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BIRD SPECIATION IN SUBTROPICAL SOUTH AMERICA IN RELATION TO FOREST EXPANSION AND RETRACTION

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ABSTRACT.—I analyzed two patterns of bird distribution in subtropical South America. The first was the disjunct distribution of pairs of species and subspecies between the southern Yungas and the Paranense forests, which are separated by 700 km of xerophytic Chaco woodland. Forest birds penetrate up to 200 km into the Chaco along gallery forests, but do not cross the rest of the Chaco, which constitutes an effective barrier. The second pattern involved several zones of secondary contact located in the Chaco lowland, where several woodland and grassland species and subspecies interact. I conclude that both bird-distribution patterns were produced by forest expansions along the Bermejo and Pilcomayo rivers that connected the southern Yungas to the Paranense region and interrupted the arid vegetation in the center of the Chaco. Vegetational fluctuations probably occurred several times during the Quaternary and produced phenotypic differentiation of sister taxa, both in the now-disjunct forests and in the currently continuous Chaco. *Received 26 June 1990, accepted 10 January 1992.*

THE FOREST and woodland area located around the Tropic of Capricorn in South America is biogeographically complex. The region shows two distinct features: (1) the southernmost extension of tropical South American forests (Paranense and southern Yungas), with a high degree of avian endemism (Cracraft 1985, Nores 1989); and (2) the central Chaco woodland, with low avian endemism (Short 1975). Relatively little is known about the climatic history of the area and the effects of Quaternary climatic changes on the dispersal and differentiation of bird species. Understanding shifts in the region's vegetation during the Quaternary could help to provide clues about events in the rest of South America (B. Simpson, pers. comm.).

Two separate patterns in the distribution of the avifauna probably resulted from large-scale vegetational dynamics during the Quaternary. First, there are several species and subspecies pairs that have disjunct populations in the southern Yungas and Paranense forests, separated by 700 km of xerophytic Chaco woodland (Fig. 1). Second, a zone of disjunction occurs in the Chaco, along the Bermejo and Pilcomayo rivers, where the distribution of several species and subspecies pairs of woodland and grassland birds meet (Fig. 1).

The first pattern was previously pointed out by Olrog (1963), who noted that several bird species of the southern Yungas also occur in the Paranense forest, or are represented there by another subspecies. Later, he (Olrog 1979a) concluded that the Paranense forest of Misiones was once continuous, through Paraguay, with the Yungas of Tucumán-Bolivia. However, Olrog (1984) reversed this idea when he presented a present-day ornithogeographic map of Argentina in which he connected both regions by a continuous gallery forest along the Pilcomayo River. With regard to the second pattern, Short (1975) identified the area of the Bermejo and Pilcomayo rivers as a zone that marks a disjuction in bird distribution in South America.

Research carried out in South America over the last 30 years has shown that, during the Quaternary, semiarid conditions alternated with humid phases. These cycles caused shrinkages of formerly widespread forests into humid pockets (refuges), followed by their subsequent reexpansion (Garner 1959, Bigarella and Andrade 1965, Haffer 1969, 1974, Mayr 1969, Mayr and O'Hara 1986, Vanzolini and Williams 1970, Vuilleumier 1971, Prance 1974, Van der Hammen 1974, 1982, Tricart 1974, 1975, Simpson and Haffer 1978, Absy 1979, 1982, Schubert 1988). Paleoecological data and present distribution patterns of animals and plants suggest that during interglacial phases there were periods when temperature and humidity were higher and forests more widely distributed than today (Groeber 1936, Smith 1962, Vanzolini 1968, 1974, 1981, Haffer 1974, 1985, Van der Hammen 1974, 1982, 1983, Fitzpatrick 1980, Markgraf 1985, Nores and Cerana 1990). Some authors consider the evidence of aridity during the glacial pe-

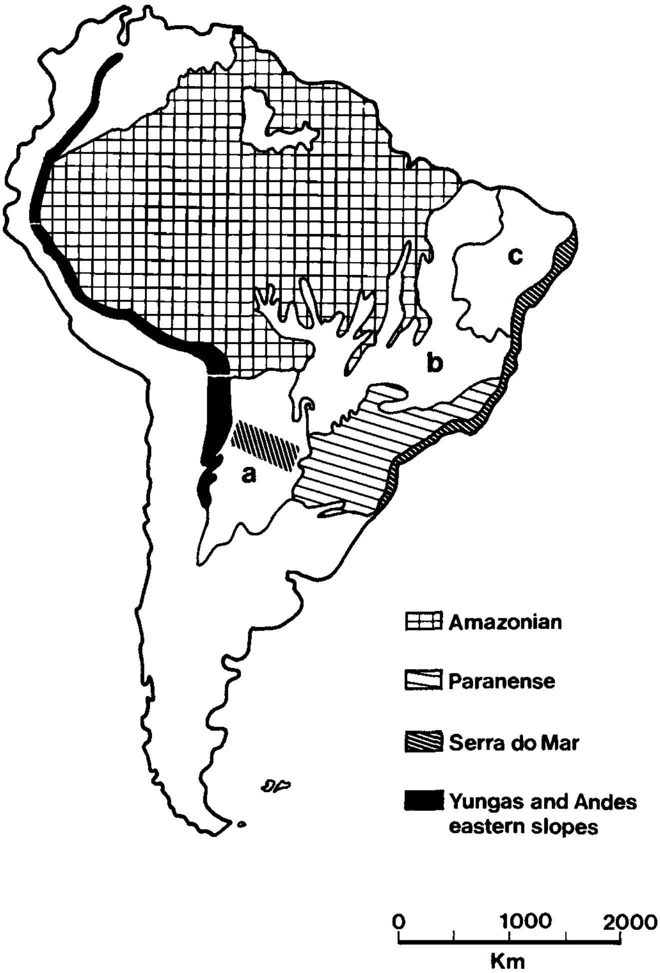


Fig. 1 Biogeographic provinces of South America, excluding the Pacific coast, most of the Andes, and southern and central Argentina (adapted from Cabrera and Willink 1973). Three regions that form the "arid diagonal" (Vanzolini 1974, Fitzpatrick 1980): (a) Chaco, showing the area of interaction of woodland and grassland birds (box with oblique lines); (b) Cerrado; and (c) Caatinga. From south to north, the breaks in the black band (representing Yungas and Andes slopes) mark the limit of the southern Yungas, northern Yungas, and eastern slopes of the northern Andes.

riods to be insufficient to indicate that the wet tropical lowlands changed substantially (Connors 1986, Colinvaux 1989). Endler (1977, 1982a, b) pointed out that current patterns of distribution are consistent with geographical divergence and adaptations to present-day conditions. Consequently, it is not necessary to postulate refuges to explain the observed distributions.

To determine if the two patterns of the avifauna are related to Quaternary climatic changes and if they have common histories, I studied the distribution of forest birds and plants in the Chaco lowland. I then compared the levels of phenotypic differentiation of the birds that inhabit the southern Yungas with those occurring in the Paranense region, and examined the ranges of woodland and grassland birds that currently interact in the center of the Chaco. Finally, I related the extent of phenotypic dif-

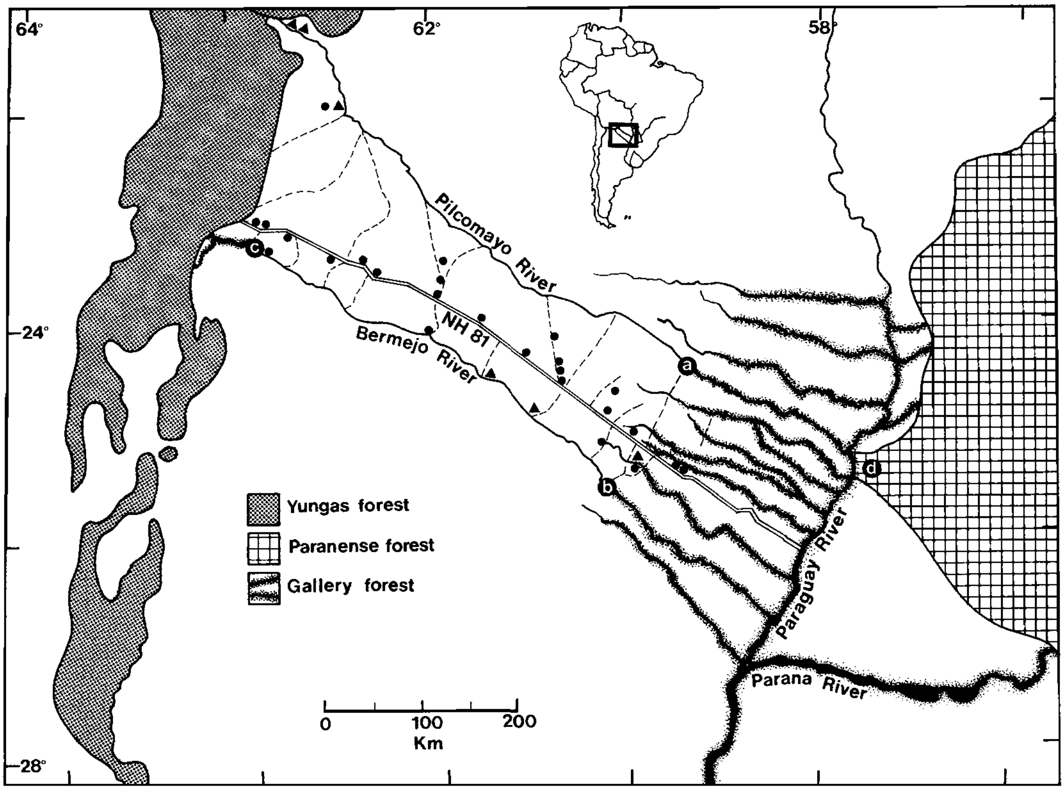


Fig. 2. Vegetation distribution in study area. Solid dots indicate location of dry riverbeds with forest patches. Triangles indicate presence of forest trees related to present-day watercourses. (a, b and c) The most extreme locations of gallery forests in Chaco lowlands. (d) Paranense forest wedge reaching Paraguay River. Gallery forests located east of Paraguay and Paraná rivers, in flooded area, are not represented (from Nores 1989).

ferentiation of these birds with vegetation changes that apparently occurred in South America during the Pleistocene and Holocene.

Study Area

The study area is subtropical South America, specifically the region drained by the Bermejo, Pilcomayo, Paraguay, and Paraná rivers (Fig. 2). From west to east it includes three components.

The first component is the forests on the eastern slopes and foothills of the Andes, and on the Sierras Pampeanas south of 18°S (southern Yungas). These forests stretch from Santa Cruz and Cochabamba departments in Bolivia to Catamarca Province in Argentina. I defined three altitudinal belts: (a) basal forest between 350 m and 600 m; (b) cloud forest between 600 and 1,500 m; and (c) montane deciduous forest between 1,400 and 2,500 m.

The second component includes the Chaco lowland drained by the Bermejo and Pilcomayo rivers and other small tributaries of the Paraguay River. Approximately 700 km wide, this area slopes gently from west to east, and extends into Argentina, Bolivia and Paraguay. Rainfall increases markedly from 500 mm in the west to 1,300 mm in the east. The Chaco, together with the "Cerrado" and "Caatinga" in Brazil, forms the "arid diagonal" (Vanzolini 1974, Fitzpatrick 1980; Fig. 1).

The third component is the forest and "campos" (Paranense region) of southeastern Brazil, eastern Paraguay and northeastern Argentina, around the upper courses of the Paraná and Uruguay rivers. Rainfall decreases towards the west from 1,700 mm to 1,300 mm. As a result, the vegetation becomes increasingly impoverished and it ends in a narrow wedge on the Paraguay River (Fig. 2, point *d*). Detailed descriptions of the study area are given in Hauman et al. (1947), Adámoli et al. (1972), Short (1975), and Cabrera (1976).

Materials and Methods

Avifauna.—I carried out field work from 1973 to 1988 in the forests and Chaco woodland of northern

Argentina, southern Bolivia, eastern Paraguay, and southern Brazil (Nores 1989). From 1986 to 1988 I concentrated on areas of particular biogeographic complexity. These included river and stream banks, forest patches on dry riverbeds, Paranense prairies, and the interaction zone in the Chaco lowland. I covered Argentine National Highway 81, which crosses the Chaco lowland from east to west, and most of the secondary roads that give access to the Bermejo and Pilcomayo rivers and other small water courses (Fig. 2). At each study site, I identified all bird species present through a combination of visual observations, song identification, song playback, and capture with mist nets.

I examined skin collections at the Fundación Miguel Lillo in Tucumán and at the Museo Argentino de Ciencias Naturales in Buenos Aires. These institutions house good bird collections from the study area, especially from the forests of Misiones, Tucumán, and Jujuy. To estimate the levels of phenotypic differentiation reached by the populations of forest and Chaco birds, I analyzed plumage pattern, color, and body measurements (wing chord, tail and exposed culmen). After applying general methods used in comparative systematics, I classified disjunct populations in terms of presence or absence of geographical variation. In those cases showing variation, I applied the terminology of Mayr (1963), Amadon (1966), and Amadon and Short (1976), but I used their categories in a more general way. I recognized *allospecies* as allopatric species with similar morphological characteristics; *megasubspecies* as subspecies that are conspicuously distinct in color or size, and *subspecies* as populations with some morphological differences, and generally with partial overlap of diagnostic characters. *Polytopic subspecies* are composed of geographically separated and indistinguishable populations.

Vegetation.—I determined the presence or absence of gallery forest and the forest tree species present at each sampling site on the Bermejo and Pilcomayo rivers, and on small rivers and streams. By visual observation, I surveyed dry riverbeds from the base of the Andes up to the Paraguay River. At each dry riverbed, I determined the presence or absence of forest patches and recorded the forest tree species present (Nores 1989).

Results

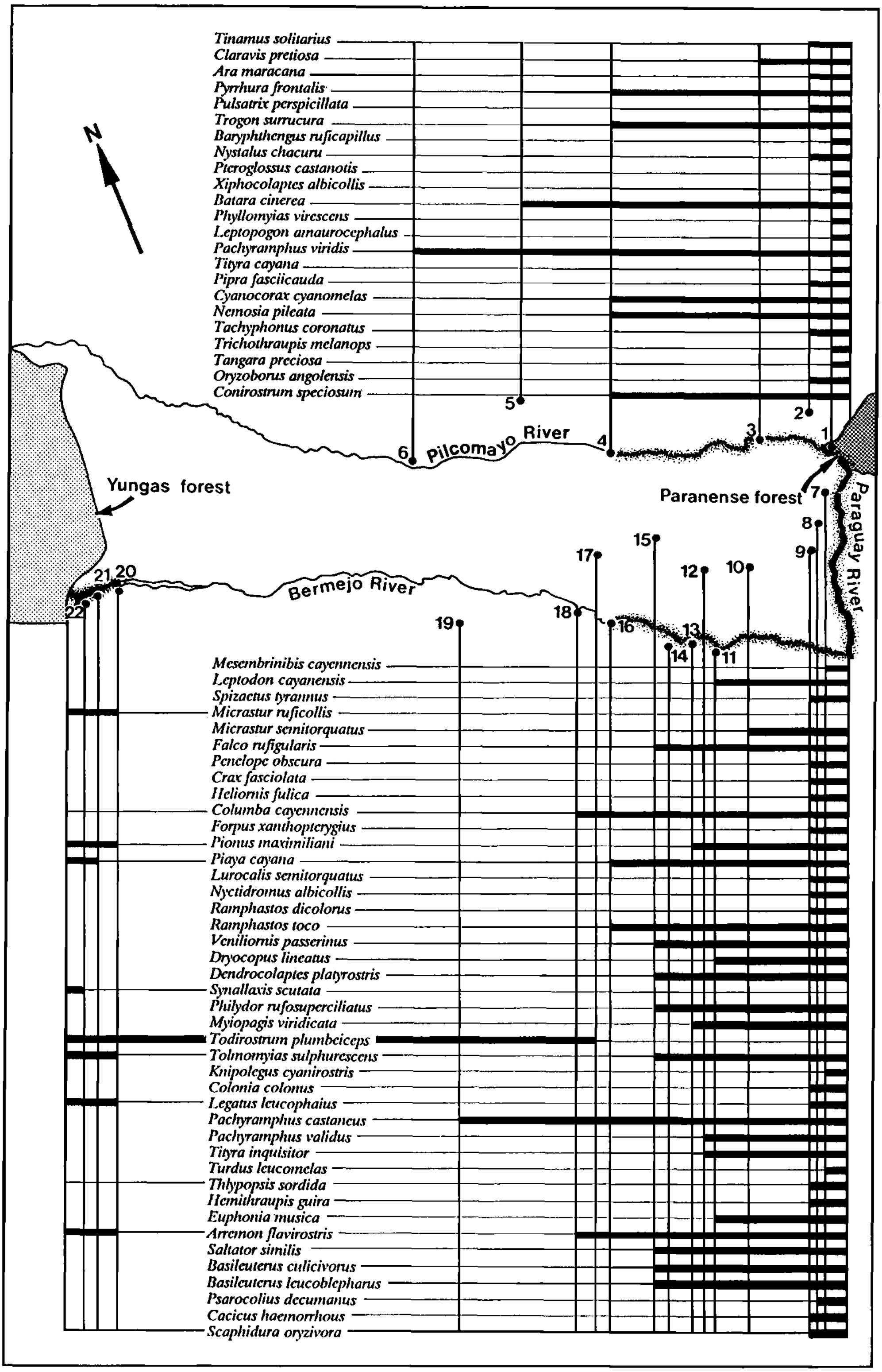
Distribution of forest vegetation.—Some forest trees occur throughout the entire Chaco (Fig. 2). This contradicts statements by Morello and Adámoli (1974), who indicated that a large semiarid gap prevents any plant species from the southern Yungas from reaching the Paranense region.

In the flooded areas of the eastern Chaco, forest vegetation occurs as narrow galleries on river and stream banks. Outside the flooded areas, the gallery forests widen considerably. On the Pilcomayo and Bermejo rivers, the gallery forests extend about 200 km to the west, reaching Fortín Sargento Primero Leyes (24°30'S, 59°23'W) and Puerto Bermejo (25°39'S, 60°08'W; see Fig. 2, points *a* and *b*). On the streams, the gallery forests are somewhat shorter.

In the central and western Chaco rainfall is lower and forest trees occur as small patches (of one to five species) on dry riverbeds, or in small groups (of one to three species) on river banks. The most common species are: *Phyllostylon rhamnoides* (Ulmaceae); *Chlorophora tinctoria* (Moraceae); *Ruprechtia laxiflora* (Polygonaceae); *Pisonia zapallo* (Nyctaginaceae); *Acacia albocorticata, Anadenanthera colubrina, Cathormion polyanthum, Enterolobium contortisiliquum, Gleditsia amorphoides, Pithecellobium scalare* and *Pterogyne nitens* (Fabaceae); *Astronium balansae* and *A. urundeuva* (Anacardiaceae); *Patagonula americana* (Boraginaceae); *Tabebuia ipe* (Bignoniaceae); and *Calycophyllum multiflorum* (Rubiaceae). Near the Andes, a short gallery forest extends eastward along the Bermejo River for about 45 km, up to Batea (23°22'S, 63°43'W; see Fig. 2, point *c*). There is no gallery forest along the Pilcomayo River in this zone. Consequently, the shortest distance between the Paranense and southern Yungas forests, about 450 km, occurs between the gallery forests along the upper and lower Bermejo River (Fig. 2).

Distribution of forest birds.—The distribution of forest birds in the Chaco lowland (Fig. 3) shows that the eastern gallery forests represent major avenues by which the Paranense birds penetrate westward into the Chaco lowland. Of 236 forest bird species recorded between 54° and 55°W, 62 (26%) reach the Paraguay River, and 54 (23%) occur in the gallery forests of the Bermejo and Pilcomayo rivers and other water courses.

In the west, the gallery forest of the Bermejo River also allows dispersal of forest birds from the southern Yungas into the Chaco, but this encroachment is not as conspicuous as in the east. Of 115 forest bird species recorded in the southern Yungas, only 10 (11%) occur in the Bermejo gallery forest. In the remainder of the central and western Chaco lowland, including the forest patches, there are virtually no forest birds. Only *Todirostrum plumbeiceps* (recorded on the Pilcomayo River [21°09'S, 63°12'W], on the Bermejo River [24°38'S, 61°25'W], and in Bru-


Tinamus solitarius
Claravis pretiosa
Ara maracana
Pyrrhura frontalis
Pulsatrix perspicillata
Trogon surrucura
Baryphthengus ruficapillus
Nystalus chacuru
Pteroglossus castanotis
Xiphocolaptes albicollis
Batara cinerea
Phyllomyias virescens
Leptopogon amaurocephalus
Pachyramphus viridis
Tityra cayana
Pipra fasciicauda
Cyanocorax cyanomelas
Nemosia pileata
Tachyphonus coronatus
Trichothraupis melanops
Tangara preciosa
Oryzoborus angolensis
Conirostrum speciosum
N
Pilcomayo River
Yungas forest
Paranense forest
Paraguay River
Bermejo River
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Mesembrinibis cayennensis
Leptodon cayanensis
Spizactus tyrannus
Micrastur ruficollis
Micrastur semitorquatus
Falco rufigularis
Penelope obscura
Crax fasciolata
Heliornis fulica
Columba cayennensis
Forpus xanthopterygius
Pionus maximiliani
Piaya cayana
Lurocalis semitorquatus
Nyctidromus albicollis
Ramphastos dicolorus
Ramphastos toco
Veniliornis passerinus
Dryocopus lineatus
Dendrocolaptes platyrostris
Synallaxis scutata
Philydor rufosuperciliatus
Myiopagis viridicata
Todirostrum plumbeiceps
Tolmomyias sulphurescens
Knipolegus cyanirostris
Colonia colonus
Legatus leucophaius
Pachyramphus castaneus
Pachyramphus validus
Tityra inquisitor
Turdus leucomelas
Thlypopsis sordida
Hemithraupis guira
Euphonia musica
Arremon flavirostris
Saltator similis
Basileuterus culicivorus
Basileuterus leucoblepharus
Psarocolius decumanus
Cacicus haemorrhous
Scaphidura oryzivora

chard [25°09′S, 59°58′W]) crossed the western Chaco from the southern Yungas along the rivers. Some Paranense birds occasionally followed the rivers or marshy lands westward beyond the limit of the gallery forests, but did not penetrate the xerophytic Chaco. Examples are *Columba cayennensis, Batara cinerea, Pachyramphus viridis, P. castaneus,* and *Arremon flavirostris* (Fig. 3).

Distribution of nonforest birds.—About 180 species of land birds occur in the Chaco zones (woodland, grassland and savanna) of northern Argentina, western Paraguay, and southeastern Bolivia (Short 1975, my study). A common pattern in the distributions of these birds is a wide range from north to south without differentiation.

In contrast to this pattern, a group of Chaco birds is represented by pairs of species or subspecies that have distributional limits in the area of the Bermejo and Pilcomayo rivers (Figs. 4–6). Six of these pairs have contact zones in this region (Figs. 4A, 4B, 4C, 5A, 5B, and 6B), two others show narrow overlap (Figs. 5C and 5D), and the remaining species (Figs. 4D and 6A) form hybrid zones. With the exception of *Thamnophilus caerulescens* and *Phacellodomus rufifrons,* which frequent Chaco woodland as well as forest, all of these species inhabit only nonforest habitats.

Levels of speciation.—My study of museum specimens from the southern Yungas and the Paranense forest showed that the species common to both regions exhibited various degrees of phenotypic differentiation (Table 1). One group (6 taxa) included polytopic subspecies and monotypic species, a second (22 taxa) included subspecies, a third (6 taxa) included megasubspecies, and a fourth (8 taxa) was composed of allospecies. Similarly, the study of specimens of Chaco birds from the interaction zone showed different levels of speciation similar to those observed in forest birds.

Discussion

At present, faunistic corridors (gallery forests and one forest wedge; Fig. 2, point *d*) allow the dispersal of the Paranense and Yungas birds from the east and west into the Chaco. However, the barrier of xerophytic vegetation, currently 450 km wide, precludes any direct connection between the birds of these two forest regions.

In the recent past (possibly during the Quaternary interglacial periods), the Chaco area may have been more humid than today (Vuilleumier 1965, Short 1975, Simpson 1979). The presence of dry riverbeds with relict forest patches, and the occurrence of forest trees in the upper part of the channels of the Bermejo and Pilcomayo rivers indicate that the area was more humid in former times. Consequently, forests advanced from the southern Yungas and the Paranense region along the Bermejo and Pilcomayo rivers deep enough to form a continuous forest bridge between both regions. Birds presumably expanded to form a continuous distribution and became isolated again in the subsequent drier period. This connection-interruption process most likely occurred several times during the Pleistocene and Holocene (Vuilleumier 1971, Van der Hammen 1974, 1983, Fitzpatrick 1980). Different levels of bird speciation currently observable in both forests (Table 1), therefore, can be tentatively related to the time elapsed since the species crossed. Thus, species that crossed during the last connection would not yet have had time to differentiate. Another group of species that show differences at subspecies level presumably crossed during an earlier connection. Slightly differentiated subspecies of this group (marked with footnote *b* in Table 1) probably belong to the first group. A third group could have crossed even earlier and differentiated to megasubspecies level. Finally, pairs of allopatric species probably represent differen-

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Fig. 3. Distribution of forest birds in Chaco lowland. Numbers indicate most extreme records: (1) Asunción City, Bernalcue and Lambaré; (2) Monte Sociedad; (3) Río Pilcomayo National Park; (4) Fortín Sgto. Primero Leyes; (5) Montelindo River, near Fortín Mcal. López; (6) Escalante Lagoon; (7) He He Stream; (8) Monte Lindo Stream; (9) Pilagá Stream; (10) Gran Guardia; (11) El Colorado; (12) 15 km NW of Pirané; (13) Presidencia Roca; (14) Guaycurú Stream, (15) El Resguardo; (16) Puerto Bermejo; (17) Bruchard; (18) Colonia Km 503; (19) Pozo de los Suris; (20) Batea and Padre Lozano; (21) El Quimilar; and (22) Las Varas (from Nores 1989).

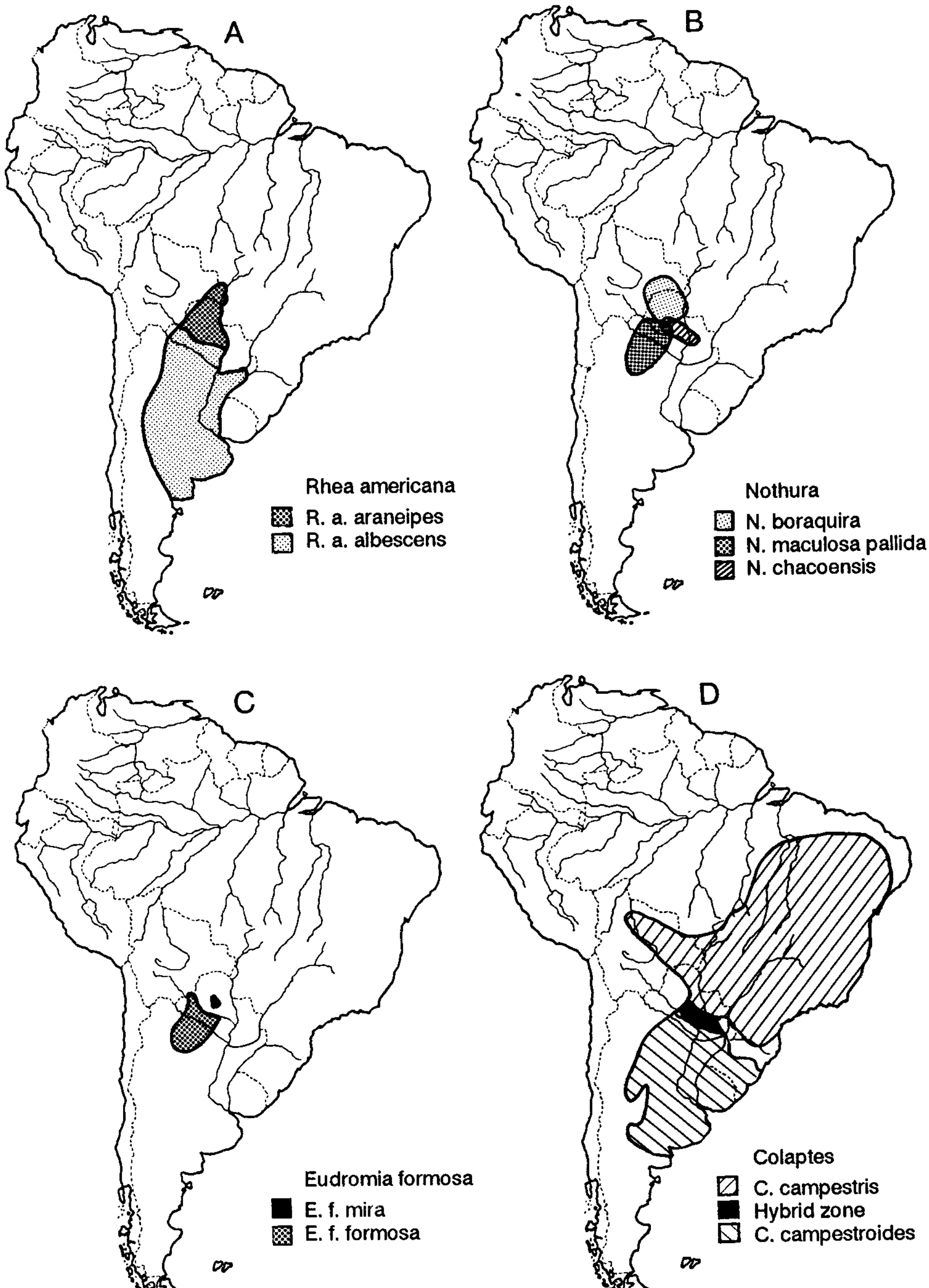

Fig. 4. (A) Ranges of two subspecies of Greater Rhea (*Rhea americana*; modified from Short 1975). The Pilcomayo River marks distribution limit of these subspecies. (B) Ranges of three species of Nothura (*Nothura*). For *N. maculosa*, only *pallida* race represented and, for *N. boraquira*, only its southern population shown. The three species overlap in center of Chaco. (C) Range of Quebracho Crested Tinamou (*Eudromia formosa*). The Pilcomayo River marks distribution limit of its two races. (D) Ranges of two allospecies of Campo Flicker (*Colaptes campestris*), showing zone of hybridization in Paraguay (from Short 1975).

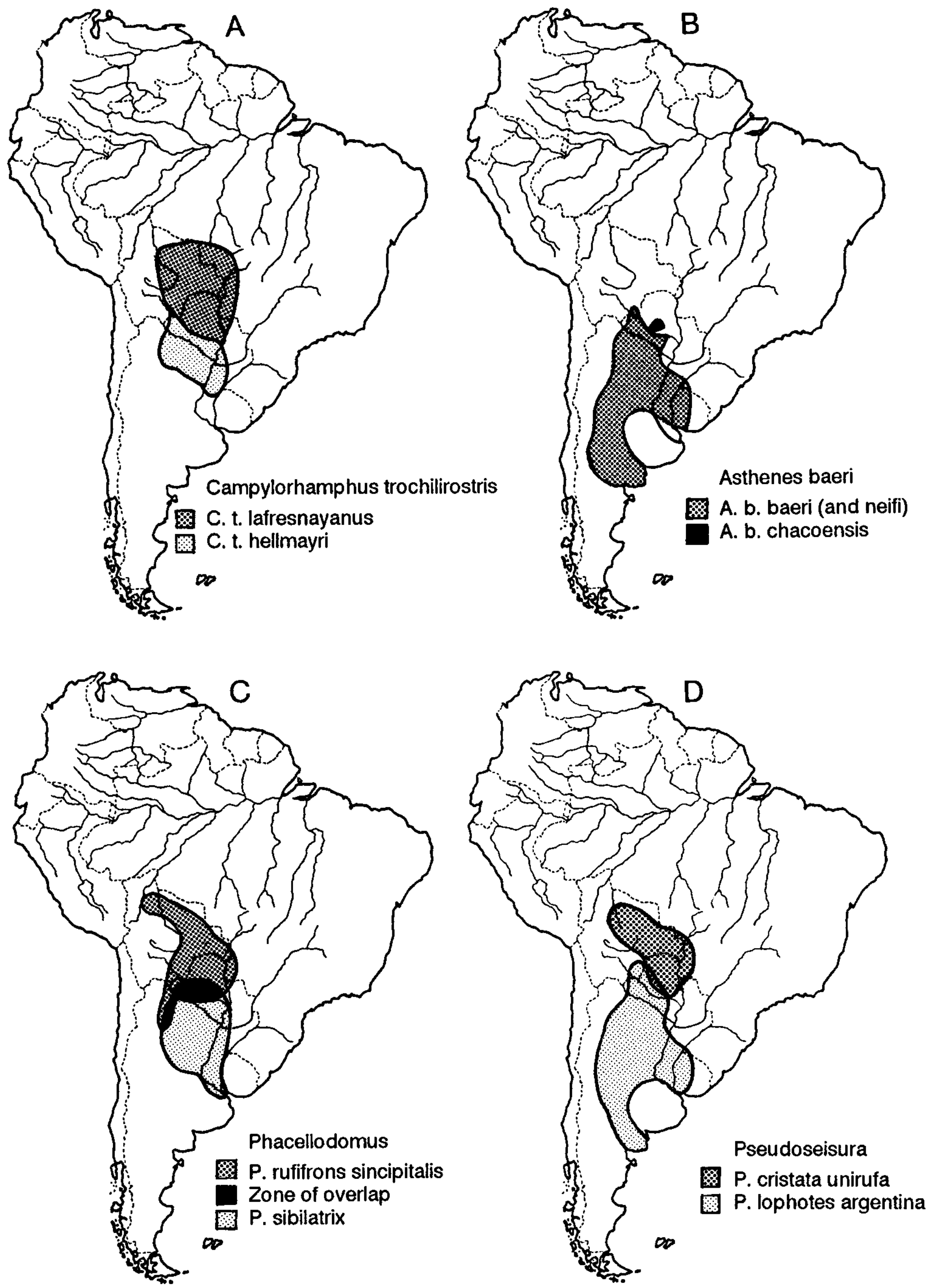

Fig. 5. (A) Ranges of two selected subspecies of Red-billed Scythebill (*Campylorhamphus trochilirostris*; modified from Short 1975). Their ranges are limited by Pilcomayo River. (B) Range of Short-billed Canastero (*Asthenes baeri*), showing distribution limit of two of its races near Pilcomayo River. (C) Ranges of southern subspecies of Rufous-fronted Thornbird (*Phacellodomus rufifrons*) and its allospecies, the Little Thornbird (*P. sibilatrix*). Overlap occurs in center of Chaco. (D) Ranges of southern race for Rufous-crested Cacholote (*Pseudoseisura cristata*; from Short 1975) and of Brown Cacholote (*P. lophotes*) showing narrow overlap in center of Chaco.

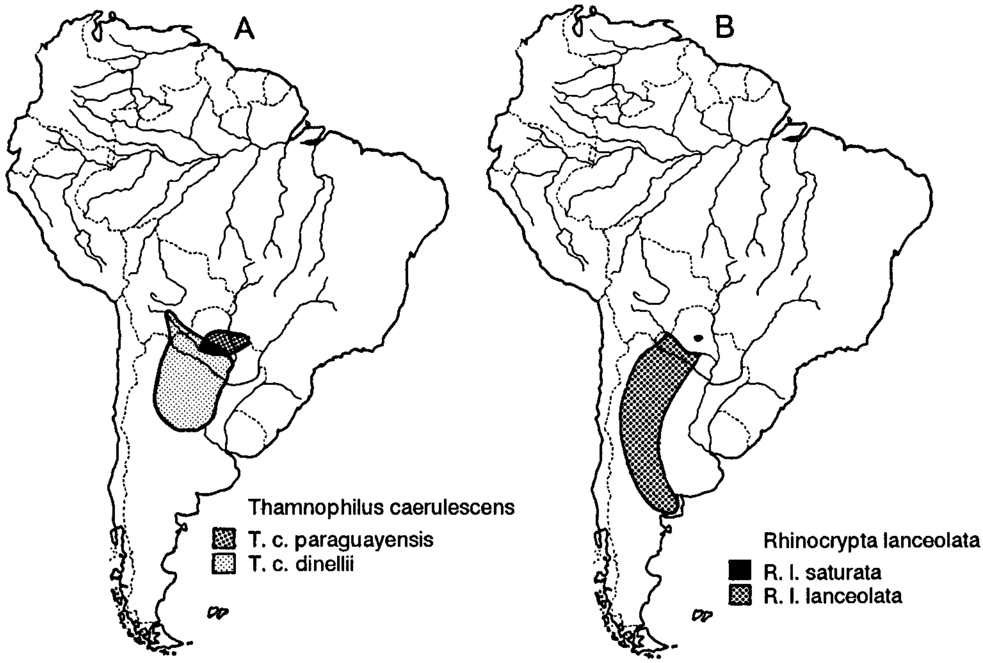

Fig. 6. (A) Ranges of two subspecies (possibly species) of Variable Antshrike (*Thamnophilus caerulescens*), showing small zone of hybridization in center of Chaco. (B) Range of Crested Gallito (*Rhinocrypta lanceolata*). Its two subspecies have their distribution limit near Pilcomayo River.

tiation that began very early in the wet-dry cycles, although it is possible that isolation and speciation began before the Quaternary. Although this classification assumes that all populations diverge at approximately the same rate, I think that other studies, such as biochemical analyses, may slightly modify this classification, and provide better data concerning relative ages of populations.

The distribution patterns of nonforest birds that interact in the center of the Chaco (Figs. 4–6) also are consistent with the former existence of a forest belt along the Bermejo and Pilcomayo rivers. Mayr (1963), Simpson and Haffer (1978), and other authors have interpreted zones of hybridization, character displacement, and narrow overlap as indicators of secondary contact between formerly isolated populations. At present, there are no geographic or ecological features in the area that suggest a plausible alternative hypothesis. Because Chaco birds are capable of crossing extensive unfavorable areas (unpubl. data), the Bermejo and Pilcomayo rivers, with a maximum width of 500 m, cannot constitute effective barriers to dispersal. Because the degrees of speciation illustrated by these birds include various species and subspecies levels, I believe that this barrier interrupted the arid diagonal several times during the Quaternary.

Forest birds may have reached the disjunct area by crossing the arid diagonal without the need of a forest bridge. Although this alternative may apply to some canopy or middle-story species, such as *Pachyramphus validus* and *Turdus nigriceps* (which colonize isolated forested areas; Nores 1989, Nores and Cerana 1990) or to *Todirostrum plumbeiceps*, it is not likely to apply to terrestrial or forest interior species (Haffer 1974: 163, Nores 1989). Mayr (1969) pointed out that savannas of all types are formidable barriers for birds of the tropical rain forest. Vuilleumier (1965) suggested that the lack of marked differentiation between two subspecies of *Penelope obscura* inhabiting these forests indicates that gene flow was continuous between them. However, a more likely explanation is that a population of this species recently crossed (probably before the last connection) and, therefore, has not yet acquired marked differences.

A second alternative is that forest birds have colonized the southern Yungas and the Paranense region from Amazonia. In the southern Yungas, this may have occurred through the

TABLE 1. Speciation levels of forest birds inhabiting southern Yungas and Paranense regions.[a]

Southern Yungas	Paranense region
Polytopic subspecies and monotypic species	
Corythopis delalandi	
Phyllomyias burmeisteri burmeisteri	
Myiopagis caniceps caniceps	
Leptopogon amaurocephalus amaurocephalus	
Trichothraupis melanops	
Euphonia musica aureata	
Trichothraupis melanops	
Euphonia musica aureata	
Subspecies	
Crypturellus obsoletus punensis	*C. o. obsoletus*
Penelope obscura bridgesi	*P. o. obscura*
Pionus maximiliani siy	*P. m. melanoblepharus*
Piaya cayana mogenseni	*P. c. macroura*
Pulsatrix perspicillata boliviana	*P. p. pulsatrix*
Aegolius harrisii dabbenei	*A. h. iheringei*[b]
Nystalus chacuru uncirostris	*N. c. chacuru*
Dendrocolaptes picumnus casaresi	*D. p. extimus*
Philydor rufosuperciliatus oleagineus	*P. r. acritus*
Philydor rufus bolivianus	*P. r. rufus*
Xenops rutilans connectens	*X. r. rutilans*[b]
Batara cinerea argentina	*B. c. cinerea*
Thamnophilus ruficapillus cochabambae	*T. r. ruficapillus*
Chamaeza campanisona boliviana	*C. c. tshororo*
Elaenia obscura obscura	*E. o. sordida*
Phylloscartes ventralis tucumanus	*P. v. ventralis*[b]
Todirostrum plumbeiceps viridiceps	*T. p. plumbeiceps*
Turdus nigriceps nigriceps	*T. n. subalaris*
Hemithraupis guira boliviana	*H. g. fosteri*
Pipraeidea melanonota venezuelensis	*P. m. melanonota*
Basileuterus culicivorus viridescens	*B. c. azarae*[b]
Phaeothlypis rivularis boliviana	*P. r. rivularis*
Megasubspecies	
Tigrisoma fasciatum pallescens	*T. f. fasciatum*
Picumnus cirratus thamnophiloides	*P. c. temminckii*
Lochmias nematura obscurata	*L. n. nematura*
Pachyramphus validus audax	*P. v. validus*
Turdus albicollis contemptus	*T. a. paraguayensis*
Arremon flavirostris dorbignii	*A. f. polionotus*
Allospecies	
Leptotila megalura	*L. rufaxilla*
Amazona tucumana	*A. pretrei*
Veniliornis frontalis	*V. passerinus*
Synallaxis superciliosa	*S. ruficapilla*
Phyllomyias sclateri	*P. virescens*
Elaenia strepera	*E. mesoleuca*
Knipolegus signatus	*K. cyanirostris*
Cyanocorax cyanomelas	*C. caeruleus*

[a] Distribution data from Peters (1934–1951, 1960–1979) and Olrog (1979b). Taxonomy follows Peters (1960–1979), Meyer de Schauensee (1966), and Short (1982).

[b] Slightly differentiated subspecies.

northern Yungas (Fig. 1). In the Paranense region, this could have occurred only in former geological times, when Amazonia may have been connected with the Paranense region and the Serra do Mar (Smith 1962, Vanzolini 1968, 1974, 1981, Haffer 1974, 1985). This hypothesis could account for the presence of only 30% of the species involved, because the remainder is not present in Amazonia. Moreover, neither of the two alternative hypothesis could account for the interaction zone in the center of the Chaco.

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