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PADRÕES DE DISTRIBUIÇÃO GEOGRÁFICA DE AVES ASSOCIADAS A AMBIENTES ALAGÁVEIS DA AMAZÔNIA

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Manaus, Amazonas

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PADRÕES DE DISTRIBUIÇÃO GEOGRÁFICA DE AVES ASSOCIADAS A AMBIENTES ALAGÁVEIS DA AMAZÔNIA

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“Usa a capacidade que tens.

A floresta ficaria mais silenciosa se só o melhor pássaro cantasse.”

Henry Van Dyke

“*Tente. Sei lá, tem sempre um pôr-do-sol esperando para ser visto, uma árvore, um pássaro,um rio, uma nuvem.*

Pelo menos sorria, procure sentir amor.

Imagine. Invente. Sonhe. Voe.”

Caio Fernando Abreu

RESUMO

Para entender os padrões de endemismo e diversidade para aves especialistasnos primeiros estágios do processo sucessional em ambientes alagáveisna Amazônia, empregamos um banco de dados incluindo 26.515 registros de ocorrência georreferenciados para70táxons.O conjunto de dados foi analisado através de duas abordagens que utilizam diferentes bases lógicas para identificar padrões de co-ocorrência de espécies, e assim verificar a congruência dos padrões recuperados:a análise de endemicidade (EA)e o Infomap Bioregions. Para definir padrões de distribuição de diversidade, identificamos mudanças na composição de taxa usando a função de Interpolação de Composição de Espécie (SCI), implementada na plataforma de modelagem ambiental, Dinâmica EGO. Essa função espacializa os padrões de diversidade Beta por meio de hexágonos e interpolação, o que identifica as mudanças mais significativas na distribuição espacial de um conjunto de dados.Nossa abordagem multi-análise recuperou3, 7 e 14 áreas de endemismo, nas resoluções espaciaisde 2º, 3º e 4º, respectivamente na análise com NDM e 6 biorregiões na análise com Infomap Bioregions. Nossa análise da diversidade mostrou três padrões composicionais distintos: um ao norte do rio Amazonas; outro a leste, incluindo as bacias dos rios Tapajós, Xingu e Tocantins; e finalmente uma região que abrange o curso principal do Amazonas e afluentes do oeste-nordeste da Bacia Amazônica.O presente trabalho consiste na primeira análise quantitativa de endemismo e diversidade de espécies deaves especialistas em ambientes alagáveis Amazônicos. Nossos resultados revelaram padrões espacialmente complexos de endemismo e diversidade, com áreas apresentando vários graus de sobreposição, aninhamento e disjunção. Em geral, as áreas de endemismo identificadas, estão associadas as três principais bacias da porção norte da América do Sul, Bacia do Amazonas, Bacia do Tocantins e Bacia do Orinoco. Táxons identificados como endêmicos para estas áreas compreendem28 % (70) das aves dependentes de sistemasalagáveis. Destes, dois estão incluídos nas categorias de ameaça (NT e VU) e dois ainda não foram avaliados de acordo com a IUCN e a BirdLife International.

ABSTRACT

With the objective of characterizing the patterns of endemism and diversity for birds specialized in floodplain environments in Amazonia, we employed a database of occurrence records, including 26,515 georeferenced occurrence records for 70taxa. The data set was analyzed employing two approaches that use different logical bases to identify patterns of co-occurrence of species, and thus verify the congruence of the recovered patterns: endemicity analysis (EA) implemented in the NDM software, and Infomap Bioregions. To define diversity distribution patterns, we identified changes in species composition using the Species Composition Interpolation (SCI) function, implemented in the environmental modeling platform, EGO Dynamics.This function analyzes Beta diversity patterns in space through hexagons and interpolation, which identifies the most significant changes in the spatial distribution of a dataset. Our multi-analytical approach recovered3, 7 and 14 areas in spatial resolutions of 2º, 3º and 4º, respectively in the NDM analyses, and six bioregions using Infomap Bioregions. Our diversity analysis showed three distinct compositional patterns, one to the north of the Amazon River, the other to the east, including the Tapajós, Xingu and Tocantins basins, and finally a region encompassing the main course of the Amazon and tributaries to the west-northeast of the Amazon Basin. We provide the first quantitative analysis of endemism and species diversity for birds specialized in seasonally flooded Amazonian environments. Our results revealed spatially complex patterns of endemism and diversity for birds in floodplain environments with areas of varying degrees of overlap, nesting, and disjunction.In general, the areas of endemism identified are associated with the three main basins of the northern portion of South America, the Amazon Basin, the Tocantins Basin and the Orinoco Basin.Taxa identified as endemic to these areas comprise 28 % (70) of avian taxa dependent on flooded systems. Of these, two are considered threatened (NT and VU) and two have not yet been evaluated by IUCN and BirdLife International.

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INTRODUÇÃO GERAL

A Amazônia, de dimensões continentais, é o bioma mais diverso da Terra. Essa alta diversidade é sobretudo um reflexo de sua heterogeneidade ambiental (Remsen&Parker, 1983).Contrariandoo imaginário popular, a Amazônia não é uma floresta homogênea,mas um mosaico formado por diversos tipos de habitats (Remsen&Parker, 1983; Vale, Cohn-Haft, Bergen, & Pim, 2008; Magnusson, Lima, Albernaz, Sanaiotti, & Guillaumet, 2008; Hess et al., 2015; Adeney, Christensen, Vicentini, & Cohn-Haft, 2016; Vale, Marques, Cohn-Haft, & Vieira, 2017).Dentre esses tipos de habitats,as florestas de terra firme (não inundada) e as áreas alagáveis, especialmente asflorestas sazonalmente inundadas (várzea e igapó), se destacamcomo os dois principais habitats da região (Borges&Carvalhaes , 2000, Vale et al., 2017).

Desses habitats, as florestas de terra firme, se destacam como habitat predominante, cobrindo aproximadamente 89% da bacia e são o seu núcleo de riqueza e diversidade de espécies (Perez, 1997; Vale et al., 2017). As áreas alagáveis, apesar de mais restritas, associadas aos grandes rios, cobrem mais de 840.000 km², o que representa aproximadamente 14%da Bacia Amazônica (Hess et al., 2015).

Asvárzeas são áreas férteis que margeiam rios de água branca ou barrenta (por exemplo, rio Madeira e Purus), cuja a cor se deve a grande quantidade de material presente em suspensão (Junk et al., 2011). Osigapós são áreas pobres em nutrientes, banhadas por rios de água preta ou clara (por exemplo, rio Negro e Tapajós, respectivamente), e apresentam baixa quantidade de sedimentos em suspensão (Junk et al., 2011).Ambos são habitas que concentram uma parcela significativa da alta riqueza de espécies e endemismos associados da Amazônia (Remsen&Parker, 1983, Borges&Carvalhaes, 2000; Conh-Haft, Naka, & Fernandes, 2007; Vale et al., 2017).

Essaexcepcional diversidade de espécies e habitatsda Amazônia e seus padrões de distribuição singulares têm sido desde o século 19, recorrentes nos estudos biogeográficos e ecológicos (Oliveira, Vasconcelos, & Santos, 2017). Especial atenção tem sido dada para compreenderos padrões de distribuição, eos processos causais da origem e manutenção dessa diversidade e dos ambientes associados, com foco em áreas de floresta de terra firme(Antonelli et al., 2018; Ribas et al., 2012; Oliveira et al., 2017; Dagosta&Pinna, 2017; Hoorn et al., 2017).

O primeiro passo na compreensão desses padrões consiste na regionalização biogeográfica, em outras palavras,na identificação de “áreas de endemismo” (Morrone, 2018).Aqui, uma “área de endemismo (AE)” deve ser entendida como uma “área geográfica definida em função dos limites de distribuição de duas ou mais espécies co-ocorrentes” (Platnick, 1991; Szumik, Cuezzo, Goloboff, & Chalup, 2002).

O reconhecimento dessas áreas com base nos padrões de distribuição de espécies é de particular interesse (Perret, Chautems, Spichiger, Barraclough, & Savalainen, 2007; Givnish et al., 2014; Tagliacollo, Roxo, Duke-Silvester, Oliveira, & Albert, 2015b; Antonelli et al., 2018). O reconhecimento é fundamental por dois motivos. Primeiro, essas áreas são tidas como unidades básicas para o estudo da evolução espacial da biota de uma região (por exemplo, Haffer, 1969; Cracraft, 1985; Ribas et al., 2012, Borges&Silva, 2012). Em segundo lugar, essas áreas potencializam o direcionamento dos esforços de conservação, visto conterem biotas exclusivas (Stattersfield, Crosby, Long, & Wege, 1998; Olson et al., 2001; de Luca, Develey, Bencke, & Goerck, 2009; Borges&Silva, 2012; Antonelli et al., 2018).

Nesse contexto, diversos estudosforam realizados buscando identificar esses padrões singulares da Biota Amazônica, principalmente os padrões da fauna associada às florestas de terra firme (Godinho& Silva, 2018).Possivelmente, a primeira proposta de regionalização da biota Amazônica veio de Wallace (1852) que, estudando a distribuição de primatas, reconheceu quatro “distritos biogeográficos” delimitados por grandes rios (Negro, Madeira, Solimões e Amazonas).Posteriormente, Haffer (1974,1978), Cracraft (1985) e Silva, Novaes, & Oren (2002)e Borges&Silva (2012), analisando dados de distribuição de aves, identificaram seis, sete, oitoe nove áreas de endemismona Amazônia, respectivamente. Assim, atualmente, para avifauna de sub-bosquede floresta de terra firme nas terras baixas da Amazônia são reconhecidas nove áreas de endemismo,delimitadas,principalmente,pelos grandes rios.

Embora certos padrões de distribuição da faunaAmazônicaestejam relativamente bem estabelecidos, principalmente para as aves de sub-bosque de terra firme,esses padrões não são concordantes para organismos que utilizam outros habitatspresentes na bacia Amazônica(Cohn-Haft et al., 2007) ou para outros grupos de organismos (Godinho & Silva, 2018). Como exposto acima, em termos biogeográficos,sabemos muito mais sobre organismos deterra firme do que aqueles que vivem ambientesalagáveis na Bacia Amazônica, como as florestas de várzea e igapós (Cohn-Haft et al., 2007; Antonelli et al., 2018).

Os estudos anteriores para ambientes alagáveis centraram-se mais em aspectos ecológicos da fauna associada do que na caracterização de padrões biogeográficos. Por exemplo, Remsen &Parker (1983) num estudo pioneiro de aves em ambientes alagáveis amazônicosdescreveram a especialização em habitats criados pelos rios, bem como em ilhas fluviais. Em termos de habitat para aves, eles caracterizaramdiferentes tipos de ambientes criados pelos rios, incluindo: bancos de areia com arbustos; florestas de beira de rio; florestas de várzea; e florestas de transição (Remsen&Parker, 1983). Eles estimaram que aproximadamente 15% das espécies (192) de aves da Bacia Amazônica são restritas a esses habitats (Petermann, 1997; Cohn-Haft et al., 2007). Posteriormente, o uso e especialização de aves em habitas de várzea, especificamente em ilhas fluviais foi melhor exploradono Peru (Rosenberg, 1990, Armacost-Jr &Capparella, 2012), na região de Manaus (Petermann, 1997) e sumarizados por (Stotz, Fitzpatrick, Parker, & Moskovits, 1996),reconhecendo assim a singularidadeda avifauna em ambientes alagáveis em relação a terra firme.

Apesar do reconhecimento da avifauna rica e diversificada presente em sistemas alagáveis, seus padrões de distribuição e endemismos ainda são pouco compreendidos. Numa primeira tentativa de elucidar esses padrões Cohn-Haft et al. (2007)com baseem uma análise qualitativa de dados de ocorrência de aves ao longo da calha dos rios Amazonas e Solimões, reconheceram três zonas de endemismo para avifauna, correspondente aos trechos alto, médio e baixo da calha dos rios Solimões-Amazonas (Cohn-Haft et al., 2007). Esses resultados contrariam a ideia de homogeneidade da avifaunaao longo dos ambientesalagáveis aparentemente contínuosao longo dos grandes rios(Cohn-Haft et al., 2007). Entretanto, métodos biogeográficos quantitativos buscando testar essa hipótese de regionalização ainda não foram aplicados nesses sistemas, bem como inexiste até hoje uma síntese de padrões de distribuição de aves em sistemas alagáveis.

Um outro aspecto da fauna Amazônica ainda pouco exploradodiz respeito a organização espacial da composição das comunidades biológicas, especialmente em ambientes alagáveis (Remsen&Parker, 1983; Buckton & Ormerod, 2002;Cintra, Sanaiotti, & Cohn-Haft,2007). A identificação de fatores que afetam a composição de espécies em uma comunidade local e, em particular, mudanças na composição entre áreas (diversidade beta) têm sido alvo de muitos estudos em ecologia (Antonelli et al., 2018; Tuomisto,& Ruokolainem, 2006; Costa&Melo, 2008; Blake&Loiselle, 2009; Dahl, Novotny, Moravec, & Richards, 2009; Jankowski, Ciecka, Meyer, & Rabenold, 2008; Melo, Rangel, & Diniz-Filho, 2009; Legendre, 2014; Balsega& Leprieur, 2015; Si, Balsega, & Ding, 2015).

No que diz respeito a conservação da diversidade biológica, a diversidade beta tende a ser mais importante que a diversidade alfa, pois mudanças na composição entre locais afetam a diversidade em grandes escalas (Condit et al., 2002). Com frequência, estudos mencionam a heterogeneidade ambiental e a dispersão como importantes processos, determinísticos e estocásticos, respectivamente, que controlam a diversidade beta em uma região (Tuomisto, 2006; Laliberté, Paquette, Legendre, & Bouchard, 2009).

Diversos estudos indicam que a riqueza de espécies está relacionada à heterogeneidade de hábitat, tanto em escala local quanto em escala regional, e enfatizam que o número e a composição de espécies em determinada assembleia são associados tanto à variação ambiental quanto às relações intra e interespecíficas (Gaston&Blackburn, 1996; Bohning-Gaese, 1997; Van Rensburg, Chown, & Gaston, 2002; Evans, Newson, Storch, Greenwood,& Gaston, 2008).

Contrastando essa ideia Hubbell (2001) em sua teoria neutra, não considera diferenças nas respostas entre os indivíduos às condições ecológicas locais, enfatizando que a dinâmica de uma comunidade pode ser modelada com poucos parâmetros, tais como tamanho populacional local e regional, taxa de especiação e taxa de migração. Sendo assim, a composição de espécies das assembleias flutua ao acaso e, em escala local, a composição se torna imprevisível, variando somente em função da distância geográfica, o que indica limitação de dispersão.Dessa forma,três hipóteses ecológicas plausíveis para estruturação espacial da composição das comunidades biológicas, em especial da diversidade beta, tem sido amplamente testadas: hipótese da heterogeneidade do habitat, a hipótese da dispersão e a hipótese da distância geográfica(Tuomisto, 2006, Mori, Isbell, & Seidl, 2018, Crouch, Capurucho, Hackett, & Bates, 2018; Piatti et al., 2019).

Para avifauna dos ambientes alagáveis o padrão de riqueza de espécies, diferentemente da terra firme, parece estar mais associado a trechos específicos dos rios, evidenciandoo padrão oeste-leste de riqueza característico para outros grupos amazônicos, dado a grande representatividade de áreas de várzea nessa porção da Amazônia (Cohn-Haft et al., 2007).Nesse contexto, uma questão de especial importância, além dessa lacuna biogeográfica e ecológica, diz respeito a vulnerabilidade iminente desses habitats e de suas espécies frente aos planos de desenvolvimento de infraestrtutra para Amazônia (Bird et al., 2012; Latrubesse et al., 2017; Fearnside, 2019).As áreas onde altas concentrações de espécies e desenvolvimento se sobrepõe são onde as espécies estarão em maior risco (Vale et al., 2008). Segundo Vale et al. (2008)os ambientes alagáveis que comportam 15% das espécies de Aves de toda Amazônia, serão os mais afetados. Especificamente, os habitats criados pelos rios, por exemplo, são áreas de aves endêmicas bem estabelecidas, e concentram muitas espécies com faixas geográficas pequenas que são de importância para conservação (EBA 067 em Stattesfield et al.,1998; Mane, Brooks, & Pimm, 1991; Manne & Pimm, 2001; Vale et al., 2008).

Nesse contexto, a preservação desses ambientes é imprescindível para conservação da diversidade total de aves amazônicas (Remsen&Parker, 1983; Rosenberg, 1990; Cohn-Haft et al., 2007).Entretanto, como exposto acima, para os ambientes alagáveis em relação aos ambientes de terra firme, pouco se tem avançado no reconhecimento dos padrões de distribuição e diversidade dessa avifauna característica e especializada.

Neste estudo investigamosos padrões de distribuição e diversidadedeaves associadas aos ambientes alagáveis da Amazônia, com foco em aves especialistas nos primeiros estágios do processo sucessional, para entender os padrões de diversidade e investigar se existem áreas de endemismo não reconhecidas.Com base emdados pontuais de ocorrência de espécies e subespécies deaves Amazônicasextraídos de bases online e coleções científicas buscamos responderas seguintes questões: (1) há áreas de endemismo para aves especializadas nos ambientes alagáveis amazônicos? (2) quais são os padrões de distribuição de diversidade (beta) presentes nas comunidades de aves especializadas nos ambientes alagáveis amazônicos?Com base em nosso conhecimento, este é o primeiro estudo a avaliar quantitativamente os padrões de distribuição de aves Amazônicas associadas a ambientes alagáveis.

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OBJETIVOS

Caracterizaros padrões de regionalização da avifauna associada a ambientes alagáveisna Amazônia, com foco em taxa especializados em formações vegetais dos primeiros estágios do processo de sucessão. Para isso buscamos identificar áreas de endemismo, definir os padrões espaciais da diversidade e correlacioná-los com os possíveis impactos das barragens propostas para Amazônia.

CAPÍTULO 1

Silva, J.V.; Laranjeiras, T.O.; Cohn-Haft, M.; Neves, M.; Fagundes, C.G. & Ribas, C.C. Biogeographic regionalization of the avifauna associated to Amazonian seasonally flooded habitats: building a baseline for environmental impact assessment. Manuscrito em preparação para Journal of Biogeography.

Original Article

Biogeographic regionalization of the avifauna associated to Amazonian seasonally flooded habitats: building a baseline for environmental impact assessment

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Running head: Patterns of endemism and diversity of birds in Amazonian floodplains

ABSTRACT

AimCharacterize the patterns of endemism and of spatial variation in species composition for the avifauna specialized in early successional vegetation in Amazonian floodplains.

Location Amazon Basin

Methods The compiled databaseincludes 26,515geo-referenced occurrence records for 70 taxa selected according to their habitat preferences. For the endemism analysis two approaches that use different logical bases to identify patterns of co-occurrence of species were employed: Endemicity analysis (EA) was performed using the NDM software, and Infomap Bioregions algorithm that identifies specific bioregions from species distribution data was applied through the interactive WEB application. To characterize the spatial distribution of diversity we identified changes in taxa composition using the Species Composition Interpolation (SCI) function, implemented in the environmental modeling platform, Ego Dynamics. This function spatializes Beta-diversity patterns through hexagons and interpolation, identifying the most significant changes.

ResultsEndemism analyses recovered3, 7 and 14 areas of endemism, inthree different spatial resolutions, as well as six bioregions, with NDM and Infomap Bioregions, respectively. Our analysis of diversity showed three distinct compositional patterns, one to the north of the Amazon, another to the east, including the Tapajós, Xingu and Tocantins River Basins, and finally a region encompassing the Amazon/Solimões main channel plus tributaries to the west-northeast.

Main conclusions We provide the first quantitative analysis of species endemism and diversity for birds in Amazonian floodplain environments. Our results revealed spatially complex patterns, with areas of endemism presenting varying degrees of overlap, nesting, and disjunction**.**In general, the areas of endemism identified are associated with the three main basins of the northern portion of South America, the Amazon Basin, the Tocantins Basin and the Orinoco Basin.Taxa identified as endemic comprise 28% (70) of the avifauna dependent on seasonally flooded habitats. Of these, two are considered threatened (NT and VU) and two have not yet been assessed according to IUCN and BirdLife International.The avifauna associated to Amazonian floodplains is heterogeneous and these patterns need to be taken into account when planning for infrastructure development along the Amazonian rivers.

Keywords: Amazon biogeography,floodplain, fluvial island,open areas,bird conservation, areas of endemism, beta diversity.

Abstract: 320 words

Main body: 5545 words

INTRODUCTION

Amazonia, with continental dimensions, is the most diverse biome on Earth (Antonelli et al., 2018). This high diversity is partly due to its environmental heterogeneity (Remsen & Parker, 1983). Contrary to the idea of a large homogeneous forest,Amazonia isa mosaic of many different kinds of habitats superimposed and intrinsically connected (Remsen & Parker, 1983, Vale, Cohn-Haft, Bergen, & Pim, 2008, Magnusson, Lima, Albernaz, Sanaiotti, & Guillaumet, 2008, Adeney, Christensen, Vicentini, & Cohn-Haft, 2016, Vale, Marques, Cohn-Haft, & Vieira, 2017).Among these,terra firme (non-flooded) forests and floodplains, especially seasonally flooded forests (várzea and igapó) stand out as the two main habitats in the region (Borges & Carvalhaes, 2000, Vale et al., 2017). Várzeas are fertile areas flooded by white water rivers like Madeira and Purus, whose color is due to a large concentration of suspended sediments (Junk et al., 2011). Igapós are nutrient poor areas, flooded by black or clear water rivers like Negro and Tapajós, with little suspended sediments (Junk et al., 2011).

Upland terra firme forest covers most of the basin and comprises the majority of known species diversity (Vale et al., 2017). The seasonally flooded habitats, although more restricted and associated with large rivers, cover more than 800,000 km², which represents approximately 14% of the basin (Junk et al., 2011; Hess et al., 2015) and harbor a significant share of the high species richness and associated endemism of Amazonia (Remsen & Parker, 1983, Borges & Carvalhaes, 2000;Conh-Haft, Naka, & Fernandes, 2007, Vale et al., 2017).

This exceptional diversity of species and habitats of the Amazon and its unique distribution patterns have been recurrent inbiogeographical and ecological studies since the 19th century (Oliveira, Vasconcelos, & Santos, 2017). Special attention has been given to understanding the patterns of distribution, and the causal processes related to the origin and maintenance of this diversity and the associated environments (Antonelli et al., 2018; Ribas et al., 2012; Oliveira et al., 2017; Dagosta & Pinna, 2017; Hoorn et al., 2017).

The first step for characterizing these patterns isbiogeographic regionalization, or the identification of "areas of endemism" (AE) (Morrone, 2018), where an AE should be understood as a "geographic area defined by the distribution boundaries of two or more co-occurring species, not occurring anywhere else" (Platnick, 1991, Szumik, Cuezzo, Goloboff, & Chalup, 2002).The recognition of AEs on the basis of species distribution patterns is of particular interest (Perret, Chautems, Spichiger, Barraclough, & Savalainen, 2007, Givnish et al., 2014, Tagliacollo, Roxo, Duke-Silvester, Oliveira, & Albert, 2015b, Antonelli et al., 2018)for two reasons. First, these areas are considered as basic units for the study of the spatial evolution of a region's biota (for example, Haffer, 1969; Cracraft, 1985; Ribas et al., 2012, Borges & Silva, 2012). Second, these areas potentiate the targeting of conservation efforts, since they contain exclusive biotas (Stattersfield, Crosby, Long, & Wege, 1998; Olson et al., 2001, de Luca, Develey, Bencke, & Goerck, 2009, Borges & Silva, 2012, Antonelli et al., 2018).

In this context, many authors have tried to summarize Amazonian bioregionalization looking at different groups of organisms, and usually, even if without noticing, focusing on upland terra firme forest taxa. Possibly the first attempt at regionalization of the Amazonian biota came from Wallace (1852), who, based on the distribution of primates, recognized four "biogeographic districts" delimited by the largestAmazonian rivers. Subsequently, Haffer (1974, 1978), Cracraft (1985), Silva, Novaes & Oren (2002) and Borges&Silva (2012), based on distribution patterns of birds from the understory of upland terra firme forest, identified, six, seven, eightand nine AEs, inAmazonia, respectively.The main difficulty in this process is the lack of knowledge about distribution patterns and even species limits for many Amazonian taxa. This explains the emphasis in birds and primates so far, as their taxonomy is better known, but even for these groups there are still many challenges related to unstable taxonomy and inaccurate information on distribution limits. Recent studies have made new attempts of regionalization focused on Amazonian birds and amphibians, with some congruence to previous studies (Godinho & Silva, 2018), but also large uncertainties in the databases concerning species taxonomy and distributions (Oliveira et al., 2017).

Another problem that has prevented advance in Amazonian regionalization is the failure in distinguishing species with specialized and distinct habitat affinities. Although some patterns of distribution of Amazonian fauna are relatively well established, mainly for birds and primates that occupy upland forests, these patterns are not necessarily representative of other groups of organisms, neither of the avifauna that occupies other Amazonian habitats, such as the seasonally flooded habitats (Cohn-Haft et al., 2007).

Previous studies of flooded environments have focused more on ecological aspects of associated fauna than on the characterization of biogeographic patterns. For example, Remsen & Parker (1983) in a pioneering study of birds in Amazonian floodplains described the specialization in habitats created by rivers as well as in river islands. They characterized different types of environments created by rivers as distinct habitats for the avifauna, including: shaded area banks; riverside forests; floodplain forests; and transitional forests (Remsen & Parker, 1983). They estimated that approximately 15% of the non aquaticbird species (192) of the Amazon Basin are restricted to habitats created by the annual flood pulse of rivers (Petermann, 1997; Cohn-Haft et al., 2007). Later, the use and specialization of birds in várzea habitats, specifically in fluvial islands, was best explored in Peru (Rosenberg, 1990, Armacost-Jr & Capparella, 2012), in the region around Manaus (Petermann, 1997) and summarized by Stotz, Fitzpatrick, Parker, & Moskovits (1996), thus recognizing the uniqueness of the avifauna specialized in seasonally flooded Amazonian environments.

Despite the recognition of rich and diversified avifauna present in seasonally flooded systems, their distributionand endemism patterns are still poorly understood. In a first attempt to elucidate these patterns Cohn-Haft et al. (2007)based on qualitative analysis of species occurrence along the Amazon-Solimões várzea, recognized three zones of endemism for the avifauna, corresponding to the upper, middle and lower reaches of the Solimões-Amazonas river channel (Cohn-Haft et al. 2007).However, quantitative biogeographic methods seeking to test this hypothesis of regionalization have not yet been applied in these systems.

Another little explored aspect ofAmazonian diversity concerns species composition in local communities, and in particular the spatial variation in community composition (beta diversity), especially in floodplain environments (Remsen & Parker, 1983; Buckton & Ormerod, 2002; Cintra, Sanaiotti, & Cohn-Haft, 2007; Antonelli et al., 2018).As far as biodiversity conservation is concerned, beta diversity tends to be more important than alpha diversity, since changes in inter-site composition affect diversity at large spatial scales (Condit et al., 2002). Studies often mention environmental heterogeneity and dispersal as important deterministic and stochastic processes, respectively, that control beta diversity in a region (Tuomisto& Ruokolainem, 2006; Laliberté, Paquette, Legendre, & Bouchard, 2009).

Several studies indicate that species richness is related to habitat heterogeneity, both locally and regionally, and emphasize that the number and composition of species in a particular assembly are associated with both environmental variation and intra and interspecific relationships (Gaston & Blackburn, 1996; Bohning-Gaese, 1997; Van Rensburg, Chown, & Gaston, 2002; Evans, Newson, Storch, Greenwood, & Gaston, 2008). For birds specialized in flooded habitats, the pattern of species richness and turnover seems to be associated with specific stretches of the rivers, showing the west-east richness pattern described for some Amazonian groups (Cohn-Haft et al. 2007), but the pattern is still largely undescribed. This knowledge gap acquires special importance concerning, the imminent vulnerability of these habitats due to the Amazon infrastructure development plans (Bird et al., 2012; Latubesse et al., 2017; Fearnside, 2019).

Areas where high concentrations of species and development projects overlap are where species are mostly at risk (Vale et al., 2008). According to Vale et al. (2008) the wetland environments, that comprise 15% of the Amazonian non-aquatic bird species, will be the most affected. Specifically, habitats created by rivers, for example, are well-established endemic bird areas, and concentrate many species with small geographic ranges that are of conservation concern (EBA 067 in Stattesfield et al., 1998; Manne, Brooks, & Pimm, 1991; Manne & Pimm, 2001; Vale et al., 2008).In this context, the preservation of these environments is essential for conservation of the total diversity of Amazonian birds (Remsen & Parker, 1983; Rosenberg, 1990; Cohn-Haft et al., 2007). However, little progress has been made in recognizing the patterns of distribution and diversity of the characteristic and specialized avifauna associated to Amazonian floodplains.

In this study, we investigate patterns of distribution and diversity of birds associated tofloodplain environments in Amazonia, focusing on habitats on river islands and on areas subjected to large periods of flooding each year, to understand diversity patterns and whether there are unrecognized areas of endemism.Based on occurrence data of species and subspeciesextracted from online databases and scientific collections, we approach the following questions: (1) Are there areas of endemism forbirds specialized in early successional floodplain Amazonian environments? (2)How does community composition vary along Amazonianearly successional floodplain environments? (3) How planning of hydroelectric generation in Amazonia can benefit from the knowledge about these patterns of diversity and endemism in order to reduce environmental impacts.

MATERIALS AND METHODS

Selection of taxa and compilation of occurrence data

Our study focused on birds specialized in the early stages of the successional process (Achard et al., 2005; Hess et al. 2015). This avifauna is especially vulnerable to changes in the hydrological cycle and sediment load, especially those caused by large dams for hydroelectric power generation (Lees, Peres, Fearnside, Schneider, & Zuanon, 2016; Latubesse et al., 2017).

The taxonomy adopted here follows the latest version of the Brazilian Ornithological Records Committee (CBRO) (Piacentini et al., 2015). The selected taxa occur specifically in new fluvial islands and open vegetation areas at the river margins, and show different degrees of dependence in relation to these environments (Remsen & Parker, 1983; Rosenberg, 1990; Stotz et al., 1996; Robinson&Terborgh, 1997; Petermann, 1997; Borges&Carvalhaes, 2000; Naka, Cohn-Haft, Mallet-Rodrigues, Santos, & Torres, 2006; Conh-haft et al., 2007; Armacost-Jr & Capparella, 2012; Laranjeiras et al., 2014). This habitat specialization is reflected in the distribution of these taxa, which for the most part are restricted to the main channels of large rivers (Vale et al., 2008, 2017).

Based on information on habitat use (Remsen&Parker, 1983; Cohn-Haft et al., 2007; Laranjeiras et al., 2014) we selected 70 taxa (species and subspecies) and builta database of occurrence records using data from ornithological collections with good representation of the Amazonian avifauna - Museu Paraense Emílio Goeldi (MPEG), National Institute of Amazonian Research (INPA), American Museum of Natural History (AMNH) and Louisiana State University Museum of Natural History (LSUMNS); and online databases – WikiAves (https://www.wikiaves.com.br/), xeno-canto (https://www.xeno-canto.org/) and Macaulay Library (https://www.macaulaylibrary.org/). The final database includes 26,515 occurrence points. Each locality of occurrence was confirmed through the Coordinate Cleaner tool (Zizka et al., 2019). This tool is especially suitable for large data sets, since inaccurate locations are a major problem when using data from large databases. We also evaluated sample bias associated with the database, using the Sampbias method (see https://azizka.shinyapps.io/sampbias), which allows quantifying the polarization effect of geographic features related to human accessibility, such as proximity to cities, rivers or roads. For non-georeferenced locations, the coordinates were estimated using online geographic dictionaries: GEOLocate (http://www.geo-locate.org/), speciesLink (http://www.splink.org.br/) and geographic dictionaries (Gazetteers) of South American countries (Stephens & Traylor Jr., 1983; Paynter Jr. & Traylor Jr., 1991). Records with insufficient information or questionable coordinates were excluded from the analysis. Along the process, the distribution maps currently available in the literature were updated for 37 species, which will be made available in a separate publication.

Endemicity analysis (NDM)

The data set was analyzed using the optimization criterion in NDM-VNDM 3.0 (Goloboff, 2004), which applies the methods of Szumik et al. (2002) and Szumik & Goloboff (2004). Endemicity analysis (EA) implements an optimization criterion based on considering the congruence between species distributions (Szumik et al., 2002). EA provides an endemicity score for each taxon (endemic taxon score = 'e'). Among potential endemism areas, the highest endemicity index (maximum endemicity value obtained for area = 'IE') is calculated as the sum of the endemic species 'e' included in the area and the highest number of species (Szumik et al., 2002; Casagranda, Taher, & Szumik, 2012). Heuristic searches were done with 50,000 replicates and areas with a minimum value of "IE" above 2.0 were saved. To describe the areas of endemism, we considered: (1) the endemicity score of each rate = 'e'; and (2) the index of endemicity = 'IE'.

The use of different grid sizes allows the investigation of distribution patterns at different scales (Casagranda, Taher, & Szumik, 2009;Szumik, Aagesen, Casagranda, Arzamendia, & Baldo, 2012; DaSilva, Pinto-da-Rocha & DeSouza, 2015; Gomes-da-Silva, Amorim, & Forzza, 2017). Analyzes were performed in three different spatial resolutions (cells of 2.0º, 3.0º and 4.0º). Analyzes using different cell sizes can retrieve different areas, all valid insofar as they are all supported by the distributional congruence of species at that resolution or scale (Szumik et al., 2012; Aagesen, Szumik, & Goloboff,2013). The optimality criterion EA can produce numerous candidate areas, and employing consensus methods simplifies the identification of areas. The consensus rules employed in this work combine all areas (set of cells) that share the endemic taxa, with cutoff values of 100% similarity (strict consensus) (see Aagesen, Szumik, Zuloaza, & Morrone, 2009; Aagesen et al., 2013).

Interactive mapping (Infomap Bioregions)

Infomap Bioregions identifies bioregions from species distribution data (Edler, Guedes, Zizka, Rosvall, & Antonelli, 2017). The user-supplied distribution data is placed on a grid with adaptive spatial resolution, that is, when the data is sparse, the grid size is large; and when the data is dense, the grid size is small. This adaptive resolution offers a considerable advantage over the conventional uniform grid when dealing with biodiversity data, which is unevenly distributed (Maldonado et al., 2015; Meyer, Weigelt, & Kreft, 2016).

The adaptive resolution generates a split network between species and grid cells, which is then grouped with the Infomap algorithm in Bioregions (Edler & Rosvall, 2015). The application also identifies the most common and most indicative species in each grid cell and bioregion. A distribution data matrix containing 26,515 records for 70 taxa with at least two points for each taxon was used, using the following parameters: minimum cell size = 1º, maximum cell size = 4º, minimum cell capacity = 10 and maximum cell capacity = 100. A split network for clusters generation was mapped to 70 taxa with 313 cells. Summary tables of the most common and most indicative species were saved for each bioregion. For the indicative species, a frequency of occurrence score was assigned. This information allowed identifying endemic species unique to a bioregion.

Analysis of species composition

To identify the spatial patterns of changes in taxa composition, we used the Species Composition Interpolation (SCI), in the biodiversity analysis package - Biodynamics, implemented in the Dinamica-EGO modeling platform (Oliveira et al., 2017). This function spatializes patterns of species composition through hexagons and interpolation, which identifies the most significant changes in spatial distribution of Beta diversity.

The same data matrix with 26,515 records for 70 taxa was used. The boundary of the study area was defined as Amazonia *sensu latissimo* (Achard et al., 2005). The size of the hexagonal sample units was defined as 1.0°. Spatial variation in species composition was expressed in a cell-cell matrix using the Bray-Curtis dissimilarity index through Non-Metric Multidimensional Scaling (NMDS). The values of the vectors were then interpolated using the function Nearest Neighbour Interporlation (NNI) generating a surface map of the variation of species composition expressed in RGB format.

To test the premise of spatial autocorrelation, we calculated the Moran index (I) for each axis of the NMDS. Hexagonal cells with less than 10 registers were excluded from the analysis because they could inflate the dissimilarity of Bray-Curtis, influencing NMDS results. All of these steps and the ordination analysis were performed in SCI function of Biodynamics.

RESULTS

Identification of areas of endemism

In the NDM analysis, 3, 7 and 14 endemism areas were identified for the 2.0, 3.0 and 4.0° cell sizes, respectively (Figures 1, 2 and 3). The areas of endemism identified in different spatial resolutions are shown in Table 1. The areas found in the different grid sizes present varying degrees of spatial overlap, nesting, and disjunction. As the cells that make up each area also include non-flooded habitats, these were plotted along with the most recent available map of Amazonian floodplains (Hess et al., 2015), which is the environment actually available for the species in question.

Table 1. Areas of endemism for birds of early sucessional habitats at different scales, with cell sizes of 2.0 °, 3.0 ° and 4.0 °. Numbers represent area size, endemic taxa and area endemicity value (IE). The areas of endemism identified for the different cell sizes carry the acronym AE.

Geographic grids				
2.0°		**Size**	**Nº.endemic taxa**	**Score – IE**
	AE0	10	3	2.039583
	AE1	32	3	2.355188
	AE2	32	3	2.132458
3.0°				
	AE0	7	5	3.366667
	AE1	5	3	2.155556

	AE2	24	8	5.277802
	AE3	28	12	7.483416
	AE4	3	2	2.000000
	AE5	22	6	4.316026
	AE6	75	10	7.910357
4.0°				
	AE0	25	17	12.29934
	AE1	24	16	11.64125
	AE2	16	6	3.959666
	AE3	7	4	3.292866
	AE4	10	3	2.305566
	AE5	5	4	2.762099
	AE6	26	17	12.30750
	AE7	19	11	8.601455
	AE8	43	14	10.69732
	AE9	14	12	8.564022
	AE10	12	11	6.711144
	AE11	3	2	2.250000
	AE12	14	13	8.498055
	AE13	42	19	13.56623

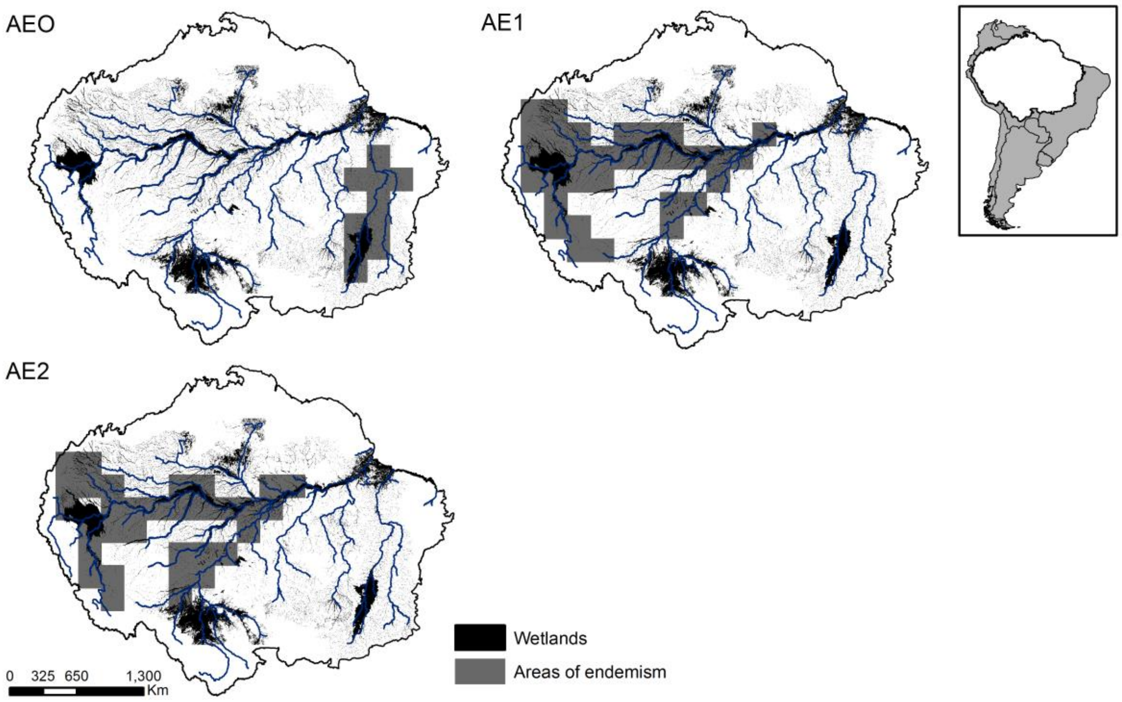

Figure 1. Areas of endemism for Amazonian birds associated with early sucessional habitatsidentified with cells of size 2.0º. The areas were identified using the method (NDM) based on species and subspecies datasets. Wetlands map of Hess et al (2015).

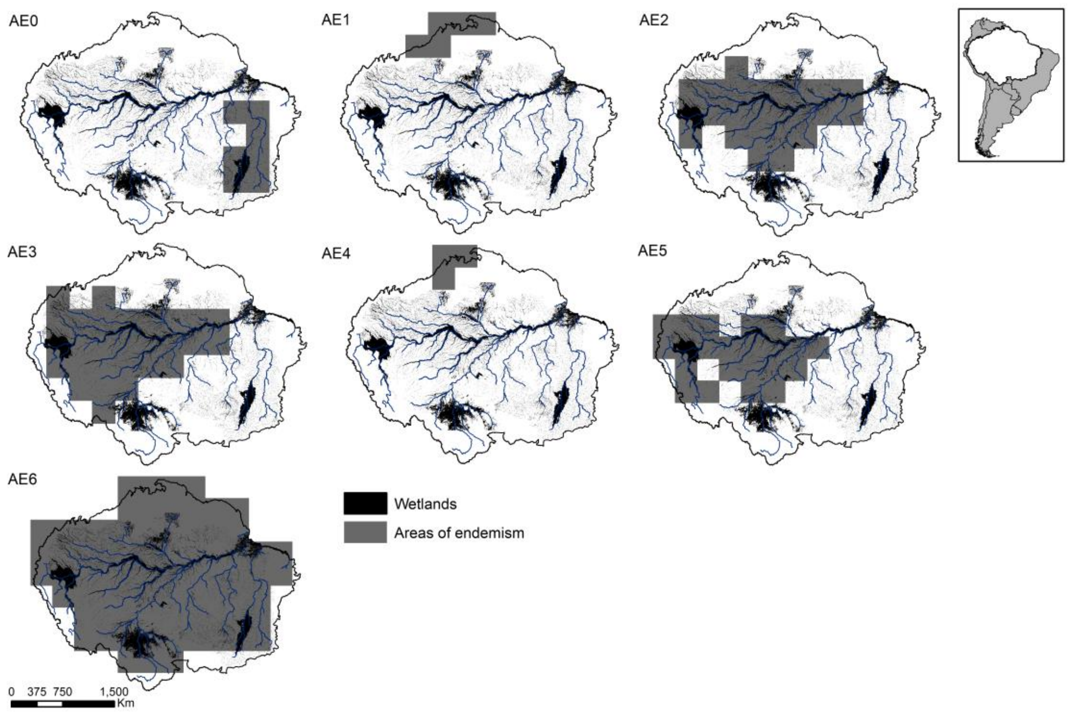

Figure 2. Areas of endemism for Amazonian birds associated with early sucessional habitats with cells of size 3.0º. The areas were identified using the method (NDM) based on species and subspecies datasets. Map of wetlands of Hess et al (2015). Map created in ArcGIS 10.6 (http://www.esri.com).

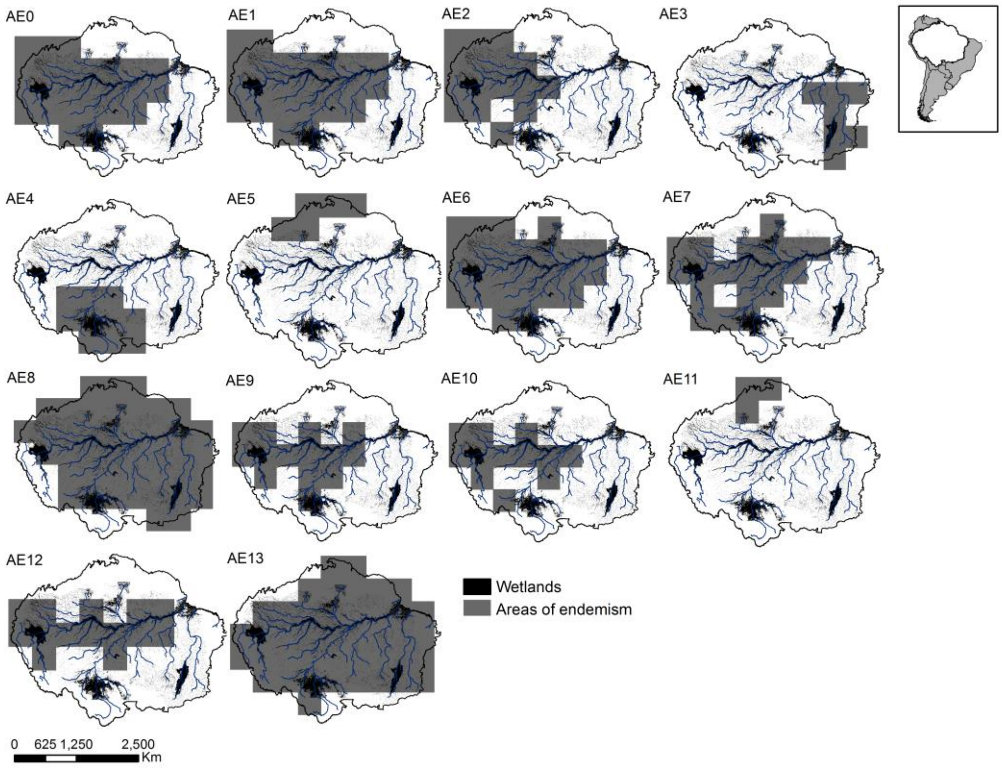

Figure 3. Areas of endemism of Amazonian birds associated with early sucessional habitats with cells of size 4.0º. The areas were identified using the method (NDM) based on species and subspecies datasets. Map of wetlands of Hess et al (2015). Map created in ArcGIS 10.6 (http://www.esri.com).

For the 2.0° grid three areas are recovered. AE0 is restricted to the Tocantins river basin and upper portions of the Xingu river basin, in southeastern Amazonia.AE1 and AE2 largely overlap in the western-central portion of the Amazon Basin,from the base of the Andes to the mouth of the Tapajós river, including the Amazon main course and its tributaries on the right bank, mainly the Madeira, middle Purus, lower Juruá and Ucayali (figure 1).None of the two areas includes the Negro river basin.Of the 70 taxa analyzed, 8 (11.42%) contribute to the identification of these areas of endemism (see supplementary material, 4).

For the 3.0° grid, seven areas were identified, ranging from widespread, as AE06 which includes the whole Amazon, Tocantins, Orinoco and Essequibo basins to quite restricted, as AEs 1 and 4, in the Orinoco basin. The other largeareas (AE2, AE3 and AE5) partially overlap in the Amazon basin, with AE5 more restricted, excluding the lower Rio Negro and reaching the mouth of the Tapajós as its Eastern limit. AE0 is restricted to the Tocantins river basin, as found in the previous analysis (figure 2). A total of 31 of the 70 taxa included in this study (44.28%) support one or more of these areas of endemism (see supplementary material, 4).

For the 4.0° grid there was great variation, with areas quite heterogeneous in their extensions. Widespread areas (AE8 and 13) are found, as well as areas corresponding to the main river basins: Tocantins (AE3), Orinoco (AE5 and 11) and Amazonas (AEs 0, 1, 2, 4, 6, 7, 9, 10, and 12), in agreement with previous analyses. Among Amazonian AEs some are restricted to parts of the basin, as AE2, restricted to the western portion of the basin, AE 4, restricted to the upper and medium Madeira river basin and AE 9, 10 and 12, that exclude the mid and lower Negro river basin (figure 3). Most Amazonian areas overlap in the central portion of the basin, including lower Solimões and Madeira rivers. A total of 48 taxa (68.57%) of 70 included in this study support one or more of these areas of endemism (see supplementary material, 4).

Infomap Bioregions

In the Infomap Bioregions analysis, 6 bioregions were identified (Figure 4).The most common species and indicators of each bioregion are presented in table 3.In common with the previous analyses, this analysis also shows evidence of distinct areas in the Orinoco basin (area **f**) and in the Tocantins basin (area **b**) with the latter extending to the west to include portions of the Tapajós and Xingú basins. In addition, area **e** corresponds to the lower Rio Negro basin, evidencing once again the unique characteristics of this basin. Areas, **a** and **b** are in agreement with the previous analyzes, highlighting the biogeographic contrast between west and southeast Amazonian floodplains.Of the 6 bioregions recovered, 3 have a pattern of disjunction, and 41% of the species included in the analyses are endemic at some spatial scale.

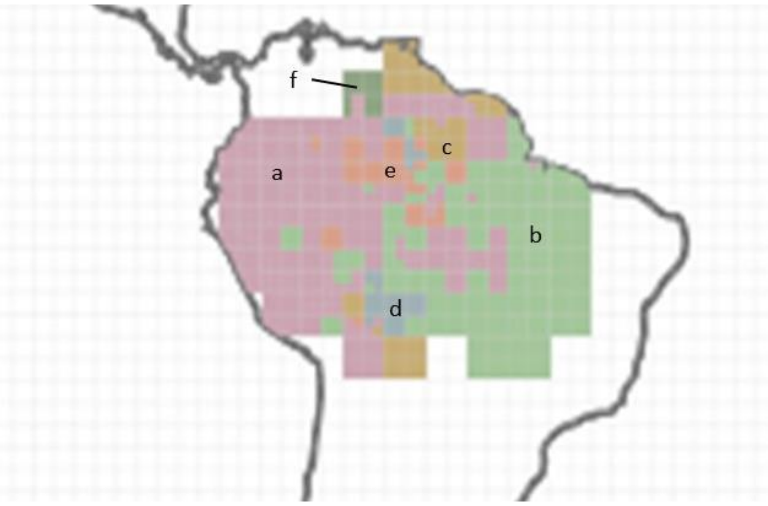

Figure 4. Bioregions of birds associated with early sucessional habitats generated with Infomap Bioregions, using records of occurrence, with their limits within the Amazonia sensu latíssimo. Map generated with web application Infomap Bioregions (http://bioregions.mapequation.org/).

Table 3. Bioregions of bird associated with early sucessional habitats.

Location	Records	Taxa	Cells	Most common species (records)	Most indicative species (score)
(a) Bioregion 1	15.767	56	152	*Atticora fasciata* (2.499)	*Agelasticus xanthophthalmus* (1.36)
(b) Bioregion 2	6.447	61	103	*Paroaria gularis* (550)	*Certhiaxis sp novum* (6.19)
(c) Bioregion 3	1.587	36	22	*Certhiaxis cinnamomeus* (281)	*Inezia caudata* (11.0)
(d) Bioregion 4	887	37	12	*Paroaria gularis* (162)	*Inezia subflava** (19.5)
(e) Bioregion 5	1.322	41	20	*Inezia subflava* (269)	*Inezia subflava* (6.26)
(f) Bioregion 6	144	26	4	*Gymnomystax mexicanus* (46)	*Paroaria nigrogenis* (148)

*Note: isolated population in the Guaporé river

Changes in taxa composition

The spatial variation in the composition of communities (beta diversity) associated with seasonally floodedenvironments is presented in figure 5.

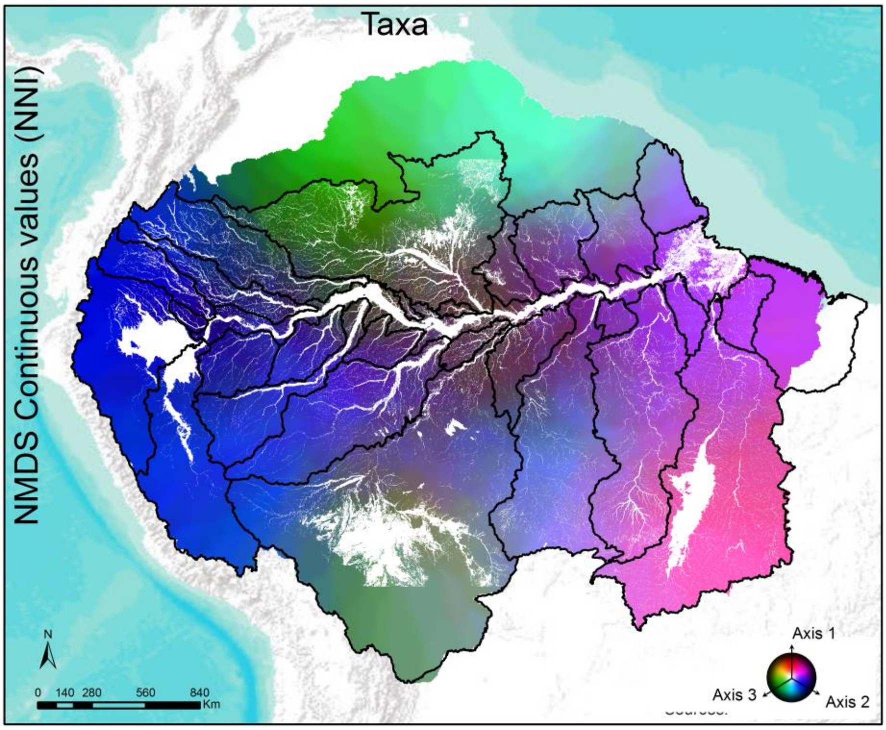

Figure 5. Spatial variation in the composition of bird taxa in Amazon floodplain environments. The composition of the taxa was obtained by interpolating the NMDS scores (three axes represented by an RGB scale). Map created in ArcGIS 10.6 (http://www.esri.com).

The NMDS analysis showed a high correlation between the observed distance and the order distance, (non-metric adjustment $R^2 = 0.96$, linear adjustment $R^2 = 0.78$), indicating that analyzes represented satisfactorily Bray-Curtis distance matrices. All axes of NMDS presented high and significant values of spatial autocorrelation (I Moran = 0.97), satisfying the premise of interpolation by Nearest Neighbor Interporlation.

The first axis of the ordinance indicates two distinct compositional divisions, the first of which is restricted to the southeast portion of the basin, evidencing the Tocantins Basin with a singular composition,as well as a transition zone along the Tapajós basin, with elements from the western Amazon and the Tocantins Basin and the other restricted to the central portion of the Amazon region, confirming previous analyzes of endemism (Figure 5).The most prominent division presented in the second axis in the analysis characterizes the western portion of the basin (Figure 5).Finally, the third axis coincides with the Orinoco River Basin in the northern portion of the Amazon River and the upper Madeira River region, reinforcing the previous analyzes (Figure 5).

DISCUSSION

Here we characterize the patterns of diversity and distribution of Amazonian birds specialized in habitats that are subject to extensive flooding during the flooding cycle that profoundly changes Amazonian landscapes every year. The habitats that remain long periods under the influence of the river water are most affected by the sediment load and sediment characteristics of the rivers. They are also the first habitats to be deposited or eroded when changes to sedimentation dynamics occur. Understanding the diversity patterns of the avifauna associated to these habitats is essential, thus, to any planning or categorization of threat sue to anthropogenic impacts in Amazonian hydrological systems, as the construction of large dams. The patterns of endemism and diversity found confirm that the avifauna associated with floodplains is not uniform throughout the basin. We further explore these identified patterns, and the implications for conservation.

Patterns of endemism and implications for conservation and planning

Based on a qualitative analysis of the occurrence birds along the floodplains of the Solimões and Amazonas rivers, Cohn-Haft et al. (2007) made the first proposal of regionalization of this avifauna. They suggested three zones of endemism. Zone 1 including the western portion of the Amazonas-Solimões floodplains, delimited to the east by the Negro and Madeira rivers. Zone 2 from the mouth of the Negro and Madeira rivers to the mouth of the Xingu River, and zone 3 between the mouth of the Xingu and the Atlantic Ocean. Here we corroborate the importance of central Amazonia, in the region of the Negro and Madeira river mouths, to the transition in species composition along the floodplains, but we do not find areas of endemism delimited by these rivers. The endemism analysis employed here identified between 3 and 14 areas of endemismand given the difference between the total area studied, taxa sampled and the analytical approachesin the two studies, it is interesting to note that the patterns prevailing in the present study also highlight the biogeographic importance of the Negro, Madeira and Xingu/Tocantins rivers for the regionalization of the avifauna associated to flooded habitats.

All of the different grid sizes employed identified an area of endemism partially corresponding to the Tocantins Basin (AE0, Fig.1; AE0, Fig. 2, AE3, Fig. 3), generally including the middle and upper reaches of the river and in some cases also including the middle and upper Xingu. This area is supported by common taxa such as *Paroaria baeri*, *Sicalis columbiana leopoldinae*and *Serpophaga hypoleuca pallida*. These results show that the history of isolation between the Tocantins and Amazonas river basinsreflected in othergroups (Hrbek et al., 2014) is also important for structuring avian distributions. Interestingly the results also agree with the biogeographic affinity between the biota associated with the aquatic environments of the Tocantins and Xingu basins (Dagosta & Pinna, 2017), suggesting past connections between them along the headwaters, independent of the main trunk rivers.The unique nature of the Tocantins basin indicates that it harbors endemic taxa that are not represented in the larger neighboring Amazon basin. This is an important information that should be taken into account when planning for the construction of new dams, besides the existing ones(Lees et al., 2016), and for the plans for developing the Araguaia-Tocantins waterway, for transportation of agricultural production from central Brazil (Castello et al., 2013). Any impact to populations of species restricted to the Tocantins-Araguaia basin should thus be evaluated in light of the total availability of habitat within this basin, and the connectivity between remnants of available habitat should be preserved, considering the vulnerability of these early successional habitats to the retention of sediments caused by dams(Rivera et al., 2019).

Another unique area recovered in all analyzes corresponds to the Orinoco basin (AE1 and AE4, Fig. 2, AE5 and AE11, Fig. 3, Bioregion F, Fig.4) and is supported by taxa such as *Knipolegus orenocensis orenocensis*, *Serpophaga hypoleuca venezuelana e Sicalis columbiana columbiana*. This is another evidence that the independent evolution of these adjacent basins has led to distinct species being associated to flooded habitats along the main rivers. The Orinoco basin is especially restricted and should be considered as an independent biogeographic unit even if some avian taxa are regarded as subspecies of Amazonian species.

Within the Amazon river basin, the areas recoveredin the analyzes reveal two main patterns.One of them (eg AE1 and AE2, Fig. 1) includes the main channel of the Amazonas / Solimões, from the western lowlands at the base of the Andesto the mouth of the Tapajós river, extending to the south along the Madeira river basin and some other southern tributaries, as the Purus and Juruá, and to the north: the middle and low Trombetas. Despite somevariations, these areas have in common the fact that they do not include the Negro River basin, and do not extend to the southeastern portionof the Amazon Basin. This endemic avifauna is characteristic of West-Central Amazonia and although it occurs mostly in white water rivers such as Madeira and Purus, it also occur in a few clear water rivers, as the Trombetas or Tapajós.

The other Amazonian pattern (eg AE6, Fig. 3) is more widespread, extending from the western end of the Amazon Basin (Beni savannah region, Bolivia) to the mouth of the Xingu.A superimposed pattern within this is restricted to Central Amazonia (centered on the middle and lower courses of the Madeira and Purus rivers, AE10, Fig.3).These patterns are also observed in the other scales of analysis, including (AE5, Fig. 2; Bioregion E, Fig. 4) in the west-central portion of the basin.It is interesting to note that in relation to the composition of fish species, the Rio Iriri, although a tributary of the Xingu, is associated with the Tapajós subbasins (Dagosta & Pinna, 2017), suggesting rearrangements between these basins in the past and fauna exchanges between the adjacent aquatic environments.

In addition to the three general patterns described above, in the grids of 3 and 4 degrees several large areas were recovered, covering a large part of the Amazon.The analysis with cells of 4º also evidenced a restricted and unique pattern. This pattern evidences the biogeographic role of the Madeira River, with an identified area (AE4, Fig. 3) restricted mainly to its basin, also represented by Bioregion D (Fig. 4), and supported by taxa such as *Inezia inornata*, *Paroaria cervicalis* and *Inezia subflava*, an isolated population in the Guaporé river. The identification of taxa endemic to the Madeira basin is very important to monitor the effects of the Madeira Hydroelectric Complex (MHC), comprised of two recently built dams (Santo Antônio and Jirau), and to plan for additional hydroelectric exploitation of this basin, as well as for assessing the impacts of the possible development of a waterway for transportation of agricultural production. The first analyses of the changes in fine suspended sediment concentration downstream of the MHC have shown a 20% decrease in the Porto Velho gauging station (Latrubesse et al., 2017, Rivera et al., 2019). This reduction may cause, in addition to the impacts to habitats subjected to flooding (upstream of the dams) long term impacts on the dynamics of deposition and erosion along the riverbanks, especially affecting the early successional habitats that the avifauna studied here occupies.

This approach of different spatial scales revealed a complex relationship of overlap, nesting, and disjunction between areas of endemism in floodplain environments.For example, of the 6 bioregions recovered, 3 of them presented the pattern of disjunction (see Fig. 4).These phenomena are imperceptible to other methods of analysis (eg Stockwell & Peter, 1999; Hausdorf & Henning, 2003; Kreft & Jetz, 2010;Bertelli et al., 2017), but these intricate patterns of endemism can be recovered if they are manifested in the data probably reflecting the action of complex biogeographic events.Such a pattern is generally ignored except in situations such as mountain tops and islands (Vuilleumier, 1978), and the prevalence of this pattern shows the complexity of the current landscape and its recent history.The Amazon Basin provided an impressive example of disarticulated areas. The northern and southern portions of the Basin also represent a disjoint bioregion (d see Fig. 4) supported by the presence of taxa as*Paroaria cervicalis*,*Stigmatura napensis napensis*,*Inezia inornata*, *Cranioleuca vulpina*, *Thamnophilus doliatus*. In addition, it showed clear differences between the western and southeastern portions of the Amazon, probably related to the geological characteristics of these regions.

It is well known that grid size directly affects the results of the analyzes performed using NDM / VNDM, (Szumik et al., 2002, Szumik, Aagesen, Casagranda, Arzamendia, & Baldo, 2012;Aagesen, Szumik, Zuloaga, & Morrone,2009).According to Szumik et al. (2002) very small grid cells will recognize small and discontinuous areas of endemism.In contrast, large cells will probably recognize large areas, with many endemic species in each area. In addition, the effect of grid size is directly correlated with the number and dispersion of localities present in the original database (see Szumik et al., 2012).

The results of the present study agree with other studies (Prado et al., 2014; Li, Chen, Jiang, & Qiao, 2017; Bertelli et al.,2017) in which several areas of endemism were identified exclusively in one of the cell sizes, and others consistently recovered in the other cell sizes adopted.According to Li et al. (2017) it is still very difficult to understand all the mechanisms by which the occurrence data of real species determine the patterns of endemism, because the patterns of true species distributions depend on many variables. However, multi-scale approach seems to be the easiest way to control and discuss these effects.

Spatial patterns of diversity and the heterogeneity of the avifauna associated to Amazonian floodplains

The spatial structure of the composition of biological communities (beta diversity) can be explained by several factors, including habitat heterogeneity, connectivity between populations, and geographic distance (see Tuomisto, 2006;Mori,,Isbell, & Seidl, 2018;Piatti et al., 2019).Global patterns of bird diversity specializedin riverine landscapes are structured by the high diversity of channel forms, habitats, as well as the high temperature and primary productivity in these systems (Buckton & Ormerod, 2002). In the Neotropical region, the high diversity of habitats and types of microhabitats, some of which unique to this region, is a major factor contributing to high bird species richness (Rosemberg, 1990).

In the Amazonian fluvial plains, flood pulse is considered the most important factor in the creation and maintenance of high beta diversity of plant and animal species (Remsem & Parker, 1983; Salo et al., 1986; Junk et al., 1989; Petermann, 1997;Costa et al., 2018).This natural disturbance shapes a high diversity of physical habitat structures that may be heterogeneous along the main channel, thus creating the basis for a diversified flora and fauna(Kell & Prance, 1979; Irion, Junk, & de Mello,1997;Junk, & Wantzen, 2004). For example, beta diversity of trees is related to river dynamics, as well as habitat heterogeneity (Salo et al., 1986; Junk, 2004; De Assis, Wittmann, Luize, & Haugaasen,2017). For bats the seasonal variation in water level mediated by the flood pulse seems to be the predominant factor in community structuring (Bobrowiec, Rosa, Gazarini, &Haugaasen, 2014). In birds differences in vegetation composition and structure explain patterns of discrepant richness between floodplain and igapó forests, as well as the existence of specific microhabitats (Remsem&Parker, 1983; Petermann, 1997; Borges & Carvalhaes, 2000).

The composition of bird species on floodplains is generally distinct from the composition found in adjacent mainland forests (Remsem & Parker, 1983). In floodplains, the general pattern of bird species richness most strongly highlights the west-east axis, given the greater extent of floodplain areas in this portion of the Amazon, and consequently greater habitat availability for birds (Cohn-Haft et al., 2007). In addition, the composition of the bird community also changes drastically along the successional Amazonian gradients, with many species confined to the initial and final stages of succession (Remsem & Parker, 1983; Rosemberg, 1990; Robinson & Terborgh, 1997). Thus, the diversity of hydrological patterns is a key element in maintaining the diversity of habitats and species in alluvial plains systems, as well as the characteristics of the shape of the flood pulse are crucial for the establishment and survival of many aquatic organisms (Junk, 2004).

Our results indicate that the greatest differences in community composition occur between the southeast, central and western Amazon(Fig. 5). The spatial variation of the composition of the taxa coincides with some identified AEs, especially those corresponding to the region of the Tocantins Basin (fig. 5).The observed patterns of composition have a strong relationship with the hydrochemistry of the rivers, which is reflected in the different colors of their waters(Junk, 2004; Junk et al. 2011; Laranjeiras et al., 2019).Junk (2004) suggests that the mobile boundary between the waters of the main river and its tributaries may become a barrier, despite the hydrological connection, depending on its hydrochemistry, structuring the patterns of community composition in the system continuum, which is reflected in the pattern of occurrence of the species.For example, the accentuated growth of aquatic macrophytes and bivalve molluscs concentrates in white waters, influenced by higher availability of nutrients and higher values of PH (Junk, 2004).

In this context, the sub-basins of western Amazonia, closer to the Andes and that receive a high sedimentary load, present a very characteristic and differentiated species composition.The composition of the communities in the Negro and Madeira sub-basins is heterogeneous, with distinct influences in the northern and southern portions. The species composition of the northern portion of the Negro subbasin is similar to the Orinoco, indicating, that despite the presence of endemic species exclusive of the Orinoco, there are several shared taxa. This may indicate a connection in the recent past, and divergence of the avifauna since its interruption. Interestingly, the communities around the middle and lower Negro river have some similarity to lower Madeira and lower Solimões communities, suggesting a possible predominance of water with higher sediment load in the past (Dagosta & Pinna, 2017). The community composition in the middle of the Madeira sub-basin in partially similar to western Amazonian composition, but the southern portion is probably influenced by the Beni grasslands and the transition to the Cerrado, and thus distinct.

In eastern Amazonia the similaritytowestern communities seems to be larger close to the Amazonas main channel, alongthe lower portionsof the rivers, that flow on the plateaus.This causes a large composition variation between the low and high stretches of rivers such as the Tapajós and Xingu. It is interesting to note the evident heterogeneity in the composition of the upper and middle Tapajós communities, which are related to the west with the communities of the Madeira basin and to the east with the communities of the Xingu basin.This result reinforces the idea of a very dynamic history of the main channels of these largeAmazonian rivers, especially the Tapajós, with drainage capturesshaping the configuration and boundaries between the basins in the recent past(Irion et al. 2006, Rossetti & Valeriano 2007, Rossetti, Valeriano, & Thalles, 2007; Dagosta & Pinna, 2017).

The results obtained here, therefore, reinforce the idea that the Amazonian sub-basins, especially those of the Brazilian shield are not distinct and independent biogeographic units, but they have recent configurations and a heterogeneous biota.Faunal similarities between adjacent basins have been reported in several recent studies, for example, between Tapajós-Xingu (Menezes, Netto-Ferreira, & Ferreira,2009), Xingu-Tocantins (Ingenito, Lima, &Buckup, 2013) and Tocantins-Paraguaia (Carvalho & Albert, 2011). Thus, our findings corroboratethe findings of Dagosta & Pinna (2017) that suggest that the Amazonian basins should not be considered a priori as distinct biogeographic units.

Implications for conservation

In order to maximize the conservation of biodiversity in the Amazon, a better understanding of the distribution of its biota and of the threatened taxa is essential (Bird et al., 2011). This better knowledge of distribution is considered a key factor for re-evaluation of the list of endangered species. In this context, the patterns of endemism and diversity are considered as guiding conservation actions(Condict et al., 2002; Stattesfield et al. 1998; Olso et al. 2001; Antonelli et al., 2018).The bird species richness in the Amazonia is dependent on a significant portion of the habitats created by the rivers, which house about 15% (192) of the non-aquatic birds endemic to the Amazon(Remsen & Parker, 1983).

Some of the identified AEs are congruent with areas of relevant conservation interest.For example, AEs at the Tocantins Basin correspond to the ecoregion - Xingu-Tocantins-Araguaia moist forest (NT0180) (Olson et al., 2001), AE4 (fig. 3) corresponds to the Madeira-Tapajós moist forest (NT0135) ecoregion of Olson et al. (2001), including mainly in its extension the Madeira River Basin, and AE2 (see Fig. 3) corresponds to the Northwest Amazon moist forest ecoregion (NT0166), restricted to the southwest portion of the basin (Olson et al., 2001).Some of these ecoregions may loose 50% of their forest cover by 2020 (Vale et al., 2008) due to infrastructure projects. This is extremely worrying given the high number of species with restricted distribution and specialized in specific microhabitats, mainly in fluvial islands (Remsem &Parker, 1983; Vale et al., 2008).

All previously recognized EBAs in the Amazon Basin are already considered priorities for conservation, classified with high and urgent grades (Stattersfield et al., 1998). Although only one species included in the analyzes, *Leucippus chlorocercus* is recognized as being of restricted distribution (Restricted-range species) according to Stattersfield et al. (1998) some of the identified AEs overlap with the recognized EBAs for the region. For example, AE2 and AE9 (Fig. 2 and 3, respectively) overlap with EBA067 (Amazon flooded forests) and AE2 (Fig. 3) with EBA068 (South-east Peruvian lowlands).

Currently, the most significant and comprehensive human impact in relation to the Amazon floodplain systems is the construction of dams for hydropower generation.The Amazon basin has a great hydroelectric potential (Borges & Carvalhaes, 2000; Lees et al., 2016; Latrubesse et al., 2017), with 191 dams built and 246 planned or under construction (Lees et al., 2016).Direct and indirect impacts of these ventures on Amazon floodplain systems, as well as their associated biodiversity, are already well documented in the scientific literature (Vale et al., 2008; Bird et al., 2011; Castello et al., 2013; Lees et al., 2016; Latrubesse et al., 2017, Forsberg et al., 2017). For example, changes in the hydrological regime (Junk, Bayley, & Sparks, 1989) affect the floristic composition of floodplain forests, the longitudinal migration of commercial fish (Lees et al., 2016), and the maintenance of specific microhabitats (eg beaches, sandbanks, successional plant formations on river islands and rocky outcrops on the Brazilian shield) (Remsem & Parker, 1983; Lees et al., 2016). The latter is especially important, since it is a crucial habitat for many species of vertebrates (eg catfish, Bats and Birds – *Atticora melanoleuca*). As well as communities of microendemic plants and birds withrestricted distributions(eg *Thamnophilus nigrocinereus* and *Picummus varzeae*) associated with várzea and igapó forest, and specifically of river islands, which will be permanently submerged upstream of the dams, and may have their processes of deposition and erosion disrupted downstream of the dams (Vale et al., 2008; Ferreira, Cunha, Chaves, Matos, & Parolin, 2013; Bird et al., 2011;Fróes&Souza, 2015).

In our analyzes, 28% of the taxa specialized in early sucessional habitats of the Amazonian floodplains are endemic at some spatial scale, which indicates that the regionalization of diversity restricted to wetland areas affects a significant part of biodiversity and should be considered in hydroelectric development planning (Latrubesse et al., 2017). The clear distinction of the communities and the areas of endemism identified for the Tocantins Basin suggest that the floodplain environments in this basin should be treated as unique in the planning of the use of this region, which already has large dams installed(Lees et al., 2016).

The results presented here reinforce the importance of connectivity and water characteristics in determining the occurrence of bird species associated with environments of primary succession in the Amazon.The main patterns revealed by both AEs and species diversity patterns indicate that the Tocantins basin and the black waters of the Rio Negro reflect important environmental filters that determine which species may occupy these regions from the white water regions that concentrate endemism and richness.The presence of the lower Solimões/lower Madeiraregion in many of the recovered Amazon Basin AEs indicates that this is a region of extreme importance for the maintenance of diversity and connectivity for the biota associated to floodplains, however, this region is also extremely dependent on sediments brought by the Solimões and Madeira, and changes in the sedimentary load may endanger the environments available forthe biota (Latrubesse et al., 2017; Forsberg et al., 2017).The separation of nutrient connectivity, that is, the influx of sediments to the main trunk of the Amazon given the dams planned for the Andean basins, will have acute effects downstream of these dams, whose rivers account for the great majority of the sediments carried to the Amazonian fluvial plains (Fine & Jenkins, 2012, Lees et al., 2016; Latrubesse et al., 2017; Forsberg et al., 2017). The Andean basins provide more than 90% of the Amazon basin sedimentary load, from which the wetlands habitats are built and maintained (Lees et al., 2016).

Thus, the results presented here underscore the spatial heterogeneity of the habitats created by river in Amazonia and the biota they sustain, reinforcing that an integrated analysis of the basin, and not just the local effects of each dam, is necessary for the planning of the expansion of the hydroelectricgeneration network (Latrubesse et al., 2017). The results found here for the avifauna suggest special attention to(1) the Tocantins basin as a unique region; (2) the impacts of the reduction of the sediment load in the lower Madeira and Solimões basin for the maintenance of diversity and connectivity across the basin; (3)the heterogeneity of the Tapajós basin and therefore the local idiosyncrasies along this basin; and (4)the distinct nature of the lower Negro river basin, which may reflect its dependence on sediments brought by the Branco River, the main white water tributary in the current configuration of this basin.

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SUPORTING INFORMATION INDEX

Informações adicionais podem ser encontradas na versão online desse artigo:

Apêndice S1 Informações gerais sobre a lista das fontes de dados dos registros geográficos, lista dos táxons utilizados no estudo e quantidade de registros, mapa com a distribuição dos pontos de ocorrência de todos os táxons, consenso das áreas de endemismo identificadas com NDM e biorregiões identifcadas com Infomap Biorregions.

BIOSKETCH

Jadson Viana da Silva is interested in ecology, natural history and biogeography of Amazonian birds. This work represents a component of his master's dissertation by the Federal University of Amazonas / National Institute of Amazonian Research, in Manaus, Amazonas.

Camila Cherem Ribas is a researcher at the National Institute of Amazonian Research (INPA) and curator of the Collection of Animal Genetic Resources. His interests are focused on the study of patterns and processes of diversification in the Neotropical region with an emphasis on the biogeographic history of the Amazon region.

Mario Cohn-Haftis a Senior Researcher and Curator of the Ornithological Collection of the National Institute of Amazonian Research (INPA). He is an ornithologist specialized in Amazon birds, with emphasis on biogeography.

Thiago Orsi Laranjeirashave experience in biogeography, ecology and bird conservation in the Amazon. Their current interests are to understand how the birds associated with the Amazonian riverside environments are distributed and protected.

Matheus Oliveira Nevesis a PhD student in the Postgraduate Program in Ecology and Conservation of the Federal University of Mato Grosso do Sul (UFMGS) and his current interests include Biogeography, Taxonomy and Conservation of Amphibians.

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Authorcontributions: J.V. conducted the research and the writing as part of requirements to achieved his Master degree; C.R and M.C. designed the study, contributed in the discussion and writing of the manuscript; T.L.contributed to preparation of the database, discussion and writing of the manuscript; M.N. contributed data analyzes and interpretation, and manuscript revision; C.F. helped in the preparation of the figures of the areas of endemism and diversity and revision of the manuscript.

SUPPORTING INFORMATION

Journal of Biogeography

MATERIAL SUPLEMENTAR

Biogeographic regionalization of the avifauna associated to Amazonian seasonally flooded habitats: building a baseline for environmental impact assessment.

Jadson Viana da Silva, Thiago Orsi Laranjeiras, Mario Cohn-Haft, Matheus OliveiraNeves, Camila G Fagundes, Camila Cherem Ribas

Appendix S1

Lista S1. Fonte de dados dos registros geográficos dos taxa

Coleções Científicas:
LSU Museum of Natural Science (LSUMNS)
Moore Laboratory of Zoology (MLZ)
Royal Ontario Museum (ROM)
University of Michigan Museum of Zoology (UMMZ)
Museum of Vertebrate Zoology at Berkeley (MVZ)
Natural History Museum of Los Angeles County (LACM)
Yale Peabody Museum of Natural History (YPMNH)
Muséum national d'Histoire naturelle (MNHN)
American Museum of Natural History (AMNH)
University of Kansas Biodiversity Institute (KUBI)
Museu de Biologia Prof. Mello Leitão (MBML)
Royal Belgian Institute of Natural Sciences (RBINS)
Instituto Nacional de Pesquisas da Amazônia (INPA)
Santa Barbara Museum of Natural History

Bases de dados online:
https://www.macaulaylibrary.org/
https://www.wikiaves.com.br/
https://www.xeno-canto.org/

https://ebird.org/home

Literatura

Ingels et al. 2012

Dados de Campo

Dados do doutorado de Thiago Orsi Laranjeiras

Table S1. Lista dostaxons (e*spécies e subespécies*) de aves utilizados no presente estudo e a quantidade de registros de distribuiçãogeorreferenciados para cada taxon.

Taxon	**Quantidade de registros**
Agelasticus xanthophthalmus Short, 1969	130
Agelasticus cyanopus xenicus (Parkes, 1966)	12
Ammodramus aurifrons (Spix, 1825)	496
Anthracothorax viridigula (Boddaert, 1783)	157
Arremonops conirostris (Bonaparte, 1850)	3
Arremonops conirostris pastazae (Krabbe & Stejskal, 2008)	5
*Arremonops conirostris*** (Bonaparte, 1850)	16
Arundinicola leucocephala (Linnaeus, 1764)	270
Atticora fasciata (Gmelin, 1789)	3007
Certhiaxis cinnamomeus (Gmelin, 1788)	738
Certhiaxis mustelinus (Sclater, 1874)	308
Certhiaxis sp novum Taxon não descrito	17
Chordeiles rupestris (Spix, 1825)	873
Chrysomus icterocephalus (Linnaeus, 1766)	538
Cnemotriccus fuscatus (Wied, 1831)	124
Cnemotriccus fuscatus fuscatior (Chapman, 1926)	13

Conirostrum bicolor minus (Hellmayr, 1935)	208
Conirostrum margaritae (Holt, 1931)	162
Conirostrum speciosum amazonum (Hellmayr, 1917)	440
Cranioleuca vulpecula (Sclater & Salvin, 1866)	257
Cranioleuca vulpina (Pelzeln, 1856)	572
Donacobius atricapilla (Linnaeus, 1766)	316
Elaenia pelzelni Berlepsch, 1907	111
Fluvicola albiventer (Spix, 1825)	120
Fluvicola pica (Boddaert, 1783)	366
Furnarius figulus pileatus Sclater & Salvin, 1878	221
Furnarius minor Pelzeln, 1858	461
Geothlypis aequinoctialis (Gmelin, 1789)	122
Gymnomystax mexicanus (Linnaeus, 1766)	1292
Hydropsalis climacocerca (Tschudi, 1844)	1066
Inezia caudata (Salvin, 1897)	244
Inezia inornata (Salvadori, 1897)	174
Inezia subflava (Sclater & Salvin, 1873)	544
*Inezia subflava**** (Sclater & Salvin, 1873)	27
Knipolegus orenocensis orenocensis Berlepsch, 1864	7
Knipolegus orenocensis sclateri Hellmayr, 1906	139

Knipolegus orenocensis xinguensis Berlepsch, 1912	39
Leucippus chlorocercus Gould, 1866	270
Mazaria propinqua (Pelzeln, 1859)	324
Muscisaxicola fluviatilis Sclater & Salvin, 1866	329
Myrmochanes hemileucus (Sclater & Salvin, 1866)	263
Nyctiprogne leucopyga (Spix, 1825)	577
Ochthornis littoralis (Pelzeln, 1868)	1793
Paroaria baeri Hellmayr, 1907	77
Paroaria cervicalis Sclater, 1862	73
Paroaria gularis (Linnaeus, 1766)	3407
Paroaria gularis gularis (Linnaeus, 1766)	59
Paroaria nigrogenis Lafresnaye, 1846	1
Paroaria xinguensis Sick, 1950	4
Phaeomyias murina (Spix, 1825)	256
Philohydor lictor (Lichtenstein, 1823)	305
Pygochelidon melanoleuca (Wied, 1820)	369
Saltator coerulescens Vieillot, 1817	301
Serpophaga hypoleuca hypoleuca Sclater & Salvin, 1866	251
Serpophaga hypoleuca pallida Snethlage, 1907	12
Serpophaga hypoleuca venezuelana J. T. Zimmer, 1940	5

	Sicalis columbiana columbiana Cabanis, 1851	42
	Sicalis columbiana goeldii Berlepsch, 1906	508
	Sicalis columbiana leopoldinae Hellmayr, 1906	66
	Sporophila americana (Gmelin, 1789)	484
	Sporophila castaneiventris Cabanis, 1849	614
	Sporophila murallae Chapman, 1915	34
	Stigmatura napensis napensis Chapman, 1926	226
	Sublegatus obscurior Todd, 1920	211
	Synallaxis albigularis Sclater, 1858	911
	Synallaxis beverlyae Hilty and Ascanio, 2009	1
	Thamnophilus doliatus (Linnaeus, 1764)	641
	Thlypopsis sordida chrysopis (Sclater & Salvin, 1880)	410
	Thlypopsis sordida orinocensis (Friedmann, 1942)	1
	Turdus ignobilis debilis Hellmayr, 1902	95
Total	**70**	**26515**

Nomeclatura taxonomica de acordo com Piacentini et al. 2015 (CBRO)

*Note: isolated population in the Branco river
**Note: isolated population in the Guaporé river

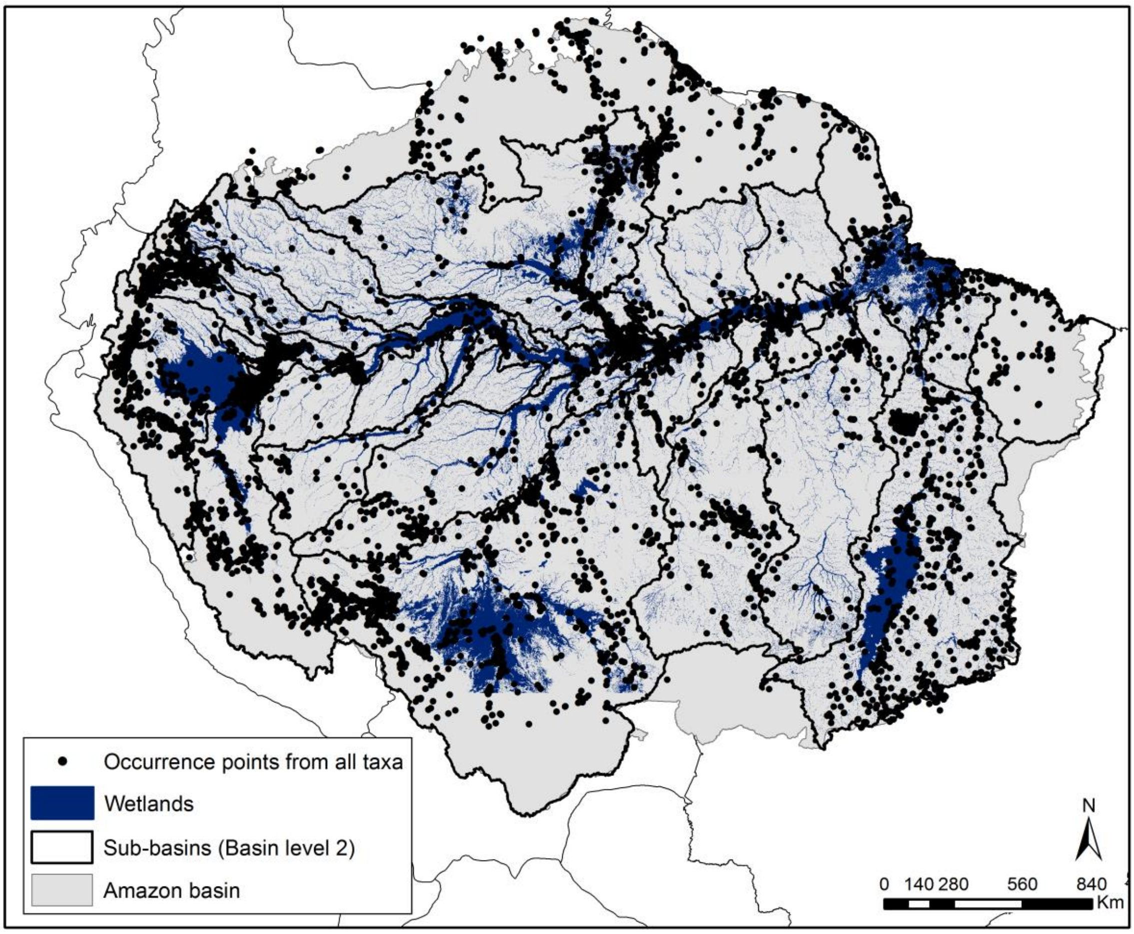
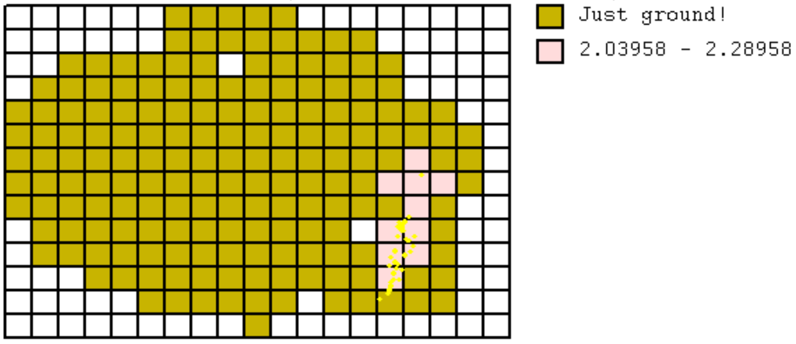


Figure S1. Todos os pontos de ocorrência dos taxa analisados no presente estudo.

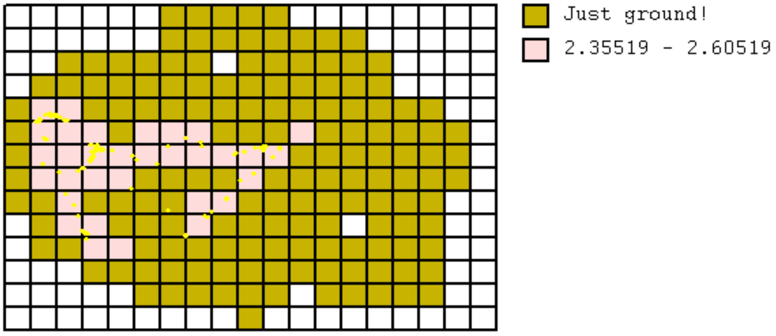
Figure S2.áreas de endemismo identificadas com NDM com base nos registros de ocorrência dos taxa - **Tamanho de célula – 2.0**

```
Consensus area 0 of 3 (from 1 areas; max. values)
```



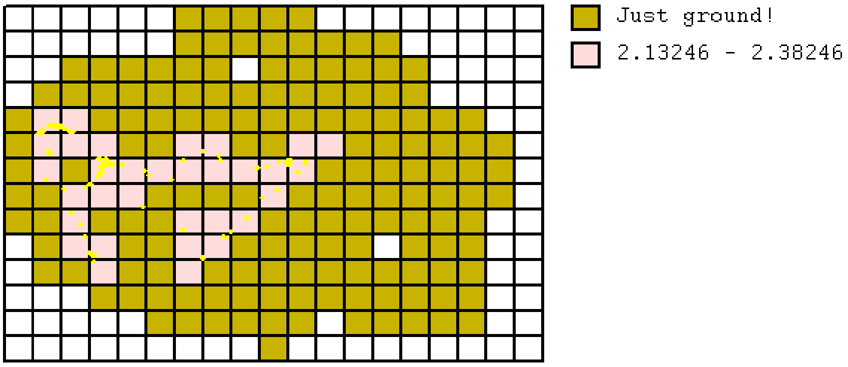
```
Showing 43; 3 species give score:
     43           Paroaria baeri(0.708)          54 Serpophaga hypoleuca pallida(0.800)
     58 Sicalis columbiana leopoldinae(0.531)
```

```
Consensus area 1 of 3 (from 1 areas; max. values)
```



```
Showing 19; 3 species give score:
     19   Cranioleuca vulpecula(0.806)          35 Knipolegus orenocensis sclateri(0.706)
     37  Leucippus chlorocercus(0.844)
```

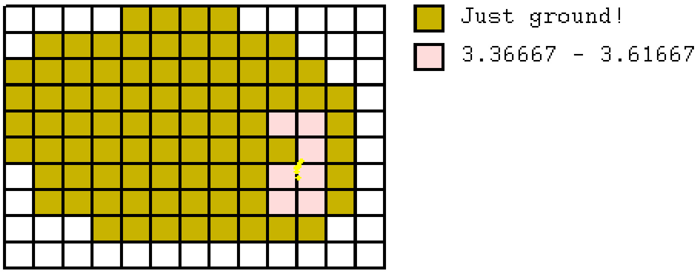
```
Consensus area 2 of 3 (from 1 areas; max. values)
```



```
Showing 19; 3 species give score:
     19   Cranioleuca vulpecula(0.938)          40  Myrmochanes hemileucus(0.824)
     69 Turdus ignobilis debilis(0.371)
```

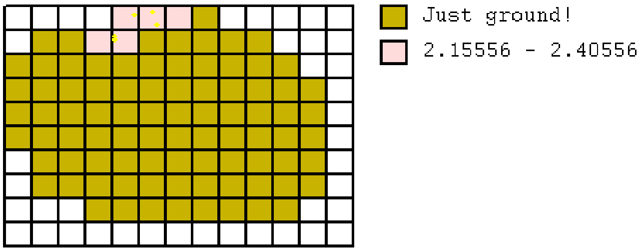
Figure S3.áreas de endemismo identificadas com NDM com base nos registros de ocorrência dos taxa - **Tamanho de célula – 3.0**

```
Consensus area 0 of 7 (from 1 areas; max. values)
```



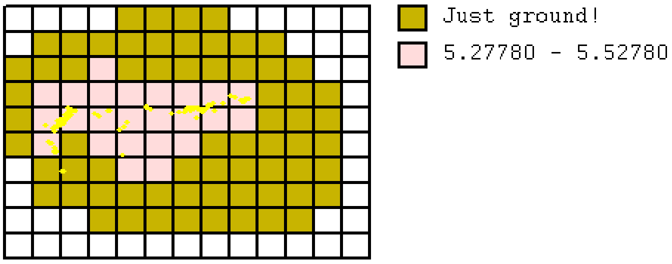
```
Showing 11; 5 species give score:
      11     Certhiaxis sp novum(0.714)          36 Knipolegus orenocensis xinguensis(0.778)
      43           Paroaria baeri(0.722)         54 Serpophaga hypoleuca pallida(0.786)
      58 Sicalis columbiana leopoldinae(0.367)
```

```
Consensus area 1 of 7 (from 1 areas; max. values)
```



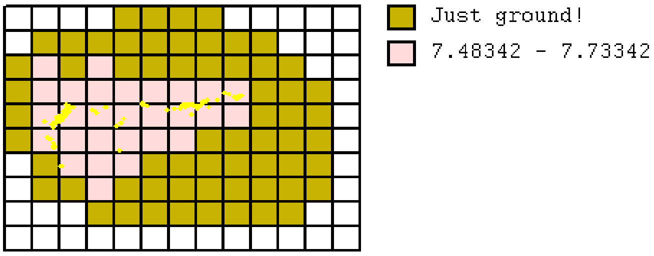
```
Showing 34; 3 species give score:
     34 Knipolegus orenocensis orenocensis(0.800)         55 Serpophaga hypoleuca venezuelana(0.800)
     56 Sicalis columbiana columbiana(0.556)
```

```
Consensus area 2 of 7 (from 1 areas; max. values)
```



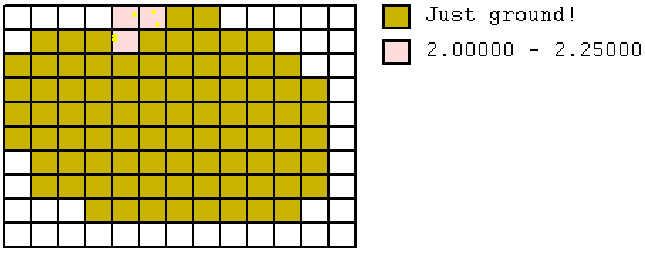
```
Showing 10; 8 species give score:
      10   Certhiaxis mustelinus(0.712)           17  Conirostrum margaritae(0.750)
      19   Cranioleuca vulpecula(0.656)           22        Elaenia pelzelni(0.771)
      26          Furnarius minor(0.609)          35 Knipolegus orenocensis sclateri(0.643)
      40  Myrmochanes hemileucus(0.559)           62 Stigmatura napensis napensis(0.578)
```

Consensus area 3 of 7 (from 1 areas; max. values)



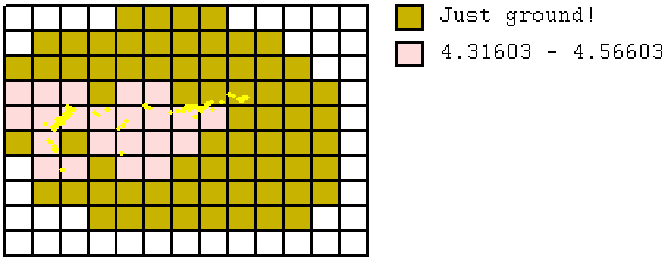
```
Showing 10; 12 species give score:
     10   Certhiaxis mustelinus(0.750)          19   Cranioleuca vulpecula(0.639)
     22        Elaenia pelzelni(0.732)          26         Furnarius minor(0.647)
     35 Knipolegus orenocensis sclateri(0.683)          37  Leucippus chlorocercus(0.603)
     40  Myrmochanes hemileucus(0.553)          53 Serpophaga hypoleuca hypoleuca(0.548)
     62 Stigmatura napensis napensis(0.618)          64  Synallaxis albigularis(0.560)
     67 Thlypopsis sordida chrysopis(0.592)          69 Turdus ignobilis debilis(0.560)
```

Consensus area 4 of 7 (from 1 areas; max. values)

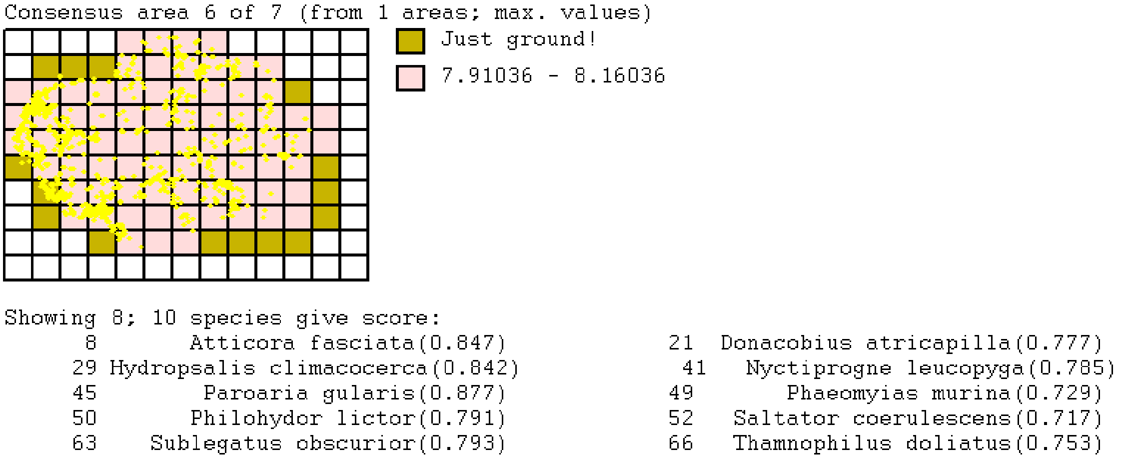


```
Showing 34; 2 species give score:
     34 Knipolegus orenocensis orenocensis(1.000)          55 Serpophaga hypoleuca venezuelana(1.000)
```

Consensus area 5 of 7 (from 1 areas; max. values)

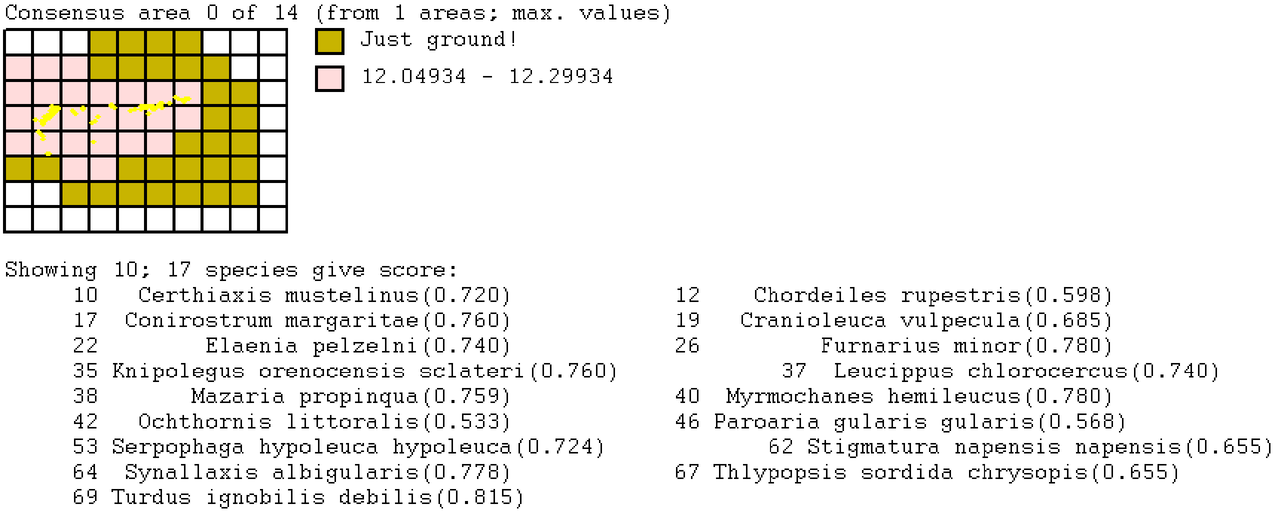


```
Showing 10; 6 species give score:
     10   Certhiaxis mustelinus(0.654)          19   Cranioleuca vulpecula(1.000)
     35 Knipolegus orenocensis sclateri(0.654)          37  Leucippus chlorocercus(0.771)
     40  Myrmochanes hemileucus(0.750)          69 Turdus ignobilis debilis(0.487)
```



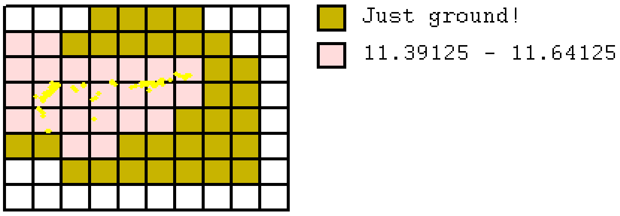
```
Consensus area 6 of 7 (from 1 areas; max. values)
                                🟨 Just ground!
                                ▨ 7.91036 - 8.16036

Showing 8; 10 species give score:
      8       Atticora fasciata(0.847)          21  Donacobius atricapilla(0.777)
     29 Hydropsalis climacocerca(0.842)          41   Nyctiprogne leucopyga(0.785)
     45         Paroaria gularis(0.877)         49        Phaeomyias murina(0.729)
     50       Philohydor lictor(0.791)          52   Saltator coerulescens(0.717)
     63    Sublegatus obscurior(0.793)          66   Thamnophilus doliatus(0.753)
```

Figure S4.áreas de endemismo identificadas com NDM com base nos registros de ocorrência dos taxa - **Tamanho de célula – 4.0**



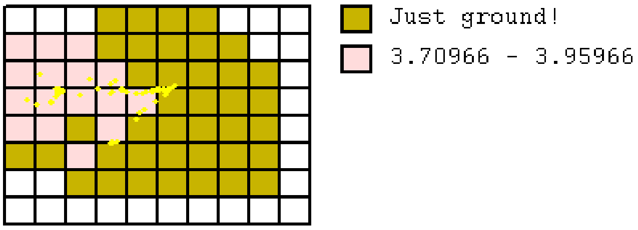
```
Consensus area 0 of 14 (from 1 areas; max. values)
                      🟨 Just ground!
                      ▨ 12.04934 - 12.29934

Showing 10; 17 species give score:
     10   Certhiaxis mustelinus(0.720)            12    Chordeiles rupestris(0.598)
     17  Conirostrum margaritae(0.760)            19   Cranioleuca vulpecula(0.685)
     22        Elaenia pelzelni(0.740)            26         Furnarius minor(0.780)
     35 Knipolegus orenocensis sclateri(0.760)           37  Leucippus chlorocercus(0.740)
     38       Mazaria propinqua(0.759)            40  Myrmochanes hemileucus(0.780)
     42   Ochthornis littoralis(0.533)            46 Paroaria gularis gularis(0.568)
     53 Serpophaga hypoleuca hypoleuca(0.724)            62 Stigmatura napensis napensis(0.655)
     64  Synallaxis albigularis(0.778)            67 Thlypopsis sordida chrysopis(0.655)
     69 Turdus ignobilis debilis(0.815)
```

```
Consensus area 1 of 14 (from 1 areas; max. values)
```



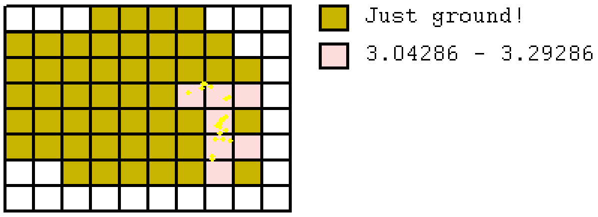
```
Showing 10; 16 species give score:
     10   Certhiaxis mustelinus(0.729)          12    Chordeiles rupestris(0.560)
     17  Conirostrum margaritae(0.771)          19   Cranioleuca vulpecula(0.692)
     22         Elaenia pelzelni(0.750)         26         Furnarius minor(0.792)
     35 Knipolegus orenocensis sclateri(0.771)          37  Leucippus chlorocercus(0.750
     38        Mazaria propinqua(0.768)         39 Muscisaxicola fluviatilis(0.514)
     40  Myrmochanes hemileucus(0.792)          46 Paroaria gularis gularis(0.569)
     53 Serpophaga hypoleuca hypoleuca(0.732)          64  Synallaxis albigularis(0.714)
     67 Thlypopsis sordida chrysopis(0.661)         69 Turdus ignobilis debilis(0.827)
```

Consensus area 2 of 14 (from 1 areas; max. values)



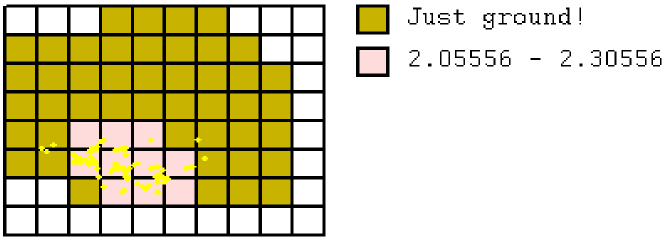
```
Showing 17; 6 species give score:
     17  Conirostrum margaritae(0.521)          19   Cranioleuca vulpecula(0.591)
     37  Leucippus chlorocercus(0.650)          40  Myrmochanes hemileucus(0.542)
     61     Sporophila murallae(0.844)          67 Thlypopsis sordida chrysopis(0.563)
```

Consensus area 3 of 14 (from 2 areas; max. values)



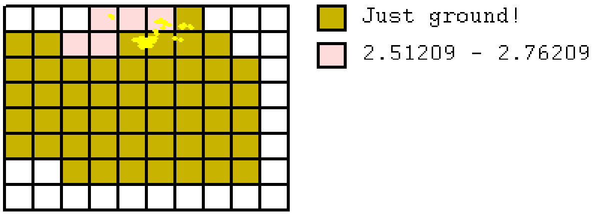
```
Showing 36; 4 species give score:
     36 Knipolegus orenocensis xinguensis(0.571-0.786)      43         Paroaria baeri(0.786-0.900)
     54 Serpophaga hypoleuca pallida(0.571-0.786)      58 Sicalis columbiana leopoldinae(0.857-1.000)
```

Consensus area 4 of 14 (from 1 areas; max. values)



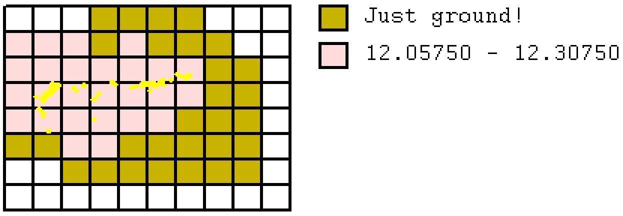
```
Showing 31; 3 species give score:
     31        Inezia inornata(0.556)          33 Inezia subflava guapore(0.600)
     44     Paroaria cervicalis(0.900)
```

Consensus area 5 of 14 (from 1 areas; max. values)



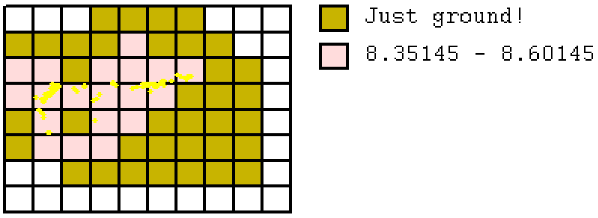
```
Showing 30; 4 species give score:
     30          Inezia caudata(0.269)           34 Knipolegus orenocensis orenocensis(0.800)
     55 Serpophaga hypoleuca venezuelana(0.800)          56 Sicalis columbiana columbiana(0.643)
```

```
Consensus area 6 of 14 (from 1 areas; max. values)
```



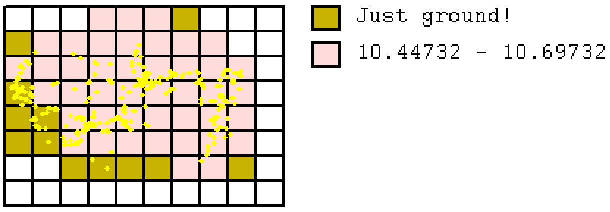
```
Showing 10; 17 species give score:
      10   Certhiaxis mustelinus(0.712)          12    Chordeiles rupestris(0.595)
      17  Conirostrum margaritae(0.750)          19   Cranioleuca vulpecula(0.679)
      22        Elaenia pelzelni(0.731)          26         Furnarius minor(0.769)
      35 Knipolegus orenocensis sclateri(0.750)        37  Leucippus chlorocercus(0.731)
      38       Mazaria propinqua(0.821)          40  Myrmochanes hemileucus(0.769)
      42   Ochthornis littoralis(0.568)          46 Paroaria gularis gularis(0.611)
      53 Serpophaga hypoleuca hypoleuca(0.786)          60 Sporophila castaneiventris(0.500)
      62 Stigmatura napensis napensis(0.714)         64  Synallaxis albigularis(0.768)
      69 Turdus ignobilis debilis(0.804)
```

```
Consensus area 7 of 14 (from 1 areas; max. values)
```



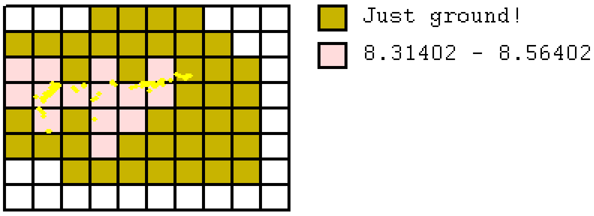
```
Showing 10; 11 species give score:
      10   Certhiaxis mustelinus(0.789)          19   Cranioleuca vulpecula(0.842)
      26         Furnarius minor(0.762)          35 Knipolegus orenocensis sclateri(0.652)
      37  Leucippus chlorocercus(0.816)          38       Mazaria propinqua(0.667)
      40  Myrmochanes hemileucus(0.868)          53 Serpophaga hypoleuca hypoleuca(1.000)
      62 Stigmatura napensis napensis(0.696)         64  Synallaxis albigularis(0.611)
      69 Turdus ignobilis debilis(0.648)
```

```
Consensus area 8 of 14 (from 1 areas; max. values)
```



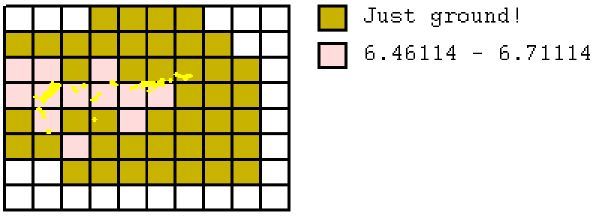
```
Showing 2; 14 species give score:
       2    Ammodramus aurifrons(0.679)          8       Atticora fasciata(0.664)
       9  Certhiaxis cinnamomeus(0.717)         20     Cranioleuca vulpina(0.765)
      21  Donacobius atricapilla(0.736)         29 Hydropsalis climacocerca(0.736)
      41   Nyctiprogne leucopyga(0.942)         45        Paroaria gularis(0.678)
      49        Phaeomyias murina(0.745)        50       Philohydor lictor(0.775)
      51 Pygochelidon melanoleuca(0.789)         52  Saltator coerulescens(0.717)
      63    Sublegatus obscurior(0.777)         66   Thamnophilus doliatus(0.728)
```

Consensus area 9 of 14 (from 1 areas; max. values)



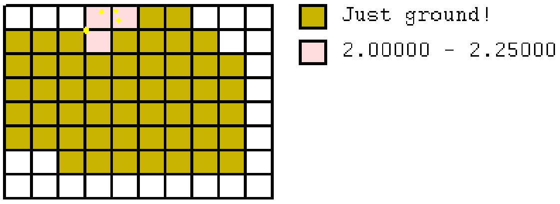
```
Showing 10; 12 species give score:
     10   Certhiaxis mustelinus(0.750)           17  Conirostrum margaritae(0.813)
     19   Cranioleuca vulpecula(0.813)           22        Elaenia pelzelni(0.781)
     26         Furnarius minor(0.722)           35 Knipolegus orenocensis sclateri(0.694)
     37  Leucippus chlorocercus(0.781)           39 Muscisaxicola fluviatilis(0.375)
     40  Myrmochanes hemileucus(1.000)           53 Serpophaga hypoleuca hypoleuca(0.583)
     67 Thlypopsis sordida chrysopis(0.568)           69 Turdus ignobilis debilis(0.433)
```

Consensus area 10 of 14 (from 1 areas; max. values)



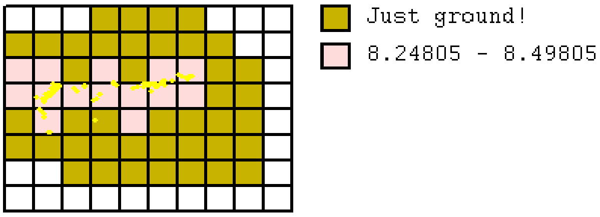
```
Showing 10; 11 species give score:
     10   Certhiaxis mustelinus(0.556)           19   Cranioleuca vulpecula(0.719)
     26         Furnarius minor(0.639)           35 Knipolegus orenocensis sclateri(0.719)
     37  Leucippus chlorocercus(1.000)           39 Muscisaxicola fluviatilis(0.328)
     40  Myrmochanes hemileucus(0.639)           53 Serpophaga hypoleuca hypoleuca(0.462)
     64  Synallaxis albigularis(0.442)           67 Thlypopsis sordida chrysopis(0.575)
     69 Turdus ignobilis debilis(0.383)
```

Consensus area 11 of 14 (from 1 areas; max. values)



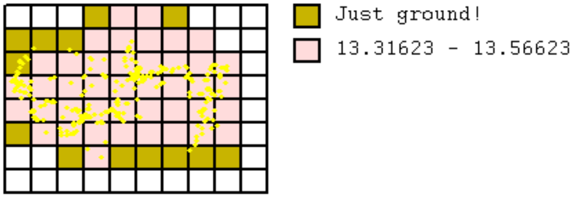
```
Showing 34; 2 species give score:
     34 Knipolegus orenocensis orenocensis(1.000)          55 Serpophaga hypoleuca venezuelana(1.000)
```

```
Consensus area 12 of 14 (from 1 areas; max. values)
```



```
Showing 10; 13 species give score:
     10   Certhiaxis mustelinus(0.750)              17  Conirostrum margaritae(0.600)
     19   Cranioleuca vulpecula(0.694)              22        Elaenia pelzelni(0.667)
     26         Furnarius minor(1.000)              35 Knipolegus orenocensis sclateri(0.813)
     37  Leucippus chlorocercus(0.781)              38       Mazaria propinqua(0.450)
     40  Myrmochanes hemileucus(0.722)              46 Paroaria gularis gularis(0.361)
     53 Serpophaga hypoleuca hypoleuca(0.519)              64  Synallaxis albigularis(0.500)
     69 Turdus ignobilis debilis(0.391)
```

```
Consensus area 13 of 14 (from 1 areas; max. values)
```



```
Showing 2; 19 species give score:
      2    Ammodramus aurifrons(0.720)             8       Atticora fasciata(0.698)
      9  Certhiaxis cinnamomeus(0.652)            14   Cnemotriccus fuscatus(0.663)
     18 Conirostrum speciosum amazonum(0.702)          20     Cranioleuca vulpina(0.657)
     21  Donacobius atricapilla(0.638)            27 Geothlypis aequinoctialis(0.700)
     29 Hydropsalis climacocerca(0.740)            41   Nyctiprogne leucopyga(0.721)
     45         Paroaria gularis(0.714)           46 Paroaria gularis gularis(0.685)
     49        Phaeomyias murina(0.750)           50       Philohydor lictor(0.670)
     52   Saltator coerulescens(0.685)            59    Sporophila americana(0.728)
     60 Sporophila castaneiventris(0.793)             63     Sublegatus obscurior(0.700)
     66   Thamnophilus doliatus(0.698)
```

Table S2. Biorregiões recuperadas com o Infomap Biorregiões para aves de ilhas fluviais e áreas abertas na Amazônia

commonSpecies	commonSpeciesCount	indicatorSpecies	indicatorSpeciesScore	bioregion	number
Atticora fasciata	2499	*Agelasticus xanthophthalmus*	1.36	a	1
Paroaria gularis	2174	*Arremonops conirostris pastazae*	1.36	a	1
Ochthornis littoralis	1549	*Thlypopsis sordida chrysopis*	1.33	a	1
Gymnomystax mexicanus	1024	*Muscisaxicola fluviatilis*	1.30	a	1
Synallaxis albigularis	867	*Leucippus chlorocercus*	1.30	a	1
Hydropsalis climacocerca	817	*Synallaxis albigularis*	1.29	a	1
Chordeiles rupestris	779	*Myrmochanes hemileucus*	1.29	a	1
Thlypopsis sordida chrysopis	400	*Cranioleuca vulpecula*	1.24	a	1
Chrysomus icterocephalus	393	*Chordeiles rupestris*	1.21	a	1
Furnarius minor	341	*Knipolegus orenocensis sclateri*	1.21	a	1
Paroaria gularis	550	*Certhiaxis sp novum*	6.19	b	2
Sporophila americana	363	*Paroaria xinguensis*	6.19	b	2
Thamnophilus doliatus	363	*Paroaria baeri*	6.19	b	2
Sporophila castaneiventris	358	*Sicalis columbiana leopoldinae*	6.19	b	2
Sicalis columbiana goeldii	309	*Agelasticus cyanopus xenicus*	6.19	b	2
Atticora fasciata	260	*Serpophaga hypoleuca pallida*	6.19	b	2
Ammodramus aurifrons	251	*Knipolegus orenocensis xinguensis*	6.03	b	2
Certhiaxis cinnamomeus	246	*Fluvicola albiventer*	5.36	b	2
Conirostrum speciosum amazonum	227	*Furnarius figulus pileatus*	4.98	b	2
Donacobius atricapilla	220	*Arundinicola leucocephala*	4.97	b	2
Certhiaxis cinnamomeus	281	*Inezia caudata*	11.03	c	3
Fluvicola pica	277	*Fluvicola pica*	9.17	c	3

Paroaria gularis	250	*Certhiaxis cinnamomeus*	4.61	c	3
Inezia caudata	222	*Anthracothorax viridigula*	3.86	c	3
Chrysomus icterocephalus	100	*Knipolegus orenocensis orenocensis*	3.46	c	3
Nyctiprogne leucopyga	63	*Arremonops conirostris**	3.03	c	3
Anthracothorax viridigula	50	*Serpophaga hypoleuca venezuelana*	2.42	c	3
Thamnophilus doliatus	40	*Chrysomus icterocephalus*	2.25	c	3
Atticora fasciata	38	*Sicalis columbiana columbiana*	1.73	c	3
Conirostrum speciosum amazonum	37	*Nyctiprogne leucopyga*	1.32	c	3
Paroaria gularis	162	*Inezia subflava***	19.47	d	4
Cranioleuca vulpina	160	*Paroaria cervicalis*	14.98	d	4
Atticora fasciata	63	*Arremonops conirostris**	14.45	d	4
Thamnophilus doliatus	54	*Cranioleuca vulpina*	5.88	d	4
Paroaria cervicalis	52	*Conirostrum bicolor minus*	3.74	d	4
Ochthornis littoralis	43	*Stigmatura napensis napensis*	2.32	d	4
Nyctiprogne leucopyga	37	*Inezia inornata*	2.29	d	4
Conirostrum bicolor minus	37	*Thamnophilus doliatus*	1.77	d	4
Hydropsalis climacocerca	36	*Mazaria propinqua*	1.62	d	4
Certhiaxis cinnamomeus	25	*Nyctiprogne leucopyga*	1.34	d	4
Inezia subflava	269	*Inezia subflava*	6.26	e	5
Paroaria gularis	220	*Nyctiprogne leucopyga*	4.63	e	5
Nyctiprogne leucopyga	211	*Sicalis columbiana goeldii*	1.64	e	5
Atticora fasciata	80	*Cranioleuca vulpina*	1.54	e	5
Cranioleuca vulpina	70	*Pygochelidon melanoleuca*	1.02	e	5
Sicalis columbiana goeldii	66	*Sublegatus obscurior*	1.02	e	5
Hydropsalis climacocerca	63	*Sporophila americana*	0.99	e	5
Sporophila castaneiventris	46	*Sporophila castaneiventris*	0.94	e	5

Ochthornis littoralis	44	*Paroaria gularis*	0.81	e	5
Sporophila americana	38	*Hydropsalis climacocerca*	0.74	e	5
Gymnomystax mexicanus	23	*Paroaria nigrogenis*	148.13	f	6
Sicalis columbiana columbiana	20	*Thlypopsis sordida orinocensis*	148.13	f	6
Pygochelidon melanoleuca	20	*Synallaxis beverlyae*	148.13	f	6
Ochthornis littoralis	17	*Knipolegus orenocensis orenocensis*	105.80	f	6
Fluvicola pica	10	*Serpophaga hypoleuca venezuelana*	88.87	f	6
Atticora fasciata	6	*Sicalis columbiana columbiana*	70.53	f	6
Paroaria gularis	5	*Arremonops conirostris*	49.37	f	6
Knipolegus orenocensis orenocensis	5	*Pygochelidon melanoleuca*	8.028	f	6
Inezia subflava	5	*Fluvicola pica*	4.047	f	6
Chrysomus icterocephalus	4	*Gymnomystax mexicanus*	2.63	f	6

*Note: isolated population in the Branco river

**Note: isolated population in the Guapore river

CONCLUSÕES

A avifauna dos ambientes alagáveis amazônicos apresentaram padrões singulares de endemismo e diversidade, e seus limites parecem não ser tão claros como os padrões aceitos para aves de terra firme. Entretando, os padrões elencados aqui confirmam que a avifauna associada aos ambientes alagáveis não é uniforme ao longo da bacia.

Nossos resultados revelaram padrões espacialmente complexos de endemismo e diversidade, com áreas de endemismo apresentando vários graus de sobreposição, aninhamento e disjunção. As diferentes análises empregadas no presente estudo identificaram entre 3 e 14 áreas de endemismo, para as quais não ficam claras as subdivisões originalmente propostas em trabalhos anteriores.Além disso, nossos resultados concordam com outros estudos em que foram identificadas várias áreas de endemismo exclusivamente em um dos tamanhos de célula, e outros foram consistentemente recuperadas nos outros tamanhos de células, bem como a análise de bioregiões mostrou diferenças claras entre as porções oeste e sudeste da bacia, provavelmente relacionados as características geológicas dessas regiões. Em geral, as áreas de endemismo identificadas estão associadas as três principais bacias da porção norte da América do Sul, Bacia do Amazonas, Bacia do Tocantins e Bacia do Orinoco.

Para os padrões de composição da comunidade, nossos resultados indicam que as maiores diferenças em composição ocorrem entre o sudeste e o oeste da Amazônia. A variação espacial da composição dos taxa coincidiu com algumas AE identificadas, em especial as correspondentes à região da Bacia do Tocantins. Os padrões de composição observados aqui apresentam uma forte relação com a hidroquímica dos rios, o que é refletido nas diferentes cores de suas águas. Dessa forma, estabelecendo os padrões de composição das comunidades no contínuo do sistema, o que é refletido no padrão de ocorrência das espécies.

Os resultados obtidos aqui, reforçam a ideia de que as sub-bacias Amazônicas, em especial as do escudo Brasileiro não são unidades biogeográficas distintas, mas possuem configurações recentes e uma biota heterôgena. Dessa forma, nossos achados substanciam os achados de Dagosta & Pinna (2017) que sugerem que as bacias hidrográficas Amazônicas não devem ser consideradas a priori como unidades biogeográficas distintas.

Dado que o melhor conhecimento da distribuição das espécies é considerado um fator chave para reavaliação da lista de espécies ameaçadas, destacamos a importância crítica da análise objetiva do endemismo no contexto do atual declínio global de biodiversidade, bem como a necessidade de acelerar a digitalização e o georreferenciamento da biodiversidade nas coleções de história natural do mundo. Além disso, propomos que os padrões identificados aqui sejam testados com outros grupos de organismos fluviais. A este respeito, no entanto, as dificuldades de se definir explicitamente ou exclusivamente os organismos de habitats ribeirinhos não devem ser subestimadas por razões delineadas nos métodos. Portanto, por enquanto, fornecemos um passo importante e fundamental para a identificação de áreas de endemismo e padrões de diversidade, contribuindo para um melhor conhecimento da biogeografia das aves associadas a ambientes alagáveis Amazônicos.

Por fim, algumas de nossas AEs identificadas , são congruentes com áreas de relevante interesse para conservação. Por exemplo, as AEs sobrepostas com a Bacia do Tocantins, correspodem à ecorregião – Xingu-Tocantins-Araguaia moist forest (NT0180) (Olson et al. 2001). Além disso, 28% dos taxa especializados em ilhas fluviais e ambientes sucessionais primários da Bacia Amazônica são endêmicos em alguma escala espacial. Destes, dois são considerados ameaçados (NT e VU) e dois ainda não foram avaliados de acordo com a IUCN e a BirdLife International. A avifauna associada às várzeas da Amazônia é heterogênea e esses padrões precisam ser levados em conta ao planejar o desenvolvimento da infraestrutura ao longo dos grandes rios amazônicos.