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# Aves especialistas de ecossistemas de areia branca no noroeste da Amazônia

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# Aves especialistas de ecossistemas de areia branca no noroeste da Amazônia

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*Dedico esta tese a todas as vítimas da COVID-19 e as aves com muito amor.*

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# Resumo

Os ecossistemas de areia branca (EAB) na Amazônia são ambientes totalmente diferentes do que se espera quando falamos em Amazônia. Grande parte da paisagem é constituída por Terra firme, e por outros ecossistemas que fazem parte da dinâmica e composição de um dos maiores Biomas da Terra. O surgimento e evolução dos ecossistemas ao longo dos anos vem sendo bem estudados, favorecendo o conhecimento dos padrões que foram moldados por múltiplos eventos geológicos, ecológicos e temporal. A história evolutiva da Amazônia pôde moldar os padrões de biodiversidade, reveladada pelos estudos em diversidade funcional, taxonômica e filogenética. O **primeiro capítulo** busca entender como a ecomorfologia das aves especialistas de EAB é em relação as espécies generalistas que usam os ambientes de EAB e outros ecossistemas da Amazônia como a Terra firme e florestas ribeirinhas. O **segundo capítulo** trata da relação da ecomorfologia e filogenia das aves dos ambientes ribeirinhos e dos EAB e quais processos evolutivos teriam influenciado a formação das comunidades nestes ecossistemas. Os resultados mostram que a ecomorfologia das aves especialistas não é diferente a ponto de serem um grupo a parte dentro do espaço funcional. A comunidade de aves de EAB são influenciadas ao longo do tempo, principalmente pelos eventos de extinção. Com modelos atuais através do processamento de dados filogenéticos e dados ecológicos, podemos contar a história evolutiva mais provável da formação das comunidades. Os EAB assim, são sumidouros de espécies, pois uma espécie pode chegar, se adaptar a um ambiente restritivo e não conseguir mais ocupar outros ecossistemas. Na história evolutiva das aves de EAB, ou elas se adaptam ou eles se extinguem. Estes resultados são inéditos e contribuem para o conhecimento da ecologia evolutiva das espécies de EAB na Amazônia.

**Palavras-chave:** comunidades, morfologia, diversidade funcional, especialização

# Abstract

The white sand ecosystems (WSE) in the Amazon are very different environments from what is expected when we talk about the Amazon. A large part of the landscape is made up of "*terra firme*" and other ecosystems that are part of the dynamics and composition of one of the largest Biomes on Earth. The emergence and evolution of ecosystems over the years have been well studied, favoring the knowledge of the patterns that were shaped by multiple geological, ecological and temporal events. The evolutionary history of the Amazon could shape biodiversity patterns, revealed by studies on functional, taxonomic, and phylogenetic diversity. The first chapter seeks to understand how the ecomorphology of WSE specialist birds is in relation to generalist species that use WSE environments and other Amazon ecosystems such as *"terra firme"* and riverine forests. The second chapter deals with the relationship between ecomorphology and phylogeny of birds from riverside environments and WSE which evolutionary processes would have influenced the formation of communities in these ecosystems. The results show that the ecomorphology of specialist birds is not different to the point of being a separate group within the functional space. WSE bird communities are influenced over time, mainly by extinction events. With current models through the processing of phylogenetic data and ecological data, we can tell the most likely evolutionary story of the formation of communities. Thus, WSE species sinks, as a species can arrive, adapt to a restrictive environment, and longer be able to occupy other ecosystems. In the evolutionary history of WSE birds, they adapt or become extinct. These results are unprecedented and contribute to the knowledge of the evolutionary ecology of WSE species in the Amazon.

**Keywords:** communities, morphology, functional diversity, specialization

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# Introdução Geral

Os organismos são capazes de tomar decisões comportamentais sobre onde viver e onde não viver dentro de suas limitações genéticas, morfológicas e ecológicas (Devictor *et al.*, 2010; Diniz-Filho & Bini 2008; Fitzgerald *et al.*, 2017). O quanto cada organismo utiliza de recursos do ambiente de onde vive, é possível diferenciar os que utilizam maior variabilidade de recursos e os que se restringem a lugares e seus recursos, podendo ser classfiados de generalistas e esécialistas. A especialização em grande parte determina as distribuições de organismos no tempo e no espaço (Ferry-Graham *et al*. 2002; Diniz-Filho *et al*., 2009). Geralmente espécies especialistas estão limitadas pelas barreiras de dispersão, extensão, qualidade do habitat, disponibilidade de recursos e interações antagonistas (Ricklefs 2012; Sobral e Cianciaruso 2015). O termo "especialista" ainda é muito controverso e pode ser estudado de várias formas, quando levamos em consideração desde a especialização individual, da população, da espécie e da comunidade (Devictor *et al*., 2010).

As limitações das espécies em um determinado habitat monta a comunidade que sofre forças da seleção natural, e para buscar respostas sobre tais processos ecológicos são sugeridos agrupamentos funcionais para facilitar o estudo dos fenômenos naturais (Cianciaruso 2009). Tratar de traços ou atributos funcionais é agrupar em subgrupos a comunidade, e apresentar características que apresentem respostas semelhantes ao ambiente e efeitos similares sobre processos ecossistêmicos, sem que esse agrupamento represente necessariamente relações filogenéticas (Diaz e Cabido 2001). As comunidades não são puramente reflexos da história evolutiva das espécies, mas também das interações com o ambiente. A estruturação filogenética na comunidade pode ou não ser desencadeada, quando atributos são fortemente conservados em determinados clados (Kraft et al. 2008).

Normalmente as espécies filogeneticamente relacionadas compartilham características fenotípicas mais semelhantes entre si, do que com as espécies distantemente aparentadas (Losos e Ricklefs 2009; Sobral e Cianciaruso 2015). Considerando as estratégias de vida das espécies/indivíduos, podemos agrupá-las em tipos que expressam "respostas" ao ambiente biológico e abiótico, no entanto algumas espécies tendem a estar mais intimamente relacionadas ao ambiente (Devictor *et al.* 2010).

Em paisagens naturalmente fragmentadas as espécies evoluem neste contexto sendo a movimentação entre manchas de habitat o fator fundamental para a persistência das populações (Petit 2001). Uma população subdivida no espaço favorece o aumento do comportamento de dispersão, na maioria das vezes para evitar a competição com co-específicos. Porém realizar movimentação entre manchas de habitat pode ser uma atividade de alto risco, aumentando a mortalidade dos indivíduos que se dispersam.

A Amazônia um dos maiores e mais biodiverso bioma do mundo, possui vários ecossistemas com histórias distintas. As dinâmicas paleoclimática e tectônica causaram mudanças na distribuição de vários tipos de vegetação de floresta e não-floresta (Haffer *et al*., 1992). Muitas áreas na região neotropical foram afetadas por mudanças cíclicas na vegetação (Figura 1). A floresta pluvial úmida em muitas regiões foi por várias vezes substituída por floresta aberta, onde a floresta pluvial foi mantida mais ou menos imutável durante uma fase seca particular formando "refúgios florestais (Haffer *et al*., 1992; Cohn-Haft *et al*., 1997). Os ciclos vegetacionais paleoclimáticos foram completos somente naquelas regiões onde a floresta pluvial foi substituída por vegetação não-florestal durante uma fase seca (Haffer *et al*., 1992).

**Figura 1:** Ecossistema de areia branca na Reserva de desenvolvimento sustentável do Uatumã. Gradiente sucessional de campinarana para área aberta com gramíneas, que parece mais com um leito de rio seco. Fonte: Grupo MAUA-FLY.

Este ecossistema de vegetação não-florestada, já foi chamado por Prance (1979) por floresta de igapó seco ou praia de rios e por Anderson (1975) de campina e campinarana. Hoje são referidos em conjunto, como "ecossistemas de areia branca -EAB" ('white-sand ecosystems' -WSE) (Adney *et al*. 2016). O padrão insular deste ecossistema é uma ótima receita para o endemismo, especiação e estudos relacionados a populações com distribuição fragmentada (Fine e Baraloto 2016; Borges 2012). Os EAB estão associados a características edáficas específicas, com diferentes níveis de alagamento e solos de areia branca (Whitmore e prance 1987; Anderson 1981)(Figura 2). Hoje cobrem cerca de 7% do bioma Amazônico no Brasil (Guimarães & Bueno 2016), predominantemente nas regiões do alto e médio rio Negro, ao sul de Roraima e noroeste do estado do Amazonas, principalmente nos interflúvios Purus-Madeira-Tapajós (Adeney *et al*. 2016; Borges *et al*. 2016; Polleto e Aleixo 2005).

**Figura 2:** Estreita faixa de Ecossistema de areia branca as margens do rio Uatumã, na Reserva de Desenvolvimento sustentável do Rio Negro. Fonte: Grupo MAUA-FLY.

Os ambientes abertos estão restritamente associados aos solos arenosos com areia branca exposta, que suportam uma vegetação arbustiva baixa densamente agregada sendo a maioria das espécies de plantas esclerófilas e vegetação rasteiras compostas por liquens, gramíneas e ciperáceas (Anderson 1981; Adeney *et al*. 2016). A medida que o solo permite uma proporção maior de material argiloso e maior acúmulo de matéria orgânica na faixa superficial do solo, há formação de uma zona de transição para a mata de terra-firme/ripária e a formação de uma vegetação com estrutura florestal, nomeada de campinarana (Ab'Sáber 2004). As campinaranas tem uma cobertura rala de arbustos e árvores (Figura 3), copa muitas vezes desigual e variando entre 5-15 metros de altura, com algumas árvores emergentes (20-30 metros de altura). A luz que chega ao solo ainda é elevada, formando um sub-bosque denso de arbustos, mas principalmente composto por árvores de troncos finos (Anderson, 1981).

**Figura 3:** Ecossistema de areia branca e seus micro-habitas de areia exposta, arbustiva e campinarana. Localidade: próximo a Comunidade Vista Bela na Reserva de Desenvolvimento Sustentável do Uatumã. Imagem de drone a 80 metros de altura. Fonte: Grupo MAUA-FLY.

A comunidade de aves que habita os EAB está totalmente adaptada a um ambiente estressante, resultando em uma comunidade pouco diversa e "pobre" em relação aos ambientes de floresta de terra firme (Alvarez Alonso *et al*. 2013; Borges *et al*. 2015). Cerca de 14% das espécies são especialistas de EAB. Estas espécies estão inseridas em uma paisagem com distribuição fragmentada sendo que tanto o contexto biogeográfico como a estrutura desta paisagem (i.e., tamanho e isolamento das manchas de habitat) tem um forte efeito sobre a estruturação das populações (Capurucho *et al*. 2013) e das comunidades de aves (Borges *et al*. 2016). Mesmo sendo animais alados o estudo da movimentação das aves é especialmente relevante, pois muitas espécies de aves apresentam uma capacidade reduzida de se dispersar na paisagem. Algumas espécies de aves florestais, por exemplo, não atravessam estradas ou clareiras ao redor de fragmentos florestais, que podem representar barreiras significativas para a dispersão (Develey e Stouffer, 2001).

Ecossistemas de areia branca podem apresentar cerca de 100 espécies de aves por hectare (Klinge e Herrera 1983; Ferreira, 2009) enquanto que nas Florestas de Terra firme são mais de 300 espécies por hectare (Valencia *et al*. 2004). Vários estudos já foram realizados nos últimos anos para entender a dinâmica das populações de aves especialistas de EAB (Oren 1981, Borges, 2004, 2006, 2013, Borges *et al*. 2015). Capurucho *et al.* (2013) estudou a filogeografia e variabilidade genética da espécie pretinho-da-campina (*Xenpipo* atronitens, Aves; Pipridae), uma espécie categorizada como restrita a este tipo de ecossistema no estudo de Borges *et al*. (2015). Matos *et al*., (2016) comparou a filogeografia de duas espécies especialistas de EAB, sanhaçu-preto (*Tachyphonus phoenicius*, Aves, Thraupidae) e do beija-flor-verde (*Polytmus theresiae*, Aves, Trochilidae). Ambos os trabalhos encontraram um pasrão de diversidade genética semelhante, com pouca estrtura, baixa diversidade e expansão demográfica recente, principalmente das populações mais ao norte da Amazônia. Estes resultados são o contraste de resultados para as aves de Floresta de Terra Firme, com alta estrutura e diversidade filogenética entre interflúvios (Ribas et al. 2012, d'Horta *et al.* 2013, Sousa-Neves *et al.* 2013, Fernandes *et al.* 2014, Thom e Aleixo 2015).

Nesta tese busco saber como as espécies de aves estão inseridas dentro da comunidade de EAB, visando entender como ocorre o processo de especialização em um ambiente "pobre" e fragmentado da Amazônia. Unir linhas de estudos é fundamental para determinar a distribuição geográfica das espécies e as fragilidades de cada uma nos tempos atuais (Brown *et al*., 1996). As lacunas no conhecimento sobre a identificação, distribuição, evolução e dinâmica da biodiversidade global precisa ser cuidadosamente reconhecida e quantificada (Hortal *et al.*, 2015). Os processos evolutivos, as características do habitat e as características ecomorfológicas podem gerar dados importantes sobre a história natural das espécies no espaço e tempo (Diniz *et al.*, 2009). Os biogeógrafos estudam os padrões espaciais de dispersão, padrões temporais, relações geográficas, filogenias e os processos que produzem esses padrões de distribuição (Cohn-Haft *et al.*, 2007; Ribas *et al.*, 2011;). Todos os estudos normalmente são tratados de forma separada. Para as florestas Neotropicais, no entanto, a saída para explicar os diversos fatores que levaram a biodiversidade ser tão elevada, é unir o conhecimento e utilizar novos e avançados modelos (Pigot *et al*., 2018).

Tratar sobre os padrões de diversidade funcional, filogenética e os processos evolutivos das aves especialistas de ecossistemas de areia branca, é complementar ainda mais os estudos realizados até o presente momento. Determinar como acontece a diversificação das espécies é fundamental para responder as questões da biologia evolutiva. Obtendo os índices de especiação, extinção e a dispersão gerados pelos modelos utilizados nesta tese, é uma forma inédita de utilizar os dados ecológicos e filogenéticos juntos. Mostramos assim, a importância de estudar os Ecossistemas de areia branca, a partir das aves especialistas e a sua história ecológica evolutiva na Amazôniam, estando nesta tese organizado em dois capítulos:

- **Capítulo 1** aborda a resposta da ecomorfologia e diversidade funcional das aves especialistas nas comunidades de EAB. Utilizamos a lista de Borges et al., 2016 e a classificação das espécies em restritas de EAB (Borges *et al.*, 2016(b), ao qual chamamos de especialistas e as espécies generalistas aquelas que não utilizam somente os EAB, mas sim outros ecossistemas amazônicos. Compilamos dados de quatro traços ecológicos das espécies e nove medidas morfológicas funcionais com média para cada uma das espécies. A partir das medidas e dados ecológicos realizamos análises multivariadas, com controle e sem controle filogenético, calculamos o índice da riqueza funcional (Villeger *et al*., 2008), e devido a diferença no número de espécies aplicamos a rarefação (Gotelli e Colwell 2001).

- **Capítulo 2** discorre sobre a existência de grupo de aves especialistas, se a campina possui estrutura filogenética e como se deu o processo de diversidifcação das aves, levando em consideração os processo evolutivos de especiação, dispersão e extinsão que mais influenciaram na composição das comunidades de aves especialistas de EAB. Utilizamos como pool de espécies a comunidade de aves dos EAB (especialistas e generalistas) e de ecossistemas ribeirinhos, do trabalho de Naka *et al.*, (2020), por considerar que o conjunto regional de espécies pode influenciar os processos geográficos e evolutivos sob análise. As espécies foram classificadas em especialistas de ecossistemas de areia branca, especialistas de ecossistemas ribeirinhos e as espécies generalistas que utilizam estes dois ambientes, mas não estão restritas a eles. Esta classificação é também uma característica ecológica das espécies. Realizamos análises de modelos comparativos inéditos para escalas locais, com resultados importantes para etender o processo evolutivo das espécies especialistas.

# CAPÍTULO 1

Lima, Gisiane Rodrigues, Sergio Henrique Borges, Marina Anciães, Cintia Cornelius. **Ecomorphology and functional diversity of generalist and specialist bird assemblages in Amazonian white-sand ecosystem habitat patches.** Manuscrito aceito para publicação no periódico *Acta Amazonica* em 08 de janeiro 2023.

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# Ecomorphology and functional diversity of generalist and specialist bird assemblages in Amazonian white-sand ecosystem habitat patches

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## Abstract

Birds that inhabit white-sand ecosystems (WSE) in the Amazon are adapted to habitats distributed as isolated patches. These environments occur in sandy soils that are extremely poor in nutrients, have low floristic diversity and support bird assemblages restricted to WSE. We investigated whether bird species specialized in WSE have morphological or ecological traits that distinguish them from generalist birds that share the same habitat but are not restricted to WSE. We collected morphological and ecological data from 22 specialist and 102 generalist bird species from WSE and described their ecomorphological diversity using multivariate analyses and measures of functional diversity. Understory insectivorous species that move alone or in pairs, were the group with the most species among specialist birds from WSE. In contrast, canopy frugivorous species that form mono- or heterospecific groups were more frequent among generalist species. Specialist and generalist birds overlapped extensively in ecomorphological space, with specialists occupying a narrower space compared to generalists. Functional diversity, however, was not different between specialist and generalist species when controlling for the number of species within the communities. Further studies comparing the ecomorphological diversity of bird assemblages of other environments in the Amazon may highlight the ecological pressures leading to the functional diversity of specialist species in WSE observed in this study.

**KEYWORDS**: environmental filter, habitat specialization, insularity, morphology, tropical ecosystems

# Ecomorfologia e diversidade funcional de assembléias de aves generalistas e especialistas em manchas de habitat de ecossistema de areia branca na Amazônia

## Resumo

As aves que habitam os ecossistemas de areia branca (EAB) na Amazônia estão adaptadas a habitats distribuídos em manchas isoladas. Esses ambientes ocorrem em solos arenosos extremamente pobres em nutrientes, possuem baixa diversidade florística e suportam assembleias de aves restritas a EAB. Investigamos se espécies de aves especializadas em EAB possuem características morfológicas ou ecológicas que as distinguem de aves generalistas que compartilham o mesmo habitat, mas não estão restritas a EAB. Coletamos dados morfológicos e ecológicos de 22 espécies de aves especialistas e 102 generalistas de EAB, e descrevemos sua diversidade ecomorfológica usando análises multivariadas e medidas de diversidade funcional. Espécies insetívoras do sub-bosque que se movem solitárias ou em pares foram o grupo com maior número de espécies dentro das aves especialistas da EAB. Em contraste, espécies frugívoras de dossel que formam grupos mono ou heteroespecíficos foram mais frequentes entre as espécies generalistas. Aves especialistas e generalistas sobrepuseram-se extensivamente no espaço ecomorfológico, com especialistas ocupando um espaço mais estreito em comparação com generalistas. A diversidade funcional, no entanto, não foi diferente entre espécies especialistas e generalistas ao controlar o número de espécies dentro das comunidades. Estudos futuros comparando a diversidade ecomorfológica de assembleias de aves de outros ambientes na Amazônia podem destacar as pressões ecológicas que levam à diversidade funcional de espécies especialistas em EAB observadas neste estudo.

**Palavras-chave:** filtro ambiental, especialização de habitat, insular, morfologia

## Introduction

Evolutionary ecologists have highlighted the study of species functions within ecosystems to connect niche-based mechanisms to assemblage patterns (Cadotte 2017; Cadotte and Tucker 2017). Species functional attributes can link population processes to environmental gradients or interactions dictating species coexistence in nature (Pigot *et al*. 2016; Cadotte 2017). Natural environments limit the distribution of animals and plants according to their ecological and morphological adaptations, which can be represented by their functional space (Tilman *et al*. 1997; Cianciaruso *et al*. 2009). Thus, variations in ecomorphological attributes selected through environmental filters can influence the species that coexist in biological assemblages (Petchey and Gaston 2002; Devictor *et al*. 2010; Clavel *et al*. 2011; Braga *et al*. 2022).

Environments with stable conditions of resource availability tend to support more diverse assemblages and require fewer specialized adaptations (Grant 1968; Cianciaruso *et al*. 2017). In contrast, environments with severe ecological conditions may require specific adaptations for survival, restricting the number of species that can persist (Pigot *et al*. 2016). Habitat insularity can also limit the number of species in an assemblage, as small, isolated habitat patches tend to harbor less species than large and connected patches (MacArthur and Wilson 1967; Rosenberg 1990; Gomes *et al.* 2008; Borges *et al*. 2016a).

Oceanic islands are examples of insular environments that impose strong selection on the number of species capable to colonize these rather severe environments (Grant 1968; Grant and Grant 2006), thus favoring phenotypes different from those found in more diverse continental environments, with greater availability of resources (Lomolino 2000). For instance, there are a number of examples of morphological trends such as dwarfism, gigantism and loss of flight capacity that have been associated to extreme environmental conditions found in oceanic islands (Boback 2003; Losos and Ricklefs 2009).

Island-like systems, habitats in an ecological context similar to islands such as mountaintops or rock outcrops, are found in several regions of the planet (Vitt *et al*. 1997; Brown *et al*. 2013; Piñeiro *et al*. 2021). Extreme environmental conditions of most of these systems can also impose strong ecological restrictions on species assemblages (Itescu 2019). However, the study of the ecological, morphological, and evolutionary distinction of species that inhabit these island-like systems has received less attention when compared to studies in assemblages that occupy true islands (but see Borges *et al*. 2016a,b). These island-like systems provide excellent opportunities to investigate how insularity and resource limitations can act as synergetic environmental filters by selecting functional attributes of the species that occupy or specialize in these environments.

White-sand ecosystems (WSE) in the Amazon are a remarkable example of an island-like habitat with severe ecological conditions. This type of low-stature vegetation occurs on sandy soils that are extremely poor in nutrients and distributed in isolated patches surrounded by tall lowland forests (Anderson 1981; Adeney *et al*. 2016; Capurucho *et al*. 2020). The flora of white-sand ecosystems is composed of plant lineages that have adapted to extreme conditions imposed by poor soils and water stress resulting in assemblages with reduced biological diversity (Adeney *et al*. 2016; Capurucho *et al*. 2020). However, WSE host a fauna and flora quite distinct from the surrounding vegetation including species that are highly specialized in the use of these environments (Anderson 1981; Oren 1981; Borges *et al*. 2016a; Fine *et al*. 2016).

The insular distribution and harsh ecological conditions make WSE excellent models to investigate the effects of environmental filters on the adaptation and specialization of animals and plants (Fine *et al*. 2016; Capurucho *et al*. 2020). In addition, WSE patches have experienced events of expansion and shrinkage of their extension throughout the geological time, evidencing a complex and dynamic evolutionary history of taxa specialized in using these systems (Capurucho *et al*. 2020; Ritter *et al*. 2021). However, we still do not know whether specialization in the use of WSE can lead to the development of distinct ecomorphological features or a peculiar arrangement of species.

Birds stand out among the taxonomic groups that specialize in the use of WSE (Oren 1981; Alonso *et al*. 2013). Some of these specialist birds are abundant locally and their ecological distribution is almost entirely restricted to WSE (Alonso *et al*. 2013; Borges *et al*. 2016*a*). It is important to emphasize that WSE are also consistently colonized and used by generalist species that also use other close by habitats such as upland forests, flooded forests, and open environments (Borges *et al*. 2016*a*).

In this study we investigated whether the specialization of birds in the use of Amazonian WSE associates with ecomorphological and evolutionary distinctions in bird species. If the limiting factors of WSE, such as scarcity of resources and insularity exerting strong selective pressure (Anderson 1981), it is expected that the specialized species would show a different and more restricted ecomorphological diversity in the functional space than generalist species that use the same environments (Julliard *et al*. 2006; Hamer *et al*. 2015; Capurucho *et al*. 2020). Alternatively, the environmental filter imposed by the ecological conditions of the WSE may not be intense enough to lead to distinct morphological or functional characteristics between specialist and generalist assemblages, but still restrict the morpho-functional space of specialist birds when compared to generalist species. We investigated these alternative hypotheses through comparisons of morphological and ecological traits of specialist and generalist birds found in WSE environments.

## Material And Methods

### Study area and bird assemblage

White-sand ecosystems (WSE) have an insular distribution in the Amazon Rainforest, forming either large and extensively connected habitat patches or small isolated patches, depending on edaphic conditions and regional paleohistory (Adeney *et al*. 2016). WSE vary along an ecological gradient from areas with open habitats dominated by grasses and shrubs (*campinas*) to forest vegetation with open understory and medium canopy height (7 to 15 m) (*campinaranas*) (Anderson 1981). In the northwest Amazon, *campinas* and *campinaranas* occupy continuous and connected areas while smaller and isolated patches of these vegetation types are more frequent in the central and western parts of the Amazon basin (Adeney *et al*. 2016).

The bird assemblage analyzed in this study was defined through a species list compilation of birds that use WSE, specifically those that occupy open vegetation dominated by herbs and shrubs (*campinas*) located in the northwest and central portion of the Amazon basin (Borges *et al*. 2016*a*). This is the most complete database available for birds associated with WSE sampled through captures in mist nets and audiovisual censuses (for details on the sampling design see Borges *et al*. (2016*b*).

We used the categorization proposed by Borges *et al*. (2016*a*) that classified bird species according to their habitat affinity with WSE in four categories: i) sporadic; ii) regular, iii) almost restricted and iv) restricted species. These categories are based on an extensive review of the literature and a qualitative assessment of the frequency at which each species is recorded in WSE and in other environments (Borges *et al*. 2016*a*). We did not consider the sporadic species category to avoid bias in subsequent analyses and considered the almost restricted and the restricted category as a single group. Thus, we worked with two groups:

1) generalist species, which regularly use WSE patches but also use other environments, classified as regular species according to Borges *et al*. (2016*a*), and 2) specialist species, which are mostly exclusively found in WSE, equivalent to the restricted and almost restricted categories in Borges *et al*. (2016a), totaling 124 species within the WSE assemblage analyzed (102 generalists and 22 specialists, see Table 1).

## Morphological and ecological data

We measured the morphological traits of a total of 316 individuals from specimen skins deposited in the Bird Collection of the Instituto Nacional de Pesquisas da Amazônia (INPA). We sampled at least three individuals of each species and measured each attribute with a digital caliper three times to estimate their averages. We followed the recommendations of (Baldwin *et al*. 1931) and obtained: body mass (g) of the individual recorded at the time of preparation; tarsus and beak length (mm); beak height and width (mm) and, length of primary and secondary remiges (mm) excluding specimens in molt. We selected these morphological traits because they are associated to organism diet (beak dimensions), foraging or locomotion (wing and tarsus) and, as such, represent species functional traits in morphological space (Devictor *et al*. 2010). Only one of the authors (GRL) conducted measurements.

Ecological traits of analyzed species were obtained from the literature (Cohn-Haft *et al*. 1997; Wilman *et al*. 2014) and field experience from authors (GRL and SHB). In this study we adopted three qualitative functional categories, classifying the species in terms of diet, foraging stratum and sociability (Table 2).

## Analyses

In order to understand ecomorphological differentiation, through habitat filtering of bird species in WSE, we proceeded with comparisons of morphological and ecological traits in functional spaces occupied by specialist and generalist species using WSE. For that, we controlled for the phylogenetic signal among species, as they might differ in functional position due to their phylogenetic distances alone (inertia) (Belmaker *et al*. 2012; Jetz *et al*. 2012).

We investigated the phylogenetic relationships between WSE generalist and specialist birds using the data available at www.birdtree.org, generating 10,000 phylogenetic trees through the PhylogenySubset tool, a platform with bird phylogenies from around the world (Jetz et al.2012; Belmaker and Jetz 2013). The phylogenies obtained were integrated into a single consensus tree (Maximum Clade Credibility Tree), maintaining branch lengths, using the phytools package and the *consensus.edges* function in the R Program. This approach has been widely used in comparative studies that takes into account the phylogenetic structure of biological assemblages (Kraft *et al*. 2007; Podani *et al*. 2018).

We chose to use a principal component analysis modality that controls for phylogenetic effects since we are considering species with different phylogenetic relationships in the same analysis. Phylogenetic principal component analysis (pPCA) serves to order multivariate data considering the phylogenetic non-independence between species. Unlike common PCA scores, scores on the pPCA axes are correlated with each other and their variances do not correspond to the eigenvalues of the phylogenetically corrected axes (Revell 2009; Callaghan *et al*. 2019). By using a pPCA analysis as a morphometric tool, we seek to interpret results explained by the adjusted eigenvectors (Polly *et al*. 2013). Ordinary PCA analyses were also performed for generalist and specialist species separately to obtain the vectors (characteristics) that are most related to the two bird groups. The SYNCSA package and *pca* function were used in program R (Debastiani and Pillar 2012; Gianuca *et al*. 2014).

We also performed a Principal Coordinate Analysis (PCoA) to explore and visualize similarities or differences including morphological and ecological categorical data. We used a dissimilarity matrix (= distance matrix) and assigned each item into a location in a low-dimensional space. For this, we used the ape package, the *gowdis* function (Gower 1971) and then the *pcoa* function in the R program (Laliberte and Legendre 2010). Thus, when including ecological data, we can better explore which attributes influenced the results the most, providing a better predictive power of morphological trends within the WSE bird assemblage.

Finally we estimated functional diversity using the Functional Richness Index (Fric) (Villeger *et al*. 2008) to quantify the representation of the reduced space of the specialist group visualized in the pPCA and PCA analyses. Functional richness (Fric) uses the space from the common convex covering all species in the community. We used the FD package, *dbFD* function by Laliberté *et al*. (2014), and obtained a Fric value for the generalist species assemblage and for the specialist species assemblage. However, because Fric values are strongly correlated to the number of species in the community, we used a rarefaction method (Gotelli and Colwell 2001), which allowed us to compare the Fric index while controlling by the effect of different number of species between the specialist and generalist assemblages. We extracted the Fric value 1000 times by randomly drawing 22 species from the 102 generalists, and compared it with the observed Fric value for the specialist bird community (with 22 species).

## Results

The WSE bird assemblage analyzed is composed by 124 bird species (2Table 1), 102 generalists (82 genera, 37 families and 18 orders) and 22 specialists (21 genera, 13 families and 4 orders). The proportions of species distributed among the major lineages (orders) were similar between generalist (17.5%) and specialist (19%) birds (Figure 1). Specialist species are grouped in different lineages when compared to generalist species and are represented by lineages throughout the bird clade (e.g., from Tinamiformes and Caprimulgiformes to Passeriformes, Figure 1).

Most specialist birds are insectivorous or omnivorous (Figure 2). In contrast, frugivorous and nectarivorous species were proportionately more diverse among generalist species (Figure 2). There is a clear predominance of understory species among specialist birds, while canopy species are more diverse among generalist species (Figure 2). Indeed, only five species that use the vegetation canopy are WSE specialists. Only one tinamou (*Crypturellus duidae*) forages on the ground within specialist species, and other 10 species within the group of generalists (Figure 2). Solitary species appear to be more common among specialists, while habitat generalist species include a slightly higher proportion of species that congregate in mono- or heterospecific flocks (Figure 2).

The first two components of pPCA accounted for 74.43% of the variations in morphological data with PC1 (61.22%) and PC2 (13.21%). Generalist and specialist species showed a wide overlap in the multidimensional morphological space, although specialist species showed reduced morphological variability (Figure 3a). On the axis 1 of the pPCA, weight (59%) was the variable that most grouped the species in the multidimensional space followed by the length of the primary wing feathers (0.77) and the tarsus length (0.68). On the axis 2, tail length (0.93) was the only morphological variable to obtain a positive value on the axis, all other morphological traits have negative values on the axis (Figure 3a). The PCA analysis without phylogenetic control showed a similar pattern to the pPCA analysis but with an even higher morphological variability between species groups (Figure 3b).

PCA analyses performed separately for each species group indicated that for the generalist species PC1 represented 61% of the morphological variations, with longer primary wing feathers for generalist species. The same value of primary wing feathers was found for specialist birds in PC1. The morphological attribute that most influenced the multidimensional space for both generalist and specialist species was the length of the primary feathers. The generalist species have longer wings, wider and heavier beaks than the specialist species. Finally, although there are some marked differences in the categorical functional traits used in this study (Figure 2), the multivariate analysis (PCoA) considering morphological and categorical ecological traits did not discriminate between specialist and generalist species based on morphology, diet, foraging strata, and sociability (Figure 4).

Functional richness measured by Fric was similar for the WSE generalist assemblage (102 species; Fric = 0.93) and for the specialist bird assemblage (22 species; Fric = 0.97), although slightly higher for specialists. Using rarefaction to take the effect of the difference in number of species between generalists and specialists, there was no significant difference in the Fric index (Figure 5) among assemblages. Functional richness as measured by the Fric index was similar between groups, with specialist birds having the same functional diversity as generalists (Figure 5).

## Discussion

White-sand ecosystems are island-like environments where ecological factors may limit the colonization of species not adapted to extreme ecological conditions (Adeney *et al.*

2016). Here, we describe and compare morphological and ecological traits of specialist and generalist species that use WSE. We did not find evidence for differentiated ecomorphological adaptations in the specialist species group associated with WSE when compared with the generalist species that also use WSE habitats besides other environments. Generalist and specialist species showed a wide overlap in the multidimensional morphological space, although specialist species showed reduced morphological variability. However, functional diversity among specialist birds is not different from functional diversity of generalists, therefore even with a reduced number of species in the specialist assemblage, functional diversity is not reduced when compared to the assemblage of generalist species.

Generalist species are more flexible in habitat use and have a greater capacity to colonize new niches and occupy the same functional space as specialist species (Pigot *et al.* 2020). On the other hand, despite low taxonomic diversity of specialists, they are more abundant locally than generalists and may represent 30% to 50% of individuals caught in mist nets (Borges *et al*. 2016*b*). This high degree of species dominance, with high local abundances, may be interpreted as a consequence of specialization and higher ability to occupy and explore resources in habitats with such stressful conditions as in WSE. In white-sand ecosystems plant communities are mostly structured by soil characteristics with flooding and oligotrophic soils imposing stressful conditions on plant communities (Damasco *et al*. 2012). As such, specialist species may have responded stronger to environmental filters than have generalist species in WSE.

Our results point to a group of specialist species from WSE mainly composed by insectivorous species that live solitarily in the understory of the shrub vegetation. We also show that the morphology of most species in the WSE community with narrow beaks is consistent with the insectivorous diet of most specialist species. Specialization should result in restrictions on habitats used rather than items fed within a given area (Morse 1971). The restrictions exerted by the patchy and harsh environment in WSE may result in a higher dependence on more reliable and constant resources such as insects, in opposition to a highly seasonal resource such as fruits, and, as a consequence, morphology related to foraging should be less variable. We show that bird species in the specialist group have mostly narrow beaks when compared to generalist birds that have wider and heavier beaks. On the other hand, generalist species will thrive primarily through behavioral plasticity switching environments when resources are scarce. The low diversity of frugivores among the specialist species may be additional evidence of an environmental filter, since the WSE are dominated by xeromorphic vegetation (Vicentini 2004) that likely provides scarce and intermittent fruit availability.

Because our comparison includes two groups of species that use WSE, it is difficult to disentangle the effects and intensity of selective pressures imposed by the stressful environmental conditions of the WSE itself. Future studies should further investigate specialization of WSE specialist birds by, for example, comparing ecomorphological traits with other groups of species that do not use WSE habitats. Furthermore, our data, do not allow comparisons of the ecomorphology of species specialized in WSE with that of their closest relatives. For instance, available phylogenies suggest that the closest relatives of birds specialized in WSE occupy extra-Amazonian biomes such as *tepuis, Cerrado, Caatinga* and Atlantic Forest (Capurucho *et al*. 2013; Matos *et al*. 2016; Crouch *et al*. 2018; Ribas and Aleixo 2019). The ancestors of these species may have occupied white sand ecosystems in periods of expansion of this environment and, subsequently, may have experienced a period of isolation long enough to have become independent species (Gubili *et al*. 2016; Capurucho 2020). Ecomorphological comparisons between specialist birds and their relatives from other environments may shed light on ecomorphological adaptations on a broader temporal scale than that adopted in the present study.

Here we show that the functional space of WSE specialist species is more restricted than that of generalists in the use of the ecomorphological space, a pattern consistent with the ecological restrictions imposed by this environment (e.g. Anderson 1981; Adeney *et al*. 2016; Capurucho *et al*. 2020). However, we also show that despite reduced taxonomic diversity of specialist species and occupation of a reduced functional space, this group does not have a reduced functional diversity when compared to the more diverse group of generalists. Specializing in such a harsh and fragile habitat can have a high evolutionary cost, and the behavior that increases movement and dispersal between patches to access resources in other habitat patches can be more advantageous than developing specific morphological structures. In addition, the dynamics of historical landscape changes resulting in expansion and increase of connectivity between patches of white-sand ecosystems may have contributed to increasing the dispersive capacity of these birds. In this sense, the behavioral functional trait of habitat use may be more relevant to specialization than the morphological or ecological traits considered in this study. However, morpho-functional comparisons between specialist bird species and their closest relatives that inhabit other environments are essential to better understand the evolution of specialization among birds in the Amazon white-sand ecosystems.

## Conclusions

A number of studies in the last decade have increased our knowledge about Amazonian white-sand ecosystems, but the ecomorphology of white-sand ecosystem specialist birds was not previously investigated. Here, we show that specialist and generalist species that use white-sand habitat patches show a wide overlap in the multidimensional morphological space, but specialist species have reduced morphological variability. Moreover, functional diversity is not reduced in the specialist species assemblage as maybe expected when compared to the assemblage of generalist species. Specializing in a patchy, harsh and fragile habitat can have a high evolutionary cost, and the behavior that increases movement and dispersal between patches to access resources in other habitat patches can be more advantageous than evolving specific habitat specializations. This study brings new insights into habitat specialization of white-sand ecosystem birds, and opens new questions on the role of environmental filters on Amazonian bird communities.

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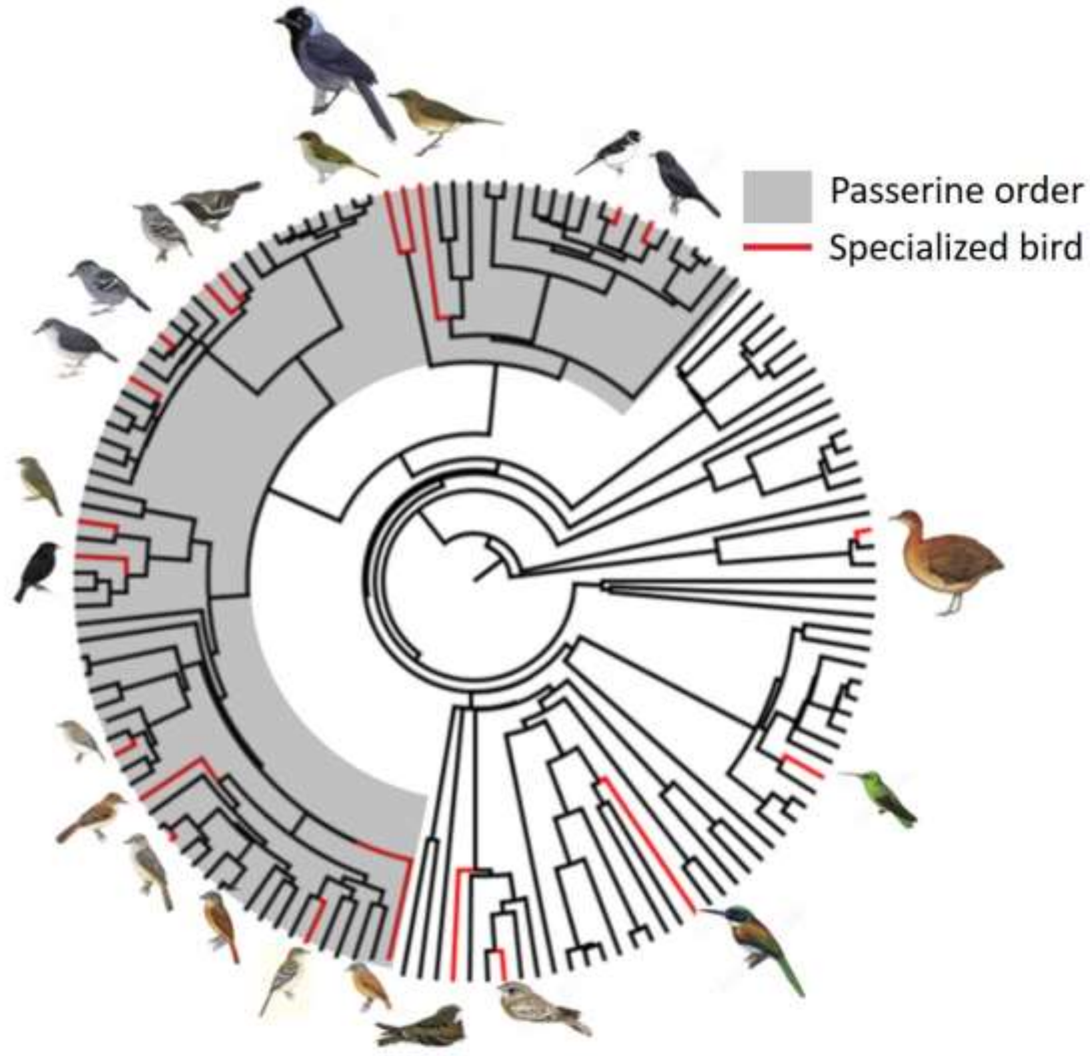

**Figure 1**. Consensus phylogenetic tree of the 102 generalist bird species (terminals with black line) and 22 species specialized in Amazonian white-sand habitat patches (terminals with red line). Data from “A Global Phylogeny of Birds” (site: www.birdtree).

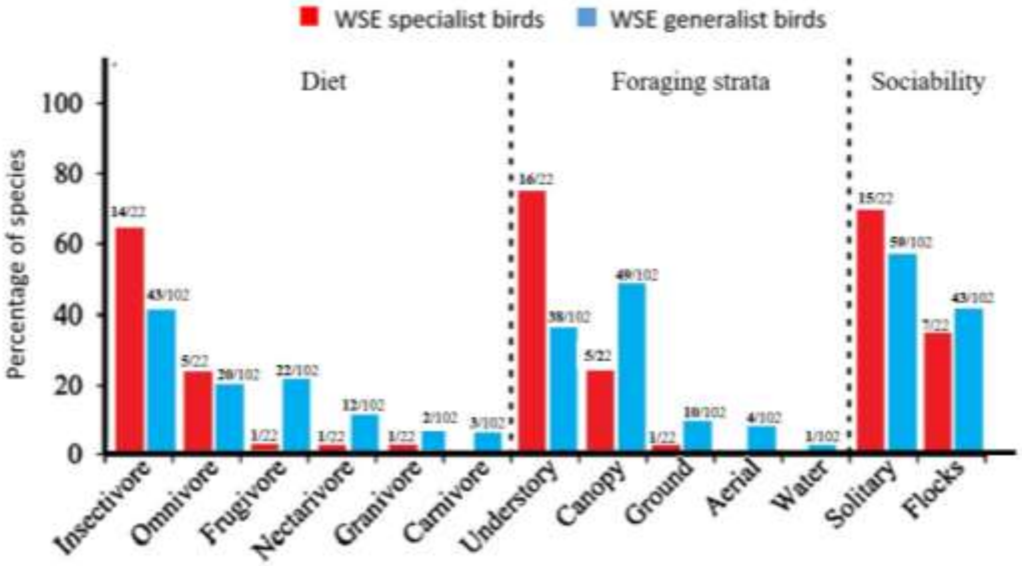

**Figure 2.** Percentage of Amazonian white-sand ecosystem bird species distributed in the major categories of diet, foraging strata and sociability. Numbers above columns are number of species within each category and total number of species for the specialist and generalist groups. Percentages within each category were calculated separately for specialist and generalist species.

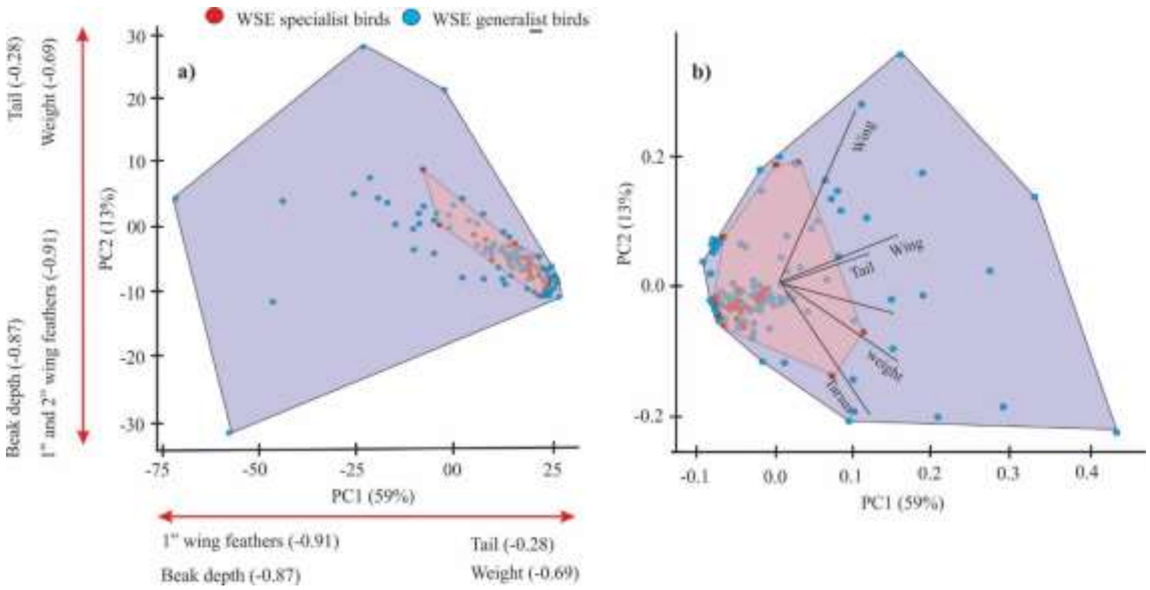

**Figure 3.** Analysis of morphological data of Amazonian white-sand ecosystem birds using: A – phylogenetic principal component analysis (pPCA); and B – principal component analysis without phylogenetic control. Blue dots represent generalist species (102 species) and red dots represent specialist species (22 species).

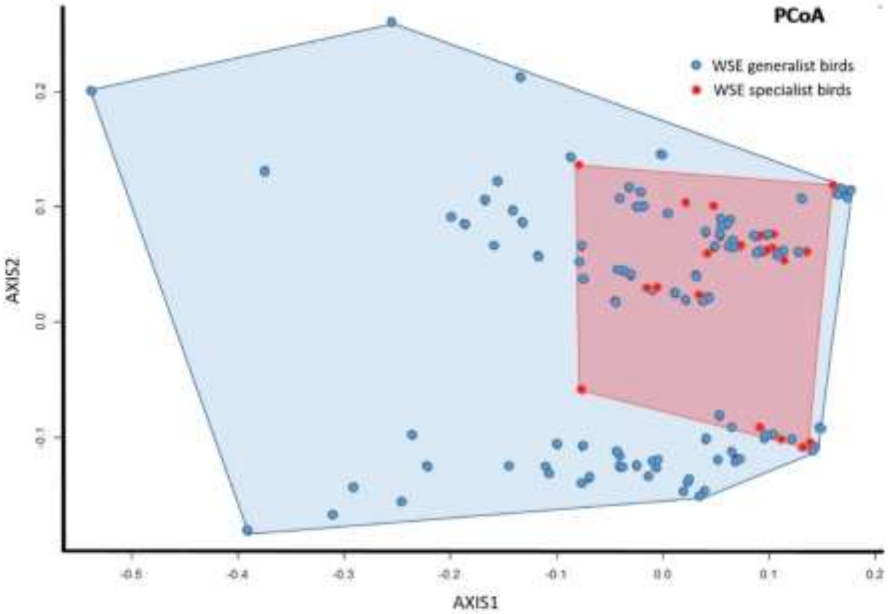

**Figure 4.** Principal Coordinate Analysis (PCoA) with morphological and ecological traits of specialist and generalist Amazonian white-sand ecosystem birds. Blue dots represent generalist species (102 species) and red dots represent specialist species (22 species).

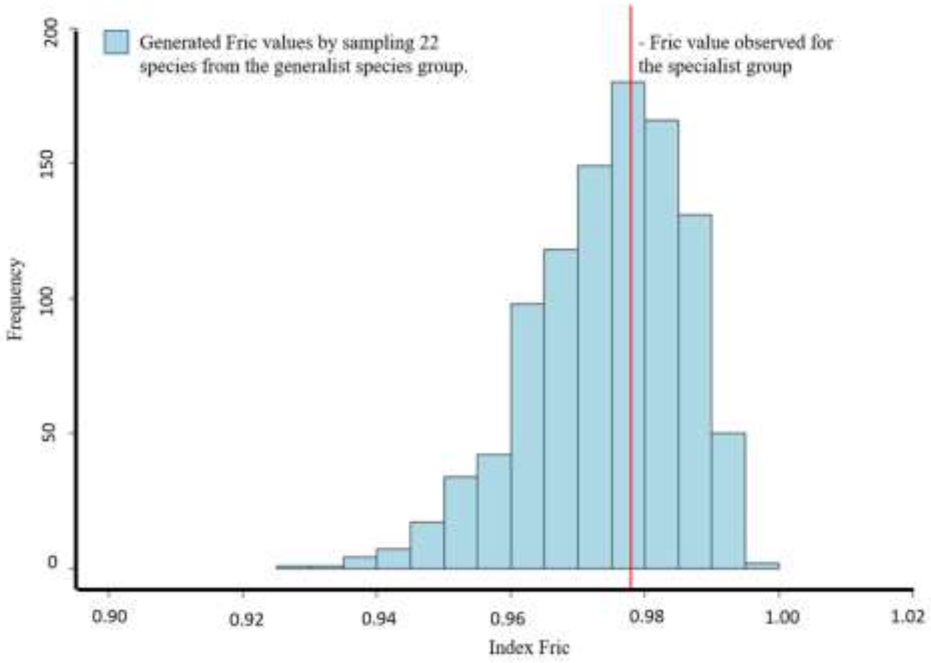

**Figure 5.** Result of the rarefaction performed with 1000 values generated for Fric by sampling 22 species from the generalist bird community (blue) in relation to the Fric value observed for the specialist community (red line) in Amazonian white-sand habitat patches.

**Table 1.** List of bird species that inhabit Amazonian white-sand habitat patches within categories and attributes analyzed in this study. The scientific nomenclature in this list is based on the list of birds from the Brazilian Committee of Ornithological Records (Pacheco *et al.* 2021). Columns with categorical ecological data were obtained from Borges *et al.* (2016), Wilman *et al.* (2014), Cohn-Haft *et al.* (1997) and personal observations (see Table 2). The nine morphological measurements were obtained by only one of the authors (GRL) and values represent the mean of three individuals measured per species.

| **Bird species** | **Habitat category** | **Diet category** | **Foraging strata** | **Sociability** | **Weight (g)** | **Tail length (mm)** | **Tarsus length (mm)** | **Beak length (mm)** | **Beak width (mm)** | **Beak depth (mm)** | **Wing prim. lenght (mm)** | **Wing secon. lenght (mm)** | **Kipp distance (mm)** |
|---|---|---|---|---|---:|---:|---:|---:|---:|---:|---:|---:|---:|
| *Amazilia fimbriata* | Generalist | Nectarivore | Understory | Solitary/pairs | 4 | 31.09 | 5.32 | 18.31 | 3.62 | 2.3 | 52.58 | 28.38 | 53.94 |
| *Amazilia versicolor* | Generalist | Nectarivore | Canopy | Solitary/pairs | 3 | 31.04 | 6.04 | 16.3 | 4.62 | 2.4 | 50.32 | 28.81 | 57.26 |
| *Amazona amazônica* | Generalist | Frugivore | Canopy | Flocks | 391.5 | 124.76 | 25.47 | 33.1 | 19.91 | 28.66 | 205.53 | 8.84 | 4.3 |
| *Ara ararauna* | Generalist | Frugivore | Canopy | Flocks | 150 | 46.03 | 43.98 | 67.1 | 30.55 | 66.73 | 383.87 | 88.83 | 23.14 |
| *Aratinga leucophthalma* | Generalist | Frugivore | Canopy | Flocks | 147.5 | 141.99 | 20.01 | 25.01 | 17.26 | 29.01 | 163.83 | 51.01 | 31.14 |
| *Aratinga pertinax* | Generalist | Frugivore | Canopy | Flocks | 79 | 97.28 | 14.74 | 19.97 | 12.38 | 21.73 | 133.01 | 41.65 | 31.22 |
| *Asio stygius* | Generalist | Carnivore | Ground | Solitary/pairs | 610 | 18.73 | 59.08 | 34.6 | 26.19 | 23.89 | 354.33 | 80.33 | 22.67 |
| *Attila cinnamomeus* | Generalist | Omnivore | Canopy | Solitary/pairs | 32.5 | 75.16 | 23.03 | 18.8 | 11.49 | 6.64 | 90.76 | 14.18 | 15.58 |
| *Attila spadiceus* | Generalist | Omnivore | Canopy | Solitary/pairs | 31.5 | 68.24 | 25.26 | 18 | 11.75 | 5.8 | 80.44 | 12.54 | 15.58 |
| *Automolus ochrolaemus* | Generalist | Insectivore | Understory | Solitary/pairs | 35 | 78.86 | 23.7 | 18.47 | 12.07 | 6.99 | 86.04 | 15.38 | 17.79 |
| *Brotogeris chrysoptera* | Generalist | Frugivore | Canopy | Flocks | 58.83 | 79.07 | 15.04 | 18.93 | 10.54 | 14.76 | 113.62 | 39.06 | 34.1 |
| *Bucco tamatiá* | Generalist | Insectivore | Understory | Solitary/pairs | 36.5 | 71.79 | 20.02 | 22.11 | 15.18 | 11.65 | 78.61 | 11.01 | 14.07 |
| *Buteo magnirostris* | Generalist | Carnivore | Understory | Solitary/pairs | 226.7 | 155.22 | 69.22 | 26.34 | 21.62 | 16.72 | 216.56 | 56.67 | 26.11 |
| *Camptostoma obsoletum* | Generalist | Insectivore | Canopy | Solitary/pairs | 7.6 | 35.78 | 12.46 | 8.41 | 6.05 | 3.52 | 44.91 | 8.19 | 18.24 |
| *Caprimulgus nigrescens* | Generalist | Insectivore | Water | Solitary/pairs | 37.5 | 104.3 | 15.26 | 9.87 | 16.87 | 3.31 | 137.41 | 55.79 | 40.63 |
| *Caprimulgus rufus* | Generalist | Insectivore | Understory | Solitary/pairs | 98 | 127.6 | 18.21 | 15.96 | 32.1 | 4.34 | 169.49 | 77.46 | 45.7 |
| *Caryothraustes canadenses* | Generalist | Frugivore | Canopy | Flocks | 29 | 72.77 | 21.27 | 15.51 | 10.82 | 10.39 | 83.46 | 12.15 | 14.56 |

| **Bird species** | **Habitat category** | **Diet category** | **Foraging strata** | **Sociability** | **Weight (g)** | **Tail length (mm)** | **Tarsus length (mm)** | **Beak length (mm)** | **Beak width (mm)** | **Beak depth (mm)** | **Wing prim. lenght (mm)** | **Wing secon. lenght (mm)** | **Kipp distance (mm)** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Celeus grammicus* | Generalist | Omnivore | Canopy | Solitary/pairs | 65 | 94.13 | 22.54 | 20.78 | 10.65 | 8.67 | 120.69 | 27.97 | 23.17 |
| *Celeus torquatus* | Generalist | Omnivore | Canopy | Solitary/pairs | 117 | 116.93 | 29.87 | 32.18 | 13.53 | 10.19 | 152.71 | 32.86 | 21.51 |
| *Cercomacra tyrannina* | Generalist | Insectivore | Understory | Solitary/pairs | 14.63 | 64.78 | 25.05 | 14.48 | 8.47 | 4.73 | 59.94 | 7.19 | 11.97 |
| *Chelidoptera tenebrosa* | Generalist | Insectivore | Aerial | Flocks | 36.33 | 57.13 | 15.87 | 18.09 | 10.99 | 7.39 | 105.5 | 14.69 | 13.88 |
| *Chloroceryle aenea* | Generalist | Carnivore | Water | Solitary/pairs | 12.33 | 38.87 | 7.57 | 20.35 | 10.72 | 6.85 | 53.9 | 12.61 | 23.33 |
| *Chlorostilbon mellisugus* | Generalist | Nectarivore | Canopy | Solitary/pairs | 4 | 24.96 | 5.82 | 14.45 | 2.69 | 1.84 | 39.9 | 24.73 | 61.98 |
| *Chrysolampis mosquitus* | Generalist | Nectarivore | Canopy | Solitary/pairs | 3.75 | 35.93 | 6 | 12.91 | 4.19 | 2.2 | 53.65 | 31.63 | 58.95 |
| *Coereba flaveola* | Generalist | Nectarivore | Canopy | Solitary/pairs | 8.25 | 35.98 | 17.85 | 11.19 | 5.29 | 3.83 | 55.07 | 10.26 | 18.52 |
| *Columbina passerina* | Generalist | Frugivore | Ground | Flocks | 35 | 67.04 | 18.2 | 11.13 | 6.19 | 4.32 | 76.47 | 14.14 | 18.49 |
| *Conopias parvus* | Generalist | Frugivore | Canopy | Flocks | 22.75 | 71.34 | 18.02 | 16.18 | 11.99 | 6.11 | 77.72 | 14.73 | 18.95 |
| *Crypturellus cinereus* | Generalist | Frugivore | Ground | Solitary/pairs | 300 | 74.81 | 55.42 | 21.8 | 18.89 | 8.52 | 169.67 | 15.4 | 9.08 |
| *Crypturellus erythropus* | Generalist | Omnivore | Ground | Solitary/pairs | 452.5 | 74.81 | 55.46 | 28.09 | 8.77 | 9.08 | 151.42 | 17.18 | 11.35 |
| *Crypturellus soui* | Generalist | Omnivore | Ground | Solitary/pairs | 180 | 51.02 | 37.92 | 17.1 | 11.44 | 5.98 | 105.21 | 9 | 8.56 |
| *Dendrocincla fuliginosa* | Generalist | Insectivore | Understory | Solitary/pairs | 39.25 | 94.34 | 26.41 | 24.64 | 10.76 | 7.99 | 101.92 | 18.19 | 17.83 |
| *Dendrocincla merula* | Generalist | Insectivore | Understory | Flocks | 46.33 | 88.23 | 26.46 | 23.42 | 11.3 | 7.69 | 103.02 | 19.32 | 18.76 |
| *Dendrocolaptes certhia* | Generalist | Insectivore | Canopy | Solitary/pairs | 80.19 | 116.86 | 34.93 | 22.74 | 13.76 | 9.27 | 123.33 | 19.13 | 16.21 |
| *Dendroplex picus* | Generalist | Insectivore | Understory | Solitary/pairs | 34 | 84.81 | 23.33 | 24.02 | 10.91 | 7.02 | 93.54 | 17.4 | 18.52 |
| *Elaenia cristata* | Generalist | Omnivore | Understory | Solitary/pairs | 18.13 | 61.58 | 20.32 | 10.87 | 9.69 | 4.91 | 65.29 | 10.73 | 16.41 |
| *Emberizoides herbicola* | Generalist | Omnivore | Understory | Solitary/pairs | 24.83 | 101.61 | 26.69 | 32.59 | 8.81 | 7.12 | 69.28 | 11.56 | 16.67 |
| *Euphonia rufiventris* | Generalist | Frugivore | Canopy | Solitary/pairs | 14.7 | 70.07 | 18.4 | 8.56 | 7.15 | 5.79 | 57.5 | 9.65 | 16.79 |
| *Hemitriccus margaritaceiventer* | Generalist | Insectivore | Understory | Solitary/pairs | 7.17 | 37.54 | 20.84 | 11.93 | 7.42 | 3.79 | 47.48 | 8.14 | 17.2 |
| *Hemitriccus minimus* | Generalist | Insectivore | Canopy | Solitary/pairs | 7.5 | 36.38 | 16.07 | 11.31 | 7.67 | 3.53 | 45.96 | 6.17 | 13.43 |
| *Heterocercus flavivertex* | Generalist | Omnivore | Canopy | Flocks | 20 | 58.92 | 16.71 | 11.67 | 10.18 | 4.58 | 81.3 | 11.36 | 13.97 |
| *Hydropsalis climacocerca* | Generalist | Insectivore | Aerial | Solitary/pairs | 55.5 | 144.22 | 23.58 | 10.84 | 23.07 | 3.72 | 145.33 | 50.27 | 34.58 |
| *Hylocharis cyanus* | Generalist | Nectarivore | Understory | Solitary/pairs | 3 | 31.09 | 4.8 | 15.94 | 4.31 | 2.27 | 48.23 | 30.2 | 62.61 |
| *Hylocharis sapphirina* | Generalist | Nectarivore | Understory | Solitary/pairs | 4.33 | 33.39 | 5.69 | 19.15 | 4.42 | 2.49 | 52.9 | 33.22 | 62.86 |
| *Laterallus exilis* | Generalist | Insectivore | Ground | Solitary/pairs | 76.5 | 36.5 | 36.81 | 18.25 | 8.73 | 8.49 | 84.06 | 7.71 | 9.16 |

| **Bird species** | **Habitat category** | **Diet category** | **Foraging strata** | **Sociability** | **Weight (g)** | **Tail length (mm)** | **Tarsus length (mm)** | **Beak length (mm)** | **Beak width (mm)** | **Beak depth (mm)** | **Wing prim. lenght (mm)** | **Wing secon. lenght (mm)** | **Kipp distance (mm)** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Leptotila rufaxilla* | Generalist | Granivore | Ground | Solitary/pairs | 152 | 110.74 | 29.36 | 16.1 | 8.11 | 5.34 | 131.75 | 24.29 | 18.33 |
| *Lipaugus vociferans* | Generalist | Omnivore | Canopy | Flocks | 67.5 | 119.53 | 22.36 | 19.83 | 16.29 | 8.31 | 121.96 | 22.7 | 18.62 |
| *Megascops choliba* | Generalist | Insectivore | Understory | Solitary/pairs | 128.33 | 96.4 | 33.71 | 21.05 | 16.55 | 13.95 | 168.11 | 42.41 | 25.23 |
| *Mionectes macconnelli* | Generalist | Insectivore | Understory | Flocks | 11.7 | 54.7 | 17.47 | 11.71 | 8.08 | 4.16 | 62.34 | 10.04 | 16.05 |
| *Mionectes oleagineus* | Generalist | Frugivore | Understory | Flocks | 10.07 | 49.87 | 16.08 | 9.44 | 6.82 | 3.45 | 59.09 | 7.31 | 12.34 |
| *Myiarchus ferox* | Generalist | Omnivore | Understory | Solitary/pairs | 25.75 | 95.33 | 23.11 | 17.75 | 11.05 | 6.26 | 87.84 | 13.17 | 14.96 |
| *Myiarchus tuberculifer* | Generalist | Insectivore | Canopy | Solitary/pairs | 20.25 | 82.04 | 21.31 | 16.43 | 10.78 | 5.45 | 81.92 | 13.12 | 16.01 |
| *Myiopagis gaimardii* | Generalist | Insectivore | Canopy | Flocks | 9.5 | 50.76 | 19.66 | 8.27 | 5.63 | 3.58 | 51.83 | 4.85 | 9.36 |
| *Myiozetetes cayanensis* | Generalist | Insectivore | Understory | Solitary/pairs | 25.25 | 81.78 | 20.73 | 12.44 | 9.13 | 5.73 | 87.06 | 12.87 | 14.73 |
| *Myrmotherula axillaris* | Generalist | Insectivore | Understory | Flocks | 7.75 | 40.43 | 17.54 | 11.48 | 6.42 | 3.89 | 50.54 | 5.04 | 9.96 |
| *Nyctibius griseus* | Generalist | Insectivore | Canopy | Solitary/pairs | 81 | 180.33 | 17.58 | 17.64 | 37.19 | 5.16 | 238.67 | 87 | 36.45 |
| *Nyctiprogne leucopyga* | Generalist | Insectivore | Canopy | Flocks | 29.33 | 106.15 | 10.51 | 5.73 | 12.42 | 2.94 | 137 | 55.63 | 40.6 |
| *Ortalis motmot* | Generalist | Frugivore | Canopy | Flocks | 546 | 256.5 | 66.01 | 22.86 | 19.14 | 12.8 | 197.5 | 11.18 | 5.74 |
| *Orthopsittaca manilata* | Generalist | Frugivore | Canopy | Flocks | 220 | 234.33 | 20.9 | 31.93 | 17.04 | 29.68 | 233 | 68.24 | 29.29 |
| *Patagioenas cayennensis* | Generalist | Frugivore | Canopy | Solitary/pairs | 156 | 134.67 | 29.15 | 17.4 | 11.65 | 6.09 | 185 | 66.33 | 35.86 |
| *Patagioenas plumbea* | Generalist | Frugivore | Canopy | Solitary/pairs | 170 | 144.33 | 19.79 | 16.74 | 9.43 | 6.28 | 172.33 | 45.55 | 26.43 |
| *Patagioenas speciosa* | Generalist | Frugivore | Canopy | Solitary/pairs | 253 | 119.74 | 24.47 | 21.08 | 10.04 | 8.56 | 183 | 62.67 | 34.27 |
| *Phaethornis malaris* | Generalist | Nectarivore | Understory | Flocks | 6 | 73.58 | 5.28 | 37.66 | 4.41 | 3.58 | 59.89 | 35.36 | 59.08 |
| *Phaethornis ruber* | Generalist | Nectarivore | Understory | Solitary/pairs | 2.25 | 36.86 | 4.82 | 22.57 | 4.05 | 2.86 | 35.61 | 19.91 | 55.84 |
| *Phaethornis superciliosus* | Generalist | Nectarivore | Understory | Flocks | 5.5 | 69.44 | 5.74 | 39.88 | 5.22 | 3.43 | 60.74 | 35.71 | 58.77 |
| *Piaya cayana* | Generalist | Insectivore | Canopy | Solitary/pairs | 98 | 269 | 40.31 | 25.91 | 15.69 | 11.66 | 137.67 | 10.44 | 7.59 |
| *Picumnus exilis* | Generalist | Insectivore | Understory | Flocks | 10 | 28.49 | 14.4 | 10.09 | 6.2 | 5.21 | 50.91 | 7.86 | 15.31 |
| *Pipra erythrocephala* | Generalist | Frugivore | Understory | Flocks | 14 | 31.28 | 14.19 | 8.79 | 8.4 | 3.81 | 58.98 | 11.81 | 20.02 |
| *Pipra pipra* | Generalist | Frugivore | Understory | Flocks | 12 | 28 | 15.24 | 8.32 | 7.83 | 4.34 | 61.86 | 8.77 | 14.19 |
| *Pitangus sulphuratus* | Generalist | Omnivore | Ground | Solitary/pairs | 54.5 | 91.21 | 25.34 | 24.09 | 12.96 | 8.96 | 110 | 18.77 | 17.07 |

| Bird species | Habitat category | Diet category | Foraging strata | Sociability | Weight (g) | Tail length (mm) | Tarsus length (mm) | Beak length (mm) | Beak width (mm) | Beak depth (mm) | Wing prim. lenght (mm) | Wing secon. lenght (mm) | Kipp distance (mm) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Polioptila plumbea* | Generalist | Insectivore | Understory | Flocks | 6.5 | 51.81 | 16.21 | 9.9 | 6.36 | 2.68 | 47.26 | 6.31 | 13.35 |
| *Psarocolius viridis* | Generalist | Omnivore | Canopy | Flocks | 170 | 155.33 | 47.01 | 48.76 | 17.41 | 16.28 | 185.33 | 43.5 | 23.47 |
| *Ramphastos tucanus* | Generalist | Frugivore | Canopy | Solitary/pairs | 663.75 | 186 | 53.12 | 153.44 | 37.87 | 51.54 | 227 | 45.9 | 20.22 |
| *Ramphastos vitellinus* | Generalist | Frugivore | Canopy | Solitary/pairs | 345 | 182.33 | 47.81 | 115.82 | 29.93 | 38.06 | 197.4 | 24.42 | 12.37 |
| *Ramphocelus carbo* | Generalist | Omnivore | Understory | Flocks | 18.5 | 79.05 | 22.1 | 13.93 | 13.18 | 8.32 | 74.23 | 9.67 | 12.97 |
| *Ramphotrigon ruficauda* | Generalist | Insectivore | Canopy | Solitary/pairs | 17 | 36.85 | 15.91 | 13.2 | 11.25 | 5.86 | 72.31 | 11.94 | 16.48 |
| *Rhytipterna simplex* | Generalist | Insectivore | Canopy | Flocks | 29 | 100.52 | 20.41 | 16.85 | 11.42 | 6.51 | 95.43 | 14.38 | 15.07 |
| *Sakesphorus canadensis* | Generalist | Insectivore | Understory | Flocks | 24.8 | 63.34 | 27.62 | 17.83 | 10.21 | 6.55 | 72.16 | 5.5 | 7.62 |
| *Schiffornis turdina* | Generalist | Omnivore | Understory | Solitary/pairs | 33.83 | 71.43 | 23.85 | 13.93 | 10.23 | 6.21 | 91.61 | 17.06 | 18.57 |
| *Sporophila angolensis* | Generalist | Granivore | Understory | Solitary/pairs | 13 | 56.02 | 17.61 | 11.62 | 9.89 | 10.72 | 57.81 | 9.19 | 15.88 |
| *Schistochlamys melanopis* | Generalist | Omnivore | Canopy | Solitary/pairs | 27.66 | 78.85 | 22.8 | 14.7 | 9.32 | 8.56 | 78.4 | 11.23 | 14.38 |
| *Sittasomus griseicapillus* | Generalist | Insectivore | Canopy | Flocks | 16.5 | 83.93 | 20.06 | 15.91 | 9.28 | 4.69 | 81.36 | 19.74 | 24.25 |
| *Stelgidopteryx ruficollis* | Generalist | Insectivore | Aerial | Flocks | 15.5 | 58.81 | 12.35 | 6.62 | 10.54 | 2.84 | 110.55 | 57.41 | 51.93 |
| *Tangara cayana* | Generalist | Frugivore | Canopy | Solitary/pairs | 18 | 55.27 | 37.04 | 10.11 | 8.99 | 5.86 | 68.82 | 17.38 | 25.27 |
| *Thalurania furcata* | Generalist | Nectarivore | Understory | Solitary/pairs | 4.17 | 37.13 | 5.04 | 20.26 | 4.6 | 2.09 | 51.1 | 31.15 | 60.95 |
| *Thamnophilus doliatus* | Generalist | Insectivore | Understory | Flocks | 24.63 | 65.1 | 29.52 | 16.07 | 9.39 | 6.46 | 74.2 | 5.94 | 7.99 |
| *Thamnophilus punctatus* | Generalist | Insectivore | Understory | Solitary/pairs | 25.56 | 62.16 | 23.23 | 15.22 | 9.61 | 6.5 | 74.02 | 11.92 | 15.36 |
| *Thraupis episcopus* | Generalist | Omnivore | Canopy | Flocks | 29.33 | 70.07 | 24.23 | 12.88 | 10.54 | 7.54 | 89.07 | 17.55 | 19.7 |
| *Thryothorus coraya* | Generalist | Insectivore | Understory | Solitary/pairs | 15.33 | 55.95 | 24.13 | 15.85 | 8.48 | 5.25 | 59.24 | 6.42 | 10.82 |
| *Tolmomyias flaviventris* | Generalist | Insectivore | Canopy | Solitary/pairs | 12.83 | 53.63 | 18.78 | 9.66 | 9.7 | 4.54 | 55.56 | 7.09 | 12.77 |
| *Tolmomyias poliocephalus* | Generalist | Insectivore | Canopy | Flocks | 11.75 | 49.21 | 18.14 | 10.66 | 9.07 | 4.09 | 54.34 | 8.64 | 15.94 |
| *Topaza pyra* | Generalist | Nectarivore | Canopy | Flocks | 14.67 | 113.49 | 7.75 | 22.1 | 7 | 3.17 | 82.94 | 50.68 | 61.1 |
| *Trogon viridis* | Generalist | Omnivore | Canopy | Solitary/pairs | 84 | 151.5 | 17.76 | 20.44 | 19.05 | 13.03 | 133.45 | 47.77 | 35.8 |
| *Tyrannulus elatus* | Generalist | Omnivore | Canopy | Flocks | 7.17 | 41.89 | 14.06 | 5.99 | 5.66 | 3.59 | 49.32 | 7.66 | 15.5 |
| *Tyrannus melancholicus* | Generalist | Insectivore | Canopy | Flocks | 41 | 93.14 | 19.41 | 19.9 | 12.84 | 7.22 | 110.49 | 27.67 | 24.96 |
| *Vanellus chilensis* | Generalist | Insectivore | Ground | Flocks | 150 | 110.59 | 70.81 | 28.11 | 10.27 | 11.45 | 207 | 11.05 | 5.3 |
| *Willisornis poecilinotus* | Generalist | Insectivore | Understory | Flocks | 18.33 | 51.07 | 25.15 | 15.17 | 10.16 | 5.52 | 66.48 | 8.43 | 12.67 |

| **Bird species** | **Habitat category** | **Diet category** | **Foraging strata** | **Sociability** | **Weight (g)** | **Tail length (mm)** | **Tarsus length (mm)** | **Beak length (mm)** | **Beak width (mm)** | **Beak depth (mm)** | **Wing prim. lenght (mm)** | **Wing secon. lenght (mm)** | **Kipp distance (mm)** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Xenops minutus* | Generalist | Insectivore | Canopy | Flocks | 11.75 | 53.68 | 16.1 | 11.28 | 6.19 | 4.72 | 64.25 | 12.44 | 19.28 |
| *Xipholena punicea* | Generalist | Frugivore | Canopy | Flocks | 66 | 76.77 | 22.9 | 14.89 | 15.73 | 6.77 | 117.34 | 16.49 | 14.05 |
| *Xiphorhynchus obsoletus* | Generalist | Insectivore | Understory | Solitary/pairs | 32.67 | 89.23 | 22.73 | 23.23 | 9.84 | 7.02 | 96.73 | 17.57 | 18.12 |
| *Xiphorhynchus ocellatus* | Generalist | Insectivore | Understory | Solitary/pairs | 32.67 | 89.23 | 22.73 | 23.23 | 9.84 | 7.02 | 96.73 | 17.57 | 18.12 |
| *Zimmerius gracilipes* | Generalist | Insectivore | Canopy | Flocks | 6.75 | 42.75 | 14.9 | 7.9 | 6.81 | 3.44 | 45.7 | 7.37 | 16.02 |
| *Zonotrichia capensis* | Generalist | Omnivore | Ground | Flocks | 15.77 | 64.82 | 23.57 | 12.12 | 7.61 | 6.64 | 65.33 | 11.6 | 17.75 |
| *Attila citriniventris* | Specialist | Insectivore | Canopy | Solitary/pairs | 33 | 68.58 | 20.82 | 19.19 | 12.55 | 5.97 | 79.91 | 14.04 | 17.61 |
| *Caprimulgus cayennensis* | Specialist | Insectivore | Understory | Solitary/pairs | 32.83 | 115.49 | 15.91 | 10.93 | 16.81 | 3.59 | 133.98 | 57.28 | 42.73 |
| *Chordeiles pusillus* | Specialist | Insectivore | Canopy | Flocks | 27.5 | 86.14 | 13.05 | 4.67 | 12.97 | 3.04 | 136.09 | 55.04 | 40.47 |
| *Cnemotriccus fuscatus* | Specialist | Insectivore | Understory | Solitary/pairs | 14 | 67.73 | 19.7 | 11.93 | 8.04 | 4.31 | 65.46 | 8.54 | 13.02 |
| *Crypturellus duidae* | Specialist | Omnivore | Ground | Solitary/pairs | 300 | 74.81 | 49.63 | 28.55 | 9.66 | 8.54 | 140.77 | 23.4 | 16.72 |
| *Cyanocorax heilprini* | Specialist | Omnivore | Understory | Flocks | 155 | 168 | 51.91 | 20.16 | 19.23 | 12.14 | 165.07 | 19.88 | 12.04 |
| *Dolospingus fringilloides* | Specialist | Granivore | Understory | Solitary/pairs | 11.75 | 54.71 | 17.53 | 13.07 | 8.62 | 8.1 | 61.25 | 10.82 | 17.64 |
| *Elaenia ruficeps* | Specialist | Omnivore | Understory | Solitary/pairs | 17.17 | 59.82 | 21.03 | 11.31 | 9.36 | 4.87 | 63.5 | 10.29 | 16.21 |
| *Formicivora grisea* | Specialist | Insectivore | Understory | Flocks | 10.5 | 49.2 | 20.64 | 12.54 | 6.49 | 3.95 | 53.53 | 5.29 | 9.89 |
| *Galbula leucogastra* | Specialist | Insectivore | Canopy | Solitary/pairs | 16.07 | 93.27 | 12.86 | 36.39 | 9.65 | 5.72 | 67.92 | 12.89 | 18.96 |
| *Hemitriccus inornatus* | Specialist | Insectivore | Canopy | Solitary/pairs | 6.6 | 34.94 | 14.8 | 11 | 7.46 | 3.31 | 46.48 | 8.68 | 18.67 |
| *Hylophilus brunneiceps* | Specialist | Insectivore | Canopy | Flocks | 10.17 | 46.41 | 18.41 | 11.32 | 8.19 | 4.86 | 56.95 | 9.14 | 16.06 |
| *Myrmeciza disjuncta* | Specialist | Insectivore | Understory | Solitary/pairs | 13.17 | 52.2 | 26.98 | 16.19 | 8.25 | 5.76 | 61.8 | 9.36 | 15.14 |
| *Myrmotherula cherriei* | Specialist | Insectivore | Understory | Flocks | 8 | 33.91 | 17.74 | 14.65 | 7.26 | 3.58 | 49.33 | 6.06 | 12.27 |
| *Neopelma chrysocephalum* | Specialist | Omnivore | Understory | Flocks | 13.81 | 55.75 | 18.29 | 11.4 | 9.91 | 4.9 | 68.97 | 12.96 | 18.82 |
| *Neopipo cinnamomea* | Specialist | Insectivore | Understory | Solitary/pairs | 6.5 | 37.05 | 14.74 | 7.85 | 7.44 | 3.14 | 49.61 | 10.1 | 20.35 |
| *Polytmus theresiae* | Specialist | Nectarivore | Understory | Solitary/pairs | 3.33 | 35.67 | 6.75 | 20.03 | 4.53 | 2.6 | 56.57 | 35.92 | 63.51 |
| *Rhytipterna immunda* | Specialist | Insectivore | Understory | Solitary/pairs | 24 | 87.63 | 22.28 | 15.85 | 11.43 | 6.54 | 86.98 | 15.49 | 17.82 |

| **Bird species** | **Habitat category** | **Diet category** | **Foraging strata** | **Sociability** | **Weight (g)** | **Tail length (mm)** | **Tarsus length (mm)** | **Beak length (mm)** | **Beak width (mm)** | **Beak depth (mm)** | **Wing prim. lenght (mm)** | **Wing secon. lenght (mm)** | **Kipp distance (mm)** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Tachyphonus phoenicius* | Specialist | Insectivore | Understory | Solitary/pairs | 19.86 | 72.45 | 22.29 | 12.48 | 8.03 | 6.96 | 71.66 | 12.67 | 17.69 |
| *Thamnophilus amazonicus* | Specialist | Insectivore | Understory | Flocks | 18 | 57.3 | 22.18 | 14.33 | 8.67 | 5.87 | 65.73 | 7.27 | 11.06 |
| *Turdus ignobilis* | Specialist | Omnivore | Understory | Solitary/pairs | 59 | 91.01 | 32.02 | 17.93 | 12.73 | 6.57 | 106.55 | 22.23 | 20.86 |
| *Xenopipo atronitens* | Specialist | Frugivore | Understory | Solitary/pairs | 14.01 | 49.98 | 16.96 | 11.43 | 10.12 | 5.13 | 69.28 | 13.77 | 19.85 |

**Table 2**. Ecological functional traits for white-sand ecosystem birds used in this study.

| **Traits** | **Categories** | **Source** |
|---|---|---|
| Diet | Frugivores<br>Insectivores<br>Omnivores<br>Carnivores<br>Nectarivore<br>Granivore | Wilman et al. 2014, GRL and SHB personal field observations |
| Foraging strata | Ground<br>Water<br>Understory<br>Canopy<br>Aerial | Wilman et al. 2014, Cohn-Haft et al. 1997, GRL and SHB personal field observations |
| Sociability | Solitary or in pairs<br>Hetero or monospecific flocks | Cohn-Haft et al. 1997, GRL and SHB personal observations |

# CAPÍTULO 2

Lima, Gisiane Rodrigues; Jardim, Lucas; Diniz-Filho, José Alexandre Felizola; Marina Anciães. **Extinction shapes the history of the communities of specialists birds in the white sand ecosystems on the Amazon.** Manuscrito submetido para publicação na revista *Ecology and Evolution* em 12 de fevereiro 2023.

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RH: Lima et al. • Extinction shapes the history of specialist bird communities in white sand ecosystems in the North of the Amazon

# Extinction shapes the history of the communities of specialist birds in the white-sand ecosystems of the Amazon

## Extinção molda a história das comunidades de aves especialistas nos ecossistemas de areia branca da Amazônia

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## Resumo

Compreender como as espécies de aves de ecossistemas de areia branca (EABs) conseguiram habitar e se especializar em um ambiente insular em meio a floresta Amazônica é fundamental para entender os processos evolutivos sobre as aves restritas a um tipo de habitat. Buscamos avaliar os processos de diversificação das espécies especialistas de aves dos ecossistemas de areia branca da bacia do Rio Negro, comparando com o pool de espécies de aves de ambientes ribeinhos. Muitos EABs podem ser leitos de Rios antigos, o que pode favorecer as espécies ribeirinhas atuais serem poteciais colonizadoras e se estabelecerem dentro dos EABs. Para isso, utilizamos uma extensão de de modelos evolutivos biogeográficos para verificar a especiação dependente do estado e modelos de extinção que explicam especificamente a presença de fatores não medidos que podem afetar as taxas de diversificação estimado para os estados de qualquer característica observada. Podemos assim, avaliar os processos evolutivos que mais atuaram na formação das comunidades de aves de EABs. Os resultados mostraram que as espécies de aves especialistas de EABs possuem diversidade funcional diferente do que esperado ao acaso. O modelo cinco foi o que se ajustou melhor, apresentando valores maiores para os índices de extinção e especiação maiores nas comunidades de aves especialistas de EABs. Os processos encontrados fazem dos EABs fonte-sumidouro de espécies ao longo do tempo, recebendo espécies generalistas e especialistas de ecossistemas ribeirinhos. Segundo os modelos analisados, uma vez que as espécies estão com grau elevado de adaptação exigido por um ecossistema com condições severas, não conseguem colonizar outros ecossistemas. A extinção é um processo importante para a dinâmica da biodiversidade na Amazônia, pois à medida que se perde muitas espécies, também há especiação e adaptação elevada. Este trabalho é um dos primeiros a utilizar as análises evolutivas locais em ecossistemas da Amazônia, e foi eficaz ao mostrar que a extinção é recorrente, e que é motivo de preocupação devido as severas e rápidas mudanças ecológicas ocorrendo atualmente.

**Palavras-chaves**: Amazônia, solos pobres, comunidades, processo evolutivos

## Abstract

Understanding how bird species from white sand ecosystems (WSEs) have managed to inhabit and specialize in an insular environment in the middle of the Amazon Rainforest is fundamental in order to understand the evolutionary processes in birds restricted to one type of habitat. We sought to evaluate the diversification processes of the specialist bird species of the white sand ecosystems of the Rio Negro basin by comparing them with the pool of bird species of riparian environments. Many WSEs may be ancient riverbeds, which may favor current riparian species to be potential colonizers and settle within the WSEs. For this, we used an extension of biogeographic evolutionary models to verify state-dependent speciation and extinction models that specifically explain the presence of unmeasured factors that can affect the estimated diversification rates for the states of any observed trait. Thus, it was possible to evaluate the evolutionary processes that most acted in the formation of bird communities of WSEs. The results showed that WSEs specialist bird species have different functional diversity to what was expected on a random basis and evolutionary models have higher extinction and speciation rates in WSEs specialist bird communities. This evidences that source-sink processes maintain WSEs over time, and that they receive generalist and specialist species from riparian ecosystems. According to the models analyzed, once the species have the high degree of adaptation required by an ecosystem with severe conditions, they cannot colonize other ecosystems. Extinction is an important process for the dynamics of biodiversity in the Amazon since, as many species are lost, there is also speciation and high adaptation. This work is one of the first to use local evolutionary analyses in Amazonian ecosystems and was effective in showing that extinction is recurrent, which is a cause for concern due to the severe and rapid ecological changes currently occurring.

Keywords: Amazon, poor soils, communities, evolutionary process

## Introduction

Ecological communities are composed of species that co-occur in a given geographic space and period, which can change in terms of variation in composition and richness (Kreft & Jetz, 2010; Schluter & Pennell, 2017). The composition of these communities is determined by temporal biotic, abiotic and ecological factors (Whittaker et al., 2001; Webb et al., 2002; Cavender-Bares et al., 2009). However, different groups of animals and plants respond differently to eco-evolutionary processes, which creates a puzzle in relation to the history of the formation of communities, both in the composition of their species, and in the ecomorphological adaptation of the species and to what extent they are able manage to disperse (Antonelli et al., 2018; Diniz-filho et al., 2009). The composition of the species is a reflection of their ecomorphological adaptation and dispersal capacity, which are fundamental for the conquest of new habitats (Weeks et al. 2022). Without abundant sources of evidence or other records showing the past geographic distribution of a lineage, the difference between *in situ* adaptation and colonization is difficult to investigate.

Studying the modifications of the natural history of species is fundamental in order to understand the evolution of the planet's ecosystems (Condamine et al., 2013). Environmental changes and extinctions are part of history, and shape the future of current ecosystems and their species. The past can favor the understanding of what can happen in this current moment of severe and rapid changes in the environment (Barnosky et al., 2011, Naeem et al., 2012). By understanding historical changes and their directions, we can assess the likely consequences in advance. According to ecological modifications, organisms and their characteristics mediate adaptation and dispersal potential (Stroud and Losos, 2016). Intense environmental pressures in certain regions can influence the characteristics of species and pressure them to similar adaptations, even if these are unrelated. Studies show that different families of plants that inhabit equally dry environments in different parts of the Earth, have leaves adapted for the storeage of water (Vicentini, 2004; Eggli & Nyffeler, 2009). The richness of birds, mammals and amphibians is similar, and responds to environmental gradients, but, according to most studies, not to competition between taxa (Powney et al., 2010).

Thus, biodiversity patterns need to be studied at spatial and temporal scales, taking into account the multiple forms of variation embedded in the complex concept of biodiversity (Antonelli et al., 2018; Diniz-filho et al., 2009), and should seek to find the specific mechanisms of characteristics (traits) and lineages, with the integration of the idea that ecological and historical biogeographic processes can act strongly in metacommunities (Vellend, 2010). Studying communities and their ecological characteristics is essential in order to understand the paths of diversification and recolonization of species in isolated places, such as islands of ecosystems surrounded by a matrix or forest fragments (Claramunt et al., 2012; Cadotte, 2017; Antonelli et al., 2018). Such transitions between environmentally different areas can allow a species maintain its characteristics and its ancestral ecological niches, which can be explained by the conservatism hypothesis (Crisp et al., 2009).

In the Neotropics, changes in habitat over time show transitions of the species from ancestral wet and forest habitats to drier environments (Lanna et al., 2022; Tucker et al., 2017). Studies suggest that investigation is essential to generalize these patterns, since one should not just look at a community, but also act in a comparative mode in relation to the diversification processes and the geographical variation of the species. One should also verify the potential to colonize and settle, and compare the species pool of a given region (Lessard et al., 2012; Carstensen et al., 2013).

Drier environments, with extreme ecological conditions such as high temperatures and water stress, require more specific adaptations for species survival, thus restricting permanence and species richness (Futuyma and Moreno, 1988; Zurita et al., 2017). One example of this type of environment is the white-sand ecosystem (WSE) that is found in the Amazon, which occurs in soils with strong water stress and which are poor in nutrients, and are distributed in isolated patches in the middle of a *terra firme* forest matrix (Anderson, 1981; Adeney et al., 2016; Capurucho et al., 2020*a*). This ecosystem presents endemic bird species adapted to its specific conditions that are similar to an island, and whose connections between the patches are probably via corridors of riparian ecosystems (Borges et al., 2016 (a); Borges, et al., 2016 (b); Capurucho et al., 2020).

Bird communities of WSEs show lower diversity and higher dominance of some species, which is probably due to the limiting pressure of an environment with low habitat complexity (Capurucho et al., 2020). Thus, the distribution of bird communities in WSEs seems to be linked to the adaptation of species to extreme conditions, their dispersal and colonization capabilities, and may be driven by the size and isolation of the spots (Borges et al., 2016). WSEs have two types of formations, i.e., the northern and southern patches of the Amazon, which have different characteristics and evolutionary histories (Matos et al., 2016; Cracraft et al., 2020). Bird communities have species turnover between the patches of WSEs across Amazon (Borges, 2013).

The formation processes of WSEs in the northern Amazon have resulted in greater heterogeneity of environments on the Guiana Shield (Adeney et al., 2016; Rossetti et al., 2012), while the WSEs patches of the southern Amazon feature fewer open areas and appear to be ancient riverbeds (Ritter et al., 2021). Thus, the connectivity of WSE areas with riparian environments are more evident in the north of the Amazon at the present time (Capurucho et al., 2020). Genetic work by WSE bird specialists corroborates a lower connectivity and recent isolation between the populations of the north and south of the Negro River (Matos et al., 2016; Capurucho et al., 2018; Norambuena and Van Els, 2020). Herein, we evaluate whether (1) WSEs act as a phylogenetic and functional filter and (2) whether WSE communities are self-sufficient in forming and maintaining their diversity or are maintained by a dispersal of species between WSEs and riparian ecosystems. Lanna et al. (2022) show that forest habitats are older, favoring dispersal to open areas. We thus expect more dispersal events from riparian forest ecosystems to open ones of WSEs. We also expect more speciation events to occur in riparian forest environments and extinction rates to be higher in WSEs due to WSE being a restrictive environment. Knowing the evolutionary processes that play an important role in the formation of WSE specialist bird communities and the evolution of bird characteristics will lead to a better understanding of what happened in the Amazon over time, especially in two important ecosystems that are currently threatened by current climate changes.

## Methods

We used two lists, one for the white-sand ecosystem (WSE) and another for the riparian ecosystem. The WSE list has 147 species and 37 families of birds, which were obtained from the work of Borges et al. (2016 (b)), for an area located in the Negro River basin. For the riparian ecosystem, we used the list from the work of Naka et al. (2020) with 439 bird species from 64 families for the Branco River, which is the main tributary of the Negro River.

Based on the species list for white-sand ecosystems and riparian environments, specimens of each of the species was measured. At least three individuals per species were measured in the zoological collections at INPA, the Goeldi Museum and the UFPE collection. Each individual was measured three times and, each time, measurements of the beak (height, length and width), tarsus, total wing length, and length of secondary feathers were otained, and the Kipp index was calculated. Via this, we obtained an average of the functional attribute for the species. All individuals were measured by the same person, always using a digital caliper and a ruler in millimeters. The functional attributes that were measured are all linked to the ecological functions of individuals in the environment (Supplementary Material 1). We ecologically classified the species using the literature of Billerman et al. (2022), Borges et al. (2016a, b) and Naka et al. (2020). Species that are restricted to one type of ecosystem were classified as specialist species, and species that are present in two or more types of Amazonian ecosystems were classified generalists. In our database, the restricted species of riparian ecosystems were represented by “0” (263 species), the restricted ones of white-sand ecosystem environments were represented by “1” (18 species), and those that use the two types of ecosystems represented by “01” (126 species).

## Environmental filtration

For the phylogenetic tree, the consensus of 10,000 bird phylogenies published by Jetz et al. (2012) was used. The consensus tree was generated using the Mesquite 3.7 program (Maddison & Maddison, 2021), and maintained the length of the branches. Only the species present in the occurrence database were maintained. Phylogenetic diversity analysis was performed to assess whether WSE communities are composed of a phylogenetic subset of riparian ecosystem communities. The phylogenetic diversity was calculated as the mean phylogenetic diversity of the community (MPD) (Webb et al., 2002). The observed MPD was compared to a null model, through a random selection of species from riparian communities, and the observed value for WSE diversity was maintained. The simulation of the null communities was repeated 1,000 times. For each repetition of the data simulation, the average MPD for the community was calculated. The significance of the phylogenetic analysis was assessed by the standardized effect size of the MPD (ses.MPD), with a significance level of 95 %. Positive and significant values of ses.MPD indicate more phylogenetically dispersed communities than what would occur by chance. Negative and significant values indicate phylogenetically grouped communities. The phylogenetic grouping analyses were performed in the *picante* package of the R software (Kembel et al., 2010).

## Filtering of the functional diversity

To evaluate the filtering of the functional attributes in the WSEs, we calculated the diversity of the functional characteristics, such as functional divergence (FDiv), functional dispersion (FDis) and functional richness (Fric) using the *FD* package (Laliberté & Legendre, 2010) do Programa RStudio 2022.07.0. The Gower distance (Gower, 1971) was used as a measure of dissimilarity between the species because it allows the use of different types of traits, whether continuous, ordinal, nominal or binary. The indices of the DAMOCLES model (dynamic assemblage model of colonization, local extinction and speciation) use estimated parameters of colonization (dispersal), local extinction and speciation events. From the generated values, 1,000 null models of community composition were simulated (Pigot and Etienne, 2015). For each simulated community, we calculated the functional diversity metrics and evaluated the significance of functional diversity using the *quantis* of 2.5 and 97.5% of these distributions of null models of functional diversity. Negative and significant values of functional diversity can indicate a grouping of the functional diversity of birds in WSEs in relation to the species pool. Positive and significant values would indicate greater dispersion of the functional attributes of WSE specialist birds.

We evaluated whether WSE communities are comprised and maintained by (1) *in loco* speciation, and have low extinction rates and diversification rates that are higher than the dispersion rates of riparian communities; 2) whether they are comprised of a source-sink dynamic. With the diversity in WSEs being formed by the dispersion of species from riparian communities, and with the extinction rate in WSEs being higher than its speciation rate. The diversification was evaluated using the GeoHiSSE model (Caetano et al., 2018) from the *hisse* v1.9.19 package (Beaulieu and O'Meara, 2016) of the software R. GeoHiSSE allows you to model how the expansion or loss of geographical states (e.g., WSE and riparian communities) (as described below) influences diversification rates. In this way, we can model how the expansion or loss of occurrence of species in WSE and riparian ecosystems can influence the rates of speciation and extinction in these ecosystems.

Geographic states were defined as WSE specialists, riparian ecosystem specialists, and generalists (occur in both ecosystems). A total of six diversification models were constructed to represent the diversification hypotheses. In Model 1, the riparian and WSE ecosystem communities are formed by the dispersion rates between geographical states, with no differences between their speciation and extinction rates. However, direct changes between specialist states are not allowed, and expansion to the generalist state is mandatory, for example specialist WSE species cannot evolve directly to specialists in riparian ecosystems, since they must expand their geographical distribution to generalist and lose the WSE state to become specialists in riparian ecosystems. Model 2 has different dispersion rates between geographic states, with the same dispersion constraints as Model 1, but has different speciation and extinction rates between geographic states. In Model 3, we add a hidden state to the model, dispersion rates are equal to those of Model 1 with the addition of dispersion between the hidden states. Speciation and extinction rates are different between the hidden states, but are equal between the geographic states. In this model, differences in speciation and extinction are caused not by geographic states, but by attributes not included in the model. Model 4 has dispersion rates that are equal to Model 3, but there are no differences in speciation and extinction rates between geographical states nor between hidden ones. In Model 5, the direct change from the status of specialist of riparian environments to WSE specialist is allowed. In Model 6, all events are present, but specialist WSE species do not change to specialists of riparian environments or to generalists. (Table 3). The models were ranked by the weights of the Akaike information criterion corrected for low sampling (wAICc) (Beier et al., 2001) and we calculated speciation, extinction and dispersal rates using the average model of the six diversification models (Caetano and Harmon, 2017; Caetano et al., 2018).

## Results

We found that the observed phylogenetic diversity was not different from that expected for a random sampling of species from riparian ecosystems (ses.MPD observed = 151.61, P = 0.25). However, WSE species presented lower functional diversity than expected by a neutral diversification and colonization process (Figure 1), thus indicating environmental filtering of species attributes in WSEs.

The best diversification models were Models 5 (wAICc = 0.39), 4 (wAICc = 0.35) and 6 (wAICc = 0.26), respectively (Table 3). In the average diversification model, WSEs had low speciation rates and high extinction rates. On the other hand, riparian ecosystems had low extinction rates and high speciation rates. Generalist species had low rates of speciation and extinction (Figure 2). We also found that there is a hidden state effect on the speciation rates of riparian ecosystems and WSE extinction rates (Figure 2). There are direct transitions between species from riparian ecosystems to WSEs, but not the other way around. In the hidden state A, the rate of transition from riparian ecosystems to WSEs (0.079) was greater than the rate in the opposite flow (0.23). In the hidden state B, the transition was greater between species from WSEs to riparian ecosystems (74.3), than the opposite transition (24.1). Therefore, WSEs are maintained mainly by the colonization of species from riparian ecosystems, since they have a low speciation rate and a high extinction rate. There is also a high flow of WSE species into riparian ecosystems, but these ecosystems are maintained primarily by their high speciation rate and low extinction rate.

## Discussion

Specialist bird communities from white-sand ecosystems (WSEs) and riparian environments were examined to try to determine whether there is environmental filter in the WSEs and whether evolutionary processes such as specialization, dispersal and extinction have shaped WSE communities. We found evidence of high extinction in WSE communities, because living in an environment different from the surroundings, with severe conditions, led populations to adapt and specialize, since they either adapt or become extinct. The results show that WSEs communities are composed of species of different evolutionary lineages, and do not differ from a random sample from riparian communities. However, WSEs specialist species are morphologically more similar than species of riparian ecosystem communities.

The models employed in this work were fundamental for answering whether the specialist species of WSEs were filtered mainly by extinction events. High adaptation to an insular environment may have driven the high speciation and endemicity rates of WSEs species. Birds may or may not be present in a given area, and may be affected by the heterogeneity of the local forest, with variation in habitat structure being fundamental in determining the distribution of species (Macarthur 1964). In the GEOHISSE model, more events were added. Including dispersal from riparian environments These modifications made to models 5 and 6 were important to test our hypotheses. WSEs and direct speciation from riparian ecosystems to WSEs (0 to 1). These modifications made to models 5 and 6 were important to test our hypotheses. By increasing the possibility of events, we obtained representative results to explain the composition of the specialist bird communities of the WSEs.Direct speciation could be performed within the models, which allows the possibility of species from open areas to return to riparian forested areas, which did not happen. Perhaps the environmental pressure is so strong that it causes the species to no longer be able to return or not find vacant niches in the riparian forest ecosystems.

With the GeoHISSE analyses, we investigated the dynamics of diversification, with transitions of species over time from riparian forest ecosystems to more open ecosystems such as WSEs. Through this work, we reinforce the potential of riparian areas for the dispersion of species in the landscape with probable corridors. In study by Capurucho et al. (2013), phytogeographic analyses were conducted that showed the expansion of populations of the specialist species black manakin (*Xenopipo atronitens*) that began after the Last Glacial Maximum. This is evidence of a likely rise in local extinctions and subsequent recolonization of patches of white sand ecosystem with species from forest ecosystems. More evidence is found in the study by Azevedo et al. (2020), which shows that open habitats in South America are younger than forest habitats, and favor the colonization of open environments by riparian forest species.

Via the models, the findings in this work show that transitions from forest ecosystems to open areas were more common than the reverse. WSEs could and can provide more empty niches and allow colonization of species from riparian forest environments. This pattern of further transitions from forest to open habitats have been covered in other studies. For example, Antonelli et al. (2018) estimated evolutionary events for six taxonomic groups of species in Neotropical biomes and found that the Amazon was a source of species for all groups of open areas. Zizka et al. (2020) identified more transition events of Bombacoideae plants from evergreen forests (forest habitats) to seasonally dry biomes (open habitats), with multiple colonization events in open habitats. The work of Zizka et al. (2020) follows Antonelli et al. (2018) in their analysis of their data at the biome level, but this can confuse the real differences by contrasting two biomes that have different extents and consequently have distinct biotic influences. Therefore, when performing the inclusion of species that occur within a single biome, we can understand how the environment shapes the dispersal and colonization processes of species within a heterogeneous biome. We therefore propose that future studies should include ecosystems, macro- and micro-habitats of species and not only general biomes in the analyses.

The models used were favorable for this work and sufficient to answer the evolutionary questions regarding the species of WSEs. We were able to show that extinction was the evolutionary process with the highest rates for the WSE. In insular conditions, colonizers experience environmental conditions that were not previously experienced by their ancestors, which cause selective pressures due to new adaptations. Pressures drive speciation rates, but they can be strong and rapid, and extinction is the process that shapes communities since species either adapt or become extinct. According to Barnosky et al. (2011), extinction is very common, but it is usually balanced by speciation. In the Amazon, several events occurred that favored the increase of in extinction and speciation in open areas, such as the fire edaphic factors and seasonal climatic factors that ended up isolating populations and increasing the selective pressure on the species (Els et al., 2021).

Morphological features do not appear to restrict species of WSEs and morphology does not preclude colonization and persistence of species in other Amazonian ecosystems. As such, the evolutionary history of species is more important in order to understand the distribution of species in the various micro- and macro-habitats of Amazonian ecosystems. This restricted association of species results in dependence and high adaptation to be able to disperse in the landscape (Lanna et al., 2022). Little is known about which corridors Amazonian birds use, and how the gene flows of the species are maintained over time. When considering transitions between ecosystems using only the species that are present and their current distributions, it is necessary to consider other factors. Species may have colonized other types of open ecosystems or forest ecosystems from other regions or even from other continents, and not transitioned between these two habitats.

Currently there are analyses with increasingly robust models to evidence evolution and its main drivers. There is still limited understanding about Amazonian communities or about species conservation within a climate change scenario. Accelerated extinction ceases to be a driving force of species selection in the Amazon and could be an unprecedented catastrophe in the history of the planet. For this reason, WSEs are considered increasingly vulnerable and are priority areas for conservation, as they are already limited environments and prone to fire. Wildfires in seasonally flooded riparian environments can abruptly transform forests into a savanna state, thus contributing to climate-induced disturbances and causing ecological transitions (Flores and Holmgren, 2021).

## Conclusion

Via the results obtaining from combining phylogenetic and ecomophological data to evidence the evolutionary history of bird species in white-sand ecosystems and riparian ecosystems of the Amazon, insights about the evolutionary processes that shape communities emerge. As seen for other animal groups, our results demonstrate a predominant pattern of transitions from forests to open habitats. The evolutionary process of extinction in the Amazon seems to be much more common than we imagined, and the WSEs are a species sink that has been important for bird speciation over time. With ecomorphological and phylogeny data we were able to generate more robust tests of evolutionary models. Tropical regions are the regions with the greatest biodiversity on the planet and are under threat, obtaining results with high numbers of extinctions is crucial for further assessments of the populations of specialist species in various ecosystems. We have identified the main drivers and have a small part of the limited understanding of how species will cope, adapt and change their distributions due to climate change. White-sand ecosystems and riparian forest ecosystems are important within the evolutionary process, and include an important tree of life dynamic within the Amazon biome.

## Acknowledgments

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## Figuras

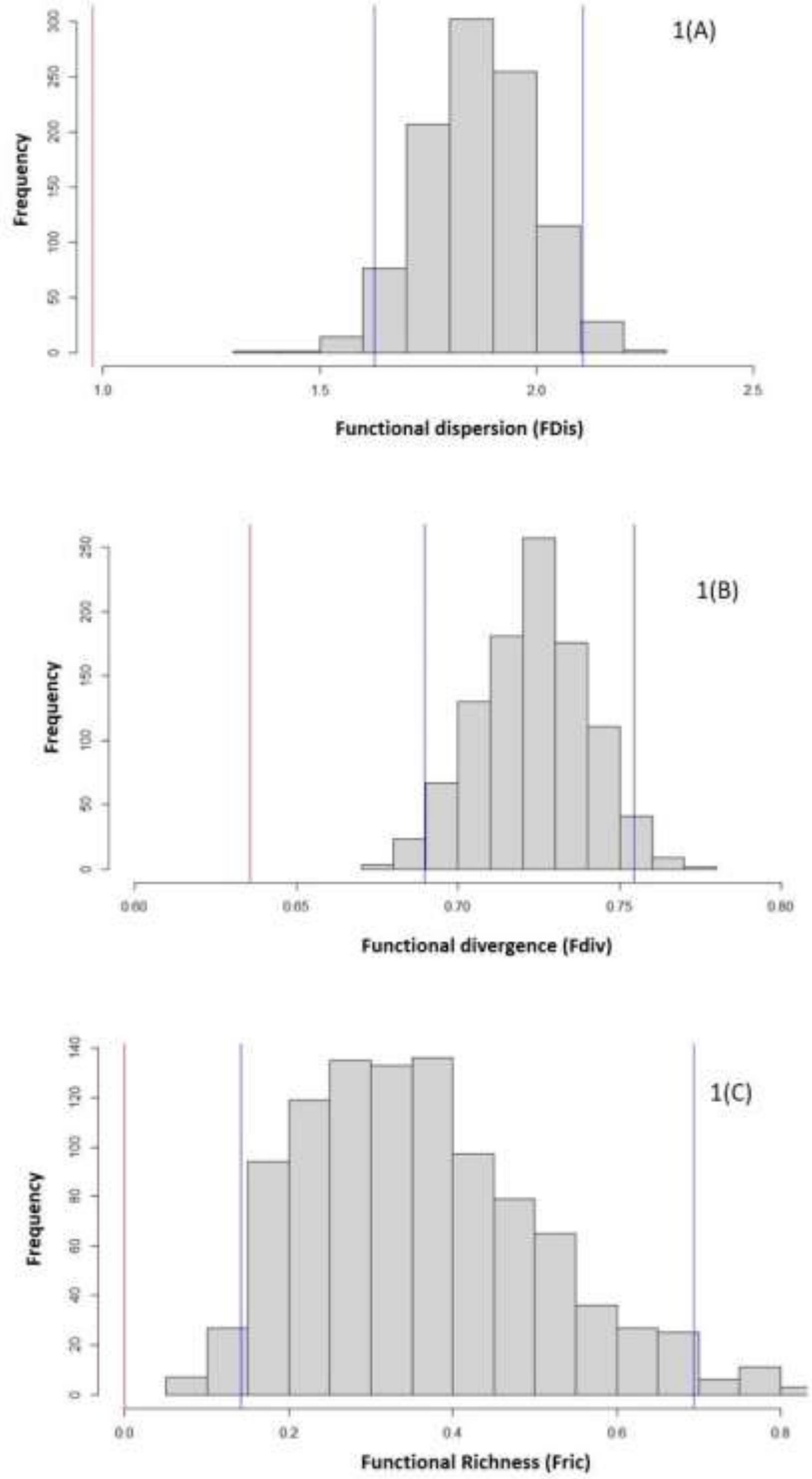

Figure 1: Phylogenetic structure of the community according to the mean distance from the nearest taxon (ses-MPD) showing the observed data patterns (represented by the red line), and the expectation using DAMOCLES, which simulated data from the rates of the indices of functional diversity estimated from 1,000 replicated simulations (variation

represented by the bars in blue). 1 (A) Functional dispersion – Fdis; 1 (B) Functional divergence – Fdiv; 1 (C) Functional Richness – Fric.

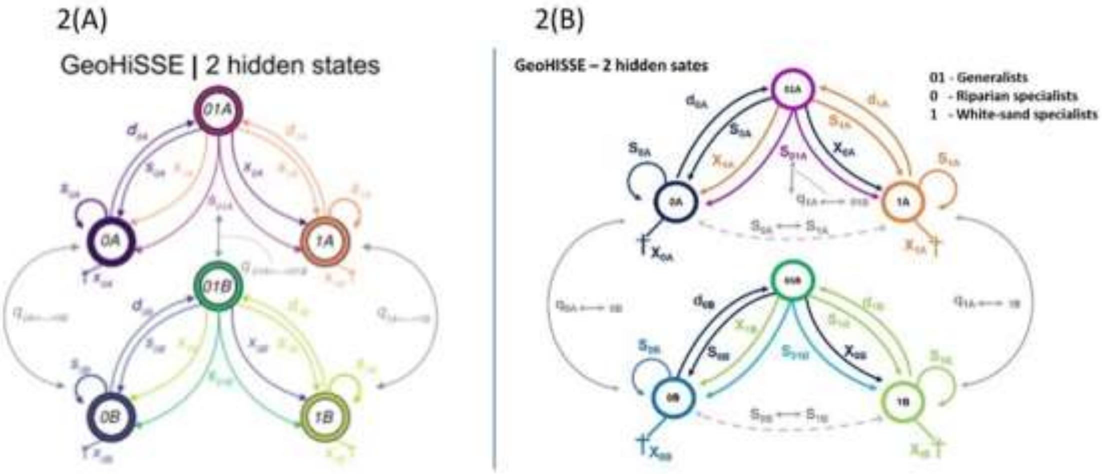

Figure 2: A – Mode GeoHisse of Caetano et al., (2018); B – Model 5 the independent area of the GeoHiSSE model (CID) has two sets of diversification parameters shown in orange and purple), and the dependent area of the GeoHiSSE model (denoted by six sets of diversification parameters shown in various colors) may have two or more hidden states. Note that all model extensions can support states. The GeoHISSE2 model has the possibility for the speciation event to occur, from the RS state (“0”) to the WSE state (“1”).

Fig.3

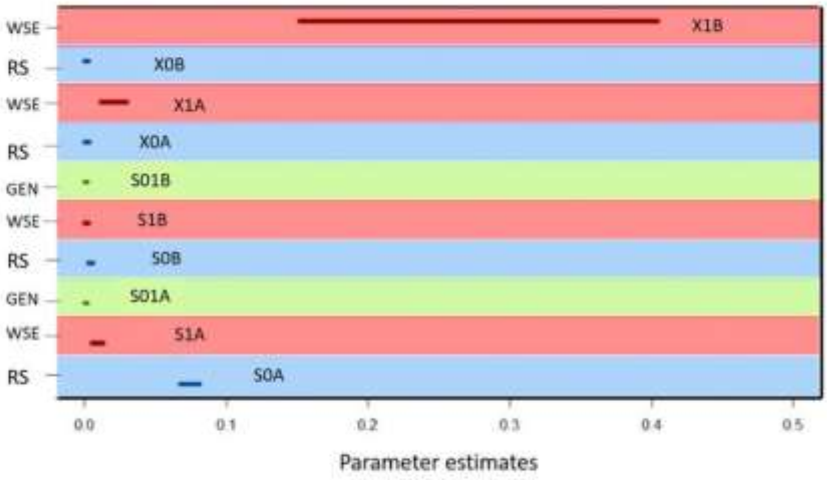

Figure 3: Result of Model 5 and the sum of evolutionary events within the tree of Model 5. The six events of S (speciation) in state 0 (RS – riparian specialists) and 1 (WSE – white-sand specialists) and 01 (GEN - generalists), irrespective of the geographical space

and four events of X (extinction), in the states of 0 (RS) and 1 (WSE), irrespective of the geographical space.

## Tabelas

**Tabela 1**. Results of the selection of models evaluating the effect of the evolutionary processes of Dispersal, Extinction and Speciation on the WSE bird community for the different states: WSE specialist condition (“1”) or riparian environments (“0”) or generalists common in both (“01”). The best models are presented in order. The ones with the highest weight have a better fit to the data and, as a result, have more weight when the mean of the model (AIC w) is used.

| **Models** | **Model description** | **Df** | **AIC*c*** | AIC *w* |
|---|---|---|---|---|
| Modelo 1 | Dispersal parameters vary only within ecosystems, with no range-dependent diversification. (HiSSE) | 7 | 3,991,6 | 0.00000001 |
| Model 2 | Canonical GeoSSE model, effect of range on diversification, from the reconstruction of phylogenies of existing species and in which speciation and extinction rates are influenced by the values of a state (0, 1 or 01). | 7 | 3,991,665 | 0.00000000002 |
| Model 3 | GeoHiSSE model, reach effect on diversification with 1 hidden area, no generalist state-dependent diversification (01) and all evolutionary processes. | 20 | 3,926,052 | 2,301.45300000 |

| | | | | |
|---|---|---|---|---|
| Model 4 | GeoHiSSE model with 1 hidden area, no generalist state-dependent diversification (01) and all evolutionary processes<br>+ variation between hidden classes. | 20 | 3,916,468 | 348,043.00000000 |
| Modelo 5 | GeoHiSSE model with 1 hidden area, no diversification dependent on the generalist state (01) and all evolutionary processes<br>+ variation between hidden classes<br>+ Jump (direct speciation) from 0 to 1. | 22 | 3,916,218 | 394,478.70000000 |
| Model 6 | GeoHiSSE model with 1 hidden area, without generalist state-dependent diversification (01)<br>+ with variation between hidden classes<br>+ Jump (direct speciation) from 0 ↔ 1<br>+ Veta dispersion of *WSE→RS* (minus two parameters) | 20 | 3,917,089 | 255,176.90000000 |

# Material Suplementar - Capítulo 2

**S1**. List of bird species that inhabit Amazonian white-sand habitat and riparian specialists, with the patches within categories and attributes analyzed in this study. The scientific nomenclature in this list is based on the list of birds from the Brazilian Committee of Ornithological Records (Pacheco et al. 2021). Columns with categorical ecological data were obtained from Borges et al. (2016), Naka et al., (2020), and personal observations. The six morphological measurements were obtained by only one of the authors (GRL) and values represent the mean of three individuals measured per species.

| **Species** | **Category GeoHisse** | **Weight (g)** | **Tarsus (mm)** | **Beak length (mm)** | **Beak width (mm)** | **Beak height (mm)** | **Kipp** |
|---|---|---|---|---|---|---|---|
| *Aburria cumanensis* | Riparian | 1450 | 82.4 | 36.7 | 20.6 | 16 | 4.1 |
| *Actitis macularius* | Riparian | 30.9 | 22.8 | 23.1 | 5.8 | 5.8 | 23.8 |
| *Agamia agami* | Riparian | 710 | 106.6 | 153.3 | 14.4 | 18.4 | 6.9 |
| *Amazona amazonica* | Generalist | 391.5 | 25.5 | 33.1 | 19.9 | 28.7 | 4.3 |
| *Amazona festiva* | Riparian | 407.5 | 31.4 | 33.8 | 20 | 29.5 | 4.9 |
| *Amazona ochrocephala* | Riparian | 425 | 25.2 | 32.5 | 21 | 33.4 | 8.8 |
| *Ammodramus aurifrons* | Riparian | 14.8 | 23.4 | 11.4 | 6.5 | 6.3 | 10.3 |
| *Ammodramus humeralis* | Riparian | 16.8 | 21.4 | 11.2 | 7.5 | 7.4 | 9.9 |
| *Anhinga anhinga* | Riparian | 1413.3 | 46.8 | 90.2 | 13.8 | 17.4 | 29.6 |
| *Anthracothorax nigricollis* | Riparian | 6 | 5.8 | 23.7 | 4.3 | 3.1 | 54.5 |
| *Antrostomus rufus* | Generalist | 98 | 18.2 | 16 | 32.1 | 4.3 | 45.7 |
| *Aprositornis disjuncta* | White-sand | 13.2 | 27 | 16.2 | 8.3 | 5.8 | 15.1 |
| *Ara ararauna* | Generalist | 150 | 44 | 67.1 | 30.6 | 66.7 | 23.1 |
| *Ara chloropterus* | Riparian | 1320 | 44.7 | 82.6 | 35.7 | 74.9 | 23.9 |

| Species | Category GeoHisse | Weight (g) | Tarsus (mm) | Beak length (mm) | Beak width (mm) | Beak height (mm) | Kipp |
|---|---|---|---|---|---|---|---|
| *Ara macao* | Riparian | 1400 | 33.1 | 73.9 | 34.9 | 73.4 | 23.4 |
| *Ara severus* | Riparian | 298 | 26.5 | 34.1 | 20.9 | 34.2 | 25 |
| *Aramides cajanea* | Riparian | 330 | 77 | 51.3 | 12.7 | 17.4 | 10.9 |
| *Aramus guarauna* | Riparian | 1530 | 121.5 | 98.8 | 10.9 | 18.4 | 9.4 |
| *Ardea cocoi* | Riparian | 1880 | 196.3 | 149.1 | 21.9 | 29.1 | 16.8 |
| *Arremon taciturnus* | Riparian | 19.5 | 25.5 | 11.1 | 9.4 | 8 | 8.1 |
| *Arremonops conirostris* | Riparian | 26.8 | 28.5 | 14.6 | 8.5 | 8.1 | 10.3 |
| *Arundinicola leucocephala* | Riparian | 12.5 | 17.7 | 12.2 | 8.7 | 4.4 | 13 |
| *Asio stygius* | Generalist | 610 | 59.1 | 34.6 | 26.2 | 23.9 | 22.7 |
| *Atticora fasciata* | Riparian | 13 | 11.5 | 6.1 | 9 | 2.9 | 62.2 |
| *Attila cinnamomeus* | Generalist | 32.5 | 23 | 18.8 | 11.5 | 6.6 | 15.6 |
| *Attila citriniventris* | White-sand | 33 | 20.8 | 19.2 | 12.6 | 6 | 17.6 |
| *Attila spadiceus* | Generalist | 31.5 | 25.1 | 18.1 | 11.6 | 5.5 | 15.9 |
| *Automolus ochrolaemus* | Generalist | 35 | 23.7 | 18.5 | 12.1 | 7 | 17.8 |
| *Automolus rufipileatus* | Riparian | 37.8 | 25.3 | 20 | 10.6 | 7.2 | 13.5 |
| *Brotogeris chrysoptera* | Generalist | 57.9 | 14.8 | 19.3 | 10.7 | 15 | 35 |
| *Bubulcus ibis* | Riparian | 259.5 | 82.7 | 54.7 | 16.5 | 14.8 | 7.7 |
| *Buteo albonotatus* | Riparian | 545 | 73.8 | 34 | 27.8 | 20.3 | 22 |
| *Buteo brachyurus* | Riparian | 210 | 69.8 | 25.3 | 21.8 | 18.2 | 31.7 |
| *Buteo nitidus* | Riparian | 480 | 81.6 | 32.1 | 25.4 | 18.7 | 15 |
| *Buteogallus schistaceus* | Riparian | 600 | 93.4 | 34.2 | 27.7 | 21.7 | 13.8 |
| *Butorides striata* | Riparian | 160 | 55.9 | 59.6 | 15.2 | 15.2 | 19.3 |
| *Cacicus cela* | Generalist | 119 | 37.1 | 35 | 11.8 | 16 | 35.7 |
| *Cairina moschata* | Riparian | 1875 | 58.3 | 58.3 | 24.4 | 26.5 | 11 |
| *Calidris melanotos* | Riparian | 43.8 | 27 | 26.5 | 5 | 5.9 | 34.8 |
| *Campephilus melanoleucos* | Riparian | 280 | 38.8 | 48.7 | 20.2 | 16.1 | 20.7 |
| *Camptostoma obsoletum* | Generalist | 7.6 | 12.5 | 8.4 | 6.1 | 3.5 | 18.2 |

| **Species** | **Category GeoHisse** | **Weight (g)** | **Tarsus (mm)** | **Beak length (mm)** | **Beak width (mm)** | **Beak height (mm)** | **Kipp** |
|---|---|---|---|---|---|---|---|
| *Campylopterus largipennis* | Generalist | 7.6 | 6.1 | 27.9 | 5.2 | 2.7 | 62.3 |
| *Campylorhamphus trochilirostris* | Riparian | 37.7 | 22.2 | 58.5 | 11 | 6.4 | 12.7 |
| *Campylorhynchus griseus* | Riparian | 48 | 32.9 | 26 | 10.4 | 7.1 | 14.2 |
| *Cantorchilus leucotis* | Riparian | 18 | 26 | 15.8 | 7.2 | 4.2 | 8.3 |
| *Capito auratus* | Riparian | 59.3 | 26 | 20.4 | 15.5 | 10 | 21.2 |
| *Capsiempis flaveola* | Riparian | 7.8 | 17.5 | 8.9 | 6.5 | 3.5 | 14.5 |
| *Caracara plancus* | Riparian | 1145 | 102.5 | 43.9 | 30.5 | 27 | 28.9 |
| *Caryothraustes canadensis* | Generalist | 29 | 21.3 | 15.5 | 10.8 | 10.4 | 14.6 |
| *Cathartes aura* | Generalist | 900 | 68 | 51.2 | 20.1 | 24.2 | 17.7 |
| *Cathartes burrovianus* | Riparian | 904.5 | 74 | 52.7 | 27.4 | 27.7 | 19.9 |
| *Cathartes melambrotus* | Riparian | 1200 | 79.1 | 53.3 | 22.3 | 27.2 | 17 |
| *Celeus elegans* | Generalist | 122.3 | 25.3 | 24.7 | 13.1 | 9.2 | 15.9 |
| *Celeus flavus* | Riparian | 98 | 31 | 23 | 12.6 | 8.6 | 16.7 |
| *Celeus torquatus* | Generalist | 117 | 29.9 | 32.2 | 13.5 | 10.2 | 21.5 |
| *Celeus undatus* | Generalist | 65 | 22.5 | 20.8 | 10.7 | 8.7 | 23.2 |
| *Cephalopterus ornatus* | Riparian | 720 | 58.3 | 47.1 | 31.2 | 21.6 | 15.1 |
| *Ceratopipra erythrocephala* | Riparian | 14 | 14.2 | 8.8 | 8.4 | 3.8 | 20 |
| *Cercomacra carbonaria* | Riparian | 15 | 25.1 | 14.4 | 7.8 | 4.6 | 10.2 |
| *Cercomacra cinerascens* | Riparian | 14.5 | 22 | 15 | 8 | 4.6 | 10.4 |
| *Cercomacra laeta* | Riparian | 16 | 25 | 15.6 | 7.4 | 4.9 | 8.3 |
| *Cercomacra nigrescens* | Riparian | 20.9 | 26.1 | 15 | 8.9 | 5 | 9.6 |
| *Cercomacra tyrannina* | Generalist | 14.6 | 25.1 | 14.5 | 8.5 | 4.7 | 12 |
| *Chaetura brachyura* | Riparian | 17.2 | 11.6 | 5.3 | 9.8 | 2.9 | 68.7 |
| *Chaetura cinereiventris* | Riparian | 14.5 | 11.1 | 4.3 | 8.2 | 2.1 | 65.2 |
| *Chelidoptera tenebrosa* | Generalist | 36.3 | 15.9 | 18.1 | 11 | 7.4 | 13.9 |
| *Chionomesa fimbriata* | White-sand | 4 | 5.3 | 18.3 | 3.6 | 2.3 | 53.9 |
| *Chiroxiphia pareola* | Riparian | 17.7 | 22.2 | 9.6 | 11.3 | 4.6 | 19.8 |

| Species | Category GeoHisse | Weight (g) | Tarsus (mm) | Beak length (mm) | Beak width (mm) | Beak height (mm) | Kipp |
|---|---|---|---|---|---|---|---|
| *Chlorestes cyanus* | Generalist | 3 | 4.8 | 15.9 | 4.3 | 2.3 | 62.6 |
| *Chlorestes notata* | Riparian | 3.5 | 5.5 | 16.9 | 3.9 | 2 | 57.9 |
| *Chloroceryle aenea* | Generalist | 12 | 8.4 | 26.9 | 10 | 7.3 | 19.4 |
| *Chloroceryle amazona* | Riparian | 100 | 16.8 | 64.1 | 21.8 | 17.1 | 14.6 |
| *Chloroceryle americana* | Riparian | 25.5 | 10.3 | 39.6 | 11.3 | 9.3 | 27.9 |
| *Chloroceryle inda* | Riparian | 52 | 13 | 49.5 | 17.7 | 11.9 | 22.2 |
| *Chlorostilbon mellisugus* | Generalist | 4 | 5.8 | 14.5 | 2.7 | 1.8 | 62 |
| *Chrysolampis mosquitus* | Generalist | 3.8 | 6 | 12.9 | 4.2 | 2.2 | 59 |
| *Chrysuronia versicolor* | Generalist | 3 | 6.9 | 15.3 | 4.2 | 2.7 | 58.5 |
| *Ciconia maguari* | Generalist | 2800 | 252.7 | 218.7 | 29.6 | 18.8 | 1.8 |
| *Cnemotriccus fuscatus* | Generalist | 14 | 19.8 | 12 | 7.9 | 4.3 | 13 |
| *Coccycua minuta* | Riparian | 43.5 | 27.8 | 19.3 | 13.5 | 6.8 | 12.8 |
| *Coccyzus melacoryphus* | Riparian | 57 | 29.2 | 23.4 | 15 | 8.5 | 27.7 |
| *Cochlearius cochlearius* | Riparian | 425 | 79.3 | 70.9 | 38.9 | 30.2 | 14.5 |
| *Coereba flaveola* | Generalist | 8.3 | 17.9 | 11.2 | 5.3 | 3.8 | 18.5 |
| *Colaptes punctigula* | Riparian | 63.7 | 24.4 | 19.5 | 10.9 | 7.2 | 16.4 |
| *Colinus cristatus* | Riparian | 100 | 27.3 | 13.3 | 8.7 | 9 | 16.1 |
| *Columbina passerina* | Generalist | 35 | 18.2 | 11.1 | 6.2 | 4.3 | 18.5 |
| *Columbina talpacoti* | Riparian | 41 | 16.9 | 12.6 | 5.4 | 4.6 | 14.8 |
| *Conirostrum bicolor* | Riparian | 9.8 | 18.4 | 9.8 | 6 | 4 | 17.8 |
| *Conirostrum speciosum* | Riparian | 11 | 16.8 | 8.9 | 5.5 | 4.5 | 22.7 |
| *Conopias parvus* | Generalist | 22.8 | 18 | 16.2 | 12 | 6.1 | 19 |
| *Conopias trivirgatus* | Riparian | 13.5 | 17.8 | 13.2 | 9 | 4.7 | 21.4 |
| *Coragyps atratus* | Riparian | 1430 | 87.2 | 57.3 | 21.2 | 20 | 10 |
| *Corythopis torquatus* | Riparian | 17 | 28.5 | 12.2 | 8.3 | 3.6 | 14.6 |
| *Cranioleuca gutturata* | Riparian | 14.8 | 19.7 | 14.1 | 6.3 | 4.2 | 18 |
| *Cranioleuca vulpina* | Riparian | 16.1 | 21.8 | 12.5 | 6.6 | 4.1 | 15.3 |

| **Species** | **Category GeoHisse** | **Weight (g)** | **Tarsus (mm)** | **Beak length (mm)** | **Beak width (mm)** | **Beak height (mm)** | **Kipp** |
|---|---|---|---|---|---|---|---|
| *Crotophaga ani* | Riparian | 189 | 37.5 | 30.7 | 13.3 | 21.7 | 20.1 |
| *Crotophaga major* | Riparian | 138 | 49.1 | 46.3 | 17.7 | 22.2 | 27.5 |
| *Crypturellus cinereus* | Generalist | 300 | 55.4 | 21.8 | 18.9 | 8.5 | 9.1 |
| *Crypturellus duidae* | White-sand | 300 | 49.6 | 28.6 | 9.7 | 8.5 | 16.7 |
| *Crypturellus erythropus* | Generalist | 452.5 | 55.5 | 28.1 | 8.8 | 9.1 | 11.4 |
| *Crypturellus soui* | Generalist | 180 | 37.9 | 17.1 | 11.4 | 6 | 8.6 |
| *Crypturellus undulatus* | Riparian | 560 | 50 | 29.4 | 15.3 | 8.2 | 6.8 |
| *Cyanocorax heilprini* | White-sand | 155 | 51.9 | 20.2 | 19.2 | 12.1 | 12 |
| *Cyanocorax violaceus* | Riparian | 252 | 53.3 | 30.3 | 18.8 | 15.6 | 11 |
| *Cyanoloxia brissonii* | Riparian | 25 | 23.7 | 17.4 | 12.1 | 13.5 | 14.2 |
| *Cyclarhis gujanensis* | Riparian | 25.5 | 25 | 15.5 | 10.5 | 7.9 | 11.7 |
| *Dacnis flaviventer* | Riparian | 13 | 18.4 | 10.4 | 6.8 | 4.2 | 21 |
| *Daptrius ater* | Riparian | 330 | 68.3 | 28.6 | 20.8 | 15.7 | 43.2 |
| *Dendrocincla fuliginosa* | Generalist | 39.3 | 26.4 | 24.9 | 11 | 7.9 | 17.8 |
| *Dendrocincla merula* | Generalist | 46.3 | 26.5 | 23.4 | 11.3 | 7.7 | 18.8 |
| *Dendrocolaptes certhia* | Generalist | 62 | 28.7 | 33.6 | 15.2 | 8.6 | 16.9 |
| *Dendrocygna autumnalis* | Riparian | 430 | 44.4 | 49.5 | 16.6 | 24.2 | 7.2 |
| *Dendroica petechia* | Riparian | 9 | 19.7 | 9.8 | 5.8 | 3.9 | 27.1 |
| *Dendroplex kienerii* | Riparian | 39.4 | 22.95 | 24.4 | 9.5 | 6.85 | 17.45 |
| *Dendroplex picus* | Generalist | 34 | 23 | 24.4 | 10.7 | 7.3 | 19.5 |
| *Deroptyus accipitrinus* | Riparian | 147 | 19.7 | 31.4 | 20.4 | 32.1 | 20.6 |
| *Diopsittaca nobilis* | Riparian | 156.5 | 21.1 | 27.1 | 18.1 | 27.7 | 31.7 |
| *Dolospingus fringilloides* | White-sand | 11.8 | 17.5 | 13.1 | 8.6 | 8.1 | 17.6 |
| *Dryocopus lineatus* | Riparian | 211 | 32.2 | 35.2 | 15.2 | 9.8 | 23.5 |
| *Egretta thula* | Riparian | 373.5 | 94.6 | 80.7 | 14.8 | 14.9 | 5.3 |
| *Elaenia cristata* | Generalist | 18.1 | 20.3 | 10.9 | 9.7 | 4.9 | 16.4 |
| *Elaenia ruficeps* | White-sand | 17.2 | 21 | 11.3 | 9.4 | 4.9 | 16.2 |

| **Species** | **Category GeoHisse** | **Weight (g)** | **Tarsus (mm)** | **Beak length (mm)** | **Beak width (mm)** | **Beak height (mm)** | **Kipp** |
|---|---|---|---|---|---|---|---|
| *Elanoides forficatus* | Generalist | 420 | 38.9 | 27.2 | 22.8 | 13.7 | 44.1 |
| *Emberizoides herbicola* | Generalist | 24.8 | 26.7 | 32.6 | 8.8 | 7.1 | 16.7 |
| *Epinecrophylla gutturalis* | Riparian | 8.5 | 17.7 | 12.1 | 6.8 | 4.1 | 13.3 |
| *Eucometis penicillata* | Riparian | 26.4 | 23.3 | 14.9 | 10.3 | 7.8 | 17.5 |
| *Euphonia chlorotica* | Generalist | 10.7 | 15.4 | 6.4 | 6.2 | 4.7 | 20.3 |
| *Euphonia chrysopasta* | Riparian | 12 | 16 | 7.9 | 4.9 | 5.6 | 23.8 |
| *Euphonia finschi* | Riparian | 10 | 15.2 | 7.5 | 6.1 | 3.9 | 21.2 |
| *Euphonia minuta* | Riparian | 9.5 | 14.3 | 6.6 | 6.7 | 3.7 | 25.7 |
| *Euphonia rufiventris* | Generalist | 14.7 | 18.4 | 8.6 | 7.2 | 5.8 | 16.8 |
| *Euphonia violacea* | Riparian | 11.7 | 14.6 | 8.3 | 8.2 | 5.4 | 19.2 |
| *Eupsittula pertinax* | Generalist | 79 | 14.7 | 20 | 12.4 | 21.7 | 31.2 |
| *Eurypyga helias* | Riparian | 172 | 54.5 | 49.1 | 11.2 | 7.9 | 18.1 |
| *Falco peregrinus* | Riparian | 566 | 57.4 | 26.5 | 23.4 | 16.3 | 36.5 |
| *Falco rufigularis* | Riparian | 150 | 41.9 | 17.4 | 16 | 13 | 42.7 |
| *Florisuga mellivora* | Generalist | 5.5 | 6.2 | 18.1 | 5.9 | 3 | 61.3 |
| *Fluvicola pica* | Riparian | 14 | 24.2 | 13.4 | 8.7 | 4.1 | 11.2 |
| *Formicarius colma* | Riparian | 46.5 | 32.3 | 16 | 9.7 | 5.6 | 13.9 |
| *Formicivora grisea* | Generalist | 10.5 | 20.6 | 12.5 | 6.5 | 3.9 | 9.9 |
| *Forpus passerinus* | Riparian | 25 | 12.6 | 12.3 | 8.7 | 14.4 | 33.6 |
| *Furnarius leucopus* | Riparian | 35.6 | 29.5 | 18.3 | 9.2 | 5.3 | 10.5 |
| *Galbula galbula* | Riparian | 22.2 | 14.6 | 43 | 8.7 | 6.8 | 14.3 |
| *Galbula leucogastra* | White-sand | 16.1 | 12.9 | 36.4 | 9.7 | 5.7 | 19 |
| *Galbula ruficauda* | Riparian | 24 | 13.2 | 47.3 | 11.5 | 7.1 | 7.6 |
| *Geotrygon montana* | Riparian | 125.7 | 27 | 12.4 | 8.6 | 6.4 | 22.1 |
| *Geranospiza caerulescens* | Riparian | 310 | 92.3 | 27 | 24.1 | 15.5 | 15.2 |
| *Glaucidium brasilianum* | Riparian | 60 | 23.7 | 11.7 | 12.6 | 9.4 | 21.9 |
| *Glaucis hirsutus* | Riparian | 6.5 | 6.2 | 29.5 | 4 | 3 | 53.3 |

| **Species** | **Category GeoHisse** | **Weight (g)** | **Tarsus (mm)** | **Beak length (mm)** | **Beak width (mm)** | **Beak height (mm)** | **Kipp** |
|---|---|---|---|---|---|---|---|
| *Glyphorynchus spirurus* | Riparian | 13.4 | 16.9 | 10.3 | 6.6 | 4 | 20.2 |
| *Granatellus pelzelni* | Riparian | 12 | 20 | 10.8 | 6.8 | 4.7 | 10.6 |
| *Gymnoderus foetidus* | Riparian | 302.5 | 37.4 | 23.4 | 21.9 | 10.7 | 15.7 |
| *Gymnopithys leucaspis* | Generalist | 24 | 27.6 | 16.7 | 10.5 | 5.4 | 14.2 |
| *Gymnopithys rufigula* | Riparian | 29.3 | 30.6 | 16.4 | 9.5 | 6.1 | 11.3 |
| *Heliomaster longirostris* | Riparian | 6.5 | 6.6 | 31.7 | 4.8 | 3 | 62.2 |
| *Heliornis fulica* | Riparian | 109 | 28.1 | 26.1 | 9.1 | 8.3 | 35.2 |
| *Heliothryx auritus* | Riparian | 5 | 5.8 | 17.5 | 4.7 | 3.1 | 62.6 |
| *Hemithraupis flavicollis* | Riparian | 14 | 17 | 10.2 | 6.2 | 5.5 | 19.4 |
| *Hemithraupis guira* | Riparian | 11.7 | 18.3 | 11.3 | 6.4 | 5 | 19.7 |
| *Hemitriccus inornatus* | White-sand | 6.6 | 14.8 | 11 | 7.5 | 3.3 | 18.7 |
| *Hemitriccus margaritaceiventer* | Generalist | 7.2 | 20.8 | 11.9 | 7.4 | 3.8 | 17.2 |
| *Hemitriccus minimus* | Generalist | 7.5 | 16.1 | 11.3 | 7.7 | 3.5 | 13.4 |
| *Hemitriccus minor* | Riparian | 6.2 | 15.5 | 10 | 6.2 | 2.9 | 11.9 |
| *Herpetotheres cachinnans* | Riparian | 610 | 69.9 | 24.3 | 20.6 | 22.7 | 19.5 |
| *Herpsilochmus dorsimaculatus* | Generalist | 9.5 | 19.6 | 13 | 7.3 | 4.2 | 14.2 |
| *Herpsilochmus rufimarginatus* | Riparian | 10 | 20.5 | 13.3 | 7.1 | 4.6 | 14.2 |
| *Heterocercus flavivertex* | Generalist | 20 | 16.7 | 11.7 | 10.2 | 4.6 | 14 |
| *Heterospizias meridionalis* | Riparian | 355 | 118.7 | 36.4 | 22.6 | 20.8 | 29.8 |
| *Hieraspiza superciliosa* | Riparian | 62 | 42.1 | 15 | 12.2 | 11.7 | 29.1 |
| *Hirundo rustica* | Riparian | 14 | 12.4 | 8 | 11.6 | 3.5 | 50.6 |
| *Hydropsalis cayennensis* | White-sand | 32.8 | 15.9 | 10.9 | 16.8 | 3.6 | 42.7 |
| *Hydropsalis climacocerca* | Generalist | 45.7 | 15.4 | 10.4 | 18.3 | 3.6 | 47.4 |
| *Hylocharis sapphirina* | Generalist | 4.3 | 5.7 | 19.2 | 4.4 | 2.5 | 62.9 |
| *Hylophilus brunneiceps* | White-sand | 10.2 | 18.4 | 11.3 | 8.2 | 4.9 | 16.1 |
| *Hylophilus pectoralis* | Riparian | 10.7 | 19.7 | 12.1 | 6.6 | 4.6 | 9.9 |
| *Hylophilus semicinereus* | Riparian | 11.5 | 20.4 | 12.1 | 7.3 | 4.4 | 12.6 |

| **Species** | **Category GeoHisse** | **Weight (g)** | **Tarsus (mm)** | **Beak length (mm)** | **Beak width (mm)** | **Beak height (mm)** | **Kipp** |
|---|---|---|---|---|---|---|---|
| *Hylophylax naevius* | Generalist | 12.8 | 23 | 14.6 | 9.2 | 4.6 | 15.3 |
| *Hylophylax punctulatus* | Riparian | 10.9 | 19.7 | 13.9 | 8.4 | 5.1 | 12.3 |
| *Hypocnemis cantator* | Riparian | 12.2 | 21.8 | 12.2 | 7.4 | 4.5 | 10.2 |
| *Hypocnemis flavescens* | Riparian | 13 | 22.7 | 11.8 | 7.7 | 4.6 | 8.5 |
| *Hypocnemoides melanopogon* | Riparian | 11.9 | 22.2 | 14.7 | 7.7 | 4 | 13 |
| *Ibycter americanus* | Riparian | 600 | 61.5 | 36.2 | 22.3 | 18.3 | 27.1 |
| *Icterus cayanensis* | Riparian | 36 | 24.6 | 21.9 | 8.9 | 7.3 | 20.8 |
| *Icterus croconotus* | Riparian | 43 | 29.3 | 22.5 | 10.9 | 9.9 | 17.5 |
| *Icterus nigrogularis* | Riparian | 36 | 29.2 | 18.7 | 9.2 | 10 | 19.9 |
| *Ictinia plumbea* | Riparian | 199 | 40.6 | 22.6 | 15.7 | 13.9 | 49 |
| *Inezia caudata* | Riparian | 7.5 | 17.2 | 8.8 | 5.8 | 3.3 | 13 |
| *Inezia subflava* | Riparian | 7 | 17.2 | 9.8 | 6 | 3.1 | 13.8 |
| *Isleria guttata* | Riparian | 10.5 | 22.1 | 11.7 | 7.1 | 3.4 | 14.6 |
| *Knipolegus poecilocercus* | Riparian | 13.8 | 19.2 | 10.4 | 7.5 | 4.1 | 16.5 |
| *Laterallus exilis* | Generalist | 34.5 | 25.5 | 16.6 | 7.5 | 6.4 | 12.6 |
| *Lathrotriccus euleri* | Riparian | 12 | 16.5 | 10.2 | 8.8 | 4.5 | 19.8 |
| *Legatus leucophaius* | Riparian | 21.5 | 17.4 | 11.8 | 10.7 | 6.4 | 19.9 |
| *Leistes militaris* | Riparian | 52 | 33.3 | 22 | 10.3 | 9.6 | 19.4 |
| *Leistes superciliaris* | Riparian | 46.3 | 14 | 34.5 | 10.2 | 8.4 | 53.1 |
| *Lepidocolaptes souleyetii* | Riparian | 20.5 | 17.9 | 25.5 | 9.1 | 5.6 | 20.3 |
| *Leptodon cayanensis* | Riparian | 460 | 49.8 | 29.8 | 23.8 | 18.2 | 21 |
| *Leptotila rufaxilla* | Generalist | 164 | 29.4 | 16 | 8.3 | 5.4 | 18.5 |
| *Leptotila verreauxi* | Riparian | 120.7 | 29.4 | 16.5 | 10.8 | 5.7 | 14.6 |
| *Lipaugus vociferans* | Generalist | 67.5 | 22.4 | 19.8 | 16.3 | 8.3 | 18.6 |
| *Lophotriccus galeatus* | Generalist | 6.5 | 15 | 9.3 | 6.1 | 3.5 | 17.8 |
| *Loriotus luctuosus* | Riparian | 11.7 | 17.6 | 11.8 | 8.2 | 6 | 14.2 |
| *Loriotus cristatus* | Riparian | 17.8 | 18.8 | 12.4 | 8.4 | 6.6 | 19.7 |

| **Species** | **Category GeoHisse** | **Weight (g)** | **Tarsus (mm)** | **Beak length (mm)** | **Beak width (mm)** | **Beak height (mm)** | **Kipp** |
|---|---|---|---|---|---|---|---|
| *Megaceryle torquata* | Riparian | 231 | 18.6 | 75.9 | 26.4 | 20.6 | 21.8 |
| *Megarynchus pitangua* | Riparian | 63 | 24 | 28.9 | 18.2 | 11.2 | 12.3 |
| *Megascops choliba* | Generalist | 128.3 | 33.7 | 21.1 | 16.6 | 14 | 25.2 |
| *Megascops watsonii* | Generalist | 133.3 | 33.2 | 18.3 | 19.8 | 12.7 | 19.2 |
| *Melanerpes cruentatus* | Riparian | 55 | 23 | 24.4 | 10.2 | 7.3 | 26.8 |
| *Mesembrinibis cayennensis* | Riparian | 600 | 72.2 | 110.4 | 14.2 | 25.3 | 10.6 |
| *Micrastur semitorquatus* | Riparian | 900 | 106.7 | 27.7 | 21.8 | 24.9 | 17.4 |
| *Microrhopias quixensis* | Riparian | 8 | 17.3 | 13.7 | 7.5 | 4.4 | 9.6 |
| *Milvago chimachima* | Riparian | 310 | 63.1 | 25 | 18.2 | 15 | 35.2 |
| *Mimus gilvus* | Riparian | 56.7 | 36.9 | 17.8 | 10.9 | 6.2 | 22.8 |
| *Mionectes macconnelli* | Generalist | 11.1 | 17.5 | 11.7 | 8.1 | 4.2 | 16.1 |
| *Mionectes oleagineus* | Generalist | 10.1 | 16.1 | 9.4 | 6.8 | 3.4 | 12.3 |
| *Molothrus bonariensis* | Riparian | 34.9 | 27.4 | 16.6 | 8.1 | 8.6 | 24.6 |
| *Molothrus oryzivorus* | Riparian | 150 | 43.2 | 30.5 | 13.6 | 13.4 | 31.2 |
| *Momotus momota* | Riparian | 117.5 | 30.7 | 37.8 | 17.8 | 12.7 | 11 |
| *Monasa atra* | Riparian | 84.9 | 24.7 | 34 | 15.4 | 13.3 | 14.1 |
| *Monasa nigrifrons* | Riparian | 79.3 | 23.8 | 31.2 | 14.6 | 13 | 15.4 |
| *Myiarchus ferox* | Generalist | 25.8 | 23.1 | 17.7 | 11.1 | 6.3 | 15 |
| *Myiarchus tuberculifer* | Generalist | 20.3 | 21.3 | 16.4 | 10.8 | 5.5 | 16 |
| *Myiarchus tyrannulus* | Riparian | 20.5 | 24.2 | 16.8 | 11.8 | 5.6 | 13.2 |
| *Myiobius barbatus* | Riparian | 10 | 16.9 | 11.1 | 7 | 3.2 | 12.4 |
| *Myiodynastes maculatus* | Riparian | 27 | 20 | 21.8 | 13.6 | 8.7 | 19 |
| *Myiopagis caniceps* | Riparian | 13 | 18.3 | 9.5 | 7.4 | 2.9 | 18.8 |
| *Myiopagis flavivertex* | Riparian | 12 | 13.5 | 9.4 | 7.7 | 4.2 | 9.9 |
| *Myiopagis gaimardii* | Generalist | 9.5 | 19.7 | 8.3 | 5.6 | 3.6 | 9.4 |
| *Myiornis ecaudatus* | Riparian | 5.8 | 11.4 | 9 | 5.1 | 2.7 | 12.9 |
| *Myiothlypis flaveola* | Riparian | 12.5 | 23.6 | 9.8 | 6.2 | 3.9 | 16.6 |

| Species | Category GeoHisse | Weight (g) | Tarsus (mm) | Beak length (mm) | Beak width (mm) | Beak height (mm) | Kipp |
|---|---|---|---|---|---|---|---|
| *Myiozetetes cayanensis* | Generalist | 25.3 | 20.7 | 12.4 | 9.1 | 5.7 | 14.7 |
| *Myrmeciza longipes* | Riparian | 23.8 | 30 | 16.4 | 9.2 | 5.8 | 8 |
| *Myrmoborus leucophrys* | Riparian | 21.3 | 27.7 | 14.5 | 8.8 | 5.2 | 11.6 |
| *Myrmoborus lugubris* | Riparian | 19.3 | 27.1 | 16.5 | 9.7 | 5.8 | 11.7 |
| *Myrmoborus myotherinus* | Generalist | 17.7 | 25.9 | 15.2 | 10 | 5.7 | 13.2 |
| *Myrmotherula assimilis* | Riparian | 9.2 | 17.9 | 12.3 | 6.7 | 3.5 | 10.7 |
| *Myrmotherula axillaris* | Generalist | 7.8 | 17.5 | 11.5 | 6.4 | 3.9 | 10 |
| *Myrmotherula brachyura* | Riparian | 7.3 | 17.3 | 11.5 | 6.1 | 3.1 | 10.5 |
| *Myrmotherula cherriei* | Generalist | 9 | 17.6 | 11.4 | 6.3 | 2.9 | 11.8 |
| *Myrmotherula klagesi* | Riparian | 8.1 | 18.7 | 12.5 | 6.1 | 3.2 | 11.6 |
| *Nannochordeiles pusillus* | White-sand | 27.5 | 13.1 | 4.7 | 13 | 3 | 40.5 |
| *Nannopterum brasilianus* | Riparian | 900 | 51.9 | 50.2 | 18.1 | 16.4 | 24.9 |
| *Nasica longirostris* | Riparian | 87.5 | 29.5 | 68.8 | 14.5 | 9.7 | 16.3 |
| *Nemosia pileata* | Riparian | 15.3 | 18.8 | 11.2 | 7.2 | 5.1 | 20.7 |
| *Neochen jubata* | Riparian | 1570 | 80.8 | 41.8 | 19.5 | 22.9 | 4.6 |
| *Neocrex erythrops* | Riparian | 51.5 | 25.9 | 19.5 | 7.3 | 8.8 | 18.9 |
| *Neopelma chrysocephalum* | White-sand | 13.8 | 18.3 | 11.4 | 9.9 | 4.9 | 18.8 |
| *Neopipo cinnamomea* | Generalist | 9 | 12.1 | 6.4 | 5.5 | 3.1 | 22.5 |
| *Notharchus macrorhynchos* | Riparian | 75 | 22.5 | 34.1 | 19.2 | 16.6 | 7.7 |
| *Notharchus tectus* | Riparian | 27 | 16.3 | 19.8 | 12.3 | 10.6 | 35.1 |
| *Nyctibius griseus* | Generalist | 81 | 17.6 | 17.6 | 37.2 | 5.2 | 36.5 |
| *Nycticorax nycticorax* | Riparian | 810 | 89.7 | 73.2 | 40.8 | 26.2 | 6.9 |
| *Nyctidromus albicollis* | Riparian | 49.5 | 28.9 | 10.1 | 19.7 | 3.7 | 39.4 |
| *Nyctipolus nigrescens* | Generalist | 37.5 | 15.3 | 9.9 | 16.9 | 3.3 | 40.6 |
| *Nyctiprogne leucopyga* | Generalist | 24 | 13.2 | 4.6 | 13 | 2.1 | 71.9 |
| *Ochthornis littoralis* | Riparian | 14.5 | 19.5 | 11.3 | 8.5 | 3.9 | 17.1 |
| *Opisthocomus hoazin* | Riparian | 600 | 76.4 | 25.4 | 20.2 | 18.5 | 14.8 |

| **Species** | **Category GeoHisse** | **Weight (g)** | **Tarsus (mm)** | **Beak length (mm)** | **Beak width (mm)** | **Beak height (mm)** | **Kipp** |
|---|---|---|---|---|---|---|---|
| *Ortalis motmot* | Generalist | 546 | 66 | 22.9 | 19.1 | 12.8 | 5.7 |
| *Orthopsittaca manilata* | Generalist | 220 | 20.9 | 31.9 | 17 | 29.7 | 29.3 |
| *Pachyramphus marginatus* | Riparian | 14.5 | 19.7 | 12 | 9.8 | 5.2 | 28.3 |
| *Pachyramphus polychopterus* | Riparian | 16.2 | 19 | 11.7 | 10.3 | 5.6 | 22.1 |
| *Pachyramphus rufus* | Riparian | 19.3 | 19.7 | 12.4 | 10 | 5.6 | 18.3 |
| *Pachysylvia muscicapina* | Riparian | 11.8 | 18 | 12.2 | 7.5 | 4.5 | 19.2 |
| *Pandion haliaetus* | Riparian | 900 | 69.3 | 38.1 | 29.4 | 19.2 | 36.8 |
| *Paroaria gularis* | Riparian | 26.6 | 24.3 | 12.8 | 7.9 | 6.5 | 16.1 |
| *Patagioenas cayennensis* | Generalist | 256 | 29.2 | 17.4 | 11.7 | 6.1 | 35.9 |
| *Patagioenas plumbea* | Generalist | 170 | 19.8 | 16.7 | 9.4 | 6.3 | 26.4 |
| *Patagioenas speciosa* | Generalist | 253 | 24.5 | 21.1 | 10 | 8.6 | 34.3 |
| *Patagioenas subvinacea* | Generalist | 132 | 24.5 | 13.3 | 11.5 | 5.7 | 24.7 |
| *Pauxi tomentosa* | Riparian | 3250 | 130.3 | 64.5 | 21.5 | 50.8 | 2 |
| *Percnostola rufifrons* | Generalist | 29.8 | 31 | 16.9 | 9.6 | 6.3 | 10.6 |
| *Phaeomyias murina* | Riparian | 10.3 | 21.4 | 9.6 | 7.7 | 4 | 15 |
| *Phaethornis malaris* | Generalist | 6 | 5.3 | 37.7 | 4.4 | 3.6 | 59.1 |
| *Phaethornis ruber* | Generalist | 2.3 | 5.1 | 22.9 | 4.4 | 3.1 | 59.5 |
| *Phaethornis rupurumii* | Riparian | 2.2 | 5 | 24.5 | 3.8 | 2.8 | 52.3 |
| *Phaethornis superciliosus* | Generalist | 5.5 | 6.2 | 33.4 | 4.8 | 3.6 | 58.2 |
| *Phaetusa simplex* | Riparian | 250 | 27.4 | 62.1 | 21.9 | 18.8 | 37.6 |
| *Pheugopedius coraya* | Riparian | 15.6 | 24.3 | 15.35 | 7.95 | 5.1 | 10.5 |
| *Philydor erythrocercum* | Riparian | 29 | 22.5 | 15.7 | 8.8 | 6.3 | 18.2 |
| *Philydor pyrrhodes* | Riparian | 30.3 | 23.2 | 17 | 9 | 6.8 | 30.3 |
| *Piaya cayana* | Generalist | 98 | 40.3 | 25.9 | 15.7 | 11.7 | 7.6 |
| *Piaya melanogaster* | Riparian | 88 | 40.5 | 29.1 | 16 | 11.2 | 7 |
| *Piculus flavigula* | Riparian | 53.3 | 20.8 | 19.1 | 10.1 | 7.4 | 22.7 |
| *Picumnus exilis* | Generalist | 10 | 14.4 | 10.1 | 6.2 | 5.2 | 15.3 |

| **Species** | **Category GeoHisse** | **Weight (g)** | **Tarsus (mm)** | **Beak length (mm)** | **Beak width (mm)** | **Beak height (mm)** | **Kipp** |
|---|---|---|---|---|---|---|---|
| *Picumnus spilogaster* | Riparian | 12.5 | 15.3 | 12.6 | 6.3 | 5.6 | 16.2 |
| *Pilherodius pileatus* | Riparian | 500 | 100.1 | 83.9 | 19.5 | 19.7 | 17 |
| *Pionites melanocephalus* | Riparian | 155 | 21.7 | 26.4 | 16.1 | 25.1 | 20.1 |
| *Pionus menstruus* | Riparian | 252.5 | 24.1 | 28.5 | 18 | 25.5 | 23.2 |
| *Pipra filicauda* | Riparian | 13.4 | 17.7 | 9.2 | 9.1 | 4.3 | 16.7 |
| *Piprites chloris* | Generalist | 15.3 | 18.2 | 9.4 | 9.4 | 4.9 | 21.4 |
| *Pitangus lictor* | Riparian | 23 | 20.6 | 20.2 | 9.1 | 5.9 | 18.05 |
| *Pitangus sulphuratus* | Generalist | 54.5 | 26.1 | 23.6 | 12.6 | 8.7 | 17 |
| *Pithys albifrons* | Riparian | 19 | 25.2 | 12.4 | 8.3 | 4.2 | 14 |
| *Pluvialis dominica* | Riparian | 116 | 41.5 | 23.3 | 7.6 | 7.1 | 41 |
| *Poecilotriccus sylvia* | Riparian | 8 | 21 | 12.2 | 6.7 | 3.8 | 16.5 |
| *Polioptila plumbea* | Generalist | 6.5 | 16.2 | 9.9 | 6.4 | 2.7 | 13.4 |
| *Polytmus theresiae* | White-sand | 3.3 | 6.8 | 20 | 4.5 | 2.6 | 63.5 |
| *Progne chalybea* | Riparian | 39.5 | 16.8 | 11 | 16 | 5.4 | 45 |
| *Progne subis* | Riparian | 51 | 15.6 | 11.4 | 16 | 5.3 | 47.9 |
| *Progne tapera* | Riparian | 37 | 16.5 | 11.3 | 13.4 | 4.9 | 49.6 |
| *Psarocolius bifasciatus* | Riparian | 238 | 48.9 | 56.1 | 19.6 | 25.9 | 22 |
| *Psarocolius decumanus* | Generalist | 355 | 54 | 64.3 | 23.5 | 27.6 | 33.8 |
| *Psarocolius viridis* | Generalist | 170 | 47 | 48.8 | 17.4 | 16.3 | 23.5 |
| *Pseudopipra pipra* | Riparian | 12 | 15.2 | 8.3 | 7.8 | 4.3 | 14.2 |
| *Psittacara leucophthalmus* | Generalist | 147.5 | 20 | 25 | 17.3 | 29 | 31.1 |
| *Pteroglossus aracari* | Riparian | 265 | 47.3 | 120.7 | 30.4 | 33.2 | 17.1 |
| *Pygiptila stellaris* | Riparian | 23.5 | 21.5 | 18.9 | 11.1 | 7.3 | 15 |
| *Pygochelidon melanoleuca* | Riparian | 14.9 | 12.05 | 5.8 | 8.25 | 2.7 | 48 |
| *Pyrocephalus rubinus* | Riparian | 12.5 | 17.6 | 12 | 7.7 | 3.9 | 19.9 |
| *Querula purpurata* | Riparian | 97 | 27.1 | 21.8 | 20.2 | 9.9 | 18.1 |
| *Ramphastos toco* | Riparian | 470 | 60.3 | 143.6 | 37.4 | 54.2 | 18.5 |

| **Species** | **Category GeoHisse** | **Weight (g)** | **Tarsus (mm)** | **Beak length (mm)** | **Beak width (mm)** | **Beak height (mm)** | **Kipp** |
|---|---|---|---|---|---|---|---|
| *Ramphastos tucanus* | Generalist | 663.8 | 53.1 | 153.4 | 37.9 | 51.5 | 20.2 |
| *Ramphastos vitellinus* | Generalist | 345 | 47.8 | 115.8 | 29.9 | 38.1 | 12.4 |
| *Ramphocaenus melanurus* | Riparian | 9.7 | 22.4 | 19.9 | 5.8 | 3.3 | 9.8 |
| *Ramphocelus carbo* | Generalist | 19.8 | 21.9 | 13.9 | 13.4 | 8.4 | 13 |
| *Ramphotrigon ruficauda* | Generalist | 17 | 15.9 | 13.2 | 11.3 | 5.9 | 16.5 |
| *Rhytipterna immunda* | White-sand | 24 | 22.3 | 15.9 | 11.4 | 6.5 | 17.8 |
| *Rhytipterna simplex* | Generalist | 29 | 20.4 | 16.9 | 11.4 | 6.5 | 15.1 |
| Rufirallus viridis | Riparian | 50.3 | 38.8 | 16.2 | 8.2 | 7.3 | 12.6 |
| *Rupornis magnirostris* | Generalist | 220 | 65.5 | 26.2 | 21.4 | 15.8 | 27.3 |
| *Rynchops niger* | Riparian | 287.5 | 33.5 | 90.9 | 24.6 | 25.6 | 40.4 |
| *Sakesphorus canadensis* | Generalist | 24.8 | 27.6 | 17.8 | 10.2 | 6.5 | 7.6 |
| *Saltator coerulescens* | Riparian | 49.3 | 28.4 | 18.5 | 11.9 | 11.7 | 14.5 |
| *Saltator grossus* | Riparian | 43.5 | 28.6 | 18.7 | 12.9 | 13.6 | 18.8 |
| *Sarcoramphus papa* | Riparian | 3000 | 114.9 | 66.6 | 32.4 | 38.5 | 2.1 |
| *Schiffornis major* | Riparian | 29.2 | 22.2 | 11.6 | 9.8 | 5.7 | 16.9 |
| *Schiffornis turdina* | Generalist | 33.8 | 23.9 | 13.9 | 10.2 | 6.2 | 18.6 |
| *Schistochlamys melanopis* | Generalist | 27.7 | 22.8 | 14.7 | 9.3 | 8.6 | 14.4 |
| *Sclateria naevia* | Riparian | 17 | 26.7 | 20.3 | 9.5 | 4.9 | 8.5 |
| *Serpophaga hypoleuca* | Riparian | 6.8 | 18.7 | 8.4 | 5.4 | 2.9 | 13.5 |
| *Setophaga pitiayumi* | Riparian | 7.8 | 17.8 | 9.6 | 6.8 | 3.5 | 19.6 |
| *Setophaga ruticilla* | Riparian | 8.5 | 19.4 | 8.4 | 7.6 | 3.6 | 20.9 |
| *Sittasomus griseicapillus* | Generalist | 16.5 | 20.1 | 15.9 | 9.3 | 4.7 | 24.3 |
| *Sporophila angolensis* | Generalist | 12 | 18 | 12.8 | 9.7 | 10.4 | 16.3 |
| *Sporophila castaneiventris* | Riparian | 11 | 15.9 | 7.9 | 6.8 | 6.5 | 11.7 |
| *Sporophila intermedia* | Riparian | 12.5 | 18.8 | 10.3 | 8.2 | 8.6 | 14.7 |
| *Sporophila lineola* | Riparian | 11.5 | 16.2 | 7.7 | 6.4 | 6.5 | 23.3 |
| *Stelgidopteryx ruficollis* | Generalist | 15.5 | 12.4 | 6.6 | 10.5 | 2.8 | 51.9 |

| **Species** | **Category GeoHisse** | **Weight (g)** | **Tarsus (mm)** | **Beak length (mm)** | **Beak width (mm)** | **Beak height (mm)** | **Kipp** |
|---|---|---|---|---|---|---|---|
| *Stigmatura napensis* | Riparian | 10.3 | 20.5 | 9.5 | 6.7 | 3.4 | 12.1 |
| *Stilpnia cayana* | Generalist | 17 | 20.7 | 10.9 | 7.8 | 5.7 | 18 |
| *Synallaxis albescens* | Riparian | 12.8 | 21.7 | 11.1 | 6.2 | 4 | 14.8 |
| *Synallaxis gujanensis* | Riparian | 17.4 | 23.8 | 12.2 | 6.8 | 4.4 | 8.7 |
| *Synallaxis propinqua* | Riparian | 18.8 | 23.8 | 14.3 | 6.9 | 3.9 | 9.4 |
| *Synallaxis rutilans* | Riparian | 18.5 | 20.6 | 10.2 | 7 | 4.4 | 8.7 |
| *Tachornis squamata* | Riparian | 9 | 7.8 | 3.8 | 7.5 | 2.3 | 64.1 |
| *Tachycineta albiventer* | Riparian | 14 | 11.2 | 8.2 | 11.5 | 3.2 | 51.4 |
| *Tachyphonus phoenicius* | White-sand | 19.8 | 22.3 | 12.5 | 8 | 7 | 17.7 |
| *Tamatia tamatia* | Generalist | 36.5 | 20 | 22.1 | 15.2 | 11.6 | 14.1 |
| *Tangara mexicana* | Riparian | 18 | 17.9 | 7.9 | 7.5 | 4.6 | 23.9 |
| *Taraba major* | Riparian | 57 | 37.3 | 25.7 | 14 | 11.4 | 8 |
| *Terenotriccus erythrurus* | Riparian | 6.6 | 16.4 | 7.6 | 7.1 | 3.3 | 13.4 |
| *Thalurania furcata* | Generalist | 4.2 | 5 | 20.3 | 4.6 | 2.1 | 61 |
| *Thamnomanes caesius* | Riparian | 15.1 | 20 | 14.8 | 9.2 | 5.2 | 12.5 |
| *Thamnophilus aethiops* | Riparian | 25.1 | 25.4 | 16.1 | 9.7 | 6.6 | 8.8 |
| *Thamnophilus amazonicus* | Generalist | 17.8 | 22.3 | 14.4 | 8.7 | 6 | 10.5 |
| *Thamnophilus doliatus* | Generalist | 24.6 | 29.5 | 16.1 | 9.4 | 6.5 | 8 |
| *Thamnophilus murinus* | Generalist | 18 | 22.8 | 14.9 | 8.8 | 5.4 | 10.8 |
| *Thamnophilus nigrocinereus* | Riparian | 25.4 | 25.3 | 18.3 | 11.7 | 7.1 | 9.7 |
| *Thamnophilus punctatus* | Generalist | 22 | 23.5 | 15.8 | 9.5 | 6.5 | 10.5 |
| *Thraupis episcopus* | Generalist | 29.3 | 24.2 | 12.9 | 10.5 | 7.5 | 19.7 |
| *Thraupis palmarum* | Riparian | 39.5 | 22.5 | 12.4 | 8.6 | 7.2 | 21.6 |
| *Threnetes leucurus* | Riparian | 5.5 | 6.3 | 29.1 | 4.9 | 3.4 | 60.9 |
| *Tigrisoma lineatum* | Riparian | 1000 | 117.6 | 112 | 19.2 | 27.5 | 14.8 |
| *Tinamus major* | Riparian | 990 | 63.9 | 30.6 | 17.1 | 14.4 | 5.8 |
| *Tityra cayana* | Riparian | 49.5 | 28.1 | 21.7 | 16.9 | 10.3 | 26.4 |

| **Species** | **Category GeoHisse** | **Weight (g)** | **Tarsus (mm)** | **Beak length (mm)** | **Beak width (mm)** | **Beak height (mm)** | **Kipp** |
|---|---|---|---|---|---|---|---|
| *Todirostrum cinereum* | Riparian | 8 | 18.7 | 13.4 | 5.4 | 3.5 | 9.8 |
| *Todirostrum maculatum* | Riparian | 7.4 | 19.4 | 12.6 | 6.1 | 3.5 | 10.8 |
| *Todirostrum pictum* | Riparian | 6 | 13.8 | 12.6 | 6.8 | 3.4 | 10.8 |
| *Tolmomyias assimilis* | Riparian | 14.5 | 19.4 | 10.8 | 9.6 | 4.4 | 16.1 |
| *Tolmomyias flaviventris* | Generalist | 11.8 | 18.2 | 9.3 | 9.2 | 4.2 | 14 |
| *Tolmomyias poliocephalus* | Generalist | 10.8 | 17.4 | 10.5 | 8.8 | 3.9 | 15.9 |
| *Tolmomyias sulphurescens* | Riparian | 14.8 | 20.1 | 11.1 | 9.7 | 4.2 | 13.3 |
| *Topaza pyra* | Generalist | 14.7 | 7.8 | 22.1 | 7 | 3.2 | 61.1 |
| *Touit huetii* | Generalist | 70 | 12.5 | 15 | 9.6 | 13.6 | 29.9 |
| *Tringa melanoleuca* | Riparian | 125.5 | 60.3 | 55 | 9.9 | 9.9 | 16.6 |
| *Tringa solitaria* | Riparian | 45 | 30.8 | 27 | 5.1 | 4.8 | 31.5 |
| *Troglodytes musculus* | Generalist | 12.75 | 20.05 | 12.9 | 6.7 | 3.8 | 11.65 |
| *Trogon melanurus* | Riparian | 107 | 19.9 | 22.6 | 21.3 | 12.7 | 36.8 |
| *Trogon violaceus* | Generalist | 48.7 | 15.8 | 15.7 | 16.4 | 9.5 | 32 |
| *Trogon viridis* | Generalist | 84 | 17.8 | 20.4 | 19.1 | 13 | 98.3 |
| *Turdus arthuri* | White-sand | 59 | 32 | 17.9 | 12.7 | 6.6 | 20.9 |
| *Turdus fumigatus* | Riparian | 64.5 | 32.8 | 18.4 | 11.4 | 7.2 | 20.4 |
| *Turdus leucomelas* | Riparian | 63.8 | 31.9 | 18.5 | 12.7 | 6.7 | 22.6 |
| *Turdus nudigenis* | Riparian | 58.8 | 34.2 | 16.7 | 12.4 | 6.3 | 19.8 |
| *Tyranneutes stolzmanni* | Generalist | 8.1 | 12.9 | 9.2 | 8 | 3.3 | 26.2 |
| *Tyrannopsis sulphurea* | Riparian | 58 | 22 | 17.3 | 15.7 | 7 | 16.3 |
| *Tyrannulus elatus* | Generalist | 6.5 | 13.7 | 6.3 | 5.2 | 4 | 15.5 |
| *Tyrannus melancholicus* | Generalist | 41 | 19.4 | 19.9 | 12.8 | 7.2 | 25 |
| *Tyrannus savana* | Riparian | 29.5 | 18.3 | 14 | 10.7 | 5.5 | 32 |
| *Urubutinga urubitinga* | Riparian | 1140 | 138 | 44.7 | 20.5 | 24.8 | 14.2 |
| *Vanellus cayanus* | Riparian | 97 | 49.3 | 23.2 | 9.5 | 8.5 | 40.1 |
| *Vanellus chilensis* | Generalist | 150 | 65.1 | 27.4 | 9.8 | 10.1 | 4.4 |

| **Species** | **Category GeoHisse** | **Weight (g)** | **Tarsus (mm)** | **Beak length (mm)** | **Beak width (mm)** | **Beak height (mm)** | **Kipp** |
|---|---|---|---|---|---|---|---|
| *Veniliornis cassini* | Riparian | 31 | 19 | 17.1 | 8.5 | 6.3 | 21.3 |
| *Veniliornis passerinus* | Riparian | 33 | 19.6 | 18.3 | 12.5 | 7.2 | 14 |
| *Vireo olivaceus* | Riparian | 16 | 20.7 | 13.2 | 7.9 | 5 | 25.5 |
| *Willisornis poecilinotus* | Generalist | 18.3 | 25.2 | 15.2 | 10.2 | 5.5 | 12.7 |
| *Xenopipo atronitens* | White-sand | 14 | 17 | 11.4 | 10.1 | 5.1 | 19.9 |
| *Xenops minutus* | Generalist | 11.7 | 16.2 | 11.2 | 6.2 | 4.7 | 18.5 |
| *Xipholena punicea* | Generalist | 66 | 22.9 | 14.9 | 15.7 | 6.8 | 14.1 |
| *Xiphorhynchus guttatus* | Riparian | 55.9 | 23.7 | 33 | 12.5 | 9.2 | 15.4 |
| *Xiphorhynchus obsoletus* | Generalist | 32.3 | 22.8 | 23.1 | 9.6 | 7.1 | 18.1 |
| *Xiphorhynchus ocellatus* | Generalist | 32.7 | 22.7 | 23.2 | 9.8 | 7 | 18.1 |
| *Xiphorhynchus pardalotus* | Riparian | 41 | 23.8 | 30 | 11.3 | 7.5 | 20.7 |
| *Zebrilus undulatus* | Riparian | 130 | 41.8 | 44.1 | 13.7 | 12.3 | 14.4 |
| *Zimmerius acer* | Riparian | 8 | 17.5 | 7.6 | 5.8 | 3.7 | 12.3 |
| *Zimmerius gracilipes* | Generalist | 6.8 | 14.9 | 7.9 | 6.8 | 3.4 | 16 |
| *Zonotrichia capensis* | Generalist | 15.8 | 23.6 | 12.1 | 7.6 | 6.6 | 17.8 |

# Considerações Finais

A linha de pesquisa neste trabalho vem sendo utilizada recentemente nas abordagens da ecologia de comunidades e evolutiva. Porém, ao lidar com grande banco de dados, relacionando dados ecológicos, morfológicos e filogenéticos, conseguimos elucidar questões importantes dentro da diversidade funcional e ecologia evolutiva das comunidades de ecossistemas de areia branca (EAB) e ser um trabalho inovador. A Amazônia um Bioma tão heterogêneo, com vários fatores que influenciaram a grande biodiversidade, não pode negligenciar as pesquisas, especialmente nos ecossistemas que mais estão vulneráveis a mudanças climáticas e ações antrópicas. Temos bons resultados para acrescentar a ciência e direcionar futuros estudos em Ecossistemas de areia branca (EAB). Assim, tentamos juntar resultados que elucidem a especialização e contar uma suposta parte da história eco-evolutiva dos EAB, colaborando com evidencias com nossos resultados que veremos a seguir:

No **Capítulo 1**, todos os resultados das analises multivariadas mostraram a assembleia das aves especialistas em um grupo reduzido e inserido no grupo mais disperso no espaço funcional das espécies das generalistas. Concluimos que há redução do espaço funcional das espécies especialistas, não sendo diferentes funcionalmente das especiesgeneralista em EAB. A especialização ecomorfológica não é evidenciada, mostrando que as aves generalistas que estão nos EAB sofrem provavelmente a mesma pressão seletiva. Nossos resultados confirmam que as espécies especialistas, possuem outras ligações históricas com o ambiente, pois a ecomofologia não impediria de colonizar novos ecossistemas amazônicos, uma vez que não são um grupo a parte no espaço funcional. O aumento do conhecimento sobre quais seriam os caminhos para estudos sobre a especialização das espécies na Amazônia em qualquer outro ecossistema, pode ajudar no direcionamento dos futuros estudos, nos planejamentos para a conservação das espécies, definição de especialistas, filtro ambiental e principalmente auxiliar no entendimento da história evolutiva das espécies e seus padrões biogeográficos. Este foi um dos estudos de EAB que mais buscou investigar as características morfológicas e ecológicas juntas, e exaurindo as possibilidades de visualizar se realmente poderia existir um grupo a parte de especialistas.

O termo “especialização” deve ser utilizado de forma clara dentro da ecologia, e sendo importante enfatizar a utilização de mais linhas de estudos para explicar a restrição das espécies em determinados locais, e em determinado espaço de tempo. Hoje existem pelo menos três linhas dentro do estudo de ecologia de comunidades que podem ser buscadas, afim de se complementarem e responder a tais questionamentos. Elas são a ecologia taxonômica, funcional e filogenética, que se utilizadas podem descrever e evidenciar importantes questões ecológicas evolutivas. Assim, para complementar os questionamentos sobre aves especialistas de EAB, usamos uma abordagem de modelos em ecologia evolutiva no segundo capítulo desta tese.

No **Capítulo 2,** nossos resultados revelam que a extinção é um evento importante na formação das comunidades de aves especialistas de Ecossistemas de areia branca (EAB). A extinção é um evento comum dentro da história evolutiva das espécies, na Amazônia ainda é pouco compreendido, assim como outros processos evolutivos e modelos que foram utilizados no trabalho. As duas analises a partir de modelos, foram utilizadas de forma pioneira, pois trabalha a composição de espécies em um único Bioma, em dois ecossistemas menos avaliados na maioria dos estudos que na maioria das vezes visam o Ecossistema de Terra Firme na Amazônia. Nossos resultados servirão de base para novos estudos sobre a especialização em ecossistemas na Amazônia que possuem história evolutiva integrada com muitos eventos biogeográficos, pressões ecológicas e atualmente processos acelaerados devido aumento das mudanças climáticas. Futuros estudos devem buscar por novas metodologias, afim de mitigar os efeitos, ter a possibilidade de estudar espécies ainda viventes e entender como ocorre o ganho e perda de espécies em ecossistemas amazônicos. É válido o desenvolvimento e utilização de todas as ferramentas possíveis para modelar os eventos passados e futuros nos diversos ecossistemas do planeta.

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