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Quaternary Vegetational Changes and Bird Differentiation in Subtropical South America

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In a recent paper (Nores 1992), I have concluded that the distribution of forest and nonforest birds in subtropical South America was the result of forest expansion 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. Silva (1994) questions practically all the points that I have discussed in that paper.

His first statement with which I do not agree is that my hypothesis can be considered as an application of the refuge model. The refuge model is related to forest retraction during arid periods and their expansion while humid conditions (like the present) prevailed. Arid periods have reduced forests to isolated blocks of various sizes that served as refugia for the fauna and flora (Haffer 1969, 1974, Vanzolini and Williams 1970, Prance 1974, Simpson and Haffer 1978, Mayr and O'Hara 1986).

My hypothesis is related to forest expansion during periods of higher than contemporary humidity and their subsequent shrinkage during periods when the climate was similar to the present. During the moister periods currently disjunct forests such as the Amazon/Atlantic regions, and the southern Yungas/Paranense regions, may have been connected. Many forest animals presumably expanded their ranges to form a continuous distribution and were separated into two populations during periods like the present. Concurrently, continuous nonforest habitats such as the Chaco-Cerrado-Caatinga diagonal would have been interrupted by forest belts of different size. Many nonforest animal ranges were presumably interrupted and the resulting differentiated populations came in contact when the forest belt disappeared (Nores 1989, 1992; see also Vanzolini 1968, 1974, 1981, Fitzpatrick 1980, Haffer 1985, Nores and Cerana 1990).

Silva's first criticism is about the lack of a precise definition of forest and nonforest birds. I think that there is not a precise definition for them. One group of forest birds inhabits forests exclusively and only disperses through forests. A second group inhabits forests but is able to reach disjunct forests by flying over unfavorable habitats. Finally, a third group inhabits forests but, occasionally or temporarily, occurs also in mesophytic habitats close to forests. Similar remarks apply to nonforest birds. In my list of forest birds, the three groups are represented. For this reason, I pointed out that: (a) some canopy or middle-story species may have reached the other disjunct forest area by crossing the arid diagonal without the need of a forest bridge; (b) 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; (c) 30% of the species would have been capable of colonizing the southern Yungas and the Paranense regions from Amazonia in former geological times; and (d) the remaining species represent genuine disjunctions between the Yungas and the Paranense regions because they are not present in Amazonia.

The first species that Silva questions is *Nystalus chacuru*, because he considers that it is a savanna species. Although this species does not occur in dense forests, it inhabits forest borders and clearings, gallery forests, and humid savannas.

He adds that some species are absent from the Argentine Chaco, but occur throughout Paraguayan and/or Bolivian Chaco. He includes the following: *Pionus maximiliani, Piaya cayana, Veniliornis passerinus, Xenops rutilans, Cyanocorax cyanomelas, Basileuterus culicivorus,* and *Hemithraupis guira.* This is undoubtedly erroneous. The Bolivian and western Paraguayan Chaco are identical to the western Argentine Chaco (pers. obs.), and any of these species can have a continuous range across that region. Some authors (Short 1975, Cabrera 1976, Hueck 1978, Ramella and Spichiger 1989) have considered, directly or indirectly, that the Chaco includes the gallery forests of eastern Paraguay and Argentina, the mesophytic areas of eastern Santa Cruz in Bolivia and western Mato Grosso in Brazil, and the forest–woodland transition of the Andes foothills. However, this does not imply that the forest birds occurring in these areas can also occur in the xerophytic Chaco. It is clear that *Piaya cayana, V. passerinus, X. rutilans,* and *H. guira* have not been found in the western Chaco (Laubmann 1939–1940, Storer 1970, Nørgaard-Olesen 1973, Short 1975, Vaurie 1980). The three remaining species (*Pionus maximiliani, C. cyanomelas,* and *B. culicivorus*) are included in Short (1975) as having a continuous distribution throughout the Chaco. I want to make clear that I have never attempted to criticize or "falsify" Short's data as implied in some parts of Silva's commentary. To the contrary, I consider that Short's (1975) paper is one of the best on Chaco birds. The westernmost records in the Paraguayan Chaco of *P. maximiliani* and *C. cyanomelas* are from 80 km west of Puerto Casado (Wetmore 1926), Fort Wheeler (Naumburg 1930), and Orloff (Steinbacher 1962). These localities are located in a mesophytic region, under the influence of permanent rivers and streams. Consequently, the records of these species there do not imply that they inhabit the xerophytic Chaco. There are no records of *B. culicivorus* in the western Chaco (Wetmore 1926, Naumburg 1930, Laubmann 1939–1940) and very few in the Cerrado (Naumburg 1930, Pinto 1944, Sick 1984). Consequently, the species has not continuous distribution from the Yungas to the Paranense forests.

Silva adds that *Philydor rufus* and *Pipraeidea melanonota* avoid the Chaco region, but are distributed almost continuously from the Yungas forest to the Paranense forest throughout central Brazil and southern Bolivia. I think that "almost continuously" is very different from "continuously," particularly in relation to forest birds. Some Paranense bird species following probably the Apa and Paraguay rivers reached the west of Mato Grosso, where some of them have formed different subspecies. This category of birds includes *Pionus maximiliani, Piaya cayana, V. passerinus, Philydor rufus, X. rutilans, C. cyanomelas,* and *Pipraeidea melanonota.* Consequently, they are distributed almost continuously, but not continuously, from the Yungas forest to the Paranense forest.

In relation to *Picumnus cirratus,* I did not present evidence to modify any taxonomic proposal, simply because my paper did not treat taxonomic problems. Therefore, I have followed Short (1982).

According to Silva, *Dendrocolaptes picumnus* does not occur in the Paranense region at all. Nevertheless, the type of *D. p. extimus* Brodkorb comes from Puerto Gibaja, Alto Paraná, Paraguay. Moreover, there is a recent record of this species from Pilagá Stream, eastern Formosa, Argentina (Chebez and Heinonen-Fortabat 1987).

Concerning nonforest birds, he questions the two species that I noted (*Thamnophilus caerulescens* and *Phacellodomus rufifrons*), as well as *Campylorhamphus trochilirostris* and *Pseudoseisura cristata.* Although *Phacellodomus rufifrons* and *Pseudoseisura cristata* can occur in forest borders and clearings, this does not invalidate their inclusion in the interaction zone in the center of the Chaco. A forest band more than 200 km wide (see below) is presumed to have connected the southern Yungas with the Paranense forests. It may have been a barrier or a severe filter (sensu Simpson 1940) to these species. It is plausible that *Phacellodomus sibilatrix* and *Pseudoseisura lophotes,* which are typical Chaco species, and *C. trochilirostris hellmayri,* which does not occur in dense gallery forests, were separated into two populations by the forest band. The ancestral species retain their characteristics as nonforest birds, whereas the resulting taxa, *Phacellodomus rufifrons, C. trochilirostris lafresnayanus* and *Pseudoseisura cristata,* are less specialized and inhabit the Chaco as well as cer-

tain forest habitats, resulting in their present distribution patterns. The case of *T. caerulescens* is more difficult to explain because this species occurs in the xerophytic Chaco, as well as in humid forests, but it also shows interaction in the center of the Chaco.

I fail to see that Silva's commentary contributes to the understanding of forest and nonforest birds. Furthermore, he concludes these two parts by stating "If one excludes the problematic species from the analysis, both distribution patterns discussed by Nores appear to be supported by other taxa."

Another criticism refers to the use of the "arid diagonal" (Fitzpatrick 1980) instead of the "open vegetation diagonal" (Ab' Saber 1977). This is only a question of terminology and I followed Fitzpatrick (1980).

Silva's next criticism concerns the secondary contact zone of birds in the central Chaco. He points out that my proposal contrasts with that of Short (1975), who suggested that this region should be considered mainly as a zone of primary intergradation rather than as a secondary contact zone. Occurrence of narrow overlaps, distributional boundaries of taxa, and a hybrid zone as found in the central Chaco indicate a secondary contact rather than a primary one, as pointed out by some authors (Mayr 1963, Remington 1968, Simpson and Haffer 1978). Furthermore, a zone of secondary contact is consistent with the existence of an earlier barrier (forest belt) that explains the distribution patterns of forest birds. In this part, Silva points out that I used 10 rough maps, 8 of which were based on maps published by Short (1975), and I did not present new detailed information. Of the 10 maps that I presented, only one (that of *Colaptes campestris* and *C. campestroides*) was taken directly from Short (1975); it was cited appropriately. Of the nine remaining, I prepared six myself, and the other three were modified from Short (1975) to include my own data obtained in the 15 last years of continued research in the region.

Silva goes on to question my proposal that "The distribution pattern of nonforest birds . . . also are [is] consistent with the former existence of a forest belt along the Bermejo and Pilcomayo rivers," because I implicitly assumed that the present-day location of this contact zone is in the same position as the barrier that separated the populations in the past. He adds that "this likely is a false assumption because there is no evidence that the courses of the Bermejo and Pilcomayo rivers have always been the same as today." It is widely agreed that the middle and lower courses of the Bermejo and Pilcomayo rivers fluctuated widely during the Quaternary. However, the total drainage area of these rivers was probably not very different than it is at present: ±50 m north and south in the middle courses (data from satellite images); and up to the Montelindo River, Paraguay, in the lower courses (Ramella and Spichiger 1989).

Silva also questions whether species that crossed during earlier connections (and remained isolated since then) may have a higher degree of differentiation than those that crossed more recently, having therefore been isolated for a shorter period. It is well known that faunas that are isolated for a long time are more differentiated than others at the same place and in the same taxonomic group, but with a shorter time of isolation. In my work, it is not possible to know if each one of the forms of the different levels of speciation that I have found between the birds of the two forests corresponds exactly to a connection. For this reason, I have tentatively related these degrees of differentiation to the time elapsed since the species crossed, but I have made it clear that biochemical analyses may slightly modify this classification and provide better data concerning relative ages of populations.

Silva adds that in my hypothesis there is another assumption, which is that different taxa showing this pattern have different propensities for dispersal, since once the connection existed some species allegedly dispersed while others waited for another opportunity. I do not think so. Since the structure of the vegetation and the duration would not have been the same in the different forest connections, the opportunities for dispersal and for reaching the former disjunct forest region would not have been the same for different species. Some species could have dispersed in more than one connection but only reached the disjunct area when they had enough time for dispersal. Others could have dispersed only at a time when the structure of the vegetation of the forest belt was appropriate for them. In figure 3 of my paper (Nores 1992) I have shown that the capacity for dispersal is very different for different species. Only 26% of Paranense birds reach the Paraguay River and 23% occur at different distances from the Paraguay River in the gallery forests of the Bermejo and Pilcomayo rivers, as well as along other water courses. From the Yungas, only 11% of forest birds occur in the gallery forest of the Bermejo River.

Silva adds that my hypothesis rests on two main paleoecological assumptions. The first assumes that "the courses of the Bermejo and Pilcomayo [rivers] were constant during all of the Quaternary." I have mentioned (Nores 1989) that the Pilcomayo River flows at present in a location several kilometers (±30) south of its "regular" course, as indicated by the location that appears on maps, forming the "Bañado La Estrella." Then it divides into three branches, which in turn flow into three different streams (Porteño, Pavado, and Tatú Piré) before reaching the Paraguay River. I have also indicated that some dry riverbeds found in the central and western Chaco could be related to the old beds of the Bermejo and Pilcomayo rivers. Therefore, I have not assumed that the courses of the Bermejo and Pilcomayo rivers were constant.

The second assumption mentioned by Silva is that "the gallery forests along these rivers were stable (at least during the interglacial periods) and, thus, could

function as faunistic corridors between the Yungas and Paranense forests." The statement of Adámoli et al. (1990) that gallery forests in the Chaco region grow mainly on river levee-banks, on top of a positive relief structure with respect to the surrounding flat land, only applies to the flooded area, which extends westward about 100 km from the Paraguay River. Outside the flooded area, the gallery forests widen considerably and merge in some sites forming continuous forest habitats (Nores 1989, 1992). In fact, at present there is a large area (ca. 150 × 70 km) where forests predominate. It is located in Formosa and Chaco provinces, west of the flooded area (Nores 1989). In addition, near Sargento Primero Leyes, located 200 km west of the Paraguay River, the gallery forest on the "regular" course of the Pilcomayo River is about 20 km wide (pers. obs.), although this river has flowed 30 km south for more than 20 years. These findings contrast with Silva's statements that the gallery forests occur only along stable water courses, and that a system of wide and continuous gallery forests would be almost inconceivable.

Another incongruence of Silva's commentary is that

> . . . if during an interglacial period (such as the one we are now in) the Chaco region was more humid than it is today (because of its poor-drainage system and flat topography), there would be a trend to great and perhaps disastrous floods of rivers. These floods would be even more severe if we also consider the melting of the Andean glaciers and raising of sea level. Thus, the region could be somewhat like a hyperseasonal savanna, dominated by grasses, palms and perhaps with mosaics of unstable patches of humid and dry gallery forests in some points of rivers.

Because the area increases in elevation from east to west, the marshes and lagoons outside the flooded area decrease in number and size, disappearing almost totally some 100 km west of the flooded area. In the remaining 500 km of xerophytic Chaco, it is possible to find mostly scattered ponds, which are dry riverbeds that retain rain water and maintain relict forest patches. Under these conditions, the disastrous floods of rivers and the formation of something like a hyperseasonal savanna, as indicated by Silva, are inconceivable. The large area where forests predominate at present in Formosa and Chaco provinces is probably a relict of a more widespread forest that occurred throughout the central and western Chaco. Considering that the forested area spreads from northeast to southwest over a distance of 150 km, it is possible to estimate that the forest belt that connected the southern Yungas to the Paranense region was more than 200 km wide.

Silva also states that many species of forest trees mentioned in my paper also occur in different types of dry forests currently distributed as islands of variable size in northeastern and central Brazil, Bolivia, and Paraguay. He adds that there is good evidence that they were more widely distributed in the past, but only during dry periods of the Quaternary or Late Tertiary. The tree species that I listed are all forest species typical of the southern Yungas and Paranense forests (Digilio and Legname 1966, Adámoli et al. 1972, Dimitri et al. 1974, Morello and Adámoli 1974, Legname 1982). They occur in the Chaco only in the gallery forests, on dry riverbeds, and in some locations along the upper parts of the channels of the Bermejo and Pilcomayo rivers. It would be surprising if forests could advance over xerophytic areas during dry periods!

In Silva's conclusion, he states that I have ignored the dynamic geological history of my study area and that I did not consider the importance of other events (e.g. Plio-Pleistocene tectonism, flooding associated with changes in sea level) that might explain (although he does not indicate how) the observed pattern as (or more) parsimoniously than interpretations based on the refuge paradigm. Of the 53 papers that I have cited, at least 30 pertain to paleoecological information. Of the five papers that Silva specifically selected, only one (Ramella and Spichiger 1989) has a relationship to my paper, but the findings of these authors do not modify my interpretation at all. The influence of Quaternary climatic changes, including fluctuations of sea level, on the distribution and differentiation of birds of Argentine and neighboring areas was analyzed in a earlier paper (Nores 1989). In conclusion, I consider that Silva's commentary is a good example of an author who, without previous knowledge of an area, attempts to discredit a well-documented paper by means of contentious criticism.

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