

ORIGINAL ARTICLE

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

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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. Understorey 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 assembleias 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 sobrepuaram-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, ecossistemas tropicais**CITE AS:** Lima, G.R.; Borges, S.H.; Anciães, M.; Cornelius, C. 2023. Ecomorphology and functional diversity of generalist and specialist bird assemblages in Amazonian white-sand ecosystem habitat patches. *Acta Amazonica* 53: 141-153.

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.* 2016a). 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.* 2016a).

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.* 2016b). 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.* (2016a).

We used the categorization proposed by Borges *et al.* (2016b) 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.* 2016b). 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.* (2016b), and 2) specialist species, which are mostly exclusively found in WSE, equivalent to the restricted and almost restricted categories in Borges *et al.* (2016b), 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 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).

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.* (2016b), 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. WSE habitat category: GEN = generalist, SPE = specialist; Diet category: Frug = frugivore, Inse = insectivore, Carn = carnivore, Omni = omnivore, Nect = nectarivore, Gran = granivore; Foraging strata: CAN = canopy, UND = understory, GRO = ground, AER = aerial, WAT = water; Sociability: Sol/pair = solitary/pairs.

Bird species	WSE 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 primaries length (mm)	Wing secondaries length (mm)	Kipp distance (mm)
<i>Amazona amazonica</i>	GEN	Frug	Can	Flocks	391.5	124.8	25.5	33.1	19.9	28.7	205.5	8.8	4.3
<i>Anrostomus rufus</i>	GEN	Inse	Und	Sol/pair	98.0	127.6	18.2	16.0	32.1	4.3	169.5	77.5	45.7
<i>Aprositornis disjuncta</i>	SPE	Inse	Und	Sol/pair	13.2	52.2	27	16.2	8.2	5.8	61.8	9.4	15.1
<i>Ara ararauna</i>	GEN	Frug	Can	Flocks	150	46.0	44.0	67.1	30.5	66.7	383.9	88.8	23.1
<i>Asio stygius</i>	GEN	Carn	Gro	Sol/pair	610	18.7	59.1	34.6	26.2	23.9	354.3	80.3	22.7
<i>Attila cinnamomeus</i>	GEN	Omni	Can	Sol/pair	32.5	75.2	23.0	18.8	11.5	6.6	90.8	14.2	15.6
<i>Attila citriniventris</i>	SPE	Inse	Can	Sol/pair	33.0	68.6	20.8	19.2	12.5	6.0	79.9	14.0	17.6
<i>Attila spadiceus</i>	GEN	Omni	Can	Sol/pair	31.5	68.2	25.3	18.0	11.7	5.8	80.4	12.5	15.6
<i>Automolus ochrolaemus</i>	GEN	Inse	Und	Sol/pair	35	78.9	23.7	18.5	12.1	7.0	86.0	15.4	17.8
<i>Brotogeris chrysoptera</i>	GEN	Frug	Can	Flocks	58.8	79.1	15.0	18.9	10.5	14.8	113.6	39.1	34.1
<i>Camptostoma obsoletum</i>	GEN	Inse	Can	Sol/pair	7.6	35.8	12.5	8.4	6.0	3.5	44.9	8.2	18.2
<i>Caryothraustes canadensis</i>	GEN	Frug	Can	Flocks	29.0	72.8	21.3	15.5	10.8	10.4	83.5	12.1	14.6
<i>Celeus torquatus</i>	GEN	Omni	Can	Sol/pair	117	116.9	29.9	32.2	13.5	10.2	152.7	32.9	21.5
<i>Celeus undatus</i>	GEN	Omni	Can	Sol/pair	65.0	94.1	22.5	20.8	10.6	8.7	120.7	28.0	23.2
<i>Ceratopira erythrocephala</i>	GEN	Frug	Und	Flocks	14.0	31.3	14.2	8.8	8.4	3.8	59.0	11.8	20.0
<i>Cercomacra tyrannina</i>	GEN	Inse	Und	Sol/pair	14.6	64.8	25.0	14.5	8.5	4.7	59.9	7.2	12.0
<i>Chelidoptera tenebrosa</i>	GEN	Inse	Aer	Flocks	36.3	57.1	15.9	18.1	11.0	7.4	105.5	14.7	13.9
<i>Chionomesa fimbriata</i>	GEN	Nect	Und	Sol/pair	4.0	31.1	5.3	18.3	3.6	2.3	52.6	28.4	53.9
<i>Chlorestes cyanus</i>	GEN	Nect	Und	Sol/pair	3.0	31.1	4.8	15.9	4.3	2.3	48.2	30.2	62.6
<i>Chloroceryle aenea</i>	GEN	Carn	Wat	Sol/pair	12.3	38.9	7.6	20.3	10.7	6.8	53.9	12.6	23.3
<i>Chlorostilbon mellisugus</i>	GEN	Nect	Can	Sol/pair	4.0	25.0	5.8	14.4	2.7	1.8	39.9	24.7	62.0
<i>Chordeiles pusillus</i>	SPE	Inse	Can	Flocks	27.5	86.1	13.0	4.7	13	3.0	136.1	55.0	40.5
<i>Chrysolampis mosquitus</i>	GEN	Nect	Can	Sol/pair	3.7	35.9	6.0	12.9	4.2	2.2	53.6	31.6	58.9
<i>Chrysuronia versicolor</i>	GEN	Nect	Can	Sol/pair	3.0	31.0	6.0	16.3	4.6	2.4	50.3	28.8	57.3
<i>Cnemotriccus fuscatus</i>	SPE	Inse	Und	Sol/pair	14.0	67.7	19.7	11.9	8.0	4.3	65.5	8.5	13.0
<i>Coereba flaveola</i>	GEN	Nect	Can	Sol/pair	8.2	36.0	17.8	11.2	5.3	3.8	55.1	10.3	18.5
<i>Columbina passerina</i>	GEN	Frug	Gro	Flocks	35.0	67.0	18.2	11.1	6.2	4.3	76.5	14.1	18.5
<i>Conopias parvus</i>	GEN	Frug	Can	Flocks	22.7	71.3	18.0	16.2	12.0	6.1	77.7	14.7	18.9
<i>Crypturellus cinereus</i>	GEN	Frug	Gro	Sol/pair	300	74.8	55.4	21.8	18.9	8.5	169.7	15.4	9.1
<i>Crypturellus duidae</i>	SPE	Omni	Gro	Sol/pair	300	74.8	49.6	28.5	9.7	8.5	140.8	23.4	16.7
<i>Crypturellus erythropus</i>	GEN	Omni	Gro	Sol/pair	452.5	74.8	55.5	28.1	8.8	9.1	151.4	17.2	11.3
<i>Crypturellus soui</i>	GEN	Omni	Gro	Sol/pair	180	51.0	37.9	17.1	11.4	6.0	105.2	9.0	8.6
<i>Cyanocorax heilprini</i>	SPE	Omni	Und	Flocks	155	168	51.9	20.2	19.2	12.1	165.1	19.9	12.0
<i>Dendrocincla fuliginosa</i>	GEN	Inse	Und	Sol/pair	39.2	94.3	26.4	24.6	10.8	8.0	101.9	18.2	17.8
<i>Dendrocincla merula</i>	GEN	Inse	Und	Flocks	46.3	88.2	26.5	23.4	11.3	7.7	103.0	19.3	18.8
<i>Dendrocolaptes certhia</i>	GEN	Inse	Can	Sol/pair	80.2	116.9	34.9	22.7	13.8	9.3	123.3	19.1	16.2

Table 1. Continued.

Bird species	WSE 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 primaries length (mm)	Wing secondaries length (mm)	Kipp distance (mm)
<i>Dendroplex picus</i>	GEN	Inse	Und	Sol/pair	34.0	84.8	23.3	24.0	10.9	7.0	93.5	17.4	18.5
<i>Dolospingus fringilloides</i>	SPE	Gran	Und	Sol/pair	11.7	54.7	17.5	13.1	8.6	8.1	61.2	10.8	17.6
<i>Elaenia cristata</i>	GEN	Omni	Und	Sol/pair	18.1	61.6	20.3	10.9	9.7	4.9	65.3	10.7	16.4
<i>Elaenia ruficeps</i>	SPE	Omni	Und	Sol/pair	17.2	59.8	21.0	11.3	9.4	4.9	63.5	10.3	16.2
<i>Emberizoides herbicola</i>	GEN	Omni	Und	Sol/pair	24.8	101.6	26.7	32.6	8.8	7.1	69.3	11.6	16.7
<i>Euphonia rufiventris</i>	GEN	Frug	Can	Sol/pair	14.7	70.1	18.4	8.6	7.1	5.8	57.5	9.6	16.8
<i>Eupsittula pertinax</i>	GEN	Frug	Can	Flocks	79.0	97.3	14.7	20.0	12.4	21.7	133.0	41.6	31.2
<i>Formicivora grisea rufiventris</i>	SPE	Inse	Und	Flocks	10.5	49.2	20.6	12.5	6.5	3.9	53.5	5.3	9.9
<i>Galbula leucogastra</i>	SPE	Inse	Can	Sol/pair	16.1	93.3	12.9	36.4	9.6	5.7	67.9	12.9	19.0
<i>Hemitriccus inornatus</i>	SPE	Inse	Can	Sol/pair	6.6	34.9	14.8	11.0	7.5	3.3	46.5	8.7	18.7
<i>Hemitriccus margaritaceiventer</i>	GEN	Inse	Und	Sol/pair	7.2	37.5	20.8	11.9	7.4	3.8	47.5	8.1	17.2
<i>Hemitriccus minimus</i>	GEN	Inse	Can	Sol/pair	7.5	36.4	16.1	11.3	7.7	3.5	46	6.2	13.4
<i>Heterocercus flavivertex</i>	GEN	Omni	Can	Flocks	20.0	58.9	16.7	11.7	10.2	4.6	81.3	11.4	14.0
<i>Hydropsalis climacocerca</i>	GEN	Inse	Aer	Sol/pair	55.5	144.2	23.6	10.8	23.1	3.7	145.3	50.3	34.6
<i>Hydropsalis cayennensis</i>	SPE	Inse	Und	Sol/pair	32.8	115.5	15.9	10.9	16.8	3.6	134	57.3	42.7
<i>Hylocharis sapphirina</i>	GEN	Nect	Und	Sol/pair	4.3	33.4	5.7	19.1	4.4	2.5	52.9	33.2	62.9
<i>Hylophilus brunneiceps</i>	SPE	Inse	Can	Flocks	10.2	46.4	18.4	11.3	8.2	4.9	56.9	9.1	16.1
<i>Laterallus exilis</i>	GEN	Inse	Gro	Sol/pair	76.5	36.5	36.8	18.2	8.7	8.5	84.1	7.7	9.2
<i>Leptotila rufaxilla</i>	GEN	Gran	Gro	Sol/pair	152	110.7	29.4	16.1	8.1	5.3	131.7	24.3	18.3
<i>Lipaugus vociferans</i>	GEN	Omni	Can	Flocks	67.5	119.5	22.4	19.8	16.3	8.3	122	22.7	18.6
<i>Megascops choliba</i>	GEN	Inse	Und	Sol/pair	128.3	96.4	33.7	21.0	16.5	13.9	168.1	42.4	25.2
<i>Mionectes macconnelli</i>	GEN	Inse	Und	Flocks	11.7	54.7	17.5	11.7	8.1	4.2	62.3	10.0	16.0
<i>Mionectes oleagineus</i>	GEN	Frug	Und	Flocks	10.1	49.9	16.1	9.4	6.8	3.4	59.1	7.3	12.3
<i>Myiarchus ferox</i>	GEN	Omni	Und	Sol/pair	25.7	95.3	23.1	17.7	11.0	6.3	87.8	13.2	15.0
<i>Myiarchus tuberculifer</i>	GEN	Inse	Can	Sol/pair	20.2	82.0	21.3	16.4	10.8	5.4	81.9	13.1	16.0
<i>Myiopagis gaimardii</i>	GEN	Inse	Can	Flocks	9.5	50.8	19.7	8.3	5.6	3.6	51.8	4.8	9.4
<i>Myiozetetes cayanensis</i>	GEN	Inse	Und	Sol/pair	25.2	81.8	20.7	12.4	9.1	5.7	87.1	12.9	14.7
<i>Myrmotherula axillaris</i>	GEN	Inse	Und	Flocks	7.7	40.4	17.5	11.5	6.4	3.9	50.5	5.0	10.0
<i>Myrmotherula cherriei</i>	SPE	Inse	Und	Flocks	8.0	33.9	17.7	14.6	7.3	3.6	49.3	6.1	12.3
<i>Neopelma chrysocephalum</i>	SPE	Omni	Und	Flocks	13.8	55.7	18.3	11.4	9.9	4.9	69.0	13	18.8
<i>Neopipo cinnamomea</i>	SPE	Inse	Und	Sol/pair	6.5	37.0	14.7	7.8	7.4	3.1	49.6	10.1	20.3
<i>Nyctibius griseus</i>	GEN	Inse	Can	Sol/pair	81	180.3	17.6	17.6	37.2	5.2	238.7	87	36.4
<i>Nyctipolus nigrescens</i>	GEN	Inse	Wat	Sol/pair	37.5	104.3	15.3	9.9	16.9	3.3	137.4	55.8	40.6
<i>Nyctiprogne leucopyga</i>	GEN	Inse	Can	Flocks	29.3	106.1	10.5	5.7	12.4	2.9	137	55.6	40.6
<i>Ortalis motmot</i>	GEN	Frug	Can	Flocks	546	256.5	66.0	22.9	19.1	12.8	197.5	11.2	5.7
<i>Orthopsittaca manillata</i>	GEN	Frug	Can	Flocks	220	234.3	20.9	31.9	17.0	29.7	233	68.2	29.3
<i>Patagioenas cayennensis</i>	GEN	Frug	Can	Sol/pair	156	134.7	29.1	17.4	11.6	6.1	185	66.3	35.9
<i>Patagioenas plumbea</i>	GEN	Frug	Can	Sol/pair	170	144.3	19.80	16.7	9.4	6.3	172.3	45.5	26.4
<i>Patagioenas speciosa</i>	GEN	Frug	Can	Sol/pair	253	119.7	24.5	21.1	10.0	8.6	183	62.7	34.3

Table 1. Continued.

Bird species	WSE 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 primaries length (mm)	Wing secondaries length (mm)	Kipp distance (mm)
<i>Phaethornis malaris</i>	GEN	Nect	Und	Flocks	6.0	73.6	5.3	37.7	4.4	3.6	59.9	35.4	59.1
<i>Phaethornis ruber</i>	GEN	Nect	Und	Sol/pair	2.2	36.7	4.8	22.6	4.0	2.9	35.6	19.9	55.8
<i>Phaethornis superciliosus</i>	GEN	Nect	Und	Flocks	5.5	69.44	5.74	39.88	5.22	3.43	60.74	35.71	58.77
<i>Pheugopedius coraya</i>	GEN	Inse	Und	Sol/pair	15.3	55.9	24.1	15.8	8.5	5.2	59.2	6.4	10.8
<i>Piaya cayana</i>	GEN	Inse	Can	Sol/pair	98.0	269	40.3	25.9	15.7	11.7	137.7	10.4	7.6
<i>Picumnus exilis</i>	GEN	Inse	Und	Flocks	10.0	28.5	14.4	10.1	6.2	5.2	50.9	7.9	15.3
<i>Pitangus sulphuratus</i>	GEN	Omni	Gro	Sol/pair	54.5	91.2	25.3	24.1	13.0	9.0	110	18.8	17.1
<i>Polioptila plumbea</i>	GEN	Inse	Und	Flocks	6.5	51.8	16.2	9.9	6.4	2.7	47.3	6.3	13.3
<i>Polytmus theresiae</i>	SPE	Nect	Und	Sol/pair	3.3	35.7	6.7	20.0	4.5	2.6	56.6	35.9	63.5
<i>Psarocolius viridis</i>	GEN	Omni	Can	Flocks	170	155.3	47.0	48.8	17.4	16.3	185.3	43.5	23.5
<i>Pseudopipra pipra</i>	GEN	Frug	Und	Flocks	12.0	28.0	15.2	8.3	7.8	4.3	61.9	8.8	14.2
<i>Psittacara leucophthalmus</i>	GEN	Frug	Can	Flocks	147.5	142	20.0	25.0	17.3	29.0	163.8	51.0	31.1
<i>Ramphastos tucanus</i>	GEN	Frug	Can	Sol/pair	663.7	186	53.1	153.4	37.9	51.5	227	45.9	20.2
<i>Ramphastos vitellinus</i>	GEN	Frug	Can	Sol/pair	345	182.3	47.8	115.8	29.9	38.1	197.4	24.4	12.4
<i>Ramphocelus carbo</i>	GEN	Omni	Und	Flocks	18.5	79.0	22.1	13.9	13.2	8.3	74.2	9.7	13
<i>Ramphotrigon ruficauda</i>	GEN	Inse	Can	Sol/pair	17.0	36.8	15.9	13.2	11.2	5.9	72.3	11.9	16.5
<i>Rhytipterna immunda</i>	SPE	Inse	Und	Sol/pair	24.0	87.6	22.3	15.8	11.4	6.5	87.0	15.5	17.8
<i>Rhytipterna simplex</i>	GEN	Inse	Can	Flocks	29.0	100.5	20.4	16.8	11.4	6.5	95.4	14.4	15.1
<i>Rupornis magnirostris</i>	GEN	Carn	Und	Sol/pair	226.7	155.2	69.2	26.3	21.6	16.7	216.6	56.7	26.1
<i>Sakesphorus canadensis</i>	GEN	Inse	Und	Flocks	24.8	63.3	27.6	17.8	10.2	6.5	72.2	5.5	7.6
<i>Schiffornis turdina</i>	GEN	Omni	Und	Sol/pair	33.8	71.4	23.8	13.9	10.2	6.2	91.6	17.1	18.6
<i>Schistochlamys melanopis</i>	GEN	Omni	Can	Sol/pair	27.7	78.8	22.8	14.7	9.3	8.6	78.4	11.2	14.4
<i>Sittasomus griseicapillus</i>	GEN	Inse	Canopy	Flocks	16.5	83.9	20.1	15.9	9.3	4.7	81.4	19.7	24.2
<i>Sporophila angolensis</i>	GEN	Gran	Und	Sol/pair	13.0	56.0	17.6	11.6	9.9	10.7	57.8	9.2	15.9
<i>Stelgidopteryx ruficollis</i>	GEN	Inse	Aer	Flocks	15.5	58.8	12.3	6.6	10.5	2.8	110.5	57.4	51.9
<i>Stilpnia cayana</i>	GEN	Frug	Can	Sol/pair	18.0	55.3	37.0	10.1	9.0	5.9	68.8	17.4	25.3
<i>Tachyphonus phoenicius</i>	SPE	Inse	Und	Sol/pair	19.9	72.4	22.3	12.5	8.0	7.0	71.7	12.7	17.7
<i>Tamatia tamatia</i>	GEN	Inse	Und	Sol/pair	36.5	71.8	20.0	22.1	15.2	11.6	78.6	11.0	14.1
<i>Thalurania furcata</i>	GEN	Nect	Und	Sol/pair	4.2	37.1	5.0	20.3	4.6	2.1	51.1	31.1	60.9
<i>Thamnophilus amazonicus</i>	SPE	Inse	Und	Flocks	18	57.3	22.2	14.3	8.7	5.9	65.7	7.3	11.1
<i>Thamnophilus doliatus</i>	GEN	Inse	Und	Flocks	24.6	65.1	29.5	16.1	9.4	6.5	74.2	5.9	8.0
<i>Thamnophilus punctatus</i>	GEN	Inse	Und	Sol/pair	25.6	62.2	23.2	15.2	9.6	6.5	74.0	11.9	15.4
<i>Thraupis episcopus</i>	GEN	Omni	Can	Flocks	29.3	70.1	24.2	12.9	10.5	7.5	89.1	17.5	19.7
<i>Tolmomyias flaviventris</i>	GEN	Inse	Can	Sol/pair	12.8	53.6	18.8	9.7	9.7	4.5	55.6	7.1	12.8
<i>Tolmomyias poliocephalus</i>	GEN	Inse	Can	Flocks	11.7	49.2	18.1	10.7	9.1	4.1	54.3	8.6	15.9
<i>Topaza pyra</i>	GEN	Nect	Can	Flocks	14.7	113.5	7.7	22.1	7.0	3.2	82.9	50.7	61.1
<i>Trogon viridis</i>	GEN	Omni	Can	Sol/pair	84.0	151.5	17.8	20.4	19.0	13.0	133.4	47.8	35.8
<i>Turdus arthuri</i>	SPE	Omni	Und	Sol/pair	59.0	91.0	32.0	17.9	12.7	6.6	106.5	22.2	20.9
<i>Tyrannulus elatus</i>	GEN	Omni	Can	Flocks	7.2	41.9	14.1	6.0	5.7	3.6	49.3	7.7	15.5

Table 1. Continued.

Bird species	WSE 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 primaries length (mm)	Wing secondaries length (mm)	Kipp distance (mm)
<i>Tyrannus melancholicus</i>	GEN	Inse	Can	Flocks	41.0	93.1	19.4	19.9	12.8	7.2	110.5	27.7	25.0
<i>Vanellus chilensis</i>	GEN	Inse	Gro	Flocks	150	110.6	70.8	28.1	10.3	11.4	207	11.0	5.3
<i>Willisornis poecilinotus</i>	GEN	Inse	Und	Flocks	18.3	51.1	25.1	15.2	10.2	5.5	66.5	8.4	12.7
<i>Xenopipo atronitens</i>	SPE	Frug	Und	Sol/pair	14.0	50.0	17.0	11.4	10.1	5.1	69.3	13.8	19.8
<i>Xenops minutus</i>	GEN	Inse	Can	Flocks	11.7	53.7	16.1	11.3	6.2	4.7	64.2	12.4	19.3
<i>Xipholena punicea</i>	GEN	Frug	Can	Flocks	66.0	76.8	22.9	14.9	15.7	6.8	117.3	16.5	14.0
<i>Xiphorhynchus obsoletus</i>	GEN	Inse	Und	Sol/pair	32.7	89.2	22.7	23.2	9.8	7.0	96.7	17.6	18.1
<i>Xiphorhynchus ocellatus</i>	GEN	Inse	Und	Sol/pair	32.7	89.2	22.7	23.2	9.8	7.0	96.7	17.6	18.1
<i>Zimmerius gracilipes</i>	GEN	Inse	Can	Flocks	6.7	42.7	14.9	7.9	6.8	3.4	45.7	7.4	16.0
<i>Zonotrichia capensis</i>	GEN	Omni	Gro	Flocks	15.8	64.8	23.6	12.1	7.6	6.6	65.3	11.6	17.7

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

Traits	Categories	Source
Diet	Frugivores	Wilman <i>et al.</i> 2014; personal field observations (GRL, SHB)
	Insectivores	
	Omnivores	
	Carnivores	
	Nectarivore	
Foraging strata	Grainivore	Wilman <i>et al.</i> 2014; Cohn-Haft <i>et al.</i> 1997; personal field observations (GRL, SHB)
	Ground	
	Water	
	Understory	
Sociability	Canopy	Cohn-Haft <i>et al.</i> 1997; personal observations (GRL, SHB)
	Aerial	
	Solitary or in pairs	
	Hetero or monospecific flocks	

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) (Villegger *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 (Table 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).

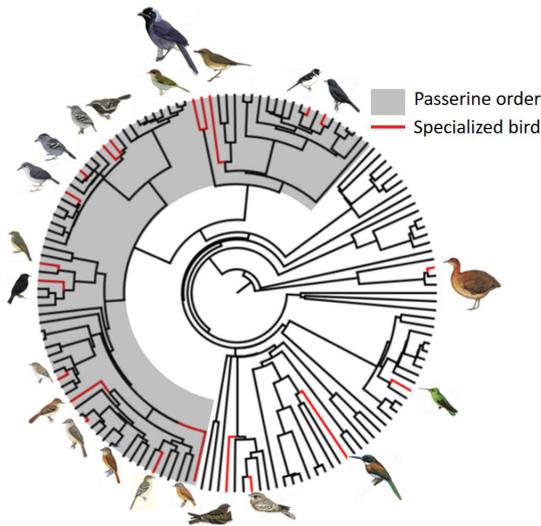


Figure 1. Consensus phylogenetic tree of the 102 generalist bird species (terminals with black line) and 22 species specialized in Amazonian white-sand habitat patches (terminals with red line). Data from “A Global Phylogeny of Birds” (www.birdtree). This figure is in color in the electronic version.

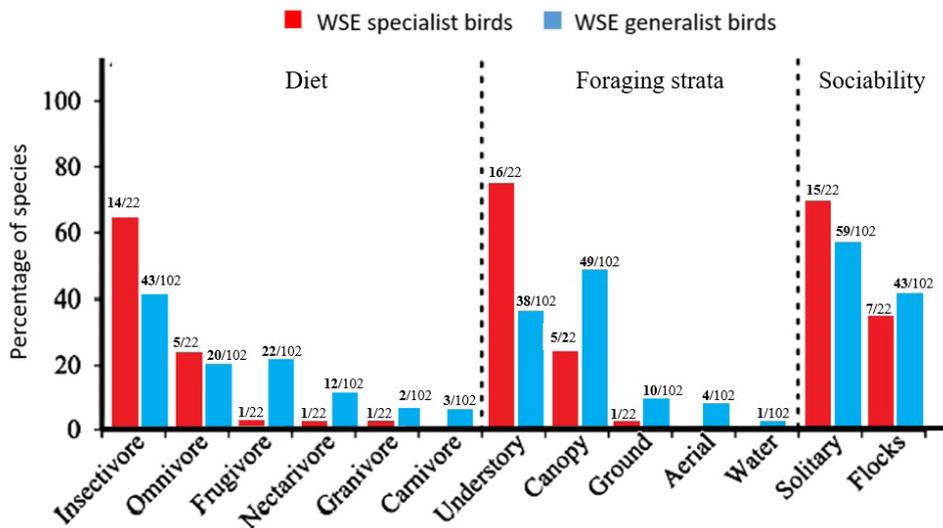


Figure 2. Percentage of Amazonian white-sand ecosystem bird species distributed in the major categories of diet, foraging strata and sociability. Numbers above columns are number of species within each category and total number of species for the specialist and generalist groups. Percentages within each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

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

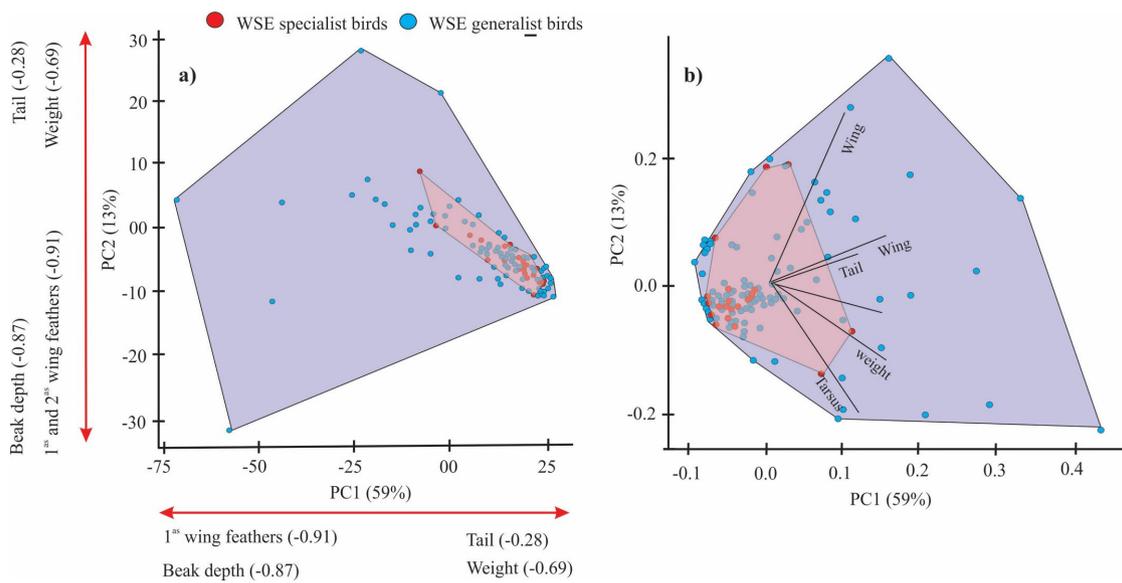


Figure 3. Analysis of morphological data of Amazonian white-sand ecosystem birds using: A – phylogenetic principal component analysis (pPCA); and B – principal component analysis without phylogenetic control. Blue dots represent generalist species (102 species) and red dots represent specialist species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

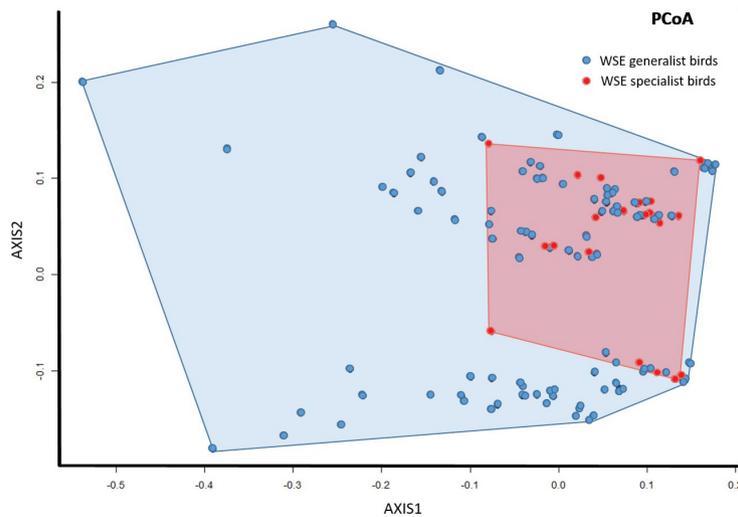


Figure 4. Principal coordinate analysis (PCoA) with morphological and ecological traits of specialist and generalist Amazonian white-sand ecosystem birds. Blue dots represent generalist species (102 species) and red dots represent specialist species (22 species). This figure is in color in the electronic version.

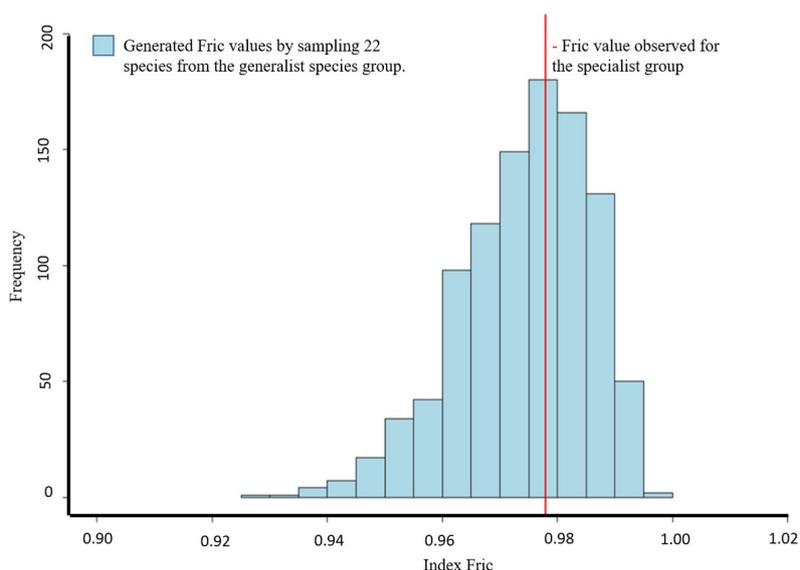


Figure 5. Result of the rarefaction performed with 1000 values generated for Fric by sampling 22 species from the generalist bird community (blue) in relation to the Fric value observed for the specialist community (red line) in Amazonian white-sand habitat patches. This figure is in color in the electronic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

of specialists, they are more abundant locally than generalists and may represent 30% to 50% of individuals caught in mist nets (Borges *et al.* 2016b). 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 may be 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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