DISTRIBUTION PATTERNS OF NEOTROPICAL PRIMATES (PLATYRRHINI) BASED ON PARSIMONY ANALYSIS OF ENDEMICITY

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(With 8 figures)

ABSTRACT

The Parsimony Analysis of Endemicity (PAE) is a method of historical biogeography that is used for detecting and connecting areas of endemism. Based on data on the distribution of Neotropical primates, we constructed matrices using quadrats, interfluvial regions and pre-determinated areas of endemism described for avians as Operative Geographic Units (OGUs). We codified the absence of a species from an OGU as 0 (zero) and its presence as 1 (one). A hypothetical area with a complete absence of primate species was used as outgroup to root the trees. All three analyses resulted in similar groupings of areas of endemism, which match the distribution of biomes in the Neotropical region. One area includes Central America and the extreme Northwest of South America, other the Amazon basin, and another the Atlantic Forest, Caatinga, Cerrado and Chaco.

Keywords: Parsimony Analysis of Endemicity, neotropical primates, Platyrrhini, distribution patterns, endemism.

RESUMO

Padrões Distribucionais de primatas Neotropicais (Platyrrhini) baseados na Análise de Parcimônia de Endemismo

A Análise de Parcimônia de Endemismo (PAE) é um método da biogeografia histórica que é usado para detectar e conectar áreas de endemismo. Baseando-se em dados de distribuição de primatas Neotropicais, construíram-se matrizes de dados utilizando-se quadrículas, regiões entre rios e áreas de endemismo pré-determinadas para aves como Unidades Geográficas Operacionais (OGUs). Codificou-se a ausência da espécie na OGU como 0 (zero) e a presença como 1 (um). Uma área hipotética com ausência total de espécies de primatas foi usada como grupo externo para polarização. Todas as três análises resultaram em grupos similares de áreas de endemismo, coincidindo com a distribuição de biomas na região Neotropical: uma área incluindo a América Central e o extremo Noroeste da América do Sul; outra, a Bacia Amazônica; e, uma terceira, a Mata Atlântica, Caatinga, Cerrado e Chaco.

Palavras-chave: Análise de Parcimônia de Endemismo; primatas neotropicais; Platyrrhini; padrões distribucionais; endemismo.

INTRODUCTION

Biogeographical methods depend on a good knowledge of the distribution and areas of endemism of a particular group of species. In biogeography, an area of endemism is defined as "the congruent distributional limits of two or more species" (Platnick, 1991). Harold & Mooi (1994) define an area of endemism as a geographic region comprising the distributions of two or more monophyletic

taxa that exhibit a phylogenetic and distributional congruence and having their respective relatives occurring in other such-defined regions. The number of species found in a given geographic area, for example, is directly related to its size, a phenomenon known as "species-area relationship" (Rosenzweig, 1995). Therefore, it is possible that scale affects the results of biogeographical studies. In this paper we test whether the choice of scale influences interpretations of the patterns of distribution of New World primates based on a Parsimony Analysis of Endemicity (PAE) and whether this method can help understanding past patterns of dispersion of the primate fauna within Latin America.

PAE is a method proposed by Rosen (1988) to relate areas historically based on the composition of their biota or part of it. This method is analog to cladistics. In the PAE method the areas (Operating Geografic Units - OGUs) represent the taxa and the taxa represent the characters. Different authors have used different ways for determining OGUs. The most common variation of the method, proposed by Morrone (1994), uses predetermined same-sized quadrats. It has been used in the study of several groups of plants and animals (*e.g.*, Posadas, 1996; Posadas *et al.*, 1997; Cavieres *et al.*, 2002; García-Barros *et al.*, 2002). Craw (1988) sugested the use of predetermined areas of endemism (see also Goldani *et al.*, 2002), whereas Silva & Oren (1996) adopted interfluvial regions as OGUs in a study of Amazonian primates. The size of individual OGUs may vary in these latter two methods.

New World monkeys are good models to test the influence of OGUs size in biogeography because their distribution is relatively well known, and most species present restrict distributions and have limited dispersion abilities. About 34% of the approximately 300 known extant primate species occur in the Neotropics (Rylands & Konstant, 2000). New World monkeys occur in forested habitats from about 30° S in Brazil and Argentina to about 20° N in Mexico (Hirsch *et al*., 2002).

MATERIALS AND METHODS

Distribution data were obtained mainly from a georeferenced data base available in the internet (BDGEOPRIM; www.icb.ufmg.br/~primatas/home_bdgeoprim.htm). BDGEOPRIM was elabo-rated and is maintained updated by André Hirsch and his colleagues of the Universidade Federal de Minas Gerais (Brazil). The data set was complemented with information from other publications (Silva & Oren, 1996; Collins & Dubach, 2000; Lehman, 2000; Chiarello & Melo, 2001).

Data analysis was based on matrices (OGUs *vs*. taxa) in which the absence of a taxon in a particular OGU is coded as 0 (zero) and its presence as 1 (one). A hypothetical area (outgroup) in which all taxa are absent (0) was added for polarization (Rosen & Smith, 1988).

Analyses were made using the Hennig86 software (Farris, 1988) with the following comands: mh* and bb* (branching bound), sw (sucessive weighting), ne (strict consensus) and ie (implicit enumeration). In the first analysis (quadrats as OGUs), areas of endemism were established in a cladogram based on the distribution of 106 species (Table 1) in 60 quadrats of 5° longitude by 5° latitude (Fig. 1) (first stage). The relationship among these areas of endemism (second stage) was determined according to the occurrence of 57 species (Table 2). Those species occurring in a single area (autapomorphies) were not included in this analysis.

The second analysis was based on the areas of endemism proposed for Neotropical birds by Cracraft (1985). Those areas with a complete absence of primates (West Peruvian Andean Subcenter, Austral Andean Center, Peruvian Arid Coastal Center, Nothofagus [Chilean Andean] Center and Patagonian Center) were excluded from the analysis, whereas a new OGU was added to the list (Central America - 31) Fig. 2). The original numbering of these areas was maintained in this paper to facilitate comparing the patterns observed with birds and primates: 1) Chocó Rainforest Center; 2) Nechí Rainforest Center; 3) Magdalena Center; 4) Santa Marta Center; 5) Guajiran Center; 6) Parian Center; 7) Venezuelan Montane Center; 8) Meridan Montane Center; 9) Perijan Montane Center; 10A) Gran Sabana Subcenter of Pantepui Center; 10B) Duida Subcenter of Pantepui Center; 11) North Andean Center; 12B) East Peruvian Andean Subcenter; 12C) South Peruvian Andean Subcenter; 14) Tumbesan Center; 16) Marañón Center; 17) Guyanan Center; 18) Imeri Center; 19) North Amazon Napo) Center; 20) South Amazon

TABLE 1

MATRIX with distributional data of 106 primate species in 60 quadrats as Operative Geografic Units.

	1	2	3	4	5	6	7	8	9	10
	123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890123456									
OG	**000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000**									
Q1	000000100000000000010000000000000000000000000000000000000000000000000000000000000000000000000000									
Q2	000001000000000000010000000000000000000000000000000000000000000000000000000000000000000000000000									
Q3	000001100000000000010000000000000000000000000000000000000000000000000000000000000000000000000000									
Q4	000000100000000000010000000000000000000000000000000000000000000000000000000000000000000000000000									
Q5	000001100000000000010000000000000000000000000000001000000000000000000000000000000000000000000000									
Q6	000001000000000000010000000000000000000000000000001000000000000000000000000000000000000000000000									
Q7	000000001001000000001000000000000000000000000000100001000000000000000000000000000000000000000100000									
Q8	000000001000000000010000000000000000000000000000100000000000000000000000000000000000000000000000									
Q9	001001000000000000010000000000000000000000000000010000000000000000000000000000100000100000000000000									
Q10	000001001001000000011000000000000000000000000000010000000000000000000000000000000000100001000000100000									
Q11	000000001011000000001000000000000000000000000000100001000001000000000000000000000000000000100000100000									
Q12	000000001000000101000000000000000000000100000000100001001000000000000000000000000100000000000000000000									
Q13	000000001000000101000000000000000000000100000000100010010000000000000000000000000100000000001000000001									
Q14	000000001000000101000010000000000000000000000000100010010000000000000000000000000000000000001000000001									
Q15	000001001001000000010000000000000000100000010000001100000000001000000000000000000000000101000000001100010									
Q16	000000001001000101000000000000000010001010000000111000000001100000000000000000000010001000100000010000010									
Q17	000000001000000101000000001000000000000010000000110001001010000000000000000000000100000001000100000001									
Q18	000000001000000101000000000000000000000100000000100001001010000000000000000000000100000000001000000001									
Q19	000000001000000100000010000000000000000000000000100010010000000000000000000000000100000000001000000001									
Q20	000000001 100000100000010000000000000000000000000100010010000000000000000000000100000000001000000001									
Q21	000001001000100011000000000000010010000001000000110000000000010000000000000000000010001010000000000010010									
Q22	000000001000010101100000010000010010000011000000101000000000010000000000000000000010001000000001010100010									
Q23	000000001000001110100000011000010000000010000000101000000011010000000000000000000011101000110001010011110									
Q24	000000001000001110100010011000010000000010000000101000100111000000000000000000000011110000110011000010111									
Q25	100010001100000100000110000000000100100000000000101000101110000000001100100100100100110100000101100000011									
Q26	100000001100000100000110000000000000100000000000010001011000000000010001001000000001100000000001010000011									
Q27	100000000100000100000100000000000000100000000000010001001000000000010000000000000010000000000000010000000									
Q28	100000000100000000000000000000000000000000000010100000100000000000000000000000000000000000000000010000000									
Q29	000000001000100001000000000000010000000010000001010000000000110000000000000000000000000100000001000000010									
Q30	000000001000001000100000010000010000000011000001010000000000100000000000000000000000101000010010000010000010									
Q31	000000001000001000100000010010010000000011000001010000000100100000000000000000000010100010010100010000110									
Q32	000000001000001000100000000010010000000010000001010000010100000000101000110110110001100100001000100001100									
Q33	100010001000000000000000000000010000000000000000100000100000000001000010000000000000000000000000000000000									
Q34	100000000100000000000000000000000010000000000000100000110000000000010000000000000010000000000000010000000									
Q35	110000000100000000000000000000000010000000101000010000000000000000000000000000000000000000000000000000000									
Q36	110000000000000000000000000000000000000000000000101000010000000000000000000000000000000000000000000000000									
Q37	100000000000000000000000000000010000000000000000101000010000000000000000000000000000000000000000000000000									
Q38	000000001000001000100000010010010000000001000000101010000010000000000000000000000000010010000010000011 0									
Q39	010000011100001100100000000010011000000001000000110010000010000000000000000000010010000010010100010000011 0									
Q40	010000011100001000100000000010001000000000000000111010001010000000000100000000100100100100000000000000110									
Q41	000000001000001000100000000001000000000000000000010000010100000000000110000000100000100000000000000000100									
Q42	010000000100000000000000000000000000000000000000100100000000000000000010000000000000000000000000000000000									
Q43	010000000100000000000000000000000000000000000001010010100000000000000000000000000000000000000000000000000									
Q44	010000000000000000000000010010000001000000000011000010010000000010000000000000000000000000000000000000000									
Q45	000100000000000000000000100100100001000000000111000000100000000100000000000000000000000000000000000000000									
Q46	000000010100000000100000000000010000000000000000000100000000000000000000000000000000010000000000000000000									
Q47	010000010100000000100000000000010000000000000000000100000000000000000000000000100100000100000000000000000									
Q48	010000000100000000000000000000010000000000000000000000000000000000000000000000010000000000000000000000000									
Q49	010000000000000000000000000000000000000000000000100001000000000000000000000000010000000000000000000000000									
Q50	010000000000000000000000000000000000000100000000100001100000000000000000000000000000000000000000000000000									
Q51	010100000000000000000000000000001010100011011000011010000000010000000000000000000000000000000000000000000									
Q52	010000000100000000000000000000001000000000000000000100000000000000000000000000010000000000000000000000000									
Q53	010000000000000000000000000000001000000000000000000000000000000000000000000000000000000000000000000000000									
Q54	010100000000000000000001000000000000000000000000000110000000000100000000000000000000000000000000000000000									
Q55	010100000000000000000011000000000000100001000010000010000000001010000000000000000000000000000000000000000									
Q56	000100000000000000000011000000000000101001111010000010000000000010000000000000000000000000000000000000000									
Q57	010100000100000000000000000000000000000000000000000010000000000000000000000000000000000000000000000000000									
Q58	010100000000000000000000000000000000000000000000000010000000000000000000000000000000000000000000000000000									
Q59	000100000000000000000010000000000000000000000000000100000000010000000000000000000000000000000000000000000									
Q60	000100000000000000000000000000000000000000000000000010000000000000000000000000000000000000000000000000000									

TABLE 1
Note

Taxa: 1 - *Alouatta belzebul*; 2 - *Alouatta caraya*; 3 - *Alouatta coibensis*; 4 - *Alouatta guariba*; 5 - *Alouatta nigerrima*; 6 - *Alouatta palliata*; 7 - *Alouatta pigra*; 8 - *Alouatta sara*; 9 - *Alouatta seniculus*; 10 - *Aotus azarae*; 11 - *Aotus hershkovitzi*; 12 - *Aotus lemurinus*; 13 - *Aotus miconax*; 14 - *Aotus nancymaae*; 15 - *Aotus nigriceps*; 16 - *Aotus trivirgatus*; 17 - *Aotus vociferans*; 18 - *Ateles belzebuth*; 19 - *Ateles chamek*; 20 - *Ateles geoffroyi*; 21 - *Ateles hybridus*; 22 - *Ateles marginatus*; 23 - *Ateles paniscus*; 24 - *Brachyteles arachnoides*; 25 - *Brachyteles hypoxanthus*; 26 - *Cacajao calvus*; 27 - *Cacajao melanocephatus*; 28 - *Callicebus barbarabrownae*; 29 - *Callicebus brunneus*; 30 - *Callicebus cinerascens*; 31 - *Callicebus coimbrai s.n.*; 32 - *Callicebus cupreus*; 33 - *Callicebus donacophilus*; 34 - *Callicebus hoffmannsi*; 35 - *Callicebus medemi*; 36 - *Callicebus melanocephalus*; 37 - *Callicebus moloch*; 38 - *Callicebus nigrifrons*; 39 - *Callicebus ornatus*; 40 - *Callicebus personatus*; 41 - *Callicebus torquatus*; 42 - *Callimico goeldii*; 43 - *Callithrix aurita*; 44 - *Callithrix flaviceps*; 45 - *Callithrix geoffroyi*; 46 - *Callithrix jacchus*; 47 - *Callithrix kuhlii*; 48 - *Callithrix penicillata*; 49 - *Cebuella pygmaea*; 50 - *Cebus albifrons*; 51 - *Cebus apella*; 52 - *Cebus capucinus*; 53 - *Cebus libidinosus*; 54 - *Cebus nigritus*; 55 - *Cebus olivaceus*; 56 - *Cebus xanthosternos*; 57 - *Chiropotes albinasus*; 58 - *Chiropotes satanas*; 59 - *Lagothrix cana*; 60 - *Lagothrix lagotricha*; 61 - *Lagothrix lugens*; 62 - *Lagothrix poeppigii*; 63 - *Oreonax flavicauda*; 64 - *Leontopithecus caissara*; 65 - *Leontopithecus chrysomelas*; 66 - *Leontopithecus chrysopygus*; 67 - *Leontopithecus rosalia*; 68 - *Mico acariensis*; 69 - *Mico argentatus*; 70 - *Mico chrysoleucus*; 71 - *Mico emiliae*; 72 - *Mico melanurus*; 73 - *Mico humeratifer*; 74 - *Mico humilis*; 75 - *Mico intermedius*; 76 - *Mico leucippe*; 77 - *Mico manicorensis*; 78 - *Mico marcai*; 79 - *Mico mauesi*; 80 - *Mico melanurus*; 81 - *Mico nigriceps*; 82 - *Mico saterei*; 83 - *Saimiri boliviensis*; 84 - *Saimiri oerstedi*; 85 - *Saimiri sciureus*; 86 - *Saimiri ustus*; 87 - *Saimiri vanzolinii*; 88 - *Saguinus bicolor*; 89 - *Saguinus fuscicollis*; 90 - *Saguinus geoffroyi*; 91 - *Saguinus graellsi*; 92 - *Saguinus imperator*; 93 - *Saguinus inustus*; 94 - *Saguinus labiatus*; 95 - *Saguinus leucopus*; 96 - *Saguinus martinsi*; 97 - *Saguinus midas*; 98 - *Saguinus mystax*; 99 - *Saguinus niger*; 100 - *Saguinus nigricollis*; 101 - *Saguinus oedipus*; 102 - *Saguinus tripartitus*; 103 - *Pithecia albicans*; 104 - *Pithecia irrorata*; 105 - *Pithecia monachus*; and 106 - *Pithecia pithecia*.

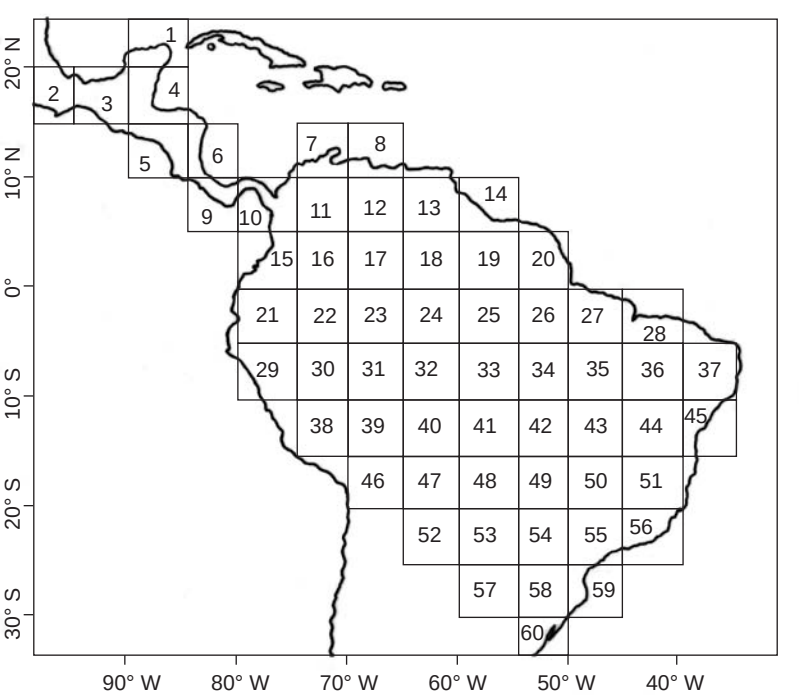

Fig. 1 — Map of the Neotropical region with the 60 quadrats of the first analysis.

TABLE 2

MATRIX with distributional data of 57 primate species in the 8 endemism areas determinated by the quadrats analysis.

		1	2	3	4	5
	12345678	**9012345678**	**9012345678**	**9012345678**	**9012345678**	**901234567**
OG	00000000	0000000000	0000000000	0000000000	0000000000	000000000
A1	00000101	0000010000	0000001000	1000010000	0000000000	010001000
A2	10010110	1001000000	0110000100	0111000010	1110010000	000010100
A3	00001101	0000110000	0000000000	0000000000	0000000000	010001000
A4	01100010	0000000100	0000000011	0000001100	0000000000	000000000
A5	01000110	1101000001	1000111110	0101000000	1011010110	100100110
A6	11100010	0000000100	0010000111	1000001100	1010000000	000010000
A7	10010110	0110001010	0111001100	1111100001	0100111001	101010011
A8	00001101	1111101011	1001111110	1111110011	0011111111	101101111

Taxa: 1 - *Alouatta belzebul*; 2 - *Alouatta caraya*; 3 - *Alouatta guariba*; 4 - *Alouatta nigerrima*; 5 - *Alouatta palliata*; 6 - *Alouatta seniculus*; 7 - *Aotus azarae*; 8 - *Aotus lemurinus*; 9 - *Aotus nigriceps*; 10 - *Aotus trivirgatus*; 11 - *Ateles belzebuth*; 12 - *Ateles chamek*; 13 - *Ateles geoffroyi*; 14 - *Ateles hybridus*; 15 - *Ateles paniscus*; 16 - *Brachyteles arachnoides*; 17 - *Cacajao melanocephalus*; 18 - *Callicebus brunneus*; 19 - *Callicebus cupreus*; 20 - *Callicebus hoffmannsi*; 21 - *Callicebus moloch*; 22 - *Callicebus torquatus*; 23 - *Callimico goeldii*; 24 - *Cebuella pygmaea*; 25 - *Cebus albifrons*; 26 - *Cebus apella*; 27 - *Cebus libidinosus*; 28 - *Cebus nigritus*; 29 - *Cebus olivaceus*; 30 - *Chiropotes albinasus*; 31 - *Chiropotes satanas*; 32 - *Lagothrix cana*; 33 - *Lagothrix lagotricha*; 34 - *Lagothrix lugens*; 35 - *Leontopithecus caissara*; 36 - *Leontopithecus chrysopygus*; 37 - *Mico acariensis*; 38 - *Mico chrysoleucus*; 39 - *Mico emiliae*; 40 - *Mico humaralifera*; 41 - *Mico melanurus*; 42 - *Saimiri boliviensis*; 43 - *Saimiri sciureus*; 44 - *Saimiri ustus*; 45 - *Saguinus bicolor*; 46 - *Saguinus fuscicollis*; 47 - *Saguinus imperator*; 48 - *Saguinus inustus*; 49 - *Saguinus labiatus*; 50 - *Saguinus leucopus*; 51 - *Saguinus midas*; 52 - *Saguinus mystax*; 53 - *Saguinus niger*; 54 - *Saguinus oedipus*; 55 - *Pithecia irrorata*; 56 - *Pithecia monachus*; and 57 - *Pithecia pithecia*.

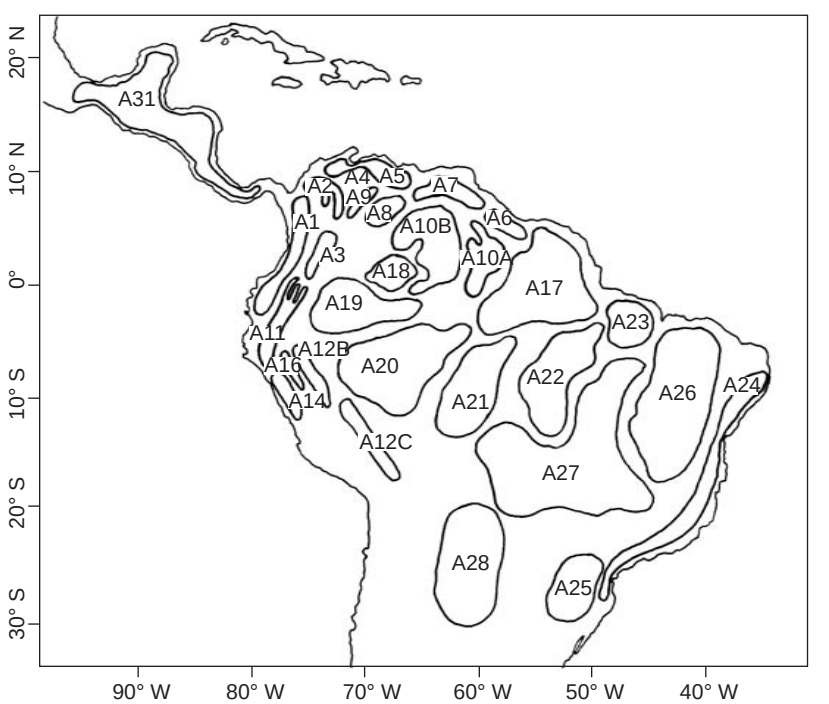

Fig. 2 — Map of the Neotropical region with the predetermined areas modified from Cracraft (1985).

Inambari) Center; 21) Rondônia Center; 22) Pará Center; 23) Belém Maranhão) Center; 24) Serra do Mar Center; 25) Paraná Center; 26) Caatinga Center; 27) Campo Cerrado Center; and 28) Chaco Center. The relationship among these areas was established based on the distribution of 69 primate species Table 3).

In the last analysis we used interfluvial regions delimited by the main rivers and the Panama Canal as OGUs (Fig. 3). According to Ayres & Clutton-Brock (1992), the main rivers may represent natural geographic barriers for some primates. Data on the distribution of 76 species were used in this analysis (Table 4). Interfluvial OGUs were delimited by: I) Panama Canal; II) Panama Canal and Magdalena river; III) Magdalena and Orinoco rivers; IV) Orinoco and Branco rivers; V) Putamayo and Maranon rivers; VI) Japura and Putamayo rivers; VII) Negro and Amazonas/Japura rivers; VIII) Branco river and Atlantic coast; IX) Maranon and Ucayali rivers; X) Ucayali and Purus rivers; XI) Purus and Madeira/Madre de Dios rivers; XII) Madeira/Guaporé and Tapajós rivers; XIII) Tapajós/Teles Pires and Xingu rivers; XIV) Xingu and Araguaia rivers; XV) Tocantins and São Francisco rivers; XVI) Madre de Dios and Guaporé rivers; XVII) Tapajós and Teles Pires rivers; XVIII) Araguaia and Tocantins rivers; XIX) São Francisco river and Atlantic coast; XX) Paraguai and Paraná/Paranaíba rivers; and XXI) Paraná/Paranaíba rivers and Atlantic coast.

RESULTS

1st analysis – Determining areas of endemism and their relationship based on quadrats

One cladogram with 669 steps, ci 0.64 and ri 0.77 was produced in the first stage (Fig. 4). It enabled the establishment of eight areas of endemism named A1 to A8 (Fig. 5). In the second stage, one cladogram with 98 steps, ci 0.58 and ri 0.54 was found (Fig. 6). Areas A1 and A3 were grouped by the presence of *Ateles hybridus* and *Saguinus leucopus*. Five species justified the grouping of areas A4 and A6: *Alouatta guariba*, *Brachyteles*

Fig. 3 — Map of the main rivers of the Neotropical region and the Panama Canal with the 21 regions used as Operative Geografic Units.

TABLE 3
Matrix with distributional data of 69 primate species in the predetermined endemism areas modified from Cracraft (1985).

		1	2	3	4	5	6
	123456789	**0123456789**	**0123456789**	**0123456789**	**0123456789**	**0123456789**	**0123456789**
OG	**000000000**	**0000000000**	**0000000000**	**0000000000**	**0000000000**	**0000000000**	**0000000000**
A1	000101010	0000100000	0100100000	0001000000	0001000000	0000010110	1010001010
A2	000001010	0000110000	0000000000	0000000000	0001000000	0000000000	0010001000
A3	000001010	0010000000	0000000100	0001000000	0001000000	0000000100	0000000010
A4	000001010	0000010000	0000000000	0001000000	0000000000	0000000000	0000000000
A5	000001010	0000010000	0000000000	0001000100	0000000000	0000000000	0000001000
A6	000001000	0000000000	0000000000	0001100000	0000000000	0000000000	0000000000
A7	000001000	0000010000	0000000000	0000000100	0000000000	0000000000	0000000000
A8	000001000	0000010000	0000000000	0001000100	0001000000	0000000000	0000000000
A9	000001010	0000010000	0000000000	0001000000	0000000000	0000000000	0000000000
A10A	000001000	0110000100	0000000010	0000000100	1010000000	0000010000	0001000001
A10B	000001000	0110000001	0000000010	0001100100	1010000000	0000010000	0001000001
A11	000001011	0110110000	0100100111	0011000000	0001100000	0000000110	0010001010
A12B	000001001	0010000000	0100000000	0010100000	0010110000	0000000100	0000000000
A12C	000001100	0001000000	1000000001	0010010000	0100000000	0000000101	0000000010
A14	000100001	0010000000	0000000000	0001100000	0000100000	0000010000	0000000010
A16	000001000	0000000000	0100000000	0010100000	0010010000	0000000100	0000000000
A17	000001100	0110000100	0000000010	0000100100	1000000000	0000011000	0001000001
A18	000001000	0110000001	0000000010	0001100100	1010000000	0000010000	1001000001
A19	000001000	0110000011	0100100011	0011100000	0010100000	0000010110	1100000010
A20	000011000	1101000010	1001000011	0010110000	0100101001	0110111101	0100100111
A21	100001100	1001001000	1001010000	0010100001	0100001111	1111011100	0100100110
A22	110000100	0000001100	0000010000	0000100001	1000000110	1000011000	0001010011
A23	100000100	0100001000	0000010000	0000100100	1000000100	0000010000	0000010000
A24	101000000	0000000000	0000001000	1100001010	0000000000	0000000000	0000000000
A25	001000000	0000000000	0000000000	0000001000	0000000000	0000000000	0000000000
A26	110000100	0000000000	0000000000	1100010010	0000000000	0000000000	0000000000
A27	111001100	1001000000	1010001000	0100111001	0100000000	0001101100	0000000110
A28	010010100	0000000000	0010000000	0000010000	0000000000	0001000000	0000000000
A31	000100010	0000100000	0000000000	0000000000	0000000000	0000000000	0000000000

Taxa: 1 - *Alouatta belzebul*; 2 - *Alouatta caraya*; 3 - *Alouatta guariba*; 4 - *Alouatta palliata*; 5 - *Alouatta sara*; 6 - *Alouatta seniculus*; 7 - *Aotus azarae*; 8 - *Aotus lemurinus*; 9 - *Aotus miconax*; 10 - *Aotus nigriceps*; 11 - *Aotus trivirgatus*; 12 - *Ateles belzebuth*; 13 - *Ateles chamek*; 14 - *Ateles geoffroyi*; 15 - *Ateles hybridus*; 16 - *Ateles marginatus*; 17 - *Ateles paniscus*; 18 - *Cacajao calvus*; 19 - *Cacajao melanocephalus*; 20 - *Callicebus brunneus*; 21 - *Callicebus cupreus*; 22 - *Callicebus donacophilus*; 23 - *Callicebus hoffmannsi*; 24 - *Callicebus medemi*; 25 - *Callicebus moloch*; 26 - *Callicebus nigrifrons*; 27 - *Callicebus ornatus*; 28 - *Callicebus torquatus*; 29 - *Callimico goeldii*; 30 - *Callithrix jacchus*; 31 - *Callithrix penicillata*; 32 - *Cebuella pygmaea*; 33 - *Cebus albifrons*; 34 - *Cebus apella*; 35 - *Cebus libidinosus*; 36 - *Cebus nigritus*; 37 - *Cebus olivaceus*; 38 - *Cebus xanthosternos*; 39 - *Chiropotes albinasus*; 40 - *Chiropotes satanas*; 41 - *Lagothrix cana*; 42 - *Lagothrix lagotricha*; 43 - *Lagothrix lugens*; 44 - *Lagothrix poeppigii*; 45 - *Oreonax flavicauda*; 46 - *Mico acariensis*; 47 - *Mico argentatus*; 48 - *Mico emiliae*; 49 - *Mico humilis*; 50 - *Mico leucippe*; 51 - *Mico manicorensis*; 52 - *Mico marcai*; 53 - *Mico melanurus*; 54 - *Saimiri boliviensis*; 55 - *Saimiri sciureus*; 56 - *Saimiri ustus*; 57 - *Saguinus fuscicollis*; 58 - *Saguinus graellsi*; 59 - *Saguinus imperator*; 60 - *Saguinus inustus*; 61 - *Saguinus labiatus*; 62 - *Saguinus leucopus*; 63 - *Saguinus midas*; 64 - *Saguinus mystax*; 65 - *Saguinus niger*; 66 - *Saguinus oedipus*; 67 - *Pithecia irrorata*; 68 - *Pithecia monachus*; and 69 - *Pithecia pithecia*.

TABLE 4
Matrix with distributional data of 76 primate species in the 21 interfluvial regions used as Operative Geografic Units.

	1	**2**	**3**	**4**	**5**	**6**	**7**	
	123456789	**0123456789**	**0123456789**	**0123456789**	**0123456789**	**0123456789**	**0123456789**	**0123456**
OG	000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000
I	000010000	0000010000	0000000000	0000000001	0000000000	0000000000	0000100000	0000000
II	000010101	0000011000	0000000000	0000000101	0000000010	0000000000	0000100000	0000000
III	000000101	0101001000	0010000000	1100000110	0010010110	0000000001	0000001010	0000001
IV	000000100	0101000010	0000000000	0100000110	0010010100	0000000001	0000000010	0000001
V	000010100	0011010000	0000100100	0110001110	0000000001	0000000001	0001000000	0110010
VI	000000100	0010100000	0100000100	0110001010	0000000000	0000000001	0101000100	0100010
VII	000000100	0111000000	0010000100	1110001010	0000000110	0000000001	0101001000	0100010
VIII	000000100	0100000010	0010000000	0000000010	0010010000	0000000001	0010000010	0000001
IX	000000100	0001100000	0000100000	0010001010	0000000001	0000000000	0001000000	0000010
X	000000100	1000100000	0100100000	0110001010	0000001001	0000000011	1101010001	0011110
XI	000001110	1100100000	0001011000	0110001010	1000001000	0000001011	1011010101	0001110
XII	000101110	1000100000	0001001000	0010000010	1000101000	0001111111	1001000101	0000110
XIII	100100010	0000000100	0000001010	0000000010	0000100000	0011110001	1000000000	0000000
XIV	110000010	0100000100	0000000010	0000000010	0000010000	0010000001	0000000000	1000000
XV	110000010	0000000000	0000000001	0000110000	1011010000	0000000001	0000000000	1000000
XVI	010001010	0000100000	0001010000	0000000100	1000000000	0000000110	0001000001	0000000
XVII	010000010	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000
XVIII	010000010	0000000000	0000000000	0000010010	1000000000	0000000000	0000000000	0000000
XIX	011000000	0000000001	1000000001	0001110000	0101000000	1100000000	0000000000	0000000
XX	011000010	0000000000	0000010000	0000000000	1000000000	0000000100	0000000000	0000000
XXI	011000000	0000000001	1000000001	0001010000	0100000000	1100000000	0000000000	0000000

Taxa: 1 - *Alouatta belzebul*; 2 - *Alouatta caraya*; 3 - *Alouatta guariba*; 4 - *Alouatta nigerrima*; 5 - *Alouatta palliata*; 6 - *Alouatta sara*; 7 - *Alouatta seniculus*; 8 - *Aotus azarae*; 9 - *Aotus lemurinus*; 10 - *Aotus nigriceps*; 11 - *Aotus trivirgatus*; 12 - *Aotus vociferans*; 13 - *Ateles belzebuth*; 14 - *Ateles chamek*; 15 - *Ateles geoffroyi*; 16 - *Ateles hybridus*; 17 - *Ateles marginatus*; 18 - *Ateles paniscus*; 19 - *Brachyteles arachnoides*; 20 - *Brachyteles hypoxanthus*; 21 - *Cacajao calvus*; 22 - *Cacajao melanocephatus*; 23 - *Callicebus brunneus*; 24 - *Callicebus cupreus*; 25 - *Callicebus donacophilus*; 26 - *Callicebus hoffmannsi*; 27 - *Callicebus medemi*; 28 - *Callicebus moloch*; 29 - *Callicebus nigrifrons*; 30 - *Callicebus ornatus*; 31 - *Callicebus torquatus*; 32 - *Callimico goeldii*; 33 - *Callithrix aurita*; 34 - *Callithrix jacchus*; 35 - *Callithrix penicillata*; 36 - *Cebuella pygmaea*; 37 - *Cebus albifrons*; 38 - *Cebus apella*; 39 - *Cebus capucinus*; 40 - *Cebus libidinosus*; 41 - *Cebus nigritus*; 42 - *Cebus olivaceus*; 43 - *Cebus xanthosternos*; 44 - *Chiropotes albinasus*; 45 - *Chiropotes satanas*; 46 - *Lagothrix cana*; 47 - *Lagothrix lagotricha*; 48 - *Lagothrix lugens*; 49 - *Lagothrix poeppigii*; 50 - *Leontopithecus chrysopygus*; 51 - *Leontopithecus rosalia*; 52 - *Mico argentatus*; 53 - *Mico emiliae*; 54 - *Mico humaralifera*; 55 - *Mico leucippe*; 56 - *Mico marcai*; 57 - *Mico melanurus*; 58 - *Saimiri boliviensis*; 59 - *Saimiri sciureus*; 60 - *Saimiri ustus*; 61 - *Saimiri vanzolinii*; 62 - *Saguinus bicolor*; 63 - *Saguinus fuscicollis*; 64 - *Saguinus geoffroyi*; 65 - *Saguinus imperator*; 66 - *Saguinus inustus*; 67 - *Saguinus labiatus*; 68 - *Saguinus midas*; 69 - *Saguinus mystax*; 70 - *Saguinus niger*; 71 - *Saguinus nigricollis*; 72 - *Saguinus tripartitus*; 73 - *Pithecia albicans*; 74 - *Pithecia irrorata*; 75 - *Pithecia monachus*; and 76 - *Pithecia pithecia*.

arachnoides, *Cebus nigritus*, *Leontopithecus caissara* and *Leontopithecus chrysopygus*. Whereas eleven primates justified the grouping of A7 and A8 (*Ateles belzebuth, Ateles paniscus, Cacajao melanocephalus, Callicebus torquatus, Lagothrix lagotricha, Mico chrysoleucus, Saimiri sciureus, Saguinus bicolor, Saguinus inustus, Saguinus midas, and Pithecia pithecia*), the branch (A2(A5(A7,A8))) was justified only by *Chiropotes albinasus, Lagothrix cana, and Saimiri ustus*.

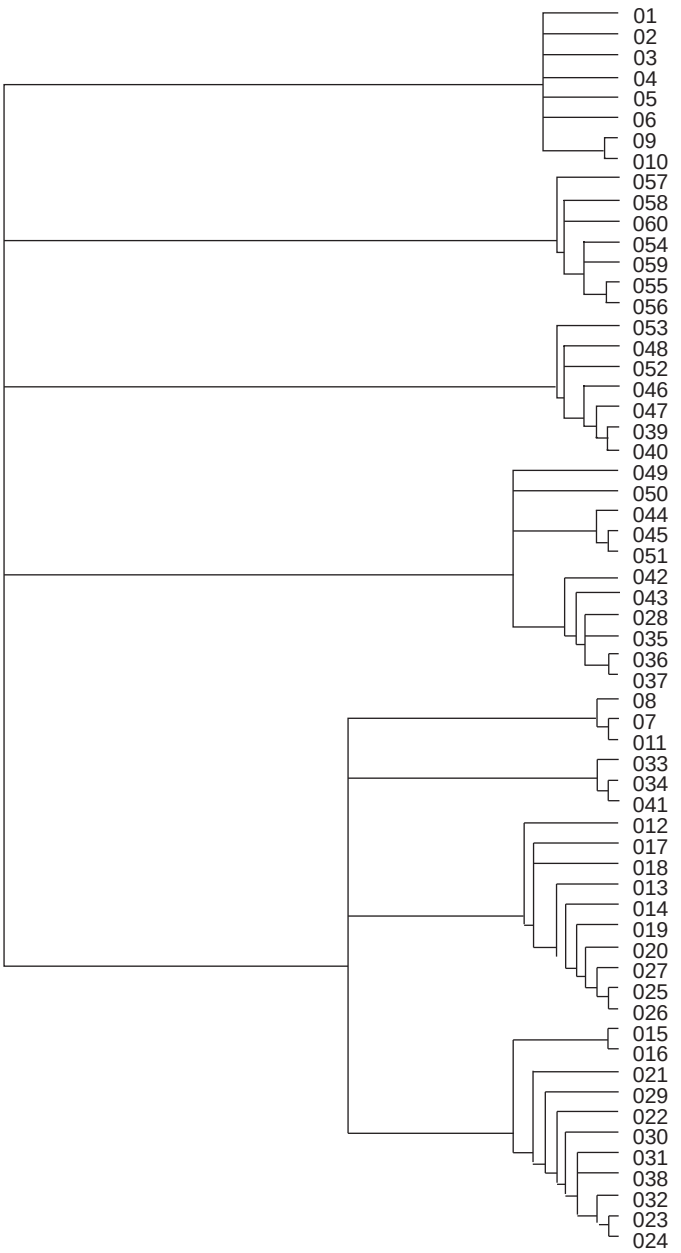

Fig. 4 — Cladogram obtained using quadrats (669 steps, consistency index 0.64 and retention index 0.77).

2nd analysis – Determining the relationship among the areas of endemism proposed for birds (modified from Cracraft, 1985) with data on primates

One cladogram with 320 steps, ci 0.72 and ri 0.84 resulted from this analysis (Fig. 7). The branches ((A10B,A18)(A10A(A17(A22, A23)))) and (A5(A2(A1,A11))) were justified by the presence of a single species, *Chiropotes satanas* and *Saguinus oedipus*, respectively. Six species grouped A20 and A21: *Callicebus hoffmannsi*, *Mico acariensis*, *Mico humilis*, *Mico manicorensis*, *Mico marcai*, and *Saguinus mystax*. The occurrence of *Ateles chamek, Callicebus*

Fig. 5 — Map of the Neotropical region with the 8 endemism areas determined by the quadrats.

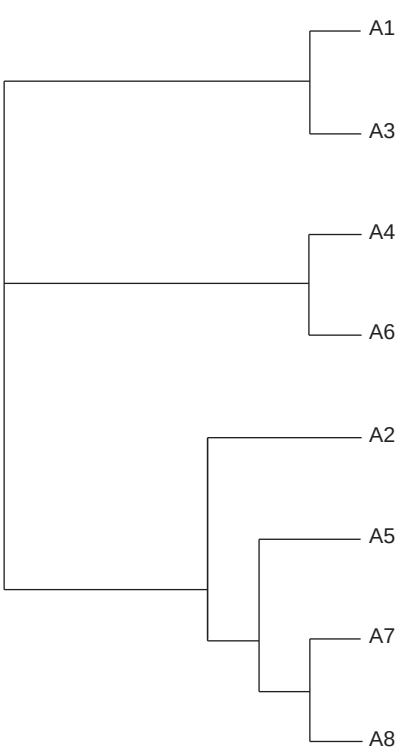

Fig. 6 — Area cladogram obtained by applying PAE (with 98 steps, consistency index 0.58 and retention index 0.54).

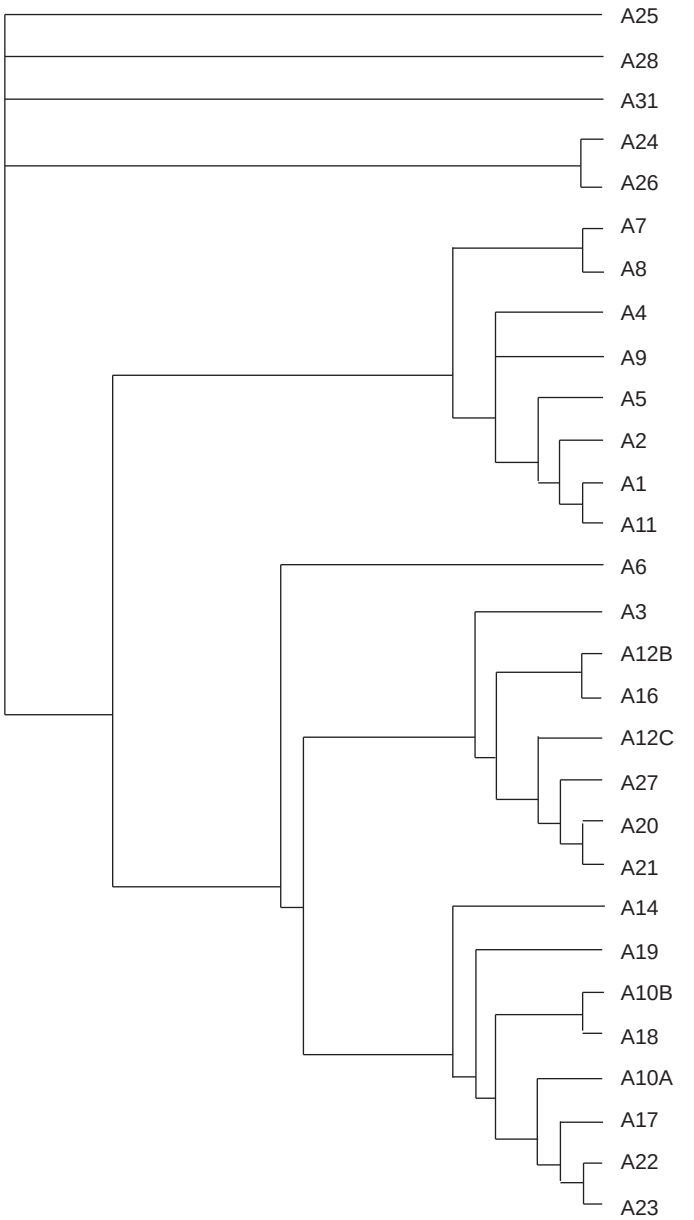

Fig. 7 — Area cladogram obtained by applying PAE (with 320 steps, consistency index 0.72 and retention index 0.84).

brunneus, and *Lagothrix cana* justified the grouping (A12C(A27(A20,A21))). Areas A24 and A26 were grouped for sharing *Callithrix jacchus* and *Cebus xanthosternos*.

3rd analysis – Determining the relationship among interfluvial areas

A cladogram with 386 steps, ci 0.79 and ri 0.89 was obtained (Fig. 8). A smaller number of species justified the groupings obtained in this analysis: a) *Cebus capucinus* justified the grouping of areas I and II; b) *Calithrix penicillata* justified the branch (XVIII(XV(XIX,XXI))); c) *Ateles marginatus*, *Callicebus moloch*, and *Mico argentatus* grouped areas XIII and XIV; d) *Saguinus midas* and *Pithecia pithecia* justified the branch (VIII(III,IV)); and e) *Callimico goeldii* and *Pithecia monachus* justified the branch (IX(VI(V,VII)(X(XI,XII)))).

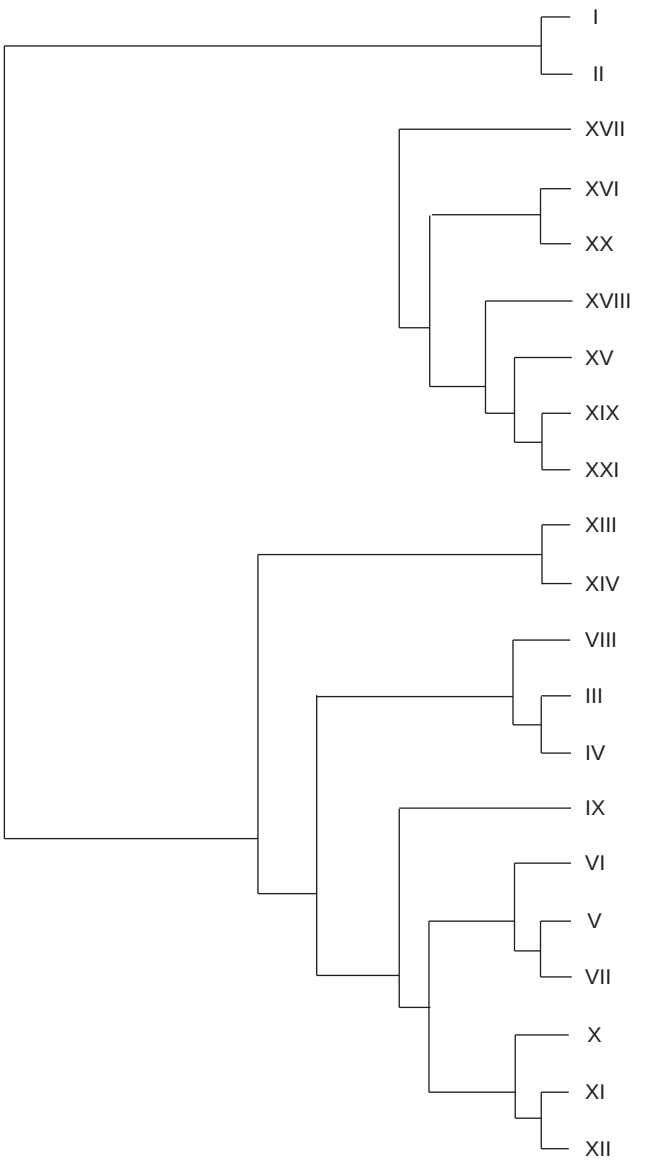

Fig. 8 — Area cladogram obtained by applying PAE (with 386 steps, consistency index 0.79 and retention index 0.89).

DISCUSSION

The cladograms produced by all three analyses were very similar, and showed the grouping of neighboring areas: a) Central America and the extreme northwest of South America; b) Amazon basin; and c) Atlantic Forest, Caatinga, Cerrado, and Chaco (see Figs 3, 5, 6, and 8). These three large areas are represented by the main biomes in Latin America. Therefore, this pattern of primate distribution suggests that in the recent past species dispersion occurred mainly within those areas than between them, probably because they may have been even less connected (or more isolated) during the Pleistocene ice ages from 1.4 mya to about 10.000 years ago (Chernicoff *et al.*, 1997) than today.

Despite this similarity, the analysis using larger OGUs (interfluvial regions) showed the highest consistency (0.79) and retention (0.89)

indices, corroborating studies with Mexican mammals (Morrone & Escalante, 2002). These values mean that the use of different OGUs enable better results with natural areas like interfluvial regions. In spite of the hypothesis that rivers may represent natural geographic barriers for primate dispersion (Ayres & Clutton-Brock, 1992), several species were widely distributed occupying more than a single interfluvial region (such as *Alouatta seniculus*, *Alouatta caraya*, *Alouatta guariba*, *Aotus azarae*, *Ateles chamek*, *Callimico goeldii*, *Cebuella pygmaea*, *Cebus albifrons*, *Saimiri sciureus*, and *Pithecia monachus*). Whereas some of these species may be good swimmers and overcome these potential barriers (*e.g.*, *Alouatta* spp.), others may have dispersed before the establishment of some of today's larger rivers, or part of its population may have been transported in natural rafts or due to river dynamics (changes in river course) from one margin to the other.

In sum, this study showed that the use of larger Operational Geographic Units (OGUs) produces more consistent results and that PAE was a useful tool for understanding the patterns of distribution and dispersion of nonhuman primates within South and Central America. Therefore, PAE shall contribute to our knowledge on the patterns of dispersion and distribution of nonhuman primates in the other three biogeographic regions where they occur (namely Africa, Madagascar, and South Asia) since similar analyses are missing.

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