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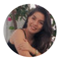

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DARK DIVERSITY OF ODONATA IN AMAZONIAN STREAMS

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Abstract

The biological diversity of a region may not be fully sampled due to the low abundance or rarity of species, or the absence of species determined by their niche specificity. Investigating these species is essential for understanding the unrealized ecological potential in different habitats, identifying gaps in local and regional communities, and gaining a better understanding of the impacts of environmental changes. Therefore, to expand knowledge about the diversity of Odonata in Eastern Amazonia considering the absent species, we tested the hypotheses that: 1) Environmental variables will influence dark diversity, with greater explanation by canopy cover where sites with lower canopy cover will have higher dark diversity values, and; 2) Functional traits associated with better species dispersal will be correlated with low dark diversity of Odonata, such as larger and wider wings for example. For this, adult Odonata specimens were sampled, while structural habitat characteristics and physical and chemical water variables were measured in 128 first- to third-order streams in the Eastern Amazon. Morphological and behavioral data were recorded for each specimen. Generalized linear models were applied to predict the effects of habitat structural characteristics and physical and chemical water variables on the dark diversity of Odonata. Additionally, we assessed which functional traits contribute most to the variation of dark diversity within these communities. Habitat structural features and physical and chemical water variables had no effect on dark diversity. Morphological traits, such as body conformation, with species having narrower wings, longer hind wings, narrower thoraxes, and shorter abdomens, comprised most of the dark diversity. The dispersal limitations of some Odonata species strongly suggest the role of space and time in nature planning and

management.

Keywords: Aquatic environments, Functional traits, Odonata, Regional pool, Species absence.

INTRODUCTION

Understanding how species are distributed along the environmental gradient and the processes and mechanisms that shape communities remains a challenging topic, resulting in many theories and hypotheses (Lewis et al., 2017). These processes and mechanisms can be affected by various factors, including resource availability, environmental conditions, climatic and anthropogenic changes, and interspecies relationships (Verberk et al., 2013). Comprehending how different species interact allows us to identify which ones have better fitness and how the loss of certain species can affect the overall stability of the community (Moeslund et al., 2017) often generating a cascading effect of biodiversity loss and ecosystem services in a locality or region.

For a species to occur in a particular environment, the environmental conditions must be within the constraints defined by its niche (Hutchison, 1957), and resource availability must not be limited, allowing for resource sharing with other species (Beaudrot et al., 2013; Weinstein et al., 2017; Carscadden et al., 2020). When species have overlapping niches and limited resources, competition becomes intense, potentially leading to niche reduction and even competitive exclusion (Bardou et al., 2021). Thus, the delicate balance between resource availability, interspecies interactions, and environmental conditions determines which species can coexist in a given ecosystem (Weinstein et al., 2017).

Within the total diversity of a region or the regional pool, we can find species that frequently co-occur in certain locations (considered ecologically equivalent) but not in others. This distribution pattern is defined as dark diversity (Pärtel et al., 2011), representing the “lost” or “hidden” potential of the community. Species that comprise dark diversity are associated with specific conditions and, even though they may not be locally present, they are capable of colonizing a habitat as long as they are regionally present (Pärtel et al., 2011; Cantanhêde et al., 2023). However, these species must have a good dispersal capacity, a trait directly related to low dark diversity. Conversely, species that have difficulty moving between habitats contribute more to the dark diversity of a region (Moeslund et al., 2017; Leitão et al., 2018).

Gathering information about dark diversity can enhance our comprehensive understanding of the regional species pool. When a community exhibits a high level of dark diversity, it suggests that many species are at risk of extinction, highlighting the need for increased conservation efforts in these areas (Lewis et al., 2016; Moeslund et al., 2017). The inference of dark diversity also includes species that evade detection through traditional inventory methods (Cornell and Harrison, 2014; Zobel, 2016). Thus, dark diversity complements alpha, beta, and gamma diversities by indicating the absence of potentially present species, providing a perspective on complementarity (Pärtel et al., 2011).

Dark diversity within a community can be influenced by factors such as species morphology, behavior, and environmental characteristics (Verberk et al., 2013; Riibak et al., 2015). Functional traits (morphological and behavioral characteristics that directly influence species fitness and ecological role within an ecosystem) influence their ability to interact with the environment and other species, thereby affecting their realized niche (Cadotte et al., 2015). Environmental filters are mechanisms that select species based on their traits, determining which species can persist in a given environment. These filters act by excluding species that do not meet certain environmental criteria, thus shaping community composition (Ronk et al., 2015; Pärtel et al., 2017). Anthropogenic disturbances, for example, can increase dark diversity within communities by modifying habitats and reducing resource availability, leading to the extinction or decline of remaining species. Even subtle changes can cause local extinction of the most sensitive species (Ronk et al., 2015; Pärtel et al., 2017; Xing and He, 2019; Zuquim et al., 2020; Rosalino et al., 2022).

Disturbance in freshwater ecosystems is a growing concern due to indiscriminate land use practices such as agriculture, livestock farming, logging, and mining, which impact both the ecological services provided by these ecosystems and their organisms (Azevedo-Santos et al., 2019; Dala-Corte et al., 2020). Loss of canopy cover, alterations in environmental integrity, and physical and chemical modifications of water are the primary causes of aquatic biodiversity loss (De Marco et al., 2015; Cantanhêde et al., 2023; Pereira-Moura et al., 2023). Deforestation of riparian zones allows increased solar radiation into aquatic ecosystems, raising air and water temperatures and carrying sediments that result in habitat loss for various aquatic organisms, leading to the turnover of species, where forest-dwelling species are replaced by those that thrive in open and sunny environments (Couceiro et al., 2010; De Marco et al., 2015).

Among aquatic organisms, insects are widely used in ecological and biomonitoring studies due to their sensitivity to environmental variations, as well as their good representation in terms of abundance, richness, and spatial distribution, making them excellent models for ecological and evolutionary studies (Mendes et al., 2017; Viana et al., 2020; Ma et al., 2021; Méndez-Rojas et al., 2021; Pereira-Moura et al., 2021). In this context, the order Odonata stands out for its notable taxonomic richness and diversity, responding to changes occurring both in streams and riparian vegetation, even when these changes are gradual rather than abrupt (De Marco et al., 2015; Miguel et al., 2017). Some Odonata species exhibit greater resilience to environmental conditions, while others are more vulnerable due to differences in behavior, morphology, and eco-physiology (Heilpern et al., 2018; Pereira et al., 2019; Basto et al., 2021a). Therefore, the compositions of local communities are is expected to result from the interaction between environmental filters and the functional traits of individuals (Verberk et al., 2013).

Given these changes, studying the dark diversity of Odonata is essential to understanding the unrealized ecological potential in different habitats. Investigating this aspect of diversity makes it possible to identify gaps in local and regional Odonata communities and better understand the impacts of environmental changes (De Marco et al., 2015; Pereira et al., 2019). Furthermore, analyzing dark diversity can guide the development of more effective conservation strategies, such as habitat restoration and the facilitation of recolonization by absent species, thereby supporting the maintenance of biodiversity and ecological balance (Pärtel et al., 2011; Cantanhêde et al., 2023). Additionally, integrating this knowledge into urban and agricultural planning can help balance human development with biodiversity conservation, ensuring a sustainable environmental legacy for future generations (Pärtel et al., 2011).

Considering the mosaic of Amazonian landscapes and the increasing advancement of land use, which creates diverse environmental gradients, this study aims to evaluate which functional traits and environmental factors influence the dark diversity of adult Odonata. We tested two hypotheses: (1) physical and chemical water properties (oxygen, pH and water temperature), habitat structure will influence the dark diversity of Odonata, with canopy cover expected to have significant explanatory power due to its direct impact on various ecological aspects of the studied group of insects; and (2) functional traits that enhance dispersal capacity, such as wing length and width, and thorax width, will be associated with lower dark diversity.

MATERIALS AND METHODS

Study Area

This study was conducted in 128 first to third-order streams (Strahler, 1957) in the cities of Belterra (n = 20), Mojuí dos Campos (n = 23), Oriximiná (n = 12), Santarém (n = 23) (Western region), and Paragominas (n = 50) (Northeast region) in the state of Pará, Eastern Amazon (Figure 1). Sampling was done during the dry season in the region, specifically in August 2010, August 2011, and July/August 2023.

In Paragominas, the predominant vegetation is originally dense tropical rainforest (Rocha et al., 2023), which has been extensively deforested primarily due to agricultural expansion and logging activities (Berenguer et al., 2014). The climate in the region is humid tropical, with a well-defined rainy season from December to May and a dry season from June to November, with an average annual temperature of around 27°C, average annual precipitation of 1,766 mm, and relative humidity around 81% (Rocha et al., 2023). In Santarém, Belterra, and Mojuí dos Campos, the vegetation consists of a mix of humid tropical rainforest and savanna areas, known as natural fields or "Amazonian cerrado" (Rente, 2006). The climate is humid equatorial, with abundant rainfall throughout the year, more concentrated between December and May (Silva, 2008). The average annual temperature is 28°C, with an average annual precipitation of 2,300 mm and relative humidity around 86% (Nepstad et al., 2002). The metropolitan region (Belterra, Mojuí dos Campos, and Santarém) faces environmental challenges such as deforestation, agricultural expansion, and urbanization (Penteado, 2013). Oriximiná has extensive areas of humid tropical rainforest, which can be subdivided into upland forests, floodplain forests (igapó), and campinaranas (low vegetation on sandy soils). The climate in Oriximiná is humid equatorial, with well-distributed rainfall throughout the year, highest from December to May, and an average annual temperature around 22°C, with an average annual precipitation of 2,250 mm and a relative humidity of approximately 85% (Cruz et al., 2022). Oriximiná also faces environmental challenges related to bauxite mining and deforestation (Bevilacqua et al., 2019).

Sampling, sorting, and identification of adult Odonata

Sampling of adult Odonata specimens followed the fixed-area sweep methodology. The sweep method establishes a 100-meter transect along stream margins, divided into 20 segments of five meters each (Batista et al., 2020), where the sampler actively collects Odonata using an entomological net. Sampling occurred from 09:00 to 14:00 hours on sunny days to ensure that all thermoregulatory groups could be active during sampling (Oliveira-Júnior and Juen, 2019), with an average time spent at each stream of one hour (Juen and De Marco, 2011). Specimens collected were stored in paper envelopes and transported to the laboratory, where they were immersed in acetone for 48 hours (Anisoptera) or 24 hours (Zygoptera) to preserve coloration and important structures for identification. Subsequently, specimens were placed in plastic envelopes on cardboard for identification and collection (Lencioni, 2017). For species identification, specialized taxonomic keys were used (e.g., Garrison et al., 2006; Lencioni, 2006, 2017; Garrison, 2009; Garrison et al., 2010; Garrison and Von Ellenrieder, 2012; Von Ellenrieder, 2015), and structures such as wings and genitals were observed under a stereomicroscope. After identification, the material was deposited in the Laboratory of Ecology and Conservation (Labeco) collection at the Federal University of Pará in Belém, where it is available for consultation.

Environmental variables

Following the published literature, we measured environmental variables that represent important structural components for the Odonata assemblage, such as canopy cover and Habitat Integrity Index (De Marco et al., 2015; Oliveira-Junior and Juen, 2019; Resende et al., 2021a). Canopy cover was measured using a convex spherical densiometer with 24 quadrants and readings taken in four directions (North, South, East, and West), positioned one meter from the water surface and facing towards the tree canopy, at the beginning, middle, and end of transects (Veras et al., 2020). The calculation of the Habitat Integrity Index (HII) includes 12 questions aimed at characterizing the landscape, generating values between 0 and 1, where values closer to 0 indicate more altered sites and values closer to 1 indicate more intact sites (Nessimian et al., 2008). The application of HII is visual, where a researcher observes the landscape and answers the questions accordingly. For the physical and chemical variables of the water, an Akso Ak88 multiparameter probe was used. Measurements of dissolved oxygen (DO), water temperature (Temp), and hydrogen potential (pH) were taken at the beginning, middle, and end of each transect to obtain average values. These variables are directly related to water quality and the surrounding environment and are important metrics for the aquatic communities (Brasil et al., 2020).

Functional traits

To represent the morphological variation of the species sampled within this study, we conducted seven morphological measurements: body total length (BTL), thorax length (TL), thorax width (TW), abdomen length (AL), forewings and hindwings length (FWL and HWL), and forewings and hindwings width (FWW and HWW). These metrics influence flight/dispersal ability and thermoregulation, which are crucial for Odonata ecology (De Marco et al., 2015; Pereira et al., 2019; Oliveira-Júnior et al., 2019). Measurements were taken for specimens sampled in 2023 using a digital caliper, while for specimens sampled in 2010/2011, measurements were extracted from the Amazon Odonata database (Ferreira et al., 2023).

Four behavioral characteristics were defined for each species: (1) flight type, (2) oviposition behavior, (3) thermoregulation strategy, and (4) territory defense. These characteristics were selected for their potential to reflect the specificities and ecology of the group. Data were extracted from the "Odonata da Amazônia" database (see Ferreira et al., 2023). When species-specific characteristics were not available, characteristics at the genus or higher taxonomic level were used. Flight type considered flying and perching groups; oviposition behavior considered endophytic, epiphytic, exophytic, and phytotelmic groups; thermoregulation strategy considered endothermic, heliothermic, and conformer groups; and territory defense considered territorialist and non-territorialist groups (May, 1976, 1991; Miguel et al., 2017).

Data analysis

To assess the efficiency of sampling, a species accumulation curve was constructed using the first-order Jackknife non-parametric richness estimator with a total of 9999 randomizations (Mendes et al., 2017). This estimator accounts for the rarity of specimens occurring in only one stream, regardless of abundance (Gotelli and Ellison, 2016).

The assumptions of normality (Shapiro-Wilk test $p = 0.198$) and homogeneity (Bartlett's test $p = 0.102$) were met. A Pearson correlation analysis and variance inflation factor (VIF) analysis were used to evaluate the correlation and multicollinearity of environmental and physical and chemical variables (variables with a correlation value of $\geq 70\%$ and multicollinearity above 10 should be removed from the model). No variable had a VIF > 10 or correlation above 70%, thus they were retained in the analysis.

To estimate species composition variation among samples (128 streams), Principal Coordinates Analysis (PCoA) with the Bray-Curtis distance matrix was employed. Principal Component Analysis (PCA) with Euclidean distance matrix was used to demonstrate variation in environmental data. Additionally, Principal Component Analysis (PCA) with Euclidean distance matrix was used to illustrate variation in morphological data.

Dark diversity

Dark diversity was estimated based on species co-occurrence patterns (Lewis et al., 2016; Cantanhêde et al., 2023). Taxa are considered components of dark diversity when they are absent in a particular stream but frequently co-occur with the same species in other locations, assuming that these species have similar ecological requirements (equivalent species) (Lewis et al., 2017). For this purpose, the Beals Index was used with presence-absence data (Beals, 1984):

$$P_{ij} = \frac{1}{S_i - I_{ij}} \sum_{k \neq j} \frac{N_{jk} I_{ik}}{N_k}$$

where S_i is the number of species at site I, I_{ij} is the incidence (0, 1) of species j at site I, N_{jk} is the number of sites where species j and k co-occur, I_{ik} is the incidence (0, 1) of species k at site I, and N_k is the number of occurrences of species k. The Beals Index was calculated using the “beals” function (De Cáceres and Legendre, 2008) in the vegan package in R (R Development Core Team, 2020). This index generates values for each species in each stream, where a value of 1 indicates that the species contributed and a value of 0 indicates that the species did not contribute to dark diversity in that stream.

To test the first hypothesis, that physical and chemical water and structural variables influence dark diversity with a stronger explanation from canopy coverage, we used a generalized linear model (GLM, quasi-Poisson due to high overdispersion) using values generated by the Beals Index mentioned earlier.

To test the second hypothesis, that functional (morphological and behavioral) traits enhancing dispersal capacity, such as wing and thorax length and width, are associated with low dark diversity, we also used a GLM. The relative contribution of a species to dark diversity was represented by the number of times it participated in dark diversity across all streams, using the formula Di × 100 / T, where Di is the number of times species i contributed to dark diversity and T is the total dark diversity of all species across all streams. GLM analyses were performed using the 'glm' function from the stats package with the quasi-Poisson family due to high overdispersion, in the R statistical environment (R Core Team, 2020).

RESULTS

We collected a total of 4031 specimens, distributed across 42 genera and 141 species (Supplementary Table 1), of which 21 species were represented by a single specimen. *Erythrodiplax basalis* (N = 330) and *Erythrodiplax fusca* (N = 247) were the most abundant Anisoptera species, while *Mnesarete aenea* (N = 310) and *Mnesarete smaragdina* (N = 272) were the most abundant Zygoptera. A sampling efficiency of 91% of the species was observed, with an estimated richness of 153.19 (±6.22) species. The analysis of the Odonata assemblage structure exhibited significant dissimilarity in species composition among the sampled streams, with Principal Coordinate Analysis explaining only 34.2% of the variation in species composition (Figure 2). This allows us to see which sites exhibit the greatest similarity in species composition, as well as which species commonly co-occur.

The sampled streams exhibited variation in their structure, with sites ranging from low integrity values (HII = 0.15) to high integrity values (HII = 0.99). Regarding canopy cover, a wide variation was observed, ranging from 2% to 99.46% vegetative coverage. The water temperature varied greatly, covering a range of 7ºC, with a minimum of 22.5ºC and a maximum of 29.9ºC. The pH ranged from 2.48 to 7.75, and dissolved oxygen levels varied between 1.47 and 16.47 (Supplementary Table 2). Aquatic environment structures exhibited considerable dissimilarity among the sampled streams, where PCA explained 61.23% of the data variation. The variables contributing most to the first axis were HII and canopy cover (positively related) and water temperature (negatively related). For the second axis, dissolved oxygen (positively related) and pH (negatively related) were the primary contributors (Figure 3). When assessing the impact of physical and chemical variables water and habitat structure on dark diversity, no model adequately explained the variation in dark diversity, as no significant variables were identified. Examining the distribution of dark diversity values highlighted higher values in areas with intensive land use, suggesting that greater alteration of natural conditions correlates with higher dark diversity (Figure 4).

The PCA explained 95.07% of the morphological data variation, demonstrating species differences (Figure 5). The variables that most contributed positively to the formation of the first axis were FWL, FWW, HWL, HWW, TW, and TL. For the second axis, the variables that contributed positively were TBL and AL (Figure 5). Behavioral traits were not significant in the model (Table 1). The functional traits that contributed most to the increase in dark diversity were collectively: FWW, HWL, TW, and AL (Table 1). The occurrence of dark diversity was negatively correlated with the width of the forewings, width of the thorax, and length of the abdomen, while it was positively correlated with the hindwing length (Table 1). The species that contributed most to dark diversity were *Neoneura luzmarina* (6.86% occurrence in dark diversity), *Argyrothemis argentea* (4.57%), *Micrathyria artemis* (4.41%), *Psaironeura tenuissima* (4.08%), *Oxystigma petiolatum* (3.75%), and *Phasmoneura exigua* (3.59%).

Table 1. GLM results showing values of morphological variables contributing to increased dark diversity in the Odonata assemblage in Amazonian streams.

Variables	Statistical values			
	Estimate	Std. Error	t	p
Forewing Width	-0.790	0.211	-3.725	<0.001
Hindwing Length	0.374	0.092	4.051	<0.001
Thorax Width	-0.691	0.305	-2.265	<0.05
Abdomen Length	-0.130	0.361	-3.604	<0.001
Flight type	-0.284	0.556	-0.511	>0.05
Oviposition behavior	-0.372	0.259	-1.433	>0.05
Thermoregulation strategy	-0.072	0.230	-0.313	>0.05
Territory defense	0.0760	0.316	0.243	>0.05

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DISCUSSION

The dark diversity was not influenced by the measured environmental characteristics, as none of the models were statistically significant. This contrasts with other studies that have found correlations between these factors and dark diversity (Riibak et al., 2015; Ronk et al., 2015; Moeslund et al., 2017; Teixeira-Santos et al., 2020; Cantanhêde et al., 2023). GLM analysis demonstrated that environmental variables had no effects on the dark diversity of Odonata adults. Although the relationship between dark diversity and canopy cover was statistically insignificant, it was inversely proportional, suggesting that higher canopy cover corresponded with lower dark diversity. Sites with lower canopy cover experience higher temperatures and more direct radiation, typically offer fewer microhabitats (lower diversity of available microhabitats). These conditions favor only a narrow range of species able to tolerate such extremes, while sites with greater canopy cover tend to support higher species diversity, leading to lower dark diversity.

Environmental factors are well known to filter taxa richness, abundance, and composition in Odonata by selecting species based on their morphological and behavioral traits (Fulan et al., 2011; De Marco et al., 2015; Alves-Martins et al., 2019; Pereira et al., 2019; Vilenica et al., 2020; Resende et al., 2021a; Rocha et al., 2023). While canopy cover and environmental integrity did not appear to influence dark diversity in this study, numerous works have demonstrated their significance in shaping Odonata distribution (De Marco et al., 2015; Bastos et al., 2021b; Dolný et al., 2021; Pereira-Moura et al., 2021; Resende et al., 2021a; Rocha et al., 2023). These environmental variables remain crucial in shaping species distribution and abundance, even if their role in dark diversity may require further exploration. Human-induced alterations such as habitat fragmentation and pollution can change these conditions, potentially increasing dark diversity (Cam et al., 2000; Ronk et al., 2015; Pärtel et al., 2017; Fernandes et al., 2019; Fløjgaard et al., 2020). Our study revealed structural differences among streams due to land use (Figure 3), as observed in sites (357-5, 369-1, UA2, and UA23) exhibiting low Habitat Integrity Index (HII) values and canopy cover, for example (Figure 3 and Supplementary Table 2). Therefore, we expected dark diversity to be influenced by environmental conditions, given its direct relationship with species presence/absence.

However, some Odonata morphological features were associated with higher values of dark diversity. More precisely, species with narrower wings have contributed more to dark diversity than those with broader wings, which is consistent with the expectation that characteristics enhancing dispersal are associated with lower values of dark diversity (Moeslund et al., 2017; Leitão et al., 2018; Cantanhêde et al., 2023). This morphological feature is directly related to flight type and duration, where narrower wings provide greater maneuverability to navigate around obstacles created by vegetation, whereas broader wings offer better efficiency for sustained flight (Wootton, 1991; Johansson et al., 2009; Pereira et al., 2019). This pattern has also been observed in other flying insects (Flockhart et al., 2017), as well as in bats (Norberg and Rayner, 1987) and birds (Voelker, 2001; Calmaestra and Moreno, 2001; Vágási et al., 2016). Studies demonstrate that airflow over wings generates small circular currents essential for lift and drag relationships during flight, and larger wings are more efficient for gliding, thereby enhancing species fitness (Thomas et al., 2004; Bomphrey et al., 2016; Blanke, 2018; Pereira et al., 2019).

The thorax width was another characteristic inversely proportional to dark diversity.

Some Odonata species may have up to 71 muscles in the thoracic region, many of which facilitate wing movement either directly or indirectly, allowing each wing to move independently, resulting in the ability to hover, glide, and even fly backwards (Büsse and Hörnschemeyer, 2013; Rüppell and Hilfert-Rüppell, 2013; Bäumler et al., 2018; Bäumler and Büsse, 2019). Alongside the wings, the thorax is responsible for flight, making them voracious hunters (Bäumler et al., 2018; Bäumler and Büsse, 2019). De Marco et al. (2015) hypothesized a relationship between body size and thermoregulation capacity, where smaller individuals, hence with smaller thoraxes, exchange heat through convection – meaning their body temperature varies with the environment – limiting the dispersal capacity of smaller species in environments where the air temperature is higher, potentially causing protein denaturation, for instance (May, 1991; Pereira-Moura et al., 2023).

In our study, we observed that species with shorter abdomen length contributed more to dark diversity, although a direct relationship between the abdomen size and Odonata dispersal has not yet been observed, it has important roles in various aspects of biology and ecology of these insects, serving purposes such as mating, oviposition, and even body temperature control (May, 1976, 2017). Many species have developed thermoregulation strategies using their abdomen, such as perching with the abdomen raised in the obelisk position, minimizing the surface exposed to sunlight. Others go further, by either maintaining hemolymph in the thorax to conserve temperature or circulating it through the abdomen to reduce thoracic temperature (May, 1976, 1991; Corbet and May, 2008). Employing these strategies, flying individuals, which spend most of their time in flight, can sustain longer flights without overheating, thereby covering greater distances compared to those unable to direct hemolymph to their abdomen (Corbet and May, 2008).

The species that have contributed the most to dark diversity (*Neoneura luzmarina*, *Argyrothemis argentea*, *Micrathyria artemis*, *Psaironeura tenuissima*, *Oxystigma petiolatum*, and *Phasmoneura exigua*) follow the pattern described by the second hypothesis model, exhibiting smaller wings, thorax, and abdomen. Even *Argyrothemis argentea* and *Micrathyria artemis*, belonging to the suborder Anisoptera, which is typically represented by larger individuals, are diminutive compared to other Anisoptera species. Although behavioral traits were not significantly associated with dark diversity, they could still have an indirect effect on it by influencing how species interact with the environment. *Neoneura luzmarina*, *Psaironeura* *tenuissima, Oxystigma petiolatum*, and *Phasmoneura exigua*, as well as many Zygoptera exigua exhibit thermal conformal thermoregulation (De Marco Jr and Vital, 2008; Brasil et al., 2014; Dalzochio et al., 2018; Silva et al., 2021), meaning their body temperature varies with the surrounding environment (May, 1976). Consequently, high temperatures can act as barriers to their dispersal, limiting their presence to locations with greater canopy cover (De Marco et al., 2015; Silva et al., 2021). In contrast, *Argyrothemis argentea* and *Micrathyria artemis* are classified as perchers and territorial species. They spend most of their time perched, flying only for short prey captures or to defend their territories. These behavioral traits thus associate them with specific habitats (Michalski, 2015). The traits contributing to their presence in dark diversity often include specialized habitat preferences, limited adaptability to altered environments, and low resilience to disturbances, making them vulnerable to habitat loss and climate change (Pärtel et al., 2011). This highlights the importance of understanding species ecological requirements and dispersal abilities when assessing dark diversity and conservation priorities.

Understanding dark diversity within communities brings interesting implications for our biodiversity comprehension. The presence of dark diversity suggests that there may be species capable of inhabiting certain habitats yet are not observed there (Pärtel et al., 2011, 2017). Exploring and discovering these species provides valuable insights into ecological dynamics and community resilience, raises questions about factors influencing species distribution, potential impacts of environmental changes on communities, and contributes to more comprehensive conservation strategies that address not only known species but also those with potential to colonize (Riibak et al., 2015; Ronk et al., 2015; Moeslund et al., 2017; Pärtel et al., 2017; Boussarie et al., 2018; Teixeira-Santos et al., 2020; Cantanhêde et al., 2023).

The literature on dark diversity has been expanding in recent years, consistently highlighting its importance for conservation and restoration practices by identifying the mechanisms and processes that determine why some species are part of dark diversity while others are not (Riibak et al., 2015; Lewis et al., 2017; Moeslund et al., 2017). The environmental effect on dark diversity has been documented in other research, such as in fish (Boussarie et al., 2018; Cantanhêde et al., 2023), plants (Riibak et al., 2015; Ronk et al., 2015; Moeslund et al., 2017), mammals (Teixeira-Santos et al., 2020), and fungi (Pärtel et al., 2017).

However, caution is warranted when using dark diversity in Odonata, as this approach has so far not effectively detected the effects of environmental gradients on absent species. While previous studies have demonstrated its efficiency for some other taxonomic groups, it has not been proven as effective for Odonata. As predicted by Pärtel et al. (2011), species with high dispersal capacity contribute less to dark diversity. As Odonata are known for their remarkable dispersal abilities, this may contribute to explaining the ineffectiveness of dark diversity in detecting the effects of the environmental gradient on species that are absent from that specific group. Essentially, the high dispersal capabilities of Odonata may limit the utility of dark diversity measures in reflecting habitat alteration or differences in habitat characteristics for this group.

Some other approaches may contribute more to our understanding of the ecology of Odonata and to the assessment of environmental quality. Studies that combining ecological niche models with occupancy-detection data can provide more robust estimates and minimize uncertainties (Medina-Romero et al., 2019; Botero-Delgadillo et al., 2022). Intensifying sampling efforts over time, increasing sample size, and covering different seasonal periods to create a temporal series, or even applying metabarcoding and environmental DNA, can help rapidly and accurately identify and monitor the biodiversity of biological communities (Deiner et al., 2017; Miya, 2022). This technique is widely used in ecological studies, conservation, environmental monitoring, and ecosystem health assessments, as it detects multiple species simultaneously, including rare, cryptic, or difficult-to-identify species using traditional methods (Botero-Delgadillo et al., 2022; Miya, 2022).

CONCLUSION

To mitigate biodiversity loss, it is crucial to develop conservation practices. To do this, we have to identify and understand mechanisms that determine why certain species are absent even in apparently suitable habitats. This is one aspect through which dark diversity can help clarify conservation issues. Despite its counterintuitive nature, the absence of certain species provides valuable insights into the health and dynamics of an ecosystem. It highlights the potential for environmental recovery, points to species that could recolonize the area, or reveals issues related to habitat fragmentation and connectivity.

Our results showed that morphological features promoting dispersal in Odonata, such as wing and thorax size, are strongly associated with dark diversity, where individuals limited by their morphological traits have contributed most to dark diversity. The dispersal limitations of some Odonata species strongly suggest the role of space and time in nature planning and management. With sufficient time and adequate corridors for dispersal, even weak dispersers can reach suitable habitats that are farther away. Given the challenges in sampling certain individuals, whether due to foraging times or extensive flight ranges, the absence of some species may have contributed to the dark diversity recorded in our study.

AUTHOR CONTRIBUTION

Conceptualization: LPM, SRMC and LJ. Developing methods: LPM, CGV and LJ. Data analysis: LPM, CGV, LJ and SRMC. Preparation of figures and tables: LPM, CGV and SRMC. Conducting the research, data interpretation, writing: LPM, CGV, LJ and SRMC.

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Figure list

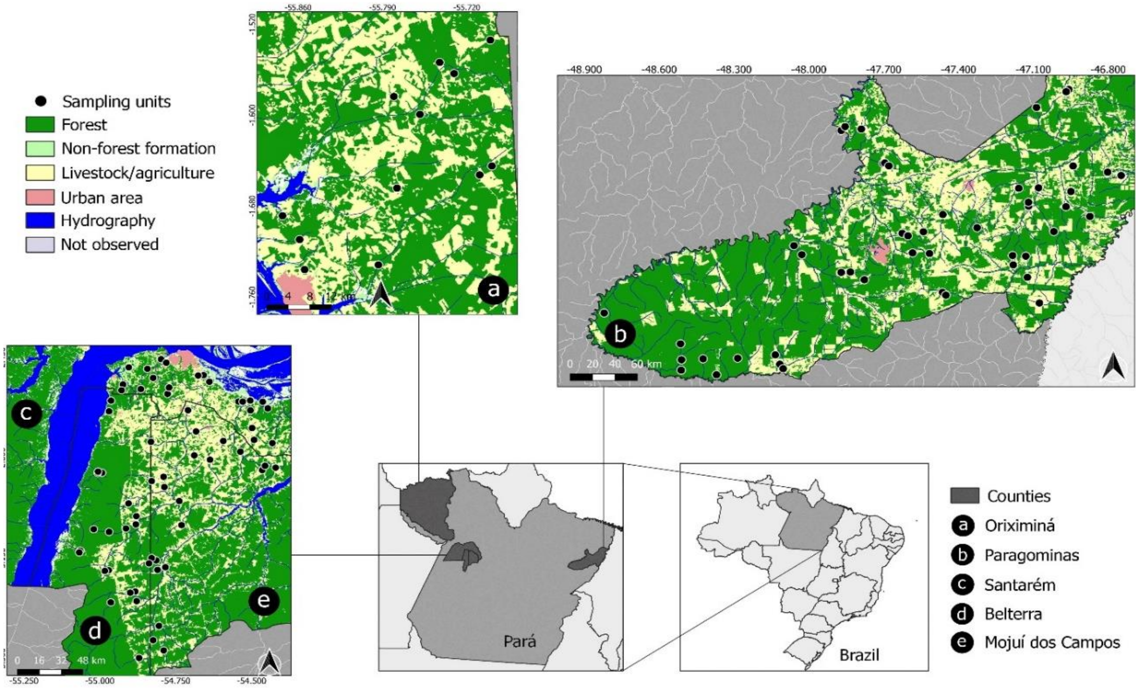


Figure 1. Sampled streams of adult Odonata in the municipalities of Belterra, Mojuí dos Campos, Oriximiná,

Santarém, and Paragominas in Pará state, Brazil.

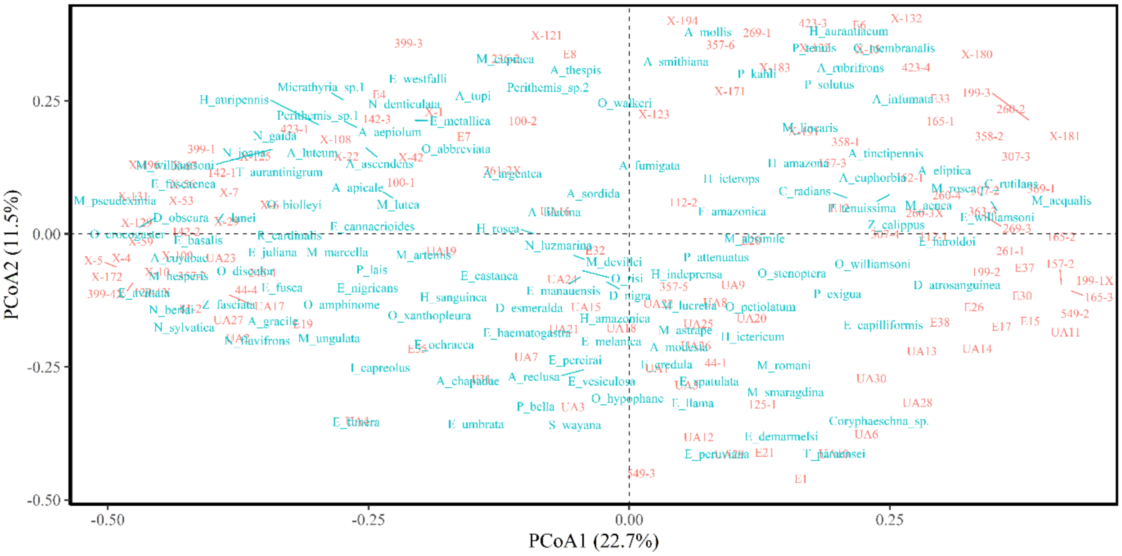


Figure 2. PCoA with variation in species composition among samples. Full species names are in Supplementary Table 1. Site coordinates are in Supplementary Table 2.

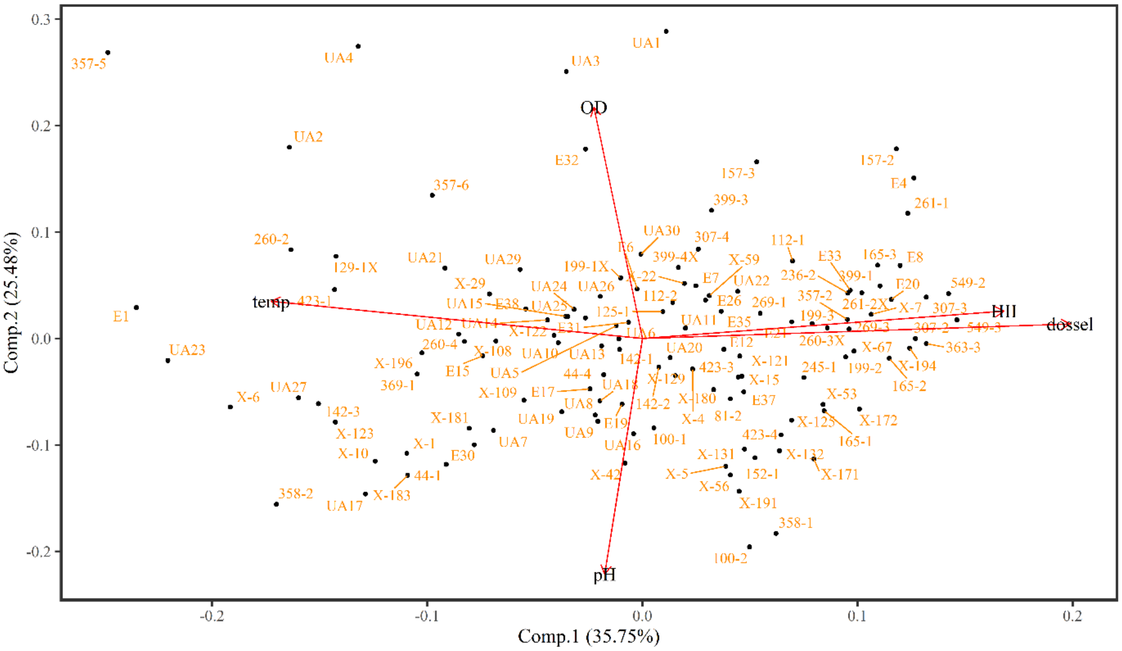


Figure 3. PCA with variation of environmental data of studied streams. OD = dissolved oxygen; temp = water temperature; pH = hydrogen potential; HII = habitat integrity index; dossel = percentage canopy cover.

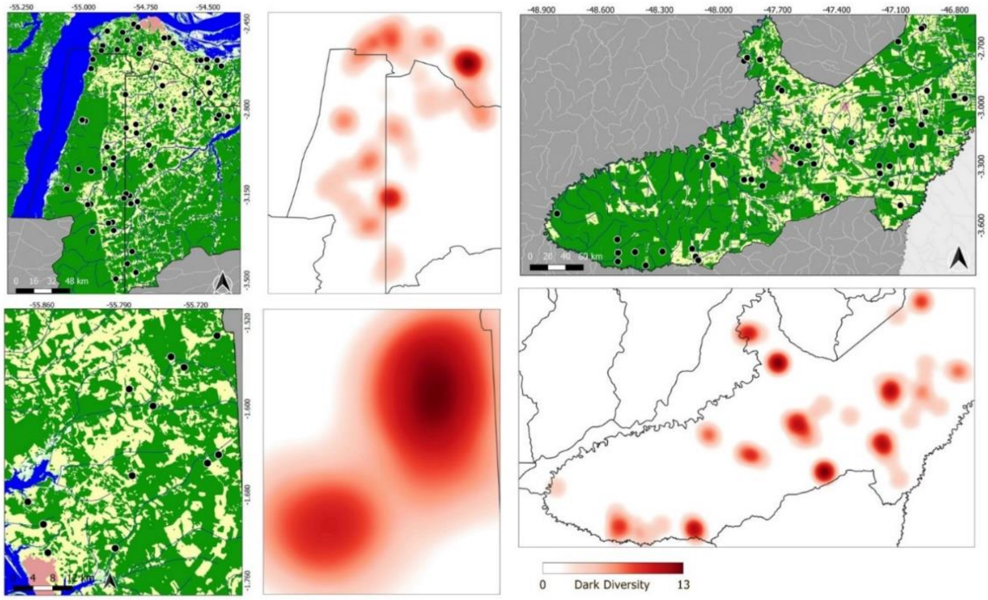


Figure 4. Heatmap showing points with higher dark diversity values within the study area, Pará state, Brazil.

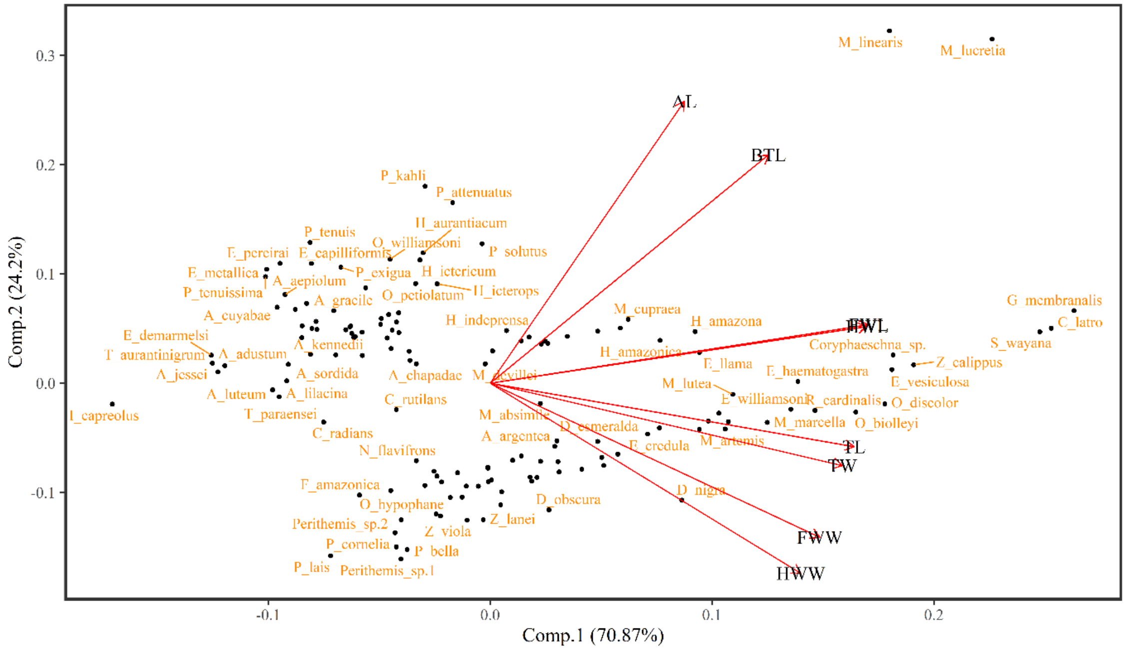
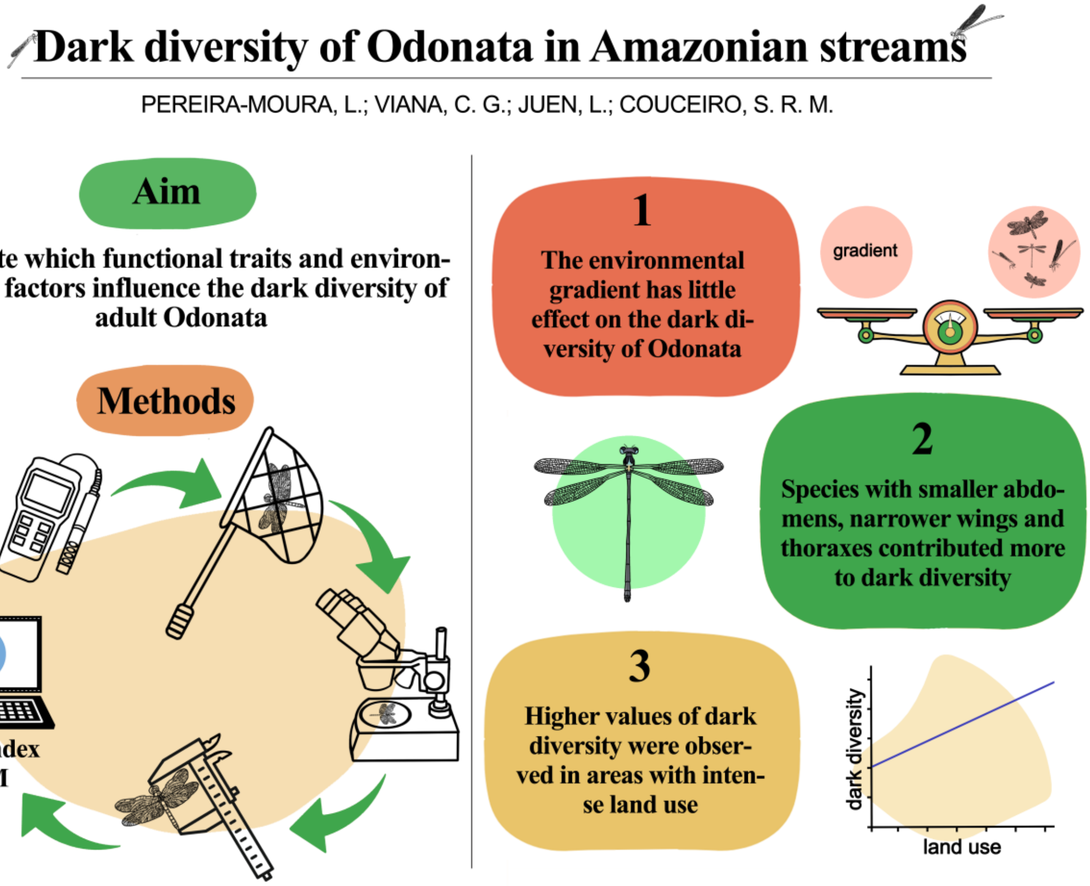


Figure 5. PCA with variation of morphological data from sampled specimens (species). BTL = Body Total Length; FWL = Forewing Length; FWW = Forewing Width; HWL = Hindwing Length; HWW = Hindwing Width; TL = Thorax Length; TW = Thorax Width; AL = Abdomen Length.

Conflict of Interest

All authors declare that there is no conflict of interest.

Graphical abstract



Dark diversity of Odonata in Amazonian streams

PEREIRA-MOURA, L.; VIANA, C. G.; JUEN, L.; COUCEIRO, S. R. M.

Aim

Evaluate which functional traits and environmental factors influence the dark diversity of adult Odonata

Methods

1

The environmental gradient has little effect on the dark diversity of Odonata

2

Species with smaller abdomens, narrower wings and thoraxes contributed more to dark diversity

3

Higher values of dark diversity were observed in areas with intense land use