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
Changes of Phylogenetic and Taxonomic Diversity of Odonata (Insecta) in Response to Land Use in Amazonia

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Abstract: Changes in natural habitats for human use can alter the distribution of biodiversity, favoring species that are more tolerant to environmental disturbance. Usually, these species comprise clades of habitat generalists, which have biological mechanisms to colonize environments with different environmental conditions. However, such effects are still poorly understood for most biological groups, such as the Amazon odonates. Therefore, this study aims to evaluate the effects of land use along an environmental gradient on the phylogenetic and taxonomic diversity of Odonata in the Amazon. We tested the following hypotheses: In deforested areas (e.g., pasture for cattle, palm plantation, and logging), the Odonata community will be more taxonomically and phylogenetically impoverished than in forested areas. We assume that the modification of the natural habitat causes loss of specialist forest species and favors specialist species of open areas and/or habitat generalists. Data sampling was performed in 195 streams under different land-use types: livestock areas, palm monoculture, timber exploitation, and forest areas taken as reference sites. Our results showed that anthropogenic impacts affected the phylogenetic diversity of odonates and the increase in shrub vegetation was related to the increase in the phylogenetic diversity of communities. On the other hand, shrub vegetation is indicative of disturbed areas, where secondary vegetation predominates, with less canopy cover due to the absence or discontinuity of the native tree cover in these habitats. Nonetheless, species richness and abundance were not related to the effects of anthropogenic land use. Finally, our results suggest that the phylogenetic diversity of Amazonian odonates is related to riparian vegetation structure.

Keywords: Amazonian streams; Brazilian Amazonian Forest; loss of natural habitat; landscape structure; phylogenetic structure

1. Introduction

The search to understand how species are distributed and what processes affect their distribution patterns has always been a major challenge for researchers addressing community ecology problems [1]. This is due to the increasing rate of environmental changes, resulting in biodiversity loss and depletion of ecosystem services [2,3]. In this context, for assessing environmental changes, some groups such as odonates are remarkably good models for studies on ecological dynamics, behavior, and evolutionary biology [4–6]. This is because of their sensitivity to changes in the aquatic environment, high species diversity, and association with different types of aquatic environments as well as living on the

boundary with the terrestrial environment [7]. Although, for Odonata, there is a noticeable recent increase in the number of ecological studies, some approaches are still scarce, such as evolutionary approaches, due to the difficulties in measuring phylogenetic relationships among species [8,9]. This knowledge gap has led many studies to consider species as independent entities with equivalent environmental importance and function [10]. However, the closer species are phylogenetically, the more likely that they will respond in a similar way to the environmental changes, both in function for ecosystem services and in response to environmental conditions [11–13].

In this perspective, environmental variation and changes in natural habitats resulting from anthropogenic uses can promote the distribution of species more tolerant to altered habitats [14,15]. Phylogenetically, it is expected that clades composed of more habitat-generalist species should be found in habitats modified for land use (e.g., monoculture, pasture, and urban habitats), as they are considered capable of colonizing environments with different environmental conditions, due to differences in behavioral responses and thermoregulatory strategies [6,16]. Due to the specificity of habitat requirements, some Odonata species are restricted to streams with vegetation cover that consists of taller plants and are represented by smaller-sized individuals that spend most of their time perched and are considered forest specialists [17]. On the other hand, many species have positive relationships with habitats in open areas and consist mostly of individuals with larger body-sizes. This latter group have the specific habit of staying in open areas where they can thermoregulate more efficiently [18]. Theoretically, odonates are classified into three thermoregulatory groups: (1) Thermal conformers, which present smaller body sizes and show higher conductance, in which body temperature varies with the environment, mainly due to heat exchange [19]; (2) Heliothermic, which have larger body sizes and consequently lower conductance, with activities determined primarily by solar irradiation; and (3) Endothermic, which are able to produce heat by controlling hemolymph movement, flight, and wing-whirring [20].

These patterns are the result of interactions between species metabolism and heat exchange with the environment. Smaller-sized individuals have a high surface-to-volume ratio and consequently thermoregulate by gaining or losing energy according to the variation in environmental temperature [21,22]. On the other hand, for larger species, the surface-to-volume ratio is lower, decreasing the efficiency of body temperature changes by environmental heat exchange [22]. Consequently, individuals from this latter group are more tolerant of solar-irradiated environments [23,24]. Due to the influence of thermoregulation strategies on species distribution, the transformation of the landscape for anthropogenic uses may cause the replacement of the forest specialists by the species from open areas and/or habitat generalists [14,25]. However, so far, it is not known whether this filter is random among the species of each group or whether there is a direct influence of evolutionary history (evolutionary inertia) on this environmental filtering [4].

In recent years, extensive use of renewable and non-renewable resources in the Amazon has occurred. Most of this exploitation is driven by rural development, resulting in a general change in land cover and consequently, high biodiversity loss [26,27]. This is most remarkable in regions with high traffic flow facilitated by roads and waterways that increase the potential for land-use change for agriculture or livestock [28]. This scenario is typical in the Belem Centre of Endemism [29], which is included in the "Arc of Deforestation", the region with the highest deforestation rates in Brazil [30]. These high rates were mainly promoted by the expansion of infrastructure (e.g., roads and hydroelectric power plants) and the emergence of new economic activities, such as mining, logging, livestock and soybean farms, and other industries [31,32]. In this region, deforestation increases land degradation and causes changes in species composition and fluctuations in climate conditions [33,34]. The effects of these changes are even more harmful to the most sensitive ecosystems such as aquatic ecosystems (e.g., small streams), which depend closely on riparian vegetation. Thus, any change in vegetation can affect biodiversity at the local and/or regional level [35–40].

At the local level, this transformation usually begins with the loss of riparian vegetation, resulting in the homogenization of substrates, contaminant leaching into water bodies, increasing margin erosion and changes in air and water temperature [41,42]. At the regional level, the loss of primary vegetation is most related to a decrease in the vegetation cover in drainage basins, leading to compaction and soil sealing, channeling of watercourses, as well as isolation among forest remnants, which can affect gene flow between areas [22]. In addition, most anthropogenic land uses can generate fragmented landscapes composed of secondary vegetation or areas in regeneration. Although secondary vegetation contributes to maintaining biodiversity, it is often not sufficient to support the physical structures in streams as expected for native forests [43]. Given these issues, this study aimed to assess the effects of land-use on the phylogenetic and taxonomic diversity of Odonata along an environmental gradient in the Amazon. Thus, we tested the following hypothesis: In deforested areas (e.g., pasture for cattle areas, palm plantation, and logging), the Odonata community will be more taxonomically and phylogenetically impoverished than in forested areas. We assumed that the modification of the natural habitat caused the loss of specialist forest species and favored species specialized in open areas and/or habitat generalists.

2. Material and Methods

2.1. Study Area

Sampling was performed in 195 streams in two areas of the eastern Amazon (Figure 1). The collections occurred along a land-use gradient, considering the land uses that most contribute to deforestation in this region of the Amazon [33]. In this framework, sampling was carried out in areas of cattle grazing [35], agriculture with palm monoculture [14], managed logging [7], and in forested areas [7,14,17]. Samplings were performed during the Amazonian dry season, from July to December of 2010 to 2017. The climate of both regions is classified as tropical forest AF (with rainfall occurring almost every month of the year) under the Köppen system [44], with an average annual temperature of 26 °C and an annual rainfall of up to 2500 mm, according to the National Meteorological Institute (INMET).
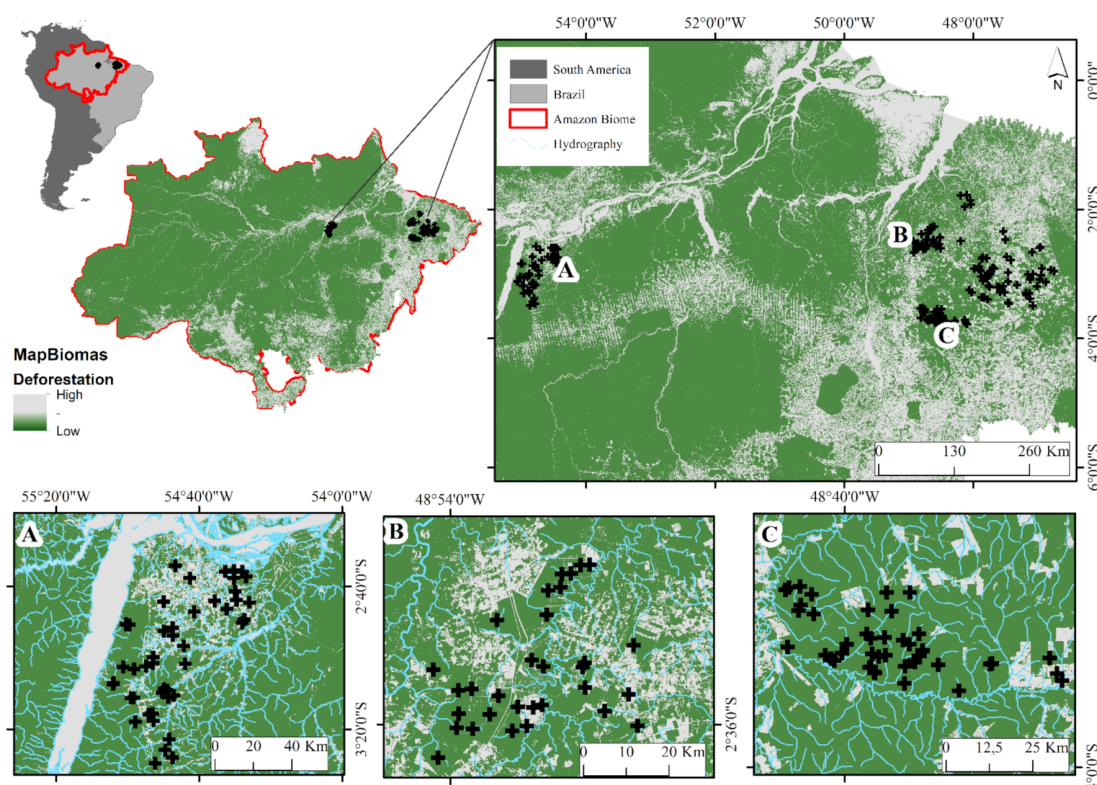

Figure 1. Study area (streams). Tapajos Basin (**A**), Capim basin (**B**) and Acará basin (**C**), in the Belém. Pará, Brazil. (Source: https://mapbiomas.org/; accessed on 20 May 2020).

2.2. Biological Sampling

The collection of Odonata specimens was based on a scanning sampling method within a fixed area, which has already been used in previous studies [45–48]. The sampling consisted of collecting adult individuals along a 150 m length of each stream; each 15 m section was divided into three segments, with sampling performed only within the two first segments, to ensure greater independence of the segments. The third segment was used to allow the observers to move among segments without disturbing the substrate (for further details, see [47]). We recognize that our sampling design does not result in complete species inventories; in particular, dragonfly species that fly far from the aquatic systems may have been omitted. However, our standardized method allows comparisons of community composition among streams. The average time spent at each sampled stream was one hour. The collections were carried out between 10 a.m. and 2 p.m.; this interval is the highest luminosity period in the riverbed [21]. These were the minimum conditions necessary to ensure that all Odonata groups (thermal conformers, heliothermics, and endothermics) were active at the time of collection [21,49]. The storage and conservation of the collected odonates followed the protocol described by Lencioni [50]. The specimens were deposited in the Zoology collection of the Laboratory of Ecology and Conservation of the Federal University of Pará.

2.3. Environmental Variables and Habitat Characterization

To assess the degree of habitat degradation, habitat variables (e.g., characteristics of riparian vegetation, channel morphology and canopy cover) were measured along each transect, following the instructions in the habitat monitoring protocol of [51,52]. Additional details and descriptions of the methods can be found in Juen et al. [53]. Dissolved oxygen (mg/L), conductivity (lS/m), hydrogen potential (pH), turbidity (mg/L), temperature (°C), and total dissolved solids (TDS) were measured and obtained with electronic equipment. To obtain the percentage of primary vegetation cover, we used images downloaded and processed by the National Water Agency (ANA). Information about microbasins was extracted following "Codification of hydrographic basins by the method of Otto Pfafstetter applied at ANA". We then used TerraClass, a project of the Brazilian government that produces systemic maps, to identify the use and coverage of deforested areas in the Brazilian Legal Amazon [54].

2.4. Phylogenetic Tree

The initial purpose was to infer a phylogenetic hypothesis containing all the Amazonian species known to date. For this, we conducted an extensive search of the literature, museum records, and unpublished data from our research group and other research groups in Latin America (members of Sociedad de Odonatologia Latinoamericana (SOL), (http://www.odonatasol.org/; accessed on 14 February 2019). We emphasize that the collection of Odonata from the Zoology Museum of the Federal University of Pará is one of those with the most significant representation of the taxon's biodiversity for the Brazilian Amazon. In addition, we also searched the Web of Science and SciELO platforms for additional information, in which the search terms phylog*, taxonom*, systematic*, clad* and Amazon* were used together with all the common scientific and common names of Amazonian odonates. After the initial research, all articles that potentially possessed phylogenetic trees were examined, and the references cited in the studies found were used to find additional publications. In total, 26 scientific studies were used to extract information on species' evolutionary relationships.

To reconstruct the phylogeny of odonates with Amazonian species (collection and scientific articles), we used the method "backbone", which is simply a taxa graft onto an existing phylogeny [55]. In this case, the phylogenetic hypothesis proposed by Waller and Svensson [56] was used as a "backbone" for the construction of the supertree (http://www.odonatephenotypicdatabase.org/shiny/shinyTree/; 10 January 2018). This phylogenetic hypothesis was built using 13 genetic markers and dated by using fossil records with

Bayesian inference. This hypothesis has all odonate families and about 21% of all described species; therefore, as far as the authors are aware, it is the most complete phylogeny. The species that occur in both oriental and occidental Amazon that were not included in the phylogeny by Waller and Svensson [56] are now manually included as polytomies at the base of their respective families or genera (Supplementary File S1). Using the phylogeny assembled by Waller and Svensson [56] as the backbone in the supertree procedure was necessary to avoid conflicts of information from different studies for the same families, as we did not carry out analyses to reconstruct the phylogeny. However, a compilation of data was the most parsimonious strategy to obtain the maximum amount of information [57].

We used the R platform to insert the Amazonian taxa and performed the following steps: Step 1: We numbered all the nodes. Next, we identified the basal nodes of the families and genera and named them with their respective names. Step 2: We inserted absent taxon in their respective basal nodes (genera or family). Step 3: In some cases, genera that were not present in the supertree were included and positioned as polytomies at the base of the family, considering their relationship according to studies that have already been established [58–61] (Figure 2). Step 4: Only valid species whose identification is largely resolved in the literature were included in the supertree, and in addition, the taxa underwent a review by specialists in the group. Taxa that presented some identification problems were not included. Step 5: From this supertree containing all Amazonian species, we generated 1000 phylogenies randomly shuffling the position of the species included as polytomies within their respective clades (Supplementary File S2). For this, we use the packages ape [62], Geiger [63], phylotools [64], adephylo [65] and Hmisc [66]. Similar approaches have already been used in other studies, which we highlight below: Duarte [67] and Debastiani et al. [68] for plant communities; Martins et al. [69] and Loyola et al. [70] for communities of Anura; Devictor et al. [71] and Gianuca et al. [72] for bird communities; Brum et al. [73] for primate communities. However, we did not find anything similar for the groups of invertebrates, which are the most difficult to perform, due to their extraordinary biodiversity and the paucity of studies on their phylogenetic relationships.
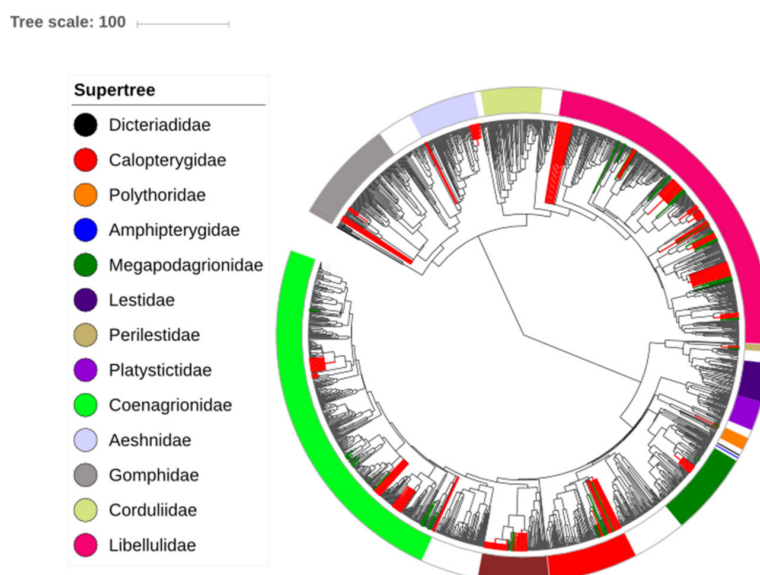

Figure 2. Phylogenetic tree of the Odonata (modified from Waller and Svensson [56]). The branches indicate the evolutionary relationships between taxa worldwide, while green branches are Amazonian taxa and red branches are Amazonian species without molecular data inserted at the root of their respective genera (which were never included before). Families listed in the legend occur in the Brazilian Amazon and are highlighted in the phylogenetic tree according to the respective color.

The tree proposed by Waller and Svensson [56] is time-calibrated with fossils downloaded from the Paleobiology Database. They considered taxonomic groups and names

found on the World Odonata List. They queried GenBank for each species in the list and then downloaded all the associated data using the R package seqinr. Two separate time-calibrated trees were generated in BEAST for computational reasons (one for Zygoptera and one for Anisoptera) and they were later combined (using the median age of the root of each subtree) into a single tree with divergence time set between the two suborders with fossils. In both analyses, the nodes of each family were named following the classification proposed in the World Odonata List (https://www.pugetsound.edu/academics/academicresources/slatermuseum/biodiversity resources/dragonflies/world-odonata-list2/; accessed on 23 July 2018).

2.5. Statistical Analysis

We calculated the standardized effect size of phylogenetic diversity (sesPD) [74], for all communities using 1000 phylogenetic trees to account for the phylogenetic uncertainty in the species relatedness. We used the null model "phylogeny. pool" to investigate whether an observed pattern could have arisen by chance [75]. Positive values indicate higher phylogenetic diversity in communities than expected according to the null model, while negative values indicate lower phylogenetic diversity than expected by the null model. To calculate sesPD, we used the picante package [76]. We used the sesPD index as a response variable, the environmental variables that described the studied sites as fixed effects, and the microbasins as a random effect. We considered the environmental variables as fixed effects in the model because they describe, in detail, the variation in the studied environments; thus, this allowed the model to test the effects of land-use changes along an environmental gradient. On the other hand, for the random effects, we selected the microbasins because, for this study, we were not testing the possible ecological effects of the microbasins on the community structure.

For each model, the parameters—Coefficient of Variation and Standard Deviation—were generated from the effects of fixed variables on community phylogenetic diversity (sesPD). We then calculated the average of the 1000 coefficients of variation and standard deviations of the fixed models. Subsequently, a type I error probability (*p*-value; $\alpha = 0.05$) was estimated for each mean of the coefficients of variation and standard deviation of the fixed variables. In addition, we generated an average of the R^2 values for fixed and random models. The values of the global index of Moran (I) were tested in the residual model [77]. To assess the effects of land use on the richness and abundance of Odonata species, we also performed a Generalized Linear Mixed Model (GLMM). We use environmental metrics as explanatory variables and the microbasins in the study area as a random variable. We conducted these analyses using the lme4 package [78] with the glmer function. To model phylogenetic diversity (sesPD), we used the Gaussian distribution. For both metrics of abundance and richness, we used a Poisson distribution.

However, before formally testing the effects of environmental variables on phylogenetic diversity, species richness, and abundance, we performed data reduction to avoid collinearity of the environmental variables. Since there were eleven habitat-structuring variables (Supplementary File S3), we used Principal Component Analysis (PCA) to calculate a small number of independent variables. The first two main components explained 54.1% of the variability in the variables of habitat structuring (Table 1, Figure 3). The variables' wood debris volume (r = 0.688), mean canopy cover (r = 0.928), Mean canopy cover of small trees (0.916), Mean canopy cover of woody understory (r = 0.863) and the proportion of mean primary vegetation cover by microbasins (r = 0.609) presented relationships greater than 60% with the first two axes [79] and were selected as predictors in the models (Figure 4). All analyses were calculated using the R software (R Development Core Team 2019).

Table 1. Results of the Principal Components Analysis (PCA) performed on the correlation matrix of the environmental variables describing the cover of different habitat types.

Variables	Axis.1	Axis.2	Comm. (%)
Wood debris volume	0.389	0.688	45.945
Mean canopy coverage of the channel	0.656	0.070	64.708
Mean canopy cover of small trees	0.916	−0.162	74.278
Mean canopy cover of woody understory	0.863	−0.229	81.912
Mean Canopy Coverage	0.928	−0.104	88.113
Mean total canopy cover	0.674	−0.403	93.487
Mean coverage of woody canopy	0.950	−0.228	97.647
Mean depth thalweg	−0.332	−0.364	99.3678
Mean channel immersion	0.500	0.450	99.799
Proportion of primary vegetation (by microbasin)	0.609	0.538	100
Total size of the microbasins	0.130	0.435	100

The values under columns Axis.1 and Axis.2 are the factor loadings and inform us of the contribution of each variable to the formation of the multidimensional space shown by the two PCA. Comm. (%) is the percentage of the total communality of each variable extracted by the PCA axes 1 and 2.
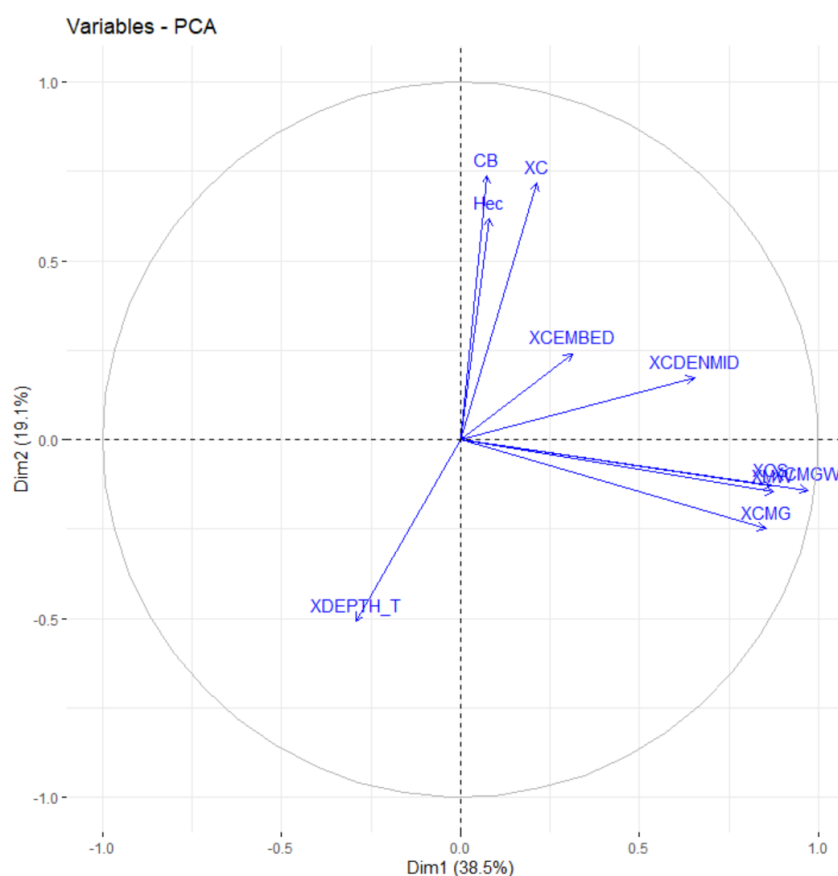

Figure 3. Principal component analysis (PCA) based on environmental variables of sampled streams. Wood debris volume (XC); Mean canopy coverage of the channel (XCDENMID); Mean canopy cover of small trees (XCS); Mean canopy cover of woody understory (XMW); Mean Canopy Coverage (XXC); Mean total canopy cover (XCMG), Mean coverage of woody canopy (XCMGW); Mean depth thalweg (XDEPTH_T); Mean Channel Immersion (XCEMBED); Proportion of primary vegetation (by microbasin) (CB); Total size of the microbasins (Hec).
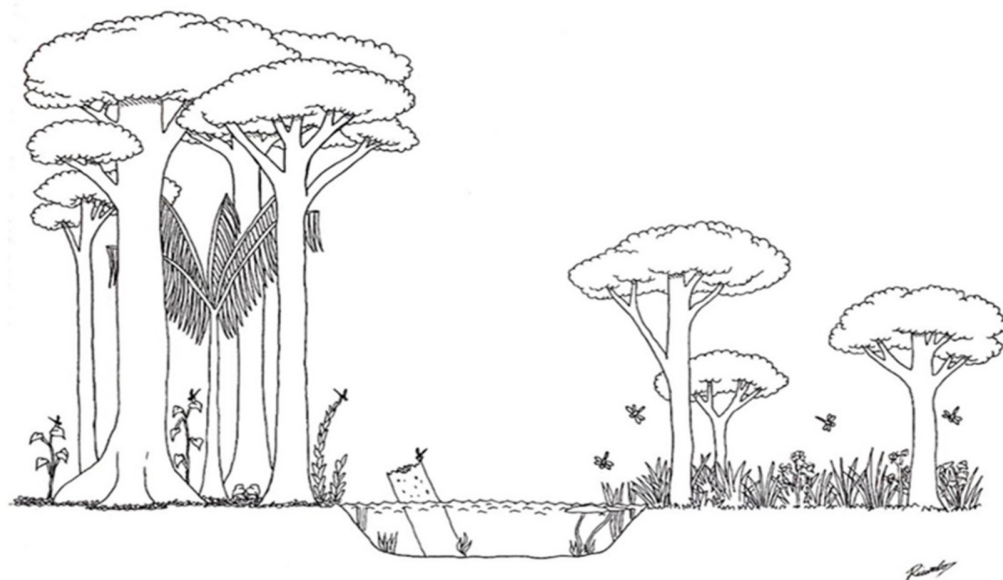
Figure 4. A hypothetical summary describing the physical structure of the streams sampled in the study, according to variables selected by the PCA axes. The left bank of the stream represents a structured forest environment, with the presence of a closed canopy formed by the canopies of large trees, which act as permanent sources of wood (perch or oviposition point) inside and outside the channel. The right side of the stream represents an environment altered for anthropogenic uses, with few and sparse large trees and a predominance of shrubs and grasses, allowing the entry of more light and heat.

3. Results

A total of 5378 individuals were collected and 126 Odonata species were identified. The families with the highest species richness were Libellulidae (n = 51 spp.), Coenagrionidae (n = 46 spp.), Calopterygidae (n = 11 spp.) and Gomphidae (n = 5 spp.). The most abundant species were *Erythrodiplax basalis* [80] (n = 424), *Chalcopteryx rutilans* [81] (n = 369), *Mnesarete aenea* [81] (n = 589), *Argia infumata* [82] (n = 335) and *Heteragrion silvarum* [82] (n = 323) (Supplementary File S1).

When evaluating the effects of physical habitat variables on the phylogenetic diversity of the Odonata community, the coefficients showed that the metrics of wood debris volume and the percent mean canopy cover of small trees had a positive relationship with the phylogenetic diversity of Odonata. However, only the mean canopy cover of small trees was significant (Estimate = 0.540; Sdt. Error = 0.078; p = 0.023), suggesting that the increase in small trees in the stream margins affected the phylogenetic diversity of Odonata. On the other hand, the variables of mean canopy cover of woody understory, mean canopy coverage and the proportion of mean primary vegetation by microbasin had a negative relationship with the phylogenetic diversity of Odonata, but none of these variables were significant in the models (Table 1). Lastly, the final mean R^2 of the coefficient of variation of the fixed portion of the model explained 66% (R^2 = 0.660) of the variation in the data, and the final mean R^2 of the random portion of the model explained 54% (R^2 = 0.540) (Table 2).

When assessing the effects of the structural physical variables of streams on species abundance, only the variable percent mean canopy cover of small trees exhibited a significant negative effect (Estimate = −0.1636; Std. Error = 0.0694; Df = 1; p-value = 0.0184). The fixed portion of the model explained 22% (R^2 = 0.223) of the variation in the data and the random portion of the model explained 7% (R^2 = 0.071). In the evaluation of the physical habitat effects on species richness, only the variable mean canopy coverage showed a significant negative effect (Estimate = −0.0524; Std. Error = 0.0129; Df = 1; p-value = 0.0057). The fixed portion of the model explained 20% (R^2 = 0.208) of the variation in the data and the random portion of the model explained 11% (R^2 = 0.114) (Table 3).

Table 2. Results of General Linear Mixed Model (GLMM) evaluating the effects of structural physical variables of streams on the phylogenetic diversity of the Odonata community (sesPD) in the Brazilian Amazon.

Parameters	Estimate	Sdt. Error	*p*-Value
Intercept	−182	0.117	0.467
Wood debris volume	0.049	0.052	0.532
Mean canopy cover of small trees	0.54	0.078	0.033
Mean canopy cover of woody understory	−0.185	0.037	0.218
Mean canopy coverage	−0.082	0.057	0.243
Proportion of primary vegetation (by microbasin)	−0.046	0.03	0.112

Table 3. Results of General Linear Mixed Model (GLMM), describing the effects of environmental variables on the abundance and taxonomic richness of Odonata in the Brazilian Amazon.

Parameters	Estimate	Std. Error	Df	*p*-Value
Taxonomic Abundance				
Wood debris volume	−0.0515	0.0612	1	0.3998
Mean canopy cover of small trees	−0.1636	0.0694	1	0.0184
Mean canopy cover of woody understory	−0.0875	0.0986	1	0.3749
Mean canopy Coverage	0.0282	0.0433	1	0.5142
Proportion of primary vegetation (micro basin)	−0.0002	0.0006	1	0.7077
Taxonomic Richness				
Wood debris volume	−0.0144	0.0112	1	0.1988
Mean canopy cover of small trees	−0.0524	0.0129	1	0.0057
Mean canopy cover of woody understory	0.0264	0.0184	1	0.1513
Mean Canopy Coverage	−0.0023	0.0081	1	0.7746
Proportion of primary vegetation (micro basin)	0.0006	0.0001	1	0.6001

4. Discussion

Our results suggest that the expansion of anthropogenic land use over the natural landscape in the Brazilian Amazon affects the phylogenetic diversity of Odonata. Physical attributes of streams that are presumably more frequent in areas modified by anthropogenic activities (shrubs around streams) had a positive relationship with the phylogenetic diversity of Odonata [4,83]. In this context, local metrics from the stream riparian zones directly affected the phylogenetic diversity of Odonata communities. On the other hand, regional metrics, such as the proportion of primary vegetation coverage by microbasins did not significantly affect phylogenetic diversity. A similar result was obtained when evaluating the expansion of land-use for anthropogenic uses on the taxonomic diversity of Odonata species (richness and abundance). Although the models were significant, they showed weak support as predictors of variation in community structure.

Notably, the variation in shrub vegetation is a metric that accounts for most habitats in open areas, as the predominance of shrub vegetation suggests the absence of large tree cover [84,85]. This may result from anthropogenic land uses, as the predominance of shrubby vegetation is more frequent on the banks of streams that drain pastures, palm monoculture, and other anthropogenic landscapes [86]. The positive relationship between the canopy of small trees and phylogenetic diversity may respond to the increased invasion of species adapted to disturbed environments [87,88]. This result is not consistent with the hypothesis proposed here that areas of anthropogenic use would show less phylogenetic diversity in response to a subset of species that would be favored by the environmental conditions created in the disturbed environments [89].

In general, areas of human use lose specialized species of forest habitats and favor habitat generalist species. This loss may be happening throughout the phylogeny and, therefore, some families may be negatively affected more than others [90]. All our results lead us to believe that land-use changes may affect specific groups within families and/or

genera. We suggest that in the future, with the availability of a better-resolved phylogeny for Neotropical species, studies should assess lineage losses within families and/or genera. In environments with higher primary vegetation, there is a predominance of some species of the genera *Acanthallagma*, *Mnesarete*, *Aeolagrion*, *Microstigma*, and *Mecistogaster*. These genera belong to the suborder Zygoptera and contain most of the species that specialize in forest habitats. When analyzing the phylogeny, these groups are closely related, as they belong almost entirely to the Coenagrionidae family [91,92]. On the other hand, in the most deforested environments, there is a predominance of species that are considered habitat generalists from the genera *Erythrodiplax*, *Orthemis*, *Acanthagrion*, and *Ischnura*, and the majority of species from the genus *Argia* [35,93–95]. In these deforested environments, they found representatives from the two suborders, Anisoptera and Zygoptera, and the two most diverse families in Amazonia, Coenagrionidae and Libellulidae, which exhibit completely antagonistic reproductive and ecophysiological behavior [19]. However, these species have particulars in common and these particulars would favor some species of the two families. For example, *Erythrodiplax fusca*, *Diastatops obscura* and *Ischnura capreolus* have a strong relationship with open areas and oviposition occurs in lentic environments [7,46]. The interaction between these families and environmental conditions has been proposed to be useful environmental indicators [73]. Furthermore, the high phylogenetic diversity found in our study may reflect the high diversity of the Libellulidae family, which, alone, represented 48% of all species observed. Most Libellulidae possess heliothermic characteristics, as they spend most of their time flying and require direct sunlight for their foraging [7,19]. It is possible that anthropogenic processes may favor species in this family, as the removal of riparian vegetation has expanded the amplitude of the spatial niche [7,19].

Similar patterns have been recorded for other taxonomic groups, such as plants [96], where smaller fragments were phylogenetically more dispersed, while larger fragments were phylogenetically more clustered, possibly in response to species invasions into small internal fragments. Lineages that tolerate environmental changes are probably among the terminal nodes of phylogeny, such as genera and species. Thus, within the same family, they could have distinct lineages with different responses to disturbed environments [9,96]. The findings from this study may also reflect the distribution of specimens in the immature stages of Odonata, since several studies have highlighted a strong congruence between the distribution of Odonata larvae and adults [97,98]. In some previous studies of Odonata, the community structure was affected by the same environmental variables when considering both adults and immature states [97,99,100]. For some genera, water temperature is an important factor for community structure; for example, the genus Acanthagrion is more tolerant of water temperature variation [101]. Dissolved oxygen is also an important predictor in the community structure of some genera and can have a strong influence on the reproductive strategies of most species. This may be related to oviposition behavior, as adult females may select the most appropriate habitats for oviposition, mainly ovipositing in more oxygenated waters [102,103].

In conclusion, the conversion of native forest to land use for anthropogenic purposes affects the phylogenetic diversity of Odonata. However, the effects found on taxonomic diversity (richness and abundance) were weak. The increase in phylogenetic diversity should be interpreted with caution because it reflects the increase in specialist species from open areas and/or habitat generalists and a decrease in specialist species from forest habitats, which are restricted to a specific range of environmental conditions. It is important to highlight that we evaluated the recent effects of land use in the Amazon (a little over 100 years) on the phylogeny of Odonata. We conclude that the effects found are not related to the evolutionary history of odonates but to the loss of more conserved lineages and the invasions of species adapted to the disturbed environments of the most phylogenetically derived clades (genera and species). The main outcome is the loss of closely related species, which probably perform similarly in the studied ecosystems. Despite being an order of predatory species, the Odonata response pattern is congruent with other orders of aquatic insects that are experiencing similar stressors [104–106].

Finally, our results showed that land use affects the phylogenetic diversity of Amazonian odonates. However, the same was not seen for taxonomic diversity since the effects found were to be weak. Certainly, our results reinforce the discussions that metrics such as phylogenetic and functional diversity may be more accurate predictors of anthropic effects than taxonomic metrics. Therefore, we do not discard the hypothesis of a possible effect of land use on the taxonomic diversity of adult Odonata. We suggest that future studies invest in multivariate analysis of matrices, as they will likely find results consistent with ours. In addition, it is necessary to increase the buffer zone on the banks of streams, to mitigate the effects of the surrounding land-use changes on forests' specialist species. However, we recommend caution when interpreting the results of phylogenetic diversity, since high values of diversity are not always linked to environmental integrity [10,96].

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