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Research Paper

## Bird species responses to forest-savanna boundaries in an Amazonian savanna

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**ABSTRACT.** Understanding how species respond to habitat boundaries in a landscape is essential because such responses influence several ecosystem processes and services. However, most studies to date are focused on boundaries between natural and human-made ecosystems, with few investigating species' responses to boundaries between natural habitats. Using a two-step approach, this paper examined how birds respond to gallery forest-savanna boundaries in an Amazonian savanna in Amapá, Brazil. First, we quantified bird species' abundance and boundary sensitivity. Then, we used phylogenetic linear regression to evaluate if five species-level characteristics (trophic level, dispersal ability, body size, niche breadth, and rarity) can be used as predictors of species' boundary sensitivities. We recorded 113 species, of which 67 had enough records to assess their responses to habitat edges. Most species (89%) crossed the boundaries between forests and savannas, with only seven species restricted to one of the habitats. Rarity is the only species trait that predicts a species' boundary sensitivity. Our results show that studies to date have underestimated the magnitude of the biological dynamics occurring along neotropical forest-savanna boundaries.

## Réponses des espèces d'oiseaux aux limites forêt-savane dans une savane amazonienne

**RÉSUMÉ.** Il est essentiel de comprendre comment les espèces réagissent aux limites de l'habitat dans un paysage, car ces réactions influencent plusieurs processus et services écosystémiques. Cependant, la plupart des études menées jusqu'à présent se sont concentrées sur les limites entre les écosystèmes naturels et celles créées par l'homme, et peu d'entre elles examinent les réponses des espèces aux frontières entre les habitats naturels. En utilisant une approche en deux étapes, cet article a examiné la façon dont les oiseaux répondent aux frontières forêt-savane dans une savane de l'Amazonie dans l'Amapá, au Brésil. Tout d'abord, nous avons quantifié l'abondance des espèces d'oiseaux et leur sensibilité aux limites. Ensuite, nous avons utilisé une régression linéaire phylogénétique pour évaluer si cinq caractéristiques au niveau des espèces (niveau trophique, capacité de dispersion, taille du corps, étendue de la niche et rareté) peuvent être utilisées comme prédicteurs de la sensibilité des espèces aux limites. Nous avons enregistré 113 espèces, dont 67 avaient suffisamment de données pour évaluer leurs réponses aux limites de l'habitat. La plupart des espèces (89%) traversent les limites entre les forêts et les savanes, seules sept espèces étant limitées à l'un des habitats. La rareté est le seul trait d'une espèce qui prédit la sensibilité de l'espèce aux frontières. Nos résultats montrent que les études menées jusqu'à présent ont sous-estimé l'ampleur des dynamiques biologiques qui se produisent le long des limites entre forêts et savanes néotropicales.

**Key Words:** *birds; forest edges; gallery forests; landscape ecology; riverine forests; tropical savannas*

## INTRODUCTION

Landscapes consist of mosaics of different habitats separated by ecological boundaries (Forman 1995, Lidicker 1999, Sisk and Battin 2002). Ecological boundaries are a product of the relationships between two habitat patches and, thus, do not have an independent existence (Kolasa 2014). They are created and maintained by either natural environmental changes or anthropogenic modifications to natural habitats. The latter becomes more common via the fragmentation of natural landscapes (e.g., Cadenasso et al. 2003, Tabarelli et al. 2004, Malhi et al. 2014). Understanding ecological boundaries is fundamental for the long-term management of landscapes because they constrain or facilitate the movements of organisms between habitats. These movements, in turn, can regulate vital ecological

processes, such as succession, which, over time, can change the location, composition, and structure of habitats within a landscape (Wiens et al. 1985, Silva et al. 1996).

Organisms respond to ecological boundaries in different ways. These responses are, in turn, a consequence of the interactions between the characteristics of those organisms and the characteristics of the adjacent habitats. To use two or more habitats, organisms must first find and cross ecological boundaries. If both habitats are distributed over large areas, the likelihood of an organism encountering a boundary is low. In contrast, if one of the habitats occupies small or narrow areas with high perimeter: area ratios, the probability that an organism encounters a boundary is high (Wiens 1992). When facing a boundary, the likelihood of an organism crossing it depends on

the boundary's permeability, defined as the degree by which a boundary constrains a species' movements (Wiens et al. 1985, Ries et al. 2004). The boundary permeability, in turn, is a function of the boundary itself and the characteristics of the organism (Wiens 1992). Thus, if two adjacent habitats have very different physiognomies, the boundary has high contrast and lower permeability. Accordingly, if the difference between habitats is not pronounced, the boundary has low contrast and higher permeability. Because organisms perceive boundaries differently, it is expected that some characteristics of organisms influence how they respond to ecological boundaries (Wiens et al. 1985, Ewers and Didham 2006b).

The response of an organism to an ecological boundary can be conceptualized as a gradient from low to high sensitivity and inferred from studies that document how the populations they belong to use two adjacent habitats within a landscape. How different species populations living together in a landscape or region at a given time are distributed along this gradient has been a recurrent research theme in modern ecology (e.g., Lees and Peres 2009, Yabe et al. 2010, Villaseñor et al. 2014, Boesing et al. 2018, Barros et al. 2019, van Schalkwyk et al. 2020). Nevertheless, most of these studies have focused on ecological boundaries created and maintained by human environmental changes rather than natural ones (Erdős et al. 2013). Therefore, there is a critical knowledge gap to be closed in this broad research agenda.

Five species-level characteristics have been proposed as significant predictors of an organism's sensitivity to ecological boundaries: dispersal ability, niche breadth, rarity, trophic level, and body mass. In general, sedentary species are less likely to cross ecological boundaries than mobile species (Ewers and Didham 2006a, Lees and Peres 2009), more specialized species are less likely to cross ecological boundaries than generalist ones (Lees and Peres 2009, Yabe et al. 2010, Peyras et al. 2013), and rare species are less likely to cross ecological boundaries than abundant species (Lees and Peres 2009). Among birds, insectivores are less likely to cross boundaries than non-insectivore species (Lindell et al. 2007). The role played by body mass on boundary sensitivity is uncertain. While some authors suggest that body mass is not a good predictor of boundary sensitivity (Ewers and Didham 2006a), others found that smaller species can be more sensitive to ecological boundaries than larger species (Lindell et al. 2007, Lees and Peres 2009).

Neotropical savannas serve as important natural laboratories where organism responses to natural ecological boundaries can be studied. These regions are dominated by landscapes composed of a matrix with open and semi-open vegetations intersected by tall (up to 25 m), evergreen gallery forests that occur naturally as relatively narrow strips (usually no more than 300 m in width) along watercourses (Ratter et al. 1997, Silva and Bates 2002). Because the boundaries between gallery forests and savannas have high contrast and possibly low permeability (Eiten 1972, Furley and Ratter 1988), most species living in these two habitats are expected to show high boundary sensitivity and, consequently, high habitat fidelity (Wiens 1992). Nevertheless, there is evidence that organisms living in neotropical savannas are not as sensitive to forest-savanna boundaries as expected (Redford and Fonseca 1986, Cavalcanti 1992, Piratelli and Blake 2006, Boss and Silva 2014). Among birds, for instance, the number of species living in

both habitats within savanna regions ranges from 20.8% in the Cerrado region (Silva 1995) to 35% in the Roraima savannas (Santos and Silva 2007).

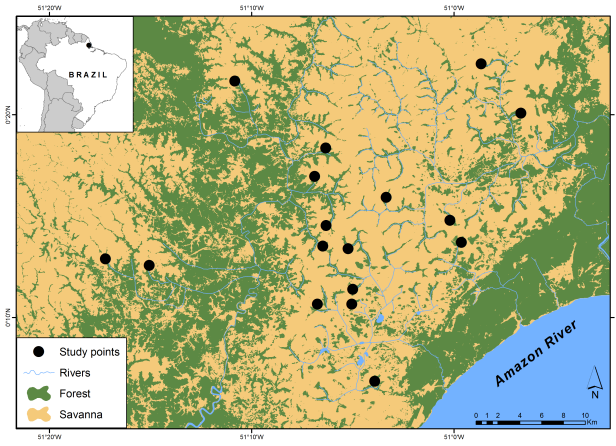
In this paper, we examined how birds use habitats along gallery forest-savanna boundaries that have not been reduced by human activities in the recent past in an Amazonian savanna in Amapá, Brazil. We selected birds because they are diverse, well-known, mobile, relatively easy to identify, access spatially dispersed resources, and contribute to the provision of several ecological services (Bibby et al. 2000, Sekercioglu et al. 2016). We used a two-step approach. First, we quantified the abundance of bird species in gallery forests and their adjacent savannas and estimated their boundary sensitivity. Then, we used phylogenetic regression to test the hypotheses that five species-level characteristics (body mass, dispersal ability, trophic level, rarity, and niche breadth) can be used to predict species boundary sensitivity and guide conservation management strategies. This study contributes to the ongoing research on ecological boundaries by studying natural rather than human-made ecological boundaries (e.g., Yabe 2009, Yabe et al. 2010, Erdős et al. 2013), and by expanding the coverage of such studies to the Amazon, the home of one of the least known neotropical savannas (Carvalho and Mustin 2017).

## MATERIALS AND METHODS

### Study area

The study was conducted in a 70,000-ha landscape (0° 16'31"N, -51°04'05"W) in the savanna region of Amapá in the Brazilian Amazon (Fig. 1). This Amapá savanna region is a narrow longitudinal strip parallel to the Atlantic coast, occupying approximately 10,021 km<sup>2</sup> (Mustin et al. 2017, Hilário et al. 2017). The climate of the region is hot (~ 27°C) and humid (average relative humidity of 81%), with high annual precipitation (2,700 mm), and a distinct dry season from August to November of high temperatures and water deficits due to reduced rainfall (~ 234.5 mm) (Boss and Silva 2014). Amapá savannas are covered primarily by upland savannas intersected by gallery forests and seasonally flooded grasslands along the rivers (Silva et al. 1997). The upland savanna has a grass layer that includes species of *Rhynchospora*, *Axonopus*, *Paspalum*, *Polygala*, *Bulbostylis*, and *Miconia*, and a woody layer that includes large shrubs and trees from 3 to 10 m, such as *Byrsonina crassifolia*, *Salvertia convallariodora*, *Ouratea hexasperma*, *Curatella americana*, *Himatanthus articulatus*, *Pallicourea rigida*, and *Hancornia speciosa* (Sanaiotti et al. 1997, Costa-Neto et al. 2017). Gallery forests are, on average, naturally narrow (~ 300 m) and found in hydromorphic soils rich in organic matter, along thin perennial streams that occur across the region (Silva et al. 1997). They are evergreen with an understory dominated by ferns, epiphytes, and palm trees. The forest canopy is dominated by trees from 15 to 30 m, such as *Jacaranda copaia*, *Symphonia globulifera*, *Desmoncus* sp., *Annona paludosa*, *Coccoloba* sp., *Ficus* sp., *Virola* sp., *Lecythis* sp., and *Hymenaea parvifolia* (Costa-Neto et al. 2017). There is no evidence that gallery forests have been reduced by human activities in the landscape in the recent past. Seasonally flooded grasslands are found in narrow valleys, where the soils are shallow and permanently flooded. These grasslands sometimes have belts of palm species, such as *Mauritia flexuosa*, *Euterpe oleracea*, and *Mauritiella aculeata* (Silva et al. 1997, Costa-Neto et al. 2017).

**Fig. 1.** The distribution of the study sites across an Amazonian savanna landscape in Amapá, Brazil.



## Bird sampling

We selected 17 sites in the study landscape (Fig. 1). These sites were chosen according to two criteria: (1) they were at least 1.5 km apart to ensure spatial independence between them (Bibby et al. 2000), and (2) forests and savannas had high contrast boundaries without gradual transitions between them. At each site, we set one 100 m linear transect perpendicular to the gallery forest, of which 50 m was within the gallery forest, and 50 m was within the immediate adjacent savanna. Because gallery forests in the landscape are relatively narrow ( $n = 17$ , Mean = 243.0 m, SD = 105.9 m), 50 m was considered enough to adequately sample populations of boundary-avoidant forest species that live in the forest interior (Stouffer 2020). We used the fixed distance transect method to estimate species abundance across the transects, counting all birds detected visually or aurally within 50 m on each transect side (Bibby et al. 2000). This method provides estimates of relative abundance that are comparable within species across different environments (Bibby et al. 2000) but does not account for differences in species detectability. Despite this limitation, Carrascal et al. (2008) demonstrated that fixed distance transects only slightly underestimate species abundance compared with methods that consider species detectability.

Birds were counted from April to September 2019, twice during the rainy season (April and June) and twice during the dry season (July and September). Thus, our counts included all the critical periods of the region's annual bird cycle (Boss and Silva 2014). We counted birds between 6:00 am, and 10:30 am to maximize species detection. Each transect was sampled at an average speed of 0.4 km/hour. The direction from which the counting began (forest  $\leftrightarrow$  savanna) was chosen randomly one day before the sampling. We recorded each count's start and end times, the species' identity (observed or heard), the number of individuals, and the forest distance interval. Species flying over the transect were noted but not counted, and therefore were not included in the analysis. The counts were made by one of us (JC) with the aid of Olympus (7×32mm) and Bushnell (10×42mm) binoculars. The vocalizations were recorded with a Sony recorder and Yoga-Ht81

directional microphone when necessary to identify a species. Because we sampled our sites with the same effort, we used the total number of detections to indicate species abundance in each habitat. Taxonomy follows Pacheco et al. (2021).

## Species characteristics

Boundary sensitivity was calculated in two steps. First, we calculated the proportion of records of a species in the savanna. Then, we used the following formula to calculate the boundary sensitivity index:

Boundary sensitivity index = Absolute value of  $(0.5 - \text{proportion of records in savanna}) / 0.5$

The boundary sensitivity index ranges from 0 to 1, with 0 representing species found equally in forests and savannas (low boundary sensitivity) and 1 representing species recorded exclusively on savannas or forests (high boundary sensitivity). We gathered the information for five species-level characteristics: body mass, dispersal ability, trophic level, rarity, and niche breadth. Data on body mass (in g) was taken from Wilman et al. (2014). We used Kipp's index of wing morphology as a proxy for avian dispersal ability (Sheard et al. 2020). Based on our field experience and, when needed, additional information from the literature (e.g., Sick 1993, Johnson et al. 2011), we classified species in three trophic levels: (a) herbivores, which include all species that feed primarily on nectar, fruits, or seeds; (b) insectivores, which include all species feeding on insects and other arthropods; and (c) omnivores, species that combine the herbivore and insectivore diets. We used the inverse ranking of species based on their total detections as the rarity score. Thus, rare species had higher rank scores than more common species. To estimate niche breadth, we used range size (in million km<sup>2</sup>). We assumed that species that maintain viable populations in a wide variety of environmental conditions (niche breadth) have large ranges. We gathered information on range size from the global database on bird species maintained by BirdLife International (<http://datazone.birdlife.org>).

## Statistical analyses

In our analyses, we excluded all species of Psittacidae (parrots and macaws), Ramphastidae (toucans and toucanets), obligate waterbirds, raptors, nocturnal species, and aerial insectivores because the methods that we used did not provide a reliable estimate of their abundances. We used Chi-Square tests to compare the number of species and the number of detections between forests and savannas.

We used phylogenetic linear regression to identify the species-level characteristics that predict a species' boundary sensitivity while considering the statistical non-independence of related species (Martins and Hansen 1997, Mundry 2014). Phylogenetic distances among species were estimated based on an updated version (available in <http://vertlife.org/phylosubsets>) of the Jetz et al.'s supertree (Jetz et al. 2012) based on the Hackett et al. (2008) bone. Before using the regression, we first examined the variance inflation factors (VIF) to ensure that the predictor variables were independent. As all predictor variables presented  $VIF < 5$ , we included them in the model (Dormann et al. 2013). All continuous predictor variables were log-transformed before the analysis. The phylogenetic linear regression was carried out in R (R Core Team 2021) using the package "phylolm" (Ho et al. 2020).

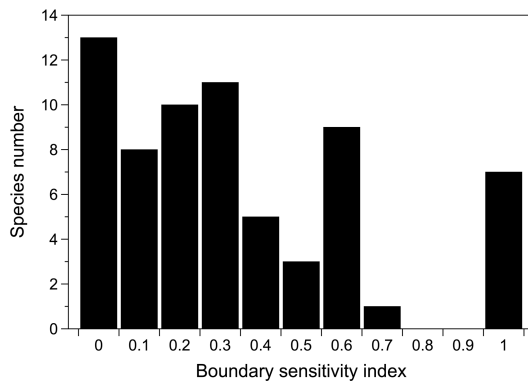


## RESULTS

We recorded 1,151 detections of 113 species along the forest-savanna boundaries (Appendix 1). More birds were detected in forests than in savannas (643 vs. 508, respectively, Chi-Square = 15.0,  $df = 1$ ,  $P < 0.0001$ ), but the difference between the number of species recorded in these two habitats (forests, 83; savannas, 102) is not significant (Chi-Square = 1.95,  $P = 0.16$ ).

The number of species with less than five detections was 46, and their habitat preferences could not be evaluated. Among the remaining 67 species (Appendix 2), most species show low boundary sensitivity, indicating that they use forests and savannas (Fig. 2). Species with the highest scores of boundary sensitivity are only seven, of which four were recorded only in forests (*Momotus momota*, *Dendrocincla fuliginosa*, and *Myrmotherula axillaris*) or three only in savannas (*Chrysolampis mosquitus*, *Myiarchus swainsoni*, *Ammodramus humeralis*, and *Piranga flava*).

**Fig. 2.** The distribution of 67 species recorded in forest-savanna boundaries in an Amazonian savanna landscape, Amapá, Brazil, along a gradient formed by the boundary sensitivity index.



The 67 species analyzed have a wide variation in all four continuous traits, with body mass showing the largest standard deviation (Table 1). Among these 67 species, 29 are omnivores, 24 are insectivores, and 14 are herbivores. The phylogenetic regression shows that only rarity can be considered a reliable predictor of a species' boundary sensitivity (Table 2). Because the boundary sensitivity index is negatively associated with rarity, it is possible to infer that abundant species are most likely to cross forest-savanna boundaries within savanna landscapes.

## DISCUSSION

Boundaries between habitats as distinct as forests and savannas are predicted to have high contrast and low permeability. However, our study failed to support this hypothesis. We found that among the species with enough detections to be included in the analyses, 89% used both forests and savannas. This percentage is higher than previous estimates at local (e.g., Piratelli and Blake 2006) and regional levels (Silva 1995, Santos and Silva 2007) and indicates that studies to date have possibly underestimated the magnitude of the biological dynamics occurring across neotropical forest-savanna boundaries.

**Table 1.** Descriptive statistics of the four continuous species traits used to predict the boundary sensitivity of 67 bird species recorded along gallery forest-savanna boundaries in an Amazonian savanna landscape, Brazil.

	Mean	Standard deviation	Minimum	Maximum
Kipp's Index	20.98	12.33	4.29	74.8
Range Size (million km <sup>2</sup> )	14.21	8.29	2.2	59.2
Body Mass (g)	59.1	91.9	2.2	502.0
Rarity	34.0	19.4	3.5	67

**Table 2.** Results of phylogenetic linear regression relating boundary sensitivity index and five species traits of 67 bird species along forest-savanna boundaries in an Amazonian savanna landscape, Amapá, Brazil. All continuous predictors were log-transformed before the analysis.

	Estimate	SE	t-value	P
Intercept	0.954	0.405	2.357	0.022
Kipp's Index	-0.050	0.201	-0.249	0.804
Range Size (million km <sup>2</sup> )	-0.103	0.143	-0.718	0.475
Body Mass (g)	-0.054	0.074	-0.732	0.467
Rarity	-0.235	0.107	-2.195	0.032
Trophic Level <sup>†</sup>				
Insectivores	0.016	0.112	0.143	0.887
Omnivores	-0.010	0.099	-0.096	0.924

<sup>†</sup>Compared to herbivores

Most species moving across ecological boundaries (i.e., species with low boundary sensitivity) were not considered core components of savanna bird assemblages in one year-round study in one of the Amapá savannas (Boss and Silva, 2015). Therefore, their presence in savanna landscapes requires gallery forests. Species observed crossing forest-savanna boundaries are, at the regional scale, associated with early-successional forest stages that occur naturally in riverine forests and scrublands across the region (e.g., Novaes 1973, Remsen and Parker 1983, Borges 2007). These species also colonize small forest patches and second-growth forests through the Amazon basin (Novaes 1973, Silva et al. 1996). Using adjacent savannas in their activities seems not to be a challenge for species with low boundary sensitivity. Most of them have behavioral adaptations to cope with open habitats as needed. They are generally insectivores or omnivores that forage in the foliage-air interface, a productive zone within habitats where full sunlight strikes the vegetation (Levey 1988). Therefore, these low boundary sensitivity species are adapted to high temperatures characteristic of open habitats and thus differ from the typical forest interior forest species that cannot even cross narrow clearings (Stouffer 2020). Although moving from forest to savannas can increase predation risk (Sisk and Battin 2002), species crossing forest-savanna boundaries regularly join mixed-species flocks to reduce this risk (Tubelis et al. 2006).

Even though they are ubiquitous and abundant, the contribution of the boundary-crossing species in savanna landscapes and regions to critical landscape-level ecological processes has been undervalued in the literature. One of these processes is seed

dispersal, as seed rains generated by species with low and moderate boundary sensitivity can facilitate forest expansion over savannas in patches where slow soil erosion improves ecological conditions. Some of these species, such as *Ortalis motmot*, have wide bills that allow them to disperse large seeds of forest trees to savannas (Moermond and Denslow 1985). However, most boundary-crossing species have narrow bills (Silva et al. 1996). Thus, they can only disperse small seeds of pioneer forest plant species to savannas (Silva and Tabarelli 2000). Good examples of these species are three tanagers (*Tangara episcopus*, *Tangara palmarum*, and *Ramphocelus carbo*) that are well known to play an essential role in accelerating forest recovery in abandoned pastures in eastern Amazonia by dispersing seeds from adjacent second-growth forests (Silva et al. 1996).

Rarity is the only characteristic that can be used to predict the sensitivity of a species to an ecological boundary. This finding is compatible with the idea that less abundant species are less likely to find and cross boundaries between different habitats (Wiens 1992). Against Ewers and Didham's (2006a) prediction, we did not find support for the hypothesis that dispersal ability (such as measured by Kipp's index) influences species sensitivity to ecological boundaries. Similarly, we did not find support for the hypotheses that body mass, niche breadth, or trophic levels can drive species responses to natural forest-savanna boundaries (Lees and Peres 2009, Yabe 2009, Yabe et al. 2010). Responses of local assemblages to ecological boundaries are a consequence of several factors, but there is a solid biogeographic factor in the case of birds living in savanna landscapes. Gallery forests are mesic corridors that allow savanna regions and landscapes to be colonized by forest-dependent birds whose ranges are centered in the adjacent forest regions (Silva 1996). To expand and maintain their ranges within savanna regions, these species must overcome several ecological filters (i.e., abiotic and biotic factors that constrain the establishment of a group of species in a given habitat). The strength of these filters is predicted to decline with the distance from the continuous forest regions (Nekola and White 1999). Based on our results, we suggest that ecological filters operating along gallery forests in Amazonian savannas favor abundant species (species with ecological traits that allow them to thrive in narrow forest patches) rather than the rare forest species that dominate most of the avifauna of the region's continuous forests (Johnson et al. 2011, Rutt et al. 2019, Stouffer et al. 2021).

In general, our results show that several species use both gallery forests and savannas and that the biological dynamics along forest-savanna boundaries are much more intense than previously thought. A potential reason for this is that because gallery forests in Amazonian savannas are narrow and have high dynamic boundaries, their bird assemblages are dominated by common species that can use the adjacent savannas for their activities rather than by rare forest species with high habitat fidelity. Alternatively, it is possible that rare species (the ones expected to show the highest boundary sensitivity according to our model) were either not detected or had a reduced number of records to have their boundary sensitivity determined (Robinson et al. 2018). Testing these two hypotheses requires standardized long-term studies along the forest-savanna boundaries of different neotropical savanna regions. In addition, there is a need to explore the roles played by species with low boundary sensitivity to critical

ecological processes, such as succession, operating at the landscape level. Our results show that maintaining bird species diversity and the environmental services in neotropical savanna landscapes requires the protection of gallery forests and their adjacent savannas, a practice that has not been followed across the region. Incorporating the biological dynamics along neotropical forest-savanna boundaries in systematic conservation planning is more relevant than ever for two reasons: 1) savanna regions are under intense pressure due to the expansion of large-scale agriculture to supply the demand of an ever-growing global population (e.g., Garcia and Ballester 2016, Hilário et al. 2017, Strassburg et al. 2017, Souza et al. 2020); and (2) current policies in most of the neotropical countries are insufficient to protect the forest-savanna gradients (Tubelis et al. 2004, Hilário et al. 2017, Stier et al. 2020).

*Responses to this article can be read online at:*  
<https://www.ace-eco.org/issues/responses.php/2138>

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#### Author Contributions:

*Jackson Cleiton de Sousa conceived and designed the experiments performed the experiments, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft. José Júlio de Toledo conceived and designed the experiments, reviewed drafts of the paper, and approved the final draft. William Douglas Carvalho analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft. José Maria Cardoso da Silva conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.*

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Appendix 1. Total detections and detections separated by habitat of bird species recorded along gallery forest-savanna boundaries in an Amazonian savanna landscape, Amapá, Brazil.

<b>Family/Species</b>	<b>Total</b>	<b>Forest</b>	<b>Savanna</b>
<b>Tinamidae</b>			
<i>Crypturellus erythropus</i>	1	1	0
<i>Crypturellus soui</i>	5	4	1
<b>Cracidae</b>			
<i>Ortalis motmot</i>	14	9	5
<b>Odontophoridae</b>			
<i>Colinus cristatus</i>	1	0	1
<b>Columbidae</b>			
<i>Columbina minuta</i>	1	0	1
<i>Columbina passerina</i>	6	1	5
<i>Columbina talpacoti</i>	4	0	4
<i>Leptotila rufaxilla</i>	7	5	2
<i>Leptotila verreauxi</i>	6	3	3
<i>Patagioenas cayennensis</i>	27	12	15
<i>Patagioenas speciosa</i>	5	3	2
<i>Zenaida auriculata</i>	2	0	2
<b>Cuculidae</b>			
<i>Coccyzua minuta</i>	3	2	1
<i>Crotophaga ani</i>	1	0	1
<i>Piaya cayana</i>	17	10	7
<b>Trochilidae</b>			
<i>Chionomesa fimbriata</i>	7	3	4
<i>Anthracothonax viridigula</i>	1	0	1
<i>Chlorestes notata</i>	3	0	3
<i>Chrysolampis mosquitus</i>	5	0	5
<i>Phaethornis ruber</i>	25	20	5
<i>Thalurania furcata</i>	1	0	1
<b>Trogonidae</b>			
<i>Trogon violaceus</i>	1	0	1
<i>Trogon viridis</i>	15	10	5
<b>Momotidae</b>			

<i>Momotus momota</i>	9	9	0
<b>Galbulidae</b>			
<i>Galbula galbula</i>	11	6	5
<b>Bucconidae</b>			
<i>Tamatia tamatia</i>	4	1	3
<i>Chelidoptera tenebrosa</i>	2	0	2
<i>Notharchus tectus</i>	1	0	1
<b>Picidae</b>			
<i>Campephilus melanoleucos</i>	6	3	3
<i>Dryocopus lineatus</i>	12	8	4
<i>Picumnus cirratus</i>	1	0	1
<i>Veniliornis passerinus</i>	1	0	1
<b>Thamnophilidae</b>			
<i>Cercomacroides tyrannina</i>	14	10	4
<i>Formicivora grisea</i>	12	6	6
<i>Formicivora rufa</i>	4	0	4
<i>Myrmeciza longipes</i>	10	6	4
<i>Myrmotherula axillaris</i>	6	6	0
<i>Pernostola rufifrons</i>	4	3	1
<i>Sclateria naevia</i>	2	1	1
<i>Taraba major</i>	1	1	0
<i>Thamnophilus doliatus</i>	8	4	4
<i>Thamnophilus punctatus</i>	26	21	5
<b>Dendrocolaptidae</b>			
<i>Dendrocincla fuliginosa</i>	7	7	0
<i>Dendroplex picus</i>	18	13	5
<i>Glyphorhynchus spirurus</i>	6	4	2
<i>Lepidocolaptes angustirostris</i>	1	0	1
<i>Xiphorhynchus guttatus</i>	19	16	3
<b>Furnariidae</b>			
<i>Berlepschia rikeri</i>	2	2	0
<b>Pipridae</b>			
<i>Chiroxiphia pareola</i>	10	5	5
<i>Manacus manacus</i>	2	1	1
<i>Pipra aureola</i>	15	8	7
<b>Tityridae</b>			

<i>Pachyramphus polychopterus</i>	18	7	11
<i>Tityra cayana</i>	1	0	1
<i>Tityra semifasciata</i>	4	4	0

#### **Rhynchocyclidae**

<i>Lophotriccus galeatus</i>	28	20	8
<i>Todirostrum cinereum</i>	8	4	4
<i>Todirostrum maculatum</i>	1	0	1
<i>Todirostrum pictum</i>	3	2	1
<i>Tolmomyias flaviventris</i>	53	37	16
<i>Tolmomyias poliocephalus</i>	7	5	2

#### **Tyrannidae**

<i>Attila cinnamomeus</i>	7	6	1
<i>Attila spadiceus</i>	2	1	1
<i>Camptostoma obsoletum</i>	12	8	4
<i>Elaenia chiriquensis</i>	2	0	2
<i>Elaenia flavogaster</i>	29	12	17
<i>Empidonomus varius</i>	6	3	3
<i>Legatus leucophaeus</i>	5	3	2
<i>Megarynchus pitangua</i>	18	11	7
<i>Myiarchus ferox</i>	8	4	4
<i>Myiarchus swainsoni</i>	7	0	7
<i>Myiarchus tyrannulus</i>	19	6	13
<i>Myiopagis flavivertex</i>	1	0	1
<i>Myiopagis gaimardii</i>	42	24	18
<i>Myiozetetes cayanensis</i>	3	1	2
<i>Phaeomyias murina</i>	6	2	4
<i>Pitangus sulphuratus</i>	18	11	7
<i>Rhytipterna simplex</i>	3	1	2
<i>Sublegatus modestus</i>	4	0	4
<i>Suiriri suiriri</i>	1	0	1
<i>Tyrannopsis sulphurea</i>	4	2	2
<i>Tyrannulus elatus</i>	4	3	1
<i>Tyrannus melancholicus</i>	27	13	14
<i>Tyrannus savana</i>	3	0	3

#### **Vireonidae**

<i>Cyclarhis gujanensis</i>	47	28	19
<i>Hylophilus pectoralis</i>	8	3	5
<i>Vireo chivi</i>	30	20	10

#### **Troglodytidae**

<i>Cantorchilus leucotis</i>	25	15	10
<i>Pheugopedius coraya</i>	1	1	0
<i>Troglodytes musculus</i>	6	1	5

#### **Poliophtilidae**

<i>Poliophtila plumbea</i>	41	17	24
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#### **Turdidae**

<i>Turdus leucomelas</i>	46	35	11
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#### **Mimidae**

<i>Mimus saturninus</i>	1	0	1
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#### **Passerellidae**

<i>Ammodramus humeralis</i>	12	0	12
<i>Zonotrichia capensis</i>	3	0	3

#### **Icteridae**

<i>Cacicus cela</i>	6	3	3
<i>Icterus cayanensis</i>	2	1	1
<i>Psarocolius viridis</i>	6	5	1

#### **Thraupidae**

<i>Coereba flaveola</i>	44	22	22
<i>Conirostrum speciosum</i>	1	1	0
<i>Cyanerpes cyaneus</i>	1	1	0
<i>Dacnis cayana</i>	7	3	4
<i>Emberizoides herbicola</i>	2	0	2
<i>Hemithraupis guira</i>	1	0	1
<i>Nemosia pileata</i>	5	4	1
<i>Ramphocelus carbo</i>	21	17	4
<i>Sporophila angolensis</i>	3	3	0
<i>Stilpnia cayana</i>	24	6	18
<i>Tangara mexicana</i>	6	2	4
<i>Thraupis episcopus</i>	26	18	8
<i>Thraupis palmarum</i>	25	17	8

#### **Cardinalidae**

<i>Piranga flava</i>	5	0	5
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#### **Fringillidae**

<i>Euphonia chlorotica</i>	9	2	7
<i>Euphonia violacea</i>	11	4	7

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Appendix 2. Abundance, boundary sensitivity, and traits of all bird species detected at least five times along gallery forest-savannas boundaries in an Amazonian savanna landscape, Amapá, Brazil.

Family/Species	Detections			Boundary sensitivity index	Body Mass (g)	Trophic Level	Range Size (million km <sup>2</sup> )	Kipp's Index	Rarity
	Total	Forest	Savanna						
<b>Tinamidae</b>									
<i>Crypturellus soui</i>	5	4	1	0.60	206.0	omnivores	15.2	26.8	64.5
<b>Cracidae</b>									
<i>Ortalis motmot</i>	14	9	5	0.28	502.0	herbivores	2.6	14.8	28.5
<b>Columbidae</b>									
<i>Columbina passerina</i>	6	1	5	0.66	32.0	herbivores	26.8	25.4	56.0
<i>Leptotila rufaxilla</i>	7	5	2	0.42	153.0	herbivores	14.3	24.4	47.0
<i>Leptotila verreauxi</i>	6	3	3	0	155.0	herbivores	26.0	21.9	56.0
<i>Patagioenas cayennensis</i>	27	12	15	0.11	260.0	herbivores	18.7	34.1	10.5
<i>Patagioenas speciosa</i>	5	3	2	0.2	261.0	herbivores	16.9	36.5	64.5
<b>Cuculidae</b>									
<i>Piaya cayana</i>	17	10	7	0.17	118.0	insectivores	16.1	11.3	25.0
<b>Trochilidae</b>									
<i>Chionomesa fimbriata</i>	7	3	4	0.14	4.3	herbivores	12.7	63.0	47.0
<i>Chrysolampis mosquitus</i>	5	0	5	1	3.0	herbivores	10.7	68.0	64.5
<i>Phaethornis ruber</i>	25	20	5	0.6	2.2	herbivores	11.3	74.8	15.0
<b>Trogonidae</b>									
<i>Trogon viridis</i>	15	10	5	0.33	84.0	omnivores	11.8	33.2	26.5
<b>Momotidae</b>									
<i>Momotus momota</i>	9	9	0	1	122.0	insectivores	11.3	18.6	38.5
<b>Galbulidae</b>									
<i>Galbula galbula</i>	11	6	5	0.09	29.0	insectivores	2.2	24.6	34.5

**Picidae**

<i>Campephilus melanoleucos</i>	6	3	3	0	220.0	omnivores	13.3	22.1	56.0
<i>Dryocopus lineatus</i>	12	8	4	0.33	200.0	insectivores	21.3	20.5	31.5

**Thamnophilidae**

<i>Cercomacroides tyrannina</i>	14	10	4	0.42	17.0	insectivores	7.0	9.3	28.5
<i>Formicivora grisea</i>	12	6	6	0	11.0	insectivores	8.8	8.2	31.5
<i>Myrmeciza longipes</i>	10	6	4	0.2	22.0	insectivores	3.2	6.4	36.5
<i>Myrmotherula axillaris</i>	6	6	0	1	8.0	insectivores	10.4	15.2	56.0
<i>Thamnophilus doliatus</i>	8	4	4	0	28.0	insectivores	18.3	9.0	41.5
<i>Thamnophilus punctatus</i>	26	21	5	0.61	20.0	insectivores	3.8	10.1	12.5

**Dendrocolaptidae**

<i>Glyphorhynchus spirurus</i>	6	4	2	0.33	14.0	insectivores	13.5	23.9	56.0
<i>Dendrocincla fuliginosa</i>	7	7	0	1	37.0	insectivores	12.3	18.3	47.0
<i>Dendroplex picus</i>	18	13	5	0.44	40.0	insectivores	12.5	17.8	22.5
<i>Xiphorhynchus guttatus</i>	19	16	3	0.68	65.0	insectivores	6.0	16.2	19.5

**Pipridae**

<i>Chiroxiphia pareola</i>	10	5	5	0	19.0	herbivores	10.9	10.4	36.5
<i>Pipra aureola</i>	15	8	7	0.06	15.0	omnivores	2.3	19.3	26.5

**Tityridae**

<i>Pachyramphus polychopterus</i>	18	7	11	0.22	20.0	insectivores	18.2	20.8	22.5
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**Rhynchocyclidae**

<i>Tolmomyias poliocephalus</i>	7	5	2	0.42	11.0	omnivores	10.0	14.9	47.0
<i>Lophotriccus galeatus</i>	28	20	8	0.43	10.0	insectivores	4.8	17.3	9.0
<i>Todirostrum cinereum</i>	8	4	4	0	7.0	insectivores	17.6	16.7	41.5
<i>Tolmomyias flaviventris</i>	53	37	16	0.39	14.0	omnivores	10.2	16.2	1.0

**Tyrannidae**

<i>Attila cinnamomeus</i>	7	6	1	0.71	33.0	insectivores	6.4	9.0	47.0
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<i>Camptostoma obsoletum</i>	12	8	4	0.33	9.0	omnivores	17.9	14.2	31.5
<i>Elaenia flavogaster</i>	29	12	17	0.17	21.3	omnivores	19.4	14.9	8.0
<i>Empidonomus varius</i>	6	3	3	0	25.0	insectivores	12.9	20.8	56.0
<i>Legatus leucophaeus</i>	5	3	2	0.2	23.0	omnivores	18.6	25.4	64.5
<i>Megarynchus pitangua</i>	18	11	7	0.22	62.0	omnivores	20.5	22.7	22.5
<i>Myiarchus ferox</i>	8	4	4	0	24.0	omnivores	13.6	12.0	41.5
<i>Myiarchus swainsoni</i>	7	0	7	1	23.5	omnivores	14.0	16.6	47.0
<i>Myiarchus tyrannulus</i>	19	6	13	0.36	29.8	omnivores	26.4	14.1	19.5
<i>Myiopagis gaimardii</i>	42	24	18	0.14	12.0	insectivores	12.1	18.4	5.0
<i>Phaeomyias murina</i>	6	2	4	0.33	10.0	omnivores	15.0	15.4	56.0
<i>Pitangus sulphuratus</i>	18	11	7	0.22	63.0	omnivores	25.8	16.7	22.5
<i>Tyrannus melancholicus</i>	27	13	14	0.04	39.0	omnivores	28.5	22.4	10.5
<b>Vireonidae</b>									
<i>Hylophilus pectoralis</i>	8	3	5	0.25	11.5	omnivores	7.8	13.9	41.5
<i>Cyclarhis gujanensis</i>	47	28	19	0.19	28.0	insectivores	21.7	17.9	2.0
<i>Vireo chivi</i>	30	20	10	0.33	15.0	omnivores	17.3	24.1	7.0
<b>Troglodytidae</b>									
<i>Cantorchilus leucotis</i>	25	15	10	0.20	16.0	insectivores	11.2	12.2	15.0
<i>Troglodytes musculus</i>	6	1	5	0.66	11.0	insectivores	59.2	14.1	56.0
<b>Poliophtilidae</b>									
<i>Poliophtila plumbea</i>	41	17	24	0.17	6.4	insectivores	15.8	12.3	6.0
<b>Turdidae</b>									
<i>Turdus leucomelas</i>	46	35	11	0.52	62.0	omnivores	13.8	22.5	3.0
<b>Passerellidae</b>									
<i>Ammodramus humeralis</i>	12	0	12	1	16.0	herbivores	16.4	4.3	31.5
<b>Icteridae</b>									
<i>Cacicus cela</i>	6	3	3	0	104.0	omnivores	11.2	27.5	56.0
<i>Psarocolius viridis</i>	6	5	1	0.66	375.0	omnivores	6.2	23.4	56.0

**Thraupidae**

<i>Coereba flaveola</i>	44	22	22	0	9.0	herbivores	22.4	19.3	4.0
<i>Dacnis cayana</i>	7	3	4	0.14	12.0	omnivores	15.7	24.4	47.0
<i>Nemosia pileata</i>	5	4	1	0.60	14.0	omnivores	13.8	20.2	64.5
<i>Ramphocelus carbo</i>	21	17	4	0.62	24.0	omnivores	11.5	17.4	18.0
<i>Stilpnia cayana</i>	24	6	18	0.50	18.5	omnivores	5.5	18.6	17.0
<i>Tangara mexicana</i>	6	2	4	0.33	20.0	herbivores	7.7	22.1	56.0
<i>Thraupis episcopus</i>	26	18	8	0.38	30.0	omnivores	13.1	22.9	12.5
<i>Thraupis palmarum</i>	25	17	8	0.36	35.0	omnivores	15.6	21.1	15.0

**Cardinalidae**

<i>Piranga flava</i>	5	0	5	1	41.1	omnivores	9.5	24.5	64.5
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**Fringillidae**

<i>Euphonia chlorotica</i>	9	2	7	0.55	11.0	herbivores	15.1	23.2	38.5
<i>Euphonia violacea</i>	11	4	7	0.27	14.0	omnivores	9.4	28.1	34.5

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