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COMPARISON OF CLOUD-FOREST AVIFAUNAS IN SOUTHEASTERN BRAZIL AND WESTERN COLOMBIA

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Resumo. Uma comparação entre as avifaunas de matas de neblina dos Andes ocidentais da Colômbia (La Planada 1800 m, Nariño, e para o norte até Valle) e das montanhas do sudeste brasileiro (Intervales 800 m, São Paulo, e para o norte até o Espirito Santo) resultaram em números muito similares de espécies em ambas as regiões (202 e 194, respectivamente). Em sua composição, os grupos ecológicos frequentemente mostraram espécies similares, com o pareamento de espécies facilmente sugerido para 167 espécies, ou 5 em cada 6 casos. Isto pode dever-se ao fato de que, com 100 das mesmas espécies ou congêneres (muitas vezes superspécies), os nichos ecológicos remanescentes podem estar restritos a espécies similares e facilmente pareadas. A presença de mais espécies de beija-flores e frugívoros do dossel na Colômbia deveu-se principalmente à existência de mais substituições ecológicas tanto altitudinais quanto latitudinais. A constatação de maior número de insetívoros de sub-bosque no Brasil deveu-se principalmente às várias espécies de aves de bambu e ao nosso limitado conhecimento das espécies de aves de bambu na Colômbia. Mais migrantes de longa distância foram notados entre as espécies insetívoras de dossel no Brasil, enquanto alguns migrantes norte-americanos parecem ter ocupado o lugar de insetívoros e frugívoros de sub-bosque na Colômbia. Migrações altitudinais a nível local ocorrem em ambas as regiões, especialmente entre os beija-flores e os frugívoros e neste último mesmo entre os de sub-bosque na Colômbia. Mais estudos são necessários, uma vez que tais espécies requerem parques e reservas com uma extensiva abrangência altitudinal para sua preservação, que são muitas vezes inexistentes, especialmente no Brasil, mas também em La Planada e outros locais importantes nos Andes. No sudeste do Brasil, em muitos casos, as espécies derivadas de grupos tropicais vivem nas matas de altitude, enquanto na Colômbia ocorrem espécies subtropicais andinas especializadas. Sugerimos que as florestas brasileiras são mais restritas altitudinalmente, carecendo de uma zona realmente tropical mais baixa devido à elevada latitude e apresentam áreas pequenas de florestas temperadas devido à extensao reduzida das cadeias de montanhas, de modo que espécies que se substituem altitudinalmente não podem ocorrer ali. Ao invés disso, as espécies tropicais de altitude (muitas vezes aparentadas à formas amazônicas) movem-se para o alto e para áreas subtropicais. A facilidade de migrações (para zonas próximas ao invés de distantes, em pequenas serras) pode também restringir a evolução de formas ocorrentes em montanhas e determinar um padrão de "tropicalização" das áreas elevadas nas matas de neblina brasileiras.

Resumen. Una comparación de la avifauna de los bosques de neblina de los Andes occidentales de Colombia (La Planada, 1800 m, de Nariño al norte hasta el Valle) y las montañas del sudeste de Brasil (Intervales, 800 m, de São Paulo al norte hasta Espirito Santo) mostró un número de especies notablemente similar, 202 a 194. Los grupos ecológicos frequentemente presentan especies similares, con el reemplazo fácilmente "pareado" sugerido en 167 especies, o 5 de cada 6. Esto puede deberse al hecho de que 100 de las especies ya sean las mismas o congenéricas (frequentemente superespecies), los nichos ecológicos restantes están probablemente restringidos a especies similares o fácilmente pareadas. La presencia de más picaflores y frugívoros de cobertura en Colombia se debió principalmente a mayores reemplazos ecológicos tanto altitudinal como latitudinal. El mayor número de insectívoros constatados en Brasil fue principalmente debido a la variedad de especies de aves de bambú y a nuestro limitado conocimiento de especies de bambú en Colombia. Algunas aves migratorias de mayor distancia fueron detectadas entre las insectívoras de cobertura en Brasil, mientras que en Colombia unas pocas aves migratorias Norte Americanas pueden haber tomado los lugares de insectívoros y frugívoros. Migraciones altitudinales locales aparecem en ambas regiones, especialmente entre los picaflores y frugívoros, esto último entre los del sotobosque en Colombia. Son necesarios más estudios para aquellas especies que requieren, parques de mayor extensión altitudinal, la que a menudo no es ofrecida especialmente en Brasil y en La Planada como tambien en otros sitios Andinos importantes. En muchos casos en el sudeste de Brasil, las especies derivadas de grupos tropicales vivem en los bosques de altura, mientras que Colombia tiene especies subtropicales andinas especializadas. Sugerimos que los bosques brasileños son altitudinalmente más restringidos careciendo de una zona realmente tropical mas baja debido a la elevada latitud, y presentando pequeñas áreas de bosques templados debido a la reducida extensión de las cadenas de montañas, de modo que las especies no pueden substituirse altitudinalmente con frecuencia mucho. Inversamente, las especies tropicales de altura (muchas veces emparentadas con las formas amazonicas) se movilizam hacia la altura

y áreas subtropicales. La facilidad de migraciones (a zonas próximas en vez de distantes, en pequeñas sierras) puede también restringir la evolución de las formas de montaña y determinar un patrón de "tropicalización" de las áreas elevadas en los bosques de neblina brasileños.

Abstract. A comparison of avifauna of cloud forests on the Western Andes of Colombia (La Planada 1800 m, Nariño, Colombia and north to Valle) and southeastern Brazilian mountains (Intervales 800 m, São Paulo and north to Espirito Santo) showed remarkably similar numbers of species, 202 to 194. Ecological groups often had similar species, with easily "paired" replacements suggested in 167 species, or 5 out of every 6 cases. This may be due to the fact that, with 100 of the species either the same or congeneric (often superspecies), remaining ecological niches are likely to be restricted to similar and easily paired species. More hummingbirds and canopy frugivores in Colombia were principally due to more altitudinal and latitudinal ecological replacements there. More understory insectivores in Brazil were mainly due to several bamboo species and our limited knowledge of bamboo species in Colombia. More long-distance migrants were noted among canopy insectivores in Brazil, while a few North American migrants in Colombia may have taken the places of understory insectivores and frugivores. Local altitudinal migrations occur in both regions, especially among hummingbirds and frugivores, the latter even from the understory in Colombia. More studies are needed, for such species require altitudinally extensive parks that are often not provided, especially in Brazil but also at La Planada and other important Andean sites. In many cases in southeastern Brazil, lowland species moved upward compared to Andean specialized montane replacements. We suggest that the Brazilian forests are narrower altitudinally, lacking a lower tropical zone due to high latitude, and with small areas of temperate forests due to small mountain ranges, so that altitudinally replacing groups cannot occur there. Instead, the upper tropical species (often related to Amazonian birds) moves up to the subtropical. Easy migrations (to nearby rather than distant lower zones, on small ranges) may also restrict evolution of montane forms and cause the "tropical-up" pattern southward. *Accepted 25 January 1993.*

Key words: Brazil, Colombia, Andes, avifaunas, cloud forests, ecological convergence, hummingbirds, migrant birds.

INTRODUCTION

One often wonders if similar habitats have similar species, especially when one sees striking convergences of one or two species, such as meadowlarks (*Sturnella* sp.) in American and pipits (*Macronyx* sp.) in African grasslands. Adaptive convergence has produced warbler-like insectivores in the Galapagos, Hawaii, the New and Old World as well as ground-foraging insectivores like pittas and antipittas in Asia and in Central and South America. Fry (1970) noted ecological convergences between jacamars of Neotropical forests and bee-eaters in the Old World.

While striking convergences do occur, it is also common to find considerable differences between continents. *Coereba*-like perching sunbirds use flowers in Africa, not hovering like hummingbirds, while larger honeyeaters use flowers in Australia. In the place of trunk-climbing Dendrocolaptidae and crosswise-clinging Formicariidae over army ants in the Neotropics, there are only horizontally-perching and poorly adapted thrushes and bulbuls over African driver ants. For some direct counterparts, there are usually many non-counterpart species. Numbers of species also vary widely.

Several authors have compared avifaunas of similar habitats in different continents, finding some similarities in numbers and niches of species. Karr & James (1975) compared tropical forest birds of four continents, finding some similar species, but not many one-to-one convergences (see also Karr 1976). Cody & Mooney (1978) compared birds of "Mediterranean" scrub in Chile, Sardinia, South Africa, and California, finding both similarities and differences, the latter often linked with localized flowering shrubs, feeding opportunities, or the absence of particular bird families.

Comparisons within a continent have also been reported. Comparing Panamanian mainland birds with those on islands off Panama, MacArthur *et al.* (1972) found some density compensation linked with lower species richness on the islands. Willis (1979) noted losses in certain ecological groups of birds in woodlots of different sizes in southeastern Brazil. Karr (1980) reported greater similarity of understory tropical birds when habitats of similar climate were not far apart (Costa Rica *versus* Panama, for instance). Haffer (1974) noted more species near the Andes in several lowland Neotropical avifaunas. Willis & Oniki (1978) compared antfollowing birds from Mexico and Argentina to the equator, finding more near the Andes and equatorially, with decreases up mountains or out into dry forests. Schluter (1990) notes that species-for-species matching has been possible in some cases, although noting that one can expect much variation between any two locations.

Meeting in early 1989 in wet cloud forests on the west side of the Colombian Andes, we wondered how the avifaunas of such forests might compare across the continent. Willis has worked extensively in cloud forests at 700—1200 m elevation from São Paulo to Espirito Santo in southeastern Brazil, and has some experience with similar forests at 1600—2000 m in western Colombia (Willis 1966a, b, c, 1988), where Schuchmann has worked intensively since 1975 (Schuchmann 1978, Schmidt-Marloh & Schuchmann 1980). In this paper, we make a first-order comparison of the two avifaunas, one (Brazil) at the border of the tropics and subject to winter cold, the other (Colombia) near the equator and relatively nonseasonal.

STUDY AREAS

We reviewed our field notes for bird species encountered at several sites in cloud forests in the two regions. For Colombia, the principal site was La Planada (00°54'N, 77°16'W, 1800—2000 m elevation) above Ricaurte in western Nariño. For Brazil, the principal site was Intervales (24°15'S, 48°20'W, 700—900 m elevation) on the Serra de Paranapiacaba in southeastern São Paulo State. Both are typical cloud forests, exactly in the zone where rising warm air condenses and drizzling rains are frequent; 4000 to 5000 mm of rain per year are normal; dense bromeliad and other epiphytes cover the trees. La Planada forests are much more moss-covered, whereas Intervales trunks are relatively free of epiphytes. Intervales has much large bamboo ("taquara") and dense tangles. Both areas have second-growth zones and clearings, but not large areas of these types.

We added to information from the two main sites by considering similar sites along the respective mountain ranges. In Colombia, we both have worked at San Antonio 1800 m, west of Cali, and Willis above Queremal at 1700 m just to the west. In Brazil, Willis & Oniki (1981) made observations at similar sites at Jacupiranga 750 m in southern São Paulo, Carlos Botelho State Park 800 m just northeast of Intervales, and Boracéia Reserve (Museu de Zoologia of the University of São Paulo) 800 m. Willis has records from Itatiaia National Park 1000—1200 m and Santa Teresa (Nova Lombardia 1000 m), in Rio de Janeiro and Espirito Santo, where zones of vegetation are higher. These localities are often less cloudy and humid than Intervales or La Planada, but their avifaunas are mostly similar.

RESULTS

Species numbers. Table 1 shows that these cloud forests are similar in number of species, 194 in the south (Brazil) and 202 in the north (Colombia). The excess in Colombia is largely due to more altitudinal (11 *versus* 3 in Brazil) or latitudinal replacements along the mountain range (4 *versus* 1 in Brazil), birds that only marginally occupy any given site together. Excluding these replacement species, 190 species are found in the Brazilian cloud forests and 187 in the Colombian cloud forests. In either case, the difference is less than 4%.

Principal differences between the two regions are excess nectarivores (hummingbirds) and canopy frugivores (trogons, parrots, thrushes) in Colombia and understory insectivores (mostly antshrikes and flycatchers) in Brazil.

Taxonomic similarities. 24 species, about 12,5%, are found in both Colombian and Brazilian cloud forests (Appendix 1). Hawks, tanagers, and aerial insectivores are the ecological groups with most species in common.

In 76 cases, about 38%, species in the same genus take similar niches north and south (Appendix 2; we include *Philodice* in *Calliphlox* and

TABLE 1. Cloud-forest birds in western Colombia and southeastern Brazil.

Bird Guild	Species	
	Colombia	Brazil
1. Seedeaters	9	10
2. Nectarivores	22	11
3. Ground frugivores		
4. Understory frugivores	3	3
5. Canopy frugivores	36	30
6. Ground insectivores	14	12
7. Understory insectivores	28	37
8. Trunk insectivores	13	12
9. Canopy insectivores	51	52
10. Aerial insectivores		3
11. Nocturnal insectivores	2	2
12. Nocturnal carnivores	4	4
13. Diurnal carnivores	8	8
14. Stream carnivores/insectivores	4	6
Total	202	194

Clytolaema in *Heliodoxa*). 15 cases of species pairs in canopy frugivores are noteworthy, and with two species in common make 17 of 30 such species in Brazil (36 in Colombia). 9 of 10 seed-eating species, all 4 nocturnal carnivores, 7 of 8 diurnal carnivores, 10 of 12 (13 in Colombia) trunk insectivores, and 4 of 6 (4 in Colombia) stream carnivores/insectivores are the same species or in the same genus. Even for understory insectivores, 12 of 37 (28 in Colombia) are accounted for, while so are 25 of 51 (52 in Colombia) canopy birds. In all, 100 or about half of the species are the same or close relatives in the same genus between the two regions.

Edge-living species, which travel widely in many cases, make up a fair proportion of species in common (9 of 24) and of congeneric species (18 of 76).

In the case of congener species pairs, a lowland form of the genus (or one with lowland relatives) moves upward elevationally in Brazil in 20 cases, whereas only one species moves upward elevationally in Colombia (*Nyctibius griseus*). We suspect that, in this last genus, we may have missed an upland species (*Nyctibius leucopterus*) probably present northward.

Counterpart species. In 57 cases, the bird that occurs in Colombia has a close ecological counterpart in the same family southward (Appendix 3). Some pairs match better than others, but none is very different. We are least certain of some counterparts among canopy insectivores/omnivores, such as suggesting that extra euphonias and a dacnis southward may take the place of part of the Colombian *Tangara* species-swarm.

In further 10 cases, we suggest species replacements by members of different families between the two regions (Appendix 4). The only extra ground fruiteater in Colombia is a dove (*Geotrygon frenata*), the only extra one south a tinamou (*Crypturellus obsoletus*), so we feel fairly certain of this case. Excess of understory antbirds south would be even worse if we did not pair them with the two excess understory wrens and two of the excess emberizids northward. We accept some differences in behavior and ecology in all these cases. Certain other cases in the following section might have been paired, as similar in ecology, but we think it sufficient that we have already "paired" 167 of the approximately 200 species in the different cloud forests, or 5 in 6.

In 33 cases in the 57 counterpart species, the southern bird is a lowland one or has lowland relatives; only *Cacicus chrysopterus* is a mostly upland species moving down (we have tentatively paired it with northern *Creurgops verticalis*, however, certainly not a lowland genus). 5 of the 10 cases of cross-family pairings represent a lowland bird moving upward in southeastern Brazil.

Where we have paired birds of different families, old South American groups have southward taken the place of worldwide or more northern families in 9 of 10 cases. In general, there is an excess of antbirds and related families southward and of nine-primaried oscines and the like northward.

Few birds in these groups are edge species; 5 of the 57 counterpart species, none of abovementioned 10. Edge species to now are 32, about 1 in 5; of course, nearby large clearings and dry valleys have more.

Unpaired species. We have not been able to pair 26 Brazilian species and 33 Colombian species, or about 1 in 6. Actually, many are simply altitudinal, latitudinal, or habitat (edge *versus* forest) replacements for a species we have already paired. Altitudinal replacements are 11 in Colombia, 3 in Brazil; latitudinal are 4 in Colombia and 1 in Brazil; edge replacements are 3 in Colombia.

The excess of hummingbirds in Colombia is partly altitudinal (3) or latitudinal (4) replacements, so that there are really 15 *versus* 11 species north/south. Snow (1986) had already noted, working at the Boracéia site in Brazil, that low numbers of visits to flowers could be caused by low hummingbird densities owing to the paucity of bird-flowering plant species. Feeding hummingbirds southward at Santa Teresa (Brazil) near one of our study sites (Nova Lombardia), does result in many species moving in from nearby habitats and in large numbers of individuals.

There are somewhat more canopy frugivores in Colombia than in Brazil even if we eliminate 5 altitudinal replacements there (*Turdus serranus*, *Trogon personatus*, *Amazona mercenaria* up the mountain, *Pionus chalcopterus* and *Pipreola jucunda* lower) and 1 in Brazil (*Brotogeris tirica* lower) plus a latitudinal replacement (*Touit surda* northward) there. If so, there are 31 in Colombia *versus* 28 in Brazil. There is a slight excess of

parakeets in Brazil (*Triclaria malachitacea*), and perhaps we should pair this with Colombian *Semnornis ramphastinus*. Otherwise, the excess birds northward are *Chamaepetes goudoti* (but *Penelope superciliaris* comes near our Brazilian sites) and a quetzal (*Pharomachrus auriceps*), unless *Trogon rufus* of the understory near our Brazilian sites could be a small replacement for it.

The real difference between Brazilian and Colombian cloud forests is in understory insectivores. Removing 2 altitudinal replacements in Brazil (*Drymophila ferruginea* downhill, *Mackenziaena leachi* uphill) still leaves 35 in Brazil *versus* 28 in Colombia. One main difference is bamboo-living insectivores southward, possibly because we were unable to study bamboo zones in the upper Anchicayá Valley west of Cali. Bamboo birds southward include an extra seedeater (*Sporophila frontalis*) and 4 understory insectivores (*Philydor fuscus* and its mimic *Biatas nigropectus* [Willis 1989]; *Drymophila rubricollis*; *Ramphotrigon megacephala*). We note that southeastern Brazil is an important zone of bamboo speciation, however, and some of the bamboo-inhabiting species occur at many sites, not just locally as in Colombia.

This leaves 5 unpaired understory birds in Colombia to 9 in Brazil (plus the unpaired understory woodpecker *Dryocopus galeatus* in Brazil, an obvious replacement for *Campephilus haematogaster* downhill from our Colombian sites). *Habia rubica* is uncommon up to Brazilian cloud forest, like its Colombian relative *Habia cristata* (Willis 1966b; not registered in cloud forest itself), and might be eliminated to leave only 3 excess species southward. In Colombia, mossy-trunk *Premnoplex brunnescens* and *Myiotriccus ornatus*, understory *Pseudotriccus pelzelni*, plus edge *Wilsonia canadensis* (a migrant) and *Iridophanes pulcherrima* seem without southern counterparts. In Brazil, there are larger flycatching species (*Trichothraupis melanops*, *Schiffornis virescens*, *Attila rufus*) and small edge flycatchers (*Myiornis auricularis*, *Hemitriccus nidipendulus*), plus several understory antbirds (*Myrmotherula gularis*, *Dysithamnus stictothorax*, *Mackenziaena severa*). *Premnoplex* may take the place of the Brazilian streamside *Lochmias nematura*, but has a wider niche, whereas *Dendrocincla tyrannina* of Colombian trunks is ecologically rather like souther *Attila rufus* (if one notes that *D. turdina* is not common up in cloud forest in Brazil and perhaps should be dropped). *Myadestes ralloides* is widespread in Colombia and may correspond to *Trichothraupis melanops* of Brazil rather than to local (Espirito Santo) *Cichlopsis leucogenys*, which could also be dropped. If so, there would only be one extra understory bird southward, other than the bamboo specialists.

Migratory species. We had thought there would be more migration in Brazil, with its cold winters, than in Colombia. This is the case among canopy insectivores/omnivores, where 8 species are summer birds in Brazil (*Pipraeidea*, *Tersina*, *Contopus borealis*, *Vireo olivaceus*, *Dacnis nigripes*, *Myiarchus swainsoni*, *Myiodynastes maculatus*, *Attila phoenicurus*) and only the first 3 plus *Dendroica fusca* in Colombia. We know there is considerable migration among hummingbirds and canopy frugivores in both regions, but lack detailed information. Edge and canopy small frugivores in the south move to nearby valleys and the base of the mountain range during cold waves, as is well known to cage-bird fanciers who even catch them out in banana plantations. How much this phenomenon occurs in Colombia is hard to say, although we know of several migrants (e.g., *Pipreola jucunda* and *Pharomachrus auriceps*). Conservation of elevational gradients is necessary to preserve altitudinal migrants, both in Colombia and other regions. Oddly, 2 of 3 understory frugivores are migratory in Colombia (*Allocotopterus*, *Catharus*) but their Brazilian counterparts are not.

Colombia receives more North American migrants than does southeastern Brazil, though *Contopus borealis* occurs in both. We have not counted *Catharus fuscescens* in Brazil, although it reaches the edge of forests there in small numbers. Rather few species of northern migrants enter cloud forest northward, too, although 2 move into the understory, where we have shown migrations of small frugivores plus deficit of resident species. Whether migrants northward force compensatory migrations in resident species or prevent some from using the understory is uncertain.

Our data indicate little migration among understory birds in Brazil or Colombia, with the exceptions noted above. Bamboo seedeaters are known to irrupt rather than migrate, moving to any region with a bamboo seed crop, but due to deforestation are now rare everywhere. The open-area seedeaters migrate, but their move-

ments are only marginally relevant to this report.

DISCUSSION

In general, we had not expected such a close correspondence between cloud-forest birds in western Colombia and southeastern Brazil. The correspondence may be caused by the large number of identical or congeneric species, 100 of the 200 or so. We suspect that, once 100 identical or similar species are thrown onto two "ecological maps," the remaining "patches" (niches) are fairly well defined and have to be occupied by ecologically similar species. At least, 67 other species in each region were easy to "pair" with their counterpart. On other continents, one would not get such a strong group of nearly-identical species, and birds could subdivide the ecological maps quite differently.

Replacement species. It is clear that Colombian sites have more altitudinal or latitudinal replacement species than do Brazilian ones. Cloud forest in Brazil is closer to the coast, both altitudinally and horizontally, for the low subtropical zone on the Tropic of Capricorn puts the cloud level lower. This leaves less room for multiple species to divide up an altitudinal gradient, for Brazil lacks the lower tropical zone coastally and hence cannot have a lower-tropical-to-lower-subtropical species. Brazil also lacks forest area and elevation above cloud forest on its smaller and lower mountain ranges. At 1400 to 2000 m there, chaparral or timberline formations take over, leaving only 500—1000 m of forest above the cloud zone rather than the 1000 to 1500 m in Colombia.

Latitudinal replacements along mountain ranges are also more common in Colombia, although not frequent in our study regions. The great length and complexity of the Andean chain, plus its subdivision compared to Brazilian ranges, may support forms that would soon go extinct or never arise, due to lack of geographical barriers, on the smaller Brazilian ranges.

Other avifaunal differences. The reduced number of hummingbirds in southeastern Brazilian cloud forests, compared with the Andes, has been attributed to lack of appropriate flowers (Snow 1986). Neither cloud forest is very favorable for hummingbirds, due to frequent rains and drizzles, so the general idea that upland cooler climates favor warm-blooded pollinators (rather than insects) may not apply. Extra movements of hummingbirds southward are needed for cold winters, so highland species are few there (*Stephanoxis*, *Leucochloris*). It may be that the reduced number of hummingbird flowers in the Brazilian uplands is a result of a habitat squeeze for hummingbirds between cold winters and the rainy cloud zone.

Canopy frugivores and understory insectivores differed less between regions than it seemed at first. Andean species do split up habitats, elevations, and geography more freely than do southern ones, so that more species occur in a wide region there even if not within any one habitat. Bamboo areas southward may increase understory diversity, while less moss on trunks there may be more favorable for birds and less for frogs, spiders, and other very small insectivores.

The large *Tangara* "species swarm" in Colombia is replaced by a few *Tangara* and several extra other small tanagers in Brazil, perhaps even by *Piprites*, *Oxyruncus*, and other species more characteristic of lower montane areas in Colombia. Antbirds take the place of wrens and nine-primaried oscines to some extent in the Brazilian area, but this mainly reflects the general tendency for lowland species and genera to move up into the subtropical zone there. Apparently, the upland avifaunas of the Andes are partly lacking southward, allowing lowland tinamou, antbird, and other groups to move upward. Also, the southeastern avifauna has been derived partly from the Andes and partly from Amazonia, so that Amazonian groups may have taken the place of Andean groups that never reached the southeast (Willis 1992). Terborgh (1973) indicated that species-rich tropical forest forms may regularly spread into "peripheral" habitats.

Absence of true upland avifaunas in Brazil, other than a few species, may also result from the narrow range of life zones there, vertically and horizontally. As noted above, even the lowlands are upper-tropical rather than lower-tropical, while upland areas are reduced and the cloud-forest and subtropical zones are generally narrow. Furthermore, cold winters and physically close and narrow elevation ranges may favor altitudinal migration and make the derivation of truly montane groups difficult.

Lack of detailed information hinders our analysis of composition of migrant species,

except that several southeastern canopy species move toward Amazonia in the winter, while North America migrants northward may push some understory species out there. Altitudinal migration needs more study both in Brazil and Colombia, since migrations make environmental protection necessary in areas with wide elevation ranges rather than the narrow isolated parks usually considered sufficient. La Planada, San Antonio and other important Colombian areas do not provide protected altitudinal habitat diversity, while Brazilian sites tend to be undergoing rapid development on the narrow coastal plains. Altitudinally extensive parks, like Munchique and the Farallones of Cali in Colombia, should go well out into lowland forests even if these areas are flat and under economic pressure.

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APPENDIX 1. Birds common to both Brazilian and Colombian cloud forests.

Zonotrichia capensis
Notiochelidon cyanoleuca
Streptoprocne zonaris
Geotrygon montana
Glaucidium minutissimum
Micrastur ruficollis
Accipiter bicolor
Buteo leucorrhous
Elanoides forficatus
Pyroderus scutatus
Chloroceryle amazona
Tigrisoma fasciatum
Platyrinchus mystaceus
Piranga flava
Tersina viridis
Pipraeidea melanonota
Euphonia xanthogaster
Euphonia musica
Parula pitiayumi
Dryocopus lineatus
Amazona farinosa
Philydor rufus
Contopus borealis

APPENDIX 2. Congener pairs found in Brazilian and Colombian cloud forests.

Carduelis magellanica/xanthogastra
Sporophila caerulescens/nigricollis
Sporophila falcirostris/schistacea
Haplospiza concolor/rustica
Amaurospiza moesta/concolor
Tiaris fuliginosa/obscura
Claravis geoffroyi/mondetoura
Odontophorus capueira/melanonota
Phaethornis squalidus/griseogularis
Phaethornis eurynome/guy
Calliphlox amethystina/mitchelli
Heliodoxa rubricauda/rubinoides
Nyctibius aethereus/griseus
Pulsatrix koeniswaldiana/melanota
Otus atricapillus/columbianus
Ciccaba virgata/albitarsus
Accipiter superciliosus/striatus
Leucopternis polionota/princeps
Selenidera maculirostris/spectabilis
Trogon surrucura/collaris
Trogon viridis/melanurus
Saltator maxillosus/atripennis
Sclerurus scansor/mexicanus
Grallaria varia/gigantea
Scytalopus indigoticus/femoralis
Scytalopus speluncae/unicolor
Basileuterus rivularis/fulvicauda
Serpophaga nigricans/cinerea
Ramphocelus bresilius/flammigerus
Hylophilus poicilotis/semibrunneus
Basileuterus culicivorus/tristriatus
Syndactyla rufosuperciliata/subalaris
Synallaxis ruficapilla/brachyura
Thamnophilus caerulescens/unicolor
Drymophila malura/caudata
Knipolegus cyanirostris/poecilurus
Campephilus robustus/pollens
Melanerpes flavifrons/formicivorus
Veniliornis spilogaster/dignus
Piculus aurulentus/rubiginosus
Picumnus cirratus/granadensis
Dendrocincla turdina/tyrannina
Xiphocolaptes albicollis/promeropirhynchus
Lepidocolaptes squamatus/affinis
Campylorhamphus falcularius/pusillus
Platycichla flavipes/leucops
Turdus albicollis/obsoletus
Turdus amaurochalinus/ignobilis
Columba cayennensis/fasciata
Columba plumbea/subvinacea
Forpus xanthopterygius/conspicillatus
Touit melanonota/stictoptera
Pionopsitta pileata/pulchra
Pionus maximiliani/seniloides
Penelope obscura/ortoni
Lipaugus lanioides/cryptolophus
Mionectes rufiventris/striaticollis
Myiobius atricaudus/villosus
Pogonotriccus eximius/poicilotis
Thraupsis ornata/cyanocephala
Vireo olivaceus/leucophrys
Euphonia violacea/laniirostris
Pachyramphus castaneus/versicolor
Tangara desmaresti/ruficervix
Tangara cyanocephala/nigroviridis
Tangara seledon/rufigula
Tangara preciosa/vitriolina
Hemithraupis ruficapilla/guira
Cyclarhis gujanensis/nigrirostris
Dacnis nigripes/hartlaubi
Cranioleuca pallida/erythrops
Terenura maculata/callinota
Phyllomyias griseocapillus/cinereiceps
Myiarchus swainsonii/tuberculifer
Conopias trivirgata/cinchoneti
Myiodynastes maculatus/chrysocephalus

APPENDIX 3. Ecologically similar species of cloud forests (Brazil/Colombia).

Volatinia jacarina/Tiaris olivacea
Chaetura cinereiventris/Cypseloides rutilus
Tinamus solitarius/Nothocercus bonapartei
Ramphodon naevius/Androdon aequatorialis
Glaucis hirsuta/Doryfera ludoviciae
Thalurania glaucopis/Haplophaedia lugens
Lophornis chalybea/Ocreatus underwoodii
Leucochloris albicollis/Schistes geoffroyi
Melanotrochilus fuscus/Colibri coruscans
Stephanoxis lalandii/Lesbia victoriae
Macropsalis creagra/Uropsalis lyra
Spizaetus tyrannus/Oraetus isidori
Chiroxiphia caudata/Masius chrysopterus
Ilicura militaris/Allocotopterus deliciosus
Cichlopsis leucogenys/Myadestes ralloides
Turdus rufiventris/Entomodestes coracinus
Pyrrhura frontalis/Bolborhynchus lineata
Pipile jacutinga/Aburria aburri
Procnias nudicollis/Rupicola peruviana
Carpornis cucullatus/Pipreola riefferi
Tityra cayana/Ampelioides tschudii
Phibalura flavirostris/Ampelion rufaxilla
Baillonius bailloni/Aulacorhynchus prasinus
Ramphastos dicolurus/Andigena laminirostris
Arremon taciturnus/Atlapetes torquatus
Basileuterus leucoblepharus/Atlapetes brunneinucha
Chamaeza meruloides/Formicarius rufipectus
Chamaeza campanisona/Grallaria flavotincta
Conopophaga lineata/Grallaricula flavirostris
Pyriglena leucoptera/Myrmeciza immaculata
Pyrrhocoma ruficeps/Atlapetes tricolor
Tachyphonus coronatus/Iridosornis porphyrocephala
Philydor amaurotis/Premnoplex guttuligera
Philydor atricapillus/Thripadectes virgaticeps
Todirostrum plumbeiceps/Poecilotriccus ruficeps
Leptopogon amaurocephalus/Rhynchocyclus fulvipectus

Hemitriccus diops/Pseudotriccus ruficeps
Pitylus fuliginosus/Bangsia edwardsi
Orthogonys chloricterus/Buthraupis montana
Cissopis leveriana/Chlorornis riefferi
Tachyphonus cristatus/Chlorospingus semifuscus
Stephanophorus diadematus/Anisognathus flavinucha
Thraupis cyanoptera/Anisognathus notabilis
Euphonia pectoralis/Tangara parzudakii
Euphonia chalybea/Tangara heinei
Dacnis cayana/Tangara labradorides
Cacicus chrysopterus/Creurgops verticalis
Coereba flaveola/Diglossa albilatera
Conirostrum speciosum/Dendroica fusca
Philydor leucophrys/Thripadectes virgaticeps
Philydor lichtensteini/Pseudocolaptes sp.
Xenops contaminatus/Margarornis squamiger
Phyllomyias fasciatus/Camptostoma obsoletum
Colonia colonus/Contopus fumigatus
Phylloscartes oustaleti/Myiophobus pulcher
Tolmomyias sulphurescens/Myiophobus flavicans
Myiopagis caniceps/Phyllomyias plumbeiceps

APPENDIX 4. Ecologically similar pairs (Brazil/Colombia) in different families.

Crypturellus obsoletus/Geotrygon frenata
Hylopezus nattereri/Cyphorhinus thoracicus
Myrmeciza squamosa/Oreothraupis arremonops
Neopelma aurifrons/Catharus ustulatus
Drymophila ochropyga/Henicorhina leucophrys
Batara cinerea/Cyanolyca pulchra
Dysithamnus mentalis/Chlorochrysa nitidissima
Oxyruncus cristatus/Chlorochrysa phoenicotis
Phylloscartes ventralis/Myioborus miniatus
Orchesticus abeillei/Cinnycerthia peruana

APPENDIX 5. Unpaired species.

Colombia

Edge
- *Veniliornis fumigatus*
- *Piculus rivolii*
- *Basileuterus coronatus*

Altitudinal Replacement
- *Phaethornis superciliosus*
- *Phaethornis longuemareus*
- *Amazilia tzacatl*
- *Turdus serranus*
- *Pionus chalcopterus*
- *Amazona mercenaria*
- *Trogon personatus*
- *Pipreola jucunda*
- *Lysurus castaneiceps*
- *Scytalopus senilis*
- *Diglossa indigotica*

Latitudinal Replacement
- *Lesbia nuna*
- *Haplophaedia aureliae*
- *Aglaiocercus kingi*
- *Boissonneaua flavescens*

Others
- *Eutoxeres aquila*
- *Coeligena wilsoni*
- *Aglaiocercus coelestis*
- *Boissonneaua jardini*
- *Ognorhynchus icterotis*
- *Chamaepetes goudoti*
- *Semnornis ramphastinus*
- *Pharomachrus auriceps*
- *Wilsonia canadensis*
- *Premnoplex brunnescens*
- *Pseudotriccus pelzelni*
- *Myiotriccus ornatus*
- *Iridophanes pulcherrima*
- *Zimmerius viridiflavus*
- *Pyrrhomyias cinnamomea*

Brazil

Edge
- *Myiornis auricularis*
- *Hemitriccus nidipendulus*

Altitudinal Replacement
- *Brotogeris tirica*
- *Mackenziaena leachi*
- *Drymophila ferruginea*

Latitudinal Replacement
- *Touit surda*

Others
- *Dryocopus galeatus*
- *Triclaria malachitacea*
- *Aramides saracura*
- *Lochmias nematura*
- *Habia rubica*
- *Trichothraupis melanops*
- *Schiffornis virescens*
- *Mackenziaena severa*
- *Myrmotherula gularis*
- *Dysithamnus stictothorax*
- *Attila rufus*
- *Xenops rutilans*
- *Herpsilochmus rufimarginatus*
- *Dysithamnus xanthopterus*
- *Attila phoeniceus*