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Biogeography of forest relics in the mountains of northwestern Argentina

Biogeografía de relictos de selva y bosque húmedo de las montañas del noroeste de Argentina

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ABSTRACT

The Quaternary was an age of major climatic changes in South America with retraction of forests in the glacial phases and their expansion in the interglacial periods. There is also evidence that during the interglacial phases humidity was, sometimes, higher than at present; consequently the forests could lave had an even wider distribution than today.

The analysis of the composition of bird and plant species in various natural forest patches in the ranges of northwestern Argentina suggests that these forests are relics of a former continuous band of vegetation and may therefore be considered present refugia. The reason why these forested areas have persisted until the present in a semiarid environment can be ascribed to the combined action of the relief and the presence of streams. The occurrence of obligatory forest birds in these patches (some of which show subspecific morphological differences) suggests that these birds evolved from a common ancestor after the band of forest vegetation had been broken up into patches. Retraction and expansion of these forests probably occurred several times during the Quaternary succession of glacial and interglacial cycles. The present patches, therefore, could not be older than the end of the last period of great humidity i.e. about 7,500 or 10,000 yr BP.

Key words: Birds, plants, relics, speciation, Quaternary.

RESUMEN

El período Cuaternario fue una época de grandes cambios climáticos en Sudamérica, con retracción de las selvas en las fases glaciales y expansión de las mismas en períodos interglaciales. Hay también evidencias de que durante los períodos interglaciales la humedad fue en algunos momentos más alta que en el presente y como consecuencia de esto las selvas habrían tenido una distribución más amplia que la que tienen actualmente.

El análisis de la composición de aves y plantas de varios manchones naturales de selva y bosque húmedo existentes en las montañas del noroeste de Argentina sugiere que los mismos son relictos de una banda continua de selvas y bosques húmedos que habría existido anteriormente, por lo que los manchones pueden considerarse refugios actuales. La razón por la cual estas áreas de selva han persistido hasta el momento en un medio semiárido puede ser atribuida a la acción combinada del relieve y de la presencia de arroyos. La existencia de aves típicas de selvas en los manchones (varias de las cuales muestran diferencias subespecíficas) sugiere que estas aves han evolucionado de un antepasado común, después que la banda de selva habría sido fragmentada. La retracción y expansión de esta selva probablemente se produjo varias veces en el Cuaternario, durante la sucesión de ciclos glaciales e interglaciales; por esta razón los manchones actuales no pueden ser más antiguos que el final del último período de gran humedad, o sea, alrededor de 7.500 ó 10.000 años AP.

Palabras claves: Aves, plantas, relictos, especiación, Cuaternario.

INTRODUCTION

It is widely accepted that the Quaternary was an age of major climatic changes in South America. The glaciations and the associated phenomena must have had a major effect on the flora and fauna, causing extinction, differentiation and changes in the geographic distribution of species (Haffer 1969, 1974, Vuilleumier 1971, Van der Hammen 1974, Simpson and Haffer 1978). The glaciations must have produced contraction of the forests during the arid phases and their expansion during the humid phases (Bigarella and Andrade 1965, Haffer 1969, 1974, 1987, Vanzolini and Williams 1970, Prance 1974, Tricart 1974, Mayr and O'Hara 1986). Arid phases must have reduced forests to patches of different

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sizes which served as refugia for the flora and fauna. As a result of isolation and selective pressure, the differentiation of a large fraction of the species could have been produced; other forest species may have gone extinct or remained without change (Refuge theory: Haffer 1969, 1974).

During the interglacial phases, the climatic conditions and the forest distribution seem to have been, in general, similar to the present but there is also evidence that there were periods when humidity was higher than at present which produced an even wider distribution of forests than today. This assumption is supported by paleoecological studies and by the present distribution patterns of animals and plants.

Groeber (1936) points out that in Argentina there was a lacustrine period with heavier precipitation at the end of the glaciation and that it was latter replaced by a drier climate which heightened up to the present.

Pollen and charcoal analyses carried out by Markgraf (1985) at 4,000 m in northwestern Argentina show that the period between 10,000 and 7,500 yr BP was somewhat moister and/or cooler than the present with increased summer precipitation. Van der Hammen (1974, 1983) also points out that in the Colombian Andes the climate was slightly moister and warmer than today by the beginning of the Holocene.

Fernández (1984-1985) states that an extinct horse found in the Altiplano of Jujuy between 12,600 and 10,000 yr ago suggests extensive Paramo-like grassland instead of Puna.

In Peru, pollen analysis at an altitude of 4,100 m indicates that from about 12,000 yr BP until some time after 3,000 yr BP, about 30% of the pollen was carried in by the easterly winds from the east Andean forest, which today are at least 600 m lower in elevation (Hansen *et al.* 1984).

Fairbridge (1972, 1976) also presents evidence for a period warmer and wetter than today which ocurred all over the earth, indicating that it was strongly not synchronous between the tropics and the northern latitudes.

In regard to animal distribution, Vanzolini (1968, 1974, 1981) suggests that the present distribution patterns of lizard fauna in northwestern Brazil would be the consequence of a broad continuity between the Amazone and the Atlantic forests in relatively recent times. Today, both forests are separated by a wide band of xerophytic vegetation which still has relictual Amazone forest patches around several mountains. Haffer (1985) also points out that the large isolated forests in central Brazil with an Amazonian bird fauna suggest that the Amazon forest and the Atlantic forest were at one time more or less continuous.

The distribution patterns of forest birds of the mountains of northwestern Argentina and southern Bolivia (Yungas vegetation) and those of the Paranense forest of southern Brazil, eastern Paraguay and northeastern Argentina suggest that both regions have been connected in the past. The presence of small isolated forest stands in dead rivers along the Bermejo and Pilcomayo River system indicates that they could be relics of a forest bridge that must have connected the Yungas forest with the Paranense forest. At the same time, this forest bridge may have interrupted the Chaco region causing differentiation of woodland and grassland birds (Nores 1989).

In this work, we present data on the avifauna and vegetation composition of several forest patches located in the mountains of northwestern Argentina. Subsequently, we discuss the probable origin of the species, their route of colonization and the time of isolation. Finally, we correlate our findings with climatic changes that may have occurred in South America during the Pleistocene and Holocene. We postulate that these areas of forest are relics of a former continuous forest band that existed during a period more humid than the present.

STUDY AREA

The mountain ranges where the study region is located are part of the Sierras Pampeanas system. The principal study site (El Cantadero) is situated in the Sierra de Ve-

lasco, Dpto. Capital, La Rioja, near the locality El Cantadero, 29°11'S, 66°44'W (Fig. 1), and was briefly described by Nores and Yzurieta (1982). The forested area is located between 950 and 1300 m along streams from three drainage basins. The three basins have common sources forming a single watershed that covers an estimated surface of 3,000 hectares. It is separated from the nearest zone of continuous forest on the eastern slope of Sierra de Ancasti (Ramblones) by about 140 km of semiarid vegetation and by 60 km from the nearest forest patch (Trampasacha-Chumbicha) (Fig. 1).

Other study sites are located in the Sierra de Ambato, Province of Catamarca and show similar features. They are undisturbed forested areas located in humid canyons surrounded by xerophytic vegetation (Chaco woodland or Monte desert). This xerophytic vegetation constitutes the natural vegetation of the region (Lorentz 1876, Vervoorst 1982) and it has been little disturbed.

The forest patches are in general similar in aspect and composition to the southern part of the continuous forest on the eastern slope of Sierra de Ancasti. The patches with a predominance of *Podocarpus* (the Las Juntas and Concepción-Los Angeles sites) are very similar to those that occur in the provinces of Salta, Jujuy, and Tucumán. In general, there is a decreasing

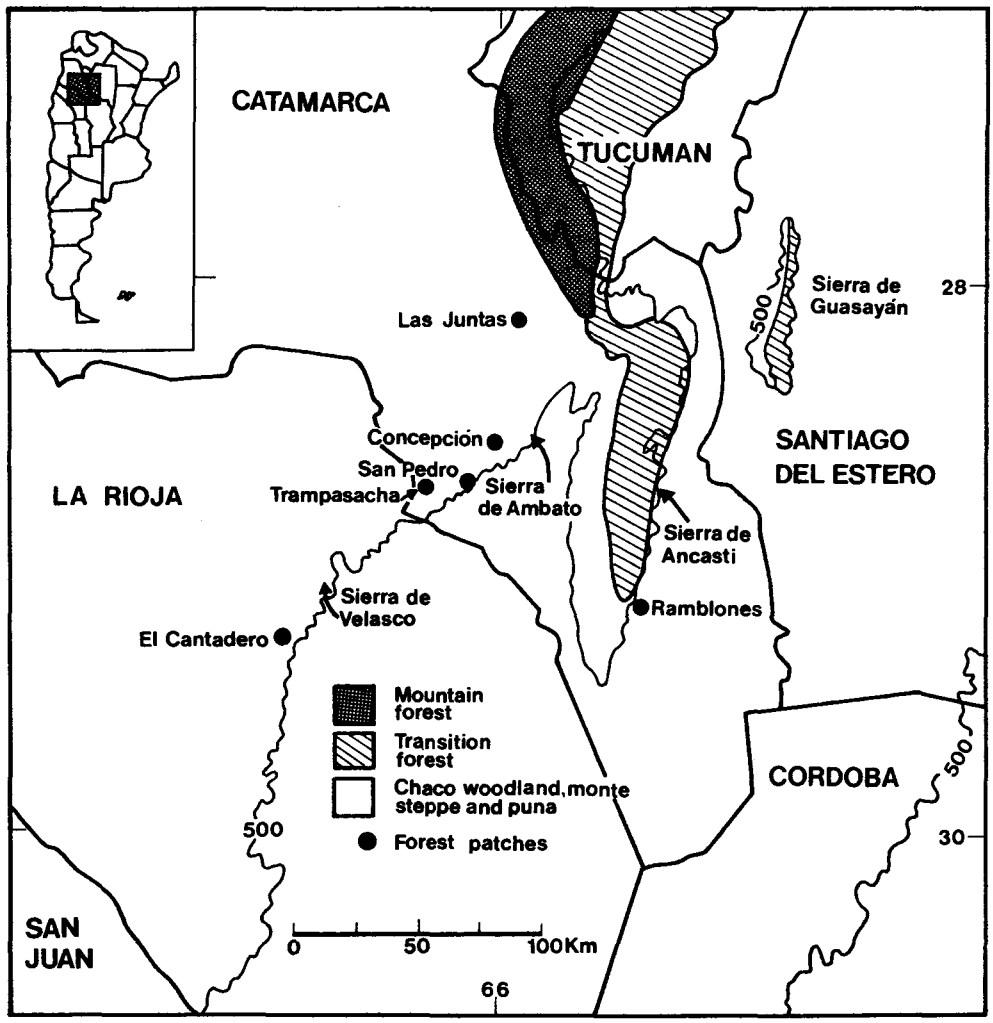

Fig. 1: Mountain ranges in northwestern Argentina showing forest distribution and location of forest patches.

Montañas del noroeste argentino mostrando la distribución de la selva y la localización de los parches.

gradient of forest plant species from the Las Juntas site to the El Cantadero site, but there are also local conditions that influence the composition and structure of the vegetation and the avifauna.

Birds were also censused during three visits to the Sierra de Guasayán (Santiago del Estero) in 1980-1981. This mountain range has features which are slightly different from those of the afore mentioned forested areas; its humidity depends mainly upon the humid eastern winds and not on the streams. It is isolated from the nearest similar environment, in the Sierra de Ancasti, by about 30 km of lowland with xerophitic Chaco vegetation (Fig. 1).

METHODS

Birds

From 1981 to 1987 the El Cantadero site was visited seven times in different seasons. The visits lasted from one to four days during which the species were recorded, including an estimate of species density based on the number of birds observed, heard, and captured with mist nets. The mist nets were set up in the early moring and pulled up after sunset. Abundance of birds was noted in the following categories: common, fairly common, uncommon, and rare (Parker *et al.* 1982).

Wings, tails and culmen length of the specimens captured with mist nets were recorded. Specimens of forest species were also collected and later compared to specimens in museums. In the other study sites visits were fewer but a list of the birds observed was made up in each case. Specimens of a few species were also collected in the site of Las Juntas.

Vegetation

A floristic survey was carried out in the El Cantadero site and specimens of the collected plants are kept at the Museo Botánico of Córdoba (CORD).

The vegetation was sampled in 15 transects 50 m long x 1 m wide, along the stream banks and in the forest interior. All trees in each transect were counted and data are presented as percentage of the number of individuals of each species (relative abundance). Percent cover of forest understory vegetation was estimated by species, and the results are given according to the modified scale of Braun-Blanquet (Matteucci and Colma 1982).

Less detailed floristic studies were carried out in the other study sites and in the Sierra de Guasayán.

RESULTS

Avifaunal composition

The 74 species recorded in the El Cantadero site are listed in Appendix 1, including relative abundance and seasonal activity for each species. Fifteen species are occasional winter visitors, casual vagrants or have only been recorded flying through the zone, and only 59 species can be considered local residents.

Fourteen (23.7%) of the 59 breeding species can be classified as "forest species" because they inhabit mostly the forest (Table 1). Six of them (10.1%) comprising *Leptotila megalura, Phacellodomus maculipectus, Scytalopus superciliaris, Phylloscartes ventralis, Arremon flavirostris* and *Poospiza erythrophrys,* inhabit exclusively the forest or humid shrub-covered ravines that are connected to the forest and only disperse through forest. Therefore they can be considered obligatory forest birds. In regard to these six species, their presence in the El Cantadero site implies a distribution from 60 to 200 km outside their continuous range.

The remaining eight species, *Accipiter bicolor, Amazilia chionogaster, Pachyramphus validus, Mecocerculus leucophrys, Elaenia strepera, Myioborus brunniceps, Pheucticus aureoventris* and *Turdus nigriceps,* have also been found in humid shrub ravines which are not connected to forest, or in neighbouring areas of the Chaco region.

Composition of forest bird species in the other study sites is also listed in Table 1.

TABLE 1

Forest birds recorded in the different study sites.
Aves de selva registradas en las diferentes zonas de estudio.

Species	El Cantadero	Trampasacha	San Pedro	Concepción	Las Juntas	Sierra de Guasayán
Obligatory forest birds[1]						
Leptotila megalura	X	X	X	X	X	–
Microstilbon burmeisteri	–	–	–	–	X	–
Piculus rubiginosus	–	–	–	X	–	–
Phacellodomus maculipectus[2]	X	X	X	X	X	–
Philydor rufosuperciliatus	–	X	–	X	X	–
Scytalopus superciliaris	X	–	–	–	X	–
Phylloscartes ventralis	X	–	–	–	–	–
Knipolegus signatus	–	–	–	–	X	–
Pipraeidea melanonota	–	–	–	–	X	–
Atlapetes citrinellus	–	–	–	X	X	–
Arremon flavirostris	X	X	X	X	X	–
Poospiza erythrophrys[2]	X	–	–	–	X	–
Total No. of species	6	4	3	6	10	0
Non-obligatory forest birds						
Merganetta armata	–	–	–	–	X	–
Accipiter bicolor	X	–	–	–	X	X
Aratinga mitrata	–	–	–	–	X	–
Amazilia chionogaster	X	X	X	X	X	X
Pachyramphus polychopterus	–	–	X	–	–	X
Pachyramphus validus	X	X	X	X	X	X
Myiopagis viridicata	–	–	–	–	–	X
Elaenia strepera	X	–	–	X	X	–
Mecocerculus leucophrys	X	X	X	X	X	–
Sayornis nigricans	–	X	–	X	–	–
Turdus nigriceps	X	X	X	X	X	–
Myioborus brunniceps	X	X	X	X	X	–
Pheucticus aureoventris	X	X	X	X	X	X
Total No. of species	8	7	7	8	10	6
Total of both	14	11	10	14	20	6

1. See text for definition.
2. The records of *Poospiza erythrophrys* and *Phacellodomus maculipectus* for the Chaco zones of La Rioja (Hayward 1967) and Santiago del Estero (Zotta 1944) respectively are wrong. In the first case the species corresponds to *Poospiza ornata* (pers. obs.) and in the second case the locality El Suncho belongs to Catamarca or Tucumán.

Degrees of differentiation of the avifauna

At least, five species at the El Cantadero site were subspecifically different from those in the provinces of Salta, Jujuy, Tucumán and Catamarca (Nores, unpublished). Morphological differences were marked in the species *Scytalopus superciliaris* and *Phacellodomus maculipectus* and only slight in *Mecocerculus leucophrys, Arremon flavirostris* and *Poospiza erythrophrys* (Table 2). It may be necessary to collect additional specimens of the last two species to assess the level of differentiation. In the Las Juntas site at least two species also showed differences at the subspecific level (Nores, unpublished) (Table 2).

Vegetation composition

Species recorded in the El Cantadero site are listed in Appendix 2. They are grouped under the two major vegetation classes: 1) the vegetation of the stream banks, 2) the vegetation of the interior of forest (Table 3). On the stream banks the dominant shrubs are *Cestrum parqui – C. lorentzianum, Pisoniella arborescens, Vassobia breviflora, Solanum tucumanense* and *Eupatorium lasiophthalmum.*

TABLE 2

Morphological differences of the bird subspecies of the El Cantadero and the Las Juntas sites.
Diferencias morfológicas de las subespecies de El Cantadero y Las Juntas.

	El Cantadero	Las Juntas	Northwestern Argentina
Phacellodomus maculipectus			
Forecrown	dark chestnut, no contrasting		rufous, contrasting
Upperparts	dark chestnut olivaceous	–	cinnamon brown
Scytalopus superciliaris			
Upperparts	dull cinnamon brown	light ochraceous brown	cinnamon brown
Throat	white area much broader, extended on to the chest	white area smaller not extended on to the chest	white area smaller not extended on to the chest
Chest	ashy gray	ashy gray	slaty gray
Mecocerculus leucophrys			
Upperparts	dull olive brown	brownish gray	olive brown
Belly	yellow	pale yellow	yellow
Wings	black; wing bars buff or buffy yellow	dark brown; wing bars whitish	dark brown; wing bars pale yellow
Arremon flavirostris			
Head and pectoral band	black		brownish black
Underparts	pure white	–	dull white
Shoulders	bright yellow		yellow
Poospiza erythrophrys			
Back	dull olive gray		olive gray
Underparts and eyebrow	dull rusty rufous	–	rusty rufous

In the interior of the forest, shrub composition is similar although *Cestrum parqui* – *C. lorentzianum* are not so important and young tree specimens of *Celtis tala* and *Bougainvillea stipitata* become more important. Among the trees of the stream banks *Celtis tala, Acacia visco* and *Bougainvillea stipitata* are predominant whereas in the interior of forest the dominant species are *Acacia visco, Condalia buxifolia, Celtis tala* and *Fagara coco.*

In general there is a prevalence of shrubs over trees in the stream banks, whereas in the interior of forest the trees predominate.

Of all the plant species listed in Appendix 2, 11 (7.9%) are forest species found in the shrubby and herbaceous strata. Seven of them: *Adiantum lorentzii, Pisoniella arborescens, Cestrum lorentzianum, Nicotiana sylvestris, Eupatorium schickendantzii, Trixis grisebachii* and *Hieracium microcephalum,* are characteristic of the forest of the eastern slope of the Andes known as Yungas, with a distributional range from Bolivia or southern Peru to Argentina (Toursarkissian 1975, Cabrera 1978, 1983).

The remaining species *Solanum tucumanense, Sicyos warmingii, Eupatorium lasiophthalmum* and *Baccharis flexuosa* have a wider distribution. Their range includes the Yungas and extends into northeastern Argentina, eastern Paraguay and southern Brazil (Martínez Crovetto 1964, Morton 1976, Cabrera 1978). If these species are compared to the non-forest species in Table 3, it is evident that some of the forest species participate with a high percentage in the shrub cover. For this reason, the habitat shows forest aspect although there are no forest trees.

TABLE 3

Vegetation of the El Cantadero site.
Vegetación de El Cantadero.

	Cover %			Relative abundance %	
Shrubs	Stream banks	Interior of forest	Trees	Stream banks	Interior of forest
Pisoniella arborescens	25-50	25-50	Celtis tala	50.00	24.25
Cestrum parqui-C. lorentzianum	25-50	15-25	Acacia visco[3]	16.66	32.33
Vassobia breviflora	15-25	15-25	Bougainvillea stipitata	16.66	–
Eupatorium lasiophthalmum	5-15	5-15	Condalia buxifolia	8.33	27.00
Anredera cordifolia	1-5	1-5	Fagara coco	2.77	13.42
Fagara coco[1]	1-5	1-5	Lithrea molleoides	2.77	2.75
Lycium cestroides	1-5	<1	Jodina rhombifolia	2.77	–
Solanum aff. kurtzianum[2]	1-5	<1			
Cynanchum bonariense	1-5	<1			
Senecio deferens[2]	1-5	–			
Jungia polita	1-5	–			
Mikania periplocifolia	<1	–			
Sicyos warmingii	<1	–			
Nicotiana glauca	<1	–			
Cassia hookeriana	<1	–			
Celtis tala[1]	–	15-25			
Bougainvillea stipitata[1]	–	5-15			
Jodina rhombifolia[1]	–	1-5			
Condalia x montana	–	1-5			
Lithrea molleoides[1]	–	<1			
Porlieria microphylla	–	<1			

1. Shrub-like trees.
2. Shrub-like herbs.
3. Cited as *Parapiptadenia excelsa* in Nores and Yzurieta (1982).

In the other study areas forest species were also recorded but systematical surveys were not carried out. In the Trampasacha-Chumbicha site (Fig. 1:2), for instance, the vegetation has physiognomic characteristics similar to the El Cantadero site but the Trampasacha-Chumbicha site is a little more humid as suggested by the occurrence of *Anadenanthera colubrina, Eugenia mato, Carica quercifolia, Celtis iguanea* and *Rhipsalis* sp. In the San Pedro site (Fig. 1:3) *Juglans australis* appears; in the Concepción-Los Angeles site (Fig. 1:4) there are forest of *Juglans australis* and *Podocarpus parlatorei.* In the Las Juntas site (Fig. 1:5) the dominant tree species is *Podocarpus parlatorei* along with *Eugenia mato, Citharexylum jorgensenii, Sambucus peruvianus,* and *Eupatorium lasiophthalmum.*

In the Sierra de Guasayán the only forest tree species is *Anadenanthera colubrina* with and abundance of about 30%. Other forest plant species found in this site are: *Carica quercifolia, Peperomia lilloi, Dioscorea megalantha, Turnefortia rubicunda* and *Rhipsalis aculeata* (Roig and Villaverde 1987).

DISCUSSION

The presence of bird and plant species typical of forest in small and isolated patches at the El Cantadero site and other sites in the Sierra de Ambato, and the fact that several bird species have evolved morphological differences at the subspecific level pose the following questions:

1) How do the forest patches persist in a semiarid environment?

2) Is the distribution of birds and plants due to vicariance or dispersal?

3) How long have the forest patches been isolated?

With respect to the first question, the persistence of forest vegetation in a semiarid environment with approximately only

600 mm precipitation per year is probably due to the combination of the presence of streams and the local relief that results in a suitable microhabitat with permanent humidity.

The most probable explanation of the second question is that the forest plants and birds in these patches are relics of a former continuous band of forest along the eastern slope of the Sierras de Ambato and Sierra de Velasco, during a period moister than the present. Existence of a moister period between 10,000 and 7,500 yr BP was suggested by Markgraf (1985) for the Altiplano in the Province of Jujuy; or between 12,600 and 10,000 according to Fernández (1984-1985). An alternative explanation would require that birds and plants dispersed across the arid gap reaching the patches directly or using the nearest patches like stepping stones. This second possibility is not very likely since some of the bird species present in the El Cantadero site as well as in the other sites are closely tied to forest habitat and need forest in order to disperse. This is probably also true for some plant species such as *Adiantum lorentzii, Pisoniella arborescens, Nicotiana sylvestris* and *Trixis grisebachii;* however, due to their dispersal modes some plant species could have dispersed across the arid gaps, for example *Anadenanthera colubrina, Juglans australis* and *Carica quercifolia.*

The distribution patterns of the birds observed in the forest on the eastern slope of Sierra de Guasayán support the hypothesis of a continuous forest band. The xeric gap that separates this range from the continuous forest in Sierra de Ancasti probably existed even during periods more humid than the present because it lies in the rainshade caused by the sierra itself.

Although the habitat of the Sierra de Guasayán site is suitable for several forest birds found in the El Cantadero site and in the other forested areas only species capable of crossing arid gaps colonized this range, such as *Accipiter bicolor, Amazilia chionogaster, Pachyramphus polychopterus, Pachyramphus validus, Myiopagis viridicata,* and *Pheucticus aureoventris* (Table 1).

The third question concerns the time of isolation of the patches and their age. We assume that the patches would have formed after periods of maximum humidity and disappeared during arid periods. Consequently the present-day patches and their avifauna could not be older than the end of the last period of maximum moisture probably close to the Pleistocene-Holocene boundary, i.e. about 7,500 yr BP (Markgraf 1985) or 10,000 yr BP (Fernández 1984-1985). Furthermore, if the Pleistocene forest refugia are relics of a continuous forest formation (Haffer 1969, 1974) the patches of the Velasco and Ambato Ranges could be considered present-day refugia.

A similar process must have taken place on the western slopes of the Peruvian Andes (Koepcke and Koepcke 1958, Koepcke 1961, Vuilleumier 1971, Simpson 1975a, 1975b). There, isolated forest pockets located in humid canyons in the mountains, have also been considered relics of a more or less continuous forest band that may have existed in a period more humid than the present; however, unlike the Argentine situation, in western Peru the maximum humidity was assumed to have occurred during the glacial phase (Simpson 1975b).

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APPENDIX 1

List and status of birds recorded in El Cantadero site, La Rioja*

Lista y status de las aves registradas en El Cantadero, La Rioja.

Species	Abundance	Occurrence
Nothoprocta pentlandii	Fairly common	Permanent
Coragyps atratus	Fairly common	Permanent
Cathartes aura	Fairly common	Permanent
Vultur gryphus	Uncommon	Casual visitor
Sarcoramphus papa	Rare	Casual visitor
Accipiter striatus	Rare	Permanent ?
Accipiter bicolor	Uncommon	Pérmanent
Buteo magnirostris	Fairly common	Permanent
Buteo polyosoma	Rare	Casual visitor
Geranoetus melanoleucus	Rare	Casual visitor
Harpyhaliaetus coronatus	Rare	Casual visitor
Falco peregrinus	Rare	Casual visitor
Aramides cajanea	Rare	Casual visitor
Zenaida auriculata	Rare	Casual visitor
Leptotila megalura	Common	Permanent
Aratinga acuticaudata	Common	Permanent
Coccyzus melacoryphus	Rare	Summer visitor
Tyto alba	Uncommon	Permanent
Otus choliba	Fairly common	Permanent
Glaucidium sp.	Uncommon	Permanent
Aeronautes andecolus	Uncommon	Casual visitor
Chlorostilbon aureoventris	Common	Summer visitor
Amazilia chionogaster	Common	Summer visitor
Sappho sparganura	Common	Permanent ?
Picumnus cirratus	Uncommon	Permanent
Campephilus leucopogon	Rare	Permanent ?
Upucerthia certhioides	Fairly common	Permanent
Cinclodes fuscus	Rare	Casual visitor
Leptasthenura fuliginiceps	Uncommon	Winter visitor
Synallaxis frontalis	Common	Permanent
Certhiaxis pyrrhophia	Fairly common	Permanent
Phacellodomus maculipectus	Common	Permanent
Thamnophilus caerulescens	Common	Permanent
Melanopareia maximiliani	Uncommon	Permanent ?
Scytalopus superciliaris	Fairly common	Permanent
Pachyrhamphus validus	Fairly common	Summer visitor
Myiophobus fasciatus	Uncommon	Summer visitor
Camptostoma obsoletum	Uncommon	Permanent ?
Phaeomyias murina	Common	Summer visitor
Suiriri suiriri	Uncommon	Permanent ?
Elaenia parvirostris	Common	Summer visitor
Elaenia strepera	Common	Summer visitor
Mecocerculus leucophrys	Common	Permanent
Serpophaga munda	Uncommon	Permanent ?
Phylloscartes ventralis	Uncommon	Permanent ?
Todirostrum margaritaceiventer	Uncommon	Permanent ?
Ochthoeca leucophrys	Uncommon	Permanent ?
Knipolegus aterrimus	Uncommon	Permanent ?
Tyrannus melancholicus	Uncommon	Summer visitor
Progne modesta	Fairly common	Summer visitor
Notiochelidon cyanoleuca	Uncommon	Casual visitor
Troglodytes aedon	Common	Permanent
Turdus chiguanco	Fairly common	Permanent
Turdus nigriceps	Common	Summer visitor
Parula americana	Fairly common	Permanent ?
Geothlypis aequinoctialis	Common	Summer visitor
Myioborus brunniceps	Common	Permanent
Cyclarhis gujanensis	Rare	Permanent ?
Vireo olivaceus	Common	Summer visitor
Junco capensis	Common	Permanent
Poospiza erythrophrys	Common	Permanent
Poospiza nigrorufa	Fairly common	Permanent
Poospiza cinerea	Common	Permanent
Sporophila caerulescens	Uncommon	Summer visitor
Catamenia analis	Uncommon	Winter visitor
Arremon flavirostris	Common	Permanent
Pheucticus aureoventris	Fairly common	Summer visitor
Saltator aurantiirostris	Fairly common	Permanent
Passerina brissonii	Uncommon	Permanent
Piranga flava	Fairly common	Permanent ?
Thraupis bonariensis	Fairly common	Permanent
Euphonia chlorotica	Fairly common	Permanent ?
Icterus cayanensis	Rare	Casual visitor
Carduelis magellanica	Fairly common	Summer visitor

* Taxonomy follows Peters (1960-1979), Meyer de Schauensee (1966) and Vaurie (1980).

APPENDIX 2

List of plant species recorded in El Cantadero site, La Rioja*

Lista de especies de plantas registradas en El Cantadero, La Rioja

Tree stratum

Celtis tala (Ulmaceae)*
Jodina rhombifolia (Santalaceae)
Ruprechtia apetala (Polygonaceae)
Bougainvillea stipitata (Nyctaginaceae)
Acacia aroma (Fabaceae)
Acacia visco (Fabaceae)
Prosopis nigra (Fabaceae)
Fagara coco (Rutaceae)
Lithrea molleoides (Anacardiaceae)
Schinopsis haenkeana (Anacardiaceae)
Schinus piliferus (Anacardiaceae)
Maytenus spinosa (Celastraceae)
Condalia buxifolia (Rhamnaceae)
Trichocereus terscheckii (Cactaceae)
Aspidosperma quebrachoblanco (Apocynaceae)

Shrub stratum

Ephedra triandra (Ephedraceae)
Phoradendron argentinum (Viscaceae)
Muehlenbeckia sagittifolia (Polygonaceae)
Pisoniella arborescens (Nyctaginaceae)
Anredera cordifolia (Basellaceae)
Clematis montevidensis (Ranunculaceae)
Cassia hookeriana (Fabaceae)
Cassia morongii (Fabaceae)
Porlieria microphylla (Zygophyllaceae)
Cardiospermum halicacabum (Sapindaceae)
Colletia spinosissima (Rhamnaceae)
Condalia x montana (Rhamnaceae)
Abutilon virgatum (Malvaceae)
Cajophora cernua (Loasaceae)
Cereus validus (Cactaceae)
Plumbago caerulea (Plumbaginaceae)
Cynanchum bonariense (Asclepiadaceae)
Ipomoea purpurea (Convolvulaceae)
Ipomoea rubriflora (Convolvulaceae)
Aloysia scorodonioides (Verbenaceae)
Cestrum lorentzianum (Solanaceae)
Cestrum parqui (Solanaceae)
Lycium cestroides (Solanaceae)
Nicotiana glauca (Solanaceae)
Solanum aff. diflorum (Solanaceae)
Solanum lorentzii (Solanaceae)
Solanum tucumanense (Solanaceae)
Vassobia breviflora (Solanaceae)
Cayaponia citrullifolia (Cucurbitaceae)
Cyclanthera histrix (Cucurbitaceae)
Sicyos warmingii (Cucurbitaceae)
Baccharis flexuosa (Asteraceae)
Eupatorium lasiophthalmum (Asteraceae)
Eupatorium viscidum (Asteraceae)
Jungia polita (Asteraceae)
Mikania periplocifolia (Asteraceae)
Senecio rudbeckiaefolius (Asteraceae)
Trixis grisebachii (Asteraceae)
Vernonia saltensis (Asteraceae)

Herb stratum

Anemia tomentosa (Schizaeaceae)
Adiantum lorentzii (Pteridaceae)
Pellaea ovata (Pteridaceae)
Cystopteris diaphana (Aspidiaceae)
Asplenium gilliesii (Aspleniaceae)
Cyperus sp. (Cyperaceae)
Tillandsia argentina (Bromeliaceae)
Tillandsia funebris (Bromeliaceae)
Tillandsia hieronymi (Bromeliaceae)
Commelina erecta (Commelinaceae)
Digitaria adscendens (Poaceae)
Leptochloa dominguensis (Poaceae)
Poa pratensis (Poaceae)
Parietaria debilis (Urticaceae)
Urtica urens (Urticaceae)
Polygonum convolvulus (Polygonaceae)
Rumex conglomeratus (Polygonaceae)
Chenopodium ambrosioides (Chenopodiaceae)
Alternanthera pungens (Amaranthaceae)
Amaranthus quitensis (Amaranthaceae)
Iresine diffusa (Amaranthaceae)
Rivina humilis (Phytolaccaceae)
Paronychia setigera (Caryophyllaceae)
Silene antirrhina (Caryophyllaceae)
Stellaria media (Caryophyllaceae)
Halimolobus montanus (Brassicaceae)
Lepidium sp. (Brassicaceae)
Rorippa nasturtium-aquaticum (Brassicaceae)
Sisymbrium gilliesii (Brassicaceae)
Potentilla norvegica (Rosaceae)
Oxalis sp. (Oxalidaceae)
Geranium patagonicum (Geraniaceae)
Anoda cristata (Malvaceae)
Malvastrum coromandelianum (Malvaceae)
Modiolastrum malvifolium (Malvaceae)
Sida rhombifolia (Malvaceae)
Parodia sp. (Cactaceae)
Heimia salicifolia (Lythraceae)
Oenothera sp. (Onagraceae)
Bowlesia incana (Apiaceae)
Anagallis arvensis (Primulaceae)
Samolus valerandi (Primulaceae)
Nama jamaicense (Hydrophyllaceae)
Heliotropium amplexicaule (Boraginaceae)
Glandularia pulchella (Verbenaceae)
Hyptis mutabilis (Lamiaceae)
Lepechinia floribunda (Lamiaceae)
Marrubium vulgare (Lamiaceae)
Minthostachys mollis (Lamiaceae)
Salvia aff. gilliesii (Lamiaceae)
Stachys gilliesii (Lamiaceae)
Nicotiana sylvestris (Solanaceae)
Petunia axillaris (Solanaceae)
Physalis neesiana (Solanaceae)
Salpichroa origanifolia (Solanaceae)
Solanum aff. kurtzianum (Solanaceae)
Maurandya scandens (Schrophulariaceae)
Mimulus glabratus (Schrophulariaceae)
Dicliptera scutellata (Acanthaceae)
Justicia squarrosa (Acanthaceae)
Plantago sp. (Plantaginaceae)
Richardia brasiliensis (Rubiaceae)
Valeriana effusa (Valerianaceae)
Triodanis biflora (Campanulaceae)
Wahlenbergia linarioides (Campanulaceae)
Acanthospermum hispidum (Asteraceae)
Aster squamatus (Asteraceae)
Bidens subalternans (Asteraceae)
Conyza bonariensis (Asteraceae)
Eupatorium clematideum (Asteraceae)
Eupatorium schickendantzii (Asteraceae)
Facelis retusa (Asteraceae)
Flaveria bidentis (Asteraceae)
Galinsoga parviflora (Asteraceae)
Gamochaeta argentina (Asteraceae)
Gamochaeta simplicicaulis (Asteraceae)
Gamochaeta spicata (Asteraceae)
Gnaphalium gaudichaudianum (Asteraceae)
Heterosperma ovatifolia (Asteraceae)
Parthenium hysterophorus (Asteraceae)
Senecio deferens (Asteraceae)
Senecio hieronymi (Asteraceae)
Stevia gilliesii (Asteraceae)
Tagetes minuta (Asteraceae)
Verbesina encelioides (Asteraceae)

* Nomenclature follows the modified system of Engler and Prantl (1887-1912).