



## BIRD ASSEMBLAGES AT THE SOUTHERN LIMIT OF THE BRAZILIAN ATLANTIC FOREST: A COMPARISON BETWEEN TWO FOREST PHYSIOGNOMIES AT THE APARADOS DA SERRA NATIONAL PARK

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**Abstract:** The Atlantic Forest is one of the world's biodiversity hotspots harbouring at least 900 species of birds. Covering less than 7% of its original distribution, conservation strategies for this biome depend on information about diversity patterns and the mechanisms behind them. Here we evaluated the composition, richness, and taxonomic and functional diversity of the bird assemblage in two forest physiognomies, corresponding to two elevation ranges, at the southernmost federal protected area within the Brazilian Atlantic Forest, the Aparados da Serra National Park. Birds were sampled with mist nets in two environments: *Araucaria* forest, at elevation ranging above 900 m a.s.l., and dense ombrophilous forest, at elevations between 0 and 200 m a.s.l.. We found no differences in species richness between the two environments but species composition was dissimilar, as revealed by ANOSIM. Also, dense ombrophilous forest was functionally richer, while *Araucaria* forest presented higher functional divergence. No dominance pattern was found in dense ombrophilous forest, while in *Araucaria* forest a few species dominated the assemblage. The evidence that the bird assemblages of the two forests are distinct both in terms of species composition and functionality indicates that the conservation and management of the bird communities at the two environments is fundamental for the maintenance of the Southern Atlantic Forest's bird species pool.

**Keywords:** Bird assembly; functional diversity; taxonomic diversity.

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### INTRODUCTION

The Atlantic Forest is a biome of tropical and subtropical forests ranging across the east, southeast and south of Brazil, east of Paraguay and the Misiones province in Argentina; it is composed by distinct forest physiognomies that originally

distributed along 1.300.000 km<sup>2</sup> in 17 Brazilian states (SOS Mata Atlântica & INPE 2014). In the southernmost portion of the biome, two main forest physiognomies occur: dense ombrophilous forest dominate the lowlands and, as elevation increases, hillside formations such as cloud forests appear, and finally at the highest elevations, usually

above 700 m, the plateaus harbour *Araucaria* forest formations interspersed with highland grasslands (Bencke & Kindel 1999). Pristine forest cover in the Atlantic Forest corresponds only to 7% of the original forest cover (SOS Mata Atlântica & INPE 2014). However, while extremely fragmented, the Atlantic Forest still harbours high levels of biodiversity and endemism (Backes & Irlang 2004), including 900 bird species (Lagos & Muller 2007) and is one of the “hottest biodiversity hotspots” of the world (Gallindo-Leal & Câmara 2005).

The structuring of biological communities is determined by both historical and contemporary factors: abiotic conditions, in combination with biotic interactions (such as food availability), define the boundaries within which a particular species of the regional pool can inhabit a given area; the competition will then define stable combinations of species that have passed the first environmental filter (Ricklefs 1987). At large spatial scales, community assembly is largely determined by both biogeographic history (Reif *et al.* 2010) and climate (Gaston & Blackburn 1995, Brown & Gibson 1998, Hawkins *et al.* 2003), while competition, predation, habitat complexity and plant succession are key in defining the structure of biological assemblages at a local level (Eisenberg 1990, Brown & Gibson 1998, Casas *et al.* 2016).

In forest environments, large tree species provide shade and a favourable environment for the recruitment of other species, forming different strata in the vegetation. In the southern Atlantic Forest biome, few studies have evaluated patterns and processes that structure bird communities. Some studies found that vegetation characteristics influence taxonomic diversity and trophic guilds, with forest bird communities having a vertical structure, that is, species associated to different strata and substrata of the forest (*e.g.*, Casas *et al.* 2016). The processes behind the patterns of community assembly act on ecological redundancies and complementarities of organisms and not just directly on the number of species present in a certain region; as such, the analysis of metrics such as functional richness, evenness, divergence and dispersion may contribute to our understanding of the mechanisms behind the structuring of biological communities (Mouillot *et al.* 2011).

Here we evaluated composition, taxonomic and functional diversity, and relative abundance

of birds in two physiognomies of the Aparados da Serra National Park, one of the southernmost federal preserved area within the Brazilian Atlantic Forest. Based on data from bird captures in dense ombrophilous forest between 0 and 200 m a.s.l. and *Araucaria* forest (above 900 m a.s.l.) we tested the following hypotheses:

1. Bird assemblages from the two forest types differ in composition and species richness. We predicted:

**a.** Higher species richness in dense ombrophilous forest, given the greater structural complexity of vegetation in this physiognomy;

**b.** The presence of more species typical of dense understory in dense ombrophilous forest, and more species adapted to high elevations present in the *Araucaria* forest.

2. The assemblages are structured by environmental filtering, which is more severe at *Araucaria* forest. We thus predict:

**a.** Higher abundance of species with frugivorous diet and morphological traits linked to a greater number of strata in the vegetation in the dense ombrophilous forest, and higher abundance of more generalist species with morphological characteristics related to environments with little or no understory in the *Araucaria* forest.

**b.** Higher functional diversity at the dense ombrophilous forest, given the expected higher number of species and a greater number of partitionable niches.

## MATERIAL AND METHODS

### *Study area*

The study was carried out in the Aparados da Serra National Park (Figure 1). Occupying an area of 10,250 ha, the park is located on the eastern border of the Araucarias plateau (29°05' S, 50°00' W – 29°15' S, 50°15' W) on the boundary between the states of Rio Grande do Sul and Santa Catarina, and contributes with 0.02% to the 2.44% Federal Preserved Areas (“Conservation Units” in Brazil) within the Atlantic Forest biome (IBAMA/MMA 2004).

The physiognomy of the region is composed of three main physiognomies: i) *Araucaria* forests, a formation of patches of highland grasslands

interspersed with *Araucaria angustifolia* trees predominate in the highest plateaus, above 900 m a.s.l.; ii) continuous areas of dense ombrophilous forest in the lowlands (between 0 and 200 m a.s.l.); and iii) escarpments forming vertical walls in the abrupt limits of the plateaus, as the relief is deeply cut by rivers, creating a landscape of canyons (Hasenack *et al.* 2009, Graeff 2015, Pillar & Lange 2015).

At the highest elevations, the climate is one of the coldest in Brazil, with winter temperatures going down to 10°C; in the lowlands, temperatures are considerably higher, with monthly averages over 22°C throughout the year (Nimer 1979). Rainfall is high at the highest elevations and in the lowlands, and homogeneously distributed throughout the year (annual average between 1750 and 2252 mm).

### Bird survey

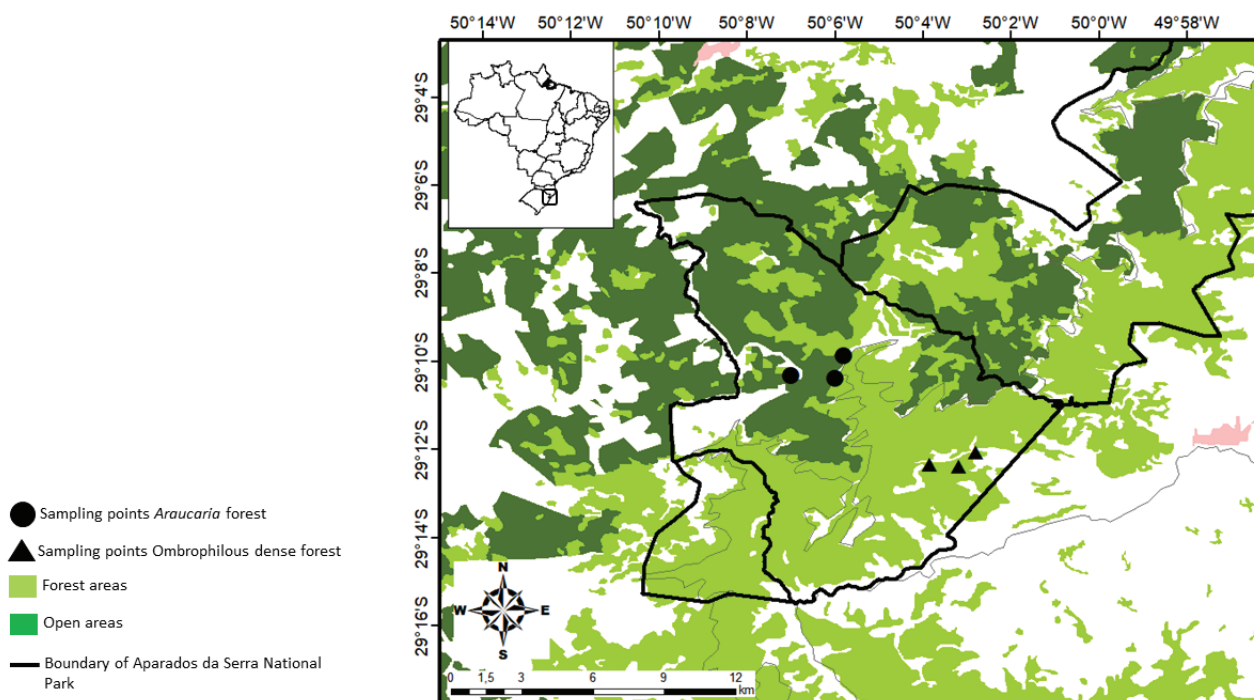
Birds were sampled with mist nets set in the understory between September 2015 and October 2016. Birds were sampled twice in each season in three sampling points distant 1 km from each other in each physiognomy: *Araucaria* forest and dense ombrophilous forest (Figure 1). At each sampling point, two lines of 150 m of nets were installed

(using 3x15 m, 22 mm nets), totaling a sampling effort of 203,040 h/net (Supplementary Material 1). Nets remained opened from sunrise to 13:00 h and were kept at the same sampling point for two consecutive days, as capture rate tends to decline considerably after that period (Marques *et al.* 2013).

Birds captured were identified in the field, marked with CEMAVE (National Center for Research and Conservation of Wild Birds) standard rings and released at the capture site as soon as they were tagged and all the following measures were obtained: tarsus – distance of the intersection with the tibia to the most distal tarsus squama; naris to tips – distance from the most distal part of the nostril to the tip of the beak; beak width – measured at the nostrils; beak height – measured at the nostrils; and body mass: weight of each individual in grams.

Bird species were characterized according to diet type: omnivore, insectivore, nectarivore, granivore, frugivore, and carnivore. Data on the diet of each species were obtained from the literature and followed Del Hoyo *et al.* (2016). Bird nomenclature followed Piacentini *et al.* (2015).

The capture of birds with mist nets is a widely used method in bird monitoring. As a method of capture, mist nets are far superior to other methods, both



**Figure 1.** Sampling points located in the Aparados da Serra National Park (ASNP), Rio Grande do Sul and Santa Catarina states, Brazil. Circles: Sampling Points in *Araucaria* Forest; Triangles: Sampling points located in ombrophilous dense Forest. Black line: ASNP boundary.

for the versatility and variety of species captured, besides allowing sampling standardization in long term studies (Gosler 2004). However, mist nets are still selective and only survey a portion of the avifauna present at a given site (Martin *et al.* 2017). Other complementary methods, such as acoustic sampling are necessary for more complete surveys, but time, logistical and financial limitations did not allow for those complementary techniques to be used here.

The study was approved by the Universidade Federal do Rio Grande do Sul Research (COMPESQ/UFRGS) and Ethics (CEUA/UFRGS) Committees (project 28645), and all the necessary permits for bird capture and ringing were obtained from the competent national agencies (SISBIO license 49050 and CEMAVE license 4026/1).

### **Data analysis**

Differences in taxonomic richness between the assemblages of the two forests types were evaluated by individual-based rarefaction and nonparametric extrapolation. Rarefaction was based on species richness estimates for a given number of individual samples, as differences in the number of species may result from differences in sample size (Oksanen *et al.* 2013). Rarefaction by non-parametric extrapolation projects the rarefaction curves beyond the size of the reference sample (Colwell & Coddington 1994), allowing more robust comparisons of the number of species between the sampled physiognomies.

To characterize the distribution of abundances of all species within each of the assemblages the Species Abundance Distribution (SAD) was used; to evaluate diversity Rényi Series profiles were used. These diversity profiles result in different values equivalent to different diversity indexes according to the variation in the order of the parameter  $\alpha$ , where  $\alpha = 0$  is species richness,  $\alpha = 1$  is Shannon index and  $\alpha = 2$  is Simpson index (Tóthmérész 1995). The assumptions of the ecological models of SAD's are examined according to the assumptions of the following models: Broken-stick (McArthur 1957) assumes that resources are equally distributed among species; Niche-preemption (Motomura 1932) postulates that the level of abundance of each species is a sequential and constant proportion of the total number of individuals in a community; log-normal (Preston

1948) assumes that the abundance of the species follows a normal distribution; Zipf (Zipf 1949) and Zipf-Mandelbrot (Gray 1987), characteristic of communities in ecological succession, postulating that late colonizing species greater need for specialized niches and are therefore rarer than the initial colonizing species.

To test for differences in bird species composition between the two forest physiognomies an Analysis of similarities (ANOSIM) was performed based on the abundance matrix. ANOSIM allows to statistically testing differences between two or more groups of sample units using a dissimilarity matrix. Subsequently, to evaluate which species contributed more to the differences found a percentage of similarity analysis (SIMPER) was used.

Functional diversity is a complex concept, and modern approaches recognize that diversity is a multifaceted issue, and therefore advocate the use of multiple metrics (Laliberté & Legendre 2010). The functional matrix was composed by five columns (four with morphological traits and one with diet information). For the morphological traits (except weight), measures were standardized by bird size allowing comparisons of those traits between species, as the influence of size on those traits is removed. Here the approach of Villéger *et al.* (2008) was followed, which is based on the distance between the assemblages in the multivariate trait space (based on the PCoA axes of a distance matrix), and incorporates information on the relative abundance of the species; four distinct metrics were calculated: i) functional richness which represents the amount of functional space occupied by a community of species; proposed as a multivariate analogue of the amplitude of a single trait (Villéger *et al.* 2008), is not weighted by abundance and therefore sensitive to outliers (Laliberté & Legendre 2010); ii) functional evenness that corresponds to how regularly species abundances are distributed in the functional space; higher values indicate that the distances between the nearest neighbouring pairs are similar, tending to zero with increasingly clustered points; iii) functional divergence that defines how distant the species abundances are from the center of the functional space (Mouchet *et al.* 2010); high values of divergence indicate that abundant species are close to the vertices of the functional space; the values approach zero as

abundant species approach the center of space; and iv) functional dispersion that was proposed to combine the strengths of the first three measures (Laliberté & Legendre 2010), incorporating abundance information such as evenness and divergence but, unlike these two metrics, as well as functional richness, considers the dispersion of species in a space of attributes. In essence, the dispersion is the average distance of each individual to the centroid of the community. To test for differences between the functional diversity metrics in the two forest physiognomies Student t tests were applied.

## RESULTS

A total of 651 individuals (disregarding recaptures) of 95 species distributed in 30 families were recorded (Table 1). Of these, 206 individuals from 49 species were captured at the *Araucaria* forest and 445 individuals from 73 species at the dense ombrophilous forest. Sampling sufficiency analysis showed that for both environments understory birds are reasonably well-sampled (Figure 2).

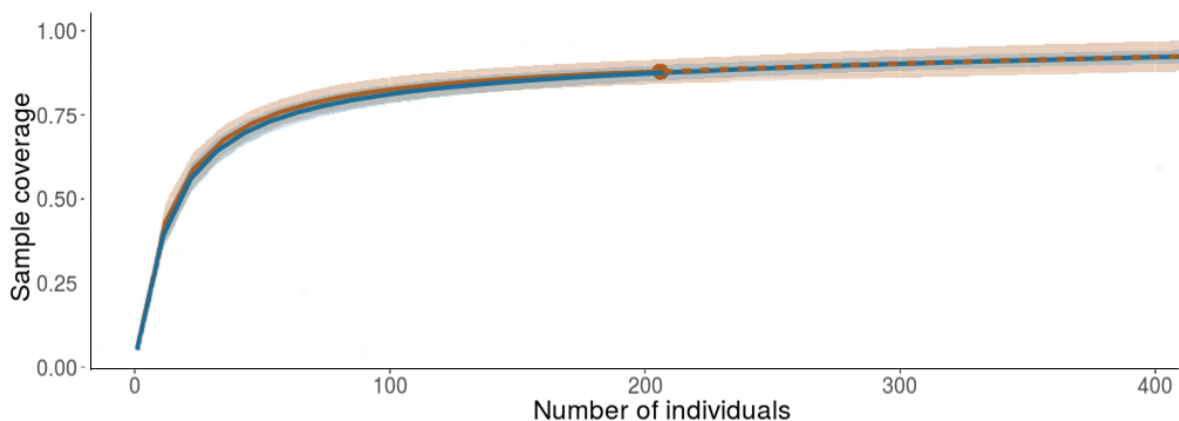
Rarefaction analysis showed no differences in species richness between the two assemblages (Figure 3). However, according to the Rényi diversity profile, the dense ombrophilous forest bird assemblage is more diverse for both the Shannon index and the Simpson index (Figure 4). It also showed a more uniform distribution, *i.e.*, a greater

evenness in the distribution of species, according to the Species Abundance Distribution (Figure 5). The distribution of the relative abundance curves did not reveal any apparent dominance in the dense ombrophilous forest assemblage, whereas there was evident dominance of a few species – *Turdus rufigiventris* (25 individuals), *Zonotrichia capensis* (24 individuals) and the complex *Elaenia* sp. (26 individuals) – in the *Araucaria* forest bird assemblage (Table 1).

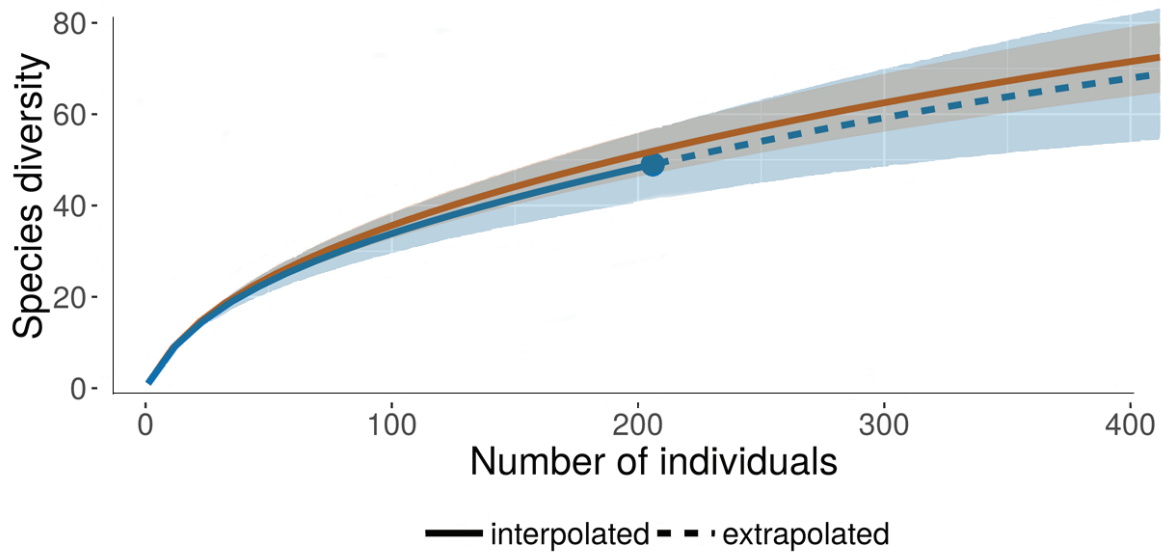
The abundance distribution curve also shows that in the lowland dense ombrophilous forest more rare species occur than in the *Araucaria* forest. The best-adjusted ecological model for SAD was Mandelbrot, which postulates that late colonizing species have the greatest needs for a specialized niche and are therefore rarer than the initial colonizing species.

ANOSIM revealed slight but significant differences in species composition between the assemblages ( $R = 0.10$ ;  $p = 0.05$ ). Some bird species, exclusive to one or the other assemblage, contributed most to the differences found: at the *Araucaria* forest these were *Z. capensis* (0.044) and *Elaenia* sp. (0.046), while at dense ombrophilous forest it were *Habia rubica* (0.064) and *Tricothraupis melanops* (0.031) (Figure 6).

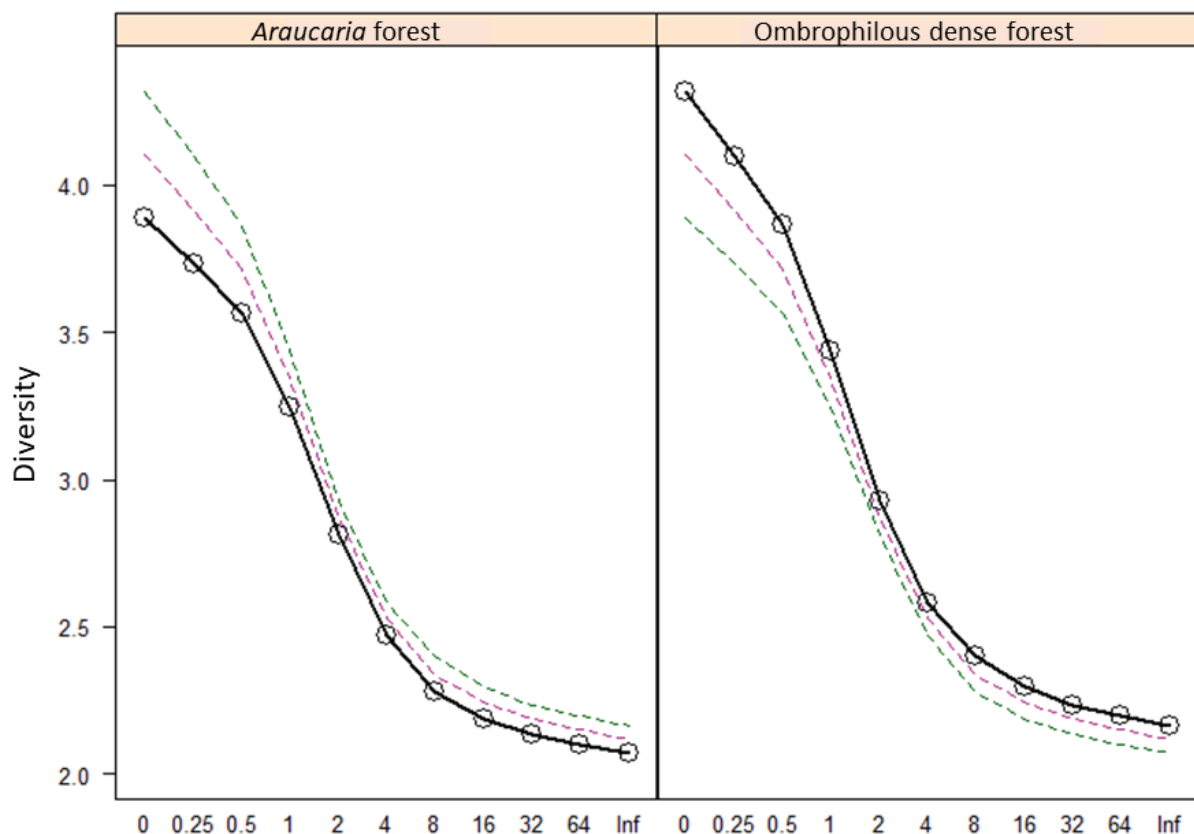
No significant differences were found in functional dispersion ( $t = -0.98$ ;  $p = 0.37$ ) or evenness ( $t = 0.49$ ;  $p = 0.64$ ) between the two assemblages (Figure 7). However, functional richness ( $t = 2.23$ ;  $p = 0.01$ ) was significantly higher at the dense



**Figure 2.** Curve of accumulation of bird species sampled between September 2015 and October in the Aparados da Serra National Park, Rio Grande do Sul and Santa Catarina states, Brazil. Smoothed solid line: 95% confidence intervals. Orange line: ombrophilous dense Forest. Blue line: *Araucaria* Forest.



**Figure 3.** Species rarefaction curve for bird species sampled between September 2015 and October in the Aparados da Serra National Park, Rio Grande do Sul and Santa Catarina states, Brazil. Blue line: *Araucaria* Forest. Orange line: ombrophilous dense Forest. Dotted line: extrapolation. Solid line: interpolation. The shading around each line corresponds to the confidence interval of each estimate (95%).



**Figure 4.** Profile of Rényi diversity in the two forest formations for bird species sampled between September 2015 and October in the Aparados da Serra National Park, Rio Grande do Sul and Santa Catarina states, Brazil. Each point on the curve represents an index of diversity. The central pink line corresponds to the median of the data and the dark green lines to the extremes of the data. The abscissa axis corresponds to the change in parameter  $\alpha$ .

**Table 1.** Species of birds captured with mist nets in the Aparados da Serra National Park, Brazil, between September 2015 and October 2016. FLOM1, FLOM2 and FLOM3: area of *Araucaria* forest (900-1020 m). FLOD1, FLOD2 and FLOD3: area of ombrophilous dense forest (100-200 m). N = Total of individuals.

ESPECIES	FLOM1	FLOM2	FLOM3	FLOD1	FLOD2	FLOD3	N
<b>TINAMIDAE</b>							
<i>Crypturellus tataupa</i>				1			1
<b>COLUMBIDAE</b>							
<i>Geotrygon montana</i>						1	1
<i>Leptotila rufaxilla</i>				2			2
<b>CUCULIDAE</b>							
<i>Tapera naevia</i>				1			1
<b>CAPRIMULGIDAE</b>							
<i>Hydropsalis parvula</i>	1						1
<b>TROCHILIDAE</b>							
<i>Amazilia versicolor</i>				1			1
<i>Chlorostilbon lucidus</i>				1	1		2
<i>Heliodoxa rubricauda</i>		3		1			4
<i>Leucochloris albicollis</i>	4	5	3	2			14
<i>Phaethornis eurynome</i>	1			6	5	5	17
<i>Stephanoxis loddigesii</i>	2	8	2	3	3		18
<i>Thalurania glaucopis</i>	1	6		11	3	12	33
<b>TROGONIDAE</b>							
<i>Trogon rufus</i>				1		1	2
<i>Trogon surrucura</i>				1			1
<b>PICIDAE</b>							
<i>Colaptes melanochloros</i>	1						
<i>Picumnus temminckii</i>				3			3
<i>Veniliornis spilogaster</i>			1	1			2
<b>FALCONIDAE</b>							
<i>Micrastur ruficollis</i>					1		1
<b>PSITACIDAE</b>							
<i>Pyrrhura frontalis</i>			1				1
<i>Triclaria malachitacea</i>					1		1
<b>THAMNOPHILIDAE</b>							
<i>Dysithamnus mentalis</i>				1		1	2
<i>Batara cinerea</i>				1			1
<i>Myrmoderus squamosus</i>				1			1
<i>Pyriglena leucoptera</i>				7		2	9
<i>Thamnophilus caeruleus</i>		1		1			2
<b>CONOPOPHAGIDAE</b>							
<i>Conopophaga lineata</i>	1			1	1	3	6
<b>FORMICARIIDAE</b>							
<i>Chamaeza campanisona</i>				1			1

Table 1. Continued on next page...

Table 1. ...Continued

ESPECIES	FLOM1	FLOM2	FLOM3	FLOD1	FLOD2	FLOD3	N
<b>SCLERURIDAE</b>							
<i>Sclerurus scansor</i>				4	3	5	12
<b>DENDROCOLAPTIDAE</b>							
<i>Dendrocolaptes platyrostris</i>	1			1		1	3
<i>Lepidocolaptes falcinellus</i>	1			1	1	1	4
<i>Sittasomus griseicapillus</i>		1		1	1	2	5
<i>Xiphocolaptes albicollis</i>		1					
<i>Xiphorhynchus fuscus</i>				1	5	5	11
<b>XENOPIIDAE</b>							
<i>Xenops rutilans</i>				1		1	2
<b>FURNARIIDAE</b>							
<i>Anabacerthia amaurotis</i>					1		1
<i>Automolus leucophthalmus</i>				2			2
<i>Cranioleuca obsoleta</i>				1			1
<i>Heliobletus contaminatus</i>		3	3			1	7
<i>Leptasthenura striolata</i>	1		1				2
<i>Philydor atricapillus</i>						2	2
<i>Philydor rufum</i>				1			1
<i>Synallaxis spixi</i>				1			
<i>Syndactyla rufosuperciliata</i>		2	1		1	2	6
<b>PIPRIDAE</b>							
<i>Chiroxiphia caudata</i>		1		4	4	6	15
<b>TITYRIDAE</b>							
<i>Schiffornis virescens</i>				2	3	3	8
<b>PLATIRINCHYDAE</b>							
<i>Platyrinchus mystaceus</i>		1		13	11	21	46
<b>RHYNCOCYCLIDAE</b>							
<i>Hemitriccus obsoletus</i>		1					
<i>Leptopogon amaurocephalus</i>				2	3	3	8
<i>Mionectes rufiventris</i>				1	1		2
<i>Poecilotriccus plumbeiceps</i>				2			2
<i>Tolmomyias sulphurescens</i>				1		2	3
<b>TYRANIDAE</b>							
<i>Camptostoma obsoletum</i>		1					
<i>knipolegus nigerrimus</i>				1			1
<i>Knipolegus cyanirostris</i>	1		2				3
<i>Lathrotriccus euleri</i>				2	2		4
<i>Myiarchus swainsoni</i>	1		1				
<i>Myiodynastes maculatus</i>	1						1
<i>Myiophobus fasciatus</i>	1						
<i>Myiornis auricularis</i>				1			1

Table 1. Continued on next page...



Table 1. ...Continued

ESPECIES	FLOM1	FLOM2	FLOM3	FLOD1	FLOD2	FLOD3	N
<i>Phyllomyias fasciatus</i>					1	1	2
<i>Phyllomyias virescens</i>		2					2
<i>Phylloscartes ventralis</i>	1	6	3				10
<i>Serpophaga subcristata</i>		1		1			2
<i>Elaenia</i> sp.	18	5	3				26
<i>Tyrannus melancholicus</i>				1			
<b>VIREONIDAE</b>							
<i>Cyclarhis gujanensis</i>			1				1
<i>Vireo chivi</i>		1		1			2
<b>TROGLODYTIDAE</b>							
<i>Troglodytes musculus</i>				4			4
<b>TURDIDAE</b>							
<i>Turdus albicollis</i>	1	2	2	24	10	17	56
<i>Turdus amaurochalinus</i>			1	1			2
<i>Turdus flavipes</i>	3	1			1		5
<i>Turdus leucomelas</i>	2						2
<i>Turdus rufiventris</i>	5	8	9	1		2	25
<i>Turdus subalaris</i>	3	3	1				7
<b>PASSERELLIDAE</b>							
<i>Zonotrichia capensis</i>	17		7				24
<b>PARULIDAE</b>							
<i>Basileuterus culicivorus</i>	1			16	14	14	45
<i>Geothlypis aequinoctialis</i>				4			4
<i>Myiothlypis leucoblephara</i>	2	4	2	4	4	11	27
<i>Setophaga pitiayumi</i>			1	1			2
<b>ICTERIDAE</b>							
<i>Cacicus chrysopterus</i>				1			1
<b>THRAUPIDAE</b>							
<i>Coereba flaveola</i>						1	
<i>Haplospiza unicolor</i>	1	2	1	1	8	2	15
<i>Microspingus cabanisi</i>	2	5	2				9
<i>Pyrrhocomma ruficeps</i>				3			
<i>Saltator similis</i>	1			2			3
<i>Sicalis flaveola</i>	1					1	2
<i>Sporophila caerulescens</i>				1			
<i>Stephanophorus diadematus</i>	1		1	1			3
<i>Tachyphonus coronatus</i>				8	1	1	10
<i>Tangara cyanocephala</i>				1			1
<i>Tangara preciosa</i>	3		1				4
<i>Tangara sayaca</i>		2		1			3
<i>Trichothraupis melanops</i>				10	2	9	21

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Table 1. ...Continued

ESPECIES	FLOM1	FLOM2	FLOM3	FLOD1	FLOD2	FLOD3	N
<b>FRINGILLIDAE</b>							
<i>Euphonia chalybea</i>					2		2
<b>CARDINALIDAE</b>							
<i>Habia rubica</i>				6	12	16	34

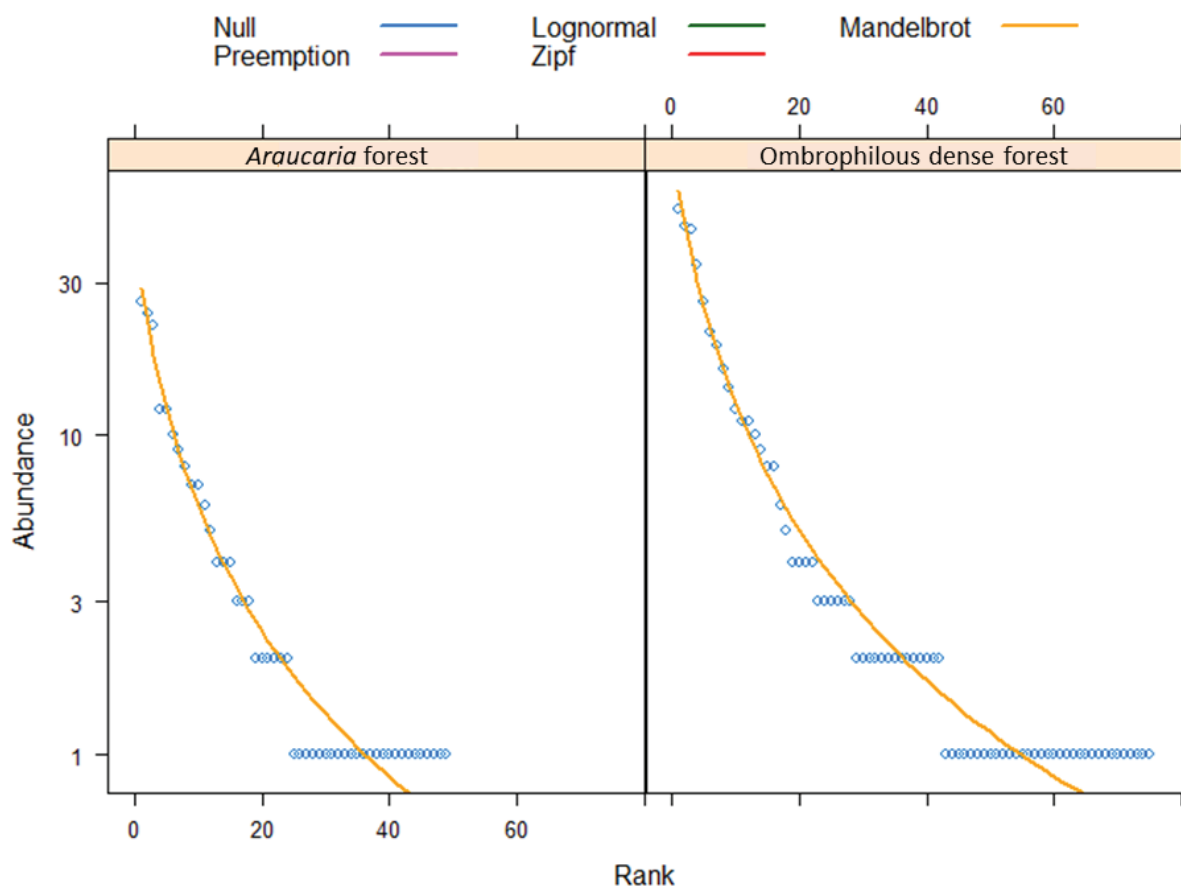
ombrophilous forest assemblage, while functional divergence ( $t = 4.86$ ;  $p = 0.01$ ) was significantly higher at the *Araucaria* forest assemblage.

### DISCUSSION

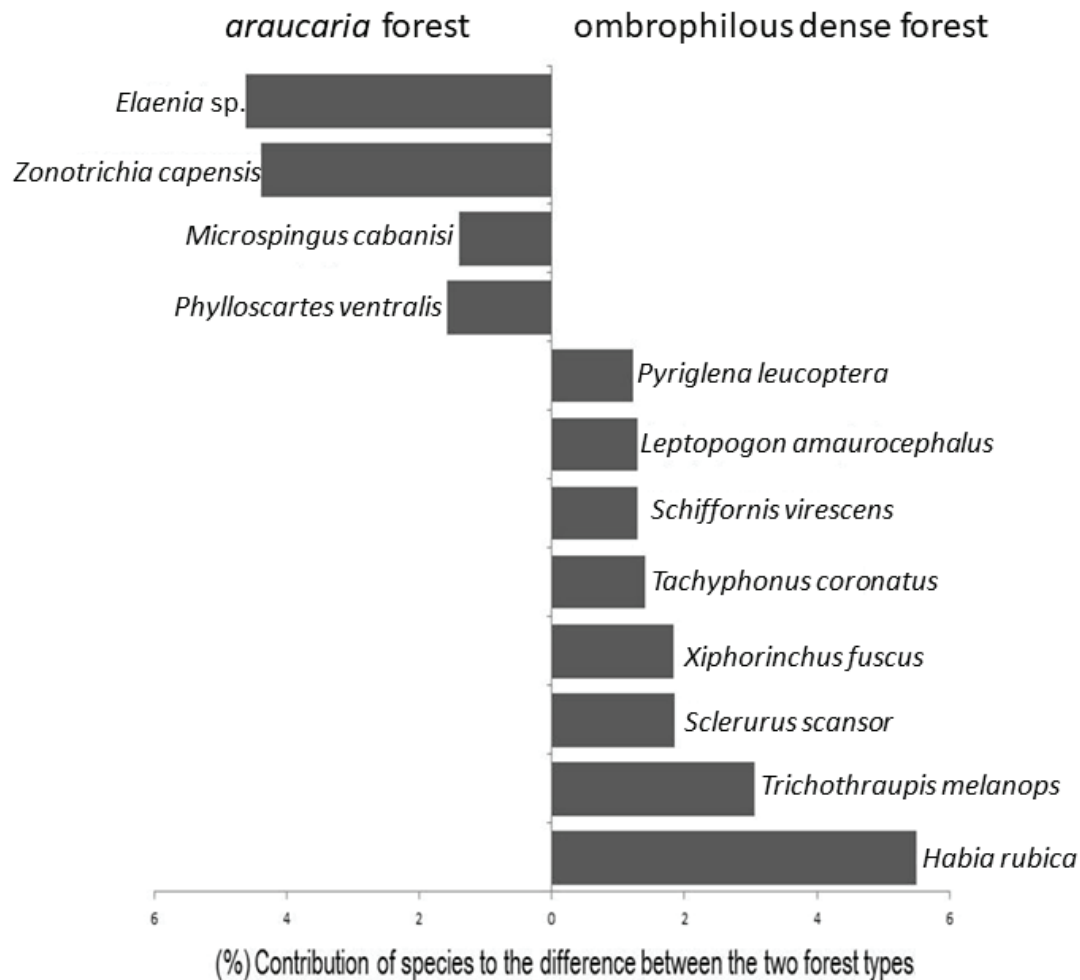
Although a higher structural vegetation complexity, usually closely linked to the number of species found in a locality, is usually found at lower elevations (Franchin *et al.* 2004), we found no significant

differences in taxonomic richness between the assemblages of the dense ombrophilous forest and the *Araucaria* forest. Our results only reflect understory bird composition and structuring, and particularly, those taxa well-sampled through mist nets; the use of complementary sampling schemes, *e.g.*, acoustic monitoring, could result in different patterns.

The model that best fitted the distribution of abundances of the species is characteristic of environments in ecological succession. Forest



**Figure 5.** Species Abundance Distribution for bird species sampled between September 2015 and October in the Aparados da Serra National Park, Rio Grande do Sul and Santa Catarina states, Brazil. The lines indicate the model that best fits the data and the points indicate the abundance of each species, so that the most abundant species are in the upper right portion of the graph and the rarer species are in the lower left portion of the graph.



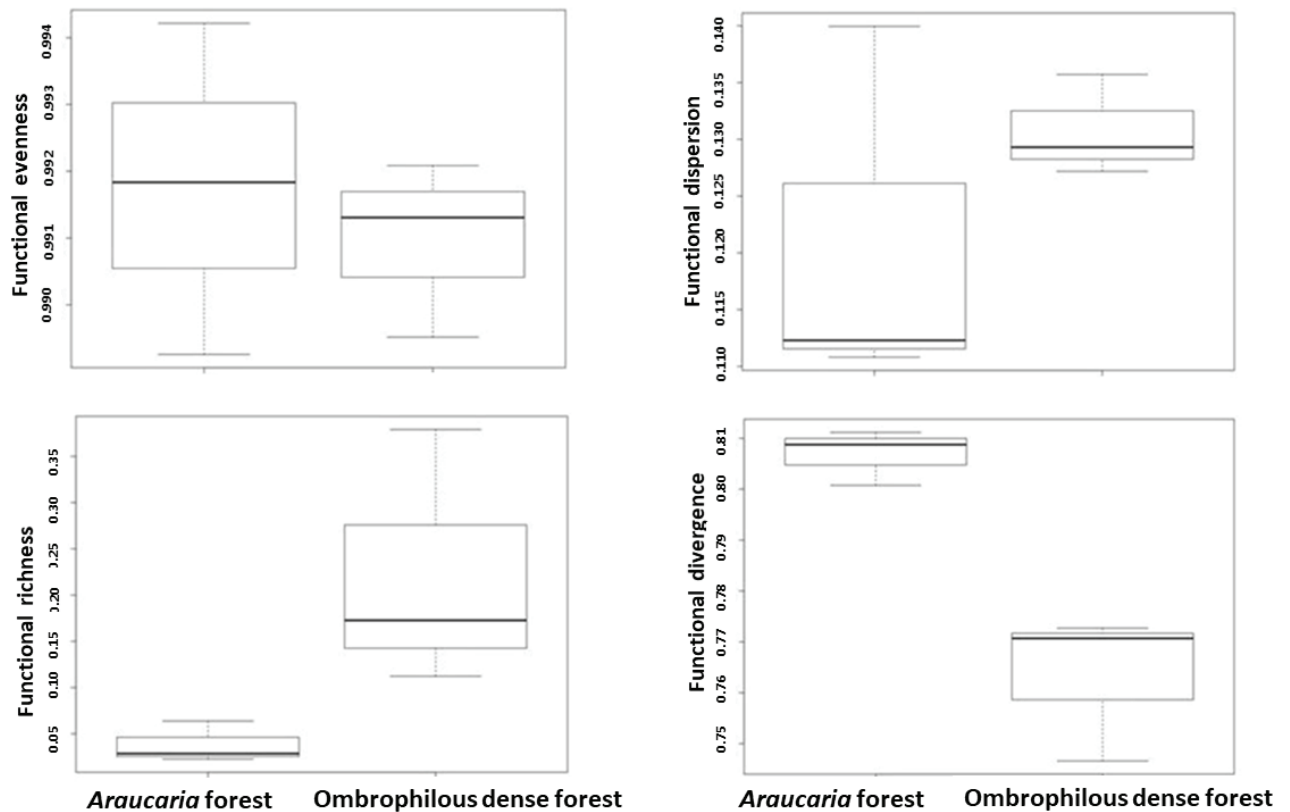
**Figure 6.** Exclusive bird species for *Araucaria* Forest (left side) and ombrophilous dense Forest (right side) with the largest contribution (1-5%) for dissimilarity between the two environments, in the Aparados da Serra National Park, Rio Grande do Sul and Santa Catarina states, Brazil.

environments in a higher successional stage tend to provide greater amount of food resources and habitats for birds, and this is probably the reason why the dense ombrophilous forest was functionally richer than the *Araucaria* forest (Aleixo 1999, Casas *et al.* 2016). Our results also showed that the dense ombrophilous forest present greater taxonomic bird diversity. The more diverse well-developed vegetation strata potentially provide a greater number of microhabitats and resources for birds, probably leading to a more equitable distribution of the number of individuals by the species present in the dense ombrophilous forest (Mendonça-Lima 2012).

Bird species contributing the most to the differences found between the assemblages of the dense ombrophilous forest and the *Araucaria* forest are either birds typical of more open areas or forest

edges, or species of dense and humid forest interior or that require large forest patches to survive, more characteristic of forested continuums still preserved in the valleys of the southernmost portion of the Atlantic Forest. *Zonotrichia capensis* and *Elaenia* sp. represent the former. Indeed, *Z. capensis* is characteristic of open environments and forest edges of colder climates from sea level up to 4,600 m (Rising & Jaramillo 2017); and *Elaenia* sp. is more common in forest edges and open areas (Bencke & Kindel 1999). On the other hand, *H. rubica* and *T. melanops* are typical humid forest understory birds (Hilty 2017a,b).

The dense ombrophilous forest bird assemblage was functionally richer and less divergent than the *Araucaria* forest bird assemblage; nonetheless, there were no differences in functional dispersion and evenness between the



**Figure 7.** Box-plot with the functional diversity metrics according to the forest type for bird species sampled between September 2015 and October in the Aparados da Serra National Park, Rio Grande do Sul and Santa Catarina states, Brazil. The boxes indicate the value and the lines the confidence interval (95%). Only richness and divergence showed significant differences between the *Araucaria* Forest and the ombrophilous dense Forest (see text for statistics).

two environments. Functional richness reflects the full range of all traits simultaneously but is not weighted by abundance and, therefore, can be inflated even by a single individual with unusual characteristics. The presence of some large-bodied species such as *Micrastur ruficollis* (Falconidae), *Trichloria malachitacea* (Psittacidae), *Batara cinerea* (Thamnophilidae), *Crypturellus tataupa* (Tinamidae), *Trogon rufus* and *Trogon surrucura* (Trogonidae) and of others of smaller size, but also functionally distinct with respect to the beak, tarsus and forage stratum as *Xenops rutilans* (Xenopidae), *Picumnus temminckii* (Picidae), *Platyrinchus mystaceus* (Platyrinchidae), *Myrmoderus squamosus* (Thamnophilidae) and *Cacicus chrysopterus* (Icteridae) would have the effect of increasing functional richness in the dense ombrophilous forest assemblage.

The higher functional divergence found in *Araucaria* forest suggests a higher degree of niche differentiation between species, indicating low competition for resources in this physiognomy.

In fact, the landscape of the plateaus is organized as a mosaic of patches of *Araucaria* trees inserted in an open grassland matrix (Pillar & Lange 2015), allowing the occurrence of both forest birds and edge or even open-space birds. This landscape configuration potentially allows for a more varied occupation of habitats and niches, ensuring an efficient use of all or most of the available foraging and nesting resources. The lack of differences in functional evenness and dispersion between the two forests suggests that the two bird assemblages occupy similar functional hypervolumes, though each of those volumes is positioned in different regions of the available functional hyperspace.

The evidence that the assemblages of the two forests are distinct, and that the ecological optima of the species is influenced by the complexity of the vegetation, has immediate consequences for the management and conservation of birds in the Atlantic Forest and particularly in the Aparados da Serra National Park. The maintenance of the regional species richness depends on the preservation of

the species present at the physiognomies, as they harbour distinct compositions and contribute, similarly, to the region's species pool. This association of some bird species with a particular type of forest suggests that both physiognomies are relevant to the regional diversity of the Atlantic Forest, a pattern already found by Beja *et al.* (2010) for the lowland Amazonian forests, underlining the importance of maintaining the natural mosaic of physiognomies that characterizes the Atlantic Forest towards the conservation of its unique and diversified avifauna. Protected areas like the Aparados da Serra National Park, which comprise different environments, are more efficient for environmental preservation, as already suggested by several authors (*e.g.*, Law & Dickman 1998, Smith *et al.* 2014). The Aparados da Serra National Park should receive special conservation attention given the great pressure on converting forest to agriculture and exotic forestry in its surroundings.

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### REFERENCES

- Aleixo, A. 1999. Effects of selective logging on a bird community in the Brazilian Atlantic forest. *The Condor*, 101, 537–548. DOI: 10.2307/1370183
- Backes, P., & Irlang, B. 2004. *Mata Atlântica: as árvores e a paisagem*. Porto Alegre: Editora Paisagem do Sul: p. 393.
- Beja, P., Santos, C. D., Santana, J., Pereira, M. J., Marques, J. T., Queiroz, H. L., & Palmeirim, J. M. 2010. Seasonal patterns of spatial variation in understory bird assemblages across a mosaic of flooded and unflooded Amazonian forests. *Biodiversity & Conservation*, 19(1), 129. DOI: 10.1007/s10531-009-9711-6
- Bencke, G. A., & Kindel, A. 1999. Bird counts along an altitudinal gradient of Atlantic Forest in northeastern Rio Grande do Sul, Brazil. *Ararajuba*, 7, 91–107.
- Brown, J. H., & Gibson, A. C. 1998. *Biogeography*. St. Louis, MO: The C. V. Mosby Company.
- Casas, G., Darski, B., Ferreira P. M. A., & Müller S. C. 2016. Habitat structure influences the diversity, richness and composition of bird assemblages in successional Atlantic rain forests. *Tropical Conservation Science*, 9, 503–524. DOI: 10.1177/194008291600900126
- Colwell, R. K., & Coddington, J. A. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 345(1311), 101–118. DOI: 10.1098/rstb.1994.0091
- Del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A., & Juana, E. 2016. *Handbook of the birds of the world alive*. Barcelona: Lynx Editions.
- Eisenberg, J. F. 1990. Neotropical mammal communities. In: A. H. Gentry. (Ed.), *Four Neotropical Rainforests*. pp. 358–368. Yale: Yale University Press.
- Franchin, A. G., Oliveira, G. M., Melo, C., Tomé, C. E. R., & Junior, O. M. 2004. Avifauna do Campus Umuarama, Universidade Federal de Uberlândia (Uberlândia, MG). *Revista Brasileira de Zootecias*, 6(2), 219–230.
- Gallindo-leal, C. E., & Câmara, I. G. 2005. *Mata Atlântica: biodiversidade, ameaças e perspectivas*. Belo Horizonte: Fundação SOS Mata Atlântica and Conservação Internacional.
- Gaston, K. J., & Blackburn, T. M. 1995. Mapping biodiversity using surrogates for species richness: macro-scales and New World birds. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 262, 335–341. DOI: 10.1098/rspb.1995.0214
- Gosler, A., 2004. *Birds in the hand. Bird ecology and conservation: a handbook of techniques*, 85–118.
- Graeff, O. 2015. *Fitogeografia do Brasil: bases e conceitos*. NAU Editora.
- Gray, J. S. 1987. Species-abundance patterns. In: J. H. R. Gee, & P. S. Giller (Eds.), *Organization of communities - past and present*. pp. 53–67. Oxford, UK: Blackwell Science.
- Hasenack, H., Cordeiro, J. L. P., & Both, R. 2009. *Unidades de paisagem. Biodiversidade dos campos do planalto das araucárias*. Brasília, DF: MMA.
- Hawkins, B. A., Field, R., Cornell, H. V., Currie, D. J., Guegan, J. F., Kaufman, D. M., Kerr, J. T.,

- Mittelbach, G. G., Oberdorff, T., & O'Brien, E. M. 2003. Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, 84, 3105–3117. DOI: 10.1890/03-8006
- Hilty, S. 2017. Black-goggled Tanager (*Trichothraupis melanops*). In: J. Del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, & E. Juana (Eds.), *Handbook of the birds of the world alive*. Barcelona: Lynx Editions. Retrieved on 20 January, 2017, from <http://www.hbw.com/node/61610>
- Hilty S. 2017. Red-crowned Ant-tanager (*Habia rubica*). In: J. Del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, & E. Juana (Eds.), *Handbook of the birds of the world alive*. Barcelona: Lynx Editions. Retrieved on 20 January, 2017, from <http://www.hbw.com/node/61836>
- IBAMA/MMA. 2004. Plano de manejo do Parque Nacional de Aparados da Serra e Serra Geral. Brasília, DF: Ministério do Meio Ambiente.
- Lagos, A. R., & Muller, B. L. A. 1994. Hotspot Brasileiro - Mata Atlântica. *Saúde & Ambiente em Revista*, 2(2), 35–45.
- Laliberté, E., & Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91(1), 299–305. DOI: 10.1890/08-2244.1
- Law, B. S., & Dickman, C. R. 1998. The use of habitat mosaics by terrestrial vertebrate fauna: implications for conservation and management. *Biodiversity & Conservation*, 7, 327–333. DOI: 10.1023/A:1008877611726
- Marques, J. T., Ramos Pereira, M. J., Marques, T. A., Santos, C. D., Santana, J., Beja, P., & Palmeirim, J. M. 2013. Optimizing sampling design to deal with mist-net avoidance in Amazonian birds and bats. *PLoS One*, 8(9), e74505. DOI: 10.1371/journal.pone.0074505
- Martin, T. E., Nightingale, J., Baddams, J., Monkhouse, J., Kaban, A., Sastranegara, H., & Simcox, W. 2017. Variability in the effectiveness of two ornithological survey methods between Tropical forest ecosystems. *PloS one*, 12(1), e0169786. DOI: 10.1371/journal.pone.0169786
- MacArthur, R. H. 1957. On the relative abundance of bird species. *Proceedings of the National Academy of Sciences of the United States of America*, 43(3), 293–295. DOI: 10.1073/pnas.43.3.293
- Mendonça-Lima, A. 2012. Estrutura de habitat, diversidade e comportamento da avifauna em sistemas de silvicultura em Floresta Ombrófila Mista. Doctoral Thesis. Departamento de Ecologia da Universidade Federal Rio Grande do Sul. p. 149.
- Motomura, I. 1932. A statistical treatment of ecological communities. *Zoological Magazine*, 44, 379–383.
- Mouchet, M. A., Villéger, S. V., Mason, N. W. H., & Moullot, D. 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, 24(4), 867–876. DOI: 10.1111/j.1365-2435.2010.01695.x
- Moullot, D., Villéger, S., Scherer-Lorenzen, M., & Mason, N. W. 2011. Functional structure of biological communities predicts ecosystem multifunctionality. *PloS one*, 6(3), e17476. DOI: 10.1371/journal.pone.0017476
- Nimer, E. 1979. Climatologia da região sul: Introdução à climatologia dinâmica - Subsídios à geografia regional do Brasil. *Climatologia do Brasil*, 3–65.
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., & Wagner, H. 2013. Package 'vegan' (<http://cran.r-project.org>, <http://vegan.r-forge.r-project.org/>). Available at: <http://cran.r-project.org/>.
- Piacentini, V. D. Q., Aleixo, A., Agne, C. E. *et al.* 2015. Lista comentada das aves do Brasil pelo Comitê Brasileiro de Registros Ornitológicos. *Revista Brasileira de Ornitologia*, 23(2), 91–298.
- Pillar, V. D. P., & Lange, O. 2015. Os campos do Sul. Porto Alegre: Rede Campos Sulinos – UFRGS.
- Preston, F. W. 1948. The commonness, and rarity, of species. *Ecology*, 29(3), 254–283. DOI: 10.2307/1930989
- Reif, J., Stastny, K., & Bejcek, V. 2010. Contrasting effects of climatic and habitat changes on birds with northern range limits in central Europe as revealed by an analysis of breeding bird distribution in the Czech Republic. *Acta Ornithologica*, 45(1), 83–90. DOI: 10.3161/000164510X516128
- Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. *Science*, 235(4785), 167–171. DOI: 10.1126/science.235.4785.167
- Rising, J., & Jaramillo, A. 2017. Rufous-collared Sparrow (*Zonotrichia capensis*). In: J. Del Hoyo,

- A. Elliott, J. Sargatal, D. A. Christie, & E. Juana (Eds.), Handbook of the birds of the world alive. Barcelona: Lynx Edicions. <http://www.hbw.com/node/61910>, accessed on 20 January 2017.
- Smith, T. B., Kinnison, M. T., Strauss, S. Y., Fuller, T. L., & Carroll, S. P. 2014. Prescriptive evolution to conserve and manage biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 45, 1–22.
- SOS Mata Atlantica, & INPE. 2014. Atlas of forest remnants of the Atlantic Forest 2013-2014. Retrieved on 10 April, 2016, from <https://www.sosma.org.br/en/project/atlas-of-the-atlantic-forest-remains/>
- Villéger, S, Mason, N. W. H., & Mouillot, D. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89, 2290–2301. DOI: 10.1890/07-1206.1
- Tóthmérész, B., 1995. Comparison of different methods for diversity ordering. *Journal of Vegetation Science*, 6, 283–290. DOI: 10.2307/3236223
- Zipf, G. K. 1949. Human behavior and the principle of least effort. Cambridge, Massachusetts: Addison-Wesley: p. 573.

**Supplementary Material 1.** Location of sampling points in the Aparados da Serra National Park, Cambará do Sul (RS) and Praia Grande (SC) municipalities, Brazil.

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