Diversity and Distributions, (Diversity Distrib.) (2005) **11**, 205–217

BIODIVERSITY RESEARCH

Dispersal of forest birds and trees along the Uruguay River in southern South America

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ABSTRACT

The Uruguay River starts in Serra do Mar in Brazil, runs through the Paranense forest, and flows southward through grassland and savannas. It has a continuous gallery forest of 750 km from the southern border of the Paranense forest to the river mouth. The gallery forest extends for 100 km more along the Río de la Plata. 125 (68.7%) of the 182 species of forest birds recorded in the southern Paranense forest penetrate into the gallery forest of the Uruguay River and only 13 (7.1%) reach the end of the gallery forest (Punta Lara). The number of bird species is inversely correlated ($r^2 = 0.942$) with distance and the slope of the regression is 58.10. This means a decline in diversity with 32% of species lost per unit distance. A hundred and eighty forest tree species were recorded in the southern Paranense forest, of which 113 (62.8%) penetrate into the gallery forest of the Uruguay River, and 28 (15.6%) reach Punta Lara. The number of tree species is inversely correlated ($r^2 = 0.976$) with distance and the slope of the regression is −45.62. This means a decline in diversity with 25% of species lost per unit distance. The Uruguay River enables the dispersal of many species of forest birds and trees from the rain forest, but species richness tends to decrease with increased distance from the source area. A clear association pattern was found for birds between size, diet, habitat use and distance reached into the gallery forest. Species of smaller body size, granivores, insectivores and those that use both the interior and exterior parts of the gallery forest advanced noticeably further along the river than larger species, carnivores, nectarivores or frugivores, and those that frequent only a part of the forest. Similarly, a clear association between dispersal mechanism, water dependence and distance reached into the gallery forest was found for trees. Species with vegetative reproduction, zoochorous species and riparian species advanced markedly longer distances along the river than, anemochorous species and non-riparian species.

Key words

Birds, trees, distribution, gallery forest, Paranense Region, species/distance, South America.

INTRODUCTION

Rivers, with their associated vegetation, are crucial sources of food, refuge, and other resources for animals (Carothers *et al.*, 1974). Within rain forest, riparian forest is barely evident, but in open areas it forms conspicuous galleries (Hueck, 1972). Although gallery forests are finger-like extensions of rain forest, ecologically they are somewhat different. They occur in regions where natural conditions are not favourable for forest and allow vast extensions in the range of forest dwelling species.

Despite the numerous studies of riparian wildlife (Bell, 1974; Hupp, 1982, 1983; Knopf, 1985; Nilsson, 1986, 1992; Tabacchi *et al.*, 1990; Gregory *et al.*, 1991; Kalliola *et al.*, 1992; Naiman *et al.*, 1993; Mares & Ernest, 1995; Stromberg *et al.*, 1996; Nilsson *et al.*, 1997, 1999; Kellman *et al.*, 1998; Johnson *et al.*, 1999), few authors have examined patterns of species richness along the entire course of a river (Short & Horne, 1981; Nilsson, 1986; Nilsson *et al.*, 1989; Silva, 1996).

Around the Tropic of Capricorn, in eastern South America, two major vegetation types cover virtually all the area: the rain forest (Paranense–Atlantic forest), extending through eastern and south-eastern Brazil, eastern Paraguay, and north-eastern Argentina, and non-forest vegetation (grassland and savannas) in central and southern Brazil, south-eastern Paraguay, eastern

  DOI: 10.1111/j.1366-9516.2005.00141.x

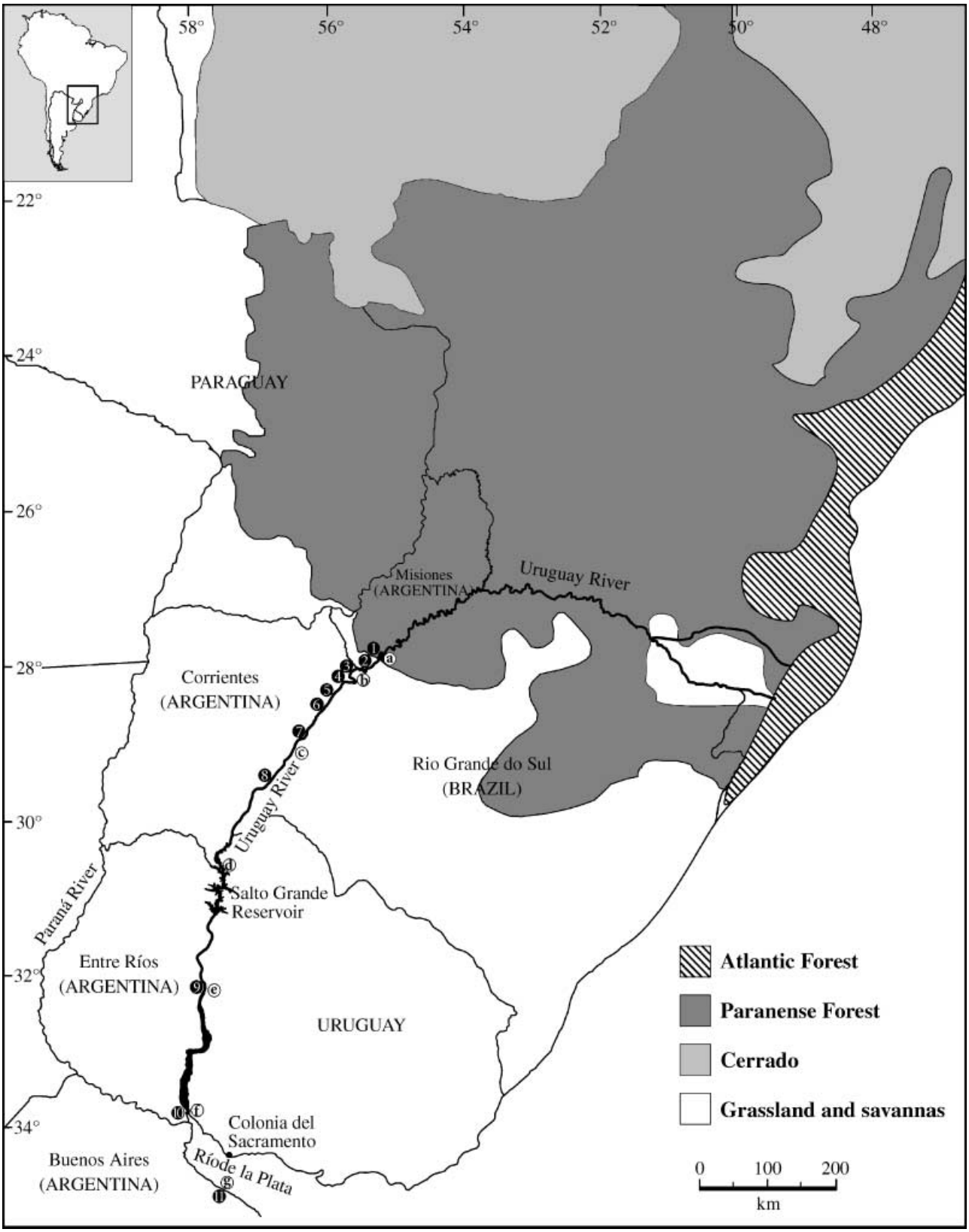

Figure 1 Map of the study area showing the location of forest and non-forest vegetation and location of the distribution points. Numbers indicate bird points: (1) Paranense forest border (2) Colonia Santa María (3) Garruchos (4) Colonia Garabí (5) Santo Tomé (6) Torrent (7) Alvear (8) Yapeyú (9) Colón (10) lower Paraná Delta, and (11) Punta Lara. Letters indicate tree points: (a) Paranense forest border (b) northern Corrientes (c) southern Corrientes (d) northern Entre Ríos (e) southern Entre Ríos (f) lower Paraná Delta, and (g) Punta Lara.

Argentina, and Uruguay (Fig. 1). In predominantly non-forest regions (Cerrado, Chaco and Pampas), narrow and well-defined gallery forests occur along rivers and streams (Hueck, 1972). Gallery forests enable many forest species to disperse from the rain forest (Darrieu, 1986; Redford & da Fonseca, 1986; Nores, 1992; Mares & Ernest, 1995; Darrieu & Camperi, 1996; Silva, 1996). However, species richness tends to decrease with increased distance from source areas (Silva & Oniki, 1988; Nores, 1992; Silva, 1996).

To the south of the Tropic of Capricorn, gallery forests generally occur where annual precipitation is at least 900 mm and they have a close relation to the microclimate of rivers. According to Martínez Crovetto (1963), morning fogs protect the vegetation from winter frost and allow tropical and subtropical species to survive in temperate regions.

A major river of subtropical South America is the Uruguay River, with a total course of 1600 km starting in the southern part of the Atlantic forest, running through the Paranense forest and flowing southward through grassland and savannas (Fig. 1). It is 1.3 km wide at the beginning of the gallery forest and 13 km wide near its mouth. It joins the Paraná River and together they form the Río de la Plata. The Uruguay River has a conspicuous gallery forest of 750 km that extends for 100 km more along the first part of the Río de la Plata. The Paraná River, however, does not have a continuous gallery forest in this area. The gallery forest follows a decreasing temperature and rainfall gradient ranging from 20 °C and 1600 mm (annual average) at its beginning in southern Misiones and north-western Rio Grande do Sul to 16 °C and 900 mm at the end of the gallery forest in the Río de la Plata. During the rainy season the Uruguay River raises several meters and floods gallery forest along most of its course.

In this paper we describe the distance that Paranense birds and trees have advanced along the gallery forest of the Uruguay River (and its extension along the first part of the Río de la Plata) and evaluate the relationship between these distances and some ecological characteristics of the species. We also compare our bird data with Atlantic–Paranense bird data from gallery forests in the Cerrado region (Silva, 1996).

METHODS

The study was conducted from February 1999 to June 2001. These data were supplemented by data we had obtained previously at various sites of the Paranense–Atlantic forest of Brazil, Paraguay and Argentina, and along gallery forests of several rivers and streams originating in these forests. We covered most of the roads that give access to the Uruguay River (and to the first part of the Río de la Plata) to verify the presence or absence of gallery forest and determined the extent and continuity of the gallery forest using satellite images.

We selected all those species of forest birds and trees recorded in the gallery forest of the Uruguay River (and the first part of the Río de la Plata) and assumed that these species have expanded their range from the Paranense–Atlantic forest by following the gallery forest of these rivers. We evaluated the distance that forest birds and trees have advanced along the Uruguay River (and the Río de la Plata) by considering the distance for each species from the source area to its southernmost record. For this reason, we generated the figures treating the species as all continuously distributed.

Forest bird distribution along the Uruguay River (and the Río de la Plata) was determined from three sources: (i) the huge collection made by William Partridge in the 1960s, which was communicated mainly by Darrieu and colleagues (Darrieu & Martínez, 1984; Darrieu, 1986, 1987, 1990; Darrieu & Camperi, 1988, 1991, 1992, 1993a, 1993b, 1994, 1996, 1998); (ii) literature from Brazil (mainly from the works of Belton, 1984, 1985, 1994), Argentina, and Uruguay; and (iii) surveys conducted at various sites where Partridge did not collect, especially Santa María, Yapeyú, Colón and Punta Lara. Some occasional records, particularly from Buenos Aires Province (Narosky & Di Giacomo, 1993), were evidently from escapees or vagrants. Most of these species are cage birds, recorded in unsuitable habitats, geographically far from their normal range. They were therefore excluded from further analysis. We surveyed bird species by visual and audio identification, and occasional mist netting.

To represent forest bird distribution along the river, 11 points were established that correspond to Partridge's collection sites and our ornithological surveys. Point 1 was on the southern border of the Paranense forest in southern Misiones and north-eastern Rio Grande do Sul. Points 2–10 were located along the gallery forest of the Uruguay River, and point 11 at the end of the gallery forest on the Río de la Plata (Fig. 1).

Forest tree distribution along the Uruguay River (and the Río de la Plata) was determined from botanical literature from Brazil, Argentina and Uruguay, mainly the work of Dimitri *et al.* (1998). Additional sources used were taxonomic and geographical reviews, such as Hauman (1925); Cabrera & Dawson (1944); Martínez-Crovetto (1963); Reitz (1965–89); Burkart (1969–79); Dimitri (1974); Jozami & Muñoz (1983); Troncoso & Bacigalupo (1987); Hunziker (1994–2000); Daviña *et al.* (1999).

To represent forest tree distribution along the rivers we established seven points, in locations similar to those of the bird points as above (Fig. 1).

To analyse the relationship between the distance reached by Paranense birds into the gallery forest and some of their ecological characteristics, we classified each taxon in categories of size, diet, habitat use and migratory status. Size categories are the following: very small up to 12 cm, small 13–20, medium 21–30 and large more than 30 cm. Diet categories include insectivores (species whose diet includes mostly insects and other arthropods), frugivores (species whose diet is mainly based on fruits, and rarely on insects), carnivores (species that feed mainly on terrestrial vertebrates or fishes), granivores (species whose diet is based primarily on grains and seeds, generally including some insects and other arthropods), nectarivores (species that feed mainly on nectar, generally including some arthropods), and omnivores (species whose diet includes fruits/seeds and insects/small vertebrates in similar proportions). Habitat use: interior (species that concentrate their activities mainly in the understorey and subcanopy of the gallery forest), exterior (species that concentrate their activities mainly in the canopy and/or borders) and both (species that use both interior and exterior of the gallery forest) (Silva, 1996). Migratory status: migratory species and residents.

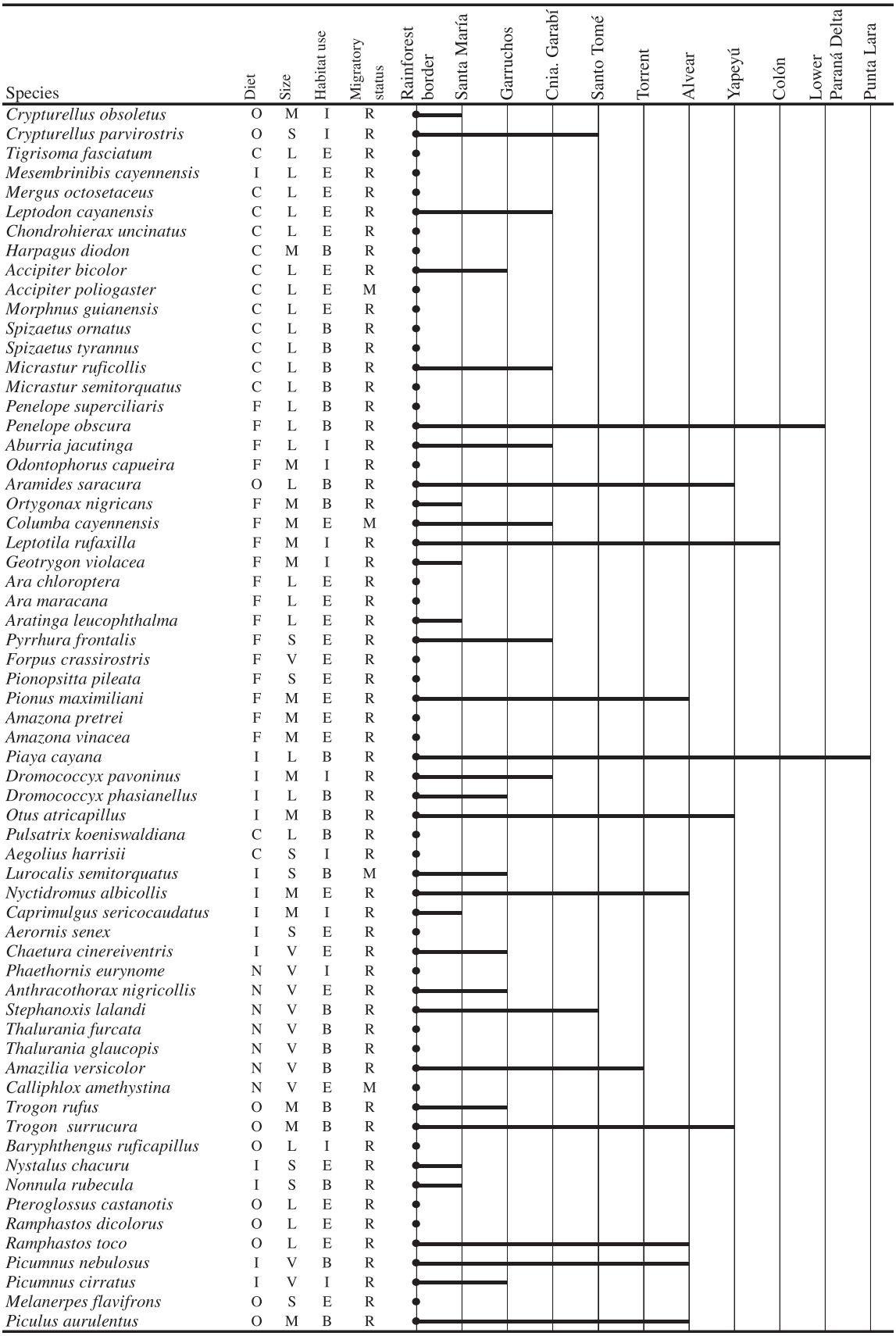

Figure 2 Ecological characteristics and distribution of forest birds along the gallery forest of the Uruguay River and in the first part of the Río de la Plata. The black lines indicate the distance that each species advances from the source area to its southernmost record.

Species	Diet	Size	Habitat use	Migratory status	Rainforest border	Santa María	Garruchos	Cnia. Garabí	Santo Tomé	Torrent	Alvear	Yapeyú	Colón	Lower Paraná Delta	Punta Lara
Colaptes melanochloros	O	M	E	R	●	●	●	●	●	●					
Dryocopus galeatus	O	L	B	R	●	●									
Dryocopus lineatus	O	L	E	R	●	●	●	●	●	●	●				
Campephilus robustus	O	L	B	R	●	●	●								
Dendrocincla fuliginosa	I	S	I	R	●	●	●								
Sittasomus griseicapillus	I	S	I	R	●	●	●	●	●						
Xiphocolaptes albicollis	I	M	I	R	●	●	●	●	●	●	●				
Dendrocolapes platyrostris	I	M	I	R	●	●	●	●	●	●	●				
Lepidocolaptes fuscus	I	S	I	R	●										
Lepidocolaptes squamatus	I	S	I	R	●	●	●	●	●						
Campylorhamphus falcularius	I	S	I	R	●	●	●	●							
Clibanornis dendrocolaptoides	I	S	I	R	●										
Synallaxis cinerascens	I	S	I	R	●	●	●	●							
Synallaxis ruficapilla	I	S	B	R	●	●	●	●							
Synallaxis spixi	I	S	B	R	●	●	●	●	●	●	●	●	●	●	●
Cranioleuca obsoleta	I	S	B	R	●	●	●	●	●	●	●	●			
Syndactyla rufosuperciliata	I	S	B	R	●	●	●	●	●	●	●	●	●	●	●
Philydor lichtensteini	I	S	I	R	●	●	●								
Philydor rufus	I	S	B	R	●	●	●								
Automolus leucophthalmus	I	S	I	R	●	●	●								
Heliobletus contaminatus	I	V	B	R	●	●									
Xenops minutus	I	V	B	R	●										
Xenops rutilans	I	V	B	R	●	●	●	●							
Sclerurus scansor	I	S	I	R	●	●	●								
Hypoedaleus guttatus	I	S	B	R	●	●									
Batara cinerea	I	L	I	R	●	●	●								
Mackenziaena leachi	I	M	I	R	●	●	●	●	●						
Mackenziaena severa	I	M	I	R	●	●									
Thamnophilus ruficapillus	I	S	B	R	●	●	●	●	●	●	●	●	●	●	●
Dysithamnus mentalis	I	V	I	R	●	●	●	●	●						
Herpsilochmus rufimarginatus	I	V	I	R	●										
Drymophila ferruginea	I	S	I	R	●										
Drymophila malura	I	S	I	R	●	●	●	●							
Pyriglena leucoptera	I	S	I	R	●										
Chamaeza campanisona	I	S	I	R	●	●	●	●							
Grallaria varia	I	S	I	R	●	●	●								
Hylopezus ochroleucus	I	S	I	R	●										
Conopophaga lineata	I	V	I	R	●	●	●	●							
Phyllomyias burmeisteri	I	V	E	M	●	●	●								
Phyllomyias fasciatus	I	V	E	M	●										
Phyllomyias virescens	I	V	E	R	●	●	●	●	●	●					
Myiopagis caniceps	I	V	I	R	●	●	●	●							
Myopagis viridicata	I	V	I	M	●	●	●	●							
Elaenia mesoleuca	F	S	E	M	●	●	●								
Elaenia obscura	F	S	B	R	●	●	●	●	●	●	●				
Mionectes rufiventris	O	S	I	R	●	●									
Leptopogon amaurocephalus	I	V	I	R	●	●	●	●	●	●	●	●			
Phylloscartes eximius	I	V	I	R	●	●									
Phylloscartes flaveolus	I	V	B	R	●	●									
Phylloscartes ventralis	I	V	B	R	●	●	●	●	●	●	●	●	●	●	●
Corythopis delalandi	I	S	I	R	●	●	●	●	●	●					
Myiornis auricularis	I	V	I	R	●	●	●	●							
Hemitriccus diops	I	V	I	R	●	●									
Todirostrum plumbeiceps	I	V	I	R	●	●	●	●	●	●	●	●			
Tolmomyias sulphurescens	I	S	I	R	●	●	●	●	●	●	●				
Platyrinchus mystaceus	I	V	I	R	●	●	●	●	●	●					
Cnemotriccus fuscatus	I	S	B	M	●	●	●	●	●	●	●				
Knipolegus cyanirostris	I	S	B	M	●	●	●	●	●	●	●	●	●	●	●
Colonia colonus	I	M	E	R	●	●									
Muscipipra vetula	I	M	E	R	●	●	●	●	●	●					
Attila phoenicurus	I	S	E	R	●										
Sirystes sibilator	I	S	E	R	●	●	●	●							

Figure 2 *Continued*

Species	Diet	Size	Habitat use	Migratory status	Rainforest border	Santa María	Garruchos	Cnia. Garabí	Santo Tomé	Torrent	Alvear	Yapeyú	Colón	Lower Paraná Delta	Punta Lara
Myiozetetes similis	I	S	E	R	●	●									
Conopias trivirgata	I	S	E	R	●										
Legatus leucophaius	I	S	E	R	●										
Pachyramphus castaneus	O	S	B	R	●	●	●	●							
Pachyramphus validus	O	S	E	M	●										
Pachyramphus viridis	O	S	E	R	●	●	●	●	●	●	●	●	●	●	
Tityra cayana	O	S	E	M	●	●	●	●							
Tityra inquisitor	O	S	E	R	●	●	●	●							
Schiffornis virescens	F	S	I	R	●	●	●								
Piprites chloris	F	V	I	R	●										
Manacus manacus	F	V	I	R	●										
Chiroxiphia caudata	F	S	B	R	●	●	●	●							
Pyroderus scutatus	F	L	E	R	●	●	●								
Procnias nudicollis	F	M	B	M	●										
Atticora melanoleuca	I	S	E	R	●										
Tachycineta albiventer	I	S	E	M	●	●	●	●	●	●					
Turdus albicollis	O	S	I	R	●	●	●	●	●	●	●	●			
Turdus leucomelas	O	M	B	R	●	●	●	●							
Turdus nigriceps	O	S	E	R	●	●	●								
Polioptila lactea	I	V	B	R	●	●	●	●							
Haplospiza unicolor	G	V	I	R	●	●	●	●	●						
Poospiza lateralis	G	S	B	R	●	●	●	●	●	●	●	●	●	●	●
Oryzoborus angolensis	G	V	I	R	●										
Amaurospiza moesta	G	S	I	R	●	●	●	●							
Arremon flavirostris	G	S	I	R	●										
Pitylus fuliginosus	G	S	I	R	●										
Saltator similis	G	S	B	R	●	●	●	●	●	●	●	●	●	●	●
Passerina glaucocaerulea	G	S	B	M	●	●	●	●	●	●	●	●	●	●	●
Cissopis leveriana	O	M	E	R	●										
Pyrrhocoma ruficeps	O	S	I	R	●	●	●	●	●	●	●				
Thlypopsis sordida	O	S	E	R	●										
Hemithraupis guira	O	S	E	R	●	●	●	●	●	●	●				
Nemosia pileata	O	S	E	R	●	●	●								
Tachyphonus coronatus	O	S	B	R	●	●	●	●							
Trichothraupis melanops	O	S	I	R	●	●	●	●	●	●	●	●			
Habia rubica	O	S	I	R	●	●									
Stephanophorus diadematus	O	S	E	R	●	●	●	●	●	●	●	●	●	●	●
Pipraeidea melanonota	O	S	E	R	●	●	●	●	●	●	●	●	●	●	●
Euphonia chalybea	F	V	E	R	●	●	●	●							
Euphonia musica	F	V	E	R	●										
Euphonia violacea	F	V	E	R	●	●	●								
Chlorophonia cyanea	F	V	E	R	●	●	●	●							
Tangara cayana	O	S	E	R	●										
Tangara preciosa	O	S	E	R	●	●	●	●	●	●	●	●			
Tangara seledon	O	S	E	R	●										
Dacnis cayana	O	V	E	R	●	●	●	●							
Tersina viridis	O	S	E	M	●										
Basileuterus culicivorus	I	V	I	R	●	●	●	●	●	●	●	●	●	●	●
Basileuterus leucoblepharus	I	V	I	R	●	●	●	●	●	●	●	●	●	●	●
Conirostrum speciosum	O	V	E	R	●	●	●	●							
Coereba flaveola	N	V	E	R	●	●	●	●	●	●	●				
Hylophilus poicilotis	O	S	B	R	●	●	●								
Cacicus haemorrhous	O	M	E	R	●	●	●	●	●	●					
Psarocolius decumanus	O	L	E	R	●										
Scaphidura oryzivora	O	L	E	R	●										
Cyanocorax cyanomelas	O	L	E	R	●										
Cyanocorax caeruleus	O	L	E	R	●	●	●	●	●	●					
					182	125	107	84	55	48	39	25	16	15	13

Figure 2 *Continued*

Table 1 Distribution of forest birds by categories of diet, size, habitat use migratory status and distance reached into the gallery forest of the Uruguay River and the Rió de la Plata I: insectivores, F: frugivores, C: carnivores, G: granivores, N: nectarivores, O: omnivores. VM: very small, S: small, M: medium, L: large. I: interior, E: exterior, B: both. M: migratory, R: resident

		Diet						Size				Habitat		Migratory Status		
	Total	I	F	C	G	N	O	VS	S	M	L	I	E	B	M	R
Rainforest border	182	77	29	14	8	8	46	45	72	31	34	61	71	50	17	165
Santa María	125	63	17	3	5	4	33	33	52	25	15	46	39	40	11	114
Garruchos	107	52	14	3	5	4	29	29	46	18	14	38	35	34	11	96
Cnia. Garabí	84	40	10	2	5	3	24	23	36	16	9	30	26	28	7	77
Santo Tomé	55	27	4	0	4	3	17	13	24	12	6	19	16	20	4	51
Torrent	48	23	4	0	3	2	16	10	21	11	6	13	16	19	4	44
Alvear	39	18	4	0	3	1	13	7	19	8	5	11	10	18	3	36
Yapeyú	25	12	2	0	3	0	8	5	14	3	3	7	4	14	2	23
Colón	16	8	2	0	3	0	3	3	10	1	2	3	3	10	2	14
Lower Paraná Delta	15	8	1	0	3	0	3	3	10	0	2	2	3	10	2	13
Punta Lara	13	8	0	0	3	0	2	3	9	0	1	2	2	9	2	11
%	7.1	10.39	0	0	37	0	4.35	6.66	12.5	0	2.94	3.28	2.81	18	11.76	6.66

For trees we classified each taxon in categories of water dependence (riparian and non-riparian species) and dispersal mechanism: V: vegetative reproduction, Z: zoochorous species, A: anemochorous species, H: hydrochorous species.

The order of the families and the generic and specific names of bird species follow Stotz *et al.* (1996). Tree families are arranged following the Angiosperm Phylogeny Group II (APG II, 2003), and genera and species are in alphabetical order. Nomenclature follows Zuloaga *et al.* (1994), and Zuloaga & Morrone (1996–99).

We used a semilog regression to determine the relation between the number of species and distance of birds and trees along the river and a chi-square analysis to compare the number of riparian and non-riparian species of trees that go into the gallery forest or reach the end of the gallery forest.

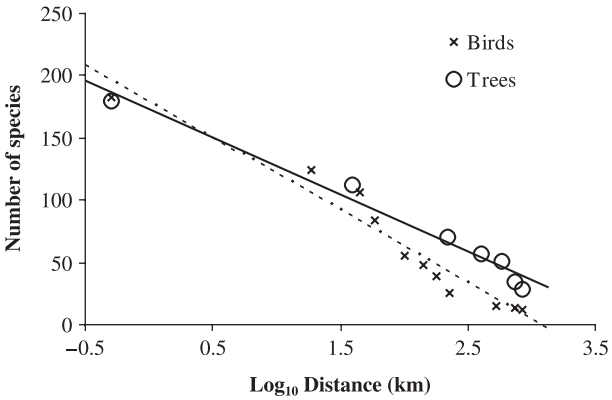

Figure 3 Species/distance curve for forest birds and trees on the Uruguay River and in the first part of the Río de la Plata.

RESULTS

Satellite images and survey data reveal that the Uruguay River formerly had a continuous gallery forest from southern Misiones and north-western Rio Grande do Sul to its mouth in the Río de la Plata, with a maximum width of 1000 m on each side of the river. We found only one apparently natural short interruption, where the gallery forest is replaced by xerophytic woodland. It is located in Monte Caseros (Corrientes) and is about 2 km long. From the mouth of the Uruguay River, the gallery forest extends for 100 km more along the Argentine coast of the Río de la Plata to Punta Lara (Cabrera & Dawson, 1944) and for 60 km along the Uruguayan side to 7 km upstream of the city of Colonia de Sacramento (pers. obs.).

During the 20th century, human constructions and forest exploitation interrupted the gallery forest in several places or changed the floristic composition of the vegetation. The most important disturbance by far is the Salto Grande reservoir which flooded and destroyed 100 km of gallery forest (Fig. 1). In spite of the fact that more than 20 years have passed since Salto Grande was constructed, there is no evidence that gallery forest is forming on its margins.

Hundred and twenty five (68.7%) of the 182 species of forest birds recorded in the Paranense forest in southern Misiones and north-western Rio Grande do Sul (Belton, 1984, 1985, 1994; Chebez, 1996) go into the gallery forest of the Uruguay River and only 13 (7.1%) reach Punta Lara (Fig. 2). The number of species is inversely correlated ($r^2 = 0.942$) with distance and the slope of the regression is −58.10; SE 4.81(Fig. 3). This means a decline in diversity with 32% of species lost per unit distance.

A clear association pattern was found for birds between size, diet, habitat use and distance reached into the gallery forest. Species of smaller body size, granivores, insectivores and those that use both the interior and exterior parts of the gallery forest advanced markedly longer distances along the river than the other groups (Table 1). Eleven migratory species (*Columba cayennensis*, *Lurocalis semitorquatus*, *Anthracothorax nigricollis*, *Phyllomyias burmeisteri*, *Myiopagis viridicata*, *Elaenia mesoleuca*, *Cnemotriccus fuscatus*, *Knipolegus cyanirostris*, *Tityra cayana*,

Table 2 Distribution of forest trees by categories of water dependence, dispersal mechanism and distance reached into the gallery forest of the Uruguay River and the Rió de la Plata

		Dispersal mechanism			Water dependence	
	Total	V	Z	A	R	NR
Rainforest border	180	4	142	34	43	137
Northern Corrientes	112	2	85	26	30	83
Southern Corrientes	69	2	56	12	25	45
Northern Entre Ríos	56	2	47	8	21	36
Southern Entre Ríos	50	1	43	7	19	32
Lower Paraná Delta	35	1	29	5	15	20
Punta Lara	28	1	24	3	13	15
%	15.6	25	16.9	8.8	30.2	10.9

V: vegetative reproduction, Z: zoochorous, A: anemochorous, H: hydrochorous. R: riparian, NR: non-riparian

Tachycineta albiventer, and *Passerina glaucocaerulea*) were recorded in the gallery forest of the Uruguay River. With the exception of *Knipolegus cyanirostris* and *Passerina glaucocaerulea* that reach Punta Lara, all of them only penetrate a short distance (maximum 180 km) along the Uruguay River.

In the Paranense forest in southern Misiones and northwestern Rio Grande do Sul 180 forest tree species were recorded, of which 43 are restricted to riparian habitats (Martínez Crovetto, 1963). From the total of species recorded 113 (62.8%) go into the gallery forest of the Uruguay River and 28 (15.6%) reach the end of the gallery forest (Fig. 4). The number of species is inversely correlated ($r^2 = 0.976$) with distance and the slope of the regression is –45.62; SE 3.11 (Fig. 3). This means a decline in diversity with 25% of species lost per unit distance.

A clear association pattern was also found for trees between ecological characteristics and distance reached into the gallery forest (Table 2). Vegetative reproduction species, zoochorous species and riparian species advanced markedly greater distances along the river than anemochorous species and non-riparian species. The species that reproduce mainly vegetatively were those that advanced more distance along the Uruguay River. However, this has little influence on the system because only four species are in this category.

DISCUSSION

The distribution of forest birds and trees along the Uruguay River shows that the river enables many species to disperse from the rain forest. But, as expected in this type of study (Silva & Oniki, 1988; Nores, 1992; Silva, 1996), the importance of the river decreases with increasing distance from the source area.

The passage from the Paranense forest to the gallery forest of the Uruguay River implies that species must not only pass the bottleneck of the change from the broad rain forest to the narrow gallery forest but must also meet all the biological requirements of a small and narrow area. This constitutes a 'filter' which 31.3% of birds and 37.2% of tree species do not pass through. Lastly, to advance down the Uruguay River implies that species must at least have a tolerance for cooler and drier environments.

Although distribution patterns along the Uruguay River are similar for birds and trees, trees have a higher percentage of species reaching the end of the gallery forest (15.6% vs. 7.1%) and a less steep species/distance slope (–45.62 vs. –58.10).

Riparian species of trees advanced markedly longer distances along the river than non-riparian species (Table 2). A question arising from this pattern is whether being a riparian species facilitates passage from the Paranense forest to the gallery forest, or makes advance along the river easier. The results suggest the second option. Although the percentage of species entering the gallery forest is somewhat higher among riparian species (69.7%) than non-riparian species (60.6%), the difference is not significant ($\chi^2 = 1.18$; Df = 1; $P = 0.277$), but the percentage of riparian species (30.2%) that reach the end of the gallery forest is significantly higher ($\chi^2 = 9.26$; Df = 1; $P = 0.0023$) than that of non-riparian species (10.9%). The presence of a relatively high number of riparian species of trees would explain why trees have a higher percentage of species reaching the end of the gallery forest and a less steep species/distance slope than birds. In the Paranense forest there are also some riparian species of birds but only one (*Knipolegus cyanirostris*) reaches the end of the gallery forest.

Silva (1996) studied distribution along gallery forests in the Cerrado region of forest birds from two sources: Atlantic–Paranense forest and Amazonia. To compare our results with those of Silva's Atlantic–Paranense forest, we grouped the bird data according to his distance categories (0–250 km, 251–500 km, 501–750 km, and more than 750 km). In the Uruguay River the first category (0–250 km) is approximately in the subtropical zone and the remaining categories are in the temperate zone.

One unexpected difference between the two systems is that the number of species of Atlantic–Paranense birds recorded in the gallery forests of the Cerrado rivers (78) is much lower than the number of species recorded in the Uruguay River (125), even though the source area species pool is larger in the former than in the latter. Another difference is in the bird distribution pattern. In the Cerrado only 50% of the species that go into the gallery forests maintain their ranges within 0–250 km, while in the Uruguay River 87% of the species are restricted to this distance category. This is probably because gallery forests of the Cerrado region are in the tropical zone with a more uniform temperature, while in the Uruguay River the gallery forest occurs in the subtropical and temperate zone and follows a decreasing temperature gradient.

Of the 16 remaining species that go beyond 250 km in the Uruguay River, one extends to 500 km, two extend to 750 km, and 13 exceed 750 km and reach Punta Lara. This means that most of the species which pass the first 250 km reach the end of the gallery forest. These are species with higher adaptability and most of them can sometimes go some distance outside gallery forests and colonize isolated — natural or exotic — forest habitats (e.g. *Synallaxis spixi*, *Syndactyla rufosuperciliata*, *Thamnophilus*

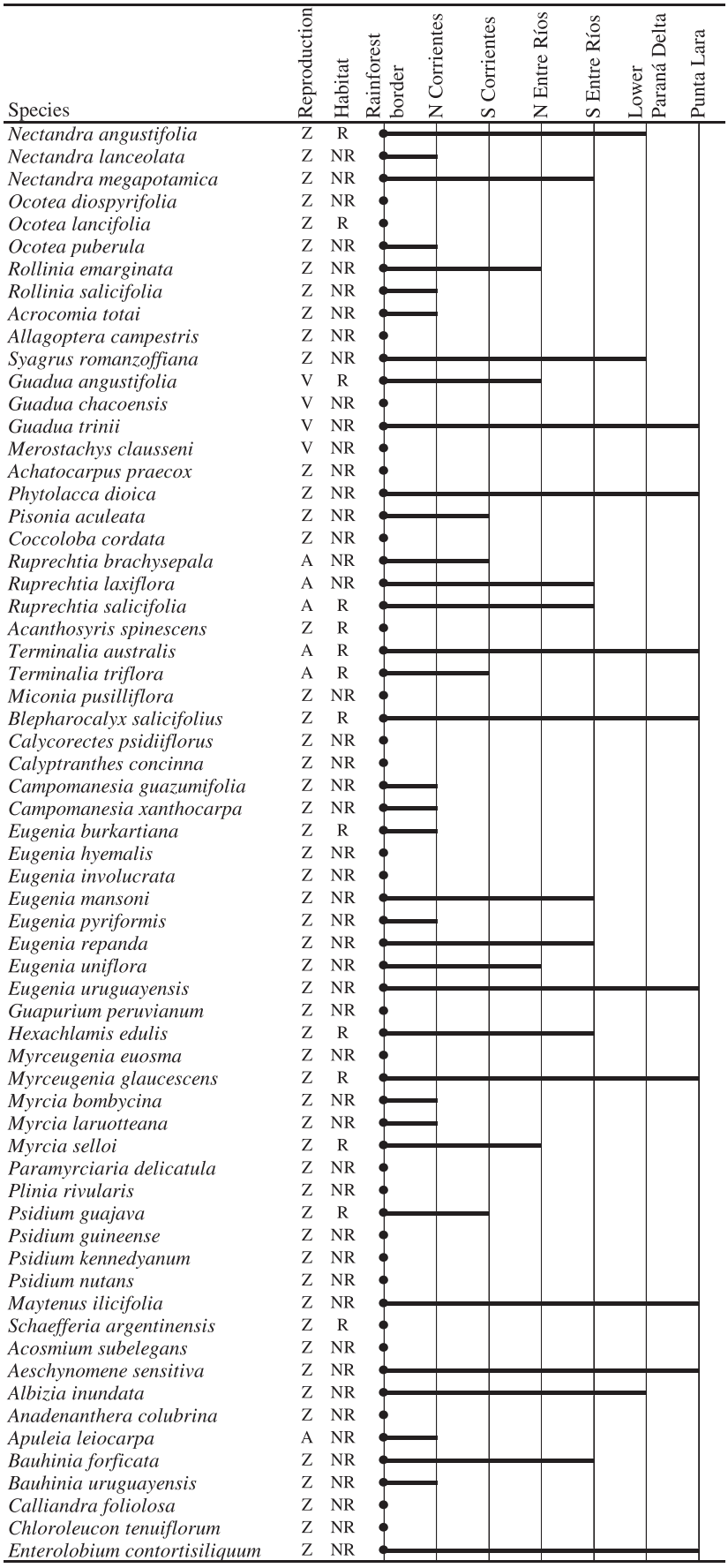

Figure 4 Ecological characteristics and distribution of forest trees along the Uruguay River and in the first part of the Río de la Plata. The black line indicates for each species the distance from the source area to its southernmost record.

Species	Reproduction	Habitat	Rainforest border	N Corrientes	S Corrientes	N Entre Ríos	S Entre Ríos	Lower Paraná Delta	Punta Lara
Gleditsia amorphoides	Z	NR	●	●	●	●	●		
Holocalyx balansae	Z	NR	●	●					
Inga semialata	Z	NR	●	●					
Inga verna	Z	R	●	●	●	●	●	●	●
Lonchocarpus leucanthus	A	NR	●	●	●				
Lonchocarpus muehlbergianus	A	NR	●	●					
Lonchocarpus nitidus	A	NR	●	●	●	●	●	●	●
Machaerium aculeatum	A	R	●						
Machaerium minutiflorum	A	R	●						
Machaerium nyctitans	A	NR	●	●					
Machaerium paraguariense	A	R	●	●					
Mimosa bimucronata	Z	R	●						
Myrocarpus frondosus	A	NR	●	●					
Parapiptadenia rigida	A	NR	●	●					
Peltophorum dubium	A	NR	●	●	●	●	●	●	
Poecilanthe parviflora	Z	R	●	●	●	●	●	●	●
Pterogyne nitens	A	NR	●	●	●	●			
Rheedia brasiliensis	Z	NR	●	●					
Alchornea triplinervia	Z	NR	●						
Croton urucurana	Z	R	●	●					
Jatropha curcas	Z	NR	●						
Manihot grahamii	Z	NR	●	●	●	●	●	●	●
Margaritaria nobilis	Z	NR	●						
Sebastiania brasiliensis	Z	NR	●	●	●	●	●	●	●
Sebastiania commersoniana	Z	R	●	●	●	●	●	●	●
Sebastiania schottiana	Z	R	●	●	●	●	●	●	●
Banara tomentosa	Z	NR	●	●					
Casearia decandra	Z	NR	●						
Casearia sylvestris	Z	R	●	●	●				
Xylosma venosa	Z	R	●	●	●	●	●		
Jacaratia spinosa	Z	NR	●	●					
Ficus adhatodaefolia	Z	NR	●						
Ficus eximia	Z	NR	●						
Ficus luschnathiana	Z	NR	●	●	●	●	●	●	
Maclura tinctoria	Z	NR	●						
Sorocea bonplandii	Z	NR	●						
Cecropia pachystachya	Z	NR	●	●	●	●			
Colubrina retusa	Z	NR	●						
Quillaja brasiliensis	A	NR	●						
Celtis iguanaea	Z	R	●	●	●	●	●	●	●
Celtis pubescens	Z	R	●						
Trema micrantha	Z	NR	●	●	●	●	●		
Boehmeria caudata	Z	NR	●						
Urera baccifera	Z	NR	●						
Bastardiopsis densiflora	Z	NR	●						
Ceiba insignis	A	NR	●	●					
Heliocarpus popayanensis	A	NR	●	●					
Luehea divaricata	A	NR	●	●	●	●	●	●	●
Guazuma ulmifolia	Z	NR	●	●					
Schinus ferox	Z	NR	●						
Schinus lentiscifolia	Z	NR	●						
Schinus terebinthifolius	Z	NR	●	●					
Cabralea canjerana	Z	NR	●	●					
Cedrela fissilis	A	NR	●						
Cedrela odorata	A	NR	●						
Guarea macrophylla	Z	NR	●						
Trichilia claussenii	Z	NR	●						
Trichilia elegans	Z	NR	●						
Trichilia pallida	Z	NR	●						
Balfourodendron riedelianum	A	NR	●	●					
Esenbeckia grandiflora	Z	NR	●						
Fagara hyemalis	Z	R	●						
Fagara rhoifolia	Z	NR	●	●					
Helietta apiculata	A	NR	●	●	●				

Figure 4 *Continued*

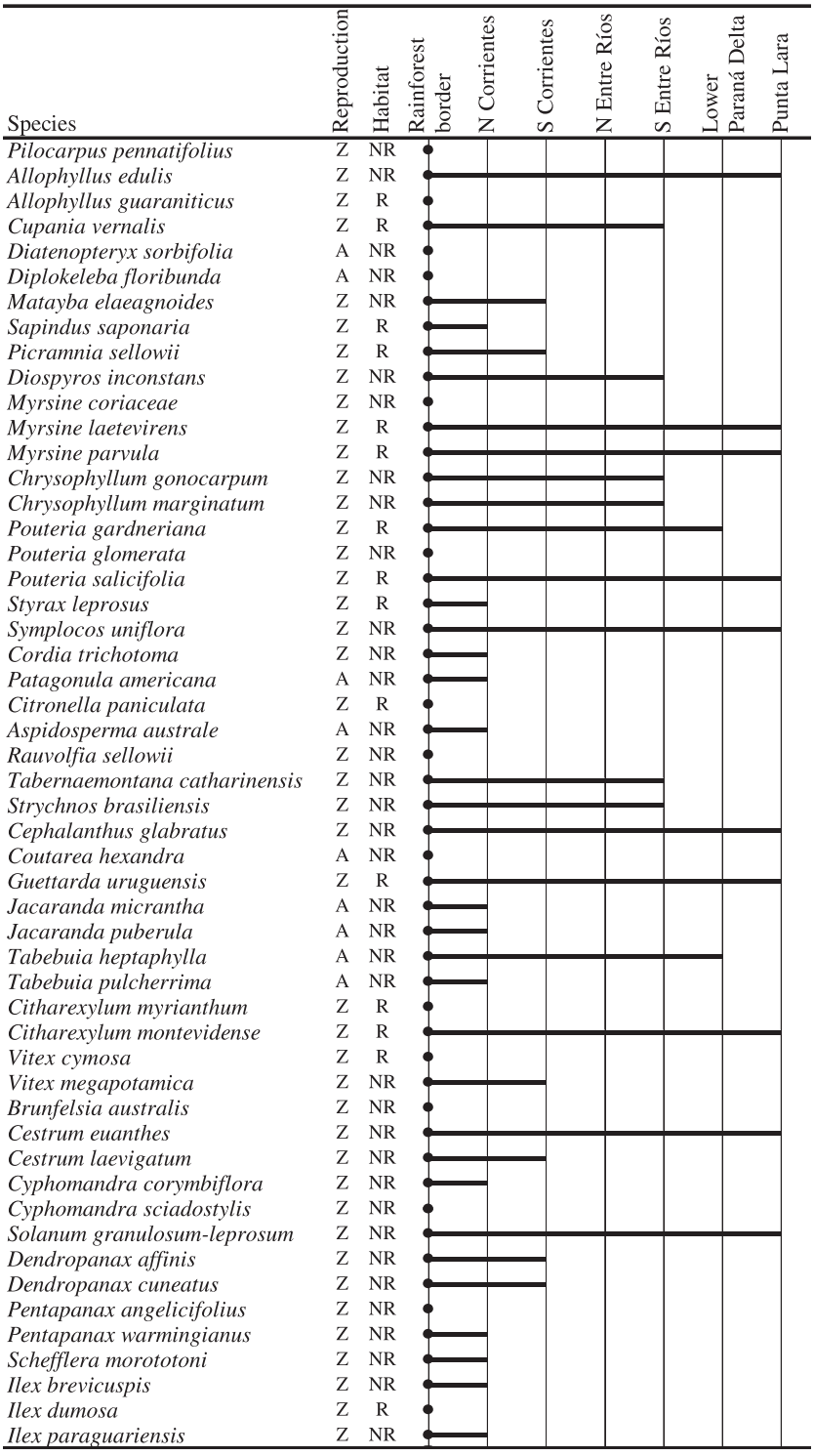

Figure 4 *Continued*

ruficapillus, *Phylloscartes ventralis*, *Turdus albicollis*, *Poospiza lateralis*, *Stephanophorus diadematus*, *Basileuterus culicivorus*, and *Basileuterus leucoblepharus* in Lussich Arboretum, near Punta del Este, Uruguay).

Thirty-three bird species are shared by the two systems, but no clear pattern of the use of gallery forests is observed. Thirteen species maintain their ranges within 0–250 km in the two systems, while the 20 remaining species differ in the distance that they advance along the rivers. For example, *Basileuterus leucoblepharus* and *Phylloscartes ventralis*, that reach the end of the gallery forest of the Uruguay River, do not go beyond 250 km in the gallery forests of the Cerrado region, while *Philydor lichtensteini*, *Automolus leucophthalmus*, *Sclerurus scansor*, *Conopophaga lineata*, *Mionectes rufiventris* and *Schiffornis virescens*, which

advance a long distance in the gallery forest of the Cerrado region, only advance a short distance (maximum 60 km) in the Uruguay River. The avifauna of the Uruguay River showed a clear association pattern between size, diet, habitat use and distance reached into the gallery forest. On the contrary, no clear pattern of association was found between ecological characteristics of birds and distance reached into the Cerrado rivers (Silva, 1996).

Despite its large size, the Salto Grande dam apparently has not caused the extinction of any species because it is located at a point in the river were only a few, adaptable species reach. All the species that extended past that point are now present downstream of the dam. A proposed dam at Colonia Garabí, northeastern Corrientes, however, constitutes a great potential hazard for the forest species of the Uruguay River. As Colonia Garabí is only 60 km downstream from the Paranense forest border, the construction of this dam would eliminate this first 60 km of gallery forest and would isolate the rest for most of the species.

ACKNOWLEDGEMENTS

Very helpful comments were made on the manuscript by D. Stotz and two anonymous reviewers. M. Tablada and M. L. Nores helped us with the data. J. Heywood and J. Brasca edited the manuscript. Fieldwork was made possible by grants from Agencia Nacional de Promoción Científica y Tecnológica and Conicor.

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