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*Research Article*

# The Western Amazonian Boundary for Avifauna Determined by Species Distribution Patterns and Geographical and Ecological Features

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In northern South America, an extensive tropical lowland runs 5,000 km from the Atlantic coast to the foot of the Andes. The slope is gentle until about 500 m where the eastern Andes rise abruptly. The lowland supports Amazonia, which is the most extensive tract of tropical rainforest on the planet. Most of its boundaries are well defined, but the boundary between Amazonia and the forest of the eastern slopes of the Andes has not been clearly defined. To determine for avifauna whether Amazonia is restricted to the lowland of northern South America or whether it also extends up into the eastern slopes of the Andes, different types of data were used. The results indicate that Amazonia may be restricted to the lowland that extends from the Atlantic coast to the foot of the Andes, up to about 500 m. Consequently, the number of bird species strictly endemic to Amazonia would be 290. Comparison with the distribution of vegetation on the eastern slopes of the Andes also suggests that Amazonia as a biome may be restricted to the lowland that extends from the Atlantic coast to the foot of the Andes, up to about 500 m.

## 1. Introduction

In northern South America, an extensive tropical lowland runs about 5,000 km from the Atlantic coast to the foot of the Andes. The slope from sea level to approximately 500 m is gentle and almost imperceptible, but at about 500 m the eastern Andes rise abruptly out of the plain and the elevation increases sharply [1]. The lowland supports Amazonia, which is the most extensive tract of tropical rainforest on the planet [2] and is considered the richest ecosystem in the world [3]. It covers an area of about 7 million km$^2$ and is in contact with the forest of the eastern slopes of the Andes for about 3000 km.

Most of the Amazonian boundaries are geographically or ecologically well defined although in general there is a transition zone between forest and nonforest vegetation [4]. To the northwest, Amazonia borders a vast grassland area named the Llanos of Colombia and Venezuela [4, 5]. To the northeast, it borders the Atlantic Ocean and to the south, the less humid "diagonal" formed by the Caatinga, Cerrado, and Chaco [6, 7]. To the west, however, the boundary between Amazonia and the forest of the eastern slopes of the Andes has not been clearly defined.

In general, authors that have studied bird distribution in the region consider that Amazonia, also classified as humid tropical, lowland, evergreen, and lower tropical forests, reaches an altitude of 900 m or more on the eastern slopes of the Andes [5, 8–11]. However, important topographic, ecological, and climatic changes occur at about 500 m, where the eastern Andes rise abruptly out of the plain. For this reason, it has been suggested that Amazonia does not extend above 500 m on the eastern slopes of the Andes [1]. Previously, Patterson et al. [12] also described the cutoff point between lowland and highland avifauna in the Andes of southeastern Peru as approximately 500 m.

To determine the geographical location of Amazonia, especially the limit with the forest of the eastern slopes of the Andes, is very important for two reasons, firstly, because Amazonia is the most important tropical rainforest of the world [2], and secondly, because the number of species of animals and plants characteristic of this biome changes considerably depending on how that limit is defined.

Here, bird distribution patterns and geographical and ecological features are used to delimit the bird boundary between Amazonia and the eastern slopes of the Andes. A comparison has also been made with other studies, apart from birds, to determine whether Amazonia as a biome is restricted to the lowland of northern South America or whether it also extends up into the eastern slopes of the Andes.

## 2. Method

To determine whether, for birds, Amazonia is restricted to the lowland of northern South America or whether it also extends up into the eastern slopes of the Andes, different types of data were used.

(i) *Altitudinal analysis of bird species that inhabit Amazonia and reach at least the foot of the Andes*. To select the species to include in the analysis I mainly followed Ridgely and Tudor [13, 14] and del Hoyo et al. [15]. Species that occur in other lowland forests besides Amazonia, such as the Pacific rainforest or the Atlantic Region, were not considered. The altitudes that the species reach in the western Amazonian/eastern slope of the Andes area were taken from Hilty and Brown [16] for Colombia, Ridgely and Greenfield [17] for Ecuador, and Schulenberg et al. [18] for Peru.

(ii) *Altitudinal analysis of bird species that inhabit the eastern slopes of the Andes and reach at least the foot of the Andes*. To select the species to include in the analysis I mainly followed Ridgely and Tudor [13, 14] and del Hoyo et al. [15]. Species that occur in other mountain forests besides the eastern slope of the Andes, such as the slopes of Central and Western Andes of Colombia, were not considered. The altitudes that the species reach in the Andes/Amazonia border were taken from Hilty & Brown [16] for Colombia, Ridgely and Greenfield [17] for Ecuador, and Schulenberg et al. [18] for Peru.

(iii) *Comparative censuses carried out in the western Amazonian lowland and on the lower eastern slopes of the Andes*. This procedure was to determine if there are important differences in the rainforest avifauna between the two sites indicating that they could belong to different biomes. To do that, I selected one site located in the lowland (at about 400 m) and another site located on the eastern slopes of the Andes (at about 600–700 m) in Peru and Ecuador, at the same latitude and with a distance of less than 20 km between them. Sites were of about 10 ha with a central trail. The censuses consisted in recording all the birds species observed along the trails during six days, alternating one day in the morning (6:00 to 12:00) and one day in the afternoon (13:00 to 18:00). I considered only the observed birds but used a tape recorder and a directional microphone to attract birds. In Peru, the Amazonian site was located 5 km west of Aguaytia (09 02 S-75 33 W), and the Andean site was 24 km west of Aguaytia. In Ecuador, the Amazonian site was located 4.5 km east of Cascales (00 08 N-77 19 W) and the Andean site was 6.5 km west of Cascales. The results obtained in each pair of sites were compared using the Sorensen Similarity Index.

(iv) *Geographical location of points that were accessible by road where the Andes rise abruptly out of the plain.* At these points. I recorded the geographical coordinates, altitude, and distance to the nearest city or town.

(v) Characteristics of the relief, watercourses, and general aspect of the vegetation of the sites where the Andes rise abruptly out of the plain. At these points I described whether the relief was steep, if the rivers and streams were rocky and swift, and the characteristic of the vegetation.

Table 1: Altitude that species inhabiting Amazonia reach in the west.

| Altitude (m) | Colombia (%) | Ecuador (%) | Peru (%) |
|---|---|---|---|
| <500–600 | 167 (88.35) | 113 (67.26) | 138 (51.30) |
| Between 700–1000 | 6 (2.07) | 35 (20.83) | 68 (25.28) |
| >1000 | 16 (10.58) | 20 (11.90) | 63 (23.42) |

## 3. Results

(i) *Altitudinal analysis*. Of 418 species of birds inhabiting the Amazonian forest, 284 reach the foot of the Andes. Of these, 189 species reach the foot of the Andes in Colombia, 168 in Ecuador, and 270 in Peru. The altitude that these species reach in the west is indicated in Table 1. In Colombia 166 species (88.29%), in Ecuador 113 species (67.06%), and in Peru 138 species (51.30%) do not occur at an altitude higher than 500–600 m.

(ii) *Altitudinal analysis of bird species that inhabit the eastern slopes of the Andes and reach at least the foot of the Andes.* Of 140 species of birds inhabiting the eastern slopes of the Andes, only 23 reach the foot of the Andes (500 m). Of these, 18 (78%) do not occur at an altitude lower than 500–400 m.

(iii) *Comparative surveys in the western Amazonian lowland and in the lower eastern slope of the Andes*. Bird activity and the number of species and individuals observed in the surveyed sites were extremely low. Early in the morning, there was a little activity, but during the rest of the day, it was practically nil. Similarity was low for all sites: there was only 15% similarity between the Amazonian and Andean sites in Peru and 30% in Ecuador. Species richness was similar in all the sites, being only somewhat lower in the Andean site in Peru. The number of forest bird species recorded and Sorensen Similarity Index are indicated in Table 2.

Table 2: Number of forest bird species observed in Amazonian and Andean sites in Ecuador and Peru, and Sorensen Similarity Index.

| Country | Amazonian site | Andean site | Shared species | Sorensen Index |
|---|---|---|---|---|
| Ecuador | 43 | 42 | 13 | 0.30 |
| Peru | 45 | 37 | 6 | 0.15 |

(iv) *Geographical points where the Andes rise abruptly out of the plain*. In Colombia, this point is located in Villavicencio City (04 09 N-73 37 W). In Ecuador, the points are 5 km west of Cascales (00 08 N-77 19 W) and in Puerto Napo (01 03 S-77 47 W). In Peru, the points are 2 km west of El Boquerón (09 03 S-75 39 W) (Figure 1) and in Santa Rosa (12 54 S-70 11 W). In Bolivia, the points are 10 km west of Villa Tunari (16 55 S-65 22 W) and about 3 km west of the Mataracú Station (17 33 S-63 52 W), in Amboró National Park (Figure 2).

(v) *Topographic and ecological characteristics of the points where the Andes rise abruptly out of the plain*. At all these sites elevation increases sharply, the relief becomes very steep, and rivers and streams turn rocky and swift. The forest gets gradually lower in stature than those of the adjacent lowland areas, having less buttressed trees. The canopy was often broken, having progressively fewer woody vines and more vascular epiphytes of all kinds (bromeliads, mosses, ferns, orchids, etc.).

Figure 1: The point where the Andes rise abruptly out of the plain, at 2 km west of the Boquerón, Peru.

## 4. Discussion

Obtaining a reliable altitudinal boundary for birds between two continuous forest habitats, in this case Amazonia and the eastern slopes of the Andes, is undoubtedly difficult. However, five lines of evidence suggest that the estimate of about 500 m may be close to the "true" Amazonian/eastern slopes of the Andes boundary.

The first is the marked altitudinal, geographical, and climatic changes that occur at about 500 m, where the Andes rise abruptly out of the plain, and the relief becomes very steep and rocky. The second line of evidence is that a large percentage of Amazonian bird species do not extend up into the eastern slopes of the Andes. The third is that a large percentage of bird species that inhabit the eastern slopes of the Andes do not extend into Amazonia. The fourth line of evidence is the change in vegetation, especially the gradual decrease in stature of trees and the gradual increase of epiphytic richness, produced mainly by a cloud effect. As Prance [19] pointed out, small changes in altitude can produce extremely important changes in vegetation type, physiognomy, and species composition. The fifth is the low similarity in bird species composition between sites located in western Amazonian lowland and the lower eastern slopes of the Andes. However, the importance of this last line of evidence is relative due to the low number of forest bird species observed in all sites, which is evidently a consequence of the drastic decrease of bird populations and activity in this area, which I have reported elsewhere [20]. In relation to that, Hennessey and Rubey [21] pointed out that due to habitat loss or geographic position, the Hill Tropical (500–900 m) and Lower Tropical (500 m and below) habitats around Villa Tunari, Bolivia, are not as rich in terms of bird life, adding "if your trip also includes visiting lowland habitats in another area of Bolivia, spend most of your time above 1000 m."

Amadon [22] pointed out that the failure of a lowland species to inhabit the mountains may reflect competitive exclusion, rather than inability to live under the climatic conditions prevailing there. However, recent findings have shown that most species are confined to specific elevational bands as a result of the microclimatic constraints of ambient temperature and humidity on their metabolism [23, 24] and on their preferred vegetation [25] (see also Sekercioglu et al. [26]). Moreover, in most cases in which Amazonian species do not penetrate the eastern slope of the Andes, there are no congeneric species there that can produce competitive exclusion. Although competitive exclusion is not restricted to congeners, exclusion by congeners generally constitutes an important factor [27]. Hence, changes in relief, temperature and humidity, and vegetation structure appear to be the factors explaining the 500 m border. Thus, for birds, Amazonia may be restricted to the lowland running from the Atlantic coast to the foot of the Andes.

As tropical rainforest birds are generally excellent indicators, are many in terms of species numbers, and are a characteristic component of this biome, they may be useful tools for the construction of a general scheme of the boundary between Amazonia and the eastern slopes of the Andes. Two extensive studies that include tropical rainforest birds (Ridgely and Greenfield [17], Schulenberg et al. [18]) also distinguish between a Humid Lowland Forest (Amazonia) and a Humid Montane Forest ("Foothill Forest or Upper Tropical Forest") that covers the eastern slopes of the Equatorial and Peruvian Andes from about 500–600 m upwards. Although Stotz et al. [10] considered that the Lowland Evergreen Forest occurs up to 900 m in the

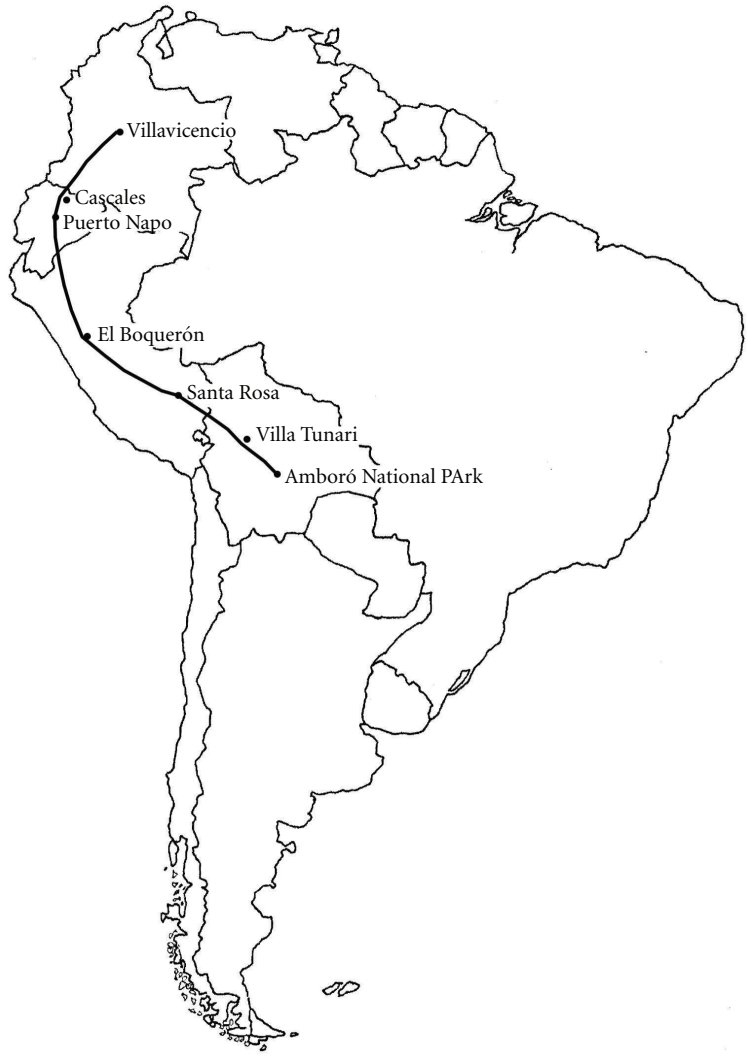


Figure 2: Western boundary of Amazonia suggested in this work.

Neotropics; they also distinguished between a Lower Tropical (lower than 500 m) and Hill Tropical (500–900 m) forest. Terborgh [28] also distinguished a Lowland Rainforest and a Montane Rainforest in the Cordillera Vilcabamba, Peru, whose limit is about 650 m. Frahm and Gradstein [29], using bryophytes as indicators also recognized in NE Peru a Tropical Lowland Forest with an upper limit at 300–500 m and a Tropical Submontane Forest from this limit to 1000–1400 m. They added that in their scheme the Submontane Forest is not placed as a subunit in the lowland forest, as in most previous studies, but recognized as a proper forest belt.

Other animals groups, however, do not agree with birds and plants in the Andes zonation. Patterson et al. [12] pointed out that in the Andes of southeastern Peru the cutoff point is 750 m for bats and 1000 m for mice. However, it seems that these differences can be better explained by the wider ecological amplitude of these groups, rather than that Amazonia also extends up into the eastern slopes of the Andes.

For these reasons, the results suggest that Amazonia may be restricted to the lowland that extends from the Atlantic coast to the foot of the Andes and of the Tepuis up to about 500 m. The western boundary of Amazonia would therefore be the line that passes along the sites where the Andes rise abruptly out of the plain (Figure 2).

Amadon [22] stated that the fact that a wide-ranging lowland species also extends up into the mountain forest should not exclude it from being considered a member of the lowland avifauna. However, this concept is valid provided that the species only inhabit a short range on the mountains or that they extend occasionally or locally up into the mountains. For this reason, I have also included in the Amazonian avifauna those species occurring at up to 700 m on the eastern slopes of the Andes and species that inhabit the lowlands up to about 500 m but were occasionally or locally recorded at higher altitudes. Thus, a total of 337 species of birds is obtained (see the appendix). Of these, 107 (31.75%) are no-passeriformes, 198 (58.75%) suboscines, and only 32

(9.49%) oscines. Of the 337 species, 46 species extend higher than 700 m up the forested slopes of the Tepuis [30]. As the forest of the Tepuis above 500 m appears not to belong to Amazonia either [1], the number of bird species of Amazonia would be 291. However, there is a great difference in the altitude that bird species reach in the west in Colombia and Ecuador in relation to Peru. For example, 39 species that do not occur above 700 m in Colombia and Ecuador extend up higher on the eastern slopes of the Andes in Peru (see the appendix). This suggests that the criterion used by Schulenberg et al. [18] to indicate the altitude that bird species reach in Peru was different to that used by Hilty and Brown [16] for Colombia and Ridgely and Greenfield [17] for Ecuador. Probably in Peru the highest altitude where the species was recorded was generally considered, while in Colombia and Ecuador, the altitude where species commonly occur was generally used. If in Peru the altitude where species commonly occur was considered, the number of strictly endemic species of birds in Amazonia would be 252.

## Appendix

Here is a check list of the birds of Amazonia distributed in centers of endemism [31]. Species marked with an asterisk extend higher than 700 m on the slopes of the Tepuis. Species marked with two asterisks do not occur above 700 m in Colombia and Ecuador but extend higher on the eastern slopes of the Andes in Peru. Species in Peru and on the slopes of the Tepuis occurring above 700 m were not included in the list. Nomenclature and order follow Remsen et al. [32].

Guiana Center. *Penelope marail, Pyrilia caica*, Amazona dufresniana*, Caprimulgus maculosus, Neomorphus rufipennis*, Phaethornis longuemareus, Lophornis ornatus*, Amazilia brevirostris, Monasa atra*, Selenidera culik*, Pteroglossus viridis, Picumnus minutissimus, P. varzeae, Veniliornis cassini, V. sanguineus, Xiphorhynchus pardalotus*, Frederickena viridis, Thamnophilus melanothorax, Myrmotherula guttata, Herpsilochmus sticturus, H. stictocephalus H. dorsimaculatus, Terenura spodioptila*, Cercomacra carbonaria, Gymnopithys rufigula*, Phylloscartes virescens, Hemitriccus josephinae, Todirostrum pictum, Contopus albogularis, Perissocephalus tricolor*, Procnias albus*, Neopelma chrysocephalum, Tyranneutes virescens, Corapipo gutturalis*, Lepidothrix serena, Iodopleura fusca, Pachyramphus surinamus, Cyanocorax cayanus*, Cyanicterus cyanicterus, Tangara varia, Euphonia plumbea*, and E. finschi*.*

Vaupés Center [33] (=Imeri Center). *Crypturellus duidae, C. casiquiare, Nonnula amaurocephala, Picumnus pumilus, Thripophaga cherriei, Myrmotherula ambigua, M. cherriei, Myrmeciza pelzelni, M. disjuncta, Hemitriccus inornatus, Cyanocorax heilprini, and Dolospingus fringilloides.*

Napo Center. *Mitu salvini, Neomorphus pucheranii, Leucippus chlorocercus, Galbalcyrhynchus leucotis, Nonnula brunnea, Thamnophilus praecox, Myrmeciza melanoceps, Pithys castaneus, Rhegmatorhina cristata, Grallaria dignissima, Heterocercus aurantiivertex, Hylopezus fulviventris, and Cacicus sclateri.*

Inambari Center. *Crypturellus atrocapillus**, *C. bartletti, Crax globulosa, Psophia leucoptera, Nannopsittaca dachilleae, Galbalcyrhynchus purusianus, Brachigalba albogularis, Galbula cyanescens, Malacoptila semicincta**, *Nonnula sclateri, Eubucco tucinkae, Picumnus castelnau, Thamnomanes schistogynus**, *Myrmoborus melanurus, Myrmeciza goeldii, Gymnopithys salvini**, *Formicarius rufifrons, Grallaria eludens, Lophotriccus eulophotes, Hemitriccus iohannis, Conioptilon mcilhennyi, Neopelma sulphureiventer, Cantorchilus griseus, Tachyphonus rufiventer**, *and Cacicus koepckeae.*

Rondonia Center. *Penelope pileata, Pyrrhura perlata, Neomorphus squamiger, Discosura letitiae, Capito brunneipectus, Dendrocolaptes hoffmannsi, Clytoctantes atrogularis, Hypocnemis ochrogyna, H. striata, Rhegmatorhina berlepschi, Rhegmatorhina hoffmannsi, Skutchia borbae, Poecilotriccus senex, Lepidothrix nattereri, and Odontorchilus cinereus.*

Pará-Belém Center. *Guarouba guarouba, Rhegmatorhina gymnops, Conopophaga roberti, and Lepidothrix vilasboasi.*

Species Inhabiting Two or More Centers of Endemism. *Tinamus guttatus, Crypturellus cinereus. C. strigulosus, C. brevirostris, Pipile cujubi, Nothocrax urumutum, Mitu tomentosum, Odontophorus stellatus**, *Cathartes melambrotus, Leucopternis schistaceus, L. melanops*, L. kuhli, Micrastur buckleyi, Psophia crepitans, P. viridis, Amaurolimnas fasciatus, Orthopsittaca manilata, Aratinga weddellii, Pyrrhura lepida, Brotogeris versicolurus, B. cyanoptera, B. chrysoptera, B. sanctithomae, Touit huetii**, *T. purpuratus, Pionites melanocephalus*, P. leucogaster, Deroptyus accipitrinus, Pyrilia barrabandi, P. vulturina, Gradydascalus brachyurus, Amazona festiva, Opisthocomus hoazin, Piaya melanogaster**, *Chordeiles rupestris, Hydropsalis climacocerca, Topaza pella, Phaethornis rupurumii, P. philippii, P. bourcieri*, Polytmus theresiae, Avocettula recurvirostris*, *Anthracothorax viridigula, Pharomachrus pavoninus**, *Galbula cyanicollis, G. galbula, G. chalcothorax, G. leucogastra*, G. dea*, Notharchus ordii, Bucco macrodactylus**, *B. tamatia, B. capensis*, Malacoptila rufa, Monasa nigrifrons, Capito aurovirens, Capito dayi, Selenidera nattereri, S. gouldii, Pteroglossus pluricinctus, P. beauharnaesii**, *P. bitorquatus, Picumnus aurifrons**, *P. spilogaster, Celeus undatus, C. elegans*, C. spectabilis*, Scleru*rus rufigularis**, *Synallaxis rutilans*, Cranioleuca gutturata**, *Tripophaga fusciceps, Metopothrix aurantiaca**, *Berlepschia rikeri, Simoxenops ucayalae**, *Ancistrops strigilatus**, *Philydor pyrrhodes, Automolus infuscatus*, A. melanopezus, A. rufipileatus, Xenops milleri, X. tenuirostris, Certhiasomus stictolaemus, Dendrocincla merula, Nasica longirostris, Dendrexetastes rufigula, Hylexetastes stresemanni, H. perrotii, Dendroplex kienerii, Xiphorhynchus obsoletus, X. elegans, Lepidocolaptes albolineatus*, *Campylorhamphus procurvoides, Frederickena unduligera, Sakesphorus luctuosus, Thamnophilus nigrocinereus, T. amazonicus, Megastictus margaritatus, Neoctantes niger, Thamnomanes saturninus, Pygiptila stellaris, Epinecrophylla gutturalis*, E. leucophthalma**, *E. haematonota*, E. erythrura**, *Myrmotherula sclateri, M. multostriata, M. hauxwelli, M. sunensis, M. iheringi, Dichrozona cincta, Herpsilochmus dugandi, H. gentryi, Hypocnemis flavescens, H. hypoxantha, Terenura humeralis, Cercomacra*

*cinerascens*, C. nigrescens, Hypocnecmoides melanopogon, H. maculicauda, Myrmochanes hemileucus, Sclateria naevia, Pernocstola rufifrons, Schistocichla schistacea, S. leucostigma*, S. caurensis*, Myrmeciza ferruginea, M. hyperythtra, M. fortis**, Pithys albifrons**, Gymnopithys lunulatus, Rhegmatorhina melanosticta**, Hylophylax punctulatus, Phlegopsis nigromaculata, P. erythroptera, Chamaeza nobilis, Hylopezus macularius, H. berlepschi, Conopophaga aurita, C. melanogaster, C. peruviana**, Liosceles thoracicus**, Myiopagis flavivertex, Elaenia ruficeps*, Lophotriccus vitiosus, L. galeatus*, Hemitriccus minor, H. fammulatus**, H. minimus, Poecilotriccus calopterus, Taeniotriccus andrei, Todirostrum maculatum, T. chrysocrotaphum**, Platyrinchus saturatus*, P. platyrhynchos**, Neopipo cinnamomea, Myiozetetes luteiventris, Conopias parvus*, Tyrannopsis sulphurea, Rhytipterna immunda, Ramphotrigon ruficauda, R. fuscicauda**, Attila cinnamomeus, A. citriniventris, A. bolivianus, Phoenicircus carnifex, P. nigricollis, Rupicola rupicola*, Haematoderus militaris, Cotinga maynana, C. cotinga, C. cayana, Porphyrolaema porphyrolaema, Xipholena punicea*, X. lamellipennis, Gymnoderus foetidus, Tyranneutes stolzmanni, Machaeropterus pyrocephalus**, Lepidothrix iris, Xenopipo atronitens, Heterocercus lineatus, Pipra aureola, Schiffornis major, Iodopleura isabellae**, Pachyramphus minor**, Hylophilus semicinereus, H. brunneiceps, H. hypoxanthus**, H. muscicapinus*, Microbates collaris*, Polioptila guianensis, Turdus hauxwelli**, T. lawrencii*, Lamprospiza melanoleuca, Lanio versicolor**, Ramphocelus nigrogularis, Tangara callophrys, Dacnis albiventris, D. flaviventer, Cyanerpes nitidus**, Granatellus pelzelni*, Periporphyrus erythromelas*, Psarocolius viridis*, P. bifasciatus, Ocyalus latirostris**, Clypicterus oseryi**, and Lampropsar tanagrinus.*

Species Inhabiting Rivers and Streams. *Furnarius torridus, Furnarius minor, Synallaxis propinqua, Cranioleuca muelleri, Certhiaxis mustelinus, Thamnophilus cryptoleucus, Myrmotherula klagesi, M. assimilis, Myrmoborus lugubris, Elaenia pelzelni, Serpophaga hypoleuca, Knipolegus poecilocercus, K. orenocensis, Ochthornis littoralis, and Conirostrum margaritae.*

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