



# Application of parsimony analysis of endemism in Amazonian biogeography: an example with primates

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The distributions of 51 non-human primate species are used for Parsimony Analysis of Endemism (PAE) to determine the relationships among 14 interfluvial regions in the Amazon basin, South America. Two most parsimonious cladograms were found. The strict consensus tree of these cladograms suggests an early separation between Lower Amazonia (eastern) and Upper Amazonia (western). The major clusters of interfluvial regions identified in the PAE cladogram are congruent with the areas of endemism delimited for birds. When interfluvial regions are converted into avian areas of endemism, the PAE cladogram is congruent with one of the two general areas cladograms suggested for Amazonia based on phylogenies of several clades of forest birds. Our analysis suggests that PAE can be used as a tool to objectively identify areas of endemism at an intra-continental scale as well as to make historical inferences. However, the value of a PAE cladogram in this latter application should be always evaluated by congruence with area cladograms built upon cladistic biogeography procedures.

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ADDITIONAL KEY WORDS: — biogeography – parsimony analysis of endemism – primates – Amazonia – Neotropical region – South America – distribution – areas of endemism – cladistic biogeography – vicariance.

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## INTRODUCTION

Two of the main questions in modern historical biogeography are how to delimit intra-continental areas of endemism, and how to determine historical relationships between these areas of endemism (Nelson & Platnick, 1981; Humphries & Parenti, 1986). The first question is usually approached by superimposing distribution maps of taxa and detecting those areas with high concentrations of overlapping ranges (Müller, 1973; Haffer, 1978; Cracraft, 1985), although difficulties may arise when a large number of species are analysed (Morrone, 1994). The second question is usually evaluated by the construction of area cladograms using the methods of cladistic biogeography (reviews in Humphries & Parenti, 1986; Humphries, 1992), that depend on a well-corroborated phylogenetic hypothesis of organisms sharing similar patterns of differentiation and distribution across three or more areas of endemism.

Rosen (1988) proposed a method to generate area cladograms directly from raw distribution data termed Parsimony Analysis of Endemicity (PAE). Several applications have been proposed for this method. Morrone (1994) has suggested that PAE area cladograms may be used as a tool to delimit areas of endemism in an intra-continental scale, when several species are included in the analysis. Rosen (1988) and Cracraft (1991) have used PAE cladograms to make inferences on historical relationships between localities and areas of endemism, respectively (for review of assumptions and limitations of using PAE for historical inference see Rosen, 1992 and Cracraft, 1994). Cracraft (1991) has found that PAE areas cladograms were quite congruent with area cladograms obtained by using methods of cladistic biogeography. Even with these promising applications, PAE has been little used to make biogeographical inferences (review in Rosen, 1992).

In this paper, we use PAE to generate an area cladogram for the major interfluvial regions in Amazonia by using the raw distribution data for species of platyrrhine monkeys. We evaluate the spatial congruence of the major groupings of these interfluvial regions in the PAE cladogram with the major Amazonian areas of avian endemism (Cracraft, 1985). Finally, after the conversion of interfluvial regions into areas of avian endemism, we compare the results of the PAE area cladogram with two other area cladograms obtained using methods of the cladistic biogeography and taxon cladograms of several clades of forest birds.

## METHODS

*Parsimony Analysis of Endemicity*

PAE is analogous to cladistic methods used in phylogenetic analysis and classifies areas (cf. taxa in cladistics) by their shared taxa (cf. characters in cladistics) according to the most parsimonious solution (Rosen, 1988). PAE cladograms consist of nested sets of endemic biotas as represented by the sample regions (Rosen, 1988, 1992; Cracraft 1991, 1994). The ideal units for a PAE analysis are point sample localities (Rosen, 1988). However, this kind of data is unavailable for most tropical regions. Alternatively, one may use as *Operative Geographical Units* (OGU) equal-size quadrats (Morrone, 1994) or pre-defined areas of endemism (Cracraft, 1991). In this case, it is assumed that localities within each OGU have historical and/or ecological features

in common. In the present analysis, we used as OGU 14 major interfluvial regions within the Amazon basin (Fig. 1). We based this procedure on the observations of early naturalists (e.g., Wallace, 1853; Sneath, 1910; Hellmayr, 1910) that rivers in Amazonia may represent important biogeographic barriers to vertebrates. This suggestion has been supported by studies with primates (Ayres, 1986; Ayres & Clutton-Brock, 1992) and birds (Sick, 1967; Haffer, 1974, 1992; Capparella, 1988, 1991).

To determine the distribution of each primate species in Amazonia, we used systematic reviews (Fooden, 1963; Hershkovitz, 1977, 1982, 1983, 1985, 1987a, 1987b, 1990; Thorington, 1988; de Vivo, 1985, 1991; Ayres, 1985, Bonvicino *et al.*, 1989; Ferrari & Lopes, 1992b; Mittermaier *et al.*, 1993) as well as recent faunistic surveys in some poorly known regions (Nunes *et al.*, 1989; Peres, 1990; Ferrari & Lopes, 1992a). We include all species of primates recorded for Amazonia, except those of the genus *Ateles*, whose species limits are problematic (Froehlich *et al.*, 1991).

The basic PAE data set is a matrix in which the absence of a species is coded as a primitive character (0) and the presence of a species as a derived (1) character of an area (Rosen, 1988). A hypothetical area that has no taxa at all (Lundberg rooting) is included in the matrix to provide a root for the resulting cladogram (Rosen, 1988). We used option 'ie\*' (implicit enumeration) in the computer program Hennig86 (Farris, 1989) to find all the most parsimonious area cladograms. If more than one

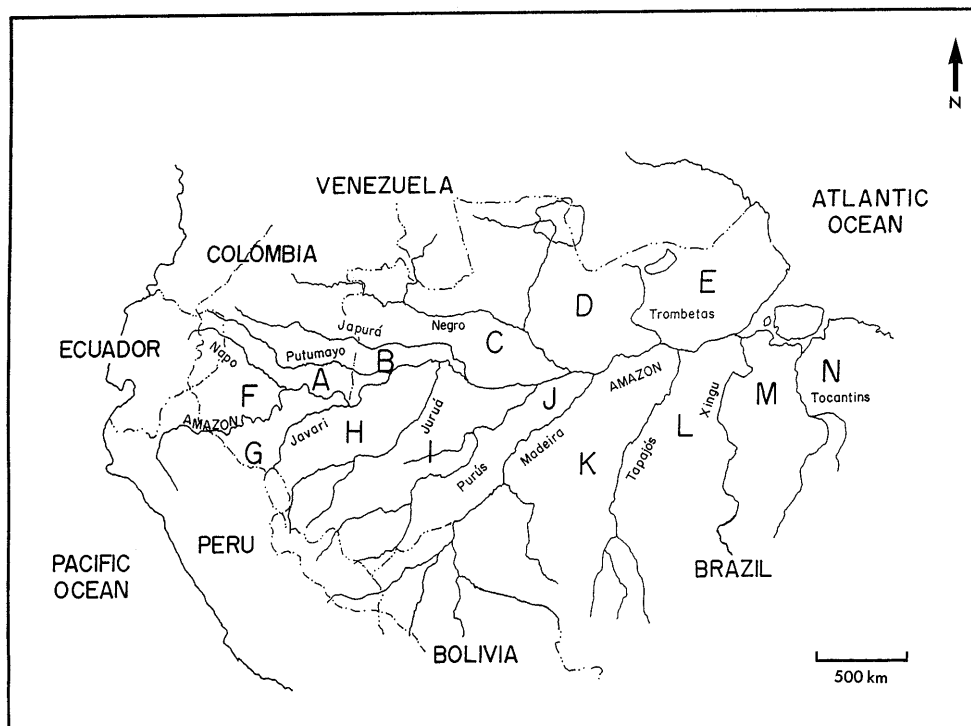


Figure 1. The Amazon basin separated into 14 major interfluvial regions. These interfluvial regions were used as Operative Geographical Units (OGUs).

more parsimonious cladogram was found, we used the option 'nelsen' of Hennig86 to find the strict consensus tree of these trees.

### *Comparisons with birds*

From a static interpretation, a PAE analysis may be used to identify areas of endemism, and the generality of this result can be evaluated by testing the congruence of these areas with those defined for other taxa (Rosen, 1988; Morrone, 1994). From a dynamic viewpoint, a PAE cladogram may indicate historical sequences of biotic divergence and isolation (Rosen, 1988; Cracraft, 1988), and its results can be evaluated by measuring congruence between the PAE area cladogram with area cladograms generated by cladistic biogeography methods (Cracraft, 1991, 1994).

To evaluate the results of the PAE analysis, we compared them with information available for birds, the only vertebrate group in Amazonia for which areas of endemism have been identified (Cracraft, 1985) and general area cladograms proposed (Prum, 1988; Cracraft & Prum, 1988). If the groups of the 14 interfluvial regions generated by PAE analysis in Amazonia are congruent with the 7 major areas of endemism recognized for birds by Cracraft (1985), we can predict the following spatial correspondence (letters refer to Fig. 1):

- (a) Guiana (interfluvial regions from the Negro River to the Atlantic coast; D and E);
- (b) Imeri (interfluvial region between the Japurá and Negro Rivers; C);
- (c) Napo (interfluvial regions between the Amazon and the Japurá Rivers; A, B, and F);
- (d) Inambari (interfluvial regions between the Amazon and Madeira Rivers; G, H, I, and J);
- (e) Rondônia (interfluvial region between the Madeira and Tapajós Rivers; K);
- (f) Pará (interfluvial regions between the Tapajós and Tocantins Rivers; L and M), and
- (g) Belém (interfluvial regions from the Tocantins River to the eastern limit of the Amazonian forests in Maranhão state; N).

If there was a good correspondence between area clusters identified by PAE analysis and avian areas of endemism, we converted interfluvial regions into areas of endemism. Thereafter, we compared the area cladogram derived from PAE analysis with the two general area cladograms proposed by Prum (1988) for avian areas of endemism in Amazonia. Prum's area cladograms were obtained from congruence analysis between individual cladograms of several clades of forest birds, following strict cladistic biogeography procedures (Nelson & Platnick, 1981). We did not include a third general area cladogram proposed by Cracraft (1988) for comparison because we think it is not a reliable estimate of area relationships within Amazonia, as three of the four clades of birds used to support its basic nodes have terminal taxa defined by characters that vary clinally (Silva, unpublished). Therefore, these taxa do not represent true 'phylogenetic species' (Cracraft, 1983) and their taxon-cladograms do not represent four-taxon statements as suggested by Cracraft (1988), but biogeographically uninformative two-taxon statements.



position in the two most parsimonious cladograms (Fig.2), suggesting that this interfluvial region may be a transitional one rather than part of one of the major areas of endemism.

When interfluvial regions occupying an unambiguous position in the PAE cladogram are converted into areas of avian endemism (Fig. 3C), the basic set of area relationships among them is very similar to one of the general area cladograms proposed for Amazonia by Prum (1988; Fig. 3A), although area relationships within the Upper Amazonia region are better resolved in the PAE cladogram.

#### DISCUSSION

Major clusters of Amazonian interfluvial regions obtained through the parsimony analysis of the distribution of monkeys agree in great part with the borders of the areas of avian endemism delimited for this large region (Cracraft, 1985). This result supports the proposal by Morrone (1994) that, at least the level of spatial generality

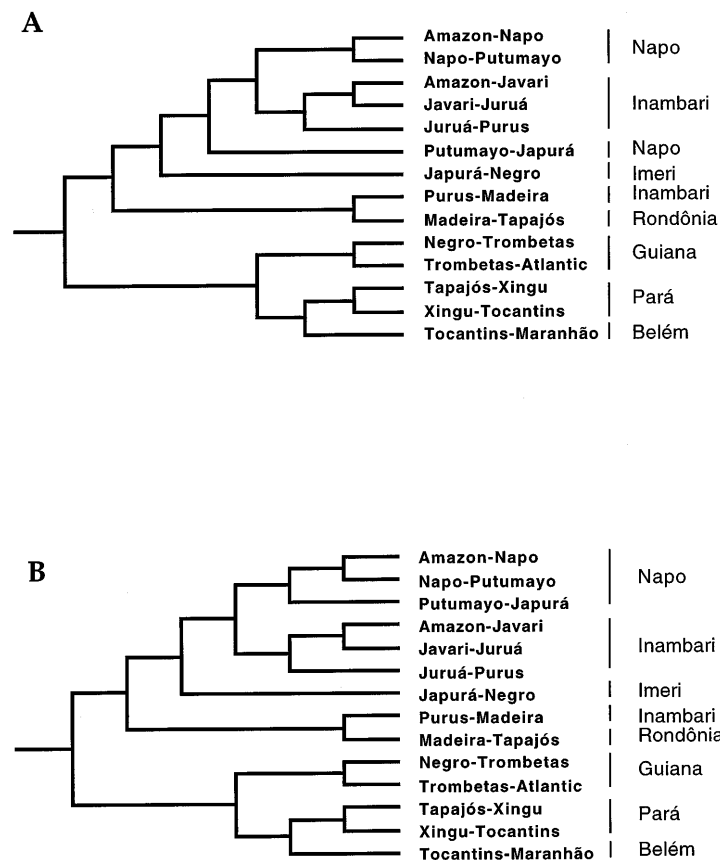


Figure 2. The two most parsimonious area cladograms (length = 78, consistency index = 0.65, retention index = 0.72) obtained by parsimony analysis of the raw distribution of 51 Amazonian primate species and their congruence with the areas of avian endemism delimited by Cracraft (1985). A hypothetical area that has no taxa at all was included in the matrix to provide a root for the resulting cladograms.

used here, PAE may be used as an important tool towards the solution of one of the basic problems in modern historical biogeography: the objective identification and delimitation of areas of endemism at an intra-continental scale.

The PAE cladogram presented here is congruent with one of the general area cladograms proposed previously for Amazonia (Fig. 3A; Prum, 1988) based on phylogenies of several forest bird clades. This is surprising, as PAE cladograms are 'tuned' to histories of distributional change of biotas as indicated by taxonomic assemblage patterns, whereas cladistic biogeography cladograms are 'tuned' primarily to histories of area isolation as implied by speciation patterns (Rosen, 1992). Cracraft (1994) suggested that congruence between a PAE cladogram and an area cladogram obtained through the use of cladistic biogeography methods might

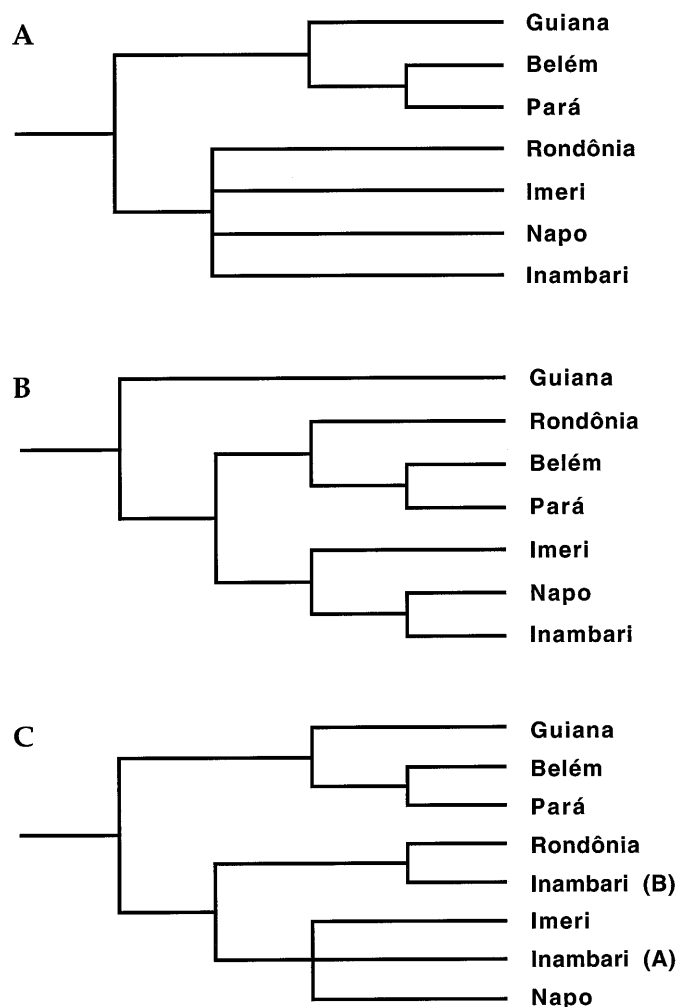


Figure 3. The three general area cladograms that have been proposed for the avian areas of endemism in the Amazon basin. (A and B) alternative area cladograms of Prum (1988), and (C) area cladogram based on the parsimony analysis of the distribution of Amazonian primate species. Area cladograms A and B were obtained from taxon cladograms of several clades of forest birds by using strict cladistic biogeography procedures.

indicate that the historical patterns of biotic distributional changes were strongly influenced by the same historical events that produced the areas of endemism. This supports the suggestion by Rosen (1988, 1992) that PAE cladograms may also be used to make historical inferences, although their value in this regard should always be evaluated by congruence with area cladograms built upon cladistic biogeography procedures (Cracraft, 1991; 1994).

The differences between the three area cladograms proposed for Amazonia to date include alternative positions for three avian areas of endemism: Guiana, Rondônia and Inambari. A simple solution to combine the historical information contained in these three area cladograms is to assume that these three somewhat 'problematic' areas have multiple histories and then duplicate them in a consensus area cladogram (Prum, 1988). The final solution (Fig. 4) resembles the general area cladogram proposed for Amazonia by Prum (1988). Although not recovered in the PAE cladogram, the separation of Guiana from the rest of the areas (Fig. 4) appears as the oldest event in the history of Amazonian areas of endemism. This is further supported by its well-marked fauna (Müller, 1973; Hoogmoed, 1979; Haffer, 1978) and flora (Maguire, 1970) that possibly evolved in isolation from the other Amazonian areas of endemism for a long time. We suggest that Guiana isolation was broken later, and an extensive biotic interchange between it and the set of areas composed of Belém, Pará, and at least part of Rondônia took place before these areas were separated again by a new cycle of vicariance. The composite nature of the Rondônia biota, which is revealed by the multiple and incongruent phylogenetic relationships of its endemic bird species (Prum, 1988), could be expected from both geological and biogeographical viewpoints. From a geological viewpoint, Rondônia is the contact zone between the Pre-Cambrian Brazilian shield, whose influence extends also into Belém and Pará, and the vast Tertiary Solimões or Pebas Formation, which covers most of the Upper Amazonian areas of endemism (Petri & Fúlvaro, 1983; Hoorn, 1993). From a biogeographical viewpoint, Rondônia is where species characteristic from both Lower and Upper Amazonian biotas have their range boundaries (Ávila Pires, 1995; Silva, unpublished data). In contrast with Rondônia, the composite nature of the large Inambari area of endemism was not revealed through bird forest phylogenies, but only through the parsimony analysis of primate distribution (Fig. 3). Hence, the historical significance of this finding is open

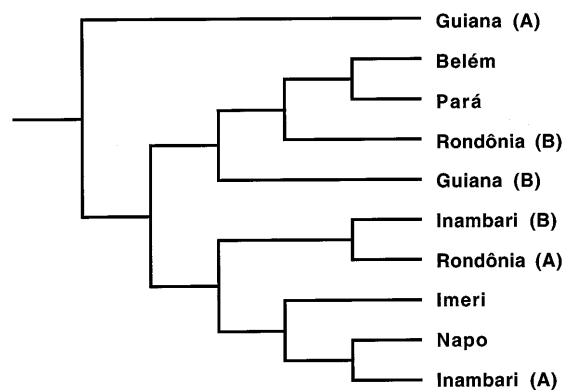


Figure 4. General area cladogram for the Amazon basin obtained by combining historical information of the three area cladograms. Areas of endemism Guiana, Rondônia and Inambari are duplicated.



to debate; an evaluation of a larger data set including other terrestrial vertebrates groups is needed. We include Inambari as a composite area in the general area cladogram (Fig. 4) in order to call attention to this hypothesis.

Amazonia had a very complex palaeoecological history throughout the Cenozoic, the period in which most of the present-day species may have originated. Several palaeoecological factors operating individually or in concert might have been important in promoting several cycles of speciation and dispersal within this region and thus contributing to the high regional and local biological diversity currently observed in this region. Among these factors are large marine incursions (Hoorn, 1993; Räsänen *et al.*, 1995), tectonic movements (Croizat, 1976; Putzer, 1984; Petri & Fúlfaro, 1983; Räsänen *et al.*, 1992), fluvial dynamics (Sick, 1967; Hershkovitz, 1977, 1990; Salo *et al.*, 1986), isolation caused by changes in sea-level (Putzer, 1984; Klamer 1984), and climatic-vegetational fluctuations caused by Milankovitch cycles (Haffer, 1974, 1993; Bigarella & Ferreira, 1985; Van der Hammen & Absy, 1994). Taking these factors in account, one could expect that the multiples cycles of vicariance and biotic intermixing could have acted in such a way that congruence between area cladograms obtained by using different methods and by analysing different groups of organisms would have a very low probability to be found. Nevertheless, the present analysis suggests that congruence is pervasive in studies of the two groups of terrestrial vertebrates evaluated so far. This opens the possibility that, complex palaeoecological history notwithstanding, biogeographical patterns of present-day organisms can reveal at least the most general chapters of the history of Amazonian biota during the Cenozoic.

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