

CONTRIBUTION OF DIFFERENT FOREST TYPES TO THE BIRD COMMUNITY OF A SAVANNA LANDSCAPE IN COLOMBIA

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Resumen. – **Contribución de diferentes tipos de bosque a la comunidad de aves en un paisaje de sabana en Colombia.** – La heterogeneidad del paisaje es particularmente importante en paisajes fragmentados, donde cada fragmento contribuye a la biodiversidad del paisaje. Este aspecto ha sido menos estudiado en paisajes naturalmente fragmentados, comparado con aquellos fragmentados por actividades antrópicas. Estudiamos las sabanas de la región de la Orinoquia en Colombia, un paisaje naturalmente fragmentado. El objetivo fue determinar la contribución de tres tipos de bosque de un mosaico de bosque-sabana (bosque de altillanura, bosques riparios anchos, bosques riparios angostos), a la avifauna del paisaje. Nos enfocamos en la estructura de la comunidad de aves, analizando la riqueza de especies y la composición de los gremios tróficos, las asociaciones de hábitat, y la movilidad relativa de las especies. Usando observaciones, grabaciones, y capturas con redes de niebla, registramos 109 especies. Los tres tipos del paisaje mostraron diferencias importantes, y complementariedad con respecto a la composición de las aves. Los análisis de gremios tróficos, movilidad, y asolación de hábitat reforzaron las diferencias entre los tipos de bosque. El bosque de altillanura presentó la mayor riqueza de aves, y a la vez también la mayor cantidad de especies únicas. Las especies de interior de bosque, y especies frugívoras e insectívoros del suelo predominaron en el bosque de altillanura, todos buenos indicadores de bosques en buen estado de conservación. Los dos tipos de bosques riparios son más parecidos entre sí, y sus diferencias con el bosque de altillanura parecen deberse a los recursos complementarios que ofrecen. Nuestro estudio resalta la complementariedad de los tres tipos de bosque para la persistencia, y por lo tanto para la conservación de la avifauna de esta región.

Abstract. – Landscape heterogeneity is particularly important in fragmented landscapes, where each fragment contributes to the landscape's biodiversity. This aspect has been less studied in naturally fragmented landscapes compared to human fragmented areas. The savannas of the Orinoco region of Colombia, a naturally fragmented landscape, were the subject of our study. The aim was to estimate the contribution of three different forest types present in the forest-grassland mosaic of the region (upland dry forest, wide riparian forest, and narrow riparian forests), to the local avifauna. We focus on the structure of the bird community, analyzing species richness and the composition of trophic guilds, habitat associations, and mobility. Using observations, recordings and mist netting, we recorded 109 species. The three forest types showed important differences and complementarities in their bird composition. Trophic guild, mobility, and habitat association analyses reinforced differences between the forests. The upland dry forest made the greatest contribution to the landscape's bird community, also showing the highest number of unique species. Forest interior species, frugivores and ground insectivores, all good forest quality indicators, predominated in the upland dry forest. Riparian forests are more similar, and differ from the upland forest by the complementary resources they offer. Our study highlights the complementarity of all three forest types for the persistence, and therefore for conservation of the avifauna of this region. *Accepted 13 May 2013.*

Key words: Bird community, upland dry forest, natural fragmentation, riparian forest, savanna.

INTRODUCTION

Landscapes are mosaics of spatially interacting and complementary elements, representing clusters of ecosystems structured in a similar way throughout (Forman & Godron 1986). Animal communities vary in relation to changes in the composition of the landscape, with their distribution responding to the spatial arrangement of the landscape elements (patches and corridors). The pattern of landscape heterogeneity is particularly important in fragmented landscapes, where each fragment contributes to the overall diversity of the landscape (Forman 1995). Although fragmented landscapes have mostly been thought of as a result of human intervention, there are numerous examples of naturally fragmented landscapes, such as riparian forests in various parts of the world (Meave & Kellman 1994), and in the savanna biome of northern South America (Etter 1998).

Studies of animal communities tend to cover limited geographical areas including only some elements of the landscape mosaic, therefore contributing only partially to the knowledge of the overall biota of the entire landscape, because each landscape element contains only part of the biota (Forman 1995). By targeting only one or a few of the landscape elements, such studies cannot account for the complementarity among elements that is inherent to most landscapes, an aspect which has been highlighted for studies relating bird richness and ecosystems (Mitchell *et al.* 2006).

Most studies addressing bird communities related to landscape heterogeneity have focused on human-induced fragmented landscapes (McIntyre 1995, Turner 1996, Graham & Blake 2001, Renjifo 2001b, Shirley & Smith 2005). Research on naturally fragmented landscapes has been done in Australia (Martin *et al.* 2006, Palmer & Bennett 2006, Woinarski *et al.* 2008), while for the Neotropics the infor-

mation about such landscapes could still be widely enriched.

Natural landscapes which are naturally fragmented, such as in many savanna ecosystems where mosaics of forest and grassland vegetation coexist, are highly diverse due to the variety of habitats that can be found. This is the case of large tracts of savanna landscapes of the Orinoco basin in northern South America, where forests are intermingled over a grassland matrix (Meave & Kellman 1994, Etter 1998). The size and shape of these forests is often not a result of human activities but rather the consequence of differences in soil and relief. A large part of the forests in these biomes occurs along watercourses, also known as riparian or gallery forests that form an extensive network of corridors. Riparian forests are among the most diverse ecosystems on Earth, drawing global interest for conservation due to their function as habitat, pollution filters and erosion traps (Sabo *et al.* 2005). However, these ecosystems are also vulnerable to sudden changes due to the high quantity of forest edge, resulting from their narrow shape (Martin *et al.* 2006). Bird studies in riparian forests have mostly focused on their use as corridors (Machtans *et al.* 1996), their importance to conservation (Palmer & Bennett 2006), and the assessment of the minimum width needed to support healthy animal communities (Spackman & Hughes 1995, Hagar 1999, Rodewald & Bakermans 2006). Understanding the importance of forests in these naturally fragmented landscapes could give insights on the effects of future processes of forest loss.

Latin America's savannas and their associated riparian forests, are under increasing pressure due to the role these ecosystems are playing in the world's food supply (Brannstrom *et al.* 2008). The Llanos of the Orinoco region in northeastern South America cover some 45 million ha of natural savannas that

with planted pastures form a matrix associated to riparian and dryland corridors and isolated patches (Etter 1998). In Colombia, these savannas cover over 17 million ha, more area than any other ecosystem in the Colombian Orinoco region, and have been an agricultural frontier where an ongoing expansion started some 30 years ago and continues to accelerate (Romero-Ruiz *et al.* 2010, Etter *et al.* 2011). Major drivers of land cover changes in Colombia include savanna replacement with exotic *Brachiaria* grasses, intensive annual crops of corn and soy, and oil palm plantations. The geographic conditions, geological history, humidity conditions, ecological factors, and anthropogenic activities in the region determine the presence of a great biological diversity (Romero-Ruiz 2009). The Orinoco region houses some 877 bird species (Murillo 2005), which represent almost 40% of the total of Colombia's bird species, but still is one of the least studied avifauna in the country (Umaña *et al.* 2009).

The aim of our study was to estimate the contribution of three different forest types (upland dry forest, wide riparian forest, and narrow riparian forests) of the forest-grassland mosaic to the avifauna of a naturally fragmented landscape in the savannas of the Orinoco region in Colombia. We focus on the structure of the bird community, analyzing trophic guilds, habitat association, and mobility. We propose the mobility as a new attribute that can offer further understanding of bird communities and their relationship to the landscape. We also discuss the importance of these landscape elements for the conservation of the regional biodiversity.

METHODS

Study site. The study area is located in the piedmont of the Eastern Andes (Fig. 1), originally covered by dense tropical forests intermixed with large savanna patches. Most of these

piedmont forests were cleared decades ago for agriculture. In the savannas, the natural grasslands have been partly replaced by pastures of introduced African grasses to increase cattle ranching productivity, but most of the associated gallery forests have subsisted, and are the target of our study.

This study was conducted specifically in three private nature reserves established in 1993 that cover 6887 ha ("Las Unamas," "Rey Zamuro," and "Matarredonda") and are located in the municipality of San Martín de los Llanos (Meta Department) (Fig. 1A). The study area is part of the piedmont plain of the Eastern Andean Cordillera, with average altitude of 200 m a.s.l. and less than 50 m of relief variations. The study area is part of three small watersheds: Cumaral, Chunaipo and Camoa. This landscape is dominated by a grassland matrix where riparian and upland dry forests appear as corridors and isolated patches (Fig. 1B). The climate is tropical seasonal humid with an annual average temperature of 24°C, and a mean annual rainfall of 2500 mm with two to four dry months. The area in and around these reserves is generally well conserved as indicated by the presence of large animals, such as jaguars (*Panthera onca*), tapirs (*Tapirus terrestris*), and peccaries (*Tajassu* spp.).

For the purpose of the study, we divided the forest fragments of the study area into three classes: i) upland dry forest (DF); ii) wide riparian forest (WRF), and iii) narrow riparian forest (NRF). We selected seven fragments (study sites): one for the only upland dry forest remnant (DF: 1071 ha), three for the wide riparian forests (WRF 1, WRF 2, WRF 3; average width > 250 m, and three for the narrow riparian forests (NRF 1, NRF 2, NRF 3; average width < 250 m) (Fig. 1B). Site selections were based on field surveys and aerial photographs. We chose the 250 m figure as a limit between the wide from narrow riparian forests, because it is a natural cut

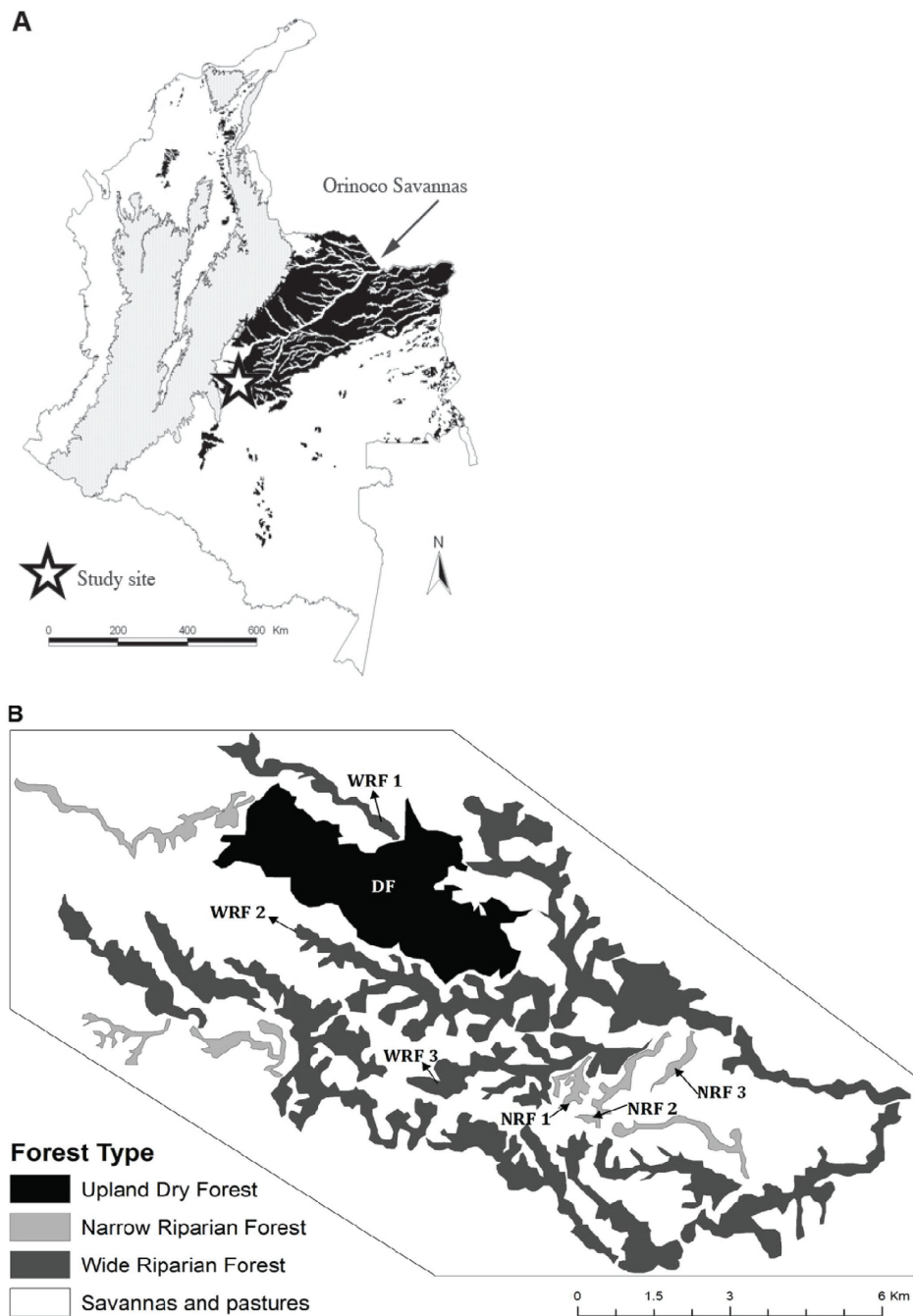


FIG. 1. Study area in San Martín de los Llanos, Meta, Colombia indicating: A. Location of study site with savannas in black (Etter 1998); B. General land cover map of the study area showing forest types.

since all narrow forests had mean widths of less than 200 m, and all wide riparian forests had widths exceeding 250 m.

The upland dry forests are non-riparian forests of the piedmont of the Eastern Andes. The vegetation resembles that of an Amazonian forest with tall canopies (25–40 m), a low vegetation density in the understory, and high plant diversity. Presence of big mammals and primates is common.

Wide riparian forests are typical riparian forests that do not flood for a period longer than several days; the courses of water they surround are approximately 4–5 m wide and maintain some of their water during the dry season. The canopy is of 15–25 m and the understory stratum has dense vegetation. All riparian forests selected for this study had widths of over 300 m. Narrow riparian forests flood seasonally and are found around courses of water that do not exceed one meter in width, these may dry out during the dry season, depending on the year. The canopy generally does not exceed 20 m, the stems of trees are thinner, and the understory less dense.

Field methods. We visited each study site nine times (six census visits and three mist-netting days) for bird sampling during the dry season between 12 January and 30 March 2009. Sampling during the dry season was appropriate to avoid the effect of precipitation on our data, to ensure continuity of the samples, and comparability among forest types. Since the aim of our study was not to record all the species present but rather determine the contribution of each forest type to the landscape's avifauna, sampling during both seasons was not imperative. We located five 100-m line transects (Bibby *et al.* 1992), each separated by 50 m, along the watersheds in the direction of running water in riparian forests, and in the least perturbed trail in the upland dry forest. For the censuses, each transect was walked by one

observer (NOP) at constant speed during ten minutes recording every bird seen or heard. We sampled between 06:00–09:00 h, visiting two sites per day, alternating the order. Because recordings provide additional information on the presence of rare, inconspicuous and patchily distributed species, as well as mixed species flocks foraging in the canopy (Parker III 1991), we recorded bird sounds for 10 min in each transect during half of the censuses for identification of additional species.

We located our mist-nets in one of the transects of each study site. During three consecutive days per site, between 06:00–11:00 h, one person (NOP) ran three 12-m and seven 6-m (all 36-mm mesh size) nets for a total effort of 97.5 h/net per site. The mist-netting protocol and data recording followed the methodology suggested by (Ralph *et al.* 1996). Bird censuses and mist-netting was not done in days of inclement weather (strong winds or rain).

Data analysis. We compared bird richness on the three forest types, and complemented the analysis by also comparing the composition of trophic guilds, mobility and habitat association. The upland dry forest data was complemented with a data set from Garzon (2009), who compared the success of observations, song recording and mist-netting in the same patch of upland dry forest (DF) during the same period of study. This data set was useful because the other two forest types had three replicas each, but this forest type had only one.

In order to measure species richness on each site, and for the three forest types, we used a null model to estimate non-parametric richness. We calculated indices Chao 2 and Jackknife 1 and 2, and also performed a bootstrap analysis to estimate species richness, and then compared it to the observed number of species.

We calculated *alpha* and *beta* richness for species and bird families for the seven sites (*alpha*), and the three forest types (*beta*). To compare bird richness between the study sites, and among forest types we used a Jaccard similarity analysis. The trophic guild composition, mobility, and habitat association complemented this analysis.

Trophic guilds. We classified each species in a trophic guild based on information from Hilty & Brown (1986), and personal observations. Each species was classified in one or more of the 14 trophic guilds as proposed by Stiles & Rosselli (1998). One species could be part of more than one guild, in which case they were added as a proportion of one. For instance, if a hummingbird species eats insects and nectar, 0.5 was added to each guild.

Mobility. We called “mobility” the movement of birds across the landscape, and classified bird species based on personal observations, in one of three categories: i) Low mobility: territorial species, restricted to a specific forest area or patch; ii) Medium mobility: species that move between forest patches and corridors, always under forest cover; iii) High mobility: species that fly across the matrix moving between forest patches and corridors. This measure refers to individual behavior and does not reflect the dispersal ability of a species.

Habitat association. We placed species on one of the four categories based on personal observations and information from Hilty & Brown (1986): i) Interior: species sensitive to edge effects, prefer forest interior; ii) Edge: species that prefer moving along the forest edge and are not common inside the forest; iii) Forest: species that are found indistinctly in forest edge and interior; iv) Non-forest: typical of areas not covered by forest.

RESULTS

During this study, we recorded 109 bird species (cf. Appendix). Of these, 27 species were unique to upland dry forest, 15 to wide riparian forests, and 15 to narrow riparian forests, while 52 species (48%) were shared between pairs of forest types (Table 1). Four species corresponded to boreal migratory species: Blackpoll Warbler (*Dendroica striata*), Blackburnian Warbler (*Dendroica fusca*), Swainson’s Thrush (*Catharus ustulatus*), and Summer Tanager (*Piranga rubra*).

Of the 1046 records we obtained during the censuses, 89% of were only by voice. We recorded 85 species from 30 families during the censuses and captured 121 individuals of 26 species (14 families) with mist-nets.

Forest types and bird composition. The recorded bird species richness of all forest types was lower than the minimum and maximum number of species estimated by the indices used for the null model (Fig. 2). The three forest types shared 33 species corresponding to one third of the birds (Table 1).

Similarity between the seven study sites was always below 0.6, and under 0.5 for forest types (Fig. 3). The three narrow riparian forests grouped together, this group also included WRF 3. Wide riparian forests did not group clearly, WRF 2 is most similar to DF, and WRF 1 is lightly similar to the narrow riparian forest group. Forest types were grouped by riparian types (wide and narrow), and the upland dry forest differed the most from these.

A total of 36 species (33%) were unique to one of the three forest types. The upland dry forest had six unique species, mostly typical of dense, almost Amazonic-like forests, such as Screaming Piha (*Lipaugus vociferans*), Spangled Cotinga (*Cotinga cayana*), Rufous-capped Antthrush (*Formicarius colma*), Black-headed Parrot (*Pionites melanocephalus*), Scaly-breasted

TABLE 1. Number of unique and shared bird species of three forest types in San Martin, Meta, Colombia (upland dry forest - DF, narrow riparian forest - NRF, and wide riparian forest - WRF); percentages shown in parenthesis are of each forest type's total.

Unique species			Shared species		
DF	NRF	WRF	DF-NRF	DF-WRF	NRF-WRF
27 (36)	11 (15)	3 (4)			
11 (17)	15 (23)	5 (8)	33 (52)	33 (59)	33 (45)
3 (5)	5 (9)	15 (27)			

Woodpecker (*Celex grammicus*), and Bicoloured Antbird (*Gymnophrys leucaspis*) (Hilty & Brown 1986, Ridgely & Greenfield 2001, Restall *et al.* 2006).

The wide riparian forests had 15 unique species, comprising mostly species that are typical of riparian vegetation, but also some forest interior ones: Cream-coloured Woodpecker (*Celex flavus*), Ringed Woodpecker (*Celex torquatus*), Short-billed Leaf-tosser (*Sclerurus rufifigularis*), Sunbittern (*Eurypyga helias*), White-browed Antbird (*Myrmoborus leucophrys*), Crested Oropendola (*Psarocolius decumanus*), and Olive Oropendola (*Psarocolius bifasciatus*) (Hilty & Brown 1986, Ridgely & Greenfield 2001, Restall *et al.* 2006).

The narrow riparian forests showed 15 unique species, conforming to a wider array of species including edge species, such as Black-billed Thrush (*Turdus ignobilis*), Pale-breasted Thrush (*T. leucomelas*), and Cocoa Thrush (*T. fumigatus*), which easily adapt to different forest types including second-growth and riparian (Hilty & Brown 1986). The Smooth-billed Ani (*Crotophaga ani*) is a bird commonly observed in open areas and occasionally on forest edge (Hilty & Brown 1986), often associated to cattle grazing and transformed landscapes, as is the Yellow-headed Caracara (*Milvago chimachima*), which rarely seen inside the forest but mostly perched amongst trees in savannas (Restall *et al.* 2006).

Trophic guild, mobility and habitat association. The species richness analysis was complemented by categorizing each species by trophic guild (Table 2), mobility, and habitat association (Fig. 4). In terms of trophic guilds, for both riparian forests the largest number of species corresponded to the flying insectivores under the canopy guild. For the upland dry forest, frugivores consuming large fruits from canopy and forest edge were the dominant guild. All forests had species representing most of the guilds, however only the wide riparian forest had a species in insectivores and aquatic invertebrate consumers guild, and aerial insectivores were found only in the upland dry forest. The guild of ground and low understory insectivores was evenly distributed in upland dry forest and wide riparian forests, with less representation in the narrow riparian forest. In general, all insectivore guilds are better represented in both riparian forests, and frugivore guilds in upland dry forest.

In terms of mobility, the three forest types showed different patterns. The upland dry forest birds presented a dominance of species of medium mobility, and of species typical for forest interior conditions. Although the wide and narrow riparian forests showed more similar patterns when mobility and habitat association were analyzed (Fig. 4), wide riparian forests had more species typical of forest edge, while narrow riparian forests had more of forest. Only one species used all forest types, always recorded as passing bird, the

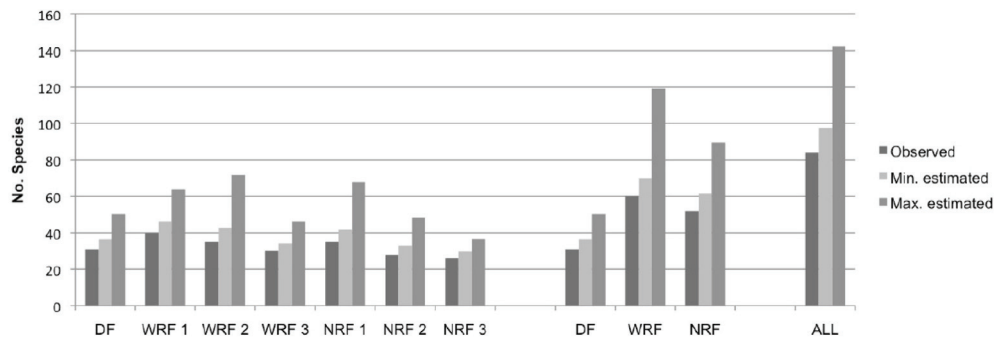


FIG. 2. Observed number of bird species in San Martin, Meta, Colombia compared to minimum and maximum richness estimations by Chao 2, Jackknife 1 and 2, and bootstrap analysis.

Red-bellied Macaw (*Orthopsittaca manilata*). We observed this species nesting in WRF 1 and feeding in all other sites.

DISCUSSION

Our study indicates that the remnant riparian forests of the Orinoco savannas harbor an important number of bird species, and that the spatial pattern of the forest type markedly influences their distribution in the landscape. Although some areas are protected by small private reserves, the increasing pressure exerted by concurrent land use changes in the region (Etter *et al.* 2011), implies that these landscape elements are under increasing threats. This is probably more so for the upland dry forests, which have a better agricultural suitability.

The studied forests contain 33.6% of the bird species reported for the Orinoco Tropical Humid Zonobiome and 41.4% of the species reported for San Martin Municipality (Umaña *et al.* 2009). This small study area also contains at least 12% of the bird species registered for the entire Orinoco region (Murillo 2005). This high bird diversity of the study site could be explained by the ecological and landscape transitions it presents, including the upland dry forests which are similar to Amazonian forests, the continuous water-land

dynamic of the riparian forests (Naiman & Décamps 1997), and the ecotones that form in the contact areas between the forests and the natural savannas.

All forest types and study sites had lower species richness than that expected by the null model (Fig. 2). Longer studies would therefore result in an increased number of species, also taking into account that many species found in these areas are inconspicuous, and that our study covered only parts of each forest patch.

When comparing the seven sites, WRF 1 had the highest species richness and NRF 2 the lowest (Table 3). WRF 1 has a complex vegetation structure and is connected to an upland dry forest patch (Fig. 1), assuring the presence of riparian forest species and interior forest birds from the upland dry forest. NRF 3 and WRF 3 are the most similar sites, and DF and WRF 2 form an out-group (Fig. 3), but no pair of sites exceeds a 60% similarity. In a similar study, Martin *et al.* (2006) found larger differences between forest patches than those found in our study. Probably species in this landscape respond to patterns at a larger scale and less to patch processes.

Forest type comparison. We compared the three forest types analyzing species richness (Table

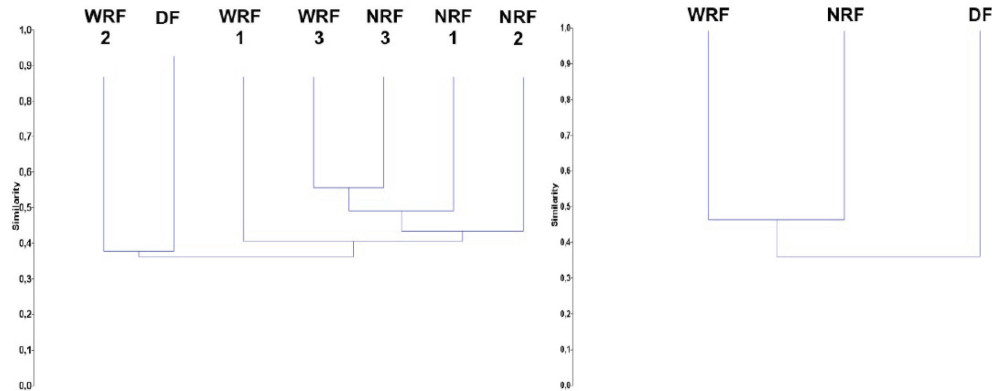


FIG. 3. Jaccard dendrograms comparing bird species richness between seven study sites (left) and three forest types (right) in San Martín, Meta, Colombia.

1). Differences between forest types are evident, aiding in determining the contribution of each forest type to the landscape's avifauna. Upland dry forest had the highest species and family richness, as well as the highest proportion of unique species (36%) of the total species in the forest type. This forest is the only non-riparian of the three types, with a significantly larger core area and a more compact and continuous forest cover, plausibly offering wider nesting and feeding resources. It also has a marked influence of Amazonian avifauna, and through its connection to WRF 1 probably receives some influx of riparian species. Eleven species are shared between this and the wide riparian forest, probably due to the greater connectivity amongst these two forest types (Fig. 1).

Wide riparian forests have the second highest number of species and families, and 23% of their species are unique. Narrow riparian forests follow with 27% unique species, but 59% shared with other forest types (Table 1). Narrow forests are flooded seasonally, have more edge, and less interior area, which may affect the presence of some species (tinamous, ground-doves). Wide and narrow riparian forests share 10 species, which most likely prefer riparian habitats.

The upland dry forest makes the largest contribution of unique species to the landscape's avifauna. McIntyre (1995) also found significant differences between bigger and more continuous forests compared to smaller and more fragmented ones. The upland dry forest offers resources for birds that can be complementary, or absent in riparian habitat (Martin *et al.* 2006). Wide riparian forests contribute mildly more than narrow ones. Rodewald & Bakermans (2006) documented that wider riparian forests support a more diverse and abundant bird community, and have less nest predation related to edge effect than their narrow counterparts.

Trophic guilds. In general, the upland dry forest had a more even distribution of species among all trophic guilds, with significantly high numbers in guilds that depict need of forest interior or large areas (Table 2). One of the two guilds with the highest number of species for this forest type were frugivores (FDPB and FGDB). Loiselle & Blake (1992) explain that species that depend on the availability of highly variable resources, such as fruits and nectar, need to move along larger areas and tend to be more susceptible to forest fragmentation. Frugivores like Screaming

TABLE 2. Trophic guilds and the number of species assigned to each guild in forest habitats of San Martín, Meta, Colombia; total percentages over forest type (upland dry forest - DF, narrow riparian forest - NRF, and wide riparian forest - WRF) shown in parenthesis.

Trophic guild definition	Abbreviation	DF	NRF	WRF
Flying insectivores under the canopy	IHSM	9.5 (12.9)	8.5 (15.3)	10 (15.3)
Flying insectivores of the canopy and the forest edge	IHDB	2 (2.7)	3 (5.4)	5 (7.6)
Ground and low understory insectivores	ISFS	9.6 (13.0)	5.1 (9.2)	9.5 (14.4)
Insectivores of understory foliage and small branches	IFSM	5 (6.8)	6.5 (11.7)	5 (7.6)
Canopy and edge foliage insectivores	IFDB	3.8 (5.2)	3 (5.4)	3 (4.6)
Insectivores and aquatic invertebrate consumers	IIPA	0	0	1 (1.5)
Insects or small vertebrates on or inside trunk or big branches consumers	ITR	8.3 (11.2)	4.3 (7.7)	5.3 (8)
Big insects and small vertebrates of the foliage and small branches consumers	IGF	4.6 (6.3)	3.3 (5.9)	4.8 (7.3)
Carnivores (big vertebrates)	CAV	3 (4.1)	4 (7.2)	2 (3)
Ground and low understory fruit and seed pickers	FSSB	5.1 (6.9)	4.5 (8.1)	4.5 (6.8)
Small fruits from the canopy and forest edge consumers	FPDB	8.6 (11.7)	6.1 (11)	7 (10.6)
Large fruits from the canopy and forest edge consumers	FGDB	11.6 (15.8)	5.8 (10.4)	7.8 (11.8)
Nectarivores	NEC	1.5 (2.0)	1.5 (2.7)	1 (1.5)
Aerial insectivores	IAE	1 (1.4)	0	0
TOTAL	14	73.6 (100%)	55.6 (100%)	65.9 (100%)

Piha, Spangled Cotinga, and others in the genus *Tangara* were unique to this forest type. Large frugivores like pihás and cotingas have been found to be extinction prone in earlier studies due to their dependence on spatially and temporally patchy resources (Willis 1979, Kattan *et al.* 1994). Renjifo (2001b) also found cotingas to be more susceptible to forest fragmentation in the Central Andes of Colombia. The guild corresponding to woodpeckers and wood creepers (ITR) was better represented in this forest type too. Drever *et al.* (2008) found a positive correlation between woodpecker diversity and general bird diversity arguing that birds of this family are good indicators of bird richness in most ecosystems; our study appears to confirm this rule since the upland dry forest had the largest number of species in this guild.

The effects of larger and more continuous forest areas are made evident by the larger

number of ground and low understory insectivores (ISFS) in the upland dry and wide riparian forests. Ground insectivores (Thamnophilidae, Formicariidae) have been described as a guild typical of forest interior (Canaday 1996), highly susceptible to forest fragmentation (Renjifo 2001a) and more prone to extinction processes (Kattan *et al.* 1994). These two forest types that house these guilds have a larger total area and a smaller edge-to-interior ratio with a consequently larger interior area than narrow riparian forests, favoring the presence of ground insectivores (Canaday 1996, Martensen *et al.* 2008).

The insectivore guilds were well-represented in both riparian forest types of our study, which corresponds to high amount of insects observed during fieldwork. The high insect density in these forests could be a result of higher humidity conditions, denser foliage and higher stem density (Chettri *et al.*

TABLE 3. *Alpha* (DF, NRF 1, NRF 2, NRF 3, WRF 1, WRF 2, WRF 3) and *beta* (upland dry forest, narrow riparian forest, wide riparian forest) avian diversity in San Martín, Meta, Colombia. *Including 35 species from Garzon (2009).

<i>Alpha</i>	DF	NRF 1	NRF 2	NRF 3	WRF 1	WRF 2	WRF 3
<i>Beta</i>	Upland dry forest	Narrow riparian forests			Wide riparian forests		
Species (<i>alpha</i>)	38	38	29	35	42	35	35
Species (<i>beta</i>)	73*	56	56	56	64	64	64
Families (<i>alpha</i>)	21	21	17	18	20	17	20
Families (<i>beta</i>)	29*	27	27	27	28	28	28

2005). The amount of insects characteristic of riparian forests makes them of high nutritive quality for insectivorous birds (Whitaker *et al.* 2000). The exclusive presence of the Sun-bittern (IIPA) in the riparian forests of this study can be explained by this insectivorous species being always associated with water areas in forests (Hilty & Brown 1986).

Carnivores (CAV) and Insectivores of understory foliage and small branches (IFSM) were more diverse in narrow riparian forests. This could be explained because carnivores may find a good amount of forest edge to perch on, from where they can observe their prey and hunt it on the pastures or savanna, or inside the forest. Indeed, most of the records for this guild were birds perched on the edge and looking away from the forest and into the open areas of the landscape matrix. Species of the understory insectivore guild find a suitable preying habitat in the complex and dense understory of small branches, and high stem density.

The trophic guild analysis confirmed differences of forest types observed in terms of species richness. The upland dry forests had again the most unique distribution of species among the trophic guilds, showing especially marked differences in frugivore guilds. Both riparian forests were more similar between them, and differed in guild composition from their non-riparian counterpart.

Mobility. Although we expected significant differences between forest types, this analysis exhibited milder trends than the other analyses. In general, species with low mobility preferred the upland dry and wide riparian forests. These forests have larger areas, and are therefore more likely to support populations of territorial birds. The upland dry forest had the largest number of species with medium mobility, which could be explained by the combination of a large forest cover and high connectivity with other patches through forest corridors. The species of high mobility were evenly distributed in all forest types. The ability to move through the landscape gives these species an advantage when critical situations arise, they are less vulnerable to local extinction because their populations can be supplemented by immigration and re-colonization (Burkey 1989).

Habitat association. The analysis of this variable showed significant results regarding forest interior species. Upland dry forest, due to its large area, had the largest amount of forest interior species and the lowest of forest edge (Fig. 4). Although a larger number of forest edge species was expected in narrow riparian forests (Shirley & Smith 2005), the other two forest types had more of these species. Species typical of non-forest habitats were not significantly represented in any of the evaluated forests, which suggests a low

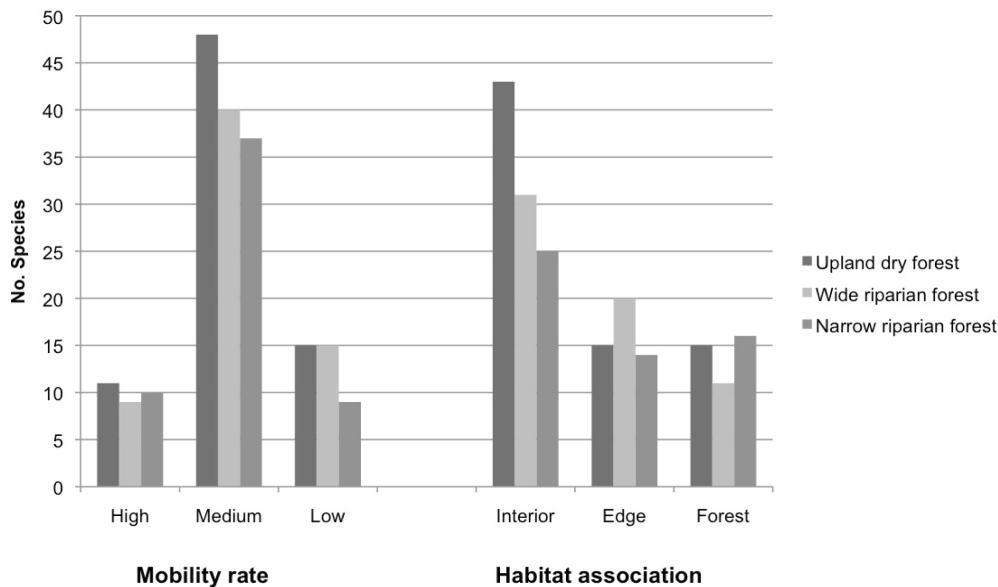


FIG. 4. Number of bird species of each category of mobility (left) and habitat association (right) in three forest types in San Martín, Meta, Colombia.

direct influence of the savanna matrix on the forest bird community. Most species typical of savannas and cattle pastures did not enter the forest, and were only observed in the forest edge.

Conclusions. This study contributes to the body of knowledge on the Orinoco's avifauna and the importance of the variety of forest elements for its conservation. Studying birds in naturally fragmented landscapes permits to learn how species distribution responds to natural spatial patterns of the landscapes. This information complements our understanding of how species adapt to man-made fragmented landscapes. Such knowledge can contribute to improve the impact of biodiversity conservation plans that guide the management of human disturbance regimes (Lindenmayer & Hunter 2010).

No single forest type can adequately represent the whole bird diversity of a landscape composed by different forest types. This is

true not only in terms of number of species, but also in terms of the guilds represented by them. Each forest type plays therefore a different role in functioning of the landscape as seen through its bird composition. The upland dry forest was the most unique forest, contributing a larger number of species than other forest types and also showing a wide variety of trophic guilds and large availability of forest interior. Because the studied remnant patch of forest is one of the last of its size in the region, with many of the species being found nowhere else, it deserves special attention. However, the riparian forests offer resources that are complementary to those of the upland dry forest. It is therefore important to implement conservation measures for all fragments in this savanna landscape.

The dynamic expansion of the agricultural frontier and the intensification of agriculture in the region (Etter *et al.* 2011) poses a latent threat to remnant ecosystems. A regional monitoring of the state of the riparian and

upland dry forest remnants needs be carried out at regular intervals to ensure that timely information is available. Conserving all three forest types should have priority, aiding to the survival of a wide array of species with different ecological niches. If decisions have to be made on prioritizing conservation actions in the region, those targeting the upland dry forests should be of high priority, but also those guaranteeing some representation of riparian forests, since these are complementary for the region's bird diversity. Although the current private reserves in the area are in support of conservation at the local level, actions towards a higher regional level of impact are urgently needed.

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APPENDIX 1. List of all the bird species recorded with their trophic guild, mobility and habitat association in San Martín, Meta, Colombia.

Family	Species	Upland dry forest			Narrow riparian forests			Wide riparian forests			Trophic guild	Mobility	Habitat association
		DF	NRF 1	NRF 2	NRF 3	WRF 1	WRF 2	WRF 3	WRF 1	WRF 2			
Accipitridae	<i>Buteo magnirostris</i>	0	1	1	1	0	0	0	0	0	CAV	High	Forest
Caprimulgidae	<i>Caprimulgus longirostris</i>	0	0	1	0	0	0	0	0	0	IHDB	Medium	Edge
Caprimulgidae	<i>Caprimulgus maculicaudus</i>	1	0	0	0	0	0	0	0	0	IHDB	Medium	Edge
Caprimulgidae	<i>Nyctinomus albicollis</i>	1	0	0	0	1	1	1	1	0	IHDB	Medium	Edge
Columbidae	<i>Patagioenas cayennensis</i>	0	1	1	1	1	1	1	1	1	FPDB	Medium	Forest
Columbidae	<i>Leptotila rufaxilla</i>	1	1	1	1	1	1	1	1	1	FPDB	Medium	Edge
Columbidae	<i>Leptotila verreauxi</i>	1	0	0	0	0	0	0	0	0	FPDB	Medium	Edge
Corvidae	<i>Cyanocorax violaceus</i>	0	1	1	1	1	1	1	1	1	FGDB, IGF, ITR	High	Forest
Cotingidae	<i>Lipaugus vociferans</i>	1	0	0	0	0	0	0	0	0	FGDB	Medium	Interior
Cracidae	<i>Ortalis motmot</i>	0	0	0	0	1	1	1	1	0	FGDB	Medium	Edge
Cracidae	<i>Penelope jacquacu</i>	1	0	0	1	1	1	1	1	0	FGDB	Medium	Edge
Cuculidae	<i>Crotophaga ani</i>	0	1	0	0	0	0	0	0	0	IFDB, IGF	High	No Forest
Cuculidae	<i>Crotophaga major</i>	1	0	0	0	1	0	0	0	0	IGF	High	No Forest
Dendrocolaptidae	<i>Dendrocincla fuliginosa</i>	1	1	1	1	1	1	1	0	1	ITR	Medium	Forest
Dendrocolaptidae	<i>Xiphobhynchus ocellatus*</i>	1	0	0	0	0	0	0	0	0	ITR	Medium	Interior
Emberizidae	<i>Arremon taeniurus</i>	1	0	0	0	0	0	0	0	0	ISFS, FSSB	Low	Interior
Eurypygidae	<i>Eurypyga helias</i>	0	0	0	0	0	0	0	0	1	IIPA	Medium	No Forest
Falconidae	<i>Herpaelithes cachinnans</i>	0	0	0	0	0	0	1	1	0	CAV	Medium	Edge
Falconidae	<i>Micrastur semitorquatus</i>	1	1	0	0	1	1	1	1	1	CAV	Medium	Interior
Falconidae	<i>Mibago chimachima</i>	0	1	0	0	0	0	0	0	0	CAV	High	Forest
Furnariidae	<i>Sclerurus rufigularis*</i>	0	0	0	0	0	0	0	0	1	ISFS, FSSB	Low	Interior
Galbulidae	<i>Galbula tombacea</i>	0	0	0	1	1	1	1	0	0	IHSM	Low	Interior
Icteridae	<i>Cactus vela</i>	1	0	0	0	1	1	0	0	0	FGDB, IFDB, IGF	High	Forest
Icteridae	<i>Psarocolius bifasciatus</i>	0	0	0	0	1	1	0	0	0	FGDB, IFDB, IGF	High	Edge
Icteridae	<i>Psarocolius decumanus</i>	0	0	0	0	1	1	1	1	1	FGDB, IFDB, IGF	High	Edge
Mimidae	<i>Mimus gilvus</i>	0	0	0	1	0	1	1	0	1	ISFS, FSSB	Medium	Edge
Momotidae	<i>Momotus momota</i>	1	1	1	1	1	1	1	1	1	IGF	Medium	Forest

APPENDIX 1. Continuation.

Family	Species	Upland dry forest	NRF1	NRF2	NRF3	Wide riparian forests	WRF1	WRF2	WRF3	Trophic guild	Mobility	Habitat association
Parulidae	<i>Dendroica fusca</i>	0	0	0	1	0	0	0	0	IFDB, IFSM	Medium	Forest
Parulidae	<i>Dendroica striata</i>	0	1	1	0	0	0	0	1	IFDB, IFSM	Medium	Forest
Picidae	<i>Ceileus elegans*</i>	0	0	0	1	0	0	0	0	ITR	Medium	Interior
Picidae	<i>Ceileus flamm</i>	0	0	0	0	1	0	0	0	ITR	Medium	Interior
Picidae	<i>Ceileus grammicus</i>	1	0	0	0	0	0	0	0	ITR	Medium	Interior
Picidae	<i>Ceileus torquatus</i>	0	0	0	0	1	0	0	0	ITR	Medium	Interior
Picidae	<i>Melanerpes orientatus</i>	0	0	0	0	1	0	0	0	ITR	Medium	Edge
Picidae	<i>Picumnus squamulatus</i>	1	1	0	0	0	0	0	0	ITR	Medium	Edge
Picidae	<i>Veniliornis passerinus</i>	0	0	0	1	0	0	0	1	ITR	Medium	Edge
Pipridae	<i>Machaeropterus regulus</i>	1	0	1	0	0	1	0	0	FPDB, IFSM	Low	Interior
Pipridae	<i>Manacus manacus</i>	1	1	1	1	1	1	1	1	FPDB, IFSM	Low	Edge
Pipridae	<i>Pipra erythrocephala</i>	1	1	1	1	1	0	1	1	FPDB, IFSM	Low	Interior
Pipridae	<i>Tyrannutes stokesmani</i>	1	1	1	1	0	0	0	1	FPDB, IFSM	Low	Interior
Psittacidae	<i>Amazona ochrocephala</i>	0	1	1	1	1	1	1	0	FGDB	High	Forest
Psittacidae	<i>Orthopsittacus manilata</i>	1	1	0	0	0	0	1	0	FGDB	High	Forest
Psittacidae	<i>Aratinga pertinax</i>	0	1	0	0	0	0	0	0	FGDB	High	Forest
Ramphastidae	<i>Pteroglossus castanotis</i>	0	0	0	0	0	1	0	0	FGDB	Medium	Edge
Ramphastidae	<i>Pteroglossus azara</i>	1	0	0	0	0	0	0	0	FGDB	Medium	Interior
Ramphastidae	<i>Ramphastos tacurus</i>	1	1	0	1	1	1	1	1	FGDB, IGF	High	Forest
Ramphastidae	<i>Ramphastos vitellinus</i>	0	0	0	1	1	1	1	1	FGDB, IGF	High	Forest
Strigidae	<i>Megascops choliba</i>	0	1	0	0	0	0	0	0	CAV	High	Forest
Tersinidae	<i>Tersina viridis</i>	0	1	0	1	1	1	0	1	IHSM, FPDB	Medium	Interior
Thamnophilidae	<i>Gymnotiplys leucaspis</i>	1	0	0	0	0	0	0	0	ISFS	Low	Interior
Thamnophilidae	<i>Hypocnemoides melanopogon</i>	0	0	0	0	1	0	0	0	ISFS	Low	Interior
Thamnophilidae	<i>Myrmeciza atrorhorax</i>	1	0	0	1	1	0	1	1	ISFS	Low	Interior
Thamnophilidae	<i>Myrmoborus leucophrys</i>	0	0	0	0	0	0	0	1	ISFS	Low	Interior
Thamnophilidae	<i>Myrmotherula axillaris</i>	1	0	0	0	1	0	0	0	ISFS	Low	Interior

APPENDIX 1. Continuation.

Family	Species	Upland dry forest			Narrow riparian forests			Wide riparian forests			Trophic guild	Mobility	Habitat association
		DF	NRF 1	NRF 2	NRF 3	WRF 1	WRF 2	WRF 3	WRF 1	WRF 2			
Thamnophilidae	<i>Thamnophilus amazonicus</i>	1	1	1	0	1	0	1	0	1	ISFS	Low	Interior
Thamnophilidae	<i>Thamnophilus palliatus</i>	0	0	0	0	0	0	0	0	1	ISFS	Low	Interior
Thamnophilidae	<i>Thamnophilus punctatus</i>	1	1	1	1	1	1	1	1	1	ISFS	Low	Interior
Thraupidae	<i>Eucometis penicillata</i>	0	0	0	0	0	1	0	0	0	IFDB, FPDB	Medium	Interior
Thraupidae	<i>Tachyphonus surinamensis</i>	1	0	0	0	0	0	0	10	0	IFDB, FPDB	Medium	Interior
Thraupidae	<i>Tangara cayana</i>	0	0	0	0	0	0	0	10	0	IFDB, FPDB	Medium	Edge
Thraupidae	<i>Tangara chilensis</i>	0	0	0	0	0	0	0	10	0	IFDB, FPDB	Medium	Interior
Tinamidae	<i>Crypturellus cinereus</i>	0	1	1	1	1	1	1	0	1	FSSB	Medium	Interior
Tinamidae	<i>Crypturellus undulatus</i>	1	1	1	1	1	1	1	1	1	FSSB	Medium	Interior
Tinamidae	<i>Tinamus major</i>	1	1	1	1	1	1	1	10	0	FSSB	Medium	Interior
Trochilidae	<i>Campylopterus largipennis</i>	0	0	1	0	0	0	0	0	0	NEC, IFDB	Medium	Edge
Trochilidae	<i>Glaucois birstutus</i>	0	1	0	1	0	1	1	0	1	NEC, IFSM	Medium	Interior
Trochilidae	<i>Phaethornis griseogularis</i>	1	1	0	1	0	1	1	1	1	NEC, IFSM	Medium	Interior
Troglodytidae	<i>Henicorbina leucosticta</i>	0	0	0	0	0	0	1	0	0	ISFS, IFSM	Low	Interior
Troglodytidae	<i>Thryothorus leucotis</i>	0	0	1	0	1	0	1	0	0	ISFS, IFSM	Low	Interior
Troglodytidae	<i>Troglodytes aedon</i>	0	1	0	0	0	0	0	0	0	ISFS, IFSM	Medium	Edge
Trogonidae	<i>Trogon viridis</i>	1	1	1	1	1	1	1	1	1	FGDB, IGF	Medium	Interior
Turdidae	<i>Calbarnus ustulatus*</i>	0	0	0	0	1	0	0	0	1	IFSM, FPDB	Medium	Forest
Turdidae	<i>Turdus albicollis</i>	1	0	0	0	0	0	0	0	0	FSSB, FPDB, ISFS	Medium	Interior
Turdidae	<i>Turdus fumigatus</i>	0	0	1	0	0	0	0	0	0	FPDB, IFSM, FSSB	Medium	Interior
Turdidae	<i>Turdus ignobilis</i>	0	1	0	0	0	0	0	0	0	FSSB, FPDB, ISFS	Medium	Edge
Turdidae	<i>Turdus leucomelas*</i>	0	1	0	0	0	0	0	0	0	FSSB, FPDB, ISFS	Medium	Edge
Tyrannidae	<i>Atalapha pilaris</i>	1	1	1	1	1	1	1	1	1	IHSM	Medium	Interior
Tyrannidae	<i>Camplostoma obsoletum</i>	0	0	0	0	0	0	0	10	0	IHSM	Medium	Edge
Tyrannidae	<i>Contopus virens</i>	0	0	0	0	0	0	0	10	0	IHSM	Medium	Edge
Tyrannidae	<i>Legatus leucophaius</i>	1	0	1	0	1	0	1	1	1	IHSM	Medium	Interior
Tyrannidae	<i>Leptopogon amaurocephalus</i>	1	1	1	1	1	1	0	1	1	IHSM	Medium	Interior

APPENDIX 1. Continuation.

Family	Species	Upland dry forest			Narrow riparian forests			Wide riparian forests			Trophic guild	Mobility	Habitat association
		DF	NRF 1	NRF 2	NRF 3	WRF 1	WRF 2	WRF 3	WRF 1	WRF 2			
Tyrannidae	<i>Mionectes olaginea</i>	1	1	1	1	1	1	1	1	1	IHSM	Medium	Interior
Tyrannidae	<i>Myiarchus tyrannulus</i>	0	1	0	0	1	0	1	0	0	IHDB	Medium	Edge
Tyrannidae	<i>Myiozetetes cayennensis</i>	0	0	0	0	0	0	1	1	0	IHDB	Medium	Edge
Tyrannidae	<i>Myiozetetes similis</i>	0	0	0	0	1	0	1	0	0	IHDB	Medium	Edge
Tyrannidae	<i>Pitangus sulphuratus</i>	0	1	0	1	1	1	1	1	0	IHDB	Medium	Edge
Tyrannidae	<i>Ramphotrigon megacephala</i>	0	0	1	0	0	0	0	0	0	IHSM	Medium	Interior
Tyrannidae	<i>Tolmomyias flaviventris</i>	1	1	1	1	0	1	1	1	1	IHSM	Medium	Interior
Tyrannidae	<i>Tolmomyias sulphureus</i>	0	1	0	1	0	1	0	0	0	IHSM	Medium	Interior
Tyrutidae	<i>Pachyrhamphus marginatus</i>	0	0	0	0	0	0	0	0	1	IHSM, FPDB	Medium	Interior
Virconidae	<i>Vireo olivaceus</i>	0	0	1	0	0	0	0	0	0	IFDB, IFSM	Medium	Forest
TOTAL	No. species	38	38	29	35	42	35	42	35	35			

