SINP)

The park comprises three mountain ranges (Serra de Itabaiana, Serra Comprida, and Serra do Cajueiro) and covers approximately 7966 ha across the municipalities of Areia Branca, Itabaiana, Laranjeiras, Itaporanga d'Ajuda, and Campo do Brito in Sergipe [54,55]. It is one of the state's most important protected areas, encompassing both the Atlantic Forest and Caatinga biomes [54,55]. All sampling points were located in lotic habitats (Coqueiros, Água Fria, Negros, and Vermelho streams) with riparian vegetation cover. Signs of anthropogenic disturbance were observed in some streams, mainly because of litter associated with tourism and recreational activities (Table 1; Figure 2C–F).

Each sampling point was surveyed only once, resulting in a total sampling effort of 90 h, distributed among the study areas according to the number of sampling points within each area. The sampling effort totalled 2 h at FUS and INF, 4 h at PF, 6 h at FIS, 8 h at MJ, 22 h at MC, and 46 h at SINP. Nevertheless, we consider the sampling effort to have been standardized, as it was proportional to the size of each study area, accessibility, and the availability of aquatic habitats and water bodies.

2.2. Odonates Sampling

Sampling was conducted on sunny days between 07:00 and 17:00 h, conditions under which species are expected to be actively foraging and exhibiting full activity regardless of the functional group [56]. This sampling approach has been widely applied in previous studies in the region (for example, refs. [35,57]). Only adult individuals were sampled using entomological nets by two collectors for one hour along a 100 m transect bordering lakes, streams, and rivers ranging from first- to fourth-order systems (adapted from [35,56,57]).

All Odonata sampling was conducted between December 2020 and February 2021, corresponding to the dry season in the region. The collected specimens were stored in paper envelopes and transported to the Laboratory of Ecology and Biodiversity (LEBIO). Subsequently, specimens were preserved in pure acetone [58], which promotes lipid dissolution and improves the long-term preservation of body structures and colour patterns. Specimens were identified to the lowest possible taxonomic level by Prof. Dr. Vilela, D. S., one of the study's authors. All specimens are deposited in the Odonatological Collection of the Laboratory of Ecology and Biodiversity (COLEBIO), Department of Ecology, Federal University of Sergipe, São Cristóvão, Sergipe, Brazil, except for two specimens of *Heteragrion lencionii* Vilela, Farias & Santos, 2021, which are deposited in the Frederico A. A. Lencioni Collection (FAAL), Jacareí, São Paulo, Brazil.

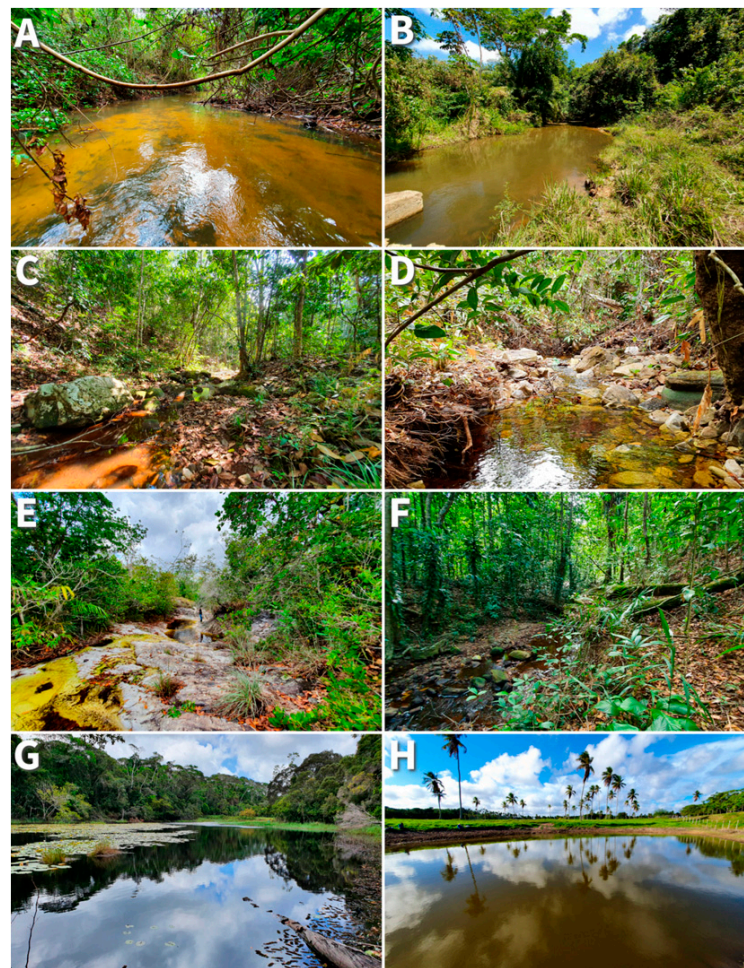


Figure 2. Sampling points in the Atlantic Forest of Sergipe, Brazil. ((A)—FIS; (B)—FIS; (C)—SINP; (D)—SINP; (E)—SINP; (F)—SINP; (G)—CF; (H)—CF). Photos: Farias, A.B.S. (2021).

2.3. Statistical Analyses

2.3.1. Spatial Autocorrelation and Sampling Sufficiency

Spatial autocorrelation was assessed using a Mantel test, correlating a geographic distance matrix (based on geodesic distances) with a Bray–Curtis dissimilarity matrix derived from the Hellinger-transformed abundance data. The results indicated a positive correlation between geographic distance and community dissimilarity ($r = 0.595$, $p = 0.001$), suggesting strong spatial structuring among the sampling points. Additionally, a Minimum Spanning Tree (MST) was constructed to represent spatial connectivity among sampling points, from which neighbourhood structures were derived and used to extract Moran's

Eigenvector Maps (MEMs). The importance of spatial components was evaluated using Redundancy Analysis (RDA), which identified two significant axes (RDA1: $p = 0.001$; RDA2: $p = 0.006$). Forward selection identified six significant MEM variables, indicating a substantial contribution of spatial processes to the community structure. Significant MEMs were included as covariates in a distance-based RDA (dbRDA) following [59], and the effect of habitat was tested. Variance partitioning was performed using ANOVA to assess the pure effects of habitat ($F_{df} = 1 = 2.2395$, $p = 0.001$) and space ($F_{df} = 11 = 1.9441$, $p = 0.001$). The spatial autocorrelation of the model residuals was subsequently evaluated using a Mantel test, which showed no significant pattern ($r = 0.274$, $p = 0.23$).

2.3.2. Species Richness and Composition in Lentic and Lotic Habitats

To estimate species richness and evaluate sampling effort efficiency, interpolation and extrapolation curves were constructed for all the sampled areas/points. The curves (Hill number $q = 0$) were based on species abundance, and 95% confidence intervals were obtained using 1000 bootstrap replicates [60,61], with extrapolation projected to twice the observed sample size [60]. In addition, species abundance distributions were plotted to visually compare patterns of species dominance for the overall assemblage, for each suborder separately, and between lotic and lentic habitats.

Species richness in lentic and lotic habitats was compared using Student's t -test for independent samples. Data normality ($W = 0.9656$, $p = 0.2003$) and homogeneity of variance ($F_{2,43} = 0.3743$, $p = 0.5439$) were assessed using the Shapiro–Wilk and Levene tests, respectively. A permutational multivariate analysis of variance (PERMANOVA) was conducted to compare the Odonata community composition between lotic and lentic habitats. Significant MEMs were included as covariates to disentangle variation driven by habitat and spatial structure (Supplementary Table S1). Results were visualized using non-metric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarity matrices computed from species abundance data (Supplementary Figure S1). The homogeneity of multivariate dispersion was assessed using a multivariate dispersion analysis (BETADISPER), following Anderson and Walsh [62].

2.3.3. Beta Diversity

The beta diversity approach used in this study was based on quantitative species abundance data using the Chao index, which measures the differences in species composition among sampling points. This index is considered robust because it is independent of species richness [63]. The Sørensen dissimilarity index, based on incidence data, was also used. This framework allows beta diversity to be partitioned into turnover and nestedness components. Total beta diversity ($\beta_{s\text{or}}$) was calculated based on species abundance, ranging from 0 to 1, where values closer to 1 indicate higher beta diversity among the sampling units. Partitioning of beta diversity yielded two components: (i) species turnover (β_{sim}), measured using the Simpson index, representing species replacement among sites driven by environmental filtering, life-history traits, dispersal barriers, and biotic interactions [64]; and (ii) nestedness (β_{nes}), which reflects situations in which species assemblages in a given site represent subsets of richer communities. Thus, the total beta diversity is expressed as $\beta_{s\text{or}} = \beta_{\text{sim}} + \beta_{\text{nes}}$. Total beta diversity was calculated across all sampling sites and within habitat types (lentic vs. lotic) [64–66], as well as separately for the two suborders (Anisoptera and Zygoptera). The proportional contributions of turnover and nestedness ($\beta_{\text{sim}}/\beta_{\text{nes}}$) followed Baselga and Orme [66].

To obtain Local Contribution to Beta Diversity–LCBD and Species Contribution to Beta Diversity–SCBD (taxonomic) values, we used the `beta.div` function from the `adespatial` package [67] on a Hellinger-transformed abundance matrix, which computes the total

beta diversity based on the total variance of the community matrix. This value was then partitioned into local contributions as the sum of squares for each sampling unit divided by the total sum of squares of the community matrix. Species contributions were calculated as the sum of squares for each species divided by the total sum of squares of the community matrix [68]. The significance of the LCBD values was assessed using 9999 permutations.

Beta diversity analyses were performed in R (software) version 4.3.3 [69] using the vegan [70] and betapart [71] packages.

3. Results

3.1. Odonate Species Inventory

A total of 1468 specimens belonging to the suborders Anisoptera and Zygoptera were sampled, distributed across eight families, 32 genera, and 66 species (γ diversity), with each sampling site exhibiting a mean of 6.6 species (α diversity). This study recorded 14 new species in the state of Sergipe (Table 2). The rarefaction curve for all sampling points in Sergipe showed no indication of stabilization, suggesting that additional sampling effort may yield further Odonata species (66 observed spp. vs. 92 estimated spp.) (Figure 3A). Estimated richness was 59 spp. for lentic habitats, 67 spp. for lotic habitats, and 64 spp. and 28 spp. for the suborders Anisoptera and Zygoptera, respectively (Figure 3A). Sampling coverage indicated that only Anisoptera may still yield additional species with increased sampling effort, whereas for the other groups, further effort is unlikely to result in new records (Figure 3B). Species richness per sampling area was 12 spp. at FUS, 6 spp. at INF, 17 spp. at FIS, 27 spp. at CF, 15 spp. at FP, 16 spp. at MJ, and 32 spp. at SINP. Rarefaction curves indicated stabilization only for INF and FUS, while none of the remaining areas approached an asymptote (Figure 4A). The highest sampling effort was directed toward SINP and CF, which are among the largest Atlantic Forest remnants in the state. For these areas, the estimated richness was 52 and 39 spp., respectively (Figure 4A), and only these two areas showed sampling coverage, suggesting that additional effort is unlikely to substantially increase species richness (Figure 4B).

Table 2. List of Odonata species sampled in Sergipe, Brazil. Aquatic habitat types: (Lo) lotic, (Le) lentic; IUCN Red List status: (LC) Least Concern, (DD) Data Deficient, (-) not assessed in the IUCN Red List; (*) new records for the state of Sergipe; occurrence points follow the numbering provided in Table 1; (N) abundance.

Taxon	Habitat	IUCN Status	New Records (*) and References	Sampling Point	N
ZYGOPTERA Calopterigidae <i>Hetaerina auripennis</i> (Burmeister, 1839)	Lo	LC	[35]	P3LO, P31LO, P37LO, P38LO, P39LO P18LO, P24LO, P27LO, P28LO, P30LO, P31LO, P32LO, P33LO, P34LO, P35LO, P36LO, P28LO, P39LO, P40LO, P41LO, P42LO, P43LO, P44LO, P45LO	18
<i>Hetaerina longipes</i> Hagen in Selys, 1853	Lo	LC	[35]	P3LO, P20LO, P21LO, P22LO, P30LO, P31LO, P32LO, P34LO, P35LO, P36LO, P37LO, P38LO, P41LO, P42LO	86
<i>Hetaerina rosea</i> Selys, 1853	Lo	LC	[38]		78

Table 2. Cont.

Taxon	Habitat	IUCN Status	New Records (*) and References	Sampling Point	N
Coenagrionidae					
<i>Acanthagrion gracile</i> (Rambur, 1842)	Le, Lo	LC	[38]	P2LE, P18LO, P19LE, P20LO, P22LO, P26LO	26
<i>Acanthagrion longispinosum</i> Leonard, 1977	Lo	LC	[35]	P36LO	1
<i>Acanthagrion minutum</i> Leonard, 1977	Le	LC	*	P7LE	1
<i>Acanthagrion truncatum</i> Selys, 1876	Le	LC	*	P7LE, P9LE, P10LE	9
<i>Argia modesta</i> Selys, 1865	Lo	LC	[35]	P3LO, P18LO, P20LO, P22LO, P27LO, P29LO, P30LO, P31LO, P32LO, P33LO, P34LO, P35LO, P38LO, P39LO, P40LO, P41LO, P43LO, P44LO, P45LO	57
<i>Argia reclusa</i> Selys, 1865	Lo	LC	[35]	P18LO, P20LO, P21LO, P24LO, P25LO, P27LO, P28LO, P29LO, P30LO, P31LO, P32LO, P33LO, P34LO, P35LO, P36LO, P37LO, P38LO, P39LO, P40LO, P42LO, P43LO, P44LO, P45LO	167
<i>Argia smithiana</i> Calvert, 1909	Lo	LC	[35]	P21LO, P23LO, P24LO, P26LO, P30LO, P32LO, P33LO, P34LO, P35LO, P36LO, P40LO, P41LO, P42LO, P45LO	112
<i>Argia tamoyo</i> Calvert, 1909	Lo	LC	[35]	P43LO, P44LO	15
<i>Ischnura capreolus</i> (Hagen, 1861)	Le	LC	[38]	P2LE, P8LE, P9LE, P10LE, P11LE, P12LE, P15LE, P17LE, P19LE	67
<i>Ischnura fluviatilis</i> Selys, 1876	Le, Lo	LC	[72]	P4LO, P6LE, P11LE	9
<i>Nehalennia minuta</i> (Selys in Sagra, 1857)	Le	LC	*	P16LE	8
<i>Oxyagrion chapadense</i> Costa, 1978	Lo	LC	[35]	P18LO, P20LO, P26LO, P27LO, P43LO, P45LO	20
<i>Oxyagrion impunctatum</i> Calvert, 1909	Lo	LC	[35]	P23LO	1
<i>Telebasis corallina</i> (Selys, 1876)	Le	LC	*	P11LE, P12LE, P15LE, P19LE	25
<i>Telebasis filiola</i> (Perty, 1834)	Le, Lo	LC	[35]	P1LE, P5LE, P8LE, P19LE, P34LO, P37LO, P38LO	54
Heteragrionidae					
<i>Heteragrion aurantiacum</i> Selys, 1862	Lo	LC	[35]	P3LO, P20LO, P21LO, P22LO, P24LO, P25LO, P26LO, P27LO, P28LO, P29LO, P30LO, P31LO, P32LO, P33LO, P34LO, P35LO, P36LO, P38LO, P39LO, P40LO, P42LO, P43LO, P44LO, P45LO	220
<i>Heteragrion lencionii</i> Vilela, Farias & Santos, 2021	Lo	-	[39]	P3LO, P21LO, P22LO, P39LO	8
Protoneuridae					

Table 2. Cont.

Taxon	Habitat	IUCN Status	New Records (*) and References	Sampling Point	N
<i>Epipleoneura metallica</i> Rácenis, 1955	Lo	LC	[35]	P20LO, P22LO, P31LO, P32LO, P38LO, P39LO, P40LO	36
<i>Neoneura confundens</i> Wasscher & van 't Bosch, 2013	Lo	LC	[57]	P3LO	2
<i>Neoneura sylvatica</i> Hagen in Selys, 1886 Perilestidae	Le, Lo	LC	[38]	P2LE, P3LO, P19LE	15
<i>Perilestes fragilis</i> Hagen in Selys, 1862	Lo	LC	[73]	P25LO, P29LO, P30LO, P34LO, P35LO, P39LO, P42LO	12
ANISOPTERA Aeshnidae					
<i>Castoraeschna cf. longfieldae</i> (Kimmins, 1929)	Lo	LC	[35]	P33LO, P35LO, P43LO	6
<i>Castoraeschna colorata</i> (Martin, 1908)	Lo	LC	[35]	P36LO	1
<i>Coryphaeschna adnexa</i> (Hagen, 1861)	Le	LC	*	P5LE	3
<i>Gynacantha bifida</i> Rambur, 1842 Gomphidae	Lo	LC	[35]	P22LO	1
<i>Phyllocycla murrea</i> Belle, 1988 Libellulidae	Le	DD	[74]	P17LE	1
<i>Anatya guttata</i> (Erichson in Schomburgk, 1848)	Le	LC	[57]	P1LE	2
<i>Brachymesia herbida</i> (Gundlach, 1889)	Le, Lo	LC	[35]	P15LE, P37LO	2
<i>Dasythemis esmeralda</i> Ris, 1910	Le	LC	[38]	P10LE	1
<i>Dasythemis venosa</i> (Burmeister, 1839)	Le	LC	*	P10LE	1
<i>Diastatops obscura</i> (Fabricius, 1775)	Lo	LC	[35]	P4LO	1
<i>Dythemis nigra</i> Martin, 1897	Le, Lo	LC	[38]	P1LE, P18LO, P26LO, P33LO, P37LO, P41LO, P42LO	17
<i>Elasmothermis cannaerioides</i> (Calvert, 1906)	Lo	LC	[35]	P4LO, P30LO	2
<i>Erythemis credula</i> (Hagen, 1861)	Le	LC	*	P6LE, P11LE, P15LE	17
<i>Erythemis haematogastra</i> (Burmeister, 1839)	Le	LC	*	P1LE, P6LE	4
<i>Erythemis mithroides</i> (Brauer, 1900)	Le, Lo	LC	[35]	P1LE, P37LO	3
<i>Erythemis peruviana</i> (Rambur, 1842)	Le, Lo	LC	[35]	P1LE, P4LO, P5LE, P6LE, P7LE, P9LE, P12LE, P13LE, P15LE, P37LO	51
<i>Erythemis plebeja</i> (Burmeister, 1839)	Le	LC	*	P1LE	2
<i>Erythrodiplax basalis</i> (Kirby, 1897)	Le	LC	[57]	P1LE, P2LE, P7LE, P9LE, P10LE, P12LE, P13LE, P14LE, P16LE	91

Table 2. Cont.

Taxon	Habitat	IUCN Status	New Records (*) and References	Sampling Point	N
<i>Erythrodiplax castanea</i> (Burmeister, 1839)	Lo	LC	[38]	P18LO	1
<i>Erythrodiplax famula</i> (Erichson in Schomburgk, 1848)	Le	LC	[57]	P7LE, P10LE, P11LE, P12LE, P16LE	32
<i>Erythrodiplax fusca</i> (Rambur, 1842)	Le, Lo	LC	[38]	P1LE, P2LE, P4LO, P9LE, P14LE, P18LO, P32LO, P37LO	23
<i>Erythrodiplax juliana</i> Ris, 1911	Le, Lo	LC	[35]	P9LE, P10LE, P18LO, P42LO	33
<i>Erythrodiplax latimaculata</i> Ris, 1911	Le, Lo	LC	[38]	P19LE, P26LO	5
<i>Erythrodiplax paraguayensis</i> (Forster, 1905)	Le	LC	*	P7LE, P12LE	5
<i>Erythrodiplax umbrata</i> (Linnaeus, 1758)	Le	LC	[38]	P1LE, P11LE	4
<i>Idiataphe amazonica</i> (Kirby, 1889)	Le	LC	[57]	P6LE	1
<i>Idiataphe longipes</i> (Hagen, 1861)	Le	LC	*	P11LE	2
<i>Macrothemis rupicola</i> Racenis, 1957	Lo	LC	[35]	P23LO	1
<i>Miathyria marcella</i> (Selys in Sagra, 1857)	Lo	LC	[38]	P37LO	1
<i>Miathyria simplex</i> (Rambur, 1842)	Lo	LC	[35]	P35LO	1
<i>Micrathyria catenata</i> Calvert, 1909	Le	LC	*	P11LE, P15LE, P16LE	24
<i>Micrathyria didyma</i> (Selys in Sagra, 1857)	Le	LC	*	P1LE	1
<i>Micrathyria eximia</i> Kirby, 1897	Le	LC	*	P15LE	1
<i>Micrathyria ocellata</i> Martin, 1897	Le, Lo	LC	[35]	P5LE, P6LE, P9LE, P11LE, P15LE, P16LE, P37LO	8
<i>Micrathyria</i> cf. <i>pirassunungae</i> Santos, 1953	Le	LC	[38]	P19LE	1
<i>Nephepeltia flavifrons</i> (Karsch, 1889)	Le, Lo	LC	[57]	P4LO, P9LE, P13LE, P15LE, P17LE	22
<i>Orthemis discolor</i> (Burmeister, 1839)	Le	LC	[38]	P1LE, P10LE, P13LE, P14LE, P17LE	15
<i>Orthemis flavopicta</i> Kirby, 1889	Le	LC	[35]	P5LE	1
<i>Perithemis lais</i> (Perty, 1834)	Lo	LC	[38]	P27LO, P31LO, P37LO, P38LO	12
<i>Perithemis tenera</i> (Say, 1839)	Le	LC	[38]	P2LE, P17LE	4
<i>Uracis imbuta</i> (Burmeister, 1839)	Lo	LC	[35]	P18LO, P44LO	5
<i>Zenithoptera anceps</i> Pujol-Luz, 1993	Le	LC	[57]	P7LE, P9LE, P16LE	12
8 families, 32 genera and 66 species			* 14 New records		1468

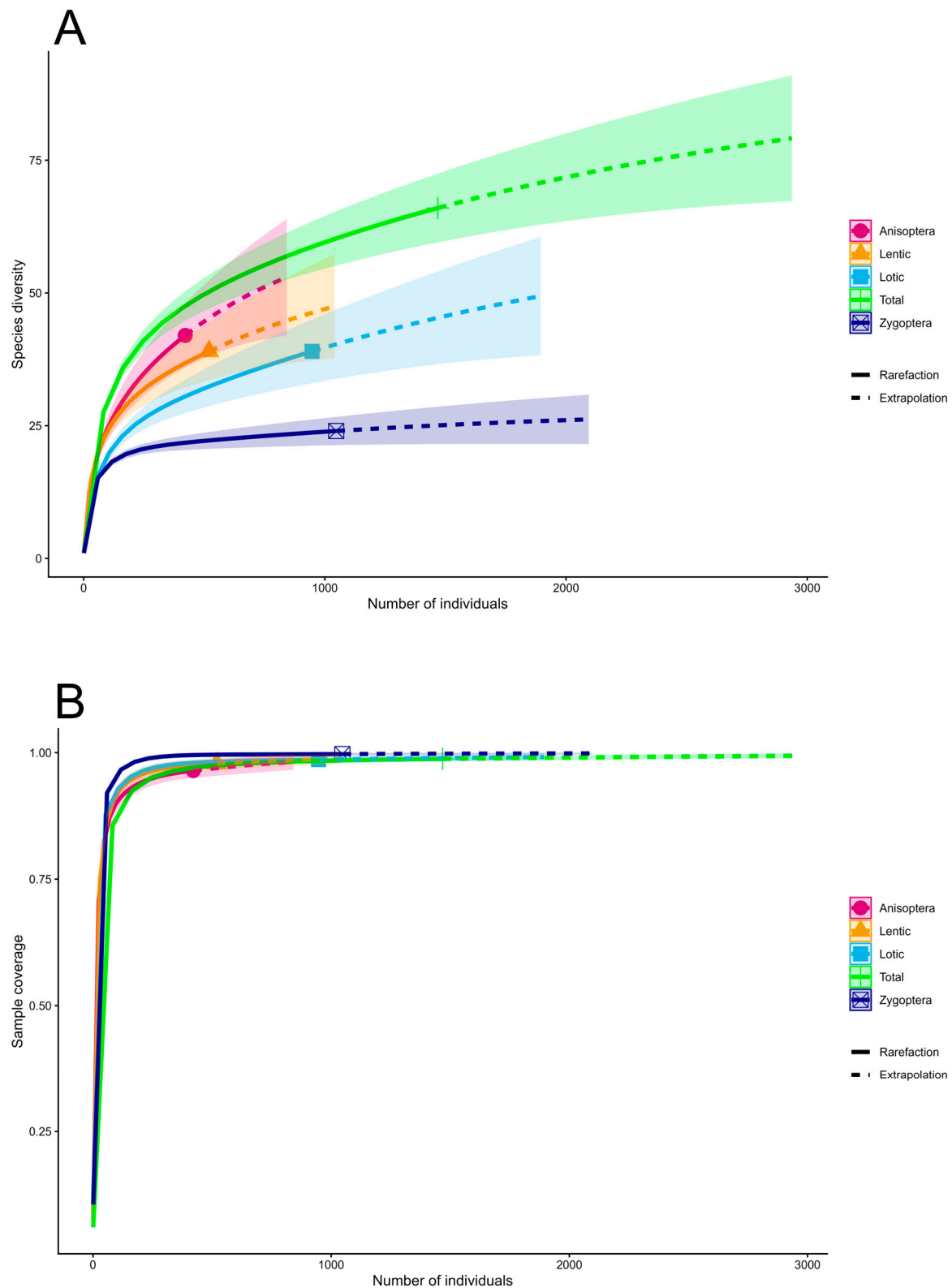


Figure 3. Rarefaction curves with 95% confidence intervals for the Odonata species sampled in the Atlantic Forest of Sergipe. (A)—Interpolation and extrapolation curves for Odonata sampling: total, suborders (Anisoptera and Zygoptera), and habitat types (lentic and lotic); (B)—Sample coverage curves for total Odonata, suborders (Anisoptera and Zygoptera), and habitat types (lentic and lotic). The solid line represents the interpolation of observed species richness, and the dashed line represents the extrapolation of expected richness with increased sampling effort.

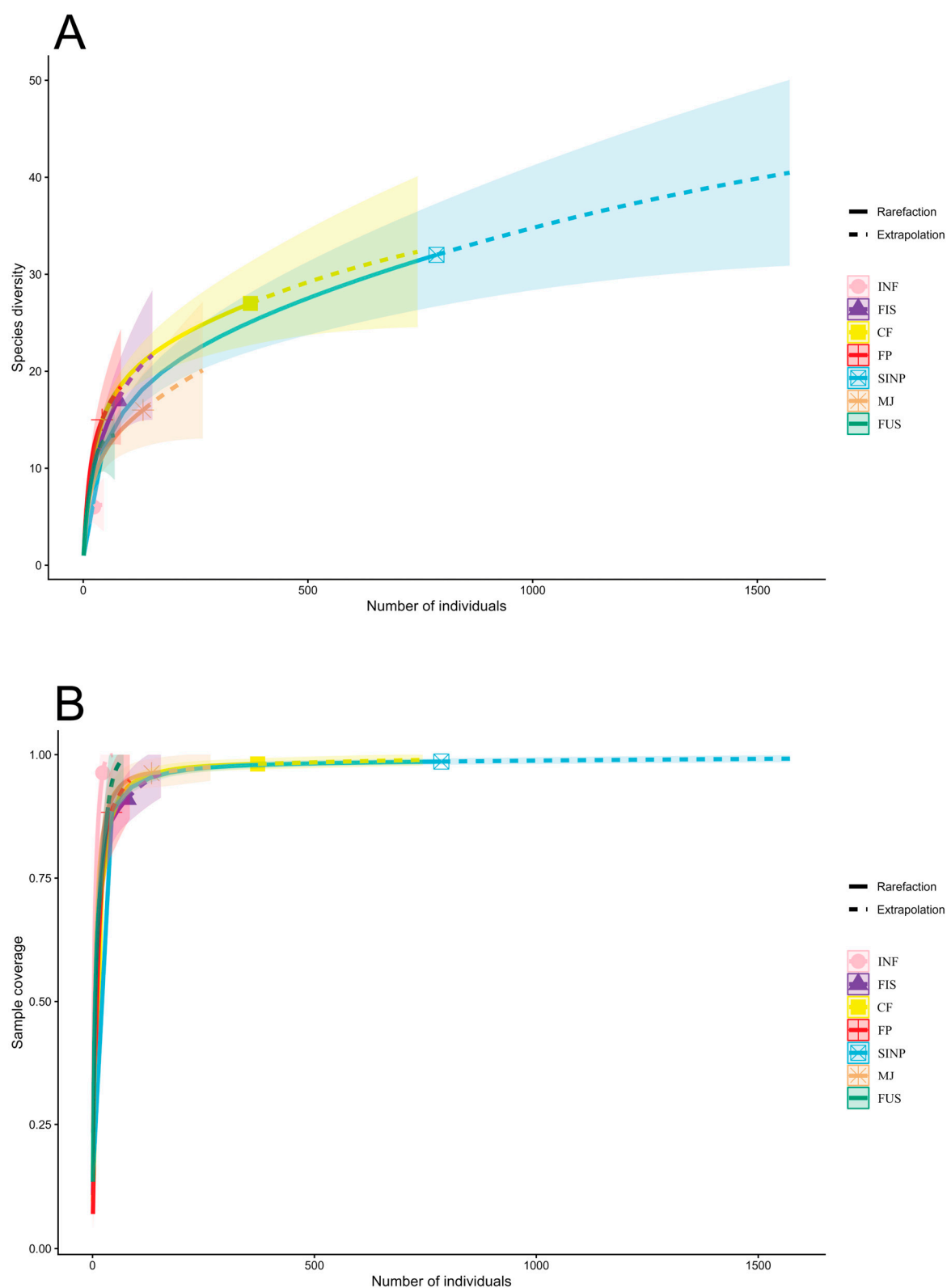


Figure 4. Rarefaction curves with 95% confidence intervals for Odonata species sampled in the Atlantic Forest of Sergipe, Brazil. **(A)**—Interpolation and extrapolation curves for Odonata sampling in the study areas; **(B)**—Sample coverage curve for total Odonata sampled in the study areas. (FUS—Federal University of Sergipe; INF—Iburá National Forest; FIS—Federal Institute of Sergipe; CF—Crasto's Forest; MJ—Mata do Junco Wildlife Refuge; FP—Falcons Park; SINP—Serra de Itabaiana National Park). The solid line indicates the interpolation of observed species richness, and the dashed line shows the extrapolated richness expected with increased sampling effort.

Anisoptera comprised 42 species and 421 individuals, accounting for 63% of the total species richness and 29% of the total abundance sampled. Three families were recorded within this suborder: Aeshnidae (4 spp./11 individuals), Gomphidae (1 spp./1 individual), and Libellulidae (37 spp./409 individuals). The most species-rich genera were *Erythrodiplax* (8 spp.), *Erythemis* (5 spp.), and *Micrathyria* (5 spp.). The most abundant species was *Erythrodiplax basalis* Kirby, 1897 (91 individuals), followed by *Erythemis peruviana* Rambur, 1842 (51 individuals), and *Erythrodiplax juliana* Ris, 1911 (33 individuals). The most widely distributed species were *Erythemis peruviana*, recorded at 10 of the 45 sampling points; *Erythrodiplax fusca* (Rambur, 1842) (Figure 5D), present at eight points; and *Dythemis nigra* (Martin, 1897), *Erythrodiplax basalis*, and *Micrathyria ocellata* Martin, 1897, each occurring at seven points (Table 2). The following species were classified as singletons, each represented by a single individual: *Castoraeschna colorata* (Martin, 1908), *Gynacantha bifida* Rambur, 1842, *Phyllocycla murrea* Belle, 1988, *Dasythemis esmeralda* Ris, 1910, *Dasythemis venosa* Burmeister, 1839, *Diastatops obscura* Fabricius, 1775, *Erythrodiplax castanea* (Burmeister, 1839), *Idiataphe amazonica* Kirby, 1889, *Macrothemis rupicola* (Racenis, 1957), *Miathyria marcella* Selys, 1857, *Miathyria simplex* (Rambur, 1842), *Micrathyria didyma* Selys, 1857, *Micrathyria eximia* Kirby, 1897, *Micrathyria* cf. *pirassunungae* Santos, 1953, and *Orthemis flavopicta* Kirby, 1889. The following species were classified as doubletons, each represented by two specimens: *Anatya guttata* Erichson, 1848, *Brachymesia herbida* Gundlach, 1889, *Elasmothermis cannaerioides* (Calvert, 1906), *Erythemis plebeja* Burmeister, 1839, and *Idiataphe longipes* Hagen, 1861 (Table 2).

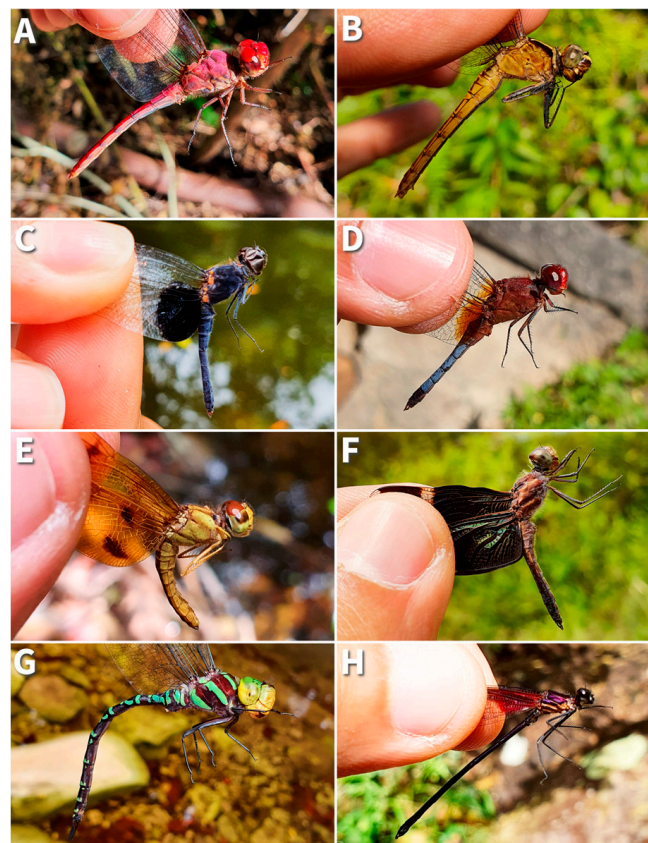


Figure 5. Odonata species collected from the Atlantic Forest of Sergipe, Brazil. ((A)—*Orthemis discolor* (Burmeister, 1839); (B)—*Erythemis peruviana* (Rambur, 1842); (C)—*Erythrodiplax latimaculata* Ris, 1911; (D)—*Erythrodiplax fusca* (Rambur, 1842); (E)—*Perithemis lais* (Perty, 1834); (F)—*Zenithoptera anceps* (Pujol-Luz, 1993); (G)—*Castoraeschna* cf. *longfieldae* (Kimmings, 1929); (H)—*Hetaerina rosea* Selys, 1853. Photos: Farias, A.B.S. (2021).

For Zygoptera, 1047 specimens were collected, distributed across 24 species, corresponding to 37% of the total richness and 71% of the total abundance sampled. Five families were recorded: Calopterygidae (3 spp./182 individuals), Coenagrionidae (15 spp./572 individuals), Protoneuridae (3 spp./53 individuals), Heteragrionidae (2 spp./228 individuals), and Perilestidae (1 spp./12 individuals). The most species-rich genera were *Acanthagrion* and *Argia*, each with four species, followed by *Hetaerina* with three species (Table 2). *Heteragrion aurantiacum* Selys, 1862 was the most abundant species (220 individuals), followed by *Argia reclusa* (Selys, 1865) (167 individuals) and *Argia smithiana* (Calvert, 1909) (112 individuals). Among the most frequently recorded species was *Heteragrion aurantiacum*, which occurred at 24 of the 45 sampling points, *Argia reclusa* at 23 points, and *Hetaerina longipes* Hagen, 1853 at 19 points (Table 2). Three species were classified as singletons: *Acanthagrion longispinosum* (Leonard, 1977), recorded in lotic habitats; *Acanthagrion minutum* Leonard, 1977, recorded in lentic habitats; and *Oxyagrion impunctatum* (Calvert, 1909), recorded in lotic habitats. Only one species was classified as a doubleton: *Neoneura confundens* Wasscher & van't Bosch, 2013, which was recorded in lotic habitats (Table 2). Coenagrionidae included four species restricted to specific points: *Acanthagrion longispinosum* at point 36 (SINP), *Acanthagrion minutum* and *Nehalennia minuta* Selys, 1857 at points 7 and 16, respectively (CF), and *Neoneura confundens* at point 3 (FIS).

Sampling point 9 (CF) showed the highest abundance, with 66 individuals. This point is characterised by open areas, lentic conditions, high solar incidence, adjacent forests, wetland habitats, and the presence of a spring. Sampling points 1 and 37 (FUS and SINP, respectively) exhibited the highest species richness, with 12 species. Point 1 also had the highest number of exclusive species ($n = 3$): *Anatya guttata* Erichson, 1848, *Erythemis plebeja* Burmeister, 1839, and *Micrathyria didyma* Selys, 1857, all of which belong to the family Libellulidae (Table 2). This site is located in an urban area characterised by a mixed habitat with open and closed vegetation, partial shading, anthropogenic disturbance, nearby buildings, and an adjacent flooded area.

3.2. Species Richness and Composition Across Aquatic Habitats Type

In lotic habitats, 880 individuals (59.9%) were collected, representing 26 exclusive species (39%) across both suborders (Anisoptera and Zygoptera). As previously noted, *H. aurantiacum*, *A. reclusa*, and *A. smithiana* were the most abundant species, with their occurrences strictly restricted to lotic environments. Among Anisoptera, *D. nigra* (16 individuals) was the most abundant species in the lotic habitats. In lentic habitats, 335 individuals (22.8%) were sampled, representing 27 exclusive species (41%). *E. basalis* (91 individuals) and *Ischnura capreolus* Hagen, 1861 (67 individuals), were the most abundant species restricted to lentic environments, followed by *E. peruviana* with 40 individuals, which was shared between both habitat types. Overall, 13 species (20%) were common to both lotic and lentic habitats.

When comparing suborders across habitat types, Anisoptera showed 32 individuals (7.6%) and 11 exclusive species (26%) in lotic habitats and 225 individuals (%) and 22 exclusive species (53.4%) in lentic habitats, in addition to nine shared species (20.6%) between lotic and lentic environments (Figure 6A). For Zygoptera, 833 individuals (79.5%) and 15 exclusive species (62.5%) were associated with lotic habitats, whereas 110 individuals (10.5%) and five exclusive species (20.8%) occurred in lentic habitats, with four species (16.7%) shared between both habitat types (Figure 6B).

3.3. Alpha and Beta Diversity

There was no statistically significant difference in Odonata species richness between the two sampled habitat types (lotic and lentic) ($t = -0.21$, $p = 0.84$) (Figure 7). However,

species composition differed significantly between lentic and lotic habitats, even after controlling for spatial autocorrelation using Moran's Eigenvector Maps (dbRDA: $F_{df=43} = 2.96$, $p = 0.001$) (Figure 8). Habitat explained 3.3% (adjusted $R^2 = 0.334$) of the variation in community composition, independent of spatial structure. After accounting for spatial structure, multivariate dispersion did not differ between habitats (PERMDISP, $F_{df=43} = 3.87$, $p = 0.055$), indicating that the observed differences primarily reflected compositional turnover between lentic and lotic groups.

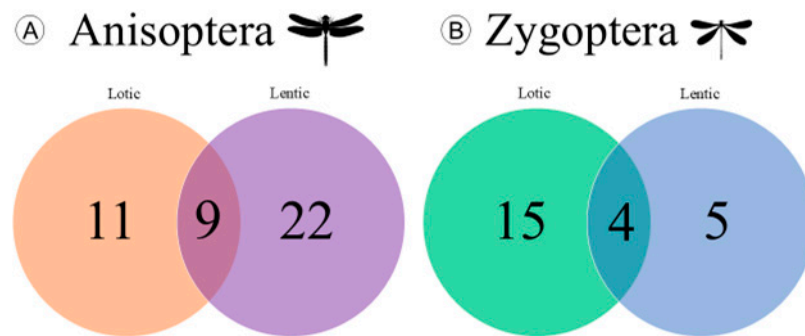


Figure 6. Venn diagram showing species richness of both Odonata suborders across the sampled habitat types in the Atlantic Forest of Sergipe, Brazil. (A)—Exclusive and shared Anisoptera species between lotic and lentic habitats; (B)—Exclusive and shared Zygoptera species between lotic and lentic habitats.

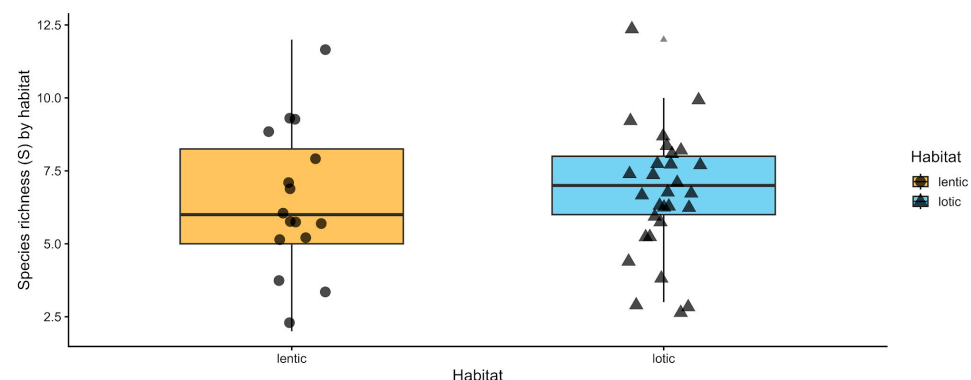


Figure 7. Odonata species richness in lentic and lotic habitats in the Atlantic Forest of Sergipe, Brazil. Vertical boxes represent the interquartile range (Q3–Q1), with a horizontal line indicating the median value. Whiskers show the minimum and maximum values within a $1.5 \times$ interquartile range. Black symbols (circle and triangle) represent individual values for each sampling site.

Total beta diversity was high ($\beta_{sor} = 0.956$), driven primarily by species turnover, which accounted for 98.6% of the variation ($\beta_{sim} = 0.943$), whereas nestedness contributed only 1.4% ($\beta_{nes} = 0.013$) (Figure 9A; Table 3; Supplementary Figure S3). Several communities showed maximum dissimilarity (e.g., P21LO, P23LO, P24LO, P25LO, P27LO, P28LO, and P29LO compared to P2LE; and P1LE, P10LE, and P11LE compared to P3LO; $\beta_{sor} = 1$) (Figure 6A; Supplementary Figure S3). These sampling points exhibited complete community replacement, as all comparisons reached the maximum turnover ($\beta_{sim} = 1$) (Figure 9A; Supplementary Figure S3). In contrast, nestedness showed its highest values in comparisons between P1LE and P14LE ($\beta_{nes} = 0.600$), P8LE and P19LE ($\beta_{nes} = 0.555$), and P25LO and P35LO ($\beta_{nes} = 0.500$) (Figure 9A; Supplementary Figure S3).

and P41LO ($\beta_{\text{nes}} = 0.833$), as well as between P27LO and P37LO ($\beta_{\text{nes}} = 0.777$) (Figure 9B; Supplementary Figure S6). Zygoptera communities were also highly dissimilar and primarily structured by species turnover, with maximum values observed between P1LE and P2LE, P10LE, P11LE, P12LE, P15LE, P16LE, and P18LO ($\beta_{\text{sor}} = 1$ and $\beta_{\text{sim}} = 1$). Nestedness was highest between P1LE and P34LO, P5LE and P34LO, and P5LE and P38LO, all showing $\beta_{\text{nes}} = 0.777$ (Figure 9C; Supplementary Figure S7).

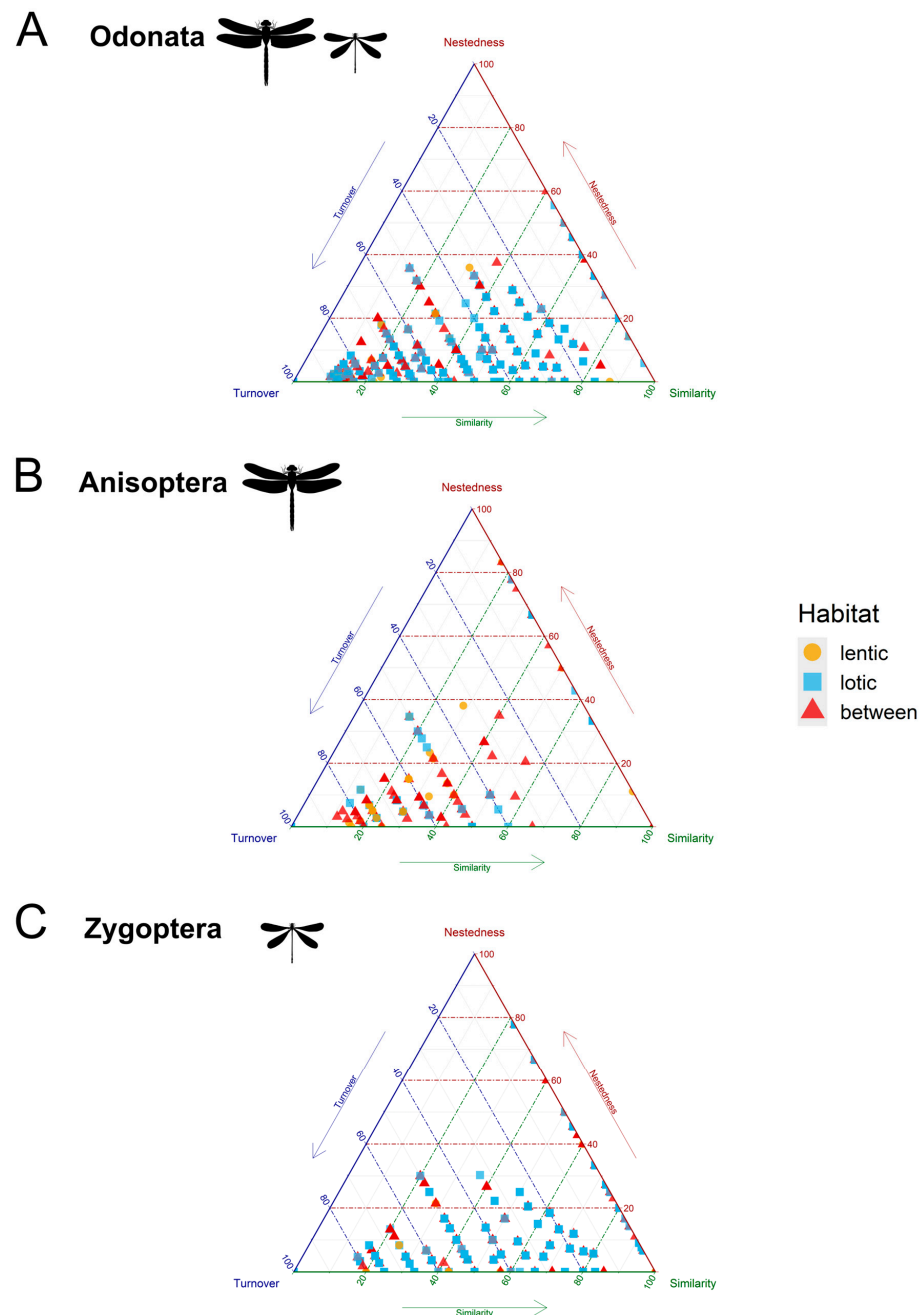


Figure 9. Ternary diagram comparing the components of beta diversity [turnover (β_{sim}) and nestedness (β_{nes})] for Odonata (A) and its suborders ((B)—Anisoptera and (C)—Zygoptera), as well as habitat types (lentic and lotic). The horizontal axis indicates similarity ($1 - \beta_{\text{sor}}$), the left axis represents species turnover, and the right axis represents species nestedness between the communities. Each symbol represents a pairwise comparison of the Odonata communities. Yellow circles represent lentic vs. lentic comparisons; blue squares represent lotic vs. lotic comparisons; and red triangles represent lentic vs. lotic comparisons.

The LCBD values ranged from 0.0119 to 0.0320, with half of the sites above the mean contribution (mean = 0.0222). Additionally, eight points (two lotic and six lentic) showed statistically significant values (P4LO, P6LE, P8LE, P10LE, P11LE, P15LE, P17LE, and P19LE; $p = 0.047, 0.038, 0.029, 0.049, 0.025, 0.027, 0.021, \text{ and } 0.022$, respectively) (Figure 10A–C; Supplementary Table S2). Regarding SCBD, values ranged from 0.0005 to 0.1150 (mean = 0.0132), with 21 species exceeding the mean contribution threshold (Supplementary Table S2). *Heteragrion aurantiacum*, *Argia smithiana*, and *Argia reclusa* were the species that contributed most to the compositional dissimilarity among the sampling points, with SCBD values of 0.1150, 0.0805, and 0.0750, respectively (Figure 11; Supplementary Table S2).

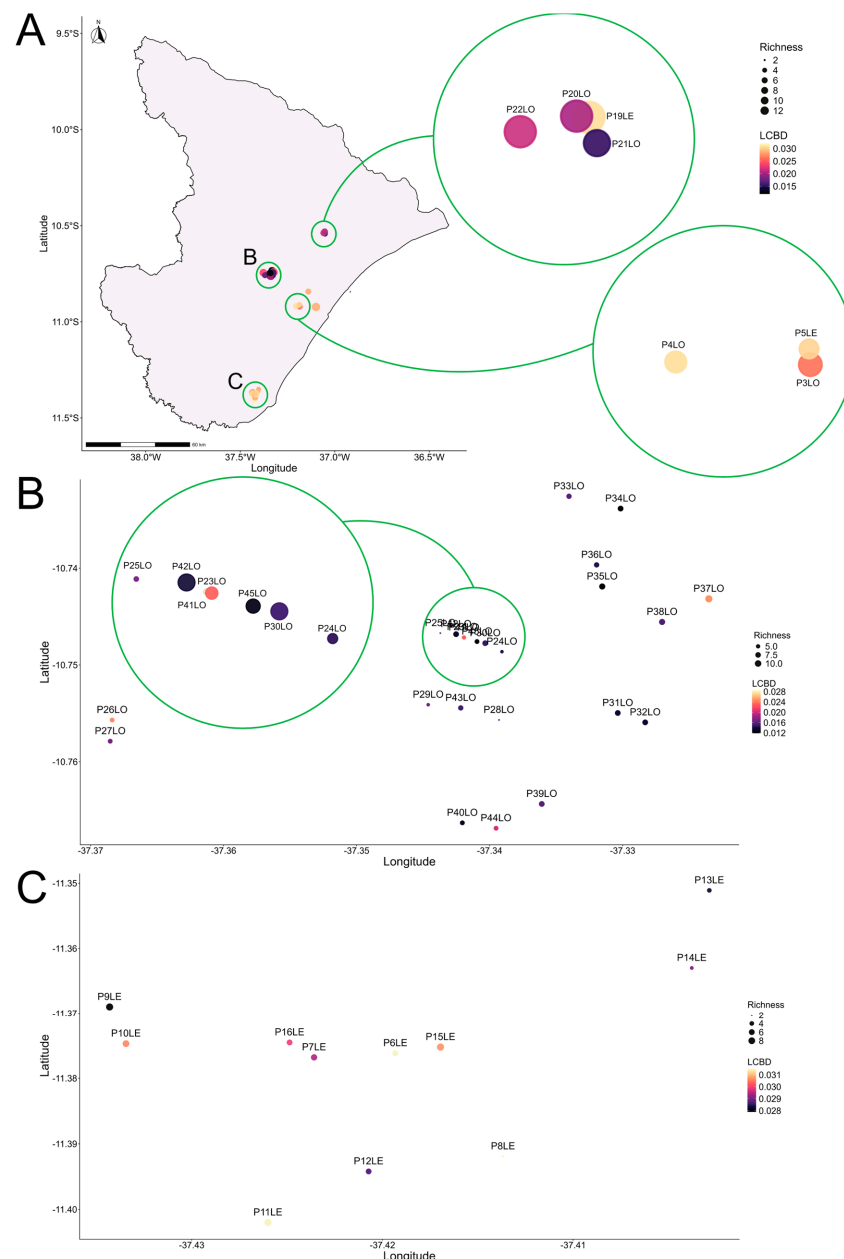


Figure 10. Local contribution to total beta diversity. (A)—Local contribution to total beta diversity of Odonata sampled in Sergipe; (B)—enlarged view of sampling points from Serra de Itabaiana National Park; and (C)—enlarged view of sampling points from Crasto's Forest. Warmer colours indicate higher LCBD values.

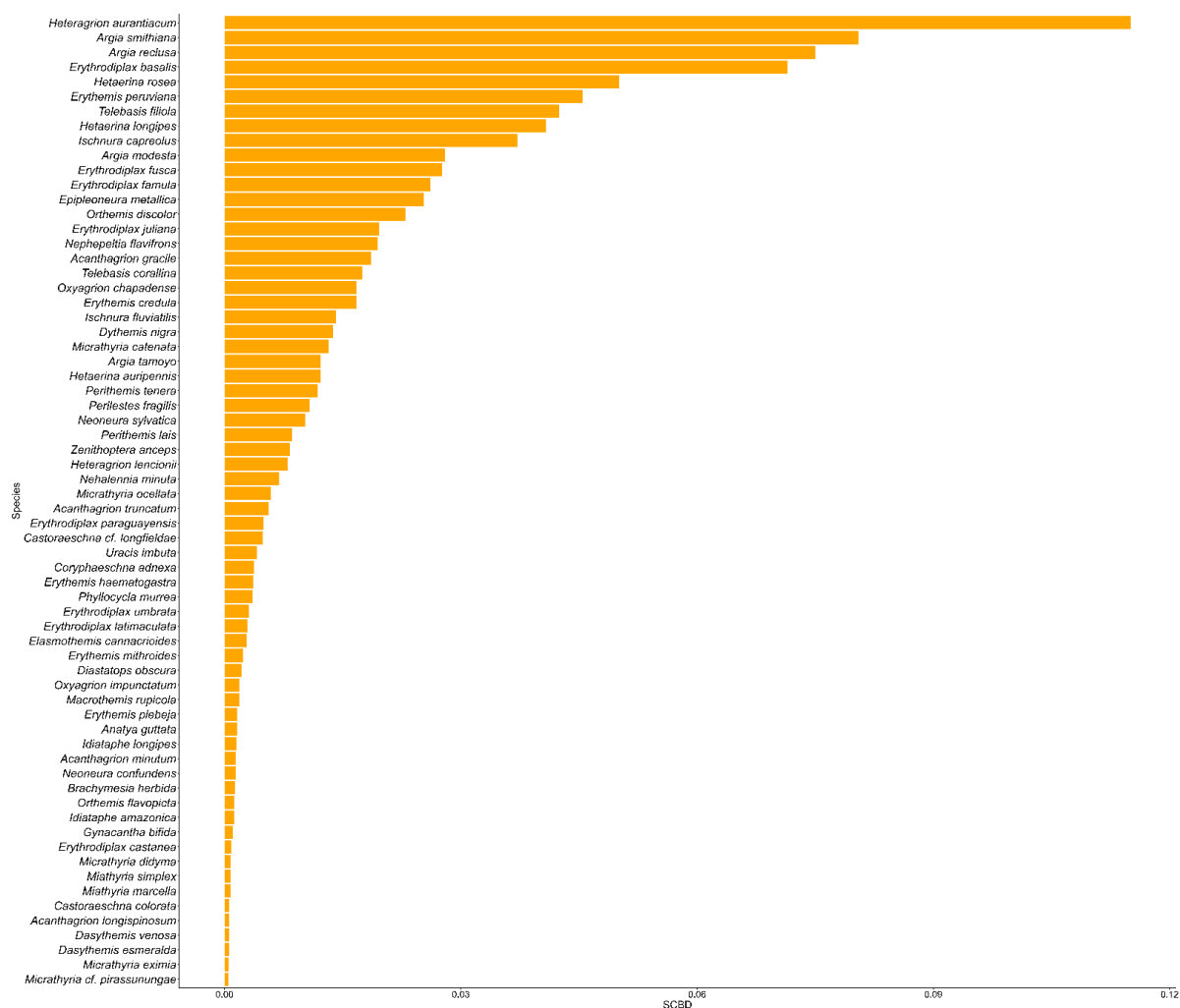


Figure 11. Species contribution (SCBD) to the total beta diversity.

4. Discussion

4.1. Odonata Species Inventory

Currently, 81 odonate species are known to inhabit Sergipe [57]. We added 14 new records, raising the total to 95 species, which places Sergipe as the second Brazilian state in the Northeast with the highest number of recorded species, second only to Bahia, which has 182 recorded species [57]. Despite being the smallest state in Brazil, we highlight the high species diversity already recorded; however, additional species are expected to be recorded in the state.

One of the major limitations faced by conservation biology in tropical forests is the scarcity of accumulated information that would allow efforts to be focused and priority areas to be established [36]. Faunal surveys are an important tool for conservation; however, the low number of inventories limits our knowledge of species distribution and abundance [33,34,36]. Until 2005, only 29% of the Brazilian territory had data on Odonata richness and distribution [36]. Most (70%) studies on Odonata in Brazil are taxonomic, although they are mainly concentrated in the Southeast and North regions [33]. In terms of Odonata knowledge, northeastern Brazil accounts for 9.2% of studies [33]. In the preliminary species lists for Alagoas, 56 species have been recorded [75,76].

When compared to other studies conducted in Atlantic Forest environments, our results are comparable, although differences in sampling effort must be considered: Ferreira-Peruquetti & De Marco (2002) recorded 28 spp. [13], Dalzochio et al. (2018) recorded 57

spp. [44], Renner et al. (2013) recorded 34 spp. [46], Renner et al. (2016) recorded 46 spp. [48], and Gomes et al. (2025) recorded 41 species [57]. In this sense, the results presented here represent a significant advance and are highly relevant, highlighting the importance of Sergipe, northeastern Brazil, and the Brazilian Atlantic Forest in terms of Odonata knowledge.

In addition, we have contributed new distribution records for a highly fragmented and threatened ecosystem, such as the Atlantic Forest. Some regions, such as the restinga and Caatinga areas in Sergipe, are currently being surveyed and will likely further increase the number of recorded species, helping to reduce the Linnean and Wallacean shortfalls for Odonata in the state. The importance of these findings for ecosystem management, conservation, and environmental monitoring is emphasised, given the widespread use of this group as bioindicators [18,42,50,77]. This underscores the urgent need for conservation actions aimed at protecting the remaining habitats and restoring degraded areas.

4.2. Main Families, Genera, and Species Recorded of the Brazilian Atlantic Forest

The families Libellulidae (Anisoptera) and Coenagrionidae (Zygoptera) were the most diverse, and similar patterns have been previously reported for southeastern, central, and more recently in our study, northeastern Brazil (for example, refs. [6,34,35,38,42,44,57,78–82]). Gomphidae (Anisoptera) was represented by only a single specimen, which reinforces the importance of using alternative sampling methods [83], as some species exhibit crepuscular activity patterns [84] and fly at high altitudes and high speeds, which is generally true for Anisoptera as a whole.

Anisopterans tend to dominate forest clearings [85]. Some Libellulidae species, particularly those of the genera *Erythrodiplex* and *Micrathyria*, are habitat generalists and are abundant in open areas [86]. In this study, approximately one-third of the sampling points exhibited open or mixed habitat characteristics, with a high incidence of plant species from the family Juncaceae along the margins of water bodies (e.g., points P1LE, P2LE, P4LO, P5LE, P6LE, P7LE, P8LE, P9LE, P10LE, P12LE, P15LE, and P16LE). These characteristics may explain why the aforementioned genera were the most representative and support the tendency for anisopterans to be more dominant in lentic environments in this study. For instance, *Erythrodiplex fusca* (Libellulidae) is a common species in disturbed environments [45,87] and was recorded at six sampling areas (FUS, INF, FIS, CF, FP, and SINP), with its highest abundance detected at INF.

Species of *Heteragrion* (Heteragrionidae) were widely distributed across the sampling points at the three areas, specifically FIS, MJ, and SINP, all of which are within protected areas. This genus shows a strong dependence on riparian vegetation in the Atlantic Forest, mainly associated with its specialization in oviposition sites [13]. Resende et al. [88] found that *H. aurantiacum* was strongly associated with more preserved streams. Our findings support these results, as both *Heteragrion* species (*H. aurantiacum* and *H. lencionii*) were recorded only at points with well-preserved riparian vegetation, with the latter occurring at sites with lower anthropogenic pressure (e.g., points P3LO, P21LO, P22LO, and P24LO).

Finally, *I. capreolus* should be highlighted. Renner et al. [48] described this species as an indicator of fragmented Atlantic Forest environments with some degree of disturbance. This result is supported by our findings, as this species was recorded at points where some level of environmental alteration was observed. For example, point P17LE in the FP is an artificial pond used for duck rearing, where litter was observed along the entire shoreline.

4.3. Richness and Species Composition Among Aquatic Habitat Types

Although no difference in mean species richness was observed between lotic and lentic habitats, the species composition differed markedly between these environments.

Species composition is linked to biotic and abiotic factors that determine the establishment of species or groups according to their ecophysiological constraints [41,89]. This pattern can be explained by the specialization of the respiratory systems in the larval stages of the suborders. In Anisoptera, the larval respiratory system extracts oxygen directly from water through specialized rectal gill tissue, which, depending on the family, may take different forms, such as simple, undulated, papillae-like, double foliate, or double lamellar structures [90]. Naturally, anisopteran larvae are not found in strong current environments; their dorsoventrally flattened body shape is considered an adaptation to a burrowing and hiding lifestyle [91]. In contrast, Zygoptera respire through water conduction across the epithelium, which is supplied by the tracheal system directly connected to the caudal lamellae. Under low oxygen availability, they can compensate by increasing the frequency and amplitude of caudal lamella movements [90]. They may also present a thicker cuticle and, in some cases, dorsal abdominal projections or hooks that provide stabilization in flowing water and protection against hydrodynamic forces [91]. Owing to these specializations and the contrasting characteristics of the two habitat types, anisopteran larvae are better established in lentic habitats, whereas zygopterans are better established in lotic habitats. Consequently, adult assemblages reflect this larval pattern, corroborating our results.

A distinction was also evident in the association and higher abundance of Anisoptera in lentic environments and Zygoptera in lotic environments. In this study, zygopterans showed a clear preference for lotic habitats, which generally present well-structured riparian vegetation, corroborating findings in the literature [41]. Zygoptera exhibit morphological and ecological traits associated with limited dispersal capacity; that is, they show stronger environmental requirements owing to their perching behaviour, in which they defend territories for courtship, mating, and oviposition [85]. Therefore, they are more dependent on local environmental conditions [22]. In Anisoptera, the association with lentic habitats is more evident, given their greater dispersal ability and tendency to include more generalist species that benefit from open-canopy environments [22,85]. Additionally, anisopterans often show higher richness and abundance in environments with some level of disturbance due to the higher proportion of species adapted to open areas and/or habitats that have lost their natural riparian vegetation, as well as aquatic environments under anthropogenic pressure [41,85,92]. These factors reflect the ecological particularities of Odonata in terms of establishment in natural environments that favour thermoregulation, dispersal, survival, and reproduction.

Finally, when sampling sites were analyzed individually, points P4LO and P37LO (lotic habitats) tended to cluster in composition with lentic habitats. This pattern may be explained by the presence of small water impoundments at both points. Although they are broadly classified as lotic habitats, these points locally function as lentic systems. This is due to anthropogenic alterations, such as the construction of the Rio Poxim dam, which modified the habitat structure at point P4LO, and the Jacarecica II dam, which influenced the habitat conditions at point P37LO.

4.4. Variation in Species Distribution at a Regional Scale (Beta Diversity)

We recorded high regional beta diversity, indicating strong environmental heterogeneity in the region. The results show that species turnover is the main mechanism driving beta diversity variation in Odonata communities in the Atlantic Forest of Sergipe, supporting the hypothesis proposed here. The same pattern was observed for both Anisoptera and Zygoptera, as well as for lotic and lentic habitats in the present study. Environmental and landscape characteristics are expected to influence species distribution [26,93]. For organisms with specific ecological requirements, such as odonates, the influence of landscape elements is even more evident [94,95]. Here, we show that even at small spatial

scales of a few hundred meters—for example, among points P3LO, P4LO, and P5LE (FIS), P6LE and P8LE (CF), and P23LO, P24LO, P25LO, P30LO, P41LO, P42LO AND P45LO (SINP)—there is sufficient environmental variation to drive differences in species composition among points.

In addition, clear differences in community structure were observed between the lotic and lentic habitats. Pires et al. [26] found a relationship between beta diversity in Odonata larvae in the Atlantic Forest of southern Brazil, analyzing the two suborders separately. They reported that for Anisoptera, beta diversity and turnover were significantly related to regional-scale factors, whereas for Zygoptera, beta diversity and turnover were more strongly associated with habitat structure than regional-scale factors. A similar pattern was observed in the present study, although adults were used as the study model. In this study, we found that lotic habitats had a higher proportion of zygopterans associated with this environment, particularly because of the riparian vegetation present in virtually all the studied lotic sites. Most species in this group are associated with shaded environments because of their vulnerability to solar exposure, which can lead to overheating and water loss [93]. This is also supported by Pires et al. [26], who found Odonata beta diversity to be related to riparian vegetation presence, as previously reported in other studies (for example, ref. [77]). This interpretation is consistent with the dependence of this group on riparian vegetation for foraging, sexual maturation, thermoregulation, and oviposition-site selection [13]. Overall, these factors highlight the importance of natural vegetation along stream margins and adjacent forested areas in maintaining the diversity of zygopterans.

The spatial extent of this study, with sampling areas/points separated by distances ranging from a few hundred meters to more than 100 km, allows inferences about the influence of spatial processes on Odonata communities in the Atlantic Forest of Sergipe. In a study of streams in the Amazon, Juen and De Marco [93] found low beta diversity for Zygoptera at small spatial distances, with no relationship between local environmental variables and beta diversity. They attributed this result to the spatial scale considered, while not ruling out the possibility that Odonata diversity responds to effects operating at larger distances [93]. The authors also argue that certain environmental variables, together with distance, may shape beta diversity patterns depending on the spatial scale of the analysis. Henriques-Silva et al. [96] highlighted that, at regional scales, factors influencing dispersal ability may outweigh climatic factors in structuring communities, particularly for taxa with limited dispersal capacity. As species differ in their dispersal abilities, they are expected to respond differently to spatial predictors [26]. The present study shows that in the Atlantic Forest of Sergipe, high beta diversity is observed at both small (local) and large (regional) spatial scales, explaining the compositional differences among the sampling sites. This pattern holds for Anisoptera, especially in lotic habitats, and for Zygoptera in both lotic and lentic habitats in the Brazilian Cerrado. As previously demonstrated for larval stages, these results indicate that Odonata communities are structured by both local and regional processes [97].

We agree that the unequal number of sampling sites and the uneven representation of habitat types among localities constitute an important limitation. This sampling imbalance reflects the natural availability and accessibility of aquatic habitats within each protected area, rather than differences in sampling intensity. Because our objective was to describe regional patterns across all available habitats, we retained all the sampled sites in the analyses. We explicitly acknowledge that part of the observed beta diversity may be influenced by this sampling imbalance and that future studies using balanced sampling designs will be necessary to disentangle the relative contributions of habitat type and geographic location to beta diversity. Nevertheless, our results should be interpreted

primarily as patterns of community differentiation rather than strict comparisons among equally sampled landscapes.

Anisopterans exhibit larger body sizes, which influence their higher dispersal capacity and are indirectly related to thermoregulatory ability [93]. Generalist species with greater dispersal capacity, such as anisopterans, tend to show more similar, that is, more homogeneous, community patterns. This is evident when considering only the Anisoptera communities in this study, where lower beta diversity values were observed among points P1LE–P16LE, mostly associated with lentic habitats, compared to the overall pattern. These points present lentic habitat characteristics with open areas, factors that favour the establishment and dispersal of these organisms due to their lower habitat specialization. In contrast, zygopterans, which generally exhibit lower dispersal capacity [21,85] and are more strongly influenced by local landscape features [22], tend to show high beta diversity in both lotic and lentic habitats. The nestedness pattern observed for this group in both habitat types reflects their dispersal limitations, which was expected given that they are more specialized organisms dependent on specific environmental conditions and have reduced dispersal ability [26,41,85].

At PNSI, anisopterans exhibited a high degree of species turnover, even among relatively close sampling points, including forest fragments adjacent to each other and different sections of the same stream. Given the ecological characteristics of this group, particularly their generalist habits and higher dispersal ability [26,86,93], it is expected that under these environmental conditions, community structure would be more strongly driven by nestedness. A possible explanation for this pattern is that anisopteran species tend to concentrate near sites with pools, ponds, or impoundments where water flow is reduced, as observed at point P37LO and in some segments of points P23LO, P26LO, P30LO, P31LO, P36LO, P37LO, and P41LO. Another contributing factor may be territorial behaviour, as observed in the field, given the lower availability of habitats that are more suitable for oviposition within the area.

Environmental variations in lower intensity are more readily reflected in organisms with low dispersal ability; under this scenario, species turnover tends to be the structuring component of these communities [98]. The results presented here support this pattern in Zygoptera communities. Finally, it is important to consider habitat preferences and/or specific environmental requirements of each species, as deterministic mechanisms are more strongly associated with species ecological constraints, which not only favour survival but also influence co-existence and reduce interspecific competition.

5. Conclusions

The drastic reduction in the territorial extent of the Atlantic Forest due to human activities has negatively impacted its biodiversity, making detailed knowledge of the species comprising this megadiverse ecosystem essential for its conservation. This study significantly contributes to filling knowledge gaps regarding Odonata diversity and distribution in the Atlantic Forest of Sergipe State, highlighting the importance of inventorying species and analyzing beta diversity patterns to understand community structure along environmental and spatial gradients. The results demonstrated that although species richness did not differ significantly between lentic and lotic habitats, community composition was strongly influenced by species turnover, reflecting environmental heterogeneity and the ecological specificities of the suborders Anisoptera and Zygoptera. The ecological distinction between these groups, combined with the influence of local and regional factors, underscores the need to conserve a variety of aquatic habitats and associated riparian vegetation to maintain odonate diversity and functionality. Thus, this study provides crucial data to guide conservation and management strategies in the Atlantic Forest of

Northeastern Brazil, emphasizing the role of odonates as bioindicators of environmental integrity and reinforcing the urgency of actions aimed at preserving this threatened biome.

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