

LEANDRO SCHLEMMER BRASIL

**Padrões de diversidade e suas implicações para a conservação de
Odonata (Insecta) em igarapés amazônicos**

Belém, 2018

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Tese apresentada ao Programa de Pós-graduação em Zoologia, do convênio da Universidade Federal do Pará e Museu Paraense Emílio Goeldi, como requisito parcial para obtenção do título de Doutor em Zoologia.

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LEANDRO SCHLEMMER BRASIL

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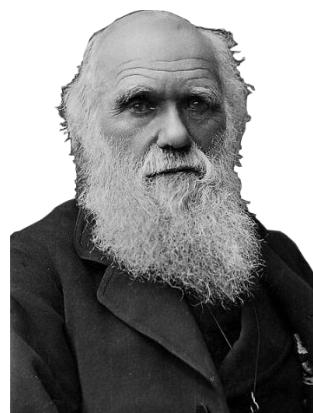
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Aos meus pais, Sadi e Ivanir.



“Para ser um bom observador é preciso ser um bom teórico”.

Charles Darwin

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Padrões de diversidade e suas implicações para a conservação de Odonata (Insecta) em igarapés amazônicos

RESUMO GERAL

Conhecer os padrões de distribuição de espécies ao longo da paisagem e entender os mecanismos que os geram são perguntas extremamente relevantes, para que possamos avançar no conhecimento ecológico das comunidades biológicas. Essas questões supracitadas são essenciais para o gerenciamento e tomada de decisão sobre a conservação da biodiversidade, das condições ambientais e dos recursos ecossistêmicos. Nesta tese, utilizamos as comunidades de Zygoptera (Insecta: Odonata) de igarapés da Amazônia brasileira para investigarmos seus padrões de diversidade alfa (Capítulo 1), diversidade beta (Capítulo 2), elementos que estruturavam suas metacomunidades (Capítulos 3) e para uma análise de priorização espacial para conservação da ordem estudada na Amazônia (Capítulo 4). Utilizamos preditoras ambientais, biogeográficas e espaciais para investigar os mecanismos estruturantes para a distribuição das comunidades alvos da tese. Analisando a diversidade alfa (Capítulo 1) as hipóteses de heterogeneidade ambiental (clima) e produtividade primária foram mais importantes para os padrões de riqueza de espécies de Zygoptera. Considerando a diversidade beta (Capítulo 2), o turnover foi o componente mais importante para a mudança na composição de espécies ao longo da paisagem, conjuntamente com a distância espacial entre os sítios e a região biogeográfica (áreas de endemismo) foram as preditoras mais importantes para os padrões de diversidade beta de Zygoptera. Analisando os padrões de metacomunidades (Capítulo 3) verificamos que em comunidades de igarapés ambientalmente preservadas o padrão é Clementiano, mas em comunidades de igarapés ambientalmente alterados o padrão é alterado para aninhamento de comunidades, onde estes igarapés representariam subconjuntos dos locais mais preservados. No quarto capítulo evidenciamos que a distribuição espacial das unidades de conservação da Amazônia não as torna eficiente para conservar o habitat de grandes porções de diversidade beta de Odonata. Uma vez que as áreas prioritárias estão localizadas principalmente na região sul da Amazônia e a maior parte destas áreas já está desmatada, pois estão inseridas dentro do arco do desmatamento, em seguida, considerando apenas áreas florestadas, as áreas prioritárias deslocam-se para a faixa mais central da Amazônia. Apartir daí sugerimos a criação de

novas unidades de conservação ou incentivos para atividades de baixo impacto nas regiões mais centrais, prioritárias e ainda florestadas, bem como, o incentivo para a restauração das áreas prioritárias já desmatadas. Uma possibilidade para isso, seria a implementação de programas que pagam por serviços ecossistêmicos, como créditos de carbono provenientes de reflorestamento, e/ou o desenvolvimento de atividades com menor impacto sobre a biodiversidade, como agrosilvicultura. Contribui consideravelmente para diminuir as lacunas wallaceanas e hutchisonianas de Zygoptera na Amazônia brasileira.

Palavras chave: Alterações ambientais, diversidade amazônica, ecologia de riachos, meta-comunidade, modelagem de nicho ecológico, priorização espacial.

Patterns of diversity of the Odonata (Insecta) in Amazonian streams and implications for Conservation

GENERAL ABSTRACT

The distribution of species within a landscape and the mechanisms that determine this distribution are fundamental questions for the understanding of the ecology of biological communities. The understanding of these phenomena is essential for the management of ecosystems and decision-making on the conservation of biodiversity, environmental conditions, and ecosystem resources. In this dissertation, we focused on the communities of the damselflies, suborder Zygoptera (Insecta: Odonata), found in streams in the Brazilian Amazon region to investigate their alpha diversity (Chapter 1), beta diversity (Chapter 2), and the elements that structure metacommunities (Chapters 3), as well as the spatial priorities for the conservation of Amazonian odonates (Chapter 4). We used environmental, biogeographic, and spatial predictors to investigate the mechanisms that structure the distribution of the communities analyzed in this dissertation. In the case of alpha diversity (Chapter 1), environmental heterogeneity (climate) and primary productivity were the most important determinants of zygoteran species richness. For beta diversity (Chapter 2), turnover was the most important component of changes in species composition within the landscape, together with the spatial distance between sites, and the biogeographic region (centers of endemism), which were the most important predictors of zygoteran beta diversity. In our analysis of metacommunity patterns (Chapter 3), we found a Clementsian pattern in well-preserved streams, with a major change in the configuration of the communities in streams with environmental alterations, which represented subsets of the better preserved areas. In Chapter 4, we show that the spatial distribution of the conservation units in the Amazon region is relatively ineffective for the conservation of most of the beta diversity of the region's odonates. As the priority areas are located predominantly in southern Amazonia, and most of these areas have already been deforested, given that they lie within the arc of deforestation, the priority areas were displaced toward the forested environments located nearer the center of the Amazon region. Based on this analysis, we suggest the creation of new conservation units or the implementation of incentives for the establishment of activities that cause reduced environmental impacts in more central, priority areas, which are still forested, as well as

the restoration of priority areas that have already been deforested. One possibility here would be the implementation of programs that pay for ecosystem services, such as carbon credits obtained through reforestation and/or the development of activities with a reduced impact on biodiversity, such as agroforestry. This study also makes a major contribution to the reduction of the Wallacean and Hutchisonian shortfalls on the zygopterans of the Brazilian Amazon region.

Key words: Environmental alterations, Amazonian diversity, stream ecology, meta-community, ecological niche modeling, spatial prioritization.

INTRODUÇÃO GERAL

Compreender os processos espaciais e temporais que influenciam os padrões atuais de diversidade de espécies é uma questão amplamente estudada e discutida em ecologia de comunidades (Ricklefs & Schlüter, 1993; Magurran, 2013). A distribuição das espécies está condicionada a fatores históricos, como a dinâmica de barreiras geográficas ao longo da paisagem (Hoorn & Wesselingh, 2011), bem como a fatores ecológicos recentes, como a interação entre as espécies e o conjunto de condições ambientais, que proporcionam um habitat favorável, ou não, ao estabelecimento das mesmas (Soberón, 2007). Desta forma, tanto processos ambientais quanto processos espaciais tem sido apontado como importantes para a estruturação das comunidades (Cottenie, 2005).

De acordo com os pressupostos da Teoria do Nicho hipervolumétrico, as espécies só conseguiram viver em ambientes cuja disponibilidade de habitat fossem condizentes com suas exigências ambientais (p. ex. temperatura e precipitação). Portanto, a disponibilidade de habitat estaria intrinsecamente relacionada à distribuição das espécies, pois seu estabelecimento e sobrevivência são condicionados a limiares mínimos de condições ambientais específicas (Chase & Leibold, 2003; Popielarz & Neal, 2007). Proposta por Hutchinson em 1957, a Teoria do Nicho prediz que as variáveis ambientais e interações bióticas são as principais forças que determinam a distribuição das espécies e que em ambientes com condições ambientais semelhantes, a composição de espécies deve ser similar (Chase & Leibold, 2003; Popielarz & Neal, 2007). Assim, quando as condições ambientais relacionadas ao nicho das espécies são alteradas (p. ex. clima), sua distribuição pode ser modificada (Hutchinson, 1957). Quando o limiar máximo de tolerância da espécie é ultrapassado por uma ou muitas ambientais isso torna-se um filtro ambiental que pode inviabilizar totalmente ou parcialmente sua abundância ou até mesmo a ocorrência em um dado local (Poff, 1997).

Por outro lado, a Teoria Neutra proposta por Hubbell (2001) prediz que os processos de deriva ecológica e a existência de barreiras geográficas são cruciais para explicar os padrões de diversidade que encontramos nos ambientes. Nessa perspectiva, a composição das comunidades seria principalmente afetada por processos de dispersão, especiação e extinção nas comunidades locais, e as variações históricas dessas taxas

causariam as variações espaciais de diversidade de espécies no presente (Cadotte & Fukami, 2005; Vandvik & Goldberg, 2006).

Além das condições ambientais e dos processos espaciais (Hutchinson, 1957; Hubbell, 2001), fatores históricos que desencadearam mudanças biogeográficas são importantes para os padrões de diversidade (Silva et al., 2005; Haffer, 2008; Ribas et al., 2012). Na bacia Amazônica, por exemplo, a formação dos grandes rios foi um evento marcante para a diversificação das espécies em diversos grupos, incluindo desde os vertebrados, como aves e macacos, como para os invertebrados, como borboletas e libélulas (Wallace, 1852; Hall & Donald, 2002; Juen & De Marco, 2012; Ribas et al., 2012). Essa diversificação ocorreu devido a processos de vicariância gerados pelas barreiras geográficas impostas pelos grandes rios, que causaram aumentos nas taxas de especiação dentro de seus interflúvios, tornando-se importantes para os padrões de diversidade no presente (Silva et al., 2005; Haffer, 2008).

Portanto, para compreender a dinâmica da distribuição das espécies diversas teorias buscam explicar os mecanismos que geram os padrões da biodiversidade ao longo da paisagem (De Marco, 2006). Neste contexto, fatores ou processos como o nicho (Hutchinson, 1957), quantidade de energia presente no sistema (evapotranspiração) (Wright, 1983), produtividade (produtividade primária) (Waide et al., 1999), água e energia (quantidade água e evapotranspiração) (O'Brien, 1998), heterogeneidade ambiental (Kerr & Packer, 1997) e fatores biogeográficos como o tamanho e isolamento da área de habitat disponível (MacArthur & Wilson, 1967), tem sido apontados como determinantes para os padrões de diversidade de vários grupos biológicos. Considerando aspectos biogeográficos históricos, na Amazônia vale acrescentar que as teorias de isolamento por rios (constituindo-se barreiras a dispersão), formando áreas de endemismo em seus interflúvios (Hipótese de Rios) e o isolamento causado pelo avanço e/ou retração da floresta úmida sobre florestas secas e savanas, durante os períodos climáticos secos do Terciário e Quaternário (Hipótese de refúgios), também são fatores importantes para entender os padrões atuais de diversidade de espécies em larga escala (Haffer, 2008).

Para investigar esses padrões de diversidade avançando além das formas tradicionais de diversidade que abordavam principalmente as diferenças na riqueza de espécies (MacArthur & Wilson, 1967; Kerr & Packer, 1997; O'Brien, 1998; Waide et al., 1999; Wright, 1983), a avaliação das mudanças na composição de espécies vem ganhando destaque desde a década de 70 (Whittaker, 1972). A diversidade pode ser dividida em diferentes componentes: a diversidade alfa (α), que representa a diversidade local de

espécies, a diversidade gama (γ) que considera o número de espécies regional de espécies e a diversidade beta (β), que considera as mudanças na composição de espécies entre diferentes locais (Buschini & Woiski, 2008). Sobre a diversidade beta, quanto mais dissimilar é a composição de espécies entre dois locais maior será a diversidade beta (Baselga, 2010; Apgaua et al., 2014). Essa variação da diversidade beta pode ser causada por dois fenômenos: (i) o *turnover*, que é a substituição de espécies entre locais, e (ii) o aninhamento, que é a variação da composição de espécies causada por um gradiente de riqueza onde um local é um subconjunto de espécies de outro local mais diversos (Baselga, 2010). Por essas razões, para uma compreensão mais ampla dos padrões de diversidade, além da diversidade alfa é importante verificar a diversidade beta e a contribuição de seus componentes *turnover* e aninhamento (Baselga, 2010; Apgaua et al., 2014).

Além dos aspectos de diversidade supracitados, também é importante salientar que entre algumas comunidades pode existir migração (comunidade abertas), enquanto que em outras não (comunidades fechadas). Portanto para que possamos tentar compreender os mecanismos que desencadeiam os padrões locais de diversidade é necessário levar em conta a dinâmica espacial e a conectividade entre as comunidades dos diferentes locais (Leibold et al., 2004). À partir disso, considerando aspectos da ecologia de paisagem junto com a ecologia de comunidades de uma forma integrada, foi proposta a teoria de metacomunidades, cujo objetivo é avaliar a dinâmica da distribuição das espécies em conjuntos de comunidades que se localizam em uma unidade geográfica onde é possível que haja dispersão de indivíduos de diferentes espécies entre as comunidades (Wilson, 1992). Nessa abordagem busca-se identificar padrões de coocorrência das espécies que refletem suas interações, relações com gradientes ambientais e com a estrutura espacial, que são interpretados a partir de mecanismos que geram os padrões de distribuição das espécies na paisagem (Leibold & Mikkelsen, 2002; Leibold et al., 2004; Presley et al., 2010) (Tabela 1).

Tabela 1. Mecanismos e padrões relacionados a distribuição de espécies em metacomunidades. Tabela baseada nas tabelas de Leibold et al. (2004) e López-González et al. (2012). (*) padrões quase-estruturados definidos por Presley et al. (2010).

| | Termo original | Definição |
|-------------------------------------|--|--|
| Mecanismos de meta-comunidades | <i>Patch dynamics</i> | Existem manchas ambientais (<i>patches</i>) similares, e todas capazes de manter populações. A diversidade das <i>patches</i> é definida por um <i>trade-off</i> entre a capacidade de colonização e de competição das espécies. |
| | <i>Species-sorting</i> | Considera mudanças nas comunidades ao longo de gradientes ambientais. As condições abióticas seriam importantes para as interações entre as espécies e consequentemente, para as taxas populacionais locais. |
| | <i>Mass-effect</i> | Mecanismos de dinâmica espacial em que um fluxo líquido de indivíduos é criado por diferenças no tamanho da população em diferentes manchas ambientais. |
| | <i>Neutral perspective</i> | Em uma perspectiva neutra as espécies são semelhantes em suas capacidades de competição, reprodução e dispersão. As interações entre populações são de ordem aleatória, e assim não alteram sistematicamente as relações entre populações e suas densidades. A razão entre probabilidades de extinção ou emigração e imigração ou especiação são responsáveis pela diversidade de espécies do pool regional. |
| Padrões de coocorrência de espécies | <i>Checkerboards</i> | Pares de espécies com exclusão mutua, com fortes indícios de competição. |
| | <i>Nested subsets</i> e <i>Quasi-nested subsets*</i> | Locais que são subconjuntos de espécies (comunidades pobres) de locais com maior riqueza de espécies (comunidades mais ricas), conhecidos como modelos aninhados. |
| | <i>Clementsian</i> e <i>Quasi-Clementsian*</i> | Comunidades discretas formando agrupamentos de espécies similares que podem refletir unidades biogeográficas. |
| | <i>Gleasonian</i> e <i>Quasi-Gleasonian*</i> | Gradientes com substituição contínua de espécies (<i>turnover</i>), mas que localmente tem padrões aleatórios. |
| | <i>Evenly spaced gradients</i> e <i>Quasi-evenly spaced*</i> | Gradientes que não forma comunidades discretas, mas que localmente é mais homogêneo do que o esperado pelo acaso. |
| | <i>Random</i> | Não existem gradientes ou padrões de agrupamento, a coocorrência é uma organização espacial aleatória. |

Integrar essas relações dos padrões observados com os possíveis mecanismos estruturantes é muito importante, no entanto é comum que diferentes mecanismos levem a padrões similares (Steve Presley, comunicação pessoal). Um padrão Clementsiano, por exemplo, pode ser gerado tanto por um mecanismo biogeográfico onde existem barreiras à dispersão dos organismos que criaram historicamente agrupamentos com composição

de espécies similares ao longo da paisagem (Brasil et al., 2018), quanto por um ecótono ambiental, como por exemplo, no encontro de um ecossistema árido com outro tropical (López-Gonzálues et al., 2012). Neste caso, gerado por um mecanismo ambiental, e não biogeográfico (López-Gonzálues et al., 2012). Portanto, relacionar diretamente padrões e mecanismos de forma fixa dentro do contexto da teoria de metacomunidades não é uma boa estratégia sem uma análise profunda dos fatores históricos e recentes que possivelmente atuam sobre os padrões de diversidade.

Compreender os padrões naturais de diversidade, avaliados em diferentes perspectivas (p. ex. abundância, riqueza de espécies e diversidade beta) é importante, complexo e desafiador para ciência (Whittaker, 1972; Wilson, 1992; Ricklefs & Schlüter, 1993; Magurran, 2013). No entanto, com o frequente avanço das alterações ambientais de origem antrópica sobre as paisagens naturais (Fearnside, 2005; Brando et al., 2013; Laurance et al., 2014), compreender esses padrões de diversidade tornou-se imprescindível para propor medidas mitigadoras do impacto das atividades antrópicas sobre a biodiversidade (Nobrega & De Marco, 2011). Por isso, é muito importante integrar uma análise de padrões de diversidade com gradientes de condições ambientais, como os gerados por distúrbios de origem antrópica (Brasil et al., 2017).

A obtenção de informações ambientais, principalmente relacionadas ao clima, podem ser obtidas com os modelos climáticos globais, por exemplo *WorldClim - Global Climate Data* (Hijmans et al., 2005). A dinâmica de uso e ocupação da terra pode ser obtida pelos mapas de uso da terra, como por exemplo Soares-Filho et al., (2014), e as ocorrências das espécies a partir de artigos científicos, dissertações e teses, registros em museus e coleções zoológicas ou até em banco de dados globais *on line*. A partir daí, avaliando a distribuição das ocorrências das espécies é possível compreender suas relações com as condições ambientais e, posteriormente, extrapolar para a paisagem modelos de adequabilidade ambiental das espécies que devem refletir sua distribuição potencial ao longo da paisagem, os chamados Modelos de Nicho Ecológico (MNE) (Peterson, 2001). A utilização de MNE permite que mesmo em áreas onde existam poucos registros (regiões com grandes déficits Wallaceanos) consiga-se avaliar sua importância para a conservação e risco devido à perda de habitat (Diniz-Filho et al., 2009), e isso pode ser discutido sobre diferentes cenários do passado, presente e futuro (Nobrega & De Marco, 2011; Ribeiro et al., 2016). Isso é útil para avaliar a eficiência das unidades de conservação para preservar o habitat de determinados grupos (Frederico et al., 2018) e

indicar áreas prioritárias para conservação, complementares às unidades de conservação já estabelecidas (Brum et al., 2017).

Considerando estudos de padrões de diversidade e/ou conservacionistas, um dos grupos mais promissores e negligenciados são os invertebrados, especialmente os insetos (Diniz-Filho et al., 2010). Entre as milhões de espécies que compõem a diversidade biológica, eles são os organismos multicelulares mais diversos e bem-sucedidos do planeta (Labandeira & Sepkoski, 1993). Tem grande importância ecológica para a polinização, controle de pragas, decomposição de matéria orgânica e manutenção de espécies nativas (Losey & Vaughan, 2006). Além disso, tem importante valor econômico, pois com a redução das áreas naturais e o aumento das áreas de monoculturas agrícolas, há a redução dos serviços ecossistêmicos prestados por eles como por exemplo, os polinizadores, decompósitos, predadores e parasitoides, cujas ausências podem levar a aumentos de pragas indesejáveis à agricultura, impactando significativamente a economia mundial (Potts et al., 2010; Losey & Vaughan, 2006). Em várias regiões, muitos dos vertebrados já foram eliminados por escassez de área de vida ou por terem sido caçados, ambientes que, nem por isso, deixam de ter um certo valor para a conservação (Freitas et al. 2003) e podem ser definidos e monitorados com comunidades de insetos.

Dentre os insetos, a ordem Odonata destaca-se por sua grande diversidade de espécies (Corbet, 1999). São insetos hemimetábolos (cuja ninfa é aquática e o adulto é terrestre, predadores, que na sua fase imatura vivem preferencialmente em riachos sombreados se alimentando de presas vivas (Corbet, 1999). Na fase adulta, utilizam o canal dos riachos para se reproduzir e as regiões ripárias e seus entornos para forragear (Corbet, 1980; Corbet, 1999). Nas regiões neotropicais, os Odonata dividem-se em duas subordens: os Anisoptera e Zygoptera. Os Zygoptera adultos são pequenos e esguios, com asas anteriores e posteriores semelhantes e apresentando baixa velocidade de voo (Corbet, 1999; De Marco & Vianna, 2005; Heiser & Schmitt, 2010). Ambientalmente, devido a características de termorregulação, a maior parte dos Zygoptera ocorrem em ambientes mais sombreados (De Marco et al., 2015) e são sensíveis a alterações ambientais (Oliveria-Júnior et al., 2015; Miguel et al., 2017).

As espécies de Odonata ocorrem em todos os habitats aquáticos de água doce, tem larvas sensíveis a mudanças ambientais e que são relativamente sedentárias (Mendes et al., 2018). Os adultos são facilmente observados devido ao seu comportamento territorialista, tendo importante papel ecológico tanto nos sistemas aquáticos quanto terrestres (Carle, 1979; Oertli, 2008). Devido a todas essas características, são

frequentemente utilizados em investigações ambientais tanto menor escala, no riacho ou na bacia hidrográfica (Silva et al., 2010; Silva-Pinto et al., 2012; Oliveira-Junior et al., 2015) quanto em escala de paisagem, ao longo de um bioma, ou país (Diniz-Filho et al., 2010; Nobrega & De Marco, 2011; Juen & De Marco, 2012; De Marco & Vianna, 2012; Brasil et al., 2017, 2018), pois suas fortes relações com as condições ambientais, ao processos espaciais e biogeográficos históricos tornam-nas um grupo qualificado para testes de hipóteses ecológicas (Miguel et al., 2017).

OBJETIVOS DA TESE

O objetivo geral da desta tese é investigar a relação de condições ambientais, fatores espaciais e aspectos históricos sobre a distribuição das espécies de Zygoptera em riachos amazônicos sob diferenças perspectivas metacomunidades e modelagem de nicho ecológico). Para responder esse objetivo geral a tese foi estruturada em quatro capítulos que foram transformados em artigos científicos. No primeiro pretendemos usar uma abordagem teórica para investigar qual ou quais teorias ecológicas são mais adequadas para explicar os padrões de riqueza de espécies de Zygoptera em riachos amazônicos. O segundo investiga a influência de fatores ambientais, espaciais e aspectos biogeográficos sobre a diversidade beta de Zygoptera. O terceiro testa como a variação de integridade ambiental dos riachos atua sobre os elementos que estruturam as metacomunidades de Zygoptera. E, por fim, no quarto capítulo analizamos em escala de paisagem os padrões de diversidade beta, a eficiência das unidades de conservação da Amazônia para conservação de Odonata e indicamos áreas prioritárias para sua conservação complementares as já existentes, considerando a dinâmica atual de uso e ocupação da terra na Amazônia braileira.

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CAPÍTULO 1

Net primary productivity, seasonality of evapotranspiration and land surface temperature are predictors of species-richness of the Damselflies in the Amazonia

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Net primary productivity, seasonality of evapotranspiration and land surface temperature are predictors of species-richness of the Damselflies in the Amazonia

Abstract - Several hypotheses have been proposed to explain the mechanisms that generate temporal and spatial species richness patterns. We tested four common hypotheses (water-energy, energy, habitat heterogeneity and net primary productivity) to evaluate which factors best explain patterns of Zygoptera species richness. Of these, we predicted that habitat heterogeneity, as represented by spatial variability of climate stability, would be the most important predictor for Zygoptera richness patterns. We sampled communities of adult Zygoptera in 212 small Amazonian streams and based on generalized linear mixed models (GLMM), we evaluated which of hypotheses best explains the observed patterns of species richness. The model comprising the net primary productivity and climate seasonality hypotheses was the best model of Zygoptera species richness in Amazonian streams. The results indicate that species richness increases by one species per 1 kg of biomass per square meter in NPP, or with an increase of 2°C in air temperature variability. These results suggest that greater spatial variability in climate provides more niche heterogeneity and more diverse environmental resources, which increase species diversity.

Keywords: Alpha diversity, aquatic diversity, climate heterogeneity, Amazon, tropical diversity

Introduction

Characterizing species distributions and richness, and understanding the underlying mechanisms driving these patterns is one of the central issues in community ecology (Arrhenius 1921, MacArthur and Wilson 1967, Wright 1983, O'Brien 1998, Kerr and Packer 1999, Waide et al. 1999, Hubbell 2001). Even after decades of research on distribution patterns of species richness (Gillman et al. 2015, Kuglerova et al. 2015, Bertuzzo et al. 2016, Coyle and Hurlbert 2016, Gainsbury and Meiri 2017, Haddad et al. 2017), key questions remain. Several hypotheses have been used to explain the patterns of species richness at a macro-ecological scale. Most of these focus on the variety and

quantity of resources available to particular taxonomic groups. For example, the energy hypothesis predicts that sites with higher energy flow (evapotranspiration) support more species (energy hypothesis) (Wright 1983). Likewise, the water-energy hypothesis considers the amount of available energy and water to be the key drivers of species richness. Sites with higher precipitation and evapotranspiration are thus expected to have more species (O'Brien 1998). The habitat heterogeneity hypothesis predicts that sites with greater environmental heterogeneity over time (e.g. climatic variability) will have more species. Environmental variability enables the coexistence of species with different environmental requirements, such that the site would exhibit greater species richness over time (Waide et al. 1999). Finally, the net primary productivity hypothesis relates productivity per unit area to species richness patterns, such that more productive areas are expected to have more species (Waide et al. 1999).

Zygoptera are a relatively diverse group in tropical regions (Corbet 1999, Kalkman et al. 2008, Clausnitzer et al. 2009), inhabiting small streams with preserved riparian vegetation (De Marco et al. 2015). Spatial patterns of Zygoptera diversity are related to historical factors such as the emergence of geographical barriers and to environmental conditions (De Marco et al. 2015) such as plant cover (Rodrigues et al. 2016) and climate (Hickling et al. 2005). Given these characteristics, Zygoptera are an ideal study system for understanding the environmental controls on patterns of diversity (Brasil et al. 2018), as well as the impacts of ecosystem change due to anthropogenic disturbances (Brasil et al. 2017) and global climate changes (Dingemanse and Kalkman 2008).

The aim of this study was to evaluate which variables or sets of variables best explain the distribution patterns of Zygoptera species richness in Amazonian streams. To do this, we tested a series of models associated with the (i) energy, (ii) water-energy, (iii) habitat heterogeneity, and (iv) net primary productivity hypotheses. We expected that a model comprised of variables representing habitat heterogeneity would have the greatest predictive power to explain Zygoptera species richness patterns in Amazonian streams. This is based on the premise that sites with greater environmental heterogeneity over time provide environmental conditions for a wider range of species (Kerr and Packer 1999).

Materials and methods

Study area

We surveyed 212 wadeable streams in the Brazilian Amazon distributed in five regions that span a large area (~ 2300 km latitudinally and ~ 1400 km longitudinally) (Fig. 1). The streams in northern and central Amazonia occurred on terra firme, meaning they were not subject to seasonal flooding and were naturally surrounded by dense ombrophylous Amazon forests. The streams located in southern Amazonia were in a Cerrado-Amazon transitional zone and surrounded by gallery forest.

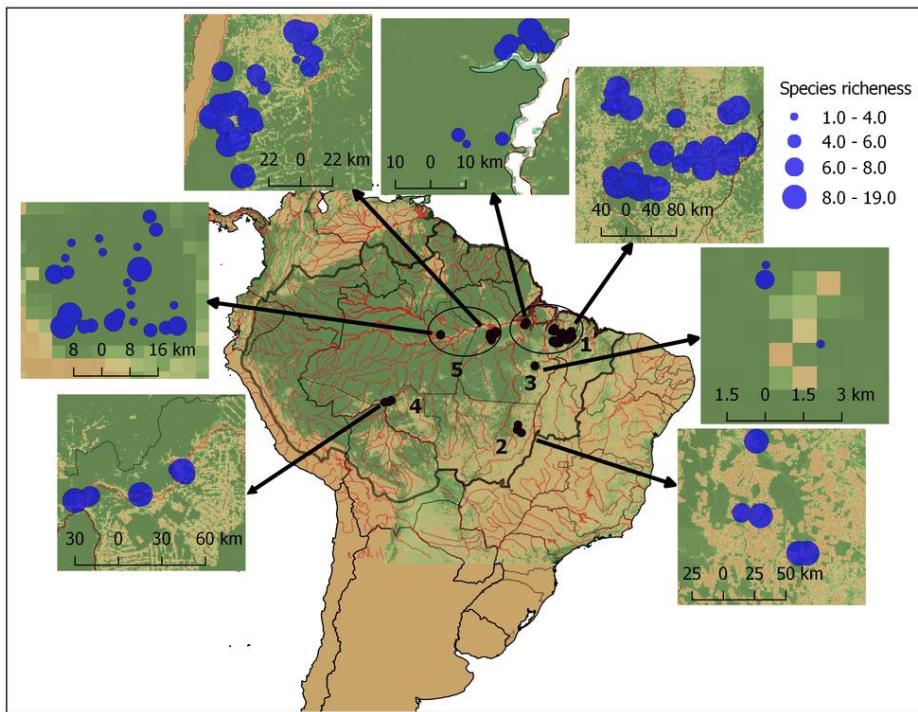


Fig. 1. Location of the Zygoptera collection sites in streams of the Brazilian Amazon. The sizes of the circles represent species richness classes.

The areas sampled occurred in three macroclimatic zones: Am in the north, Aw in the south, and Af to the east, according to the updated Koppen classification (Peel et al. 2007, Alvares et al. 2013). Am has a tropical rainy climate, influenced by the South American Monsoon; Aw has a highly seasonal tropical climate with a dry winter; and Af has a humid tropical climate called the equatorial climate (Peel et al. 2007, Alvares et al. 2013). Previous studies have provided detailed descriptions of the environmental conditions at streams in Amazonia (Frederico et al. 2014, Leal et al. 2016, Benone et al. 2017).

Biotic data

We collected adult Zygoptera individuals in streams with maximum width and depth of 5 and 0.8 meters, respectively. The collection was carried out during the dry seasons (July to November) from 2009 to 2013. We chose this period because the intensity of precipitation during the rainy season hinders both access to sites and sampling procedures. Moreover, the greatest diversity of aquatic insects is expected during the dry season in both central Amazonia (Baptista et al. 2001, Oliveira-Junior et al. 2015) and southern Amazonia (Cerrado-Amazon transition) (Brasil et al. 2017a).

In each stream we established a linear transect of 100 meters, where we captured all the observed adults Zygoptera individuals. We sampled streams for one hour by a collector using an insect net with 40-cm diameter and 65-cm length. The collections occurred between 10 a.m. and 2 p.m. on sunny days, with sunlight on the stream bed (Brasil et al. 2014, De Marco et al. 2015).

We identified all specimens collected using taxonomic keys and specialized illustrated guides (Garrison 1990, Lencioni 2005, Lencioni 2006, Garrison et al. 2010). Once identified, we packed specimens following the protocol proposed by Lencioni (Lencioni 2005) and stored them in the zoological collection of the Zoology Museum of the Federal University of Pará, Belém, Brazil (northern and central sites) and in the James Alexander Ratter Zoobotanical collection, of the State University of Mato Grosso, Nova Xavantina, Mato Grosso (southern sites).

Abiotic data

We used the original predictor variables published in the literature describing each hypothesis. To test the energy hypothesis, we calculated the mean evapotranspiration (ET), the sum of evaporation and plant transpiration from the land surface to the atmosphere, in January (AETJan) and June (AETJun) (Wright 1983). We used ET from MOD16, with a resolution of 1km (Mu et al. 2011). To test the water-energy hypothesis, we used the average of ET in January (AETJan), and June (AETJun), and the yearly average of monthly precipitation (PPT) (Waide et al. 1999). We used precipitation data from the Tropical Rainfall Measuring Mission (TRMM), with resolution of 0.25°. To test the net primary productivity hypothesis, we used the mean values of net primary productivity of forests (Waide et al. 1999). The NPP is a proxy for the energy/nutrients reaching the system, and a measure of the quality of litter inputs to the system which drive more productive and diverse food webs in tropical streams. We used the NPP from

MODIS17A3 product that estimate biomass in Kg C/m²/year, with a resolution of 1 km. To test the habitat (climate) heterogeneity hypothesis, we used yearly standard deviation of precipitation (PPT_{SD}) from TRMM, and standard deviation of the land surface temperature (T_{SD}) from the daytime land surface temperature (LST) from the MOD11A2 product. To calculate these environmental variables, we used a 12-year time series (2000–2012) for all products (ET, PPT, LST and NPP). We calculate the average of each variable for the entire time series, than we extracted the values for each sample location using the extract function in the raster package (Hijmans and Etten 2015), in the R Programming Environment (Team R 2013).

Data analysis

To minimize biases related to biotic sampling, we used a technique that evaluates the sampling coverage (efficiency) at each site based on the number of individuals collected (Chao et al. 2014). Our analysis only included sites where sampling was classified as efficient (minimum of 60% sample coverage) (Calvão et al. 2016). This approach based on individuals is important when looking for richness patterns, as there is a strong relationship between richness and abundance in most cases (Costa and Melo 2008). These methods are intended to flag and eliminate sites with potential sampling issues (Chao et al. 2014).

To control for possible biases in Zygoptera diversity patterns due to differences in anthropogenic disturbances across sites, we applied the Habitat Integrity Index (HII) proposed by Nessimian et al. (2008). This index scores each stream on a scale of 0 (very altered) to 1 (high integrity). The HII values represent the overall similarity between the sample location and an undisturbed stream, as measured by land use, riparian forest, and channel structure characteristics (Nessimian et al. 2008). In this study, we considered only streams with environmental HII values > 0.6 (Brasil et al. 2018). The final dataset included only communities collected in stream sites with ≥ 60% sample coverage (Calvão et al. 2016) and relatively little environmental change (HII > 0.6) (Brasil et al. 2018). Species richness at a site was the response variable for all models, while the predictor variables were selected to represent each of the ecological hypotheses tested (Table 1).

Table 1. Predictors for each of the five hypotheses about species richness patterns of Zygoptera species richness in Amazonian streams. AET_{JAN} = Atmosphere in January;

AET_{Jun} = Atmosphere in Juny; PPT = average of monthly precipitation; T_{SD} = land surface temperature;

| Hypothesis | Predictor variables | Variable code |
|-----------------------|---|-------------------------------|
| Energy | Evapotranspiration in January and June | $AET_{JAN} + AET_{JUN}$ |
| Productivity | Net Primary Productivity | NPP |
| Water-energy | Precipitation, AET_{Jun} , and AET_{Jan} . | $PPT + AET_{JAN} + AET_{JUN}$ |
| Habitat heterogeneity | Temporal variation of temperature and precipitation | $T_{SD} + PPT_{SD}$ |

To test which hypothesizes best explains Zygoptera species richness in Amazonian streams, we built Generalized Linear Mixed Models (GLMM) with Poisson distribution, using species richness as response variable and as predictors the different combinations of the variables associated with the hypotheses described above. As random effect for all the models we included the regions and sample coverage index. We used the Akaike Information Criterion (AIC) to compare models and select the model with the greatest explanatory power (Akaike 1974). The model with the lowest ΔAIC value was considered the best model (Burnham and Anderson 1998). We calculated also two approximated r-squared: the marginal r^2 , that is the proportion of variance explained by the fixed effects alone; and the conditional r^2 , proportion of variance explained by the fixed and random effects jointly (Nakagawa and Schielzeth 2013). All these analyses were done using R software (Team R 2013).

To test for spatial autocorrelation between the models, we evaluated Moran's I values for the residuals of each model. We considered Moran's I values > 0.15 as an indication of spatial autocorrelation, and Moran's I values ≤ 0.15 as an indication that the models had no significant spatial structure. To implement the spatial autocorrelation assumption tests we used the Spatial Analysis in Macroecology Software (SAM) (Rangel et al. 2010). We also tested the collinearity between predictor variables (Legendre and Legendre 1998) (S1 Table).

Results

The most common species was *Argia tinctipennis* (Selys, 1865). This species was found at 101 of the sampled sites (52%). *A. tinctipennis* was followed by *Mnesarete aenea* (Selys, 1853), found at 74 sites (35%), and by *Chalcopteryx rutilans* (Rambur, 1842),

found at 58 sites (27%). Twenty species (18%) were found at only one of the sampled sites.

None of the models considered showed evidence of significant spatial autocorrelation, Moran's I < 0.15 (S2 Table). The model comprising NPP and climate seasonality (habitat heterogeneity) hypotheses was the best predictor of Zygoptera species richness in Amazonian streams, with a pseudo r² of 25% (Table 2). The summary of best model indicates significant influence of NPP and surface temperature seasonality (Table 3), and the Fig 2 shows the response of the species richness to changes on these variables. For example, one zygotperan species is gained for every 1 kg of carbon per square meter in NPP, or with an increase of 2°C in the air temperature variability.

Table 2. Generalized linear mixed models, representing different hypotheses to explain patterns of Zygoptera species richness in Amazonian streams. For a detailed description of each model, please refer to the Supplementary Materials. For a detailed review of the variables used to test the hypotheses see Table 1.

| Model | Hypotheses | AICc df | AICc | Pseudo r ² |
|---|-----------------------------|---------|------|-----------------------|
| NPP + PPT _{SD} + T _{SD} | Prod/Heterogen | 6 | 952 | 0.247 |
| NPP | Productivity | 4 | 954 | 0.096 |
| PPT _{SD} + T _{SD} | Heterogeneity | 5 | 955 | 0.202 |
| PPT _{SD} + T _{SD} + PPT + AET _{JAN} + AET _{JUN} | Heterogen/Water-Energy | 8 | 956 | 0.242 |
| NPP + PPT _{SD} + T _{SD} + PPT + AET _{JAN} + AET _{JUN} | Prod/Heterogen/Water-Energy | 9 | 957 | 0.247 |
| PPT + AET _{JAN} + AET _{JUN} | Water-Energy | 6 | 958 | 0.1 |
| | Null | 3 | 958 | 0 |
| NPP + PPT + AET _{JAN} + AET _{JUN} | Prod/Water-Energy | 7 | 959 | 0.108 |
| AET _{JAN} + AET _{JUN} | Energy | 5 | 961 | 0.003 |

Table 3. Description of the model more adjusted to explain the richness patterns of Zygoptera species of Amazonian streams. For a detailed comparison between all models is shown in table 2.

| | Estimate | Std. Error | z value | Pr(> z) |
|-----------|----------|------------|---------|----------|
| Intercept | 0.885 | 0.476 | 1.858 | 0.063 |
| NPP | 0.178 | 0.077 | 2.319 | 0.020* |
| PPTSD | -0.007 | 0.007 | -1.014 | 0.310 |
| TSD | 0.089 | 0.041 | 2.145 | 0.031* |

Discussion

The best model to explain the observed patterns of Zygoptera species richness included net primary production (NPP), and climate variability (PPTSD and TSD), supporting an integrated form of the net primary productivity (NPP) and habitat heterogeneity hypotheses. Habitat heterogeneity and its interaction with net primary productivity explained most of the variation in species richness. Our results suggest that habitat heterogeneity (in space and time) is among the primary factors driving Zygoptera distributions, likely because it promotes greater niche variation and more diverse environmental resources, which increase species diversity (Bazzaz 1975, Tews et al. 2004).

Seasonality is a key-driver of the climate heterogeneity in the Amazon and is most pronounced in the transition zones (Nobre et al. 2009). In our study we included sites in the Cerrado-Amazon transition, where two of the most diverse biomes on the planet meet (Brando et al. 2013). In these regions, the rainy Amazonian climate is influenced by the climatic seasonality of the Cerrado (Balch et al. 2008), providing an environment that alternates between climatic conditions favoring species typical of rainy Amazonian environments and those typical of drier Cerrado environments (Brasil et al. 2014, Juen et al. 2014). This variation likely contributes to higher species richness in these more environmentally heterogeneous regions (Risser 1995, Gonçalves et al. 2017, Juen et al. 2017).

We found productivity alone to be a weak predictor of Zygoptera diversity. Although several authors have found robust relationships between species richness and primary productivity for other organisms (Connell and Orias 1964, Leigh 1965,

MacArthur and Pianka 1966, Brown 1973, Korell et al. 2016), the mechanisms and responses of this relationship are idiosyncratic. There is no clear mechanism for this richness-productivity relationship generalizable across taxonomic groups and different spatial scales (Waide et al. 1999), so the positive relation of the richness of Zygoptera with productivity can be derived from an indirect mechanism associated with their interaction with the climate. This is because it observes greater net primary productivity in places where vegetation is more diverse (Silva et al. 2015). Zygoptera communities have a moderate and direct congruence with plant communities, (Rodrigues et al. 2016, Bried et al. 2007) which may help explain the relationships with climatic heterogeneity observed in our study.

Considering the interaction between habitat heterogeneity and net primary productivity, Van Rensburg et al. (2002) found similar pattern analyzing richness patterns of birds in Africa. They noted that climatically heterogeneous regions have dry periods that may restrict net primary productivity. Therefore, there is an associated relationship between these predictors (climatic heterogeneity and net primary productivity) that generates environmental conditions conducive to the coexistence of multiple species of birds (Van Rensburg et al. 2002).

This same environmental gradient is correlated with tree richness because regions with greater climatic variation experience greater water restriction and an associated decrease in the rates of photosynthesis. These factors are directly correlated with the number of woody plant species (O'Brien 1993). However, the mechanisms that act on the richness of Zygoptera may be distinct due to the specificities of each group. Zygoptera richness patterns in the Amazon are likely modulated by interactions among the ecological variables measured in the present (e.g. climatic heterogeneity and productivity) and the historical dynamics of migration in the forest-savanna ecotone, transition zones with great species diversity (Risser 1995, Gonçalves et al. 2017, Juen et al. 2017).

In conclusion, this study showed that the temporal variation in climate and net primary productivity were the best predictors of spatial variation in species richness of Zygoptera in Amazonian streams. This work is the first to investigate Odonata richness patterns in the Amazon at this macroecological spatial scale and across a large number of streams. The patterns of richness observed here resemble those found in other taxonomic groups in Africa (O'Brien 1993, Van Rensburg et al. 2002). These patterns are strongly related to environmental conditions in the transition between the Cerrado savanna and

Amazon forest - two globally important ecosystems high in biodiversity and possess the environmental characteristics needed to generate and sustain that diversity.

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Supplementary material

S1 Table. Pearson's Correlation analysis of predictor variables considered in the candidate models.

| | AET_{JAN} | AET_{JUN} | NPP | PPT | PPT_{SD} | T_{SD} |
|--------------------------|--------------------------|--------------------------|------------|------------|-------------------------|-----------------------|
| AET_{JAN} | 1 | | | | | |
| AET_{JUN} | 0.04 | 1 | | | | |
| NPP | 0.38 | -0.21 | 1 | | | |
| PPT | 0.38 | -0.21 | 0.11 | 1 | | |
| PPT_{SD} | 0.16 | 0.09 | 0.14 | 0.13 | 1 | |
| T_{SD} | 0.39 | -0.53 | 0.51 | 0.51 | 0.26 | 1 |

AET_{JAN} = Evapotranspiration in January

AET_{JUN} = Evapotranspiration in June

NPP = Net Primary Productivity

PPT = Precipitation

PPT_{SD} = Precipitation (standard deviation)

T_{SD} = Temperature (standard deviation)

S2 Table. Test of spatial autocorrelation of the residuals of the models using Moran test.

| Model 1 | | | | | | Model 2 | | | | | | |
|---------|----------|-----------|-------|---------|----------|---------|----------|-----------|-------|---------|----------|-------|
| D.Class | DistCntr | Moran's I | P | I (max) | I/I(max) | D.Class | DistCntr | Moran's I | P | I (max) | I/I(max) | |
| 1 | 0.125 | -0.007 | 0.819 | 0.345 | -0.02 | | 0.125 | -0.01 | 0.583 | 0.343 | -0.037 | |
| 2 | 0.455 | 0.011 | 0.613 | 0.253 | 0.042 | | 0.455 | 0.011 | 0.643 | 0.249 | 0.044 | |
| 3 | 0.841 | -0.065 | 0.02 | 0.388 | -0.17 | | 0.841 | -0.06 | 0.025 | 0.38 | -0.165 | |
| 4 | 1.114 | <.001 | 1 | 0.316 | -0 | | 1.114 | 0.003 | 0.879 | 0.316 | 0.009 | |
| 5 | 1.434 | -0.005 | 0.819 | 0.182 | -0.03 | | 1.434 | -0 | 0.854 | 0.173 | -0.024 | |
| 6 | 2.228 | 0.017 | 0.382 | 0.371 | 0.046 | | 2.228 | 0.016 | 0.352 | 0.356 | 0.045 | |
| 7 | 3.134 | -0.01 | 0.538 | 0.21 | -0.05 | | 3.134 | -0.01 | 0.628 | 0.208 | -0.041 | |
| 8 | 3.785 | -0.01 | 0.628 | 0.211 | -0.05 | | 3.785 | -0.01 | 0.613 | 0.203 | -0.041 | |
| 9 | 5.068 | -0.039 | 0.121 | 0.478 | -0.08 | | 5.068 | -0.04 | 0.131 | 0.464 | -0.081 | |
| 10 | 6.212 | 0.05 | 0.04 | 0.556 | 0.089 | | 6.212 | 0.046 | 0.07 | 0.551 | 0.084 | |
| 11 | 6.707 | 0.005 | 0.834 | 0.597 | 0.008 | | 6.707 | 0.003 | 0.864 | 0.593 | 0.005 | |
| 12 | 9.377 | -0.016 | 0.367 | 0.479 | -0.03 | | 9.377 | -0.01 | 0.367 | 0.494 | -0.028 | |
| 13 | 12.27 | -0.006 | 0.663 | 0.195 | -0.03 | | 12.269 | -0 | 0.819 | 0.163 | -0.024 | |
| 14 | 13.68 | 0.01 | 0.487 | 0.187 | 0.055 | | 13.681 | 0.008 | 0.538 | 0.165 | 0.048 | |
| Model 3 | | | | | | Model 4 | | | | | | |
| D.Class | DistCntr | Moran's I | P | I (max) | I/I(max) | D.Class | DistCntr | Moran's I | P | I (max) | I/I(max) | |
| 1 | 0.125 | -0.007 | 0.774 | 0.352 | -0.02 | | -0.125 | 0.005 | 0.839 | 0. | -368 | 0.012 |
| 2 | 0.455 | 0.008 | 0.754 | 0.249 | 0.032 | | 0.455 | 0.007 | 0.754 | 0.307 | 0.022 | |
| 3 | 0.841 | -0.061 | 0.025 | 0.385 | -0.16 | | 0.841 | -0.06 | 0.005 | 0.413 | -0.15 | |
| 4 | 1.114 | -0.004 | 0.814 | 0.308 | -0.01 | | 1.114 | 0.007 | 0.734 | 0.333 | 0.022 | |
| 5 | 1.434 | -0.001 | 0.965 | 0.187 | -0.01 | | 1.434 | -0 | 0.925 | 0.336 | -0.008 | |
| 6 | 2.228 | 0.013 | 0.462 | 0.374 | 0.036 | | 2.228 | -0.01 | 0.739 | 0.415 | -0.016 | |
| 7 | 3.134 | -0.008 | 0.683 | 0.228 | -0.04 | | 3.134 | 0.014 | 0.422 | 0.339 | 0.042 | |
| 8 | 3.785 | -0.008 | 0.653 | 0.198 | -0.04 | | 3.785 | -0 | 0.844 | 0.175 | -0.014 | |
| 9 | 5.068 | -0.038 | 0.126 | 0.467 | -0.08 | | 5.068 | -0.03 | 0.131 | 0.479 | -0.068 | |
| 10 | 6.212 | 0.05 | 0.05 | 0.554 | 0.091 | | 6.212 | 0.04 | 0.06 | 0.53 | 0.076 | |
| 11 | 6.707 | 0.003 | 0.879 | 0.596 | 0.004 | | 6.707 | -0.02 | 0.186 | 0.565 | -0.037 | |
| 12 | 9.377 | -0.016 | 0.372 | 0.494 | -0.03 | | 9.377 | -0.01 | 0.548 | 0.489 | -0.018 | |
| 13 | 12.27 | -0.002 | 0.864 | 0.163 | -0.01 | | 12.269 | 0.002 | 0.925 | 0.204 | 0.008 | |
| 14 | 13.68 | 0.006 | 0.588 | 0.164 | 0.038 | | 13.681 | 0.005 | 0.673 | 0.198 | 0.027 | |

| Model 5 | | | | | | Model 6 | | | | | |
|---------|----------|-----------|--------|---------|----------|---------|----------|-----------|-------|---------|----------|
| D.Class | DistCntr | Moran's I | P | I (max) | I/I(max) | D.Class | DistCntr | Moran's I | P | I (max) | I/I(max) |
| 1 | 0.125 | 0.005 | 0.839 | 0.392 | 0.014 | 3164 | 0.125 | 0.011 | 0.618 | 0.402 | |
| 2 | 0.455 | 0.012 | 0.593 | 0.279 | 0.044 | 3164 | 0.455 | 0.011 | 0.623 | 0.282 | |
| 3 | 0.841 | -0.073 | 0.015 | 0.422 | -0.17 | 3162 | 0.841 | -0.07 | 0.01 | 0.426 | |
| 4 | 1.114 | -0.001 | 0.975 | 0.357 | -0 | 3164 | 1.114 | -0.008 | 0.663 | 0.344 | |
| 5 | 1.434 | -0.006 | 0.764 | 0.201 | -0.03 | 3162 | 1.434 | -0.005 | 0.809 | 0.217 | |
| 6 | 2.228 | 0.019 | 0.312 | 0.429 | 0.043 | 3164 | 2.228 | 0.016 | 0.367 | 0.447 | |
| 7 | 3.134 | -0.015 | 0.397 | 0.275 | -0.05 | 3162 | 3.134 | -0.016 | 0.387 | 0.296 | |
| 8 | 3.785 | -0.012 | 0.518 | 0.263 | -0.05 | 3164 | 3.785 | -0.012 | 0.467 | 0.265 | |
| 9 | 5.068 | -0.035 | 0.151 | 0.574 | -0.06 | 3162 | 5.068 | -0.035 | 0.106 | 0.577 | |
| 10 | 6.212 | 0.049 | 0.09 | 0.605 | 0.081 | 3164 | 6.212 | 0.053 | 0.03 | 0.608 | |
| 11 | 6.707 | 0.015 | 0.427 | 0.664 | 0.022 | 3162 | 6.707 | 0.014 | 0.457 | 0.668 | |
| 12 | 9.377 | -0.024 | 0.151 | 0.521 | -0.05 | 3164 | 9.377 | -0.027 | 0.176 | 0.521 | |
| 13 | 12.27 | -0.008 | 0.598 | 0.252 | -0.03 | 3162 | 12.27 | -0.007 | 0.573 | 0.254 | |
| 14 | 13.68 | 0.01 | 0.427 | 0.159 | 0.065 | 3164 | 13.68 | 0.009 | 0.503 | 0.16 | |
| Model 7 | | | | | | Model 8 | | | | | |
| D.Class | DistCntr | Moran's I | P | I (max) | I/I(max) | D.Class | DistCntr | Moran's I | P | I (max) | I/I(max) |
| 1 | 3164 | 0.125 | 0.013 | 0.553 | 0.39 | 1 | 0.125 | 0.026 | 0.302 | 0.449 | |
| 2 | 3164 | 0.455 | 0.013 | 0.608 | 0.285 | 2 | 0.455 | 0.002 | 0.955 | 0.285 | |
| 3 | 3162 | 0.841 | -0.073 | 0.01 | 0.441 | 3 | 0.841 | -0.082 | 0.005 | 0.437 | |
| 4 | 3164 | 1.114 | -0.008 | 0.729 | 0.355 | 4 | 1.114 | 0.01 | 0.628 | 0.379 | |
| 5 | 3162 | 1.434 | -0.01 | 0.643 | 0.224 | 5 | 1.434 | 0.002 | 0.915 | 0.304 | |
| 6 | 3164 | 2.228 | 0.021 | 0.281 | 0.444 | 6 | 2.228 | -0.015 | 0.412 | 0.533 | |
| 7 | 3162 | 3.134 | -0.018 | 0.397 | 0.287 | 7 | 3.134 | 0.005 | 0.789 | 0.431 | |
| 8 | 3164 | 3.785 | -0.013 | 0.508 | 0.272 | 8 | 3.785 | -0.004 | 0.779 | 0.157 | |
| 9 | 3162 | 5.068 | -0.036 | 0.111 | 0.589 | 9 | 5.068 | -0.019 | 0.387 | 0.611 | |
| 10 | 3164 | 6.212 | 0.055 | 0.05 | 0.617 | 10 | 6.212 | 0.042 | 0.07 | 0.618 | |
| 11 | 3162 | 6.707 | 0.019 | 0.317 | 0.677 | 11 | 6.707 | -0.015 | 0.462 | 0.674 | |
| 12 | 3164 | 9.377 | -0.03 | 0.171 | 0.511 | 12 | 9.377 | -0.023 | 0.136 | 0.548 | |
| 13 | 3162 | 12.269 | -0.01 | 0.538 | 0.278 | 13 | 12.27 | -0.007 | 0.719 | 0.223 | |
| 14 | 3164 | 13.681 | 0.011 | 0.422 | 0.177 | 14 | 13.68 | 0.013 | 0.342 | 0.147 | |

Continuação...

| Model 9 | | | | | |
|----------------|-----------------|------------------|----------|----------------|-----------------|
| D.Class | DistCntr | Moran's I | P | I (max) | I/I(max) |
| 1 | 0.125 | 0.03 | 0.191 | 0.439 | 0.067 |
| 2 | 0.455 | <.001 | 0.96 | 0.283 | 0.003 |
| 3 | 0.841 | -0.084 | 0.015 | 0.45 | -0.19 |
| 4 | 1.114 | 0.005 | 0.824 | 0.383 | 0.013 |
| 5 | 1.434 | 0.004 | 0.859 | 0.292 | 0.013 |
| 6 | 2.228 | -0.012 | 0.548 | 0.545 | -0.02 |
| 7 | 3.134 | 0.003 | 0.829 | 0.436 | 0.006 |
| 8 | 3.785 | -0.004 | 0.809 | 0.155 | -0.03 |
| 9 | 5.068 | -0.02 | 0.322 | 0.623 | -0.03 |
| 10 | 6.212 | 0.046 | 0.05 | 0.629 | 0.073 |
| 11 | 6.707 | -0.012 | 0.472 | 0.685 | -0.02 |
| 12 | 9.377 | -0.028 | 0.151 | 0.537 | -0.05 |
| 13 | 12.27 | -0.009 | 0.523 | 0.248 | -0.04 |
| 14 | 13.68 | 0.016 | 0.302 | 0.163 | 0.096 |

CAPÍTULO 2

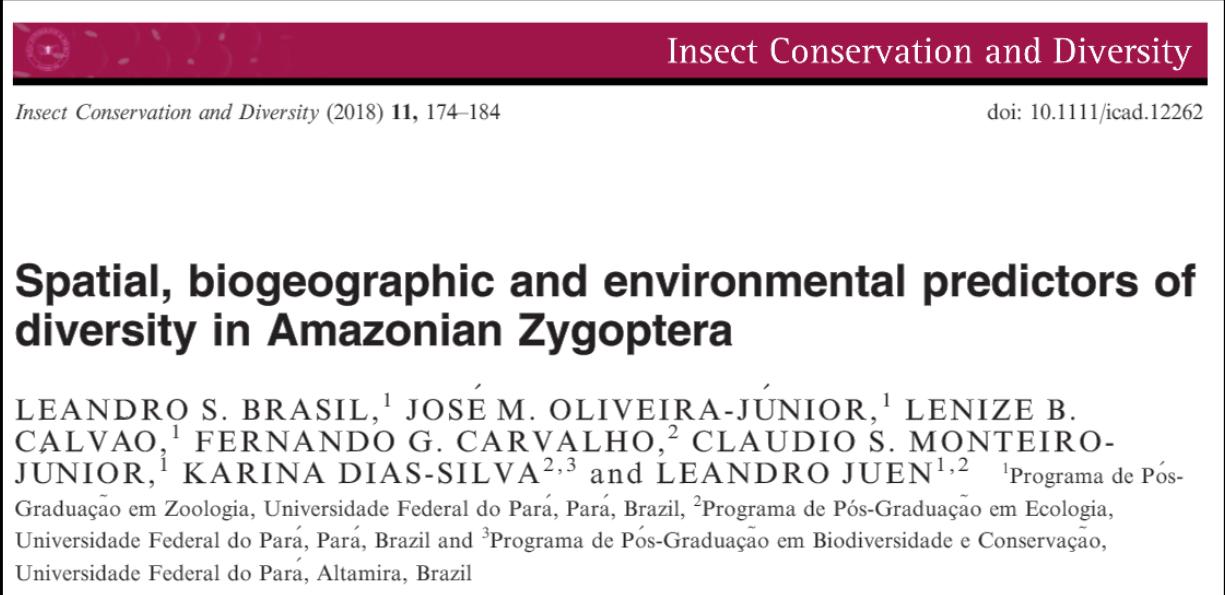
Spatial, biogeographic and environmental predictors of diversity in Amazonian Zygoptera

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The image shows the front cover of a journal issue. At the top, there is a decorative header with the text 'INSECT CONSERVATION AND DIVERSITY' in white. Below this, the journal title 'Insect Conservation and Diversity' is written in a serif font. Underneath the title, the volume information 'Insect Conservation and Diversity (2018) 11, 174–184' is displayed. To the right of the volume info, the DOI 'doi: 10.1111/icad.12262' is shown. The main title of the article, 'Spatial, biogeographic and environmental predictors of diversity in Amazonian Zygoptera', is centered below the journal title. Below the article title, the authors' names are listed: LEANDRO S. BRASIL, JOSÉ M. OLIVEIRA-JÚNIOR, LENIZE B. CALVAO, FERNANDO G. CARVALHO, CLAUDIO S. MONTEIRO-JÚNIOR, KARINA DIAS-SILVA, and LEANDRO JUEN. A small note indicates that LEANDRO JUEN is affiliated with the Programa de Pós-Graduação em Zoologia at the Universidade Federal do Pará. The authors are from the Universidade Federal do Pará, Pará, Brazil. The article is associated with two programs: Programa de Pós-Graduação em Ecologia and Programa de Pós-Graduação em Biodiversidade e Conservação.

Spatial, biogeographic and environmental predictors of diversity in Amazonian Zygoptera

Abstract

1. Our objectives were to assess how turnover and nestedness contribute to beta diversity patterns of the Zygoptera in Amazonian streams, and to relate these components of beta diversity to environmental, spatial and biogeographic predictors. Our first hypothesis is that the turnover is the most important component of beta diversity patterns, due to the historical isolation of all or part of the areas located in the interfluves of the major Amazonian rivers. Our second hypothesis is that the interaction between environmental conditions and the area of endemism (biogeography) would be the most important predictor of beta diversity patterns.
2. To test these hypotheses, we compiled data on the Zygoptera communities from 172 Amazonian streams. We used three sets of predictor variables: (i) environmental variables, (ii) area of endemism (biogeographic) and (iii) spatial filters.
3. The turnover explained 99.36% of the beta diversity, corroborating our first hypothesis. Together, environmental and biogeographic variables were the best predictors of beta diversity patterns. However, for turnover, the biogeographic variables were the best predictors, contrary to our second hypothesis.
4. We found high gamma diversity, but low alpha diversity in the Zygoptera communities. This paradox is explained by the high turnover among sites within the study landscape. This pattern of diversity is related to both historical biogeographic factors and the spatial structuring of environmental conditions in the Amazon region. In the light of our results (high turnover and beta diversity), and their correspondence with areas of endemism,

adequate conservation of Amazonian Zygoptera diversity will depend on the establishment of so-called mega-reserves throughout the major Amazonian interfluves and, whenever possible, in the areas with adequate environmental conditions for the greatest possible number of species, otherwise, most species may be at a constant risk of extinction.

Keywords: Beta diversity, area of endemism, species turnover, Amazonian diversity.

Introduction

The understanding of the processes that contribute to the establishment and/or maintenance of species diversity is one of the major challenges in ecological research (Hutchinson, 1959; Hubbell, 2001; Püttker *et al.*, 2014; Tucker *et al.*, 2015), given the vastly complex nature of these processes and the potential relationships among species. The principal theoretical approaches to this question are based on either environmental factors, derived from the niche theory of Hutchinson (1959), which considers environmental conditions to be selective species filters (Van der Gucht *et al.*, 2007), or neutral processes that consider organisms have similar abilities in dispersal, speciation, birth and death rates, and therefore, independent of their identity, the main drivers of diversity patterns will be the geographic distance between sites (Hubbell, 2001).

In community ecology, research questions that focus on phenomena at large spatial scales normally use niche models based on macroclimatic variables (Nobrega & De Marco, 2011; Juen & De Marco, 2012; Collins & McIntyre, 2015). This approach encompasses the Grinellian aspect of the niche, which has a direct effect on species distribution (Soberon, 2007). However, environmental conditions also determine the structure of biological communities, acting as filters on the distribution of individual species along different ecological gradients (De Marco *et al.*, 2015). The effect of

environmental gradients on species distributions is discussed in species sorting theory, where populations of a given species are more abundant in areas where environmental conditions are more favorable to its development (Henriques-Silva et al., 2013).

A simplified landscape model based on spatial features under similar environmental conditions with no geographic barriers and species with restricted dispersal capacity will predict that sites located more closely together will share more species (Legendre, 1993; Hubbell, 2001; Austin, 2002). In natural environments, however, the existence of geographic barriers makes the long-term spatial dynamics of regional biodiversity a more complex process (Hoorn et al., 2010). Given this, the analysis of spatial processes such as migration or species movements, must take the existence of geographic barriers and the dispersal capacity of the different species into account, in their role as fundamental determinants of biogeographic dynamics (Juen & de Marco, 2012; Dambros et al., 2016).

The theory of isolation by river barriers proposed by Alfred Russell Wallace (Wallace, 1854) as result of his research in the Amazon basin, discusses dispersal processes in the context of the role of the major rivers, which have provoked historical processes of vicariance, resulting in the formation of centers of endemism (Haffer, 2008). These areas of endemism can be divided into eight regions, limited by the confluences of the principal Amazonian rivers (Da Silva et al., 2005), forming the principal biogeographic divisions of species diversity within the basin (Haffer, 1969; Ribas et al., 2012). The taxonomic and phylogenetic diversity of some animal groups, such as primates and birds, is known to be strongly related to the formation and structure of these interfluves (Wallace, 1854; Ayres & Clutton-Brock, 1992; Ribas et al., 2012; Pomara et al., 2014). In the specific case of the Odonata, at large spatial scales, the distribution of species of the Zygoptera is closely related to areas of endemism (Brasil et al., 2017). This is because the Zygoptera have a reduced capacity for dispersal, making the major

Amazonian rivers important geographical barriers to their dispersion, and thus over time, forming areas of endemism corresponding to the interfluviums of these major rivers (Juen & de Marco, 2012).

Zygoptera species conform to environmental conditions in both the immature, aquatic phase and the adult, terrestrial-aerial phase (Valente-Neto *et al.*, 2015; Mendes et al 2017). In the immature phase, there is a high degree of correlation with the physical structure of the stream and the physical and chemical characteristics of the water (Mendes *et al.*, 2015), whereas in the adult phase, there is a strong relationship with the incidence of sunlight, a factor related directly to the microclimatic conditions of temperature and humidity (Monteiro-Júnior *et al.*, 2014; De Marco *et al.*, 2015; Oliveira-Junior *et al.*, 2015; Miguel *et al* 2017a). In general, Zygoptera are small-bodied, with low flying speeds (Corbet, 1999), and their geographic distribution tends to be well-structured in spatial terms (Heiser & Schmitt, 2010; Siepielski & McPeek, 2013). These characteristics (relationships with environmental variables and spatial distribution) make the Zygoptera an appropriate group for ecological studies on the spatial distribution of diversity (Miguel *et al* 2017b).

Considering the theoretical framework regarding community ecology and Zygoptera characteristics, it becomes clear that there is a need for a broad investigation that takes into account several aspects in order to understand its distribution patterns within Amazonia. Three major aspects must be taken into consideration: i) the effect of the environmental conditions on the distribution of species, expressed as the degree of environmental suitability for its establishment over the landscape (Grinnell, 1917; Hutchinson), ii) biogeographical patterns and historical barriers for dispersal (Wallace, 1985; Juen et al., 2012), and iii) the spatial effect, or how these patterns might be affected merely by geographical distance (Dambros et al., 2016).

In this context our objectives were to assess how turnover and nestedness contribute to the beta diversity patterns of the Zygoptera in Amazonian streams, and relate the most important component of beta diversity (turnover or nestedness) to environmental, spatial and biogeographic predictors. Our first hypothesis was that turnover is the most important component for beta diversity patterns, due to the historical isolation in all or part of the areas of endemism located in the interfluves of the major Amazonian rivers. Our second hypothesis is that the interaction of environmental conditions and areas of endemism (biogeography) would be the most important predictors of beta diversity patterns, as a result of both environmental gradients (Henriques-Silva et al., 2013) and biogeographic processes (Juen and De Marco, 2012) acting together.

Materials and Methods

Study area

We sampled the Zygoptera communities found in 172 small streams (up to 5 m in width and 0.8 m mean depth, classified as wadeable streams) in the Brazilian Amazon basin (Fig. 1). The streams are located in five different areas of endemism, including 72 streams (42% of the total) in the Belém area of endemism, 24 (14%) in the Guiana area, 21 (12%) in the Rondônia area, 27 (16%) in the Tapajos area of endemism, and 28 (16%) in the Xingu area of endemism (Fig. 2).



Fig. 1. (A) Example of a study stream in the Brazilian Amazon region, and (B) one of the Zyoptera species analyzed in the present study.

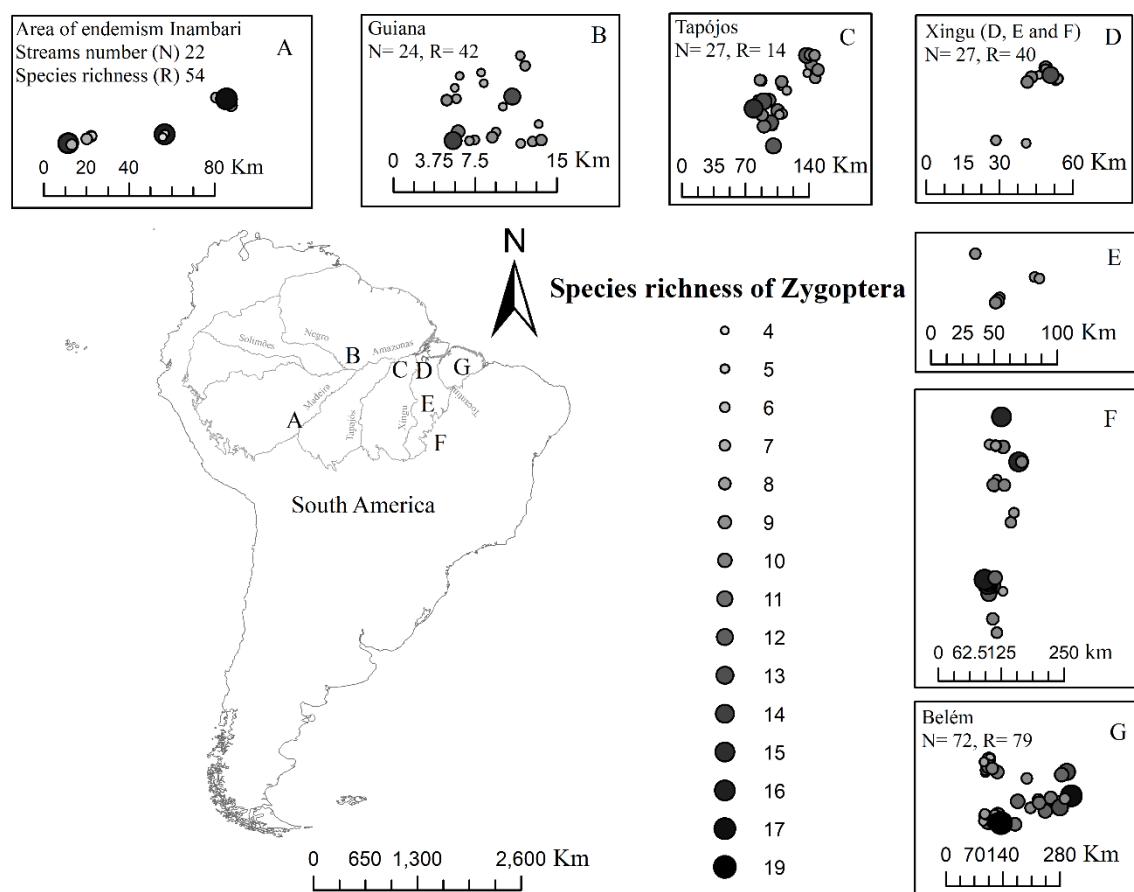


Fig. 2. The spatial distribution of the collecting points for the Zyoptera communities sampled in the Brazilian Amazon: A= Inambari center of endemism; B= Guiana center of endemism; C= Tapajós center of endemism; D= northern Xingu center of endemism;

E= central Xingu center of endemism; F= southern Xingu center of endemism. G= Belém center of endemism. The size and color of the circles vary in accordance with Zygoptera species richness.

All the streams are located within areas of dense *terra firme* rainforest, with altitudes of over 100 meters, have large amounts of biomass and are distributed widely throughout the Neotropics (Myster, 2016). We measured the integrity of the habitat at all the sites using the index proposed by Nessimian *et al.* (2008), which varies from 0 to 1, with higher values indicating the streams with the highest integrity. To control for possible biases related to the influence of anthropogenic pressures, we restricted sampling to streams with a HII of at least 0.6, following Nessimian *et al.* (2008).

We used three sets of predictor variables. The first set (Environmental variables) were based on niche theory (Grinnell, 1917; Hutchinson, 1959; Soberon, 2007). The second set of predictor variables (Biogeographic variables) were based on the areas of endemism from biogeographic analyses of the Zygoptera, presented by Juen & de Marco (2012). The third set of predictors (Spatial variables) was derived from the spatial filters (Dray *et al.*, 2006), and considers both demographic stochasticity and limited dispersal.

Environmental variables

The set of environmental variables was based on niche theory (Grinnell, 1917; Hutchinson, 1959; Soberon, 2007), for which we used 19 climatic environmental variables extracted from the WorldClim database, version 1.4 (<http://www.worldclim.org/>): (1) annual mean temperature; (2) mean diurnal temperature range; (3) isothermality; (4) temperature seasonality; (5) maximum temperature of the warmest month; (6) minimum temperature of the coldest month; (7) annual temperature

range; (8) mean temperature of the wettest quarter; (9) mean temperature of the driest quarter; (10) mean temperature of the warmest quarter; (11) mean temperature of the coldest quarter; (12) annual precipitation; (13) precipitation of the wettest month; (14) precipitation of the driest month; (15) seasonality of the precipitation; (16) precipitation of the wettest quarter; (17) precipitation of the driest quarter; (18) precipitation of the warmest quarter; and (19) precipitation of the coldest quarter. A resolution of approximately 1 km was used, considering the latitude at the equator (30 arc-seconds). This set of variables was selected because it is the most popular model of species distribution based on environmental determinants used for the Odonata (Collins & McIntyre, 2015).

Biogeography variables

The standard protocol for the analysis of the influence of biogeographic processes on diversity in the Amazon region is to use the areas of endemism formed between the major rivers (for more information, see Silva et al., 2005). In this study, we consider five regions (areas of endemism): Guiana (formed by the Amazon and Negro rivers), Rondônia (formed by the Solimões and Tapajós rivers), Tapajós (formed by the Tapajós and Xingu rivers), Belém (formed by the Tocantins river and/or mouth of Amazon river) and Xingu (formed by the Xingu and Tocantins rivers). These divisions were initially proposed based on the observations of Wallace (1985), and have been found to be important predictors for the distribution of bird species (Ribas et al., 2012) and Zygoptera in the Brazilian Amazon basin (Juen and De Marco, 2012).

Spatial variables (Principal Coordinates of Neighbour Matrices - PCNM)

Due to spatial autocorrelation, it is expected that the closer the areas, the more similar species composition will be, which is related to species movement and how difficult it would be for a species to reach more distant areas (Koenig, 1999; Koenig & Knops, 1998; Dormann et al., 2007). For this reason, we must take in consideration this purely spatial effect when testing hypothesis about what factors determine the distribution patterns of species (Dambros et al., 2016). We used spatial filters to understand how the spatial distribution of sites influenced patterns of beta diversity and its components, turnover and nestedness (Rangel et al., 2010). This ensures that environmental and biogeographical predictors are not affected by any underlying spatial structures, and thus avoids any confounding effects of spatial autocorrelation on our analyses (Bini et al., 2009). A Principal Coordinates of Neighbour Matrices (PCNM) approach (Dray et al., 2006) was used to spatially represent the sites.

Biotic variables

We collected biotic data between 2009 and 2013, in the dry season (July-November), which is when the greatest diversity of aquatic insects is expected in the Amazon region (Baptista et al., 2001), and sampling is least likely to be affected by climatic conditions. In each stream, we demarcated a linear transect of 100 meters, and captured all the adult Zygoptera specimens observed along the transect, with a mean sampling period of one hour, using an entomological hand-net of 40-cm in diameter and 65-cm in length. To minimize bias related to the different types of thermoregulation (thermal conformers, heliotherms and endotherms: May, 1976), we collected specimens only on sunny days between 10:00 a.m. and 2:00 p.m., when the sun's rays reach the principal channel of the

streams (Juen & De Marco, 2011; Brasil *et al.*, 2014b; Miguel *et al.*, 2017a).

We prepared all the specimens collected based on the protocol of Lencioni (2006) and identified the material using taxonomic keys and specialized illustrated guidebooks (Garrison 1990; Lencioni 2005; 2006; Garrison *et al.*, 2010). Whenever necessary, we sent material to specialists. The specimens were deposited as vouchers in the collection of the Zoology Museum on the Belém campus of the Federal University of Pará (UFPA), Brazil. All insects were collected by members of the UFPA Ecology and Conservation Laboratory (LABECO) of the Federal University of Pará (UFPA), under authorization from the Brazilian Institute for the Environment and Renewable Resources (IBAMA, Licence No. #1993421). All data collected are available on the SISBIO platform (<http://www.icmbio.gov.br/sisbio/>).

Data analysis

The mean beta diversity (β_{sor}) considers the number of species not shared between a sampling unit and all other sampling units (α -diversity), providing an index that varies from 0 to 1. The lower the value of this index, the greater the β diversity of the sampling unit. The mean nestedness index (β_{nes}) provides a measure of the extent to which the set of species recorded in the sampling unit represents a subset of the total species diversity of all the sampling units, with values closest to zero indicating the highest level of local nestedness. The mean turnover index (β_{sim}) evaluates the exchange of species in each sampling unit relative to the total diversity of all the samples, with values closest to zero indicating the highest local turnover (Baselga, 2010; Baselga & Orme, 2012; Si *et al.*, 2015).

To calculate beta diversity, turnover and local nestedness (mean beta diversity) we

averaged each row of the dissimilarity matrix to enable pairwise comparison between sites. Thus, beta diversity, turnover and nestedness represent the mean value of beta diversity, turnover and nestedness of each site compared with all the other study sites. This beta diversity approach, when based on homogenized mean values for pairs of sites, may result in a loss of information, although it permits the integrated interpretation of a set of sites to demonstrate general patterns of diversity, which facilitates the investigation of their relationship with environmental or spatial gradients, which may be structuring diversity at a landscape level (see Boyero *et al.*, 2015; Solar *et al.*, 2015; Datry *et al.*, 2016). We used the beta.sor, beta.sim and beta.nes functions to calculate the β_{sor} , β_{sim} and β_{nes} vectors, respectively (Baselga, 2010) (Supplementary Material).

The climatic parameters used in the models were derived from the 19 macroclimatic variables extracted from WorldClim. To avoid instability in the regression models derived from multicollinearity among the variables, we ran a Principal Components Analysis (PCA) on the 19 variables and then used the axes of this analysis as predictors for the regressions. For this, we used the first five axes of the PCA that together accounted for more than 97.62% of the observed environmental variation, in an attempt to use the smallest possible number of axes to best represent the empirical pattern of environmental variation. For the PCA, the matrix of climatic data was first standardized, to permit the comparison of parameters measured on different scales. The environmental data were standardized for the PCA using the decostand function of the vegan package (Oksanen *et al.*, 2013) and the PCA what was run in the princomp function of the stats package, using correlation.

The spatial variables used as predictors were the spatial features calculated by the Principal Coordinates of Neighbour Matrices (PCNM) (Dray *et al.* 2006). We used the latitude and longitude of each collecting point to calculate the spatial filters for the β_{sor} ,

β_{sim} and β_{nes} vectors in the SAM (Spatial Analysis in Macroecology) program (Rangel et al., 2010). We used the vector with the information on the centres of endemism of all the sites (Belém, Xingu, Tapajós, Guiana and Inambari) to compile the biogeographic variables to be used as predictors. We then ran an ordination analysis (PCA) on this vector, using the dudi.hillsmith function in the ade4 package (Dray and Dufour, 2007). We then used the eigenvectors of this ordination as the biogeographic predictors.

To test our first hypothesis, i.e., that turnover would be the most important component of the patterns of diversity, we calculated the beta diversity (β_{sor}), and the contribution of turnover (β_{sim}) and nestedness (β_{nes}) to the total diversity (beta values, and the turnover and nestedness of the whole set of sites). Then, using null models, we tested the probability that the results could be explained by chance, considering a 5% significance level, with the function ‘oecosimu’ (Oksanen et al., 2013). We used the ‘oecosimu’ function in the Vegan package to assess whether the values of the β_{sor} (Beta diversity), β_{sim} (turnover), and β_{nes} (nestedness) vectors found for the community were different from those of randomly-generated communities. The randomization process of the communities is described in the commsim function of the Vegan package (Oksanen et al., 2013).

To test our second hypothesis and check the contribution of each set of predictors (environmental, spatial and biogeographical), we applied a partial Redundancy Analysis (partial-RDA) (Legendre and Legendre, 2012). We pre-selected the predictor variables using the Forward stepwise method to determine which variables of the three data sets (environmental, spatial, and biogeographic) would be adequate predictors of β_{sor} and β_{sim} . We then determined the partition of variance using the β_{sor} as the response variable, and the pre-selected environmental, spatial, and biogeographic parameters as the predictor variables, and a second partition using β_{sim} as the response variable, and the pre-

selected environmental, spatial, and biogeographic parameters as the predictor variables. For each partition (β_{sor} and β_{sim}), we tested whether the observed relationships could be accounted for by chance, using 10,000 randomizations, with an α of 5%. The partition of variance was conducted using the varpart function of the vegan package (Oksanen et al., 2013). The codes used in the analysis of the data are listed in the supplementary material.

Results

Environmental conditions

In general, a well-defined environmental gradient was found among the study sites. The highest mean temperatures were recorded in the Inambari area of endemism and at the sites in the northern portion of the Xingu area of endemism. The sites closer to the Amazon-Cerrado transition in the Belém area of endemism, to the south of the Xingu area of endemism returned the greatest variation in temperature and precipitation (Fig. 3).

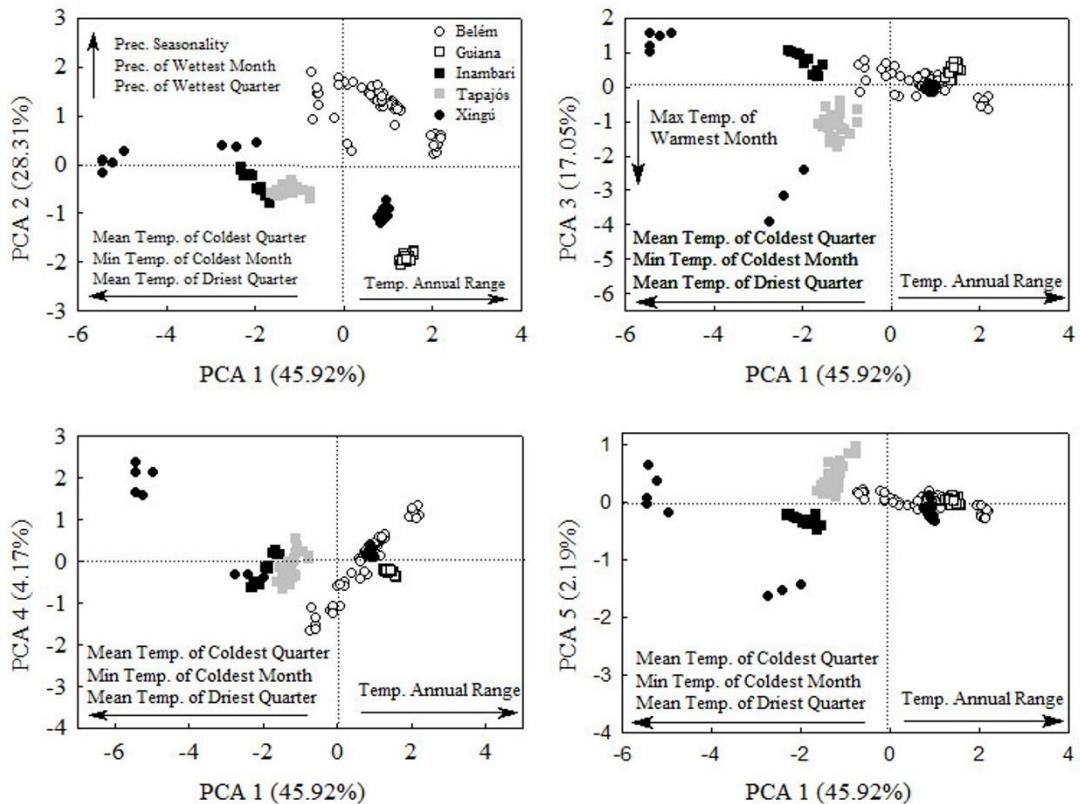


Fig. 3. Principal Components Analyses (PCAs) of the environmental conditions found at the study sites. The variables shown in each figure correlated > 70% with the respective axes.

Patterns of diversity

A total of 132 species (gamma diversity) were recorded in study. Of these, 6.7 ± 3.5 species (mean \pm standard deviation per stream) were collected on a local scale, and 45.8 ± 23.6 (mean \pm standard deviation per area of endemism) work collected on a regional scale (Fig. 4). The most widely-distributed species was *Protoneura tenuis* Selys, 1860, which occurred in 83 streams (48% of the study sites), followed by *Chalcopteryx rutilans*

(Rambur, 1842) (63 or 36%), *Argia infumata* Selys, 1865 (60 or 35%), *Argia tinctipennis* Selys, 1865 (52 or 30%) and *Mnesarete aenea* (Selys, 1853) (37 or 21%). Beta diversity in the streams was high ($\beta_{\text{soer}} = 0.987$), and was related to turnover in 99.36% of the cases ($\beta_{\text{sim}} = 0.981$), and to nestedness in only 0.6% ($\beta_{\text{nes}} = 0.006$) (Table 1).

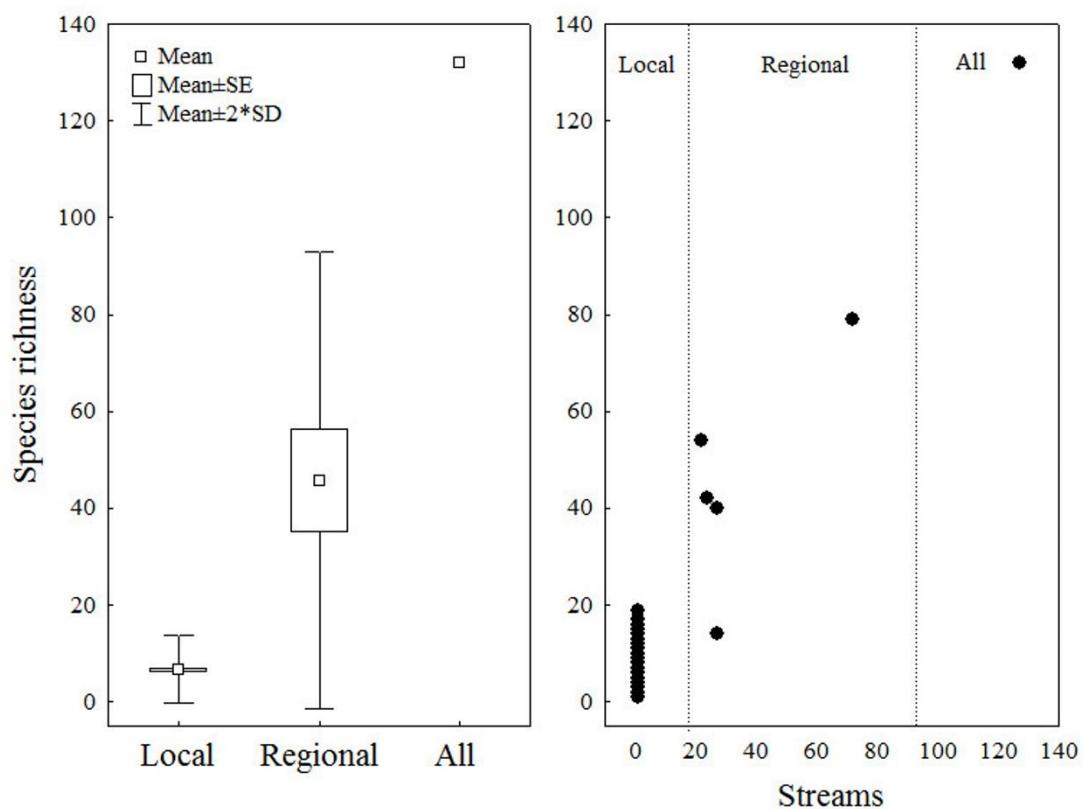


Fig. 4. Relation between the sampling effort on different spatial scales and the Zygoptera species richness.

Table 1. Values of beta diversity (β_{sor}) with the contributions of the turnover (β_{sim}) and nestedness (β_{nes}) calculated following Baselga et al. (2012). The p values were obtained using the R1 method in the ‘oecosimu’ function (Oksanen et al., 2016).

| | Statistic | SES | mean | | | | Pr (sim.) |
|--|------------------|------------|--------------|------------|--------------|-------|------------------|
| | | | 2.50% | 50% | 97.5% | | |
| Turnover (β_{sim}) | 0.981 | 2.471 | 0.981 | 0.981 | 0.981 | 0.982 | 0.019 |
| Nestedness (β_{nes}) | 0.006 | 2.664 | 0.006 | 0.005 | 0.006 | 0.006 | 0.015 |
| Beta diversity (β_{sor}) | 0.987 | 2.232 | 0.987 | 0.987 | 0.987 | 0.987 | 0.031 |

Spatial, biogeographic and environmental conditions and diversity of the Zygoptera

The best-fitting model included environmental, spatial and biogeographic variables, which together explained 29% of the variance in beta diversity (β_{sor}). Most of the explanation is derived from the interaction between environment and biogeography (14%), followed by the between all three predictors (11%), and the interaction between biogeography and space (10%). Biogeography alone also explained 8% of this model (β_{sor}) of beta diversity (Fig. 5). When the turnover model (β_{sim}) was used as the response variable, the environmental, spatial and biogeographic predictors explained 27.5% of the variance. In this case, biogeography alone in the major predictor (16%), followed by the interactions between space and biogeography (4%) and the three variables combined (3%) (Fig. 5). Nestedness (β_{nes}) explained only 0.6% of the beta diversity, and was thus excluded from the testing of the second hypothesis.

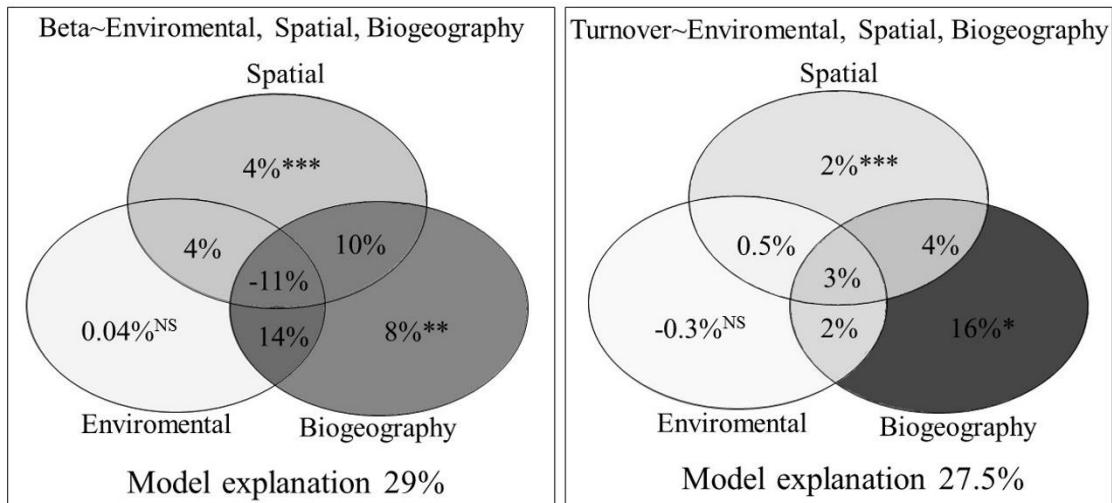


Fig. 5. Partition models of variance for the beta diversity (β_{sor}) and turnover (β_{sim}) component considering environmental, spatial and biogeography as predictors. The color gradient represents the size of the effect, with darker colors reflecting a higher degree of explanation.

DISCUSSION

Patterns of diversity

Our results indicate that turnover is the most important component of the variation in beta diversity in the Zygoptera communities of Amazonian streams, confirming the predictions of our first hypothesis. Local (alpha) species richness was relatively low in comparison with previous studies using similar sampling effort in streams of the Brazilian Atlantic Forest (Silva *et al.*, 2010), Cerrado Savanna (Carvalho *et al.*, 2013; De Marco Júnior *et al.*, 2015; Dutra & De Marco, 2015) and the Amazon-Cerrado transition zone

(Brasil *et al.*, 2014a, 2014b; Juen *et al.*, 2014). However, the Amazon region has one of the highest levels of alpha diversity found anywhere on the planet in a number of different taxonomic groups (Vinet & Zhedanov, 2010), including the Odonata (Kalkman *et al.*, 2008), which may be related to the large number of endemic species found in the different biogeographic regions (Juen & De Marco, 2012).

Our results reinforce the conclusion that species diversity is dependent primarily on spatial scaling (Gering & Crist, 2002), and that, given the high species turnover of the communities on a small scale (Juen & De Marco, 2011), studies that focus on relatively small areas may underestimate regional diversity (Caley & Schluter, 1997). Given this, we would recommend that baseline studies for environmental licensing should focus on an area larger than that impacted directly by any proposed project (e.g. resource extraction, hydroelectric projects), to avoid underestimating the number of species. Furthermore, any mitigating measures deployed on a small spatial scale are likely to be ineffective if the impacts of disturbance also occur on a larger (regional) spatial scale.

Historically, the Odonata have been widely neglected in the decision-making process and definition of conservation areas in Brazil (Nobrega & De Marco, 2011), despite their considerable importance for both aquatic and terrestrial systems (Corbet, 1999; Miguel *et al.*, 2017b). Given this, and knowing the dynamic nature of Zygoptera communities in the Amazon landscape (high turnover and beta diversity), and the relationship between the endemic species and the centers of endemism (Juen & de Marco, 2012), the best strategy for the conservation this group is likely to be the establishment of so-called mega-reserves (see Peres, 2005). These mega-reserves should be distributed in all the Amazonian interfluves, and whenever possible, in the areas with adequate conditions for the largest possible number of species, otherwise, most species may be at constant risk of extinction due to habitat loss, as observed in the Brazilian Cerrado by Nobrega & De

Marco (2011). It is important to note that, of the 1636 odonate species estimated to occur in the Neotropical region (Kalkman *et al.*, 2007), 392 are known to occur in the Brazilian Amazon, and 47.7% are endemic to a single interfluve (Juen & De Marco, 2012).

Spatial, biogeographic and environmental conditions, and diversity of the Zygoptera

Biogeographic and environmental conditions were considered to be good predictors of Zygoptera beta diversity. However, considering only turnover, the best predictor was Biogeography. Thus, our second hypothesis was not supported by our findings. From there, we concluded that climate variation and geographical barriers, created by the major Amazonian rivers, are the major drivers of the diversity pattern of Amazonian Zygoptera.

Together with biogeography, climate is an important driver of beta diversity (β_{sof}) in the Zygoptera because factors such as temperature determine which areas are appropriate for the occurrence of a given species, i.e., they act as an environmental filter (Hutchinson, 1959). Environmentally heterogeneous areas should thus have a higher diversity of species (Hutchinson, 1961). This is because, in more heterogeneous environments, individuals that occupy distinct portions of the functional space may co-occur in the same geographic space due to greater niche partitioning (Tilman, 1982; Tilman *et al.*, 1997), thus avoiding competitive exclusion (Oliveira-Júnior & Juen, *in preparation*). On a macro scale, the Amazon basin can be divided into three principal climatic types (Peel *et al.*, 2007) - (i) the western Amazon basin, with a superhumid (Af type) climate influenced strongly by the proximity of the Andes, (ii) the central Amazon basin, with a tropical sub-humid climate (Am), and (iii) the southern and eastern Amazon basin, where the tropical climate is characterized by dry winters (Aw). These macro-climatic patterns represent

environmental filters that may restrict the geographic distribution of odonate species over both time and space, due to the dynamic nature of the conditions found in the landscape (Hickling *et al.*, 2005), which are important determinants of local patterns of species diversity (Ball-Damerow *et al.*, 2014).

When we consider a climate change scenario, it is expected that suitable areas for species occurrence will be displaced in the future landscape (Ribeiro *et al.*, 2016). When we consider that displacement coupled with the natural geographic barriers that limit Zygoptera dispersal (Juen & de Marco, 2012; Brasil *et al.*, 2017) and the incessant habitat fragmentation (Fearnside, 2005), it is expected that several Zygoptera will have their suitable areas displaced to locations where they cannot reach. This combination of factors will be particularly critical for species with low adaptive capacity, as those species will not endure climatic changes and will not be able to escape from those harsh conditions.

In addition to current ecological factors, such as the climate, historical factors such as the isolation of populations by river barriers play an important role in the distribution patterns of odonates in the Amazon region (Juen & de Marco, 2012). The interfluves restrict the dispersal of the species that are unable to traverse the major rivers that delimit them (Haffer, 2008). However, beyond the geographical barrier effect mentioned above, spatially proximal locations should have a higher number of shared species (Hubbell, 2001), especially in the case of organisms with limited dispersal capacity, as in the case of most Zygoptera (Juen & De Marco, 2011; Sanchez-Herrera & Ware, 2012). These two influences, i.e., (i) distance between the sites, and (ii) the influence of major rivers as geographical barriers, are difficult to separate, as most of the sites in the same area of endemism area are spatially closer to one another than to sites in different areas of endemism (Dambros *et al.*, 2016; Oliveira *et al.*, 2017).

Clearly, it is difficult to provide a unified theory to explain diversity patterns for all

organisms across different temporal and spatial scales. As in the case of the present research, many previous studies have found evidence of the combined effects of environmental and spatial factors (Hamasaki *et al.*, 2008; Juen & De Marco, 2011; Siepielski & McPeek, 2013). In this context, we conclude that the interaction between environmental conditions, space and biogeographic processes provide the best explanation for the patterns of beta diversity of the Zyoptera in the Amazon region. Furthermore, due to the high turnover of species along the landscape, it is crucial that researchers be cautious while deriving conclusions about Zyoptera diversity patterns based only on alfa diversity and small spatial scales.

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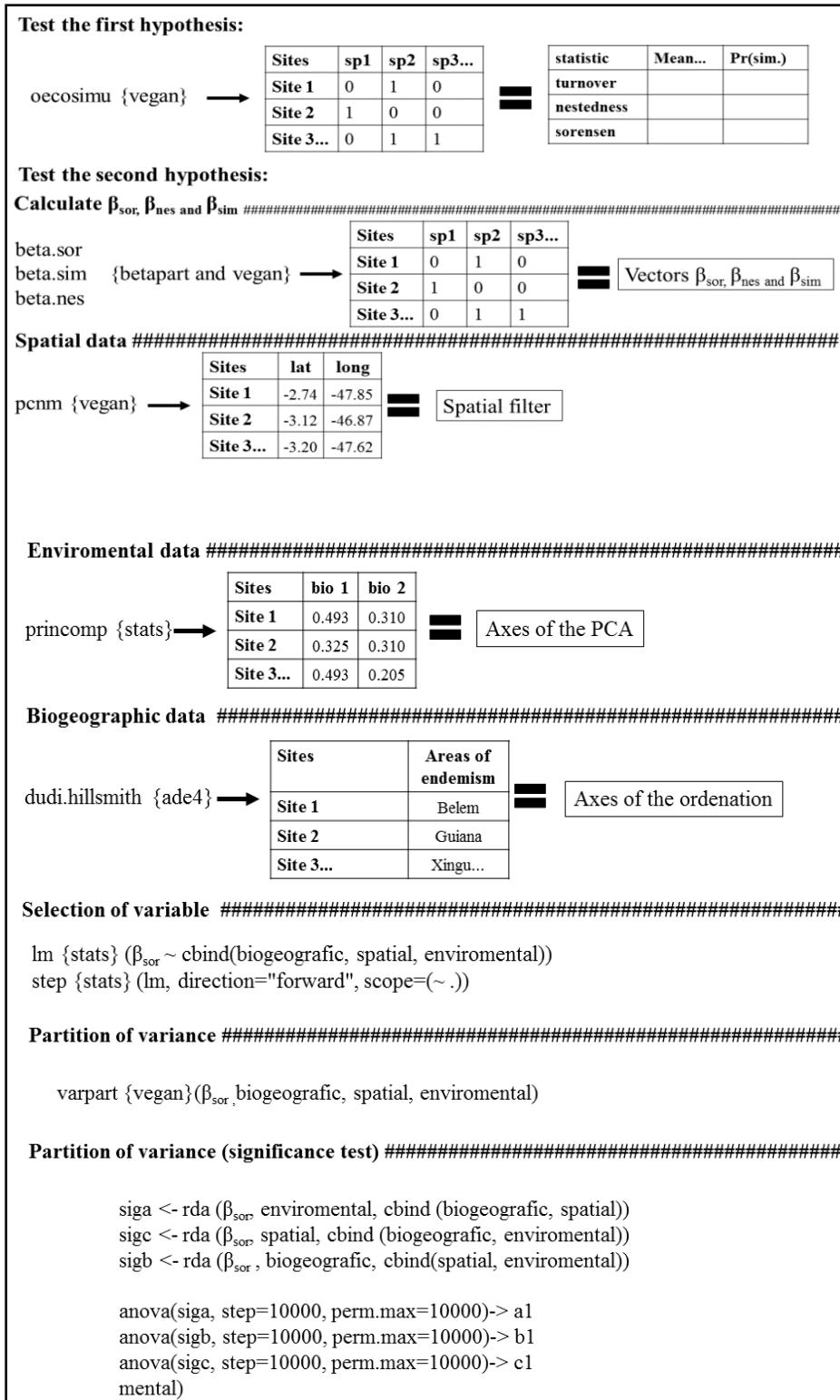
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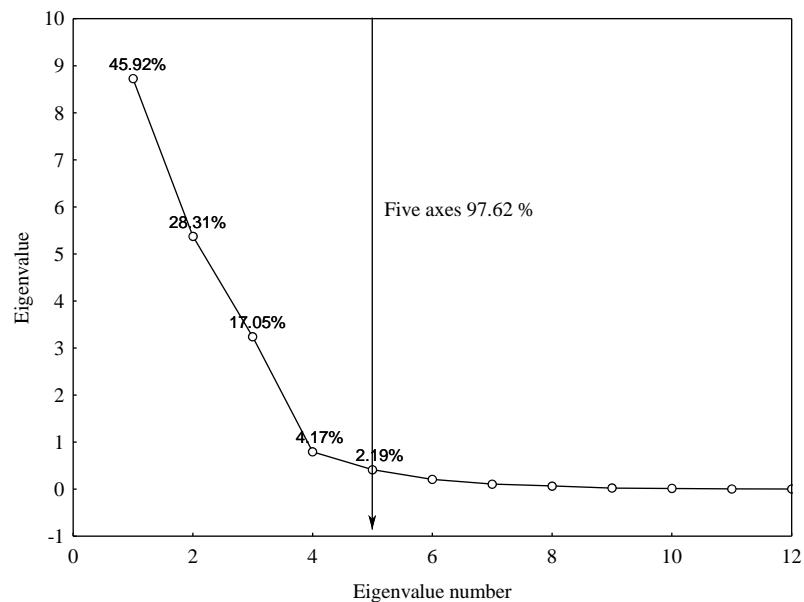
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Supplementary material

- Suggestion of statistical tests for routine replicates the work.



2. Eigenvalues of the Principal Component Analysis.



3- Checklist of the species of Zygoptera of Amazonian streams.

- Acantagrion chacoense* Calvert, 1909
Acanthagrion adustum Williamson, 1916
Acanthagrion aepiolum Tennessean, 2004
Acanthagrion apicale Selys, 1876
Acanthagrion ascendens Calvert, 1909
Acanthagrion kennedii Williamson, 1916
Acanthagrion phallicorne Leonard, 1977
Acanthagrion rubrifrons Leonard, 1977
Acanthagrion truncatum Selys, 1876
Acanthagrion sp.
Acanthallagma luteum Williamson & Williamson, 1924
Agrion dorsale (Burmeister, 1839)
Argia chapadae Calvert, 1909
Argia croceipennis Selys, 1865
Argia oculata Hagen in Selys, 1865
Argia euphorbia Fraser, 1946
Argia fumigata Hagen in Selys, 1865
Argia hasemani Calvert, 1909
Argia indicatrix Calvert, 1902
Argia infumata Selys, 1865
Argia insipida Hagen in Selys, 1865
Argia lilacina Selys, 1865
Argia modesta Selys, 1865
Argia mollis Hagen in Selys, 1865
Argia reclusa Selys, 1865
Argia smithiana Calvert, 1909
Argia subapicalis Calvert, 1909
Argia tinctipennis Selys, 1865
Argia tupi Calvert, 1909
Argia sp.
Argia sp. 1
Argia sp. 2
Argia sp. 3
Argia sp. 4
Argia sp. 5
Argia sp. 6
Argia sp. 7
collata Selys, 1865
Chalcolepteryx radians Ris, 1914
Chalcolepteryx rutilans (Rambur, 1842)
Chalcolepteryx sp.
-

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- Cyanallagma ferenigrum* De Marmels, 2003
Dicterias atrosanguinea Selys, 1853
Drepanoneura janirae Belle, 1994
Epipleoneura albuquerquei Machado, 1964
Epipleoneura capilliformis (Selys, 1886)
Epipleoneura haroldoi Santos, 1964
Epipleoneura kaxuriana Machado, 1985
Epipleoneura machadoi Rácenis, 1960
Epipleoneura metallica Rácenis, 1955
Epipleoneura pereirai Machado, 1964
Epipleoneura spatulata Rácenis, 1960
Epipleoneura tariana Machado, 1985
Epipleoneura venezuelensis Rácenis, 1955
Epipleoneura westfalli Machado, 1986
Epipleoneura williamsoni Santos, 1957
Epipleoneura sp.
Epipleoneura sp. 1
Gynacantha auricularis Martin, 1909
Gynacantha litoralis Williamson, 1923
Gynacantha membranalis Karsch, 1891
Gynacantha sp. 1
Gynothemis sp. 1
Heliocharis amazona Selys, 1853
Hetaerina amazonica Sjöstedt, 1918
Hetaerina auripennis (Burmeister, 1839)
Hetaerina cruentata (Rambur, 1842)
Hetaerina curvicauda Garrison, 1990
Hetaerina hebe Selys, 1853
Hetaerina indepresa Garrison, 1990
Hetaerina laesa Hagen in Selys, 1853
Hetaerina moribunda Hagen in Selys, 1853
Hetaerina rosea Selys, 1853
Hetaerina sanguinea Selys, 1853
Hetaerina westfalli Rácenis, 1968
Heteragrion angustipenne Selys, 1886
Heteragrion aurantiacum Selys, 1862
Heteragrion bariai De Marmels, 1989
Heteragrion icterops Selys, 1862
Heteragrion silvarum Sjöstedt, 1918
Heteragrion sp.
Heteragrion sp. 1
Heteragrion sp. 2
Homeoura nepos (Selys, 1876)
Ischnura capreolus (Hagen, 1861)
-

-
- Macrothemis absimilis* Costa, 1991
Macrothemis imitans Karsch 1890
Mesoleptobasis acuminata Santos, 1961
Metaleptobasis amazonica Sjöstedt, 1918
Metaleptobasis diceras (Selys, 1877)
Metaleptobasis selysi Santos, 1956
Metaleptobasis sp. 1
Microstigma anomalum Rambur, 1842
Microstigma rotundatum Selys, 1860
Microstigma sp.
Mnesarete aenea (Selys, 1853)
Mnesarete astrape De Marmels, 1989
Mnesarete cupraea (Selys, 1853)
Mnesarete machadoi Garrison, 2006
Mnesarete smaragdina (Selys, 1869)
Mnesarete sp.
Mnesarete williamsoni Garrison, 2006
Neoneura denticulata Williamson, 1917
Neoneura bilinearis Selys, 1860
Neoneura lucas Machado, 2002
Neoneura luzmarina De Marmels, 1989
Neoneura rubriventris Selys, 1860
Oxyagrion fernandoi Costa, 1988
Oxystigma petiolatum (Selys, 1862)
Oxystigma sp.
Perilestes attenuatus Selys, 1886
Perilestes kahli Williamson & Williamson, 1924
Perilestes minor Williamson & Williamson, 1924
Perilestes solutus Williamson & Williamson, 1924
Perissolestes aculeatus Kennedy, 1941
Perissolestes romulus Kennedy, 1941
Perithemis cornelia Ris, 1910
Phasmoneura exigua (Selys, 1886)
Phasmoneura janirae Lencioni, 1999
Phasmoneura sp. 1
Phoenicagrion sp.
Polythore vittata (Selys, 1869)
Protoneura scintilla Gloyd, 1939
Protoneura tenuis Selys, 1860
Psaironeura bifurcata (Sjöstedt, 1918)
Psaironeura tenuissima (Selys, 1886)
Telebasis carminita Calvert, 1909
Telebasis coccinea (Selys, 1876)
Telebasis griffinii (Martin, 1896)
-

Telebasis racenisi Bick & Bick, 1995

Telebasis sp.

Tigriagrion aurantinigrum Calvert, 1909

CAPÍTULO 3

Elements of metacommunity structure in Amazonian Zygoptera among streams under different spatial scales and environmental conditions

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Elements of metacommunity structure in Amazonian Zygoptera among streams under different spatial scales and environmental conditions

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Elements of metacommunity structure in Amazonian Zygoptera among streams under different spatial scales and environmental conditions

Abstract - An important aspect of conservation is to understand the founding elements and characteristics of metacommunities in natural environments, and the consequences of anthropogenic disturbance on these patterns. In natural Amazonian environments, the interfluves of the major rivers play an important role in the formation of areas of endemism through the historical isolation of species and the speciation process. We evaluated elements of metacommunity structure for Zygoptera (Insecta: Odonata) sampled in 93 Amazonian streams distributed in two distinct biogeographic regions (areas of endemism). Of sampled streams, 43 were considered to have experienced negligible anthropogenic impacts, and 50 were considered impacted by anthropogenic activities. Our hypothesis was that preserved (“negligible impact”) streams would present a Clementsian pattern, forming clusters of distinct species, reflecting the biogeographic pattern of the two regions, and that anthropogenic streams would present random patterns of metacommunity, due to the loss of more sensitive species and dominance of more tolerant species, which have higher dispersal ability and environmental tolerance. In negligible impacts streams, the Clementsian pattern reflected a strong biogeographic pattern, which we discuss considering the areas of endemism of Amazonian rivers. As for communities in human-impacted streams, a biotic homogenization was evident, in which rare species were suppressed and the most common species had become hyper-dominant. Understanding the mechanisms that trigger changes in metacommunities is an important issue for conservation, because they can help create mitigation measures for the impacts of anthropogenic activities on biological communities, and so should be expanded to studies using other taxonomic groups in both tropical and temperate systems, and, wherever possible, at multiple spatial scales.

KEYWORDS aquatic insect, diversity decline, freshwaters, integrity, landscape

1 | INTRODUCTION

A fundamental goal of community ecology is to understand patterns of species distributions (Sutherland et al., 2013). Species distributions at the metacommunity scale result from the interplay between spatial and environmental processes, and biotic interactions (Soberón, 2007). These conditions are discussed in four mechanisms of metacommunities structure: (1) patch dynamics, (2) neutral effects, (3) species sorting, and (4) mass effects, which may act either in isolation or in combination (Leibold et al., 2004), on metacommunity structures, based on their patterns of coherence, species turnover, and boundary clumping (Leibold & Mikkelsen, 2002).

Metacommunities are made up of sets of communities potentially connected through the dispersal of species (Wilson 1992). In the context of metacommunities in the Amazon biome, the distribution of some organisms, such as monkeys (Wallace 1954), birds (Ribas et al. 2012), and Zygoptera (Juen and de Marco, 2012), is determined by major rivers, which have acted historically as geographic barriers to migration, limiting the dispersal capacity of many species. Accordingly, there are eight areas of endemism, each bounded by large Amazonian rivers: Guiana (region of interfluve between the Amazon and Negro Rivers), Imeri (Negro and Solimões Rivers), Napo (Solimões and Napo Rivers), Inambari (Solimões and Madeira Rivers), Rondônia (Madeira and Tapajós Rivers), Tapajós (Tapajós and Xingu Rivers), Xingu (Xingu and Tocantins Rivers), and Belém (Tocantins and Amazonas Rivers). Given this biogeographic role of the rivers, each area of endemism probably acts as a distinct metacommunity, with the species being more likely to disperse within an area of endemism than between different areas of endemism.

However, at small spatial scales, environmental conditions of the streams are among the most important mechanisms determining community structure (Monteiro-Júnior, Juen, & Hamada, 2014; OliveiraJunior et al., 2015), as the presence or absence of species will depend on the prevailing conditions (species sorting) (Van der Gucht et al., 2007). Given this, the species composition of a community will be determined principally by environmental filters - Hutchinson's (1959) niche concept-rather than dispersal ability (Leibold et al., 2004). In the mass effect perspective, both regional and local assembly processes play a role important in structuring communities (Amarasekare, 2000). Predictions change if dispersal plays a role in structuring communities. This is because

populations will tend to be larger in more appropriate habitat patches, and due to the homogenizing effect of dispersal, communities connected by dispersal should be functionally similar to each other (Altermatt, 2013). Therefore, metacommunities should be influenced by both dispersal among sites and environmental conditions (Heino, Melo, et al., 2015). The patch dynamics approach considers patches with identical conditions, in which local species diversity is determined by dispersal, colonization, and extinctions (Pickett & Thompson, 1978); the neutral perspective assumes that at a given trophic level, species are equivalent in birth, death, dispersal, and speciation rates (Hubbell, 2001). These mechanisms are especially important on a regional scale for species distribution patterns (Cottenie, 2005).

From the processes mentioned above (species sorting, environmental filters, mass effect, and neutral concept) arise patterns in the distribution of species at the metacommunity level. To analyze these patterns, an analytical routine based on null models has been developed, which distinguishes six idealized “metacommunity structures” (Leibold & Mikkelsen, 2002; Presley, Higgins, & Willig, 2010): (1) checkerboard - the distribution of species is influenced primarily by biotic interactions, such as competitive exclusion or facilitation (Diamond & Diamond, 1975); (2) nested - the regional set of species is formed by a series of subsets nested over a spatial continuum (Patterson & Atmar, 1986), which may be related to the environmental conditions of the habitats and/or the intrinsic characteristics of the species, such as their dispersal capacity or tolerance environmental alterations (Heino, Mykrä, & Muotka, 2009); (3) Clementsian – this pattern reflects the effect of biogeographic processes and barriers, leading to the formation of discrete communities within the landscape (Clements, 1916); (4) Gleasonian - communities are structured along some gradient, but species respond to this gradient independently (Gleason, 1926); (5) uniform spacing - continuous gradients formed by the progressive turnover of species within the environment (Tilman, 1982); and (6) random - elements of metacommunity structure no different from those expected by chance (Simberloff, 1983). Additionally, the quasi-structured pattern covers the cases in which the turnover is equal to that expected by chance, thus reducing the robustness of the nested, Clementsian, Gleasonian, uniformly spaced and random patterns, leaving the metacommunity quasi-structured (Presley et al., 2010) (Figure 1).

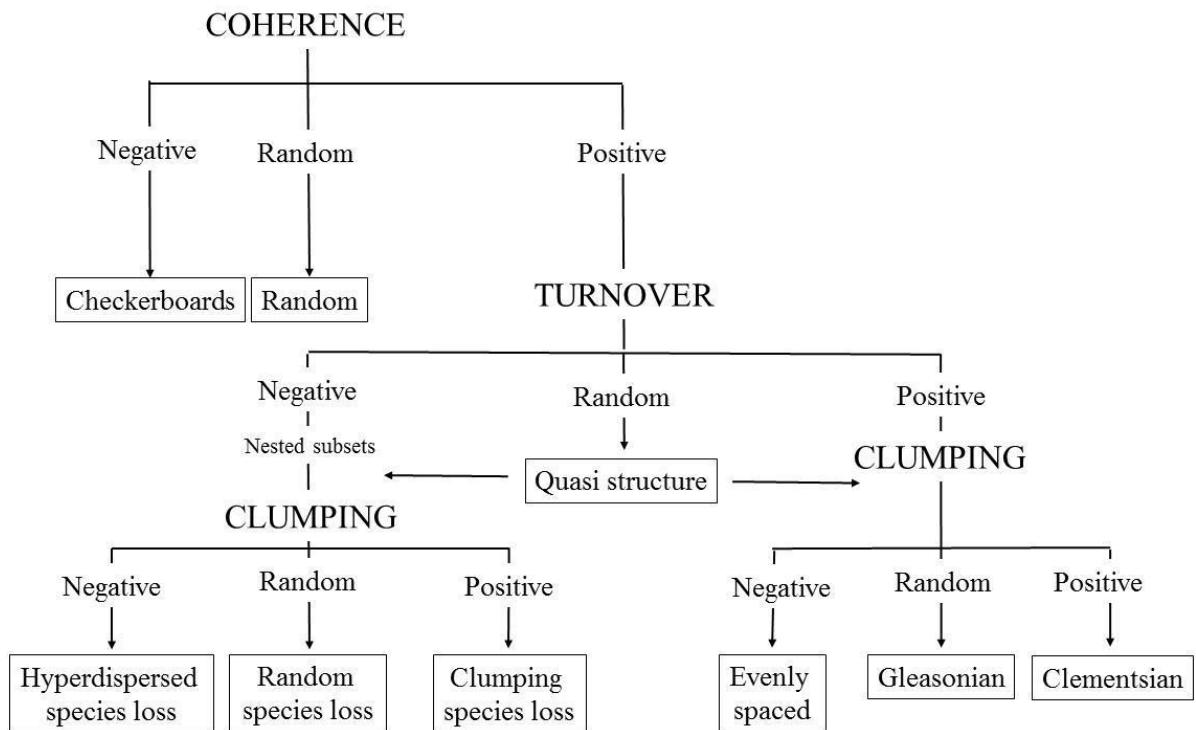


FIGURE 1. Theoretical framework of the analytical method of elements of metacommunity structure. Modified from Presley et al. (2010).

Considering recent ecological factors, the principal environmental filters for Odonata communities are the loss of habitat quality resulting from human activities (e.g., conversion of natural habitats to farmland, urban, or industrial areas) (Monteiro-Júnior et al., 2014; Oliveira-Junior et al., 2015). In addition, considering biogeographic historical factors in the Amazon, the formation of endemic areas is an important predictor of zygopteran assemblages at large spatial scales (Juen and De Marco, 2012). As the distribution of Zygoptera is related to both environmental conditions (recent ecological factors) and spatial processes (biogeographic historical factors), we believe that it is an appropriate group for the testing of hypotheses on the patterns and mechanisms that structure metacommunities.

In the present study, we investigated the elements of metacommunity structure of zygopteran species in two Amazonian areas of endemism, which include streams under different levels of anthropogenic influence. Our principal hypothesis was that the metacommunities in preserved (“negligible impact”) sites would present a Clementsian pattern, due to the biogeographic distribution of the species in the areas of endemism. However, these patterns should be modified in the impacted streams, due to homogenization of communities in impacted streams (primarily by agriculture). We also

analyzed elements of metacommunity structures at smaller spatial scales, within each area of endemism. This analysis is necessary given that Presley and Willig (2010) found that, in the case of a Clementsian pattern, each distinct geographic block can be identified, and distribution patterns can be re-analyzed within these blocks, reinforcing the overall perspective on the influence of different processes and mechanisms acting at different spatial scales.

2 | MATERIAL AND METHODS

2.1 | Study areas

We collected adult damselflies (Odonata: Zygoptera) in 93 small streams (no more than 5 m in width and 0.8 m in mean depth), located in eastern Brazilian Amazonia, in the municipalities of Santarém and Belterra in the Tapajós area of endemism (interfluvium between the Tapajós and Xingu Rivers), and the municipality of Paragominas, in the Belém area of endemism (interfluvium between the Tocantins and Amazon Rivers), all in the state of Pará, Brazil (Figure 2). Given the possible influence of isolation by rivers (Wallace 1954), which has been confirmed in Amazonian zygopteran communities (Juen and De Marco, 2012), we considered the Paragominas (located in the Belém area of endemism), and Santarém and Belterra (Tapajós area of endemism) regions, as two distinct biogeographic units in our analyses.

The study region has an Af-type climate, in the Köppen classification (Peel, Finlayson, & Mcmahon, 2007), that is, wet tropical, with short dry periods between June and December (Gardner et al., 2013). In Paragominas (1.9 Mha), mean annual precipitation is 1766 mm, mean annual temperature is 27°C, and relative humidity is 81%. Santarém (1 Mha) has a mean annual precipitation of 1,920 mm, mean temperature of 25°C, and relative humidity of 86% (Gardner et al., 2013).

The natural landscape of the two study regions is formed by equatorial rainforest or terra firme forest, although there has been extensive deforestation in many areas (Gardner et al., 2013). The anthropogenic areas are covered mainly by eucalyptus (*Eucalyptus* sp.), teak (*Tectona grandis* L.), or paricá (*Schizolobia parahyba* var. *amazonica* Huber ex Ducke) plantations, cattle pasture, and crops such as rice (*Oryza sativa* L.) and soybean (*Glycine max* L.) (Oliveira-Junior et al., 2015).

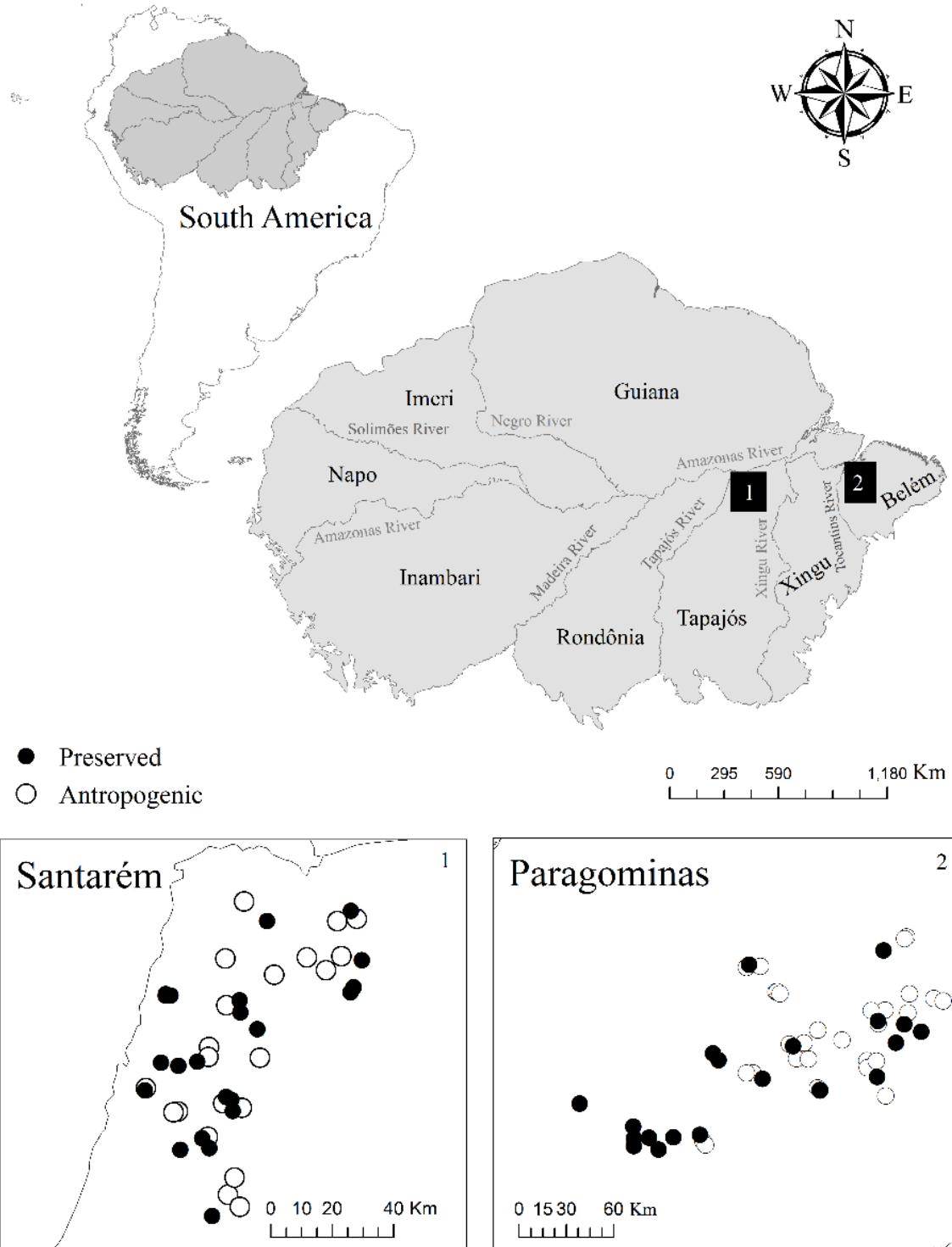


FIGURE 2 Spatial distribution of the zygopteran communities sampled in the southeastern Amazon basin, with the interfluve of the major rivers shaded gray (areas of endemism). At the left, (1) shows the sites sampled in Santarém, which is located in the Tapajós area of endemism, while at the right, (2) shows the sites sampled in Paragominas, in the Belém area of endemismo.

2.2 | Environmental characteristics

To describe the environmental conditions of the study areas, we measured 12 habitats variables included in the protocol described in Nessimian et al. (2008), which are used to calculate the Habitat Integrity Index (HII). These variables (supporting information) describe land use in the environments adjacent to the riparian zone (variable 1), the environmental conditions of the riparian forest (2-4), and the characteristics of the stream channel (5-12). Each variable is composed of four to six alternatives ranked in accordance with their perceived contribution to habitat integrity. To standardize the measures for analysis, the values were weighted in relation to the maximum value recorded for each item (see equation 1- supporting information). The final index score is the mean value of all the items measured in each habitat (equation 2 - supporting information). The result of this procedure is an index that varies from 0 to 1, providing a standardized measure of the integrity of the local conditions found in each habitat (Nessimian et al., 2008).

The HII has proven to be a valuable descriptor of the environmental integrity of Amazonian streams, and when applied to odonate fauna, it has also been shown to be a good predictor of the abundance of individuals and the species richness and composition of these communities (Brasil, Batista, et al., 2014; Brasil, Giehl, et al., 2014; Carvalho, Pinto, Oliveira-Júnior, & Juen, 2013; Juen, Oliveira-junior, & Shimano, 2014; Monteiro-Júnior, Couceiro, Hamada, & Juen, 2013; Monteiro-Júnior et al., 2014; Oliveira-Junior et al., 2015). Major alterations, principally in species composition, tend to be observed at streams with integrity values of <0.6 or 0.7. Significant changes tend to be observed in the communities found in habitats with indices lower than this (Brasil, Batista, et al., 2014; Carvalho et al., 2013; Juen et al., 2014; Monteiro-Júnior et al., 2014; Oliveira-Junior et al., 2015).

2.3 | Collection of biological material

We collected specimens in 2010 (Tapajós area of endemism) and 2011 (Belém area of endemism), during the drier part of the year between June and August, when most of the species that inhabit Amazonian streams can be found as adults (Baptista, Dorvillé, Buss, & Nessiamian, 2001; Oliveira-Junior et al., 2015). At each stream, we demarcated

a linear transect of 150 m, along which a trained technician captured all the damselflies spotted during a 60-min period, using an entomological hand-net, 40 cm in diameter and 65 cm in length (Oliveira-Junior et al., 2015). To avoid sampling bias derived from the thermoregulatory behavior of the insects, all sampling was conducted between 10:00 hr and 14:00 hr, when the sunlight reaches the stream bed, and all the different groups - thermal conformers, heliotherms, and endotherms - can be encountered (De Marco, Batista, & Cabette, 2015; De Marco & Resende, 2002; May, 1976).

The specimens were prepared and fixed following the protocol described by Lencioni (2006). Finally, we identified all the specimens collected using taxonomic keys and specialized illustrated guides (Garrison, 1990; Garrison, Ellenrieder, & Louton, 2010; Lencioni, 2005, 2006). Whenever necessary, specimens were sent to the appropriate specialists to resolve their taxonomy. All the specimens were deposited as vouchers in the collection of the Zoology Museum of the Belém campus of the Federal University of Pará, Brazil.

2.4 | Data analysis

Initially, to define the threshold of habitat integrity along the environmental gradient that divided the sites into two categories (negligibly impacted and impacted), we performed a principal component analysis (PCA) using the 12 environmental variables that make up the HII (Supplementary material 1). Based on this analysis and the findings of previous studies (Brasil, Batista, et al., 2014; Dutra & De Marco, 2015; Juen et al., 2014; Monteiro-Júnior et al., 2014; Oliveira-Junior et al., 2015), we defined a threshold of $HII = 0.7$ to separate the negligibly impacted streams ($HII \geq 0.7$) from the impacted ($HII < 0.7$) streams. While the term “negligibly impacted” is used here to facilitate the comprehension of the results, some of the sites may have suffered a certain degree of anthropogenic impact, but can be considered to be the best conserved sites, given the local context of the region, and adequate for inclusion in the analyses as control sites.

To verify the elements of metacommunity structures, we adopted the approach of Leibold and Mikkelsen (2002). The analysis consists of a sequence of tests of the coherence, turnover, and clumping. Coherence is measured by the number of absences found between the occurrences in the matrix, where fewer absences than expected by chance represent a condition of positive coherence, while a greater number than expected

by chance represents a negative coherence. Similarly, the turnover is the number of double substitutions in pairs of streams and considered to be positive when this number is larger than the expected value, and negative when the number is lower than expected by random. Clumping or boundary clumping measures the divergence in the limits of species distribution based on Morisita's index, which estimates the clumping of species distributional boundaries (Leibold & Mikkelsen, 2002). When the index is higher than one, clumping is positive, and negative when it is lower than one.

We tested the three elements, coherence, turnover and clumping, by determining the probability of accepting the null hypothesis based on 9999 randomizations with a 5% significance level (Leibold et al., 2004; Presley et al., 2010). When coherence is significantly negative, the analysis confirms a checkerboard pattern, but when the null hypothesis is accepted, a random pattern is confirmed. When coherence is significantly positive, the turnover test is implemented (positive or negative than what expected given the null distribution).

When turnover is significantly positive, the clumping is tested, and when this is significantly negative, an evenly spaced pattern is confirmed. When it is random, the pattern is Gleasonian, and Clementsian when significantly positive. In the cases where the turnover is significantly negative, and the clumping is also negative (nested subsets), the data are tested again, and a negative pattern indicates hyper-dispersed or random species loss, and clumped species loss when positive. When no significant turnover is recorded, and clumping remains positive or negative, a quasi-structured pattern is identified (Presley et al., 2010).

To identify the elements of metacommunity in zygopteran communities of Amazonian streams according to their level of impact (impacted and negligibly impacted) and biogeographic region (Belém and Tapajós areas of endemism), we divided the data into nine distinct subsets: (1) all the streams, (2) negligibly impacted streams ($HII \geq 0.7$), (3) impacted streams ($HII < 0.7$), (4) all the streams in the Belém area of endemism, (5) all the streams in the Tapajós area of endemism, (6) negligibly impacted streams in the Belém area of endemism, (7) negligibly impacted streams in the Tapajós area of endemism, (8) impacted streams in the Belém area of endemism, and (9) impacted streams in the Tapajós area of endemism. We visualized these patterns graphically through the direct ordination of the communities by the first spatial filter (principal coordinate analysis of neighbor matrices - PCNM1) derived from the geographic coordinates of the study sites (Griffith & Peres-Neto, 2006). The eigenvector-based

spatial filters (PCNM) from the geographic coordinates of the sites are simple solution to understand spatial patterns. The basic idea is to extract eigenvectors of a distance Euclidean matrix among spatial units (sites) and use these eigenvectors, which describe the spatial structure as a spatial predictor variable (Diniz-Filho & Bini, 2005).

To test the premise that there are groups of species that reflect the pattern biogeographic regions of the study, we conducted a PERMANOVA (Anderson, 2001; Anderson & Walsh, 2013), with the species composition matrix (presence and absence) including region (Paragominas and Santarém) as a categorical variable. To test whether communities in impacted areas are homogenized compared to communities of negligibly impacted areas, we compared the species composition matrix between negligibly impacted and impacted streams using tests of homogeneity of multivariate dispersion (PERMDISP) (Anderson, & Walsh, 2013).

We ran all the analyses in the R program (Team R, 2013), with the patterns of environmental conditions being tested using a principal component analysis (PCA) run with the “prcomp” function (R stats package), permutational multivariate analyses of variance (PERMANOVA) in the “adonis” function (R vegan package), and permutational analysis of multivariate dispersions (PERMDISP) in the function “betadisper” (R vegan package). To calculate spatial filters, we used the function “PCNM” (R vegan package). The metacommunities were analyzed with the metacom package, using the metacommunity function (Dallas 2014), and the ordination was produced in the vegan package using the generic function (Oksanen et al., 2013).

3 | RESULTS

3.1 | Description of the communities

We collected 71 species of Zygoptera, of which 57% were found in both negligibly impacted and impacted streams, while 25% were found exclusively in negligibly impacted streams, and 18% only in impacted streams. A quarter (25%) of the species were found in both Belem area of endemism and Tapajos area of endemism, while 21% were exclusive to Tapajos area of endemism, and 54% were exclusive to Belem area of endemism. The negligibly impacted sites were the most species-rich in both study

regions, with the negligibly impacted streams of Belém area of endemism being the richest overall, and the impacted streams of Tapajós area of endemism, the poorest (Figure 3).

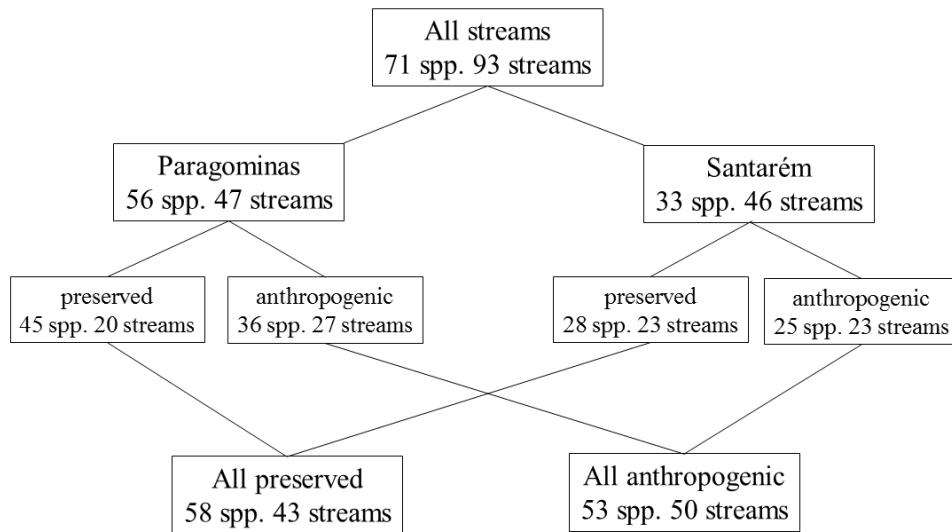


FIGURE 3 Graphic showing the number of streams (sampling units) and species (spp.) classified by integrity environmental (negligibly impacted and impacted) and biogeographic region (Belém and Tapajós) in eastern Amazonia.

3.2 | Environmental conditions of the streams

The ordination of the streams based on their characteristics of environmental integrity revealed a clearly visible separation of the sites, with those of high integrity ($HII \geq 0.7$) to the right, and the low integrity streams ($HII < 0.7$) to the left of the first axis (negligibly impacted and impacted, respectively). The variables that most contributed to this distinction were the structure of surrounding riparian vegetation (less extensive and more degraded in the impacted streams, within a radius of 10 m), and the quantity of debris in the water (higher in impacted streams). These features refer to variables 2, 3, 4, and 12 of the HII (Table 1; Figure 4).

TABLE 1 Correlation between the different variables of the environmental integrity of the streams and the first and second PCA axis (Figure 4). The highest loadings (correlation >70%) are shown in bold.

| Characteristic | Loadings | |
|---|---------------|--------|
| | Axi 1 | Axis 2 |
| 1- Land use pattern beyond the riparian zone | -0.395 | 0.193 |
| 2- Width of riparian forest | -0.876 | 0.192 |
| 3- Completeness of riparian forest | -0.851 | 0.159 |
| 4- Vegetation of riparian zone within 10 m of channel | -0.846 | 0.167 |
| 5- Retention devices | -0.674 | -0.185 |
| 6- Channel sediments | -0.612 | -0.521 |
| 7- Bank structure | -0.453 | 0.668 |
| 8- Bank undercutting | -0.644 | 0.232 |
| 9- Stream bottom | -0.268 | -0.602 |
| 10- Riffles and pools, or meanders | -0.557 | -0.295 |
| 11- Aquatic vegetation | -0.627 | -0.460 |
| 12- Detritus | -0.799 | 0.105 |

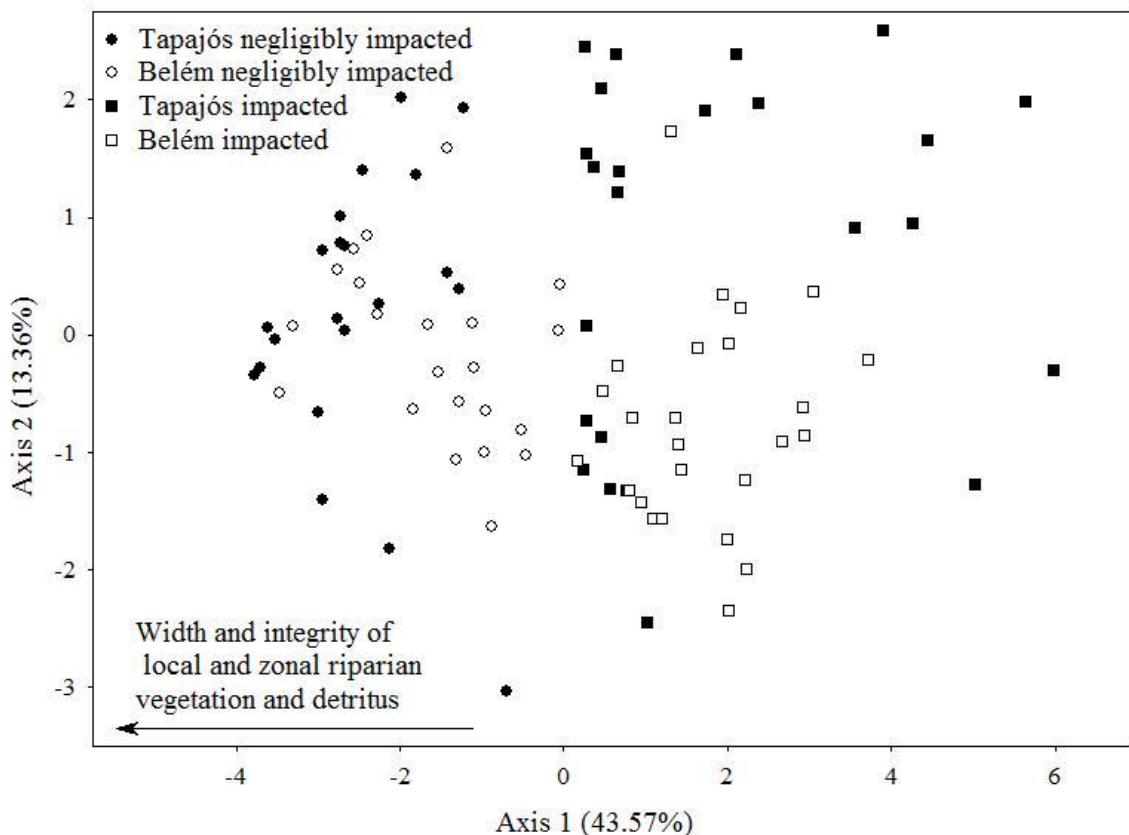


FIGURE 4 Ordination of the streams based on the 12 variables of environmental integrity used to compose the Habitat Integrity Index of Nessimian et al. (2008).

3.3 | Metacommunity structures

Considering the complete set of communities, the elements of metacommunity structures were quasi-Clementsian, given that the matrix coherence was significant and positive, although the turnover was not significantly different from what could be expected by random, while the clumping was positive and significant. When only negligibly impacted streams were analyzed, the coherence, turnover, and clumping were all significantly positive, which is consistent with a Clementsian pattern. In the case of the impacted streams, coherence did not differ from random significantly positive, but turnover was random, with values lower than expected and significant clumping, with observed values higher than one, which is consistent with a pattern of clumping species loss (Table 2).

TABLE 2 Metacommunity structures in the zygopteran of negligibly impacted and impacted streams in the Belém area of endemism (BAE) and Tapajós area of endemism (TAE).

| | | Metacommunity | | | | | | | | |
|-----------|-------------------|-------------------|---------|-----------|-------------|-------------|----------|----------------------|---------|--------|
| | | All communities | | | Preserved | | | Anthropogenic | | |
| | | All | PRG | SNT | All | PRG | SNT | All | PRG | SNT |
| Coherence | P | < 0.001 | 4.017 | 0.261 | < 0.001 | 0.001 | 0.519 | < 0.001 | 0.065 | 0.465 |
| | Embedded absences | 1898 | 795 | 603 | 766 | 286 | 231 | 520 | 280 | 178 |
| | Z | 9.073 | 5.490 | 1.123 | 5.634 | 3.139 | 0.644 | 6.313 | 1.841 | 0.730 |
| | sim. Mean | 3550.2 | 1259 | 657.879 | 1152.2 | 383 | 244.208 | 1120.6 | 348 | 192 |
| | sim.sd | 182.08 | 84.631 | 48.851 | 68.560 | 31 | 20.496 | 95.139 | 37.029 | 19.785 |
| | Method | R1 | R1 | R1 | R1 | R1 | R1 | R1 | R1 | R1 |
| Turnover | P | 0.226 | 0.560 | 0.436 | 0.0001 | 0.0008 | 0.417 | 0.995 | 0.261 | 0.427 |
| | Replacements | 486410 | 80165 | 23849 | 111874 | 19599 | 4760 | 66172 | 5801 | 5173 |
| | Z | -1.209 | -0.582 | -0.777 | -3.852 | -3.331 | -0.810 | 0.005 | 1.123 | -0.793 |
| | sim. Mean | 364287.2 | 68848 | 19463.302 | 53970.1 | 10251 | 3850.157 | 66281.4 | 9163 | 4232 |
| | sim.sd | 100984.6 | 19416 | 5640.221 | 15031.06 | 2805 | 1122.994 | 19671.7 | 2992 | 1185 |
| | Method | R1 | R1 | R1 | R1 | R1 | R1 | R1 | R1 | R1 |
| Clumping | Index | 2.918 | 3.309 | 2.546 | 2.314 | 1.911 | 2.484 | 2.181 | 3.857 | 1.434 |
| | P | < 0.001 | < 0.001 | < 0.001 | < 0.001 | 0.001 | < 0.001 | < 0.001 | < 0.001 | 0.008 |
| | | quasi-Clementsian | Random | Random | Clementsian | Clementsian | Random | Clumped species loss | Random | Random |

When we analyzed the regions separately, the impacted streams of both regions (Tapajos and Belem areas of endemism) presented a random pattern of coherence. When the negligibly impacted streams of Tapajos area of endemism were added to the analysis, the random pattern was also found. However, when we analyzed the negligibly impacted streams of the Belem area of endemism, the pattern was Clementsian, with significantly positive coherence, turnover, and clumping (Table 2), with a similar (quasi-Clementsian) pattern being found when all the communities (negligibly impacted and impacted streams) were analyzed together (Figure 5).

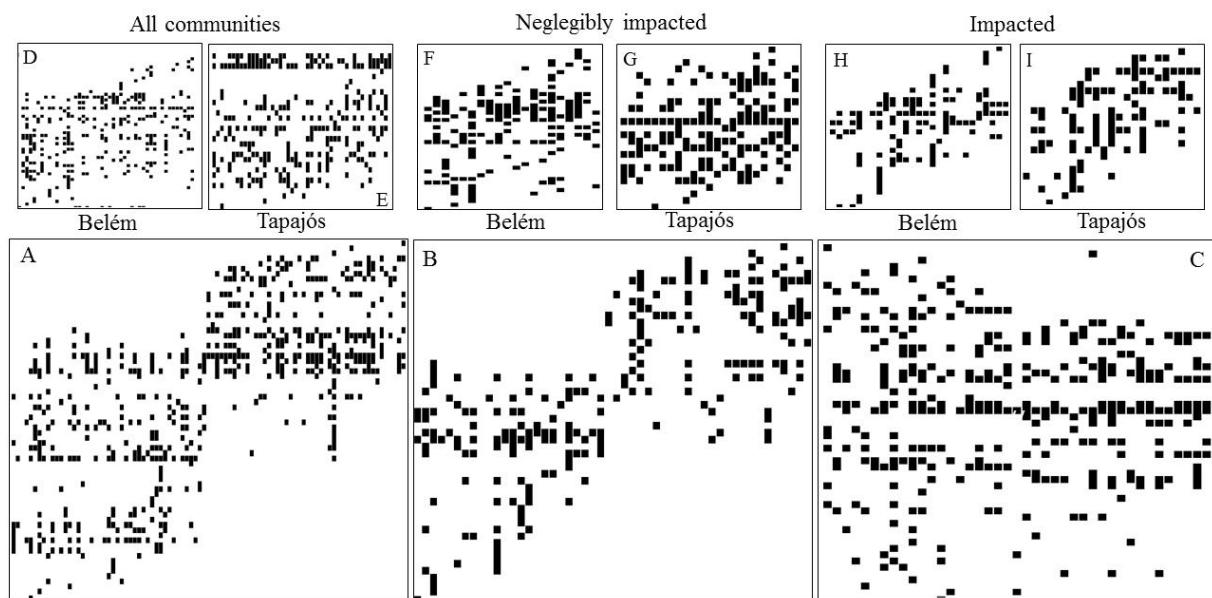


FIGURE 5 Ordination of the composition of Zygoptera communities in Amazonian streams. Horizontally represent the occurrence of species and vertically represent the spatial filter (principal coordinate analysis of neighbor matrices - PCNM1). (a) All 93 communities regardless of environmental conservation, (b) only the communities of the 43 streams negligibly impacted, (c) only the communities of the 50 streams impacted, (d) all 47 communities from Belém area of endemism, regardless of environmental conservation, (e) all 46 communities from Tapajós area of endemism, regardless of environmental conservation, (f) only 20 communities negligibly impacted streams of Belém area of endemism, (g) only 23 communities negligibly impacted streams Tapajós area of endemism, (h) only 27 communities impacted streams of Belém area of endemism, and (i) only 23 communities impacted streams of Tapajós area of endemismo.

The patterns (Clementsian and quasi-Clementsian) found in most of the metacommunities associated with negligibly impacted streams, and all communities, irrespective of region or environmental integrity, were closely related to the biogeographic configuration (areas of endemism). This pattern was particularly strong among the negligibly impacted stream communities, which differed greatly in their species composition between regions (PERMANOVA, pseudo $F = 10.541$; $p = 0.001$). The patterns of clumped and random species loss observed in all the impacted streams indicate that environmental changes have caused changes in the elements of metacommunity structure. Evidence of these changes can be seen in the homogenization of communities in impacted streams compared to communities in negligibly impacted streams (PERMDISP, pseudo $F = 67.202$ (1,96); $p = .001$) (Figure 5c).

4 | DISCUSSION

Our hypothesis that communities at sites with less impact would present a Clementsian pattern, due to the biogeographic distribution of the species in the areas of endemism, was corroborated. The Clementsian pattern of the more negligibly impacted sites reflects the biogeographic configuration of the areas of endemism (Juen and De Marco, 2012). By contrast, the evidence of clumped species loss in the case of the impacted streams reflects the changes of these communities through the loss of zygopteran species (Oliveira-Junior et al., 2015), principally in the Tapajós area of endemism, where there is a more extensive history of anthropogenic impact (Gardner et al., 2013). In this region, in fact, even the communities of the negligibly impacted streams presented a random pattern (Figure 6), giving indications that besides the intensity (negligibly impacted or impacted), the historical frequency of the alterations of the regions has also been an important process for the present communities.

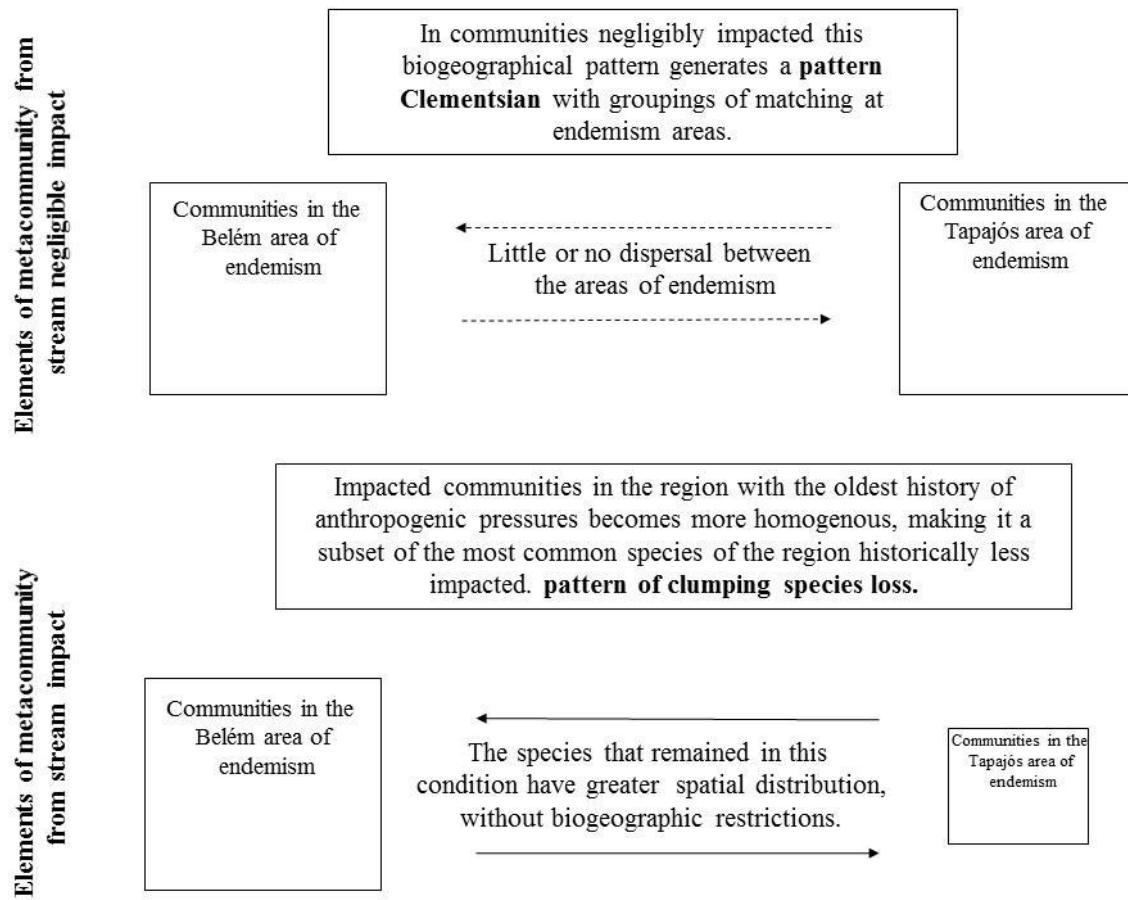


FIGURE 6 Graphical model representing the main results of the metacommunities patterns. Streams with little change a limiting dispersion (dotted arrows) and communities have distinct compositions between the two biogeographic regions (pattern Clementsian). The second result demonstrates the nested pattern found between regions whereas only impacted communities, this dispersion is not limiting prospects (unbroken lines and arrows) (pattern clumped species loss).

The intensity of the impacts on the landscape is responsible for major changes in the patterns of species diversity (Gutiérrez-Cánovas, Millán, Velasco, Vaughan, & Ormerod, 2013). In addition, the impacted streams of the Santarém region (Tapajós area of endemism) presented a subset of the species found in the communities of the impacted streams of Paragominas region (Belem area of endemism) (see Figure 5c). Comparing the same regions, Gardner et al. (2013) also found a lower taxonomic richness of bees, beetles, ephemeropterans, ants, heteropterans, plecopterans, odonates, and tricopterans in Santarém. These authors comment that whereas Santarém has been densely populated by farming communities of pre-Columbian civilizations since 1661, Paragominas was

sparingly populated until the 1980s, when the logging industry advanced into the region. Thus, the longer history of disturbance in the Santarém is the probable cause of the greater homogeneity of the biota of this region. These results reinforce the idea that the random structure indicates that species are not structured by responses to a common environmental gradient. It does not mean that there is no structure or that environment is not important, only that the responses may not be idiosyncratic along environmental gradients (Rodrigues et al., 2016) with different disturbance intensities (Petraitis, Latham, & Niesenbaum, 1989).

One fundamental aspect in metacommunity analysis is the spatial scale of the area analyzed, given that different mechanisms may operate at each scale leading to distinct patterns (local or regional) of distribution (Presley et al., 2010). This occurs because, on a smaller scale, environmental gradients and spatial processes have different effects on the distribution of species (Presley & Willig, 2010). According to the theory of isolation by rivers (Wallace 1854), for example, higher levels of dispersal are expected between the communities found in the same areas of endemism (Juen and de Marco, 2012). Given this, when we analyze small-scale patterns of elements of metacommunity structures, that is, within areas of endemism, the spatial component may be less important, as found by Juen & De Marco (2011) in communities in Amazonian streams. The random patterns observed at this scale may in fact be related to the variation in the timing and the magnitude of the environmental impacts that are or were dynamic in these landscapes, either historically, as discussed by Gardner et al. (2013), or currently (see Leal et al., 2016). Both these studies focused on the same areas analyzed in the present study. The Clementsian patterns, found in most of the negligibly impacted stream communities and at the broader spatial scale, may be structured by biogeographic processes, as observed in the bat communities of Caribbean islands (Presley & Willig, 2010), or in communities affected by major environmental variation, such as that found in the tropical desert climate ecotone in Mexico (López-González, Presley, Lozano, Stevens, & Higgins, 2012). In this case, the Clementsian pattern may be related to biogeographic features and/or environmental variations, as well as the historical factors that contribute to the spatial distribution of the species (Heino, Soininen, Alahuhta, Lappalainen, & Virtanen, 2015). Given this, we believe, on a large scale, the Clementsian pattern is related to the historical process of isolation of communities generated by the emergence of large rivers, making their areas of endemism distinct biogeographic units for Zygoptera communities in Amazonia (Juen and de Marco, 2012). However, when we consider the impacted sites

only, the effect of environmental gradients on the communities is clear, as referred to in the species-sorting perspective (Henriques-Silva et al. 2013). This mechanism is very important for the distribution of Odonata, mostly at local scale, being mainly determined by gradients of human impact, such as those induced by land use changes, where generalist species are favored in altered habitats (De Marco et al., 2015).

There is much evidence to show that environmental filter is the main mechanisms for the structure of aquatic communities, especially when you consider small spatial scale (Cottenie, 2005; Van der Gucht et al., 2007; Mykrä et al., 2007, Heino, Nokela, et al., 2015); however, whereas in large spatial scale aquatic communities have a strong relationship with biogeographic units (such as the water catchment area or areas of endemism), and with that the communities have high values of beta diversity along the landscape (explained mainly by turnover), what generates Clementsian patterns along the landscape (Heino et al. 2016).

The interpretation of changes in the patterns of metacommunity structures is an important step in the analysis of the impact of environmental disturbances on natural communities. Our results show that the natural elements of metacommunity structures are altered due to environmental pressures that interfere directly on the coexistence of species, changing the rules of community assembly. Understanding the mechanisms that trigger these changes is an important issue for conservation, because they can help to create mitigating measures of the impacts of environmental changes on communities and so should be expanded in other studies using other taxonomic groups in tropical and temperate systems, and, wherever possible, at multiple spatial scales.

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CONFLICT OF INTEREST

None declared.

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Table S1. Descriptors characteristics of the environmental conditions of the streams.
Table adapted from Nessimian et al. (2008).

| Characteristic | Condition | Score |
|---|--|-------|
| 1- Land use pattern beyond the riparian zone | Primary continue forest/100 ha fragment/10 ha fragment | 6 |
| | Cecropia secondary forest/mixed secondary forest | 5 |
| | Vismia secondary forest | 4 |
| | Pasture | 3 |
| | Perennial crops | 2 |
| | Short-cycle crops/exposed soil | 1 |
| 2- Width of riparian forest | Continuous forest | 6 |
| | Forest width between 30 and 100 m | 5 |
| | Forest width between 5 and 30 m | 4 |
| | Forest width between 1 and 5 m | 3 |
| | Riparian forest absent, but some shrub species and pioneer trees | 2 |
| | Riparian forest and shrub vegetation absent | 1 |
| 3- Completeness of riparian forest | Riparian forest intact without breaks in vegetation | 4 |
| | Breaks occurring at intervals of < 50 m | 3 |
| | Breaks frequent with gullies and scars at every 50 m | 2 |
| | Deeply scarred with gullies all along its length | 1 |
| 4- Vegetation of riparian zone within 10 m of channel | More than 90% plant density by non-pioneer trees or shrubs | 4 |
| | Mixed pioneer species and mature trees | 3 |
| | Mixed grasses and sparse pioneer trees and shrubs | 2 |
| | Grasses and few tree shrubs | 1 |
| 5- Retention devices | Channel with rocks and/or old logs firmly set in place | 4 |
| | Rocks and/or logs present but backfilled with sediment | 3 |
| | Retention devices loose, moving with floods | 2 |
| | Channel of loose sandy silt, few channel obstructions | 1 |
| 6- Channel sediments | Little or no channel enlargement resulting from sediment accumulation | 4 |
| | Some gravel bars of coarse stones and little silt | 3 |
| | Sediment bars of rocks, sand and silt common | 2 |
| | Channel divided into braids or stream channel corrected | 1 |
| 7- Bank structure | Banks inconspicuous | 5 |
| | Banks stable, with rock and soil held firmly by grasses, shrubs, or tree roots | 4 |
| | Banks firm but loosely held by grasses and shrubs | 3 |
| | Banks of loose soil held by a sparse layer of grass and shrubs | 2 |
| | Banks unstable, easily disturbed, with loose soil or sand | 1 |
| 8- Bank undercutting | Little, not evident or restricted to areas with tree root support | 4 |
| | Cutting only on curves and at constrictions | 3 |
| | Cutting frequent, undercutting of banks and roots | 2 |
| | Severe cutting along channel, banks falling in | 1 |

Continued

| Characteristic | Condition | Score |
|------------------------------------|---|--------------|
| 9- Stream bottom | Stone bottom of several sizes packed together, interstices obvious | 4 |
| | Stone bottom easily moved, with little silt | 3 |
| | Bottom of silt, gravel, and sand, stable in some places | 2 |
| | Uniform bottom of sand and silt loosely held together, stony substrate absent | 1 |
| 10- Riffles and pools, or meanders | Distinct, occurring at intervals of 5-79 the stream width | 4 |
| | Irregularly spaced | 3 |
| | Long pools separating short riffles, meanders absent | 2 |
| | Meanders and riffle/pools absent or stream corrected | 1 |
| 11- Aquatic vegetation | When present, consists of moss and patches of algae | 4 |
| | Algae dominant in pools, vascular plants along edge | 3 |
| | Algal mats present, some vascular plants, few mosses | 2 |
| | Algal mats cover bottom, vascular plants dominate channel | 1 |
| 12- Detritus | Mainly consisting of leaves and wood, without sediment | 5 |
| | Mainly consisting of leaves and wood, with sediment | 4 |
| | Few leaves and wood, fine organic debris, with sediment | 3 |
| | No leaves or woody debris, coarse and fine organic matter, with sediment | 2 |
| | Fine anaerobic sediment, no coarse debris | 1 |

Table S2. Checklist of species by environments from Belém area of endemism and Tapajós area of endemism.

| Taxa | Belém | | Tapajós | |
|---|-------------------|-----------------|-------------------|-----------------|
| | Negligible | Impacted | Negligible | Impacted |
| | impacted | | impacted | |
| <i>Acanthagrion adustum</i> Williamson, 1916 | | x | | |
| <i>Acanthagrion aepiolum</i> Tennessen, 2004 | x | x | | |
| <i>Acanthagrion apicale</i> Selys, 1876 | x | x | | x |
| <i>Acanthagrion ascendens</i> Calvert, 1909 | x | x | | |
| <i>Acanthagrion jessei</i> Leonard, 1977 | | x | | |
| <i>Acanthagrion kennedii</i> Williamson 1916 | x | x | x | x |
| <i>Acanthagrion rubrifrons</i> Leonard, 1977 | x | | | |
| <i>Acanthallagma luteum</i> Williamson and Williamson, 1924 | x | x | | |
| <i>Argia fumigata</i> Hagen in Selys, 1865 | x | x | x | x |
| <i>Argia infumata</i> Selys, 1865 | x | | x | x |
| <i>Argia insipida</i> Hagen in Selys, 1865 | x | | | |
| <i>Argia mollis</i> Hagen in Selys, 1865 | x | x | | |
| <i>Argia reclusa</i> Selys, 1865 | x | | | |
| <i>Argia smithiana</i> Calvert, 1909 | x | | | |
| <i>Argia thespis</i> Hagen in Selys, 1865 | x | x | | |
| <i>Argia tinctipennis</i> Selys, 1865 | x | x | x | x |
| <i>Argia tupi</i> Calvert, 1909 | x | | | |
| <i>Chalcopteryx rutilans</i> (Rambur, 1842) | x | | x | x |
| <i>Dicterias atrosanguinea</i> Selys, 1853 | x | | x | x |
| <i>Epipleoneura capilliformis</i> (Selys, 1886) | x | | x | x |
| <i>Epipleoneura fuscaenea</i> Williamson, 1915 | | x | | |
| <i>Epipleoneura metallica</i> Rácenis, 1955 | x | x | | |
| <i>Epipleoneura westfalli</i> Machado, 1986 | x | x | | |
| <i>Heliocharis amazona</i> Selys, 1853 | x | x | x | |
| <i>Hetaerina auripennis</i> Burmeister, 1839 | x | x | | |
| <i>Hetaerina sanguinea</i> Selys, 1853 | | x | x | x |
| <i>Heteragrion aurantiacum</i> Selys, 1862 | x | x | | |
| <i>Heteragrion icterops</i> Selys, 1862 | x | x | x | x |
| <i>Ischnura capreolus</i> (Hagen, 1861) | | x | | |
| <i>Mecistogaster linearis</i> (Fabricius, 1776) | x | | x | |
| <i>Mnesarete aenea</i> (Selys, 1853) | x | x | x | |
| <i>Mnesarete cupraea</i> (Selys, 1853) | x | | | |
| <i>Mnesarete williamsoni</i> Garrison, 2006 | x | x | | |
| <i>Neoneura denticulata</i> Williamson, 1917 | x | x | | |

Continuation

| Taxa | Belém | | Tapajós | |
|---|------------------------|--------------|------------------------|--------------|
| | Negligible impacted | Impacted | Negligible impacted | Impacted |
| <i>Neoneura bilinearis</i> Rácenis, 1953 | | x | | |
| <i>Neoneura joana</i> Williamson, 1917 | | x | | |
| <i>Neoneura luzmarina</i> Marmels, 1989 | x | x | x | x |
| <i>Neoneura rubriventris</i> Selys, 1860 | x | x | | |
| <i>Oxystigma petiolatum</i> (Selys, 1862) | x | | | |
| <i>Perilestes kahli</i> Williamson & Williamson, 1924 | x | | | |
| <i>Perilestes solutus</i> Williamson & Williamson, 1924 | x | | | |
| <i>Protoneura tenuis</i> Selys, 1860 | x | | x | |
| <i>Psaironeura tenuissima</i> (Selys, 1886) | x | | x | x |
| <i>Telebasis sanguinalis</i> Calvert, 1909 | | x | | |
| <i>Tigriagrion aurantinigrum</i> Calvert, 1909 | x | x | | |
| <i>Argia chapadae</i> Calvert, 1909 | | | | x |
| <i>Argia oculata</i> Selys, 1865 | | | x | x |
| <i>Argia euphorbia</i> Fraser, 1946 | | | x | x |
| <i>Chalcopteryx radians</i> Ris, 1914 | | | x | x |
| <i>Epipleoneura haroldoi</i> Santos, 1964 | | | x | x |
| <i>Epipleoneura pereirai</i> Machado, 1964 | | | x | |
| <i>Epipleoneura spatulata</i> Rácenis, 1960 | | | | x |
| <i>Hetaerina indeprena</i> Garrison, 1990 | | | x | x |
| <i>Hetaerina rosea</i> | | | x | |
| <i>Mnesarete smaragdina</i> (Selys, 1869) | | | x | x |
| <i>Oxystigma williamsoni</i> Geijskes, 1976 | | | x | x |
| <i>Perilestes attenuatus</i> Selys, 1886 | | | x | |
| <i>Phasmoneura exigua</i> (Selys, 1886) | | | x | |
| <i>Telebasis</i> sp. nov. | | | x | x |
| <i>Acanthagrion</i> sp.1 | | x | | |
| <i>Argia</i> sp.1 | x | x | | |
| <i>Argia</i> sp.2 | | x | | |
| <i>Argia</i> sp.3 | x | x | | |
| <i>Argia</i> sp.4 | x | | | |
| <i>Argia</i> sp.5 | x | x | | |
| <i>Argia</i> sp.6 | | x | | |
| <i>Argia</i> sp.7 | x | | | |
| <i>Argia</i> sp.8 | x | x | | |
| <i>Argia</i> sp. | | | x | x |
| <i>Heteragrion</i> sp.nov. | x | | x | x |
| Ocorrencia (%) | 64.28 | 51.42 | 35.71 | 35.71 |

Figure S3. Equations of Habitat Integrity Index, adapted from Nessimian et al. (2008). A= Equation 1, ponders the weight of the items within each feature examined, and B = 2 equation, calculates the index whereas the values obtained within 12 characteristics weighted (Equation 1). p_i = value weighted of characteristic; a_o = value observed; a_m = Maximum value; HII= Habitat Index Integrity.

A)

$$p_i = \frac{a_o}{a_m}$$

B)

$$\text{HII} = \frac{\sum_{i=1}^n P_i}{n}$$

CAPÍTULO 4

Using Beta diversity to assess protected areas efficiency and set priority areas for conservation of Odonata in the Brazilian Amazon

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Protected areas efficiency and priorities areas for conservation of Odonata in the Brazilian Amazonian

Abstract - In the Brazilian Amazon, the efficiency of protected areas and spatial prioritization for conservation has already for several vertebrate groups such as mammals and fish, but this information is unknown for invertebrate communities. Here, we assess whether the Amazon network of protected areas is effective in protecting Odonata beta diversity, a taxonomic group of invertebrates living in the immature aquatic and adult terrestrial stages. Posteriorly, using the principle of complementarity, we will carry out a spatial prioritization analysis to indicate important areas for the conservation of Odonata in the Amazon. We used ecological niche models based on 23,601 occurrences records of 503 species (Neotropical region) to respond to our objectives. We found that most of the protected areas are not efficient for the conservation of the Odonata diversity. In addition, the main priority areas for conservation, complementary to existing protected areas, are in the region of the deforestation arc, a region with high rates of deforestation. Based on these results, we advocate that strategies for conserving Odonata in Amazonia should focus on two main scenarios: create conservation units or incentives for low-impact activities in the most central, priority and forest regions, and encourage the restoration of priority areas already deforested through programs that pay for ecosystem services, such as carbon credits from reforestation, or the development of activities with less impact on biodiversity, such as agroforestry.

Keywords Aquatic conservation, spatial prioritization, invertebrates, tropical environments.

Introduction

Understanding patterns and mechanisms related to the spatial distribution of biodiversity is fundamental to guide the establishment of protected areas in face of scarce conservation resources (Chape et al. 2005). This is especially important for regions like the Amazon, where there is a geographic overlap between important areas for conservation with those addressed for agriculture, mining, logging and creation of hydroelectric (Brando et al., 2013; Laurance et al. 2014). It is known the location or size of area of protected areas in the Brazilian Amazon are not efficient for the conservation of biodiversity, as has already been tested for birds (De Carvalho et al. 2017), mammals (Ribeiro et al. 2016) and fish (Frederico et al. 2018), but this evaluation is almost non-existent in studies with groups of invertebrates (Diniz-Filho et al. 2010). Although important for the conservation of ecosystem services (Noriega et al. 2018), predation of agricultural pests (Vandermeer et al. 2010) and pollination (Boreux et al. 2013) invertebrates are neglected in decision-making on conservation (Nóbrega & De Marco 2011), and it is not known how well the network of Amazonian protected areas protects them and which areas are prioritized for their conservation.

To define which areas are most important for conservation, the procedure is to choose those that preserve the habitat of as many species as possible (De Carvalho et al. 2017). One way to do this is used the principle of complementarity (Moilanen et al. 2005), at where, priority areas are the ones that protect the ecological niche from a larger number of species per unit area (Ribeiro et al. 2016), the biogeographic crossroads (Spector 2002), and have species more dissimilar to each other. For some organisms, such as Odonata of the Amazon, have a high beta diversity due to a great turnover of species along the landscape (Juen & De Marco 2011; Brasil et al. 2018), related to the existence of areas of

endemism congruent with the interfluves of the great rivers (Juen & de Marco 2012). Historically, those interfluves acted as partial or total barriers to dispersal, making their interfluent areas regions of endemism (Da Silva et al. 2005). Under these conditions, even if protected areas have high values of alpha diversity, they could not maintain gamma diversity (Socolar et al. 2016), as regions with low alpha diversity contribute to beta diversity because they have dissimilar species compositions (Landeiro et al. 2018). This paradox of alpha diversity and beta diversity, which occurs in many taxa in the Amazon (Landeiro et al. 2018), should be considered in conservation decisions.

Historically, the creation of protected areas are not always determined by the importance of the biodiversity in the region, which compromises its existence or even its purpose of protection (Bruner 2001; Andam et al. 2008; Joppa & Pfaff 2011). As a result, protected areas were generally designed without a deep evaluation of the distribution or ecology of species and are generally biased towards certain taxonomic groups such as plants, mammals and birds (Nóbrega & De Marco 2011; Frederico et al. 2018). Some taxa are underrepresented or uncovered by protected areas (Leal 2005; Becker et al. 2010; Nóbrega & De Marco 2011; Ribeiro et al. 2016). This is particularly true for freshwater organisms, as protected areas do not consider drainage networks (Carrizo et al. 2017; Nieto et al. 2017; Frederico et al. 2018) and also for invertebrates, particularly neglected for conservation (Diniz-Filho et al. 2010). Therefore, as aquatic invertebrates are possibly one groups with the largest conservation gaps, it is important to assess the efficiency of the existent protected areas network and, if ineffective, indicate priority areas for conservation (Nóbrega & De Marco 2011).

Among aquatic invertebrates, Odonata is especially important for conservation. As they comprise both aquatic (immature) and terrestrial (adult) life stages, acting as predators in both environments (Corbet 1999), they have play a critical role for the

ecological balance of aquatic systems and adjacent areas (Samways 1989). Among aquatic invertebrates, they are possibly the group with fewer problems related to Wallacean shortfall in Brazil (spatial distribution data), with 2,317 papers published between 1993 and 2013 on the websites "Thomson-Reuters Web of Knowledge" and "Scielo" (Miguel et al. 2017). This was due to permanent data collection efforts established mainly from since 2000s (De Marco & Vianna 2005; Nóbrega & De Marco 2011; Juen & de Marco 2012). In particular, for the Amazon region several published works considerably increased the knowledge of the spatial distribution of Odonata species' (De Marmels & Neiss 2011; Juen & De Marco 2011; Fleck & Neiss 2012; Juen & De Marco 2012; Monteiro-Júnior et al. 2013; Brasil et al. 2014, 2017, 2018; Monteiro-Júnior et al. 2014; Oliveira-Junior et al., 2015, 2017; De Marco et al. 2015; Carvalho et al 2018), up to a point that enables the applicability of ecological niche models in problems related to the conservation of Odonata (Collins & McIntyre 2015).

Ecological Niche Models (ENMs) are already widespread within the field of conservation biology, both for assessing the efficiency of the currently established protected areas network (Hannah et al. 2007; Nóbrega & De Marco 2011) and for defining new priority areas for conservation (Kremen et al. 2008). Models' estimates seek to approach as best as they can the distribution of a species, not its suitable areas for occupancy, as overestimating the distribution may lead to selecting areas where species would be able to occur, but are actually absent (Guisan & Rahbek 2011; Peterson et al. 2011). Therefore, it is essential to incorporate the spatial structure in the model, which can be done by restricting the model output with convex polygons and buffers (Kremen et al. 2008), or running a cellular automata on the model output to simulate a population dynamics (De Marco et al. 2008; Engler & Guisan 2009), or even using the spatial structure as a predictor while fitting the model (Allouche et al. 2008). While there is not

a study that contrasts those alternatives, the application of any of them is essential to discuss conservation using ENMs, especially for taxons with well-defined biogeographical clusters such as the Amazonian Odonata (Juen & de Marco 2012; Brasil et al. 2018).

Here, we assess whether the Amazon network of protected areas is effective in protecting Odonata beta diversity. Our hypothesis is that the spatial distribution of conservation units in the Brazilian Amazon is inefficient for the conservation of Odonata beta diversity given that these areas are generally created without accounting for the representation of insects (Diniz-Filho et al. 2010) or aquatic organisms (Carrizo et al. 2017; Frederico et al. 2018), and because the Odonata has a lot of species turnover along the landscape (Brasil et al. 2018). Therefore, using the principle of complementarity, we will carry out a special prioritization analysis to indicate important areas for the conservation of Odonata in the Amazon, in this way complementing the already established protected areas network.

Material and methods

Occurrence data

We obtained 23,601 occurrences records of 1,234 species (neotropical region) from an extensive literature review, museums records and unpublished data from our research group and data provided by other research groups in Latin America (Members of the *Sociedad (e) de Odonatología Latinoamericana - SOL* (<http://odolatino.blogspot.com.br/>)). We also updated data found in De Marco & Vianna (2005) and Juen & de Marco (2012). We selected from the 1,234 species only those

species which occurred in the Brazilian Amazon, which left us with 19,282 occurrences from 503 species. From the remaining species, we took the caution of removing duplicated records (records for the same species that fell within the same 9.2 km² cell), an important step for fitting ENMs (Giovanni et al. 2012). We then excluded those species with a small sample size since that the minimal sample size is algorithm dependant. However, to establish a standard, we exclude from our database species with less than ten unique occurrences, the lowest acceptable species record for several algorithms (Stockwell & Peterson 2002; Pearson et al. 2007). After this procedure of selection of species, our database comprised 5,283 records from 190 species.

Ecological Niche Modeling

For our predictors, we first restricted our extent to the Neotropical region and derived Principal Components from the 19 bioclimatic variables from WorldClim (Hijmans et al. 2005). From the 19 components, we selected 8, which accounted for 95% of the total variability. Deriving Principal Components is a recommended way for reducing model complexity, avoiding collinear variables and overfitting (Jiménez-Valverde et al. 2011; Silva et al. 2014).

We used three algorithms to build ENMs: (i) Maxent (MXE) with linear and quadratic features to reduce overfitting and model complexity, particularly problematic for situations in which species have few occurrences (Anderson & Gonzalez 2011), (ii) Support Vector Machine (SVM) (Guo et al. 2005); and (iii) Random Forest (RDF) (Prasad et al. 2006). For SVM and RDF, we randomly generated pseudo-absences throughout the Neotropic, always keeping a 1:1 ratio with species' occurrences. For

Maxent, we generated 10000 background points. We created 10 replicates, randomly splitting presence and pseudo-absence data in two subsets for calibration (70%) and validation (30%) We used the replicates for model evaluation, by calculating an average TSS and its standard deviation for each algorithm within each species. For the final model we fitted ENMs using all occurrence records, again this procedure was followed for each algorithm within each species. To reduce uncertainty caused by different algorithms, we created an ensemble combining the final maps generated by the three algorithms (MXS, SVM and RDF) (Araújo & New, 2007, Diniz-Filho et al. 2009). To do so, we used the maximum specificity and sensitivity threshold to exclude all cells below the threshold (cells with low suitability) and performed a PCA on the remaining cells. We believe this is an improvement of the common PCA method used for ensemble (Marmion et al. 2009), as it eliminates a major source of variability caused by cells with low suitability.

We know that ENMs may overestimate diversity patterns, what is caused by models making predictions to areas not accessible to the species (Guisan & Rahbek 2011). To avoid overprediction, we included distance constraints to exclude suitable areas far from a species' known distribution. We did this by incorporating the cumulative distance, in which it generates new predictor with information about the sum of the distances from each cell to all the occurrences. Cells far from all occurrences receive a high distance value and are penalised while fitting models (Allouche et al. 2008). We fitted ENMs using the original 8 PCs and the species-specific cumulative distance. Overprediction is especially harmful to beta diversity calculations, since it bases those on the presence-absence of the species in a location. Therefore, the use of spatial restrictions to reduce overprediction is imperative for beta diversity calculations.

To calculate beta diversity, we first transformed ensemble suitability maps in presence-absence maps using the maximum specificity and sensitivity threshold, a threshold that balances omission and commission. We then transformed those presence-absence maps in a composition matrix, in which each line represents a cell and each column a species. Cells in which the species is considered to occurring, according to the ensemble, are given the value of 1, while on the opposite the cell receives a value of 0.

To create a composition data for each protected area, we summarized the information inside protected areas in a way that, if the species is predicted to occur (value 1) in any cell inside the protected area, the species is considered as occurring in that protected area. After defining species composition for each protected area, we calculated beta diversity with a null model. To perform the null model, we randomized protected areas in space, maintaining its shape and area, and extracted its new species composition. We performed 1000 randomizations for each protected area and, in the end, generated a Sorenson dissimilarity matrix of the original protected area against its randomizations. We then used the dissimilarity matrix to calculate the protected area's Beta diversity (β_{sor}) (Baselga 2010; Si et al. 2015) with respect to the randomizations and calculated the probability distribution for the beta diversity of the focal protected area and its randomizations. Protected areas were designated to one of three categories, based on their probability distribution: (i) Efficient PAs, in which beta diversity values' were higher than expected by chance, (ii) Random PAs, beta diversity values not different from expected by chance and (iii) Inefficient PAs, beta diversity values lower than expected by chance.

Spatial Conservation analysis

We used the software Zonation version 4 (Moilanen et al. 2005, 2014) to define priority areas for Odonata species conservation in the Amazon. Zonation produces a complementarity-based ranking of conservation priority over the entire landscape via iteratively removing cells with the smallest conservation value (Moilanen et al. 2005). The conservation value of an area (i.e. cells) is measured through its relative importance to the total conservation value of the entire planning region and is defined by the cell removal procedure used in Zonation. In this work, we used the additive benefit function (ABF) removal rule (Moilanen 2007), which favors the selection of high-quality areas for all features; i.e., species-rich areas. The principles and mathematical details of the ABF and software documentation are described in (Moilanen et al. 2014).

We used a set of configurations in Zonation to produce a more robust solution to climate change. We used the distribution interaction component in Zonation to identify a set of areas important to maintaining the connectivity between species current and future distributions. The distribution interaction favors the selection of areas where species current and future distributions overlap or on the edges of spatially segregated distributions (Rayfield et al. 2009). We also used the info-gap component in Zonation to account for uncertainties regarding future species distribution models arising from three climate models (Moilanen & Wintle 2006). In doing so, areas with greater uncertainties on species distribution are removed from the analysis. Furthermore, Zonation produces a set of priority areas that account for the level of species protection already achieved by the existing protected areas. We include federal, state and municipal PAs already established in Amazon (data source) as a mask in the spatial conservation priority analysis, which means that PAs were accounted as high-priority in solution produced.

Results

Patterns of diversity and effectiveness of protected areas

From 224 protected areas in the Brazilian Amazon, only 18 (8%) were efficient in protecting Odonata beta diversity. On the other side, 10 (4%) of the protected areas were less efficient than expected by chance in protecting Odonata beta diversity. 196 (88%) had beta diversity not different from expected by randomly real locating protected areas in the Amazon (Figure 1).

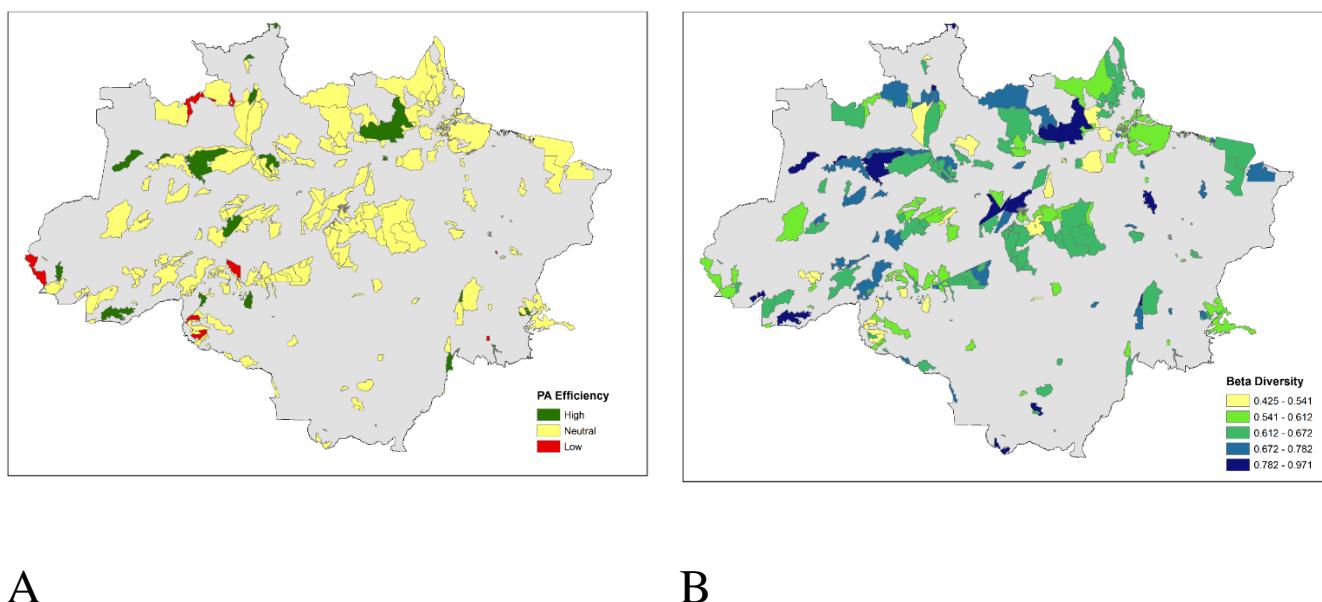


Figure 1. A: The efficiency of protected areas in the Amazon to protect areas with higher values of Odonata beta diversity. In green areas are protected with beta diversity values greater than expected in a random spatial distribution, in yellow are the protected areas where the beta diversity did not differ from that expected in a random spatial distribution and in red are the protected areas where the beta diversity was lower than expected in a random spatial distribution. B: Odonata beta diversity in protected areas of the Brazilian

Amazon, darker colors are areas with higher values of beta diversity, lighter colors are areas with lower values of beta diversity.

Space prioritization for preservation of Odonata

One of the most important principles of spatial prioritization for conservation is the complementarity. This guarantees the optimization of the solution produced, that is, to protect more species (or more endangered species) in a smaller set of areas. Thus, the map of priority areas will be very similar to a map of beta diversity, but in the prioritization it is possible to consider a greater variation of scenarios, making the results more robust for landscape management. From there we made the prioritization considering different scenarios: the first using the criterion that prioritizes areas for rare species (Core Area Zonation) (Figure 2 A). Using this criterion, it is possible to protect, on average, 34% of the species distribution. In addition, we have made special prioritization of the areas with the highest species richness. The results are similar, but these areas contain on average 37% of the species distribution, 3% more than that found using the above method (Figure 2 B).

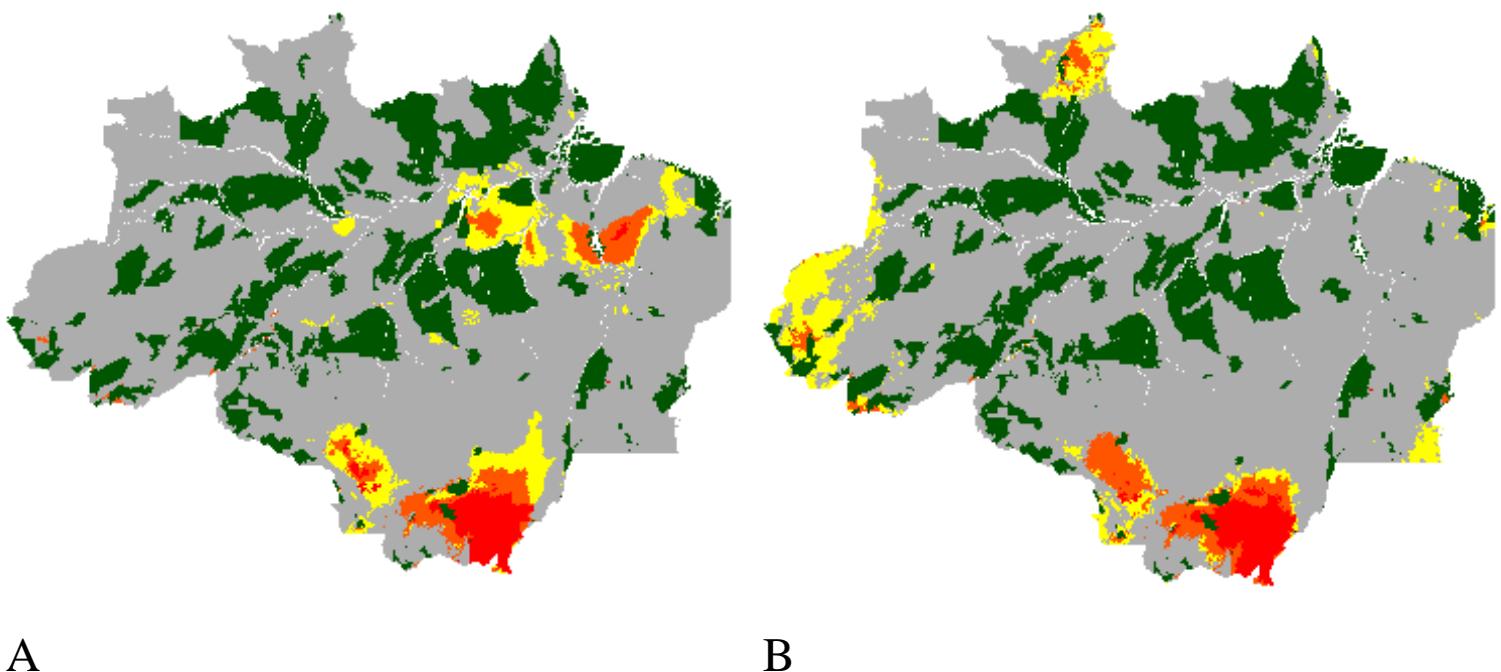


Figure 2. Special priority map for protection of Odonata in the Brazilian Amazon by priming areas with more rare species (A) and prioritizing areas with greater species richness (B). In green are the Amazon protected areas. The priority areas for conservation complementing the Amazon protected areas in red, orange and yellow represent high, medium and low priority, respectively.

We made a preliminary consideration of a land-use map of the Amazon (Soares-Filho et al. 2014) to indicate areas that will be prioritized. That is, only areas with forests will be prioritized. The set of priority areas indicated on the map below protects, on average, 30% of the species distribution (performance worse than previous solutions). This is because in this scenario, areas are chosen only in regions with forest, but with this

method we have the feeling that prioritization becomes more realistic and applicable (Figure 3).

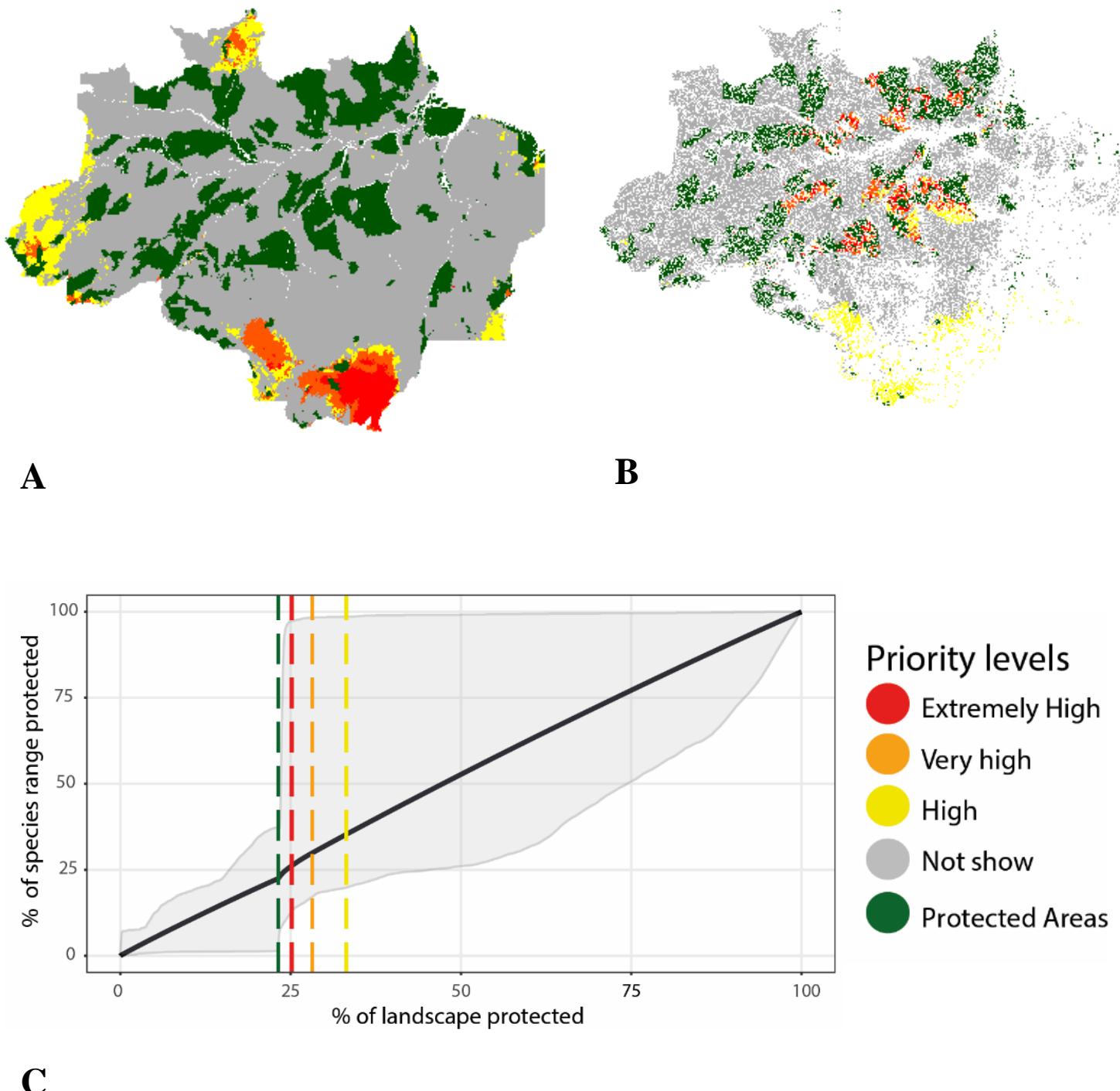


Figure 3. Areas in green are the current protected areas. In red (high priority) and yellow (medium priority) are areas of remnant forest priority for conservation, complementing already established protected areas (In green). A= Scenario of priority areas for Odonata

conservation considering the ecological niche models. B= Scenario of the priority areas for Odonata conservation considering the ecological niche models restricted by deforestation. C= Ratio of increased protection to species due to increased protected areas.

Results of spatial conservation planning analysis

On average, $22 \pm 29\%$ (mean and standard deviation) of species they represent current and future distributions in the Amazon network of PAs. The “Extremely high” set of priority areas showed in red in Figure 4 accounts for an average increase in 4% of species representation level (Figure 4). For some species poorly represented in PAs such as *Macrothemis imitans*, however, the priority areas assigned as “extremely high” may imply in an increase of species protection of ~2 to 71% (Table 1).

Figure 4. Spatial distribution of priority areas for odonata species conservation in the Brazilian Amazon. a) distribution of priority areas and Amazon protected areas (PAs) and, b) performance curves showing the mean proportion of the distribution of the current and future odonata species in the Amazon (black line). The minimal and maximal species representation is shown in the grey. Zonation produces a hierarchical e nested ranking of priority areas. Thus, the PAs are contained within the ‘extremely high’ set of priority areas (PA + 2%) of the entire Amazon, which are nested in the ‘very high priority areas’ (PA + 5%), which in turn is nested in ‘high priority areas’ (PA + 10%).

Discussion

Our results are the first to analyze the efficiency of Amazonian protected areas for a group of aquatic invertebrates and demonstrate that those areas are not efficient to protect the habitat of most species of Odonata. The Amazon is the biome with the higher amount of protected territory, 23.80% of its total area, nevertheless. This amount is still inefficient to conserve the species of Odonata. The situation might be even worse in all other biomes, in which the amount of protected territory is even lower: Atlantic Forest (6.81%), Cerrado (6.61%), Caatinga (6.26%), Pantanal (2.94%) and Pampa (2.63%) (MMA, 2010).

The low protection to conserve the habitat of Odonata species should also be invested considering other aquatic taxa, or inhabiting the riparian zone that has trophic interaction with Odonata (Samways 1993; Rice 2003). Considering the same environmental gradient, in the Amazon, the answers obtained with Odonata (Oliveira-Junior et al. 2015), are very similar to those found with fish (Leal et al. 2017; Leitão et al. 2018) and benthic aquatic insects, Ephemeroptera, Plecoptera and Trichoptera (Brito et al. 2018). Therefore, besides the conservation of Odonata, our results should also alert us to the conservation of other aquatic groups that have never been evaluated, but which have a certain level of congruence with the diversity of Odonata (Cleary et al. 2004; Lee et al. 2005; Chen et al. 2017).

This scenario is worrying in the Brazilian Amazon due to the constant conversion of natural areas into agro-systems (Brando et al. 2013; Laurance et al. 2014, 2018). Studies that analyzed Odonata communities *in situ* already verified that the conversion of the Amazon Forest into pasture for cattle breeding (Oliveira-Junior et al. 2015, 2017; Brasil et al. 2017), urbanization (Monteiro-Júnior et al. 2014), palm planting (Juen et al. 2016; Carvalho et al. 2018), logging (Calvão et al. 2016), damming of streams for the

construction of small hydroelectric (Klein et al. 2018) or for storage of water for cattle or agricultural irrigation (Brasil et al. 2014b) affect the Odonata communities and cause the loss of forest species (Carvalho et al. 2018). Considering models of future deforestation, it is likely that even species that have a good portion of the habitat preserved in the present are at risk due to future habitat loss (De Marco et al. 2015). Therefore, to conserve Amazon Odonata species it is fundamental that protected areas shelter a representative portion of the habitat of their species, since the indices of deforestation within protected areas are much smaller than the deforestation in areas of permitted use (Nolte et al. 2013).

However, in addition to protected areas, the maintenance of forest areas in private areas, or the use of agro-systems less harmful to my environment are also important measures for conservation (Soares-Filho et al. 2006). For this it is necessary that the productive sector has the possibility to generate financial resources in these areas, for example, the payments for ecosystem services (Soares-Filho et al. 2015). In the Amazon, reduced impact logging is a good alternative, generating resources that maintain most of the forest and causes minimal or undetectable damages to communities of Odonata (Calvão et al. 2016), fish (Prudente et al. 2017; 2018) and benthic aquatic insects (Nogueira et al. 2016, Cardoso et al. 2018). Agroforestry systems can be a good alternative to produce food and maintain a larger share of biodiversity, compared to areas of monoculture (Porro et al. 2012). In monocultures should havê added value when production is certified (eco-certification), respecting the legislation of the environment (Nepstad et al. 2006; Blackman & Naranjo 2012). In addition to the maintenance and creation of new indigenous areas, as they complement the protected areas very effectively for conservation (Frederico et al. 2018).

Another worrying factor to discuss about conservation is the greater anthropic pressure in certain biogeographic regions (Diniz-Filho et al. 2009a). Two areas with a

high number of endemic species, Belém and Xingu area of endemism, with 15 and 12 endemic species, respectively (Juen & de Marco 2012) are of the areas most deforested regions of the Amazon (Da Silva et al. 2005; Nolte et al. 2013) and are not very efficient for conservation of Odonata in all scenarios. In the southern and eastern parts of these areas of endemism an area of transition between the Amazon and the Cerrado biomes, is located the "arc of deforestation" (Fearnside 2005), region with many agrarian conflicts, deforestation and pressure on biodiversity (Brando et al. 2013). This region was also considered a priority for the conservation of mammals (Ribeiro et al. 2018) and fish of the streams (Frederico et al. 2018). Therefore, it is important that protected areas be created and there are forest restoration programs and implementation of activities with a lower impact on biodiversity, such as all the alterations mentioned above.

In conclusion we found that most of the protected areas are not very efficient for the conservation the species of Odonata of the Amazonian. Based on these results, we advocate that strategies for conserving Odonata in Amazonia should focus on two main scenarios: create conservation units or incentives for low-impact activities in the most central, priority and even forest regions, and encourage the restoration of priority areas already deforested through programs that pay for ecosystem services, such as carbon credits from reforestation, and or the development of activities with less impact on biodiversity, such as agroforestry.

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Supplementary.

| Species | Priority levels | | | |
|-----------------------------------|-----------------|----------------|-----------|------|
| | Protected Areas | Extremely high | Very high | High |
| <i>Macrothemis imitans</i> | 1.8 | 71.2 | 93.8 | 94.5 |
| <i>Oxyagrion evanescens</i> | 2.3 | 58.1 | 92.3 | 97.4 |
| <i>Acanthagrion hildegarda</i> | 2.5 | 97.3 | 98.3 | 98.6 |
| <i>Micrathyria almeidai</i> | 4 | 35.8 | 60 | 71 |
| <i>Ischnura fluviatilis</i> | 5.1 | 34.6 | 54.5 | 63 |
| <i>Minagrion waltheri</i> | 6.5 | 15.9 | 25.3 | 30.4 |
| <i>Hetaerina curvicauda</i> | 7.3 | 13.4 | 19.8 | 23.3 |
| <i>Brechmorhoga nubecula</i> | 8.9 | 26.6 | 38.4 | 42.9 |
| <i>Elasmothemis constricta</i> | 9 | 20.6 | 29.8 | 39.2 |
| <i>Epipleoneura westfalli</i> | 9.1 | 12.9 | 17.1 | 19.8 |
| <i>Remartinia luteipennis</i> | 9.9 | 17 | 26 | 37.6 |
| <i>Micrathyria ocellata</i> | 11.6 | 24 | 36.5 | 41.3 |
| <i>Brachympesia furcata</i> | 11.7 | 24.8 | 38.6 | 63 |
| <i>Perithemis icteroptera</i> | 12 | 59.2 | 91.5 | 92.4 |
| <i>Phyllogomphoides annectens</i> | 12.3 | 25.7 | 34.6 | 37 |
| <i>Ischnura capreolus</i> | 14.6 | 22.1 | 30.9 | 38.4 |
| <i>Elasmothemis cannacioides</i> | 15.5 | 20.2 | 25.5 | 28.7 |
| <i>Erythrodiplax castanea</i> | 17 | 20.3 | 23.8 | 31.4 |
| <i>Tramea binotata</i> | 17.5 | 19.4 | 22.4 | 28 |
| <i>Aphylla dentata</i> | 17.8 | 20.8 | 25 | 31.7 |
| <i>Micrathyria eximia</i> | 17.9 | 20.9 | 25.3 | 28.3 |
| <i>Zonophora calippus</i> | 17.9 | 21.4 | 25.9 | 30.9 |
| <i>Erythemis haematogastra</i> | 18.1 | 19.6 | 22.7 | 29.1 |
| <i>Erythrodiplax unimaculata</i> | 18.1 | 21.2 | 25.3 | 29.3 |
| <i>Erythemis attala</i> | 18.3 | 20.1 | 22.8 | 26.5 |
| <i>Metaleptobasis diceras</i> | 18.3 | 21.8 | 26 | 31 |
| <i>Neoneura luzmarina</i> | 18.3 | 21.7 | 26.6 | 34.6 |
| <i>Neoneura rubriventris</i> | 18.4 | 21.7 | 26.1 | 31.6 |
| <i>Heteragrion silvarum</i> | 18.5 | 18.5 | 20.5 | 24.4 |
| <i>Phoenicagrion flammeum</i> | 18.5 | 22 | 26.5 | 34 |
| <i>Argyrothemis argentea</i> | 18.7 | 21.8 | 25.6 | 32.8 |
| <i>Hetaerina amazonica</i> | 18.7 | 21.2 | 24.9 | 31.8 |
| <i>Erythrodiplax attenuata</i> | 19 | 22 | 26.1 | 30 |
| <i>Micrathyria atra</i> | 19.2 | 22.1 | 26 | 32 |
| <i>Hetaerina sanguinea</i> | 19.3 | 22.2 | 26.3 | 32.6 |
| <i>Hetaerina brightwelli</i> | 19.4 | 21.8 | 25.6 | 31.3 |
| <i>Oxystigma petiolatum</i> | 19.5 | 22.2 | 26.1 | 32.4 |
| <i>Uracis imbuta</i> | 19.5 | 21.4 | 24.1 | 27.5 |
| <i>Chalcopteryx rutilans</i> | 19.7 | 22.4 | 26.2 | 33.2 |
| <i>Erythrodiplax famula</i> | 19.9 | 22 | 24.9 | 30.4 |

| | | | | |
|-----------------------------------|------|------|------|------|
| <i>Phasmoneura exigua</i> | 19.9 | 22.4 | 26.1 | 32.4 |
| <i>Dasythemis esmeralda</i> | 20.1 | 21.2 | 23.6 | 30.5 |
| <i>Mecistogaster linearis</i> | 20.2 | 23 | 26.8 | 32.8 |
| <i>Psaironeura tenuissima</i> | 20.3 | 23 | 27 | 33.6 |
| <i>Tramea calverti</i> | 20.3 | 21.9 | 25 | 32.6 |
| <i>Zenithoptera anceps</i> | 20.4 | 22.4 | 25.9 | 32.2 |
| <i>Megapodagrion megalopus</i> | 20.5 | 22.6 | 25.6 | 34.2 |
| <i>Uracis infumata</i> | 20.8 | 24.1 | 27.4 | 33.2 |
| <i>Micrathyria catenata</i> | 20.9 | 29.2 | 37.6 | 42.8 |
| <i>Uracis fastigiata</i> | 20.9 | 23.9 | 27.9 | 33.6 |
| <i>Neoneura bilinearis</i> | 21.2 | 23.1 | 26.4 | 32.1 |
| <i>Uracis ovipositoria</i> | 21.2 | 22.9 | 25.5 | 34 |
| <i>Micrathyria pseudeximia</i> | 21.3 | 22.4 | 25.2 | 30.7 |
| <i>Erythrodiplax basalis</i> | 21.5 | 24.1 | 28.6 | 31.9 |
| <i>Epipleoneura kaxuriana</i> | 21.6 | 23.8 | 27.2 | 32.7 |
| <i>Uracis siemensi</i> | 21.7 | 23.4 | 26.5 | 34.7 |
| <i>Erythrodiplax lativittata</i> | 21.9 | 22.4 | 27 | 32.1 |
| <i>Oligoclada walkeri</i> | 21.9 | 24.8 | 28.5 | 36 |
| <i>Orthemis discolor</i> | 21.9 | 24.7 | 28.6 | 32.1 |
| <i>Perithemis lais</i> | 21.9 | 25.6 | 29.6 | 32.2 |
| <i>Argia hasemani</i> | 22.3 | 25.3 | 28.6 | 37.6 |
| <i>Argia infumata</i> | 22.3 | 24.6 | 28 | 33.7 |
| <i>Erythrodiplax amazonica</i> | 22.5 | 24.6 | 27.5 | 35.4 |
| <i>Oligoclada pachystigma</i> | 22.5 | 24.4 | 27.5 | 34.9 |
| <i>Epipleoneura capilliformis</i> | 22.6 | 24.9 | 28.3 | 33.8 |
| <i>Zenithoptera fasciata</i> | 22.6 | 25 | 28.3 | 35.5 |
| <i>Erythemis peruviana</i> | 22.7 | 24.4 | 26.7 | 31.8 |
| <i>Erythemis plebeja</i> | 22.7 | 24.7 | 27.2 | 32.3 |
| <i>Aeolagrion dorsale</i> | 22.8 | 24.8 | 28 | 33.1 |
| <i>Neoneura gaida</i> | 22.8 | 23.2 | 24.4 | 27.1 |
| <i>Gynacantha bifida</i> | 23 | 31.4 | 39.4 | 45.5 |
| <i>Mnesarete aenea</i> | 23 | 25.2 | 28.6 | 34.1 |
| <i>Acanthagrion peruvianum</i> | 23.2 | 25.6 | 28.7 | 31.6 |
| <i>Argia elliptica</i> | 23.2 | 25.5 | 28.7 | 34.4 |
| <i>Argia oculata</i> | 23.3 | 24.3 | 26.8 | 34.3 |
| <i>Erythrodiplax umbrata</i> | 23.3 | 23.9 | 25.5 | 30.9 |
| <i>Hetaerina indepresa</i> | 23.3 | 25.6 | 28.8 | 34.1 |
| <i>Lestes bipunctatus</i> | 23.3 | 24.8 | 27.7 | 32.7 |
| <i>Mnesarete cupraea</i> | 23.3 | 25.8 | 28.7 | 34.5 |
| <i>Argia indicatrix</i> | 23.4 | 25.4 | 28.5 | 33.6 |
| <i>Dictytes atrosanguinea</i> | 23.4 | 25.7 | 29 | 34.5 |
| <i>Erythemis credula</i> | 23.4 | 24.2 | 25.8 | 31.2 |
| <i>Erythrodiplax fusca</i> | 23.4 | 24.1 | 26.1 | 32.7 |
| <i>Tramea cophysa</i> | 23.4 | 24.4 | 26.6 | 31.6 |
| <i>Coryphaeschna adnexa</i> | 23.5 | 24.8 | 27.1 | 31.8 |
| <i>Pantala flavescens</i> | 23.5 | 24.3 | 26.4 | 31.7 |

| | | | | |
|------------------------------------|------|------|------|------|
| <i>Argyrothemis angentea</i> | 23.6 | 25.6 | 28.7 | 33.8 |
| <i>Chalcopteryx radians</i> | 23.6 | 25.7 | 28.8 | 34 |
| <i>Erythrodiplax media</i> | 23.6 | 24.4 | 26.9 | 31.9 |
| <i>Hetaerina hebe</i> | 23.6 | 24.9 | 27.4 | 32.5 |
| <i>Micrathyria stawiarskii</i> | 23.6 | 24.5 | 27.4 | 32.4 |
| <i>Oligoclada abbreviata</i> | 23.6 | 25.2 | 27.8 | 34 |
| <i>Oxyagrion microstigma</i> | 23.6 | 24.5 | 27.1 | 32.1 |
| <i>Tauriphila argo</i> | 23.6 | 24.8 | 27.1 | 32.1 |
| <i>Oxyagrion basale</i> | 23.7 | 24.3 | 26.7 | 31.7 |
| <i>Acanthagrion apicale</i> | 23.8 | 24.8 | 26.8 | 31.4 |
| <i>Brachymesia herbida</i> | 23.8 | 26.9 | 31.5 | 35.7 |
| <i>Hetaerina westfalli</i> | 23.8 | 25.8 | 28.7 | 34.5 |
| <i>Fylgia amazonica</i> | 23.9 | 26.4 | 29.9 | 35.8 |
| <i>Mnesarete pudica</i> | 23.9 | 25.2 | 27.7 | 32.3 |
| <i>Progomphus intricatus</i> | 23.9 | 24.3 | 26.3 | 33 |
| <i>Telebasis carmesina</i> | 23.9 | 24.7 | 26.9 | 30.8 |
| <i>Dythemis multipunctata</i> | 24 | 24.7 | 26.8 | 31.7 |
| <i>Micrathyria longifasciata</i> | 24 | 25.1 | 27 | 32 |
| <i>Telebasis corallina</i> | 24 | 24.6 | 26.8 | 31.8 |
| <i>Zenithoptera lanei</i> | 24.1 | 25.5 | 27.7 | 34.3 |
| <i>Orthemis ferruginea</i> | 24.2 | 24.9 | 27.2 | 33.4 |
| <i>Peristicta aeneoviridis</i> | 24.3 | 24.8 | 26.9 | 31.8 |
| <i>Acanthagrion gracile</i> | 24.4 | 25 | 26.9 | 31.8 |
| <i>Acanthagrion cuyabae</i> | 24.5 | 25.3 | 27.1 | 32.1 |
| <i>Erythrodiplax paraguayensis</i> | 24.5 | 25.2 | 26.6 | 32.1 |
| <i>Miathyria marcella</i> | 24.5 | 25.5 | 27.3 | 33.1 |
| <i>Oligoclada xanthopleura</i> | 24.5 | 26.5 | 29.4 | 34.6 |
| <i>Perithemis mooma</i> | 24.7 | 25.5 | 27.5 | 32.5 |
| <i>Acanthagrion temporale</i> | 24.8 | 25.5 | 27.2 | 32.1 |
| <i>Gynothemis venipunctata</i> | 24.8 | 25.2 | 27.1 | 32.1 |
| <i>Miathyria simplex</i> | 24.8 | 25.6 | 27.3 | 32.4 |
| <i>Micrathyria spinifera</i> | 24.8 | 26.3 | 28.5 | 34.2 |
| <i>Diastatops intensa</i> | 24.9 | 25.5 | 27.4 | 33.4 |
| <i>Gynacantha nervosa</i> | 24.9 | 25.9 | 27.2 | 32.8 |
| <i>Micrathyria spuria</i> | 24.9 | 25.3 | 26.9 | 31.4 |
| <i>Protoneura tenuis</i> | 24.9 | 25.9 | 28.1 | 33.6 |
| <i>Macrothemis heteronycha</i> | 25 | 25.3 | 27.3 | 32.2 |
| <i>Micrathyria mengeri</i> | 25 | 26.9 | 29.6 | 33.8 |
| <i>Nephepeltia phryne</i> | 25 | 25.6 | 27.5 | 31.9 |
| <i>Hetaerina rosea</i> | 25.1 | 25.4 | 27.2 | 32.2 |
| <i>Idiataphe longipes</i> | 25.1 | 25.5 | 27.1 | 32.2 |
| <i>Micrathyria pirassunungae</i> | 25.1 | 25.7 | 27.9 | 33.1 |
| <i>Argia tinctipennis</i> | 25.2 | 27.1 | 30.1 | 35.9 |
| <i>Argia lilacina</i> | 25.3 | 25.9 | 28.1 | 33 |
| <i>Cacoides latro</i> | 25.3 | 25.9 | 27.8 | 33 |
| <i>Acanthagrion truncatum</i> | 25.4 | 25.6 | 27.1 | 31.9 |

| | | | | |
|-----------------------------------|------|------|------|------|
| <i>Erythrodiplax ochracea</i> | 25.4 | 26 | 28 | 34.8 |
| <i>Micrathyria hesperis</i> | 25.4 | 26.1 | 28.2 | 33.2 |
| <i>Oxyagrion chapadense</i> | 25.4 | 25.8 | 27.7 | 32.8 |
| <i>Aphylla producta</i> | 25.5 | 28.5 | 33.4 | 38.2 |
| <i>Heliocharis amazona</i> | 25.5 | 26.1 | 27.6 | 33.3 |
| <i>Hetaerina laesa</i> | 25.5 | 26.1 | 28.2 | 36.8 |
| <i>Micrathyria ungulata</i> | 25.5 | 25.8 | 27.5 | 32.3 |
| <i>Mnesarete fuscibasis</i> | 25.5 | 25.8 | 27.4 | 32.3 |
| <i>Hetaerina auripennis</i> | 25.6 | 26.1 | 27.8 | 33 |
| <i>Oligoclada amphinome</i> | 25.6 | 28.8 | 32.7 | 35.1 |
| <i>Tholymis citrina</i> | 25.6 | 26 | 27 | 32.4 |
| <i>Aeolagrion flammeum</i> | 25.7 | 26.9 | 29.1 | 34.9 |
| <i>Erythrodiplax latimaculata</i> | 25.7 | 26.2 | 27.9 | 32.7 |
| <i>Metaleptobasis selysi</i> | 25.7 | 26.2 | 27.7 | 32.6 |
| <i>Acanthagrion ascendens</i> | 25.8 | 26.4 | 27.7 | 32.6 |
| <i>Argia reclusa</i> | 25.8 | 26.3 | 28 | 33.1 |
| <i>Diastatops obscura</i> | 25.8 | 29.5 | 33.9 | 36.8 |
| <i>Epipleoneura venezuelensis</i> | 25.8 | 26 | 27.4 | 32.4 |
| <i>Tigriagrion aurantinigrum</i> | 25.8 | 26.1 | 27.7 | 32.5 |
| <i>Zenithoptera viola</i> | 25.8 | 26.2 | 28 | 33.6 |
| <i>Cyanogomphus waltheri</i> | 25.9 | 26.2 | 27.7 | 32.7 |
| <i>Mnesarete guttifera</i> | 25.9 | 26.1 | 28.1 | 33.3 |
| <i>Aphylla theodorina</i> | 26 | 26.4 | 27.9 | 32.8 |
| <i>Oxyagrion impunctatum</i> | 26 | 26.1 | 27.9 | 32.9 |
| <i>Macrothemis hemichlora</i> | 26.1 | 26.5 | 28.2 | 33.1 |
| <i>Macrothemis musiva</i> | 26.1 | 26.9 | 28.8 | 34.4 |
| <i>Epipleoneura williamsoni</i> | 26.2 | 26.9 | 29.1 | 34.5 |
| <i>Erythrodiplax juliana</i> | 26.2 | 26.9 | 28.8 | 34 |
| <i>Heteragrion icterops</i> | 26.2 | 28.1 | 30.8 | 37.8 |
| <i>Idiataphe amazonica</i> | 26.2 | 26.8 | 28.7 | 34.7 |
| <i>Lestes forficula</i> | 26.2 | 26.6 | 28.1 | 33.3 |
| <i>Neoneura sylvatica</i> | 26.2 | 26.5 | 28.2 | 33.6 |
| <i>Telebasis racenisi</i> | 26.2 | 27.4 | 29.7 | 34.8 |
| <i>Epipleoneura machadoi</i> | 26.3 | 27.4 | 29.3 | 34.9 |
| <i>Homeoura nepos</i> | 26.3 | 26.7 | 28.2 | 33.7 |
| <i>Acanthagrion minutum</i> | 26.4 | 26.9 | 28.5 | 33.5 |
| <i>Erythrodiplax maculosa</i> | 26.4 | 27 | 29 | 34.6 |
| <i>Orthemis cultriformis</i> | 26.5 | 29 | 32.3 | 34.9 |
| <i>Erythemis vesiculosa</i> | 26.6 | 29.7 | 33.8 | 38.3 |
| <i>Telebasis coccinea</i> | 26.6 | 26.8 | 28.5 | 33.5 |
| <i>Argia mollis</i> | 26.8 | 27 | 28.3 | 33.5 |
| <i>Elga leptostyla</i> | 26.8 | 27.5 | 29.2 | 34.4 |
| <i>Neoneura denticulata</i> | 26.9 | 28.1 | 30.3 | 37.1 |
| <i>Epipleoneura metallica</i> | 27.1 | 27.7 | 29.7 | 35.9 |
| <i>Erythrodiplax nigricans</i> | 27.2 | 27.3 | 28.6 | 32.6 |
| <i>Planiplax phoenicura</i> | 27.3 | 30.8 | 35.6 | 38.7 |

| | | | | |
|-------------------------------|------|------|------|------|
| <i>Micrathyria aequalis</i> | 27.4 | 30.9 | 36.7 | 44.9 |
| <i>Micrathyria artemis</i> | 27.6 | 31.1 | 35.4 | 38.7 |
| <i>Erythemis mithroides</i> | 27.9 | 29.2 | 31.8 | 37.7 |
| <i>Heteragrion bariai</i> | 28.1 | 28.1 | 29.5 | 36 |
| <i>Hetaerina moribunda</i> | 28.2 | 28.7 | 29.9 | 30.6 |
| <i>Triacanthagyna septima</i> | 28.5 | 30.4 | 32.5 | 34.9 |
| <i>Perithemis thais</i> | 29 | 30.2 | 33 | 36.6 |
| <i>Diastatops pullata</i> | 29.1 | 29.7 | 31.5 | 34.8 |
| <i>Chalcopteryx rutillans</i> | 30.1 | 31 | 32.8 | 34.8 |
| <i>Mnesarete smaragdina</i> | 33.9 | 35 | 39.1 | 41.9 |
| <i>Nephepeltia flavifrons</i> | 34.4 | 36.7 | 39.6 | 41.8 |
| <i>Heteragrion ictericum</i> | 37.4 | 37.4 | 37.8 | 38.9 |

CONCLUSÃO GERAL

Em conclusões gerais as condições ambientais, tanto o clima quanto a estrutura do habitat, mostraram-se importantes para os padrões de diversidade de Odonata. Concomitantemente a esses preditores as áreas de endemismo foram importantes para a grande diversidade gama de Odonata da Amazônia, pois os interflúvios dos grandes rios causaram eventos de especiação que geraram altos valores de diversidade beta ao longo da paisagem. No primeiro capítulo foi evidenciado que a diversidade alfa (riqueza de espécies) é muito dinâmica ao longo da paisagem. A heterogeneidade do clima ao longo do tempo junto com as taxas de produtividade primária líquida das florestas são fatores importantes para essa diversificação. As regiões localizadas nas áreas de transição da Amazônia com o Cerrado foram as áreas onde existem as maiores variações temporais no clima e também as áreas com maiores valores de diversidade alfa de Zygoptera. Esses resultados são um reflexo tanto de suas condições ambientais, quanto da sua localização (biogeografia), por estar adjacente a dois ecossistemas extremamente diversos, a Amazônia e o Cerrado.

No segundo capítulo evidenciamos que em comparação com outros biomas brasileiros como o Cerrado e a Mata Atlântica, a Amazônia tem menores valores de diversidade alfa de Zygoptera, mas tem altos valores de diversidade gama. Isso é explicado pelos grandes valores de diversidade beta que existem entre os riachos amazônicos, assim, mesmo que a riqueza de espécies local seja relativamente baixa, o grande *turnover* de espécies ao longo da paisagem forma uma grande diversidade gama. Os principais mecanismos desencadeadores desse padrão de *turnover* é a grande extensão territorial da Amazônia (espaço) e as barreiras geográficas históricas formadas pelos grandes rios amazônicos.

Já no terceiro capítulo, considerando a dinâmica entre as comunidades de diferentes manchas de habitat ao longo da paisagem, com a dinâmica de meta-comunidades verificamos que em comunidades localizadas em igarapés ambientalmente preservados, existe um padrão clementsiano ao longo da paisagem com grupos de espécies congruentes aos interflúvios dos grandes rios. No entanto, em comunidades de igarapés ambientalmente alterados esse padrão é alterado para um agrupamento com

perda de espécies. Isso ocorre porque nos locais ambientalmente alterados as espécies generalistas e que tem maior capacidade de dispersão predominam, tornando as comunidades mais homogêneas.

No quarto capítulo evidenciamos que a distribuição espacial das unidades de conservação da Amazônia não é eficiente para conservar o habitat de grandes porções de diversidade beta de Odonata. A maior parte das áreas apontadas como prioritárias para a conservação localizam-se principalmente na região sul da Amazônia, justamente aonde está concentrado a maior parte do desmatamento na Amazônia. Se considerarmos apenas áreas florestadas, as áreas prioritárias deslocam-se para a faixa mais central da Amazônia. Apartir desses resultados sugerimos a criação de novas unidades de conservação ou incentivos para atividades de baixo impacto nas regiões mais centrais, prioritárias e ainda florestadas. Bem como, o incentivo para a restauração das áreas prioritárias já desmatadas por meio de programas que pagam por serviços ecossistêmicos, como créditos de carbono provenientes de reflorestamento, e / ou o desenvolvimento de atividades com menor impacto sobre a biodiversidade, como agrosilvicultura.

Outros resultados alcançados pela tese é a contribuição consideralmente para diminuir as lacunas wallaceanas e hutchisonianas de Zygoptera na Amazônia brasileira. Além disso, seus capítulos foram ou serão todos publicados em revistas internacionais de grande impacto, tornando-os disponíveis para toda comunidade científica internacional. Nacionalmente nossos resultados já contribuíram diretamente para a elaboração do programa de monitoramento aquático continental do ICMBio. O “Programa Monitora” capacita as comunidades tradicionais da Amazônia para que elas utilizem conhecimentos ecológicos de Odonata para o biomonitoramento da qualidade ambiental dos igarapés inseridos nas Unidade de Conservação onde elas residem, inserindo parte dos conhecimentos obtidos nesta tese na gestão ambiental da Amazônia.

OUTRAS ATIVIDADES DESENVOLVIDAS NO DOUTORADO

Nos 42 meses de doutorado, de janeiro de 2015 a julho de 2017 eu publiquei 12 artigos científicos entre os quais, dois são os capítulos dois e três desta tese:

- 1- BRASIL, LEANDRO S.; OLIVEIRA-JÚNIOR, JOSÉ M.; CALVÃO, LENIZE B.; CARVALHO, FERNANDO G.; MONTEIRO-JÚNIOR, CLAUDIO S.;**

DIAS-SILVA, KARINA; JUEN, LEANDRO. Spatial, biogeographic and environmental predictors of diversity in Amazonian Zygoptera. *Insect Conservation and Diversity*, v. 11, p. 174-184, 2018.
<https://doi.org/10.1111/icad.12262>

- 2- BRITO, T.; CONTRERA, F.; PHIFER, C.; KNOWLTON, J. L.; **LS Brasil**; MAUES, M. M.; SILVA, D. P. Effects of habitat type change on taxonomic and functional composition of orchid bees (Apidae: Euglossini) in the Brazilian Amazon. *JOURNAL OF INSECT CONSERVATION*, 2018.
<https://link.springer.com/article/10.1007%2Fs10841-018-0073-9>

- 3- JUEN, L; **L. S. Brasil**; SALLES, F. F.; BATISTA, J. D.; Cabett, H. S. R. Mayfly assemblage structure of the Pantanal Mortes/Araguaia flood plain. *MARINE AND FRESHWATER RESEARCH*, 2017.
<http://www.publish.csiro.au/mf/MF17013>

- 4- GONCALVES, G. R.; CERQUEIRA, P. V.; **BRASIL, L S**; SANTOS, M. P. D. The role of climate and environmental variables in structuring bird assemblages in the Seasonally Dry Tropical Forests (SDTFs). *PLoS One*, v. 12, p. e0176066, 2017. <https://doi.org/10.1371/journal.pone.0176066>

- 5- RAIMUNDI, E. A.; HELENA SOARES RAMOS CABETTE; **Brasil L. S.**; SALLES, F. F. A new species of Miroculis Edmunds, 1963 (Ephemeroptera: Leptophlebiidae) from Cerrado-Amazonian forest transition zone, Brazil. *ZOOTAXA (ONLINE)*, v. 4299, p. 271-278, 2017.
<http://dx.doi.org/10.11646/zootaxa.4299.2.7>

- 6- LUIZA-ANDRADE, A.; **Brasil L.S.**; BENONE, N. L.; SHIMANO, Y.; FARIA, A. P. J.; MONTAG, L. F. A.; DOLEDEC, S.; JUEN, L. Influence of oil palm monoculture on the taxonomic and functional composition of aquatic insect communities in eastern Brazilian Amazonia. *ECOLOGICAL INDICATORS*, v. 82, p. 478-483, 2017. <https://doi.org/10.1016/j.ecolind.2017.07.006>

- 7-** **Brasil L. S.**; Dias-Silva, K. Do landills affect the environmental quality of nearby streams? Biotemas, v. 30, p. 41-49, 2017.
<https://periodicos.ufsc.br/index.php/biotemas/article/download/2175-7925.2017v30n4p41/35403>
- 8-** **BRASIL, LEANDRO SCHLEMMER**; VIEIRA, THIAGO BERNARDI; DE OLIVEIRA-JUNIOR, JOSÉ MAX BARBOSA; DIAS-SILVA, KARINA; JUEN, LEANDRO. Elements of metacommunity structure in Amazonian Zygoptera among streams under different spatial scales and environmental conditions. Ecology and Evolution, v. 7, p. 3190-3200, 2017.
<https://doi.org/10.1002/ece3.2849>
- 9-** **Brasil L.S.**; GIEHL, NÚBIA FRANÇA DA SILVA; BATISTA, J. D.; RESENDE, B. O.; Cabette,H.S.R. Aquatic insects in organic and inorganic habitats in the streams on the Central Brazilian savannazilian savanna. REVISTA COLOMBIANA DE ENTOMOLOGIA, v. 43, p. 286-291, 2017.
http://www.scielo.org.co/scielo.php?script=sci_serial&pid=0120-048
- 10-** **Brasil L. S.**; Dias-Silva, K.; OLIVEIRA, J. C. A.; JUNG, A.; VIEIRA, T. B.; SABINO, U. Ambiente, espaço ou conectividade: o que estrutura as comunidades de insetos aquáticos em riachos represados? ENTOMOTROPICA, v. 31, p. 155-166, 2016. http://saber.ucv.ve/ojs/index.php/rev_ento/article/view/11819
- 11-** **BRASIL, L S**; GIEHL, N.; JUEN, L.; Cabette, H. S.R. Effect of Environmental and Temporal Factors on Patterns of Rarity of Ephemeroptera in Stream of the Brazilian Cerrado. NEOTROPICAL ENTOMOLOGY, v. 5, p. 1-7, 2016.
<https://link.springer.com/article/10.1007/s13744-016-0431-9>
- 12-** GIEHL, N.; FONSECA, P. V. B.; Dias-Silva, K.; **BRASIL, L. S.**; CABETTE, H S R. Efeito de fatores abióticos sobre Brachymetra albinervis albinervis (Heteroptera: Gerridae). IHERINGIA. SÉRIE ZOOLOGIA (ONLINE), v. 105, p. 411-415, 2015. <http://dx.doi.org/10.1590/1678-476620151054411415>.

Neste período apresentei os resultados desta tese em dois eventos científicos internacionais e fui premiado nos dois eventos. Apresentando o segundo capítulo da tese ganhei o prêmio de 2º melhor apresentação oral no I Econtro da Sociedade de Odonotologia Latinoamericana, Sociedade de Odonatologia Latinoamericana (SOL), e apresentando o 3º capítulo da tese ganhei o Prêmio Claudio Gilberto Froehlich, no Simpósio de Insetos Aquáticos Neotropicais.

Orientei três alunos de iniciação científica e trabalho de conclusão de curso:

1 - Aluno: Leonardo da Silva Novaes. Título: Novas e ameaças: panorama do grau de ameaça as espécies de Odonata descritas a partir de 2010. Graduação em Ciências Biológicas na Universidade Federal do Pará. Bolsa: Fundação Amazônia Paraense de Amparo à Pesquisa.

2 - Aluno: Viniccius Tomé Feitosa. Título: Integridade ambiental e os insetos aquáticos: Uma meta-análise em riachos tropicais. Graduação em Engenharia Florestal na Universidade Federal Rural da Amazônia. Bolsa: Conselho Nacional de Desenvolvimento Científico e Tecnológico.

3 – Aluno: Rafael Costa Bastos. Título: Implicações das condições ambientais de riachos e déficit wallaceano sobre Odonata no nordeste brasileiro. Graduação em Ciências da Natureza na Universidade Federal do Maranhão.

Por fim, no mês de junho eu fui contemplado com uma bolsa de pós-doutorado júnior a qual deve ser implementada imediatamente após a defesa e permitirá com que eu prossiga desenvolvendo minhas atividades de pesquisa junto a Universidade Federal do Pará e publique o primeiro capítulo da tese que no momento encontra-se apenas submetido e submeta o quarto capítulo que está em fase final de preparação.