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BIOGEOGRAPHICAL AFFINITIES OF THE AVIFAUNA OF THE TIBAGI RIVER BASIN, PARANA DRAINAGE SYSTEM, SOUTHERN BRAZIL

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Resumo. As origens biogeográficas e a composição da avifauna da extensa bacia hidrográfica do rio Tibagi (TRB), parte da bacia hidrográfica do rio Paraná, sul do Brasil, foi analisada considerando os maiores centros de evolução de aves na América do Sul que são Amazônia, a região Atlântica, o sul dos Andes e Patagônia, e o cerrado. Considerando registros em 19 localidades, foram obtidos dados sobre a distribuição de 473 espécies de aves nativas na BRT. Não foi possivel indicar uma relação biogeográfica para 176 destas especies (37%). A reconstrução dos padrões de distribuição e a identificação de centros de origem, entretanto, foram possíveis para as restantes 297 espécies (63%). A avifauna do norte da TRB é diferente daquela do centro e do sul da bacia. Mais da metade (53%) das 297 espécies de aves mostra clara afinidade aos taxa da região Atlântica, seguido pelo sul dos Andes (22%), Amazônia (14%) e o cerrado (9%). A influência da região Atlântica na composição da avifauna da TRB é similar no norte (33%), no centro (36%) e no sul (37%) da TRB. As afinidades com a Amazônia decrescem de norte para sul (21%, 13% e 10%). As afinidades com as espécies do sul dos Andes decrescem de sul para norte (28%, 24% e 20%). A possível ocorrência de habitats adequados na BRT, devido à similaridades florísticas e fisionômicas entre as florestas, pode ter favorecido aos colonizadores da região Atlântica, supostamente pré-adaptados. Na TRB, as aves com origem na região amazônica tiveram mais sucesso em colonizar a floresta estacional semidecidual do norte, de clima mais quente, do que a floresta ombrófila temperada mista do sul, de clima mais frio. A mais alta concentração de espécies de aves com origem no sul dos Andes é encontrada no sudeste da BRT, de clima temperado, e que corresponde à região de maiores altitudes, onde dominam os campos secos e os campos úmidos. Os nichos ecológicos das 297 espécies de aves, aquelas que apresentam claras afinidades geográficas, foram um tanto diferentes, indicando redução ou ausência de competição.

Resumen. Se analizan los orígenes biogeográficos y la composición de la avifauna de la larga cuenca hidrográfica del Río Tibagi (TRB), que forma parte del sistema de drenaje del Río Paraná en el sur de Brazil, con respecto de los centros mayores de evolución y de diferenciación de las aves en América del Sur, especialmente los de Amazonia, de la región Atlántica, de los Andes meridionales y de la Patagonia, y del cerrado. Se recolectaron datos sobre la distribución de 473 especies nativas en 19 localidades dentro de la TRB. No fue posible precisar las afinidades biogeográficas de 176 especies (37%). Sin embargo, se pudo reconstruir patrones distribucionales y identificar los centros de otigen de 297 especies (aproximadamente 63%). La avifauna del norte de la TRB es distinta de las avifaunas del centro y del sut de la cuenca. Más de la mitad (53%) de las 297 especies en la TRB poseen afinidades evidentes con taxa de la región Atlántica, y porcentajes menores y disminuyendos con los Andes meridionales (22%), la Amazonia (14%) y el cerrado (9%). La influyencia de la región Atlántica sobre la composición de la avifauna de la TRB se encuentra similar en el norte (33%), centro (36%) y sur (37%) de la cuenca. La contribución de especies de la Amazonia es más importante en el norte de la cuenca y disminuye haste el centro y el sur (21%, 13% y 10% respectivamente). Al contratio, la contribución de especies de los Andes meridionales es más importante en el sur de la cuenca y disminuye hasta el centro y el norte (28%, 24% y 20%, respectivamente). Las similitudes florísticas y fisiognómicas entre las selvas de la TRB y las selvas de la región Atlántica podrían haber ofrecido habitats apropiados para la colonización de elementos faunísticos preadaptados desde la región Atlántica. Aves de origin Amazónico fueron majores colonizadores de las selvas estacionales, relativamente abiertas y semi-decíduas del notte de la TRB, más caliente que la parte sur de la cuenca, con sus selvas más templadas y mixtas. Las concentraciones más elevadas de especies de origen Andino se encuentran en las zonas templadas altas del sureste de la TRB, donde una mezcla vegetacional con pajonales y humedales predomina. Los nichos ecológicos de las 297 especies de la TRB que tienen obvias afinidades geográficas con centros de diferenciación y evolución de América del Sur, estan bastante diferentes los unos de los otros, lo que indicaría ausencia de competencia o competencia reducida.

Abstract. The biogeographical origins and composition of the avifauna of the large Tibagi River Basin (TRB), part of the Paraná drainage system, southern Brazil, are analyzed with regard to the major centers of avian evolution and differentiation in South America, i.e., Amazonia, the Atlantic region, the southern Andes and Patagonia, and the *cerrado*. Distributional data were collected for 473 native bird species from 19 localities within the TRB. For 176 species (37%) it was not possible to specify their biogeographical affinities. For 297 species (about 63%), however, patterns of distribution could

be reconstructed and centers of origin could be identified. The northern TRB avifauna is distinct from that of the central and southern parts of the basin. More than half (53%) of the 297 species in the TRB show clear affinities to taxa of the Atlantic region, followed by the southern Andes (22%), Amazonia (14%), and the *cerrado* (9%). The influence of the Atlantic region on the composition of the TRB avifauna is similar in the northern (33%), central (36%), and southern sectors (37%). The Amazonian contribution decreases from north to south (21%, 13%, and 10%). The contribution of southern Andean species decreases from south to north (28%, 24%, and 20%). The floristic and physiognomic similarity of the TRB forests and Atlantic forests may have provided suitable habitats for preadapted colonizers from the Atlantic region. Birds of Amazonian origin were more successful in colonizing the seasonal, relatively open, semi-deciduous forests in the warmer north than the cooler, mixed temperate rain forests in the southern part of the TRB. The highest concentrations of species of Andean origin are found in the temperate southeastern TRB highlands where a mixture of grassland and wetland vegetation is dominant. The ecological niches of the 297 TRB bird species with clear geographical affinities are rather different from each other, indicating reduced or no competition. *Accepted 27 August 1997.*

Key words: Tibagi River Basin, Paraná drainage, avifauna, southern Brazil, biogeographical affinities, Atlantic influence, Amazonian influence, Andean influence, competition.

INTRODUCTION

The high number of bird species in the Neotropics, when compared to that of other major biogeographical regions, is usually explained by scenarios involving complex interplays of geohistorical, climatological, and ecological factors. The most widely accepted general hypothesis is based on the concept of centers of evolution (refugia), resulting from the cyclical contraction and expansion of various major habitats (or biomes) during the Pleistocene (e.g., Haffer 1969, 1985, 1990; Vuilleumier 1969, 1991; Terborgh 1985; Ricklefs 1987; Vuilleumier & Simberloff 1980). The biogeographical reconstruction of their phylogenetic affinities is an important prerequisite for an understanding of the present-day distribution of most Neotropical avian taxa and their ecological role in present-day communities, (e.g., Blondel 1987, 1990; Blondel *et al.* 1984; Karr 1990).

The southern Andes and Amazonia are two major Neotropical centers of species evolution that have contributed substantially to the composition of the Atlantic eastern Brazilian avifauna (e.g., Sick 1970, 1985; Müller 1973; Willis 1992). These three regions (southern Andes, Amazonia, and Atlantic) are now ecologically isolated from each other to varying degrees by areas of open vegetation such as *caatinga*, *cerrado*, and *chaco*, in central South America. The incompleteness of the ecological isolation of the southern Brazilian avifauna at various times during the Plio-Pleistocene due to riverine forest corridors connecting the Atlantic region to the southern Andes and Amazonia has been demonstrated by Nores (1992), Willis (1992), and Cardoso da Silva (1996).

In this study we analyze the composition and biogeographical origins of the species that make up the avifauna of the large Tibagi hydrographic basin (part of the Paraná drainage system) in southern Brazil. Although part of this basin is located within Cracraft's (1985) postulated Paraná Center of endemism, many bird species found there did not originate in this center but rather in Cracraft's postulated Atlantic Center. Cracraft (1985) listed a large group of endemic species as restricted to the Paraná and the Atlantic centers, thus supposedly forming a well-defined center of endemism in southeastern Brazil, which he named Paraná/Atlantic. As the resident avifauna of the Tibagi River Basin also exhibits biogeographical affinities to the southern Andes and to Amazonia, we explore this problem in detail in this paper.

STUDY AREA

The Tibagi River Basin (TRB) in the state of Paraná, southern Brazil, which drains into the Paraná River System, comprises an area of 24 530 km^2 (Fig. 1 a, b). The Tibagi River is 550 km long. As it flows from its headwaters at Santa Rita Farm in the south of Paraná state at 25°15'S, 49°55'W to its confluence in the north with the Paranapanema River at 22°50'S, 51°00'W, the altitude of the Tibagi River decreases from 1150 m to 335 m. This 815 m altitudinal difference creates a relatively high water velocity of up to 3.2 m/s in certain parts of the river system. The water volume varies from 230 ro 330 m^3/s during the year. The Tibagi River is part of a rich hydrographic network, with 65 direct tributaries and nearly 1200 smaller streams (Maack 1981, Instituto de Terras Cartografia e Florestas 1987).

The TRB can be subdivided into three distinct zones arranged from south to north according to altitude: the upper Tibagi (UT), 1150–800 m, the middle Tibagi (MT), 800–600 m, and the lower Tibagi (LT), 600–350 m (Fig. 1c). Three basic vegetation types characterize the TRB: seasonal semideciduous forest, mixed temperate rain forest, and a

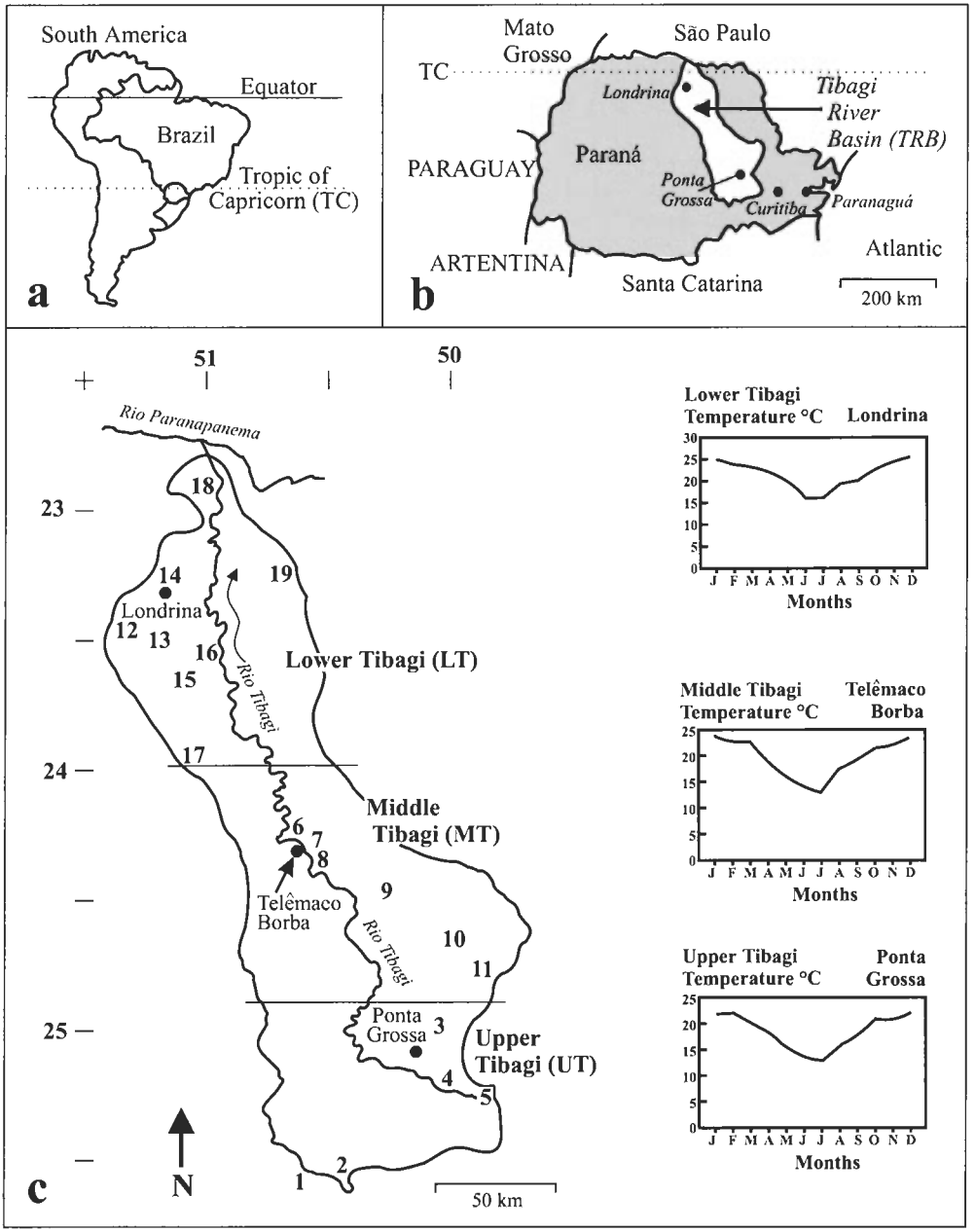

FIG. 1.a. Location of Paraná state (shaded) in Brazil. b. Location of Tibagi River Basin (TRB) with major cities in Paraná state. c. Geographical coordinates of TRB and locations of principal towns, Londrina (lower Tibagi), Telêmaco Borba (middle Tibagi), and Ponta Grossa (upper Tibagi), with their average annual temperatures. The sites studied in this survey are: 1 - Rio Azul and Mallet, 2 - Angaí, 3 - Represa de Alagados, 4 - Vila Velha State Park, 5 - Santa Rita Farm, 6 - Imbauzinho, 7 - Klabin Ecological Park, 8 - Varanal, 9 - Tibagi, 10 - Caxambú State Park, 11 - Cunhaporanga River, 12 - Rolândia, 13 - Mata dos Godoy State Park, 14 - Londrina, 15 - Guaravera, 16 - Maravillha, 17 - Serra do Cadeado, 18 - Sertaneja, 19 - Cornélio Procópio.

combination of grassland/wetland. The seasonal semi-deciduous forest (range of mean annual temperature: 20.8° C–21.6° C, range of mean annual precipitation: 1100–2000 mm) is found in the northern part of the TRB (22°50'S to 24°00'S and 50°30'W to 51°25'W) at lower altitudes (300 to 700 m) (Maack 1981). The most common tree species in the seasonal semi-deciduous forest are *Aspidosperma polyneuron* (Apocynaceae), an emergent tree reaching heights of 25–35 m, *Euterpe edulis* (Areceae) (10–20 m), *Galesia integrifolia* (Phytolaccaceae) (20–30 m), and *Ficus glabra* (Moraceae) (20–30 m) (Soares-Silva & Barroso 1992, Torezan, pers. comm.). The mixed temperate rain forest (range of mean annual temperature: 15° C–18° C, range of mean annual precipitation: 1500–2000 mm) is found at higher alritudes (600–1300 m) in the western part of the central and southern TRB (24°00'S to 25°40'S, 50°20'W to 51°00'W) (Maack 1981). The most common tree in this forest is the emergent conifer *Araucaria angustifolia* (Araucariaceae) (25–35 m). Other common trees are *Podocarpus lambertii* (Podocarpaceae) (5–15 m), *Ocotea porosa* (Lauraceae) (20–30 m), *Nectandra grandiflora* (Lauraceae) (20–30 m), and *Sebastiania commersoniana* (Euphorbiaceae) (5–15 m) (Klein 1960, Hueck 1966, Hueck & Seibert 1972, Torezan, pers. comm.).

The seasonal semi-deciduous forest has fewer tree species per ha (average 100 taxa; trees > 5 cm DBH) rhan rhe mixed temperare rain forest (average 120 taxa). The phytophysiognomy of the understory vegetation is similar in both forest types. *Aspidosperma polyneuron* and *Araucaria angustifolia* are the two tree species with highesr biomass, each contributing up to 10% of rhe total biomass in each forest type (Soares-Silva & Barroso 1992, Torezan, pers. comm.).

Grassland/werland vegetation is found ar the highest altitudes of the TRB, in the slightly undulating east-central and southern regions. Grassland and wetland are characterized by the presence of *Axonopus* spp. (Poaceae) and *Baccharis* spp. (Asteraceae). Because these open habitats occur side by side in a complex mosaic, they are considered as one ecological unit in this work. Small sparse patches of mixed temperate rain forest (usually smaller than 100 ha) also occur in the grassland/werland region. These patches of forest do not result from anthropogenic disturbance but from natural succession. Species of forest birds are present in these forest fragments within the grassland/wetland areas.

The average yearly temperature is usually higher in the LT (north) than in the UT (south) (Fig. 1c). Frosts are common in the UT during the winter (June/July) but irregular in the LT. Another latitudinal difference is precipitation: 1600 mm in the south against 1220 mm in the north. The greatest altitude of about 1300 m is in the MT whereas the lowest areas, about 300 m, are close to the junction of the Tibagi River with the Paranapanema River. The majority of the soils of the TRB are of Permian origin. However, those in the northern area are younger (Jurassic and Cretaceous) and richer in nutrients than in the east-central and south-east regions (Ordovician, Cambrian and Devonian) (Maack 1981).

METHODS

We recorded birds species (visually, aurally, mist netting) at 19 localities (see Fig. 1c; Table 1). Published data from locality no. 14, Londrina (Westcott 1980), no. 5, Santa Rita Farm (Anjos & Graf 1993), and no. 4, Vila Velha State Park (Scherer-Neto *et al.* 1992) have been included, as well as unpublished data from no. 10, Caxambú State Park (Scherer-Neto, Straube & Anjos, pers. comm.), and no. 7, Klabin Ecological Park (Berndt, pers. comms.). Data from no. 1, Rio Azul and Mallet counties (considered as a unit), have been incorporated. Alrhough these localities are actually 30–50 km outside the TRB (Pichorin & Boçon 1996), they have a similar phytogeography and thus have been included.

Periods of field study in each of these localities varied; they ranged from one visir (lasting 3 or 4 days) to several years (with monthly samples). The period of field observation, the area, and coordinates of each site are shown in Table 1. In Table 2, the species identified in the TRB are listed, largely following Meyer de Schauensee (1982) and updated for some species according to Sick (1993).

Using the axes north-south and east-west, and taking into account the phytogeography and altitude of the Tibagi River, we identified 6 distinct subregions in the TRB. These subregions with their major localities are: upper Tibagi west (1, 2), upper Tibagi east (3, 4, 5), middle Tibagi west (6, 7, 8), middle Tibagi east (9, 10, 11), lower Tibagi west (12, 13, 14, 15, 16, 17), and lower Tibagi east (18, 19) (Fig. 1c). The occurrence of each species in each subregion was recorded to ascertain their patterns of distribution within the TRB (Fig. 2).

TABLE 1. Details of the locations surveyed in the Tibagi River Basin, mapped in Fig. 1. A - area in hectares. B - dates of observation.

Locality	A	B
Upper Tibagi		
(1) Rio Azul 25°45'S, 50°47'W (1)*	unknown	monthly, February 1992–January 1993
(1) Mallet 25°55'S, 50°50'W (1)*	unknown	monthly, February 1992–January 1993
(2) Angaí 25°35'S, 50°25'W	50 ha	March 1993
(3) Represa de Alagados 25°0'S, 50°05'W	1000 ha	April 1991
(4) Vila Velha State Park 25°15'S, 50°0'W (2)*	1300 ha	every 2 months, 1984
(5) Santa Rita Farm 25°15'S, 50°0'W (3)*	2000 ha	sporadically 1984–1989, monthly 1990
Middle Tibagi		
(6) Imbauzinho 24°15'S, 50°40'W	150 ha	every two months, 1993
(7) Klabin Ecological Park 24°20'S, 50°35'W (4)*	450 ha	every two months, 1993 and 1994
(8) Varanal 24°25'S, 50°35'W	1000 ha	every two months, 1993 and 1994
(9) Tibagi 24°30'S, 50°20'W	1500 ha	March/April 1996
(10) Caxambú State Park 24°40'S, 50°0'W (5)*	1050 ha	every two months, 1984, October/November 1995
(11) Cunhaporanga river 24°50'S, 49°50'W	450 ha	October/November 1989
Lower Tibagi		
(12) Rolândia 23°50'S, 51°50'W	25 ha	September–November, 1993
(13) Mata dos Godoy State Park 23°27'S, 51°15'W	656 ha	every two months, 1993–1996
(14) Londrina 23°15'S, 51°10'W (6)*	550 ha	monthly, 1992–1996
(15) Guaravera 23°40'S, 51°05'W	50 ha	October 1994
(16) Maravilha 23°30'S, 50°57'W	15 ha	July–October 1991
(17) Serra do Cadeado 23°55'S, 51°10'W	20 ha	May 1994
(18) Sertaneja 22°58'S, 50°58'W	250 ha	March/October 1995
(19) Cornélio Procópio 23°15'S, 50°40'W	150 ha	September 1995

* *Data source*: (1) Pichorim & Boçon 1996, (2) Scherer-Neto *et al.* 1994, (3) Anjos & Graf 1993, (4) Berndt 1992, (5) Scherer-Neto *et al.* 1984, (6) Westcott 1980.

The biogeographical affinities of each bird species were determined with respect to the six major centers of evolution identified by Cracraft (1985) for South America: Andes, Amazonia, *cerrado* (open areas associated with the central plateau of the continent), Paraná, Atlantic, and Paraná/Atlantic combined. Using data on food habits published by Belton (1984, 1985), Fitzpatrick (1980), and Sick (1993), each species was assigned to one of the following feeding categories or guilds: bud-eaters, nectarivores, frugivores, frugivores/insectivores, insectivores/frugivores, insectivores, omnivores, insectivores/carnivores, carnivores/insectivores and carnivores (for a similar classification see Blondel *et al.* 1984). Simpson's (1960) index

$$D = 1 - \sum_{i=1}^{i} (P_i)^2$$

(where P_i is the proportion of individuals of species i in a community of s species) was used to measure the degree of resemblance among the TRB regions.

RESULTS AND DISCUSSION

Patterns of distribution. A total of 473 native bird species occur in the TRB (see Appendix). For 225 species (47%), that are widespread in the area, distribution patterns within the TRB cannot be identified. However, for 251 species (53%) it was possible to identify distinct patterns of distribution in the TRB (Fig. 2, Table 2).

The avifauna of the lower Tibagi River (LT) is clearly distinct from those of the middle (MT) and upper (UT) Tibagi drainages. A total of 60 species occurred only in the LT (patterns 1 to 3 in Fig. 2). The MT and the UT are represented by a lower number of exclusive species, 39 species and 32 species respectively (patterns 4 to 6 and 7 to 9 in Fig. 2). Simpson's index is higher between UT and MT (D = 86) than between either of them and LT (D = 68 and 77, respectively). Thus, MT and UT are more similar to each other, as would be expected because both regions share the same vegetation composition: mixed temperate rain forest and grassland/wetland, whereas seasonal semi-deciduous forest dominates in LT.

Some patterns of distribution shown in Fig. 2 were detected by comparing the eastern with the western parts of the TRB. For MT and UT, differences can be explained by the occurrence of grassland/wetland in the eastern part (patterns 5, 8, 10), while the western part is composed of mixed temperate rain forest (patterns 4, 7). Otherwise in LT the differences between east (pattern 2) and west

TABLE 2. Numbers of species and their origin: 0 - unknown, 1 - Paraná, 2 - Atlantic, 3 - Paraná/Atlantic, 4 - Amazonia, 5 - Andes, 6 - *cerrado*, 7 - widespread, and their pattern of distribution shown in Fig. 2.

Pattern	Biogeographical Origin								
	0	1	2	3	4	5	6	7	Σ
1	12	0	8	5	7	3	1	4	40
2	1	0	1	0	2	0	0	2	6
3	2	0	1	0	4	1	2	4	14
4	3	0	6	4	1	3	1	4	22
5	2	0	2	0	2	2	2	2	12
6	0	0	2	0	2	0	1	0	5
7	0	0	1	0	0	0	0	2	3
8	1	0	9	2	1	8	2	3	26
9	0	0	0	2	0	0	0	1	3
10	1	1	2	0	0	4	6	1	15
11	8	4	13	9	0	12	2	8	56
12	1	0	2	3	2	2	0	6	16
13	2	0	3	4	3	1	0	5	18
14	4	0	2	0	2	4	1	2	15
15	24	3	41	34	16	24	9	71	222
Σ	61	8	93	63	42	64	27	115	473

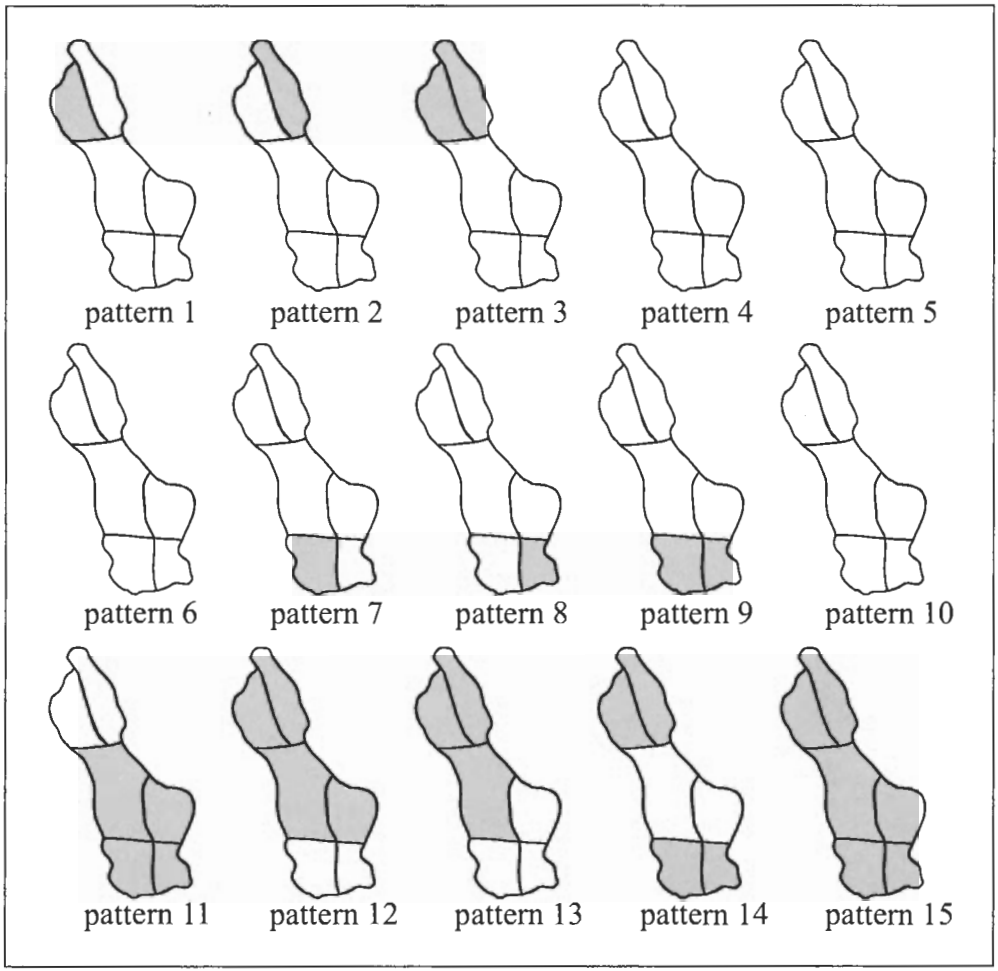

FIG. 2. Distribution patterns of birds (shaded areas) in the Tibagi River Basin. The six subregions were determined according to vegetation similarities and geographical coordinates (for further details see results and discussion).

(pattern 1) are most likely a result of habitat disturbance by man. An increase in disturbed areas can be observed from east to west in the LT.

Biogeographical affinities. We were able to assign 297 species (out of 473, 63%) to one or the other of Cracraft's (1985) biogeographical centers of evolution (Paraná, Atlantic, Paraná/Atlantic, Amazonia, Andes, *cerrado*). However, for 176 (37%) species it was not possible to make such geographical assignments because they are too widely distributed in South America (Table 2).

A total of 93 species out of 297 (31%) are associated with the Atlantic center of endemism. Taking the Atlantic center together with Cracraft's Paraná/Atlantic, an additional 63 species (21%) can then be assigned, adding up to 156 species. Thus, a total of 53% of the assignable species in the avifauna of the TRB have either closely related allies, or occur themselves, in the Atlantic center. Interestingly, only 8 species out of 297 (3%) are shared with the Paraná center: *Penelope obscura*, *Picumnus nebulosus*, *P. temminckii*, *Clibanornis dendrocolaptoides*, *Leptasthenura striolata*, *L. setaria*, *Cyanocorax caeruleus*, and

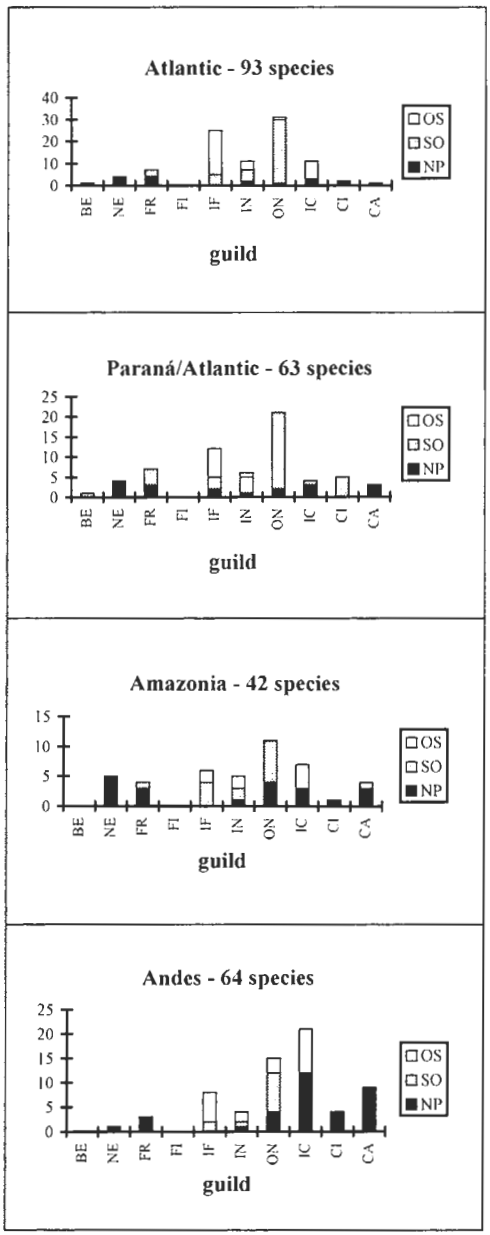

FIG. 3. Number of bird species (OS=oscines, SO=suboscines, NP=non-passerines) from the Tibagi River Basin according to guild affinities with the Atlantic, Paraná/Atlantic, Amazonian, and Andean centers of endemism. Guilds: bud eaters (BE), nectarivores (NE), frugivores (FR), frugivores/insectivotes (FI), insectivores/frugivores (IF), insectivotes (IN), omnivores (ON), insectivores/carnivores (IC), carnivores/insectivores (CI), and carnivores (CA).

Anthus nattereri. By contrast, representatives of the Andean center in the TRB avifauna are more numerous (64 species, 22%), than those from Amazonia (42 species, 14%), and from the *cerrado* (27 species, 9%).

Omnivorous suboscines (29 species), followed by insectivorous-frugivorous oscines (21 species), are the two foraging guilds best represented in species from the Atlantic center; the other avian trophic groups are represented by a smaller number of species (Fig. 3). Omnivorous suboscines also dominate the guild structure of the Paraná/Atlantic birds. The number of insectivorous-frugivorous oscines is low (7 species) (Fig. 3). Trophic organization is slightly different in the birds of Amazonian origin: omnivorous suboscines (7 species) are still the dominant group but their proportion in relation to the other groups, especially insecrivorous-frugivorous suboscines (4 species), is lower than in the Atlantic and Paraná/Atlantic centers (Fig. 3).

The three proposed centers of endemism (Atlantic, Paraná/Atlantic, and Amazonia) are associated with forest vegetation, thus certain similarities in the trophic composition of rhe avian forest guilds in the TRB can be expected. Differences in the trophic composition of guilds may be explained by the geographical distance between the Amazon and the TRB, and by the different vegetation structure of the Amazon and Atlantic forests. Neotropical non-passerines may be better adapted than passerines to disperse over long distances due to their relatively high body mass and species-specific energy regulation patterns. Neotropical passerines, usually much smaller birds, lack these prerequisites for long distance dispersal.

These general features of passerines and non-passerines may account for the higher proportion of the latter originating from the more distant Amazonia. As expected, the proximity of the Atlantic region contributes to the higher number of passerine species in the TRB. In addition, the similarity of the TRB forests with those of the Atlantic and Atlantic/Paraná regions may have provided appropriate habitats for suitable, i.e., preadapted, colonizers.

Andean birds, occuring more in open areas, utilize a different trophic structure in the TRB. Insectivorous non-passerines of Andean origin are the group with the highest number of species (12) followed by omnivorous suboscines (8). Because they problably evolved in semi-open to open areas, the niche overlap with forest species from the Atlantic and from Amazonia is reduced (Fjeldså 1985, Vuilleumier 1991).

Patterns of distribution versus *biogeographical affinities.* Because of its geographical proximity to the TRB, the Atlantic center contributed almost equally to the avian community structure throughout the entire TRB (LT 59%, MT 63%, UT 62%) (see Fig. 4).

Amazonian species reached the TRB from the north, probably via river valleys, for example along the Paranapanema river. The proportion of species from the Amazonian center decreases from LT (21%) through MT (13%) to UT (10%) (Fig. 4). The progressive north to south decline in the proportion of species from the Amazonian center of endemism is probably correlated with the seasonality of climate (frosts are common in the south of the TRB, but irregular in the north). This climatic gradient is also correlated with the gradual latitudinal change of vegetation from the warmer seasonal semi-deciduous forests near the mouth of the Tibagi river to the cooler mixed temperate rain forest of the MT and UT. These important abiotic and biotic features are obvious barriers to a dispersal of Amazonian birds in a southerly direction within the TRB. Excluding widespread species, only 3 Amazonian species (*Harpagus diodon*, *Laterallus melanophaius*, and *Lipaugus lanioides*) occur in the MT and UT (patterns 7 to 11, 14; Fig. 2, Table 2).

Species assigned to the Andean center probably reached the TRB via the open habitats of Argentina and southern Brazil (see Sick 1970, 1985). Their proportion decreases from south to north (UT 28%, MT 24%, LT 20%; Fig. 4). The highest concentration of birds of Andean origin is found in the temperate south-eastern highlands of the TRB where grassland/wetland vegetation dominates (Table 2). These environmental conditions are similar to the foothill regions of the southern Andes (Fjeldså 1985). The majority of Andean birds are not widespread in the TRB. Their pattern of distribution relates to schemes 8 and 11 (Fig. 2, Table 2).

The areas of grassland/wetland above 1000 m in the middle and upper eastern part of the TRB include some remnants of *cerrado* vegetation. Although *cerrado*-favoring birds are most abundant here (Fig. 2, Table 2), they also colonized the forest edge of seasonal semi-deciduous and mixed temperate rain forests (Cavalcanti 1992), which contributes to their wide distribution within the TRB.

Synopsis. The bird species composition of the TRB with strong Andean, Amazonian and Atlantic (in the broadest sense) origins can be attributed to distinct habitat differences (vegetational and climatic) providing suitable niches for preadapted colonizers. We postulate that niche overlaps are reduced or nonexistent between guild members of species with different biogeographical traits. Other widespread species of the TRB avifauna which could not be traced back to a center of origin are basically habitat and food generalists, benefiting from the severe man-made habitat changes in the TRB.

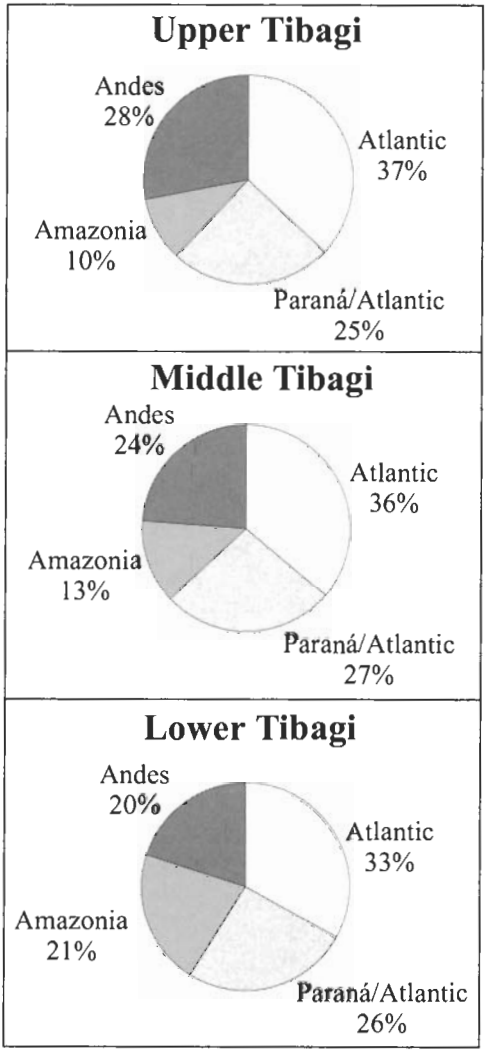

FIG. 4. Contribution of faunal elements from the Atlantic, Paraná/Atlantic, Amazonian, and Andean centers of endemism to the avifauna of the Upper, Middle, and Lower Tibagi.

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APPENDIX. Species occurring in the Tibagi River Basin, Paraná State, southern Brazil. Localities according to Fig. 1c. Upper Tibagi: 1 - Rio Azul and Mallet, 2 - Angaí, 3 - Represa de Alagados, 4 - Vila Velha State Park, 5 - Santa Rita Farm. Middle Tibagi: 6 - Imbauzinho, 7 - Klabin Ecological Park, 8 - Varanal, 9 - Tibagi, 10 - Caxambú State Park, 11 - Cunhaporanga river. Lower Tibagi: 12 - Rolândia, 13 - Mata dos Godoy State Park, 14 - Londrina, 15 - Guaravera, 16- Maravilha, 17- Serra do Cadeado, 18- Sertaneja, 19- Cornélio Procópio. Pattern of distribution (according Fig. 2). Biogeographical affinities: 0 - unknown, 1 - Paraná, 2 - Atlantic, 3 - Paraná/ Atlantic, 4 - Amazonia, 5 - Andes, 6 - *cerrado*, 7 - widespread. Guilds: BE - budeaters, NE - nectarivores, FR - frugivores, FI - frugivores/insectivores, IF - insectivores/frugivores, IN - insectivores, ON - omnivores, IC - insectivores/carnivores, CI - carnivores/insectivores, CA - carnivores. Three exotic species *Bubulbus ibis*, *Estrilda astrild*, and *Passer domesticus* are not listed. Taxonomy follows Meyer de Schauensee (1982), species marked with an (*) follow the taxonomy of Sick (1993).

Species	Upper Tibagi	Middle Tibagi	Lower Tibagi	Pattern of distribution	Biogeographical affinity	Guild
Tinamidae						
Tinamus solitarius	5	8	13	15	3	ON
Crypturellus obsoletus	1,2,3,4,5	6,8,9,10,11	13	15	0	ON
Crypturellus undulatus	–	–	13	1	0	ON
Crypturellus parvirostris	1	8	12,13,19	15	6	ON
Crypturellus tataupa	1	8,9	13,15,16	15	6	ON
Rhynchotus rufescens	2,3,5	8,9	–	11	5	ON
Nothura maculosa	2,3,5	8,9	13,14	15	5	ON
Podicipedidae						
Podiceps dominicus	4,5	9	14	15	7	CA
Podilymbus podiceps	–	8,9	14	12	7	CA
Phalacrocoracidae						
Phalacrocorax olivaceus	3,4,5	8,9	14,16,18,19	15	7	CA
Ardeidae						
Ardea cocoi	5	8	18	15	7	CA
Casmerodius albus	3,5	8,9	14,16,18,19	15	7	CA
Egretta thula	5	8,9	14,18,19	15	7	CA
Butorides striatus	–	8,9	14,15,16,18,19	12	7	CI
Syrigma sibilatrix	1,2,3,5	8,9,10,11	–	11	5	IC
Nycticorax nycticorax	–	8,9	14,18,19	12	7	CI
Tigrisoma lineatum	–	8	–	4	7	CA
Ixobrychus involucris	–	–	18	2	7	CA
Ciconiidae						
Mycteria americana	5	–	–	8	7	ON
Threskiornithidae						
Theristicus caudatus	1,3,4,5	8,9,10,11		11	5	CI
Mesembrinibis cayennensis	–	8,9,10	–	6	4	ON
Plegadis chihi	5	–	–	8	5	ON
Anatidae						
Dendrocygna viduata	–	–	13,14,16,18	3	7	BE
Amazonetta brasiliensis	1,3,4,5	8,9,10,11	14,16,18,19	15	7	BE

Species	Upper Tibagi	Middle Tibagi	Lower Tibagi	Pattern of distribution	Biogeographical affinity	Guild
Sarkidiornis melanotos	5	–	–	8	7	BE
Cairina moschata	5	8,10	18	15	7	BE
Mergus octosetaceus	–	–	18	2	2	BE
Oxyura dominica	–	10	–	5	7	BE
Cathartidae						
Sarcoramphus papa	3,5	8	13	15	0	CA
Coragyps atratus	1,3,4,5	8,9,10,11	12,13,14,16,17	15	7	CA
Cathartes aura	3,5	8,9,10,11	13,14	15	0	CA
Accipitridae						
Elanus leucurus	3,5	8,9,10,11	13,14	15	0	CI
Elanoides forficatus	1,5	6,8	13	15	0	IF
Leptodon cayanensis	1,5	6,8	–	11	0	IC
Harpagus diodon	1,5	–	13,14	14	4	IN
Ictinia plumbea	1,5	6,7,8	13	15	0	IN
Accipiter striatus	1	6	13	15	2	CA
Geranoaetus melanoleucus	5	8		11	5	CA
Buteo albicaudatus	5	–	14	14	5	CA
Buteo swainsoni	–	6	–	4	5	IN
Buteo magnirostris	1,3,4,5	6,7,8,9,10,11	12,13,14,15,16,17	15	7	CI
Buteo leucorrhous	5	9	–	11	0	CA
Buteo brachyurus	1	–	–	7	7	CA
Buteo nitidus	–	–	13	1	0	CA
Heterospizias meridionalis	5	8,9	–	11	5	CI
Buteogallus urubitinga	2	10	–	11	7	ON
Spizastur melanoleucus	–	8	–	4	7	CA
Geranospiza caerulescens	–	9,10,11	–	5	7	CA
Pandionidae						
Pandion haliaetus	–	–	18	2	7	CA
Falconidae						
Herpetotheres cachinnans	5	6,8,10	13	15	4	CA
Micrastur semitorquatus	1	8	13	15	4	CA
Micrastur ruficollis	5	6,7,8,11	13	15	4	CI
Milvago chimachima	1,2,3,4,5	6,7,8,9,10,11	13,14,18	15	5	ON
Polyborus plancus	1,2,3,4,5	8,9,10,11	13,14,16	15	5	ON
Falco peregrinus	5	–	18	14	7	CA
Falco femoralis	3,4,5	9	13,15	15	5	IC
Falco sparverius	1,2,3,4,5	8,9,10	13,14,15	15	0	IC
Cracidae						
Penelope obscura	1,2,3,4,5	6,7,8,9,10,11	–	11	1	ON
Penelope superciliaris	–	–	13	1	3	ON
Pipile jacutinga	–	–	13	1	3	FI
Crax fasciolata	–	–	13	1	4	ON
Phasianidae						
Odontophorus capueira	2,4,5	6,8,10	13	15	3	FI
Aramidae						
Aramus guarauna	–	–	14,18	3	7	CA

Species	Upper Tibagi	Middle Tibagi	Lower Tibagi	Pattern of distribution	Biogeographical affinity	Guild
Rallidae						
Rallus sanguinolentus	–	11	–	5	5	ON
Rallus nigricans	1	8,9,10,11	14,18	15	2	ON
Rallus maculatus	–	10	14	12	5	ON
Aramides cajanea	3,5	8,9,10,	14	15	7	ON
Aramides saracura	1,3,5	6,8,9,10,11	13,19	15	2	ON
Porzana albicollis	3	8	–	11	7	CI
Laterallus melanophaius	–	10	13	12	4	ON
Gallinula chloropus	1,4,	9	14,18	15	5	ON
Porphyrula martinica	1	8	14,18	15	0	ON
Porphyrula flavirostris	–	–	18,19	2	4	ON
Fulica leucoptera	–	–	14,18,19	3	5	ON
Cariamidae						
Cariama cristata	5	8,9,10		11	6	ON
Jacanidae						
Jacana jacana	3,5	8,9	14,16,18,19	15	7	CI
Charadriidae						
Vanellus chilensis	2,3,5	8,9,10,11	13,14,16,17,18,19	15	5	ON
Scolopacidae						
Tringa solitaria	4	8	14	15	0	CA
Tringa flavipes	5	10	14	15	0	CA
Tringa melanoleuca	–	–	14	1	0	CA
Actitis macularia	–	–	14	1	0	CI
Calidris fuscicollis	5	–	14	14		CA
Calidris melanotos	–	8	–	4	5	CA
Bartramia longicauda	5	–	–	8	5	IC
Gallinago gallinago	2,3,5	9,11	18	15	7	ON
Gallinago undulata	5	–	–	8	5	ON
Recurvirostridae						
Himantopus himantopus	–	–	14	1	5	CA
Columbidae						
Columba speciosa	5	6	–	11	7	FR
Columba picazuro	1,3,5	6,8,9,10,11	12,13,14,16,17,18,19	15	5	FR
Columba maculosa	5	–	18	14	5	FR
Columba cayennensis	1,3,4,5	6,7,8,9,10	13,15	15	7	FR
Columba plumbea	1,5	6,7,8	13	15	0	FR
Zenaida auriculata	1,2,3,4,5	8,9,10,11	13,14,16,17,18,19	15	0	FR
Columbina minuta	–	–	18,19	3	4	FR
Columbina talpacoti	1,2,3,4,5	8,9,10,11	12,13,14,15,17,18,19	15	7	FR
Columbina picui	2	8	12,13,14,18,19	15	5	FR
Claravis pretiosa	–	8	13	13	7	FR
Scardafella squammata	1,2	8,9	12,13,16,18	15	0	FR
Leptotila verreauxi	1,2,3,4,5	6,7,8,9,10,11	13,19	15	7	FR
Leptotila rufaxilla	3,5	6,7,8,9,10	12,13,19	15	7	FR
Geotrygon montana	5	6,7,8,11	13	15	7	FR

Species	Upper Tibagi	Middle Tibagi	Lower Tibagi	Pattern of distribution	Biogeographical affinity	Guild
Psittacidae						
Ara maracana	–	–	13	1	2	FR
Aratinga leucophthalmus	–	6,7,8	13,16	13	7	FR
Aratinga solstitialis	–	–	13	1	4	FR
Aratinga aurea	–	–	13	1	4	FR
Pyrrhura frontalis	1,3,4,5	6,7,8,9,10	13,14,16,17	15	2	FR
Forpus xanthopterygius	5	8,10	13,15,16,19	15	7	FR
Brotogeris tirica	5	7,8	13,16	15	2	FR
Pionopsitta pileata	1,2,5	6,7,8,9,10,11	13	15	3	FR
Pionus maximiliani	1,2,3,4,5	6,7,8,9	13,14,16,18	15	2	FR
Amazona aestiva	5	9	12,13,14	15	6	FR
Amazona vinacea	1,4,5	6,8	–	11	3	FR
Triclaria malachitacea	–	–	13	1	3	FR
Cuculidae						
Coccyzus americanus	5	8	13	15	4	IC
Coccyzus euleri	–	–	13	1	0	IC
Coccyzus melacoryphus	1	8,11	13,14	15		IC
Piaya cayana	1,2,3,4,5	6,7,8,9,10,11	12,13,14,17,19	15	7	IC
Crotophaga major	–	6	18	13	7	ON
Crotophaga ani	1,2,4,5	8,9,10	12,13,14,15,18,19	15	7	ON
Guira guira	1,2,3,4,5	6,8,9,10,11	12,13,14,15,16,18,19	15	5	ON
Tapera naevia	1,2,3,5	6,8,9,10	13,14,16,18	15	7	IC
Dromococcyx pavoninus	3	8	13	15	7	IC
Tytonidae						
Tyto alba	5	8,9	13	15	7	CA
Strigidae						
Otus choliba	1,3,5	8	12,13,14,16	15	7	CA
Otus atricapillus	–	8	–	4	3	CA
Bubo virginianus	–	–	13	1	5	CA
Pulsatrix perspicillata	–	–	13	1	7	CA
Pulsatrix koeniswaldiana	5	8	13	15	3	CA
Glaucidium brasilianum	5	7,8	13,14	15	7	CA
Speotyto cunicularia	1,2,3,4,5	8,9,10,11	13,14,16	15	5	CA
Ciccaba virgata	5	–	–	8	7	CA
Strix hylophila	1,2,5	8,10	13	15	3	CA
Rhinoptynx clamator	1,5	8	–	11	7	CA
Asio stygius	1,3	8	–	11	0	CA
Asio flammeus	5	–	–	8	5	CA
Nyctibiidae						
Nyctibius aethereus	–	–	13	1	5	IN
Nyctibius griseus	2,5	6,8,10	12,13	15	7	IN
Caprimulgidae						
Lurocalis semitorquatus	1,2,3,4,5	6,8,9,10	13,18	15	0	IN
Chordeiles acutipennis	–	9	13	12	0	IN
Chordeiles minor	–	–	13,14	1	0	IN

Species	Upper Tibagi	Middle Tibagi	Lower Tibagi	Pattern of distribution	Biogeographical affinity	Guild
Podager nacunda	4,5	–	13,14	14	5	IN
Nyctidromus albicollis	1,3,5	8,9	13,14,17	15	7	IN
Caprimulgus rufus	–	–	13,14,19	3	0	IN
Caprimulgus parvulus	1,3,5	–	–	9	7	IN
Hydropsalis brasiliana	–	9	–	5	4	IN
Macropsalis creagra	1,5	8,10	–	11	3	IN
Apodidae						
Streptoprocne zonaris	3,4,5	8,9,10,11	13,14	15	0	IN
Cypseloides senex	–	8,9	–	6	6	IN
Cypseloides fumigatus	5	9	–	10	0	IN
Chaetura cinereiventris	1,5	8,9	13,14	15	0	IN
Chaetura andrei	5	8	13,14	15	0	IN
Trochilidae						
Phaethornis eurynome	–	6,7,8	12,13,14	13	3	NE
Phaethornis squalidus	5	–	–	8	2	NE
Phaethornis pretrei	5	6,8	13,14	15	6	NE
Eupetomena macroura	–	8	13,14	13	4	NE
Melanotrochilus fuscus	–	8,9	13,14,17,18	12	3	NE
Colibri serrirostris	3,5	9	13,14,17	15	5	NE
Anthracothorax nigricollis	5	9	13,14,17,18	15	7	NE
Chrysolampis mosquitus	–	–	14,18	3	4	NE
Stephanoxis lalandi	3,5	8,9,10,11	13	15	3	NE
Chlorostilbon aureoventris	1,3,5	8,9,10,11	12,13,14,18	15	7	NE
Thalurania glaucopis	3,5	6,7,8	13,14	15	2	NE
Hylocharis sapphirina	–	8	13,14,18	13	4	NE
Hylocharis cyanus	–	–	18	3	2	NE
Hylocharis chrysura	–	11	12,13,14	12	4	NE
Leucochloris albicollis	1,3,4,5	6,7,8,9,10,11	12,13,14,17,18	15	3	NE
Amazilia versicolor	5	–	14	14	7	NE
Amazilia fimbriata	–	–	13	1	7	NE
Amazilia lactea	–	–	14	1	2	NE
Heliomaster squamosus	–	–	14	1	4	NE
Calliphlox amethystina	5	8	14	15	7	NE
Trogonidae						
Trogon viridis	–	–	13	1	0	IF
Trogon rufus	5	8	13	15	0	IF
Trogon surrucura	1,3,4,5	6,7,8,9,10	13,14	15	3	IF
Alcedinidae						
Ceryle torquata	1,3,4,5	8,9,10,11	14,16,18	15	7	CA
Chloroceryle amazona	3	8,9,10,11	14,19	15	7	CA
Chloroceryle americana	3,5	8,9,10,11	18	15	7	CA
Chloroceryle aenea	–	8	–	4	7	CA
Momotidae						
Baryphthengus ruficapillus	–	6,8,9	13,14	12	2	IC
Galbulidae						
Galbula ruficauda	–	–	13,14	1	4	IN

Species	Upper Tibagi	Middle Tibagi	Lower Tibagi	Pattern of distribution	Biogeographical affinity	Guild
Bucconidae						
Notharcus macrorhynchus	–	–	13	1	0	ON
Nystalus chacuru	1,2	8	13,14	15	6	ON
Nonnula rubecula	–	6,7,8	13	13	0	IN
Ramphastidae						
Pteroglossus aracari	–	–	13	1	0	ON
Selenidera maculirostris	–	–	13,14	1	0	ON
Baillonius bailloni	5	6,7,8	13	15	2	ON
Ramphastos dicolorus	1,3,4,5	6,7,8,9	13	15	3	ON
Picidae						
Picumnus nebulosus	3,5	9	13,1	15	1	IN
Picumnus temminckii	1,5	6,7,8,10,11	12,13,14,16,17	15	1	IN
Picumnus cirratus	1,3	9	–	11	7	IN
Colaptes campestris	1,2,3,4,5	8,9,10,11	13,14,17,18,19	15	5	IN
Colaptes melanochloros *	1,2,3,5	6,7,8,9,10	13,14	15	4	IF
Piculus aurulentus	1,2,3,4,5	6,7,8,10,11	13,14	15	3	IN
Celeus flavescens	–	6,7,9	13	12	7	IF
Dryocopus lineatus	1,5	6,7,8,9	13,14,18	15	7	IN
Melanerpes flavifrons	1,5	6,7,8	13,17	15	2	IF
Leuconerpes candidus	1	6,8,10	12,13,14,16,17	15	5	IF
Veniliornis spilogaster	1,2,3,4,5	6,7,8,9,10,11	12,13,14,17,19	15	2	IF
Phloeoceastes melanoleucos	–	7,8	–	4	7	IF
Phloeoceastes robustus	1,5	6,7,8	13,16	15	2	IN
Dendrocolaptidae						
Dendrocincla turdina *	5	8,9	13	15	2	IN
Sittasomus griseicapillus	1,2,3,4,5	6,7,8,9,10,11	13,14,17	15	4	IN
Xiphocolaptes albicollis	1,5	8,11	13	15	2	IC
Dendrocolaptes platyrostris	1,2,3,4,5	6,7,8,9,10	13,14,17	15	2	IN
Lepidocolaptes angustirostris	5	6,8,9	–	11	6	IN
Lepidocolaptes squamatus	1,2,3,5	6,8,10,11	–	11	2	IN
Lepidocolaptes fuscus	2,5	6,7,8,11	13,14	15	2	IN
Campylorhamphus trochilirostris	–	7,8,9	–	6	4	IN
Campylorhamphus falcularius	5	–	–	8	2	IN
Furnariidae						
Clibanornis dendrocolaptoides	1,5	6,7,8,9,10,11	–	11	1	IN
Furnarius rufus	1,2,3,5	8,9,10,11	12,13,14,17,18,19	15	5	IF
Leptasthenura striolata	1,5	8	–	11	1	IN
Leptasthenura setaria	1,2,3,4,5	7,8,9,10,11	17	15	1	IN
Synallaxis ruficapilla	1,2,3,4,5	6,7,8,9,10	12,13,14	15	2	IN
Synallaxis frontalis	3	7,8,10	12,13,14,16	15	6	IN
Synallaxis spixi	1,2,3,5	6,7,8,9,10,11	12,13,14	15	2	IN
Synallaxis cinerascens	1,2,3,4,5	6,7,8,9,10,11	13,14	15	3	IN
Certhiaxis cinnamomea	1	11	14,16,19	15	4	CI
Cranioleuca obsoleta	1,3,4,5	6,8,9,10,11	–	11	3	IN
Cranioleuca vulpina	–	–	18,19	2	0	IN
Cranioleuca pallida	3,5	10	–	10	2	IN

Species	Upper Tibagi	Middle Tibagi	Lower Tibagi	Pattern of distribution	Biogeographical affinity	Guild
Anumbius annumbi	2,3,4,5	8,9,10,11	–	11	5	IN
Anabazenops fuscus	2,5	–	–	9	3	IN
Syndactyla rufosuperciliata	1,2,3,4,5	6,7,8,9,10,11	13,14	15	2	IN
Anabacerthia amaurotis	5	6,8,9	17	15	3	IN
Philydor atricapillus	2,5	–	–	9	3	IN
Philydor dimidiatus	5	–	–	8	4	IN
Philydor lichtensteini	1	–	–	7	2	IN
Philydor rufus	2,3,5	6,7,8,10	13,14	15	3	IN
Automolus leucophthalmus	–	8,10	13,14	12	3	IN
Cichlocolaptes leucophrys	3,4,5	–	–	8	2	IN
Heliobletus contaminatus	1,2,3,4,5	6,7,8,9,10	13,14	15	3	IN
Xenops rutilans	5	6,7,8	13,14	15	4	IN
Xenops minutus	5	6,8,10,11	–	11	2	IN
Sclerurus scansor	3,5	6,7,8,9,11	13,14	15	3	IC
Lochmias nematura	1,2,3,5	6,7,8,9,10,11	14,15	15	2	IN
Formicariidae						
Hypoedaleus guttatus	–	–	13,14	1	3	IN
Batara cinerea	1,4,5	6,7,8,10,11	–	11	3	IC
Mackenziaena leachii	5	6,8,9,10	–	11	3	IC
Mackenziaena severa	5	6,7,8,9	13,14,19	15	3	IC
Biatas nigropectus	5	–	–	8	3	IN
Thamnophilus doliatus	–	–	13,14,18,19	3	4	IN
Thamnophilus caerulescens	1,2,3,4,5	6,7,8,9,10,11	12,13,14,16,17	15	0	IN
Thamnophilus ruficapillus	5	8,9,10,11	12,13,14,19	15	6	IN
Dysithamnus stictothorax	–	–	13	1	2	IN
Dysithamnus mentalis	3,4,5	6,7,8,9,10,11	12,13,14	15	3	IN
Dysithamnus xanthopterus	–	8	–	4	2	IN
Herpsilochmus rufimarginatus	–	–	13	1	3	IN
Drymophila ferruginea	1,2	7,8	13	15	2	IN
Drymophila malura	1,2,4,5	6,7,8,10	13	15	3	IN
Pyriglena leucoptera	5	6,7,8	13,17	15	3	IC
Chamaeza campanisona	1,4,5	6,7,8,9,10,11	13	15	2	IF
Chamaeza ruficauda	5	6,8,9	13	15	2	IF
Formicarius colma	5	–	–	8	3	IN
Grallaria varia	–	6,7,8	13	13	3	IF
Hylopezus ochroleucus	1,2,5	6,8	–	11	2	IN
Conopophaga lineata	1,2,3,4,5	6,7,8,9,10	13	15	2	IN
Rhinocryptidae						
Psilorhamphus guttatus	5	6,8	13	15	2	IN
Scytalopus speluncae	5	–	–	8	2	IN
Scytalopus indigoticus	5	7,8,10	13	15	2	IN
Cotingidae						
Phibalura flavirostris	–	8	13	13	3	FR
Lipaugus lanioides	5	–	13	14	4	FR
Pachyramphus viridis	1,2,5	8,11	13	15	7	FI
Pachyramphus castaneus	1,4,5	6,7,8,9,10,11	12,13,14,15,16	15	3	FI
Pachyramphus polychopterus	1,2,3,5	6,7,8,9,10,11	13	15	7	FI

Species	Upper Tibagi	Middle Tibagi	Lower Tibagi	Pattern of distribution	Biogeographical affinity	Guild
Pachyramphus validus *	1,3,5	6,7,8,9,10,11	13,14,19	15	7	FI
Tityra cayana	1,2,3,4,5	6,7,8,10	13	15	7	FI
Tityra inquisitor	5	7,8,10	13	15	7	FI
Pyroderus scutatus	–	7,8	–	4	3	FR
Procnias nudicollis	3,4,5	7,8,10	–	11	2	FR
Pipridae						
Pipra fasciicauda	–	–	13	1	4	FI
Manacus manacus	–	–	13	1	0	FI
Chiroxiphia caudata	1,2,3,4,5	6,7,8,9,10	13,14	15	3	FI
Neopelma pallescens	–	8	–	4	6	FI
Piprites pileatus	5	–	–	8	2	FI
Piprites chloris	–	–	13	1	2	FI
Schiffornis virescens	3,4,5	6,7,8,9,10,11	13,14	15	3	ON
Tyrannidae						
Xolmis cinerea	3,5	8,9,10	–	11	5	IN
Xolmis velata	–	9	–	5	5	IN
Xolmis dominicana	3,5	9,11	–	10	5	IN
Colonia colonus	1,3,5	6,8,9,10	13,14,19	15	7	IN
Gubernetes yetapa	–	9	–	5	0	IN
Alectrurus tricolor	3,5	–	–	8	6	IN
Knipolegus lophotes	3,5	9	–	10	6	IN
Knipolegus nigerrimus	3,5	9	–	10	6	IN
Knipolegus cyanirostris	5	8,10,11	12,13	15	2	IN
Muscipipra vetula	1,2,5	8,10	13	15	3	IN
Fluvicola pica	–	–	18	2	4	IN
Arundinicola leucocephala	3	8	13,14,19	15	7	IN
Pyrocephalus rubinus	3,5	8	13,14	15	5	IN
Satrapa icterophrys	5	8,9,10,11	13,14	15	7	FR
Machetornis rixosus	1,3,4,5	8,9,10	13,14,18	15	5	IN
Sirystes sibilator	–	8,10	13,14	12	3	IN
Muscivora tyrannus	1,2,3,5	8,9,11	12,13,14,19	15	4	IN
Tyrannus melancholicus	1,2,3,5	6,8,9,10,11	12,13,14,15,18,19	15	4	IF
Empidonomus varius	1,3,5	6,8,9,10,11	12,13,14,19	15	6	IF
Legatus leucophaius	1,2,3,5	6,7,8,9,10,11	–	11	7	FR
Conopias trivirgata	–	7	–	4	0	IF
Megarhynchus pitangua	1,2,3,5	6,7,8,9,10	12,13,14,16,19	15	7	IN
Myiodynastes maculatus	1,2,3,5	6,7,8,9,10,11	12,13,14,15,19	15	7	IF
Myiozetetes similis	–	8,9	13,14,19	12	7	FI
Pitangus sulphuratus	1,2,3,4,5	6,7,8,9,10,11	12,13,14,15,16,17,18,19	15	7	IF
Attila rufus	–	8	13	13	3	IN
Pseudattila phoenicurus	5	–	–	8	2	IN
Myiarchus ferox	5	7,8,10,11	–	11	7	IN
Myiarchus swainsoni	3,5	6,8,9,10,11	13,14	15	7	IN
Contopus cinereus	3,5	7,8	13,14	15	7	IN
Empidonax euleri	1,4,5	6,7,8,10,11	13,14,19	15	7	IN
Cnemotriccus fuscatus	5	8,9,11	13	15	7	IN
Myiobius barbatus	–	–	13	1	2	IN
Myiobius atricaudus	5	–	–	8	2	IN

Species	Upper Tibagi	Middle Tibagi	Lower Tibagi	Pattern of distribution	Biogeographical affinity	Guild
Myiophobus fasciatus	1,3,4,5	8,9,10,11	13,14	15	7	IN
Hirundinea ferruginea	2,3,5	8,9	–	11	0	IN
Onychorhynchus coronatus	–	7	–	4	0	IN
Platyrinchus mystaceus	1,3,4,5	6,7,8,9,10,11	13,14	15	0	IN
Tolmomyias sulphurescens	1,3,5	6,7,8,9,10	13,14,16	15	7	IN
Ramphotrigon megacephala	–	10	–	5	0	IN
Todirostrum cinereum	–	6,8	12,13,14,16,18	13	2	IN
Todirostrum plumbeiceps	1,2,3,4,5	6,7,8,9,10,11	12,13,16	15	3	IN
Idioptilon nidipendulum	5	6,8	13	15	2	IN
Idioptilon margaritaceiventer	–	–	13	1	7	IN
Myiornis auricularis	2,5	7,8,9,11	13,14	15	3	IN
Hemitriccus diops	–	7,8	–	4	3	IF
Hemitriccus obsoletus	1,5	6,8	13	15	3	IF
Phylloscartes eximius *	5	6,8	13	15	3	IF
Phylloscartes silviolus *	–	–	13	1	2	IF
Phylloscartes ventralis	1,3,4,5	6,7,8,9,10,11	13,14	15	3	IF
Phylloscartes oustaleti	5	8	13,14	15	2	IF
Phylloscartes paulistus	–	10	–	5	2	IF
Capsiempis flaveola	5	6,8,9	13,14	15	0	IF
Euscarthmus meloryphus	5	–	13	14	0	IN
Culicivora caudacuta	5	10	–	10	5	IN
Serpophaga subcristata	1,3,4,5	8,9,10,11	13,14,16,17,19	15	2	IN
Serpophaga nigricans	1,3,5	9,10,11	–	11	5	IN
Elaenia flavogaster	5	8,10	13,14,19	15	4	FI
Elaenia parvirostris	2,5	7,8,10,11	13,14,16	15	5	FI
Elaenia mesoleuca	2,5	8,9,10,11	13,14	15	5	FI
Elaenia chiriquensis	5	8	–	11	0	FI
Elaenia obscura	5	8,9,10	–	11	3	FI
Myiopagis caniceps	1,5	6,8	13,14	15	4	IF
Myiopagis viridicata	–	–	13	1	0	IF
Suiriri suiriri	5	–	–	8	6	IN
Camptostoma obsoletum	1,3,4,5	6,8,9,10,11	12,13,14,19	15	7	FI
Phyllomyias virescens *	–	6	–	4	3	FR
Phyllomyias fasciatus	5	6,7,8,10,11	–	11	2	FR
Phyllomyias griseocapilla *	–	8	–	4	2	FR
Phyllomyias burmeisteri *	1,5	–	13	14	2	IF
Leptopogon amaurocephalus	1,5	6,7,8,9,10	13,14	15	7	FI
Pipromorpha rufiventris	3,5	6,7,8,9,10	13,14	15	3	FR
Corythopis delalandi	–	7,8,9	13,14	12	2	IN
Oxyruncidae						
Oxyruncus cristatus	–	8	13	13	2	FI
Hirundinidae						
Tachycineta albiventer	–	6,8	14,18	13	7	IN
Tachycineta leucorrhoa	3,5	8,9,10,11	13,14,19	15	7	IN
Phaeprogne tapera	5	8	13,19	15	7	IN
Progne chalybea	1,5	8	12,13,15,19	15	7	IN
Notiochelidon cyanoleuca	1,3,5	6,8,9,10,11	12,13,14	15	7	IN
Alopochelidon fucata	3,5	8,11	13	15	7	IN

Species	Upper Tibagi	Middle Tibagi	Lower Tibagi	Pattern of distribution	Biogeographical affinity	Guild
Stelgidopteryx ruficollis	1,3,5	8,9,10,11	13	15	7	IN
Hirundo rustica	–	–	13,18	3	7	IN
Petrochelidon pyrrhonota	5	–	13	14	0	IN
Corvidae						
Cyanocorax caeruleus	1,2,3,5	8,10	–	11	1	ON
Cyanocorax cristatellus	–	9	–	5	6	ON
Cyanocorax chrysops	1,2,3,4,5	6,7,8,9,10	13,14	15	6	ON
Troglodytidae						
Cistothorus platensis	–	10	18	12	5	IN
Troglodytes aedon	1,2,3,4,5	6,7,8,9,10,11	12,13,14,15,16,17,18,19	15	7	IN
Mimidae						
Mimus saturninus	1,2,3,5	8,9	13,14,15,19	15	5	ON
Donacobius atricapillus	–	–	14,18,19	3	7	IN
Turdidae						
Platycichla flavipes	5	8	–	11	0	FI
Turdus nigriceps	1,2,5	7,8,9,10,11	–	11	3	FI
Turdus rufiventris	1,2,3,4,5	6,7,8,9,10,11	12,13,14,16,17	15	5	ON
Turdus leucomelas	1,2	6,7,8,9	12,13,14,17,19	15	4	FI
Turdus amaurochalinus	1,2,3,5	6,7,8,9,10,11	12,13,14,16,17	15	5	ON
Turdus albicollis	1,2,3,5	6,7,8,9,10	13,14	15	3	FI
Sylviidae						
Polioptila lactea	–	–	13	1	2	IN
Motacillidae						
Anthus hellmayri	5	9	–	10	5	ON
Anthus lutescens	3,5	–	13,14	14	5	IF
Anthus correndera	5	11	–	10	5	IF
Anthus nattereri	5	11	–	10	1	IF
Vireonidae						
Cyclarhis gujanensis	1,2,3,4,5	6,7,8,9,10,11	12,13,14,16,17,18,19	15	7	IF
Vireo olivaceus	1,2,3,5	6,7,8,9,10,11	13,14,19	15	7	IN
Hylophilus poicilotis	1,2,5	6,7,8,10,11	13,14	15	2	FI
Icteridae						
Molothrus bonariensis	1,2,3,4,5	8,9,10,11	13,14,15,19	15	7	ON
Molothrus rufoaxillaris	–	8	–	4	5	ON
Molothrus badius	5	–	–	8	5	ON
Scaphidura oryzivora	–	8	13	13	4	IF
Psarocolius decumanus	–	10	–	5	4	ON
Cacicus haemorrhous	1,5	6,7,8,9,10	13,14	15	2	ON
Cacicus chrysopterus	1,3,4,5	6,7,8,10	–	11	2	ON
Gnorimopsar chopi	1,2,3,4,5	8,9,10	13	15	2	ON
Agelaius thilius	–	8	18	13	0	ON
Agelaius ruficapillus	–	8	14,18	13	5	ON

Species	Upper Tibagi	Middle Tibagi	Lower Tibagi	Pattern of distribution	Biogeographical affinity	Guild
Agelaius cyanopus	–	8	19	13	2	ON
Icterus cayanensis	2	8,9	13,14	15	7	IN
Pseudoleistes guirahuro	1,3,5	9,10,11	–	11	2	ON
Leistes superciliaris	5	8,11	13,14,16	15	5	ON
Dolichonyx oryzivorus	5	8	–	11	0	ON
Parulidae						
Parula pitiayumi	1,2,3,4,5	6,8,9,10,11	12,13,14,16,19	15	7	IF
Geothlypis aequinoctialis	1,5	8,9,10,11	12,13,18,19	15	0	IN
Basileuterus culicivorus	1,2,3,4,5	6,7,8,9,10,11	12,13,14,16,17	15	0	IN
Basileuterus leucoblepharus	1,2,3,4,5	6,7,8,9,10,11	13,14,15,17	15	5	IN
Basileuterus rivularis	–	10,11	–	5	2	IN
Coerebidae						
Coereba flaveola	2	7,8,10	13,14	15	7	FI
Conirostrum speciosum	1,5	6,7,8,9,11	12,13,14	15	7	IF
Cyanerpes cyaneus	1,3,5	–	13,	14	0	ON
Dacnis cayana	–	7,8,9	13,14,17	12	7	ON
Dacnis nigripes	–	6	–	4	2	ON
Tersinidae						
Tersina viridis	1,3,5	6,8,9	13,14	15	7	FI
Thraupidae						
Chlorophonia cyanea	–	7,8,9	–	6	2	FI
Euphonia musica	5	–	13	14	2	FI
Euphonia chlorotica	5	9	12,13,14,16,19	15	7	FI
Euphonia violacea	–	8	13	13	7	FI
Euphonia pectoralis	5	11	13	15	3	FI
Euphonia chalybea	3,5	6,7,8,9	–	11	2	FI
Pipraeidea melanonota	1,2,3,5	7,8,9,10,11	13	15	2	ON
Tangara seledon	–	–	13	1	2	FI
Tangara desmaresti	5	–	–	8	2	FI
Tangara preciosa	1,3,5	9	13	15	2	FI
Tangara peruviana	–	7,8,11	–	6	2	FI
Tangara cayana	–	–	13,14	1	4	ON
Stephanophorus diadematus	1,2,4,5	8,9,10,11	–	11	2	FI
Thraupis sayaca	1,2,3,4,5	6,7,8,9,10,11	13,14	15	2	FI
Thraupis palmarum	2	9	–	11	7	FI
Thraupis bonariensis	1,2,5	8,10	–	11	5	FI
Ramphocelus carbo	–	–	13,18	3	4	FI
Piranga flava	1,4	6,7,8,9	13	15	4	ON
Orthogonys chloricterus	–	8	–	4	2	FI
Habia rubica	5	6,7,8,9	13,14	15	2	FI
Tachyphonus coronatus	1,3,5	6,7,8,9,10	13,14	15	3	FI
Trichothraupis melanops	3,5	6,7,8,9	13,14,17	15	2	FI
Cypsnagra hirundinacea	–	–	14,18	3	6	IF
Pyrrhocoma ruficeps	1,5	6,7,8	13,14	15	3	IF
Nemosia pileata	–	–	13,16	1	6	IF
Hemithraupis ruficapilla	5	–	–	8	2	IF

Species	Upper Tibagi	Middle Tibagi	Lower Tibagi	Pattern of distribution	Biogeographical affinity	Guild
Hemithraupis guira	1,3	6,7,8,10,11	12,13,14,19	15	4	IF
Neothraupis fasciata	–	9	–	5	6	IF
Orchesticus abeillei	–	8	–	4	2	IF
Cissopis leveriana	5	6,7,8	13,17	15	2	IF
Schistochlamys ruficapillus	5	8,9	–	10	6	IF
Fringillidae						
Saltator similis	1,2,3,4,5	6,7,8,9,10,11	12,13,14,16,17,19	15	2	FI
Saltator maxillosus	1,5	10	–	11	3	FI
Saltator atricollis	–	–	13,18	3	6	FI
Pitylus fuliginosus	5	6,8	13	15	3	FI
Paroaria coronata	5	–	–	8	0	FI
Cyanocompsa cyanea	2,5	6,7,8,10	13,16	15	2	FI
Cyanoloxia glaucocaerulea	2,3,5	10	–	11	2	FI
Volatinia jacarina	1,2,3,4,5	8,9,10,11	12,13,14,15,16,19	15	7	FI
Tiaris fuliginosa	5	10	–	10	2	FI
Sporophila falcirostris	–	7	–	4	2	FI
Sporophila plumbea	–	7	–	4	4	FI
Sporophila collaris	–	–	13,18	3	0	FI
Sporophila lineola	–	–	16	1	7	FI
Sporophila caerulescens	1,2,3,4,5	6,8,9,10,11	12,13,14,15,16,18,19	15	5	FI
Sporophila bouvreuil	3,5	–	–	8	5	FI
Sporophila hypoxantha	3,5	–	–	8	5	FI
Sporophila melanogaster	5	–	–	8	5	FI
Oryzoborus angolensis	5	8	–	10	7	FI
Amaurospiza moesta	5	6,7,8,10	–	11	2	FI
Sicalis citrina	5	9	–	10	6	FI
Sicalis flaveola	1,2,3,5	8,9,10	–	11	2	FI
Sicalis luteola	1,3,5	9,11	–	11	5	FI
Haplospiza unicolor	3,5	7,8,11	–	11	3	FI
Coryphospingus cucullatus	3	–	13,14	14	6	FI
Arremon taciturnus	–	6	–	4	0	FI
Arremon flavirostris	5	7,8	–	11	0	FI
Myospiza humeralis	3,5	8,9,11	13,14,15,19	15	4	ON
Zonotrichia capensis	1,2,3,4,5	6,7,8,9,10,11	12,13,14,16,17	15	7	ON
Emberizoides ypiranganus	5	11	–	10	6	FI
Emberizoides herbicola	3,5	9,10,11	–	10	6	FI
Donacospiza albifrons	5	8	–	11	5	IN
Poospiza nigrorufa	2	–	–	7	7	FI
Poospiza lateralis	1,3,4,5	7,8,9,10,11	–	11	2	FI
Embernagra platensis	1,3,4,5	9,10,11	–	11	5	ON
Spinus magellanicus	1,2,3,4,5	8,9,10,11	13,14,19	15	2	ON