TITULO: NUEVAS RESPUESTAS A LAS RELACIONES DE AREAS EN LA AMAZONIA DESDE BIOGEOGRAFIA DE EVENTOS[*]

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Biogeografía cladística, vicarianza, dispersión, ajuste de árboles basado en eventos, animales amazónicos

La Amazonia ha sido considerada un área biogeográfica natural. El proyecto apuntaba a determinar la historia biogeográfica de la Amazonia y evaluar los eventos responsables de su presente diversidad.

Ajuste de árboles basado en parsimonia fue usado bajo diferentes modelos de costos implementados en TREEFITTER para reconstruir un cladograma general de áreas para la Amazonía, utilizando hipótesis filogenéticas de 59 grupos de taxa amazónicos y para probar el ajuste del conjunto de datos a 20 hipótesis de áreas previamente propuestas, mediante pruebas con aleatorizaciones. El análisis de dispersión vicarianza (DIVA) fue utilizado para evaluar la frecuencia relativa de la dispersión y de la vicarianza dentro de cada grupo y su contribución relativa al conjunto de datos.

Los análisis de DIVA indicaron más eventos de vicarianza que dispersión. Los análisis de hipótesis previas utilizando los modelos de máxima vicarianza y reconciliados no mostraron constricción filogenética de los datos a ninguna de estas hipótesis. El modelo de costos óptimo fue el implementado por omisión en TREEFITTER. Las reconstrucciones realizadas produjeron diferentes cladogramas de áreas, los cuales no documentan ninguna de las relaciones de áreas tradicionales. No obstante todas consideran a Imeri y Para, áreas de origen hibrido. Fue concluido que un modelo complejo, el cual involucre duplicación, dispersión, y extinción es el óptimo para describir la historia biogeográfica de la región. Estos hallazgos sugieren que diferentes historias han estado desarrollándose en la región y que no es posible denotar ninguna de las hipótesis de áreas como “el” patrón general que describa una historia única. La Amazonia debió originarse por adición de elementos bióticos provenientes de la Guyana, Centro América, y la Mata Atlántica. Estos resultados no son del todo inesperados pues trabajos previos han encontrado algunas áreas amazónicas como hibridas, es urgente la reevaluación de las áreas denominadas como endémicas y la inclusión de más hipótesis filogenéticas.

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TITLE: NEW ANSWERS FOR AMAZONIAN RELATIONSHIPS BASED ON EVENT BIOGEOGRAPHY[*]

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Amazonia, cladistic biogeography, vicariance, dispersal, event-based treefitting, Amazonian animals.

The Amazonia has been considered a natural biogeographic area. This project aimed to determinate the biogeographic history of the Amazonia and to evaluate the events responsible for its present high diversity.

Parsimony based treefitting was used under different models implemented in TREEFITTER to reconstruct a general area cladogram for the Amazonia, based on the phylogenetic information of 59 amazonian taxa and to test the fit of the data set to 20 previous proposed area hypotheses using randomization tests. Dispersal vicariance (DIVA) analysis was used to evaluate the relative frequency of dispersal and vicariance within each group and its relative contribution to the data set.

DIVA analysis indicated more vicariance than dispersal events. The analysis of previously proposed hypotheses under Maximum Codivergence and Reconciliation models shows no phylogenetic constrictions of the data set to these models. The optimal model of costs was the default model of TREEFITTER. The different partitions of the data set produced different area cladograms, which did not document any of the traditional area relationship; nevertheless all consider Imeri and Para to be hybrid areas. It was concluded that a complex model, which involves events as duplication, dispersion, and extinction, appears to be the optimal to explain Amazonia biogeographic history. The findings suggest that different histories had took place at different moments in the region and that it is not possible to denote any of the patterns as “the” general area cladogram that describes a unique history. Amazonia must be originated by the addition of biotic elements coming from Central America, Guiana, and the Mata Atlantica. This result is not unexpected at all since previous works had found some of the amazonian areas as composite. Finally, it is demanding the revaluation of the biogeographic units used as areas of endemism and the inclusion of more phylogenetic hypotheses.

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INTRODUCTION

Amazonia, the richest and most diverse ecosystem in the world (Colinvaux, 1997), is widely recognized to comprise the Amazon basin and the lowlands of southern Colombia, southern Venezuela, eastern Ecuador, eastern Bolivia, northern Brazil, and the Guiana. Different approaches (Cabrera & Willink, 1973; Müller, 1973) have been used to identify its limits. However, the concern for a definition that makes explicit reference to its biogeographic history and that determines whether it represents a natural biogeographic unit is recent (Amorim, 2001). Just a few years ago were generated the first delimitations of the Amazonia based on quantitative approaches (Morrone, 2000; Amorim, 2001) and using phylogenetic hypotheses (Amorim, 2001). Cracraft & Prum's (1988) study gave the first steps to resolve the question about Amazonia origin, however Amorim's (2001) work was the first to question the traditional view of Amazonia as a single unit (Cabrera & Willink, 1973; see also Hooghiemstra, 1997).

These works (Cracraft & Prum, 1988; Morrone, 2000; Amorim, 2001) have made the difference within a research program where the main question about Amazonia, had not been its origin, but its diversity. But if we want to understand the biotic diversity of the Amazonia, and the reasons to explain why it supports the main endemic centers for several taxa like Anura (Ron, 2000), Aves (Nores, 2000), Lepidoptera (Brown, 1979), Primates (da Silva & Oren, 1996), and Squamata (Ron, 2000), we have to search for a reconstruction of the Amazonian history from the most direct evidence at hand, the Amazonian biota with its phylogenetic history (see Croizat, 1964; Vane-Wright *et al.,* 1991).

The earliest attempts to reconstruct the Amazonian biogeographic history were, however, non-quantitative approaches based on narrative descriptions of those events that originated today's species richness. These are known as the Amazonian *diversification hypotheses* (Wallace, 1852; Haffer, 1969; for a revision see Haffer, 1997). Although these approximations were very useful at that time because they opened the question about Amazonian diversity, since the development of quantitative biogeography approaches they have been severely criticized. In first place because they are based on explicit or implicit *a priori* assumptions (Amorim, 2001), and in a second place because their statements could not be empirically tested (Cracraft & Prum, 1988; Patton & da Silva, 1998; Alexio, 2002).

Under an explicit biogeographic framework the first cladistic and quantitative analyses, related to the Amazonian biogeographic history, began with Prum (1988) and Cracraft & Prum (1988). Although Cracraft & Prum (1988) did not explicitly describe the methodology used to obtain their area cladogram, Brooks Parsimony Analysis (BPA) is the most frequent method used. After them, da Silva & Oren (1996), Bates *et al.* (1998), Ron (2000), and Racheli & Racheli (2003, 2004) used a modification of PAE (Parsimony Analysis of Endemicity) (Cracraft, 1991) to generate their hypotheses. Amorim (2001) and Hall & Harvey (2002) proposed the latest and most recent area relationship hypotheses using phylogenetic and distributional data, under "cladistic biogeography" and BPA respectively.

In spite of all these efforts, the origin and the biogeographic history of the Amazonian diversity is still on discussion. This is evident from the amazing number of papers dealing with the subject (Peres & Terborgh, 1995; Haffer, 1997; Hooghiemstra, 1997; Marroig & Cerqueira, 1997; Colinvaux *et al.,* 2000; Bates & Demos, 2001; Rose &

Grainger, 2003). However, from the biogeographic framework, these hypotheses had failed to document explicit historical events, like those events resulted from cladogenetic events, since seven (da Silva and Oren, 1996; Bates *et al.,* 1998; Ron, 2000; Racheli & Racheli, 2003, 2004) of the 16 hypotheses have been developed not using the phylogenetic information of the Amazonian taxa, that is, using non historical methods (Garzón, *et al.* in prep.). Just recently the first formal critique to the use of PAE in the reconstruction of general area cladogram to the Amazonia (Brooks & van Veller, 2003) has been presented. Racheli (2004) also criticized the use of the Matrix Parsimony Representation technique used by Hall & Harvey (2002) to produce their combined area cladogram, questing the use of the competing topologies as source data.

Additionally most of the hypotheses have been formulated from a single taxonomic group (Aves in Prum, 1988; Cracraft & Prum, 1988; Bates *et al.*, 1998 and Racheli & Racheli, 2003; Primates in da Silva & Oren, 1996; Rodentia in Patton *et al.,* 2000; butterflies in Hall & Harvey, 2002, and Racheli & Racheli, 2004, and finally Ron, 2000 who produced separate hypotheses for Anura and Squamata). It is obvious that the history of the area had to have affected all the Amazonian taxa that coexisted along the region, producing their speciation, extinction, or dispersion pattern (s).

The geologic reconstruction of Amazonia

During the first part of the 20th century, ecological stability had prevailed as the traditional cause invoked to explain the current diversity in Amazonia (Webb, 1995; Amorim, 2001). However, after South America separation from Africa (125-130 myr) (Raven & Axelrod, 1975; Tarling, 1980) the geological history of the Amazonia has been defined mainly by the development of the Amazon basin. Many studies (Colinvaux, 1993; Räsänen *et al.*, 1995; Webb, 1995; Hoorn, 1996) have shown that numerous geologic and climatic changes as Andes uplift, glacial events, sea level changes, and aridity have affected the Amazon basin and at the same time to the lowland around it, so “the biological and ecological stability have been substituted by a conception of dynamism” (Marroig & Cerqueira, 1997 p.103). The history of the Amazonia has passed through a series of events since Cretaceous to the late Tertiary (Hooghiemstra & Van der Hammen, 1998), Amorim (2001) described that at the earliest time during the Silurian and Devonian the Amazonia was submerged. This condition, caused mainly by events like sea level variations and tectonic pressures was maintained until the Cretaceous. The followed events that affected the Amazonia were the uplifting of the Andes, the formation of the Amazon basin, and the connection of North and South America all of these, constrained to the Tertiary period (Hooghiemstra & Van der Hammen, 1998; Nores, 2004). The first Andean tectonic lift (73- 59 myr) progressively propagated the axis of the Andean foreland eastward and produced a large accumulation of sediments (Marshall & Lundberg, 1996; Hooghiemstra & Van der Hammen, 1998). The Andean tectonic events additionally produced two marine incursions into the Andean foreland that produced the earliest record of what we call now the Amazon, Orinoco, and Paraná drainage systems. There is not additional geological evidence for other marine transgressions at that time or for a possible connection between the Pebasian Sea with the Paranaense Sea, or the Pebasian Sea with the present Amazon mouth or for the present Amazon mouth with the Orinoco Sea (Hoorn, 1996; Marshall & Lundberg, 1996). By the late Miocene the rivers of the present-day Amazon basin have changed their course toward the east and the lowlands of the basin were separated from the biogeographic Chocó.

Finally, although it is recognized that the upheaval of the Andean Cordilleras and the separation from the Caribbean had its impact modeling current drainage systems (Marshall & Lundberg, 1996), on the atmospheric circulation, and on the northern of South American rain patterns (Hooghiemstra & Van der Hammen, 1998), paleoclimatic and geological data appears still unsatisfactory to reconstruct a geological area cladogram that could be tested by the diversification patterns of Amazonian animals as had been discussed (Cracraft & Prum, 1988; Racheli & Racheli, personal communication).

The diversification hypotheses

One of the first to express his concern about the diversity present in the Amazonian forests was Alfred Wallace (1852), after his voyage along the Amazonian Basin. His observations lead him to propose the first diversification hypothesis to the Amazonia, known now as "The Riverine Hypothesis". The principal argument is that the current biodiversity is the result of the vicariant events produced during the formation of the Amazon River and its tributaries. Since Wallace, there had been developed more than 16 diversification hypotheses (Nores, 2000). Nores (2000) made an extensive review of these hypotheses. All of the *diversification hypotheses* present a vicariant perspective of the Amazonian history; clearly the speciation is given by alopatric events caused by a variety of barriers to the gene flow: rivers, lagoons, ecological gradients, or the sea level.

Marroig & Cerqueira (1997) offered some of the phylogenetic and biological implications of the statements proposed by the most important hypotheses: 1) the Pleistocene Refuge hypothesis (Haffer, 1969), 2) the Riverine hypothesis (Wallace, 1852; Sick, 1967), and 3) the Gradient hypothesis (Endler, 1977). In all cases (Nores, 1999; Marroig & Cerqueira, 1997) the authors proposed a new hypothesis and gave their support to some of the 16 previous hypotheses. This has been the traditional way of work in the recent non-quantitative approach.

Previous analyses to the Amazonian's biogeographic history

The studies about the biogeographic history of the Amazonian region have increased during the last few years since the impact and acceptation of the phylogeography research program (Lougheed *et al.,* 1999; Ditchfield, 2000; Patton *et al.,* 2000; Marks *et al.,* 2002; Costa, 2003). Population genetics analysis, undoubtedly, has contributed to the "Amazonian cause", for example, testing some predictions of the riverine diversification hypothesis (Patton & da Silva, 1998; Lougheed *et al.,* 1999; Alexio, 2002), nevertheless most of these have been developed to answer the speciation history of one or two particular taxonomic groups and not to explore the relationship between the areas.

The area relationship for the Amazonia has been reconstructed twelve times (Cracraft & Prum, 1988; Prum, 1988; da Silva & Oren, 1996; Bates *et al.,* 1998; Patton *et al.,* 2000; Ron, 2000; Amorim, 2001; Hall & Harvey, 2002; Marks *et al.*, 2002; Racheli & Racheli, 2003, 2004), but at the moment there are 16 hypotheses. Table 1 shows all the area cladograms proposed for the Amazonia. All these biogeographic studies had stated that the Amazonia history was driven mainly by vicariance events that produced a hierarchical pattern (Moritz *et al.,* 2000; Ron, 2000; Amorim, 2001; Hall & Harvey, 2002). Ron (2000) and Hall & Harvey (2002), based on the congruence between the areas history for taxonomically distant groups (Butterflies, Primates, Birds, Anurans, and Lizards), presented a strong common history of vicariant isolation events proposing as the first event the disjunction between Guiana and the Atlantic Brazilian Forest. These studies also have shown some persistent relationships, for example a consistent Inambari- Napo group. However the Guiana position continues to be uncertain, its relationship with the so-called upper (Imeri and Napo) and lower (Inambari, Rondonia, Para, and Belem) Amazonia is inconsistent along the hypotheses and sometimes appears like an independent unit. It is still unclear what barriers were responsible for the proposed vicariant patterns (Ron, 2000; Hall & Harvey, 2002) and the timing of the diversification. The controversy continues at this point, a lot of hypotheses have been proposed to explain that vicariant pattern (*the diversification hypothesis*) and although the Pleistocene Refuges model (Haffer, 1969) has generated discussion, this is still the most accepted and championed one to explain the diversification for several taxa (Brower, 1994; Hall & Harvey, 2002). One major problem that enclose all above mentioned hypotheses is that were formulated to count for events of the late Pleistocene, letting out earlier periods (Cretaceous or late Tertiary) which molecular phylogenies of frogs, lizards, birds, and mammals suggest to be the timing for the main events of speciation (Moritz *et al.,* 2000; Ron, 2000).

Probably, the most important contributions about the origin of the Amazonian biota have come from recent phylogeographic studies (Patton *et al.,* 2000; Marks *et al.*, 2002; Costa, 2003). Marks *et al.* (2002) using the diversification pattern of *Glyphorynchus spirurus* showed that some Amazonian haplotypes (Imeri population) are more closely related to Central America and Chocó populations than they are to other Amazonian taxa (Napo populations), a pattern that they documented as common within the Amazonian birds (Marks *et al.*, 2002 pp. 164). Costa's (2003) analysis of the small mammal of Amazonia and the Brazilian Atlantic forest showed that these two regions (or domains in the traditional classification) are not exclusive in their fauna composition, and that the genetic similarity exhibit between the mammals of the two areas is often higher than the similarity within each of the areas. Although others works had already achieved a similar conclusion (Cracraft & Prum, 1988; Amorim, 2001), it is interesting to see how this result reappears with new taxa studied, and how wrong was the idea of two different units (provinces or domains) that now appears to be a single biogeographic unit. Another conclusion produced by Costa's (2003) work, which must be tested with strictly historical biogeographic approaches, predicts that a single hypothesis of the Neotropical area is not likely and that a single vicariance model will not explain the speciation events. Although these works are focused on Aves and mammals, they had produced new insights about the origin of the Amazonian biota and had placed new challenges to the biogeography research program.

The Events-based biogeography and the Parsimony based treefitting

The event-based analysis has gained a considerable popularity in coevolutionary (Weckstein, 2004) and in biogeographical studies (Sanmartin & Ronquist, 2004; Vilhelmsen, 2004). The fundaments of the event-based method were proposed at the molecular field (Goodman, *et al.,* 1979) to infer species tree from gene trees. Later, Page (1993a; 1994a,b) presented the analogy parasite-host and organisms-area and with Ronquist & Nylin (1990), Ronquist (1997; 1998), and Page & Charleston (1998) brought the method to the field of coevolution and biogeography, transformed as a parsimony analysis based on explicit process models. Since then, Page and Ronquist presented a variety of methods, which, Page (1994a) formalized in the computational programs COMPONENT 2.0 (Page 1993b) and TREEMAP (Page, 1995) and Ronquist (1997, 1998) in DIVA (Ronquist, 1996) and TREEFITTER (Ronquist, 2002a). The basic idea behind the event-based approach is to assign a cost, inverse to the likelihood of the event, to each of the four major processes known to affect the history of the taxa: vicariance, duplication (sympatric speciation in biogeography), switches (dispersal in biogeography), and sorting events or extinction. Parsimony is then used to estimate the minimum cost description given the data set. The explicit specification of the process' cost avoids *a posteriori* explanations of the pattern (Ronquist, 2002b) and also allows to re-evaluate patterns traditionally assumed to be originated only by vicariance (Sanmartin *et al*., 2001).

TREEFITTER offers three predefined models of cost (Table 2) although any combination could be proven (but see Wheeler, (1993) to check that triangle inequality can not be violated). These models are maximum vicariance (MV), reconciliation, and the default model (hereafter Ronquist's model). Maximum vicariance model known as maximum codivergence was proposed by Page (1994b) as an alternative of the four-event models that gives a negative cost to cospeciation and zero to the other three process, in this way MV maximizes the number of cospeciations when fits a parasite with a host tree. Reconciliation is a three-event based model that works under the assumption that no (or fairly improbable) horizontal transmission of associates (in biogeography, dispersal between areas) has occurred. The reconciliation model includes cospeciation, duplication, and sorting events. The last explicit model offered by TREEFITTER is Ronquist's model. Ronquist (2002b) proposed a combination of costs when, after an exploration of the cost space, concluded that his model was able to detect historical constrained patterns in the data under a wide range of conditions.

Optimal events cost

The possibility of an infinite combination of costs has been the main argument against approaches with explicit cost assignments (Siddall & Kluge, 1997; Grant & Kluge, 2003). Ronquist (2002b) proposed a criterion of optimization to select the optimal costs: he proposed that given an organism phylogeny (ptree) and an area cladogram (htree), we have to find the combination of costs that minimizes the probability (p-value) that a randomized data set has a lower cost than the area cladogram obtained from the original data set.

The randomization tests developed by Ronquist in TREEFITTER permit to calculate any property of the general area cladogram obtained from the observed data set (Sanmartin & Ronquist, 2004) by fitting it with other area cladograms obtained from randomizations of the data set (see Ronquist, 2002b and Sanmartin & Ronquist, 2004). To search for the optimal costs, the randomizations must be applied to the terminal's distribution of the organisms, because it is there where the phylogenetic constraints may have effect. In another context to explore whether the organism distributions are phylogenetically constrained to a given area cladogram, we should permute both areas and organisms terminals. An area cladogram previously constructed could be evaluated in terms of its success in describing the different events, however here we have to make a distinction: we must use permutations of the terminals in the area cladogram when the events under interest are vicariance and extinction and permutations of the organisms terminals when the interest is on dispersal and duplication events. Ronquist (2002b) explored the effects of randomize phylogenies and showed that they cause misleading results, therefore he consistently recommends permute only the terminals. The null hypothesis of no phylogenetic constraint (that is, the occurrence of an organism in a particular area as the product of ¨random¨ events) is rejected when less than the 5% of the general area cladograms resulted from the permutations have a lower cost than the general area cladogram obtained from the original data set. These are the combination of costs that maximize the probability to obtain phylogenetic constrained patterns.

In this paper we present an event-based analysis for the Amazonian biogeography based on phylogenetic and distributional evidence from several Amazonian animals to test previously proposed general area cladograms, evaluate the relative contribution of vicariance as a structuring factor, and to find the general biogeographic pattern of the region.

MATERIALS & METHODS

1. Data set selection for the analyses

Groups were selected following Sanmartin *et al.* (2001) choice criteria:

a) The topology must include at least three terminals.
b) The groups must be monophyletic and exclusively or predominantly of Amazonian distribution.
c) The terminals of the group must be confined to some of the provinces or area of endemism.
d) The group must be represented in at least three of the Amazonian Haffer's areas of endemism.

Additionally haplotypes from the same locality and grouped into a monophyletic group were collapsed.

We included in the analyses all the groups that we could find in the literature that agree with these criteria. However to some groups in selection criteria (d) we sometimes make exceptions an included groups present in two areas of endemism and that also occurred in some of the outgroup areas because this allow us test the monophyly of the Amazonia, and in others cases of Amazonian areas like Para. The data set compiled and references are presented in table 3. Although our data set included phylogenetic hypotheses generated from approaches with methodological and epistemological differences (maximum parsimony, maximal likelihood or bayesian inference), we agree with Ebach & Humpries (2002 pp. 429) that: “TAC [*taxonomic area cladograms*] are essentially *silent* or *passive* statements of relationship. They do not function as *active* accounts of speciation (hybridization, reticulation) or geography (migration, centers of origin)“. The cladograms found by us are the must updated phylogenetic hypothesis for the specific taxonomic group. We used 59 phylogenies and 831 terminals representing the main taxonomic groups of animals (Fig. 1A). For those phylogenies that include polytomic nodes, all the possible dichotomous resolutions were considered, although we recommend to use only supported resolutions (see Miranda-Esquivel, 2001). In total we performed the analyses with 470 dichotomic topologies. The data set was partitioned in order to make an exhaustive data exploration and to test the existence of a general pattern of area relationship for the Amazonia. The first partition is composed of haplotypes (23% of total terminals) while the second is composed of species (77% of total terminals). As insects were the richest group with the 36% of the total terminals (Fig. 1A), and could bias the analysis, we also performed a separate analysis using only the insect taxa.

2. Area definition

Since Haffer (1969) proposed the theory of Quaternary Refuges, the refuges inside the Amazonia became the most common tool for the delimitation of the region. Under the refuge theory these areas represent diversity centers. Although we recognize other traditional delimitations and definitions for the region (Cabrera & Willink, 1973; Müller, 1973; Cracraft, 1985), we performed the analyses under Haffer's (1969) units because most of the Amazonian hypotheses had been developed using these areas so we can contrast former hypotheses. Some authors (Amorim, 2001; Bates *et al.,* 1998) had found that part of Para has biotic similarities with another non-Amazonian area, the Brazilian Atlantic forest. We divided the Para area as used by Bates *et al.* (1998) to test the previous hypotheses that had used this division. Although Haffer's delimitation of the Amazonia comprises seven endemic regions, ten areas were finally identified and used in the reconstruction of the general area cladogram since areas 1, 2, and 3 were used as external areas to evaluated the common origin of Amazonian units (Fig. 3):

1. Central America (CA): We included in this area all the Central American areas, the Caribbean islands and southern North America (Mexico and Florida).
2. Chocó (CH): is the area between the Pacific cost and the west slopes of the Andes at the northern South America, below Panama to Esmaraldas Equatorial region.
3. Serra do Mar (SD): is the area that corresponds to Southern and Northern Brazilian Atlantic Forest.
4. Guiana (GU): is the interfluvial region from the Negro river to the Atlantic coast, the area includes the French Guiana, the Guiana, and Venezuelan Amazonia.
5. Imeri (IM): is the interfluvial region between the Negro River and the Japurá River, at the northern flank of the Amazon River.
6. Inambari (IN): is the area from the left flank of the Madeira River to the eastern limit of the Andean slopes following the Amazon River flow, at the southern flank of the river.
7. Napo (NP): is the area that includes all the river Napo basin, from the left flank of the Japura river, following the Amazon River flow, to the eastern limit of the Andean slopes.
8. Rondonia (RO): is the area comprising the interfluvial region between Tapajos River and the right flank of the Madeira River, at the southern flank of the Amazon River.
9. Para (PA): is the area involving the interfluvials areas between the Tapajos and Tocantis River, at the southern flank of the Amazon River.
10. Belem (BE): is the Interfluvial region from the Tocantis River to the Atlantic coast, at the southern flank of the Amazon River.

Fig. 1B shows the distribution of the terminals compiled for the analyses on the areas used.

3. Biogeographic analyses

Dispersal Vicariance Analysis

We used the dispersal vicariance analysis as implemented in DIVA 1.2 for windows (Ronquist, 1996; 1997) to calculate the dispersal/vicariance rate and to reconstruct the ancestral area for each taxonomic group, and for the partitions (see *data selection for the analysis*). DIVA approach is a widely used tool to evaluate vicariance and dispersal scenarios (Donato *et al.,* 2003; Miranda-Esquivel & Coscarón, 2003; Sanmartin, 2003) and unlike pattern-based methods DIVA does not require a hierarchical area relationship. The analyses were performed under a heuristic search, holding 100 trees; we restricted the number of areas of the ancestral distribution to a value of seven. We also quantified the most frequent dispersal and vicariance events between two areas for each taxonomic group as well for the partitions.

The Fit Of The Previous Hypotheses

To test the existence of a hierarchical constrained pattern for the Amazonia, and to evaluate whether the organisms were constrained according to any of the previous hypotheses, we fitted each of the hierarchical hypotheses to the data set compiled.

These previous hypotheses and the data set were fitted using the three predefined models of cost in TREEFITTER 1.3b (Ronquist, 2002a). Although 11 studies had been performed for the Amazonia biogeography, some of them had produced more than one hypothesis and now there are 16. In total we evaluated 20 hypotheses resulted from dichotomizing polytomic hypotheses since the program only accepts resolved trees (Table 4). To evaluate the significance of the fit, we used the randomization tests of TREEFITTER permuting 1000 times areas and organism terminals.

Since MV finds the maximum number of vicariance events that can be explained by a particular hierarchical scenario given a data set, and vicariance has been the major event assumed to model the history of the region (Table 1), then we evaluated how successful are the previous hypotheses to predict vicariance events given the data set. The fit between these scenarios and the data was calculated by counting the number of vicariance events found in the hierarchical scenarios, the larger the number of vicariance events in a hierarchical scenario, the better it explains the observed data set. We randomized 1000 times the terminals of the area topology, and in this case the *p-value* was calculated as the number of random data set having a higher or equal number of vicariance events than the observed data set given a particular scenario.

Parsimony-Based Tree Fitting To The Amazonia

Using TREEFITTER we analyzed the partitions and the whole data set under the three predefined models of cost (Table 2) to search for a general pattern for Amazonia. The randomization tests and the optimization criteria (see *Optimal events cost*) were used to choice those cost events that guarantee to obtain a general area cladogram constrained to the phylogenetic information in the data set (Ronquist, 2002b). The evaluation of the models was performed by comparing the overall cost of the cladograms from the original data set and the cost of cladograms generated from the 1000 randomizations of the organism’s distributions. To all the analyses the result was considered significant at the 0.05 level, when fewer of the 5% of the permutations fall at a lower or equal cost than the calculated to the observed data set.

All the searches were conducted using step addition, holding 1000 trees in each step and branch swapping with a reconnection limit of 25 nodes. The widespread taxa were coding as “recent origin” to focus only on ancestral events and to avoid reconstruction based on widespread taxa (Sanmartin *et al.,* 2001; Sanmartin & Ronquist, 2002)

Patterns and Taxa

We performed a search eliminating with replacement from the data set one group at a time to evaluate the contribution of each animal group to the general area cladogram. This was done until we had explored the absence of each of the 59 groups. Two additional searches were performed. First using only the taxa found to change the general pattern when they were excluded and, a second search excluding all of them at the same time. We used Ronquist’s model of cost and the same search conditions used in the tree fitting analysis (see above). The resulting topology without each group was compared with the general area cladogram obtained with the all data set by counting the number of identical nodes. We also evaluate the individual fit of each taxonomic group to the general area cladogram found with the all data set, obtaining the number of the different events required to fit the individual phylogeny and distribution to the area cladogram.

Parsimony Analysis of Endemicity (PAE)

We performed a PAE using areas as defined by Rosen (1988) to explore the information given only by the distribution of the data set and determinate the effect of excluding the phylogenetic hypotheses. In order to do so, a presence/absence matrix was constructed using the areas as terminals and the taxa as characters. An all zeroes outgroup was used to root the tree. The matrix was analyzed under a heuristic search with NONA 2.0 (Goloboff, 1998) and the equally parsimonious topologies resulted were summarized using a strict consensus.

4. New and old patterns

To evaluate the congruence between our results and the previous patterns, we compared the number of identical nodes shared by the previously proposed hypotheses and the patterns obtained in this study.

RESULTS

Dispersal Vicariance Analysis

The analysis with DIVA for each taxonomic group showed more vicariance than dispersal events in almost all of the 59 phylogenies (fig. 2). Eight groups presented more dispersal than vicariance events, five of them are Insecta groups, and the other three corresponds to one taxon of Chiroptera, one of Marsupia, and one of Primates. *Juditha* (Lepidoptera) was found to be the group with the highest number of dispersal events. Thamnophilidae (Aves) and *Thrichomys* (Mammalia) were the groups with equal number of dispersal and vicariance events. The most frequents dispersal events are recorded in fig. 3. The dispersal between Inambari and Napo in any direction was the commonest event. Eight groups supported the direction: Inambari to Napo and seven groups showed the opposite direction. The groups: *Hyla* (Anura), *Glyphorynchus spirururs, Tangara*, Thamnophilidae (Aves), and *Rutela* (Coleoptera) presented both directions of dispersal. The analyses performed to the partitions produced similar results: more vicariance events than dispersal. Although the ratio of events was smaller in the species partition (590 vicariance/ 411 dispersals events), in the haplotypes data set, there was a greater numbers of vicariance than dispersal events (214/ 49). The dispersal route Inambari to Napo was also the most frequent in the haplotypes partition, however in the species partition the most frequent events were from Guiana to Napo and from Guiana to Rondonia.

The fit of the Previous Hypotheses

Regardless of the partition used, under the MV and reconciliation models, the distribution of the organisms did not appear to be phylogenetically constrained to any of the hypotheses tested (Table 5). The results were different under Ronquist's model where the distributions were phylogenetically constrained to all the hypotheses. Table 6 shows the number of vicariance events found by each of the 20 hypotheses using the whole data set. The hypothesis of Bates *et al.* [(1998), H8] showed the best fit (the highest number of vicariance events *sensu* Sanmartin *et al.,* 2001) to the data set. In this hypothesis all the areas that conform the Amazonia are in the same clade, divided in the so-called groups upper and lower Amazonia. The terminal randomizations showed that Bates' *et al.* (1998) hypothesis did not fit the data set significantly better than expected by chance (P=0.4), 442 of the 1000 randomizations had more vicariance events than the original data set. The others hypotheses with a significant fit showed a lower number of vicariance events. This behavior is seen also using the haplotypes and the species data set. Using the haplotype data set, the hierarchical hypothesis of Marks *et al.*, [(2002), H16], produced using parsimony, showed the best fit with 43 vicariance events. Under Marks' *et al.,* hypothesis, Amazonia is a composite area, where traditional Amazonian areas as Imeri are closer to Central America than to

Amazonian areas and Para is closer to Serra do Mar than to any of the Amazonian areas. The number of vicariance events, however, was not significantly higher than expected by chance, which means that this topology did not fit the data better than expected by chance. Using the species data set two hierarchical hypotheses showed the best fit. The topology of Bates *et al.* [(1998), H8] once again had the highest number of vicariance events and shared the same number of nodes with Marks' *et al.,* (2002) Maximal Likelihood hypothesis (H17). This topology differs from H16 in Rondonia's position; Rondonia is the basal area in H16, while in H17 Rondonia appeared as the sister group for Para-Serra do Mar clade. These two topologies did not fit the data set significantly better than expected by chance, the p-value for Bate's *et al.* (1998) hypothesis was P=0.5, [596 of 1000 randomizations performed had a higher number of vicariance events]. To Marks's hypothesis (H17) the p-value was P=0.3 [303 of 1000 permutations had more vicariance events]. We must recall, nevertheless, that the hypotheses tested differ greatly in the number of terminals or areas used, so the numbers of resolved nodes were different. The number of vicariance events recovered by them might be an artifact caused by the number of internal nodes, which could imply that, the probability of more vicariance events increases. This could be a real risk if we observe that H8 as H16, and H17 had the greatest number of terminals.

Parsimony-based tree fitting to the Amazonia

Table 7 shows the fit of each cost model with the data set and partitions, given 1000 randomizations. The results are given as significant (S) or non-significant (NS) based on the number of permutations with a lower total cost than the cladogram obtained from the original data set. Regardless of the partition used, the area cladograms obtained from MV and reconciliation models did not fit the data set significantly better than expected by chance, that is, the number of randomizations with a lower cost than the original data set was no significant, so it is impossible to prefer any of these two models. Ronquist's model was found to be the optimal combination of costs that assures the reconstruction of general area cladograms phylogenetically constrained; this result was the same regardless of the partition used. The cladograms obtained under this model fit the data set much better than expected by chance; the permutations did not find a pattern that had a lower cost than the original cost. Under this model, all the topologies had more vicariance events than the expected by chance given the data set. Only the topology produced using species data set did not found a significant number of vicariance events given the randomizations (Table 8).

Fig. 4 shows the cladogram for the whole data set (*hereafter* general pattern), the main difference between the three recovered topologies was Imeri and Para 1 position related to the others terminals. This reconstruction required 8 vicariance (cospeciations), 15 events of duplication, 12 sorting events, and 144 dispersal events. The commonest dispersal events occurred from Central America to Chocó, from Guiana to Napo, from Guiana to Rondonia, from Guiana to Inambari, and from Inambari to Napo. These dispersals were also common within the analysis performed for each group with DIVA (Fig. 3). The routes Guiana to Napo, and Guiana to Rondonia were the most frequent with the species partition in DIVA analysis. Fig. 5 presents the cladograms obtained using the haplotypes partition. This reconstruction required 8 cospeciation, 15 duplications, 12 extinctions, and 69 dispersal events. The dispersal from Inambari to Rondonia was the most frequent route, the others dispersal events presented very small frequencies in relation to the required with all the data set and with the species partition. Fig. 6 presents the resulting tree using the species partition. This reconstruction required 9 cospeciation, 15 duplications, 11 extinctions, and 118 dispersal events. Dispersal from Napo to Inambari represents the most frequent dispersal event followed by the routes Central America to Guiana, Serra do Mar to Central America and Napo to Central America. The main difference among the topologies was Imeri position, however Imeri was the poorest represented area within the data set (fig. 1a); this could be one explanation to this phenomenon, otherwise this could mean that Imeri area is actually a composite area. The division of Para showed that this region is a composite area too. Both Para 1 and Para 2 appeared to be closer related to areas as Belem, Serra do Mar, or Imeri than to each other. The reconstructions obtained using species and haplotypes partitions differ drastically between each other and with the general pattern. Just two nodes were shared between the haplotypes pattern and the general pattern; these correspond to Napo-Inambari relationship and Belem position at the base of the clade. The greatest number of insects into the data set did not influence the reconstruction of the general pattern, this was evident in the low congruence between insects' topology and the reference tree called general pattern, besides insects were not the only group producing the structure in the general pattern (*see Pattern and taxa section*). In spite of this some clades like the Napo-Guiana relationship recovered with the insects and species partition, maybe due to this number superiority since only two groups of insect had topologies using haplotypes, however it is interesting that no additional clades had been shared.

Patterns and Taxa

Eight of the 59 animal taxa were found to be the main structural taxa to shape the general pattern, that is, the absence of any of these groups change the pattern. The number of nodes shared with the general pattern when they were eliminated is shown in Table 9. The contribution of these taxa to the general pattern was confirmed when we searched for a general pattern using only these eight groups (Table 9) and five of the ten nodes of the general pattern were recovered. By contrast, the pattern produced when we eliminated these eight groups at the same time differs greatly from the general pattern since only three nodes were recovered. However we found that some groups contribute to the structure in the general pattern more than others do. The patterns recovered when we eliminated six of the eight groups (*Pteroglossus viridis* group, *Pteroglossus bitorquatus* group*, Juditha, Morphinae, Charis gynea,* and *Mico*) did not differ deeply from the general pattern retaining seven, six, and five nodes respectively. The patterns resulted when *Xiphorhynchus* and *Amazona* information were eliminated differ greatly from the general pattern and only three or four nodes of the general pattern were kept. Five of these eight groups were also found to be the ones that required a high number of cospeciation in relation with the number of dispersal when we fitted their particular histories to the general pattern.

Parsimony Analysis of Endemicity

The PAE produced eleven most parsimonious topologies; the strict consensus is shown in fig. 7. Although the topology is poorly resolved with four nodes only, these nodes are pretty congruent with the previous area hypotheses proposed to the Amazonia. In fact these same nodes are the most common nodes through the entire hypotheses: Napo-Inambari, Chocó-Central America and, Para-Belem; and basically are the same that those recovered by previous hypotheses generated using PAE. The absence of phylogenetic information clearly results in the possibility of many different answers that made difficult the summary of the information in a single pattern.

Old and New Patterns

Old vs. Old

Based on node congruence, the previous hypotheses seem to be much similar between each other (Table 10) than with the topologies generated using any partition, however particular behaviors must be underlined. We found that the highest number of shared nodes appeared between the hypotheses H15 and H10; both of them produced using both distributional and phylogenetic information of Amazonian taxa. H1 and H15 also shared an important number of nodes and these two hypotheses also used distributional and phylogenetic information. No such a similar behavior was found between hypotheses produced using PAE, although the PAE hypotheses shared some nodes between each other, the numbers of common nodes were low and not congruent with the nodes shared between the hypotheses generated using phylogenetic data.

New vs. Old

We found that the general pattern recovered by us disagrees greatly with the previously proposed hypotheses (Table 10). The only informative clade shared by the general pattern and previous hypotheses was Napo-Inambari. Napo-Inambari clade is shared with the hypotheses H1, H2, H3, H6, H8, H9, H10, H11, H12, H13, H14, H15, H18, H19, and H20. The species pattern shared the node Rondonia-Para 1, with the previous hypothesis H8, H18, H19, and H20. The haplotypes' pattern and the H2, H3, and H8 hypotheses shared the nodes, Napo-Inambari and Central America-Chocó. Others hypotheses shared Napo-Inambari clade with haplotypes' pattern.

DISCUSSION

Many studies had claimed the importance of historical information to produce more realistic answers about Amazonia origin (Bates *et al.*, 1998; Lougheed *et al.* 1999; Ron, 2000). Although our study used the largest data set ever presented with distributional and phylogenetic information from several animals coexisting at the Amazonia, none of the previous hypotheses could fit the data set successfully and the patterns obtained from partitions run in opposite directions. We were not able to recognize a general area cladogram to describe a sequence of events and representing a unique history. In spite of this, our results are not unexpected at all; some authors had showed their doubts about the existence of such a hierarchical pattern for the Amazonia (Bush, 1994; Costa, 2003). Some have claimed to look back for ecological particularities (Tuomisto & Ruokolainen, 1997); others, to explain the incongruence between different patterns, have proposed that they all represent Amazonian's history but in different moments (Bates *et al.,* 1998). We considered that the area cladograms obtained from species and from haplotypes presumably document different evolutionary times. Old biogeographic events from species and more recent from haplotypes, since mitochondrial DNA focus on fast evolving sequences, characterized by high substitution rates and had been considered for diverse studies as an effective marker for recent levels of divergence (Brower, 1994; Eizirik *et al*., 1998; Avise, 2001). Nevertheless they do not document classics disjunctions as cis-trans Andean or upper-lower Amazonia. Several works had stated the old origin of the Amazonian biota (Moritz *et al.,* 2000; van der Hammen & Hooghiemstra, 2000; Amorim, 2001) and molecular phylogenies had corroborated this, finding high levels of divergence between species and populations (Clough & Summers, 2000; Patton *et al.,* 2000; Marks *et al.,* 2002; Costa, 2003; Dick *et al.,* 2003) suggesting the timing of divergence predates the Tertiary. We consider that our results date events old enough not expected to have been recovered by the previous hypotheses based only on distributional data. Cracraft (1988) stated that biogeographic patterns within continental biotas are produced by cycles of vicariance of widespread species, followed by narrow endemism, followed by dispersal of the descendant populations to produce more widespread forms, followed by new cycles of vicariance. Through this complex history it is possible that areas of endemism might be lost and others process as area hybridization, disappearance of barriers, the origin of new barriers, dispersion, and extinction, obscure the pattern making more difficult the task of the biogeographers. In other words areas of endemism within continental biotas had a deep-time history. However a real consequence of this complex history, since many barriers within continental biotas are ecological in nature, is the result that more than one general area cladogram describes aspects of “true” areas’ history. Our results seem to corroborate fairly Cracraft’s findings, however we do not suggest that there are as many patterns as taxa as some authors imply (see Ron, 2000), we are referring to the widely know differential response of some organisms to the same events or barriers (e.g. differential effects of the Amazon River in Aves see Hayes & Sewlal, 2004).

So far all the approaches used to analyze Amazonia’s biogeography had came from pattern-based methods; we are not surprising at all with the difference in their and our results, pattern-based methods tend to reduce complexity by losing of information (our PAE topology shows this behavior) (Cracraft, 1988) and most of the previous hypotheses had been developed without reference to phylogenetic relationships. Given that PAE methodology is based on distributional information of widespread taxa, we consider that the results of the previous hypotheses reflect current biotic similarities shared by the areas used and do not reflect its historical relationship. In fact, our PAE topology, although poorly resolved, did share traditional components suggested by the previous hypotheses of area relationship (Central America-Chocó, Para 1-Para 2, Belem-Para, and Napo-Inambari); These results place the incongruence in the phylogenetic information and induce us to think that most of the area relationships produced previously were biased by the information produced only by raw distribution of the Amazonian taxa.

Repeatedly through the biogeographic analysis of the Amazonia, the composite origin of some of the areas had been documented, since early approaches (Cracraft & Prum, 1988) this finding contributed also as initial evidence about a possible hybrid origin of the region. So far The Brazilian Atlantic Forest (Cracraft & Prum, 1988), Inambari (da Silva & Oren, 1996; Racheli & Racheli, 2004), Para (Bates *et al.,* 1998; Racheli & Racheli, 2004), Napo (Racheli & Racheli, 2004), Guiana (da Silva & Oren, 1996), and Rondonia (da Silva & Oren, 1996) had been discovered to have composite origins, some cases do imply the paraphyly of the region (da Silva & Oren, 1996), and other do not (Ron, 2000). These findings put several questions about the confidence on the biogeographic units that had been used and challenge our ability to identify endemic areas. Our data set includes historical information from organisms with different dispersal abilities, since the barriers to gene flow may vary greatly. Our findings make us consider that Para and possibly Imeri are composite areas. The topologies produced using the whole data set and the partitions showed ambiguous relationships of these areas related to the others. These findings about area hybridization could be the result of more time to dispersal, lost of old barriers, and new barriers to the gene flow causing the speciation at the Amazonia, implying that our patterns show older events than those shown by PAE. Area hybridization also put several questions about the causes of the speciation at the region and shows that current barriers used to define the areas of endemism are not efficient at all. Several phylogeographic studies had showed results that make us doubt about the effectiveness of rivers as real barriers to gene flow (Lougheed *et al.,* 1999; da Silva & Patton, 1998; contra Hayes & Sewlal, 2004). These results suggest that is necessary to reformulate the units used as endemism areas. New quantitative approaches are now available (Linder, 2000; Garcia-Barros *et al.,* 2002; Szumick *et al.*, 2002) to identify them efficiently. We consider that although areas of endemism to particular taxa are without doubt important to describe its evolutionary history, the biogeographic units to evaluate Amazonian history must come from the inclusion of the distributional information of the most Amazonian taxa as possible (see Kress *et al.,* 1998). Finally, and most important, area hybridization implies that to present a general area cladogram, some areas must be redefined and/or duplicated, which might mean a reticulate history of the region. This statement could found support in molecular studies that have shown deep divergence level within Amazonian populations and strong genetic similarity between Amazonian and non-Amazonian populations.

Pattern congruence found in previous analyses (Hall & Harvey, 2002; Ron, 2000) had lead to some authors to think that vicariance was the main and unique event causing speciation at the Amazonia, however our results showed that it is clear that other events than vicariance are also causing the speciation. Those models with additional processes as duplication, dispersal, and extinction fit better with the evidence than MV (Table 8). Previously proposed hypotheses tested in this study showed a similar result. They fitted the evidence better under Ronquist’s model than MV. Using MV we found that randomly permuted data set had more vicariance events than the original data, a behavior that Sanmartin *et al.* (2001) had documented to be typical under MV as the result of local diversification (duplication) patterns, that is, “terminals species are often found in the same areas as their closest relatives” (p. 368), a clear result against the preconceived idea to consider alopatric events as the main cause of diversification in the Amazonia. Although dispersal-vicariance analysis indicated that vicariance is an important event in the diversification patterns of the Amazonian animals, the Amazonian history constrained into the data set suggests that a complex model (as Ronquist’s) is necessary to describe it and to produce an area cladogram constrained to the phylogenetic information of the taxa used. This complex history cannot be described using models based only on vicariance (MV) or models without dispersal (as Reconciliation).

Although we were not able to present any of the patterns produced as “the” general area cladogram for the Amazonia, some important contributions about area relationship might be discussed. First, our analyses corroborated once again a closer relationship between Napo and Inambari, which was recovered by the haplotypes data set and the whole data set. However these two areas were also found to have the most frequent dispersal events. This result could indicate that there is not a clear distinction between the organisms coexisting in these areas and that they are moving freely through the barrier (upper Amazonian River) used to separate the areas. Phylogeographic studies although had remarked high levels of divergence between Amazonian animals populations they had failed to define the rivers as efficient barriers to gene flow (Patton & da Silva, 1998; Lougheed *et al.,* 1999; Colwell, 2000; Gascon *et al*., 2000; Patton *et al.,* 2000), recently Hayes & Sewlal (2004) showed that the effect of Amazon River as a dispersal barrier to Amazonian Aves is at least differential, habitat preference appeared as the critical factor. Their analyses demonstrated that the Amazon River was a most effective dispersal barrier along its lower portion and for species restricted to forest and *terra firme.* These results seem to be additional support to ours, basically in the presumption that Napo and Inambari are actually a single unit.

Second, given that all the reconstructions found in this study (whole data and partitions) required a higher number of dispersals than cospeciations events, we consider feasible that the diversification within continental biotas must to be greatly influenced by the wide distribution of the organisms, which move freely through a continuous forest, nevertheless again this imply that others process than vicariance must be considered.

Third, we found the highest frequency of dispersal events between two major clades that were clearly represented in the topology produced with the whole data and in the topology using haplotypes: a first clade comprised of coastal areas and a second one involved continental areas, the most frequent dispersals included routes from the coast areas to the continental ones. This result seems imply that continental areas were secondarily colonized from coastal areas and additionally implies that the organisms must have been isolated in the periphery of the continent. We considered that, probably continental areas were initially submerged and that only until the area emerges, the organisms were able to occupy it. Some *diversification hypotheses* had used a similar explanation as a probable cause of isolation (e.g. Amazon Lagoon hypothesis, Frailey *et al.,* 1988), however other approaches as geology or statigraphy have powerful tools that must be used to test this hypothesis (Ebach, 2001; Ebach & Humphries, 2003).

Fourth, we found that some of the groups that contributed more to outline the resulted topology were those with phylogenies implying fewer number of events to fit the area cladogram and included a high number of cospeciations. We believe that this is produced because event-based analysis uses parsimony as a decision tool to reconstruct the topology. In spite of this, we consider the topology reconstructed with the whole data set as highly stable, since only the absence of eight groups changes its structure. The results have shown that these eight groups produced the main structure of the topology nevertheless the complete data set is necessary to give the detailed structure that permits to reach the area cladogram obtained.

Finally, the area relationships found indicate that there is not possible to postulate a unique hierarchical pattern, in fact the analyses showed that there are different patterns for the partitions and for the whole data set, all constrained to the phylogenetic information. We think that some of these possibilities must be consider:

Diverse histories are taking place in the region and the causes of the cladogenetics events in Amazonian animals are different between some taxa.

The cladogenetics events in Amazonia predate the formations of current rivers and drainage systems, and current genetic structure could be the results of barriers that are no longer evident on the landscape (following Lougheed *et al.,* 1999).

Amazonian rivers do not work as effective barriers to the gene flow of the Amazonian animals.

Barriers used are not the main cause for the cladogenetics events of Amazonian animals; this is the reason that now almost all of these endemic areas had been found as composite areas in many of the studies made.

Obviously, we consider imperative to include in subsequent biogeographic studies, more phylogenetic hypotheses than those compiled here. The work of Kress *et al.*, (1998) have shown that to several important groups the sampling effort had been enough, which gives confidence to their distribution information. Fishes could represent the next target to generate new hypotheses about the Amazonia's history because an important number of phylogenetic hypotheses are now available (Vari & Harold, 2001; Boeger & Kritsky, 2003; Montoya-Burgos, 2003; Moyer *et al.,* 2004), however area limits have to be redrawn first; phylogenetic hypotheses from plants might be useful too, since they might be affected by different process (Sanmartin & Ronquist, 2004). These new phylogenetic hypotheses will lead us to corroborate or to re evaluate our results. If these studies corroborate our results, Cracraft (1988) warn about the possible lost of continental biotas history through the time, must be consider it. This finding must challenge us to find new solution to deal with it; maybe to look for those groups with deep divergences might be a solution.

ACKNOWLEDGEMENTS

We are deeply thankful with Isabel Sanmartin, Leonora Costa, Tommaso & Luigi Racheli, Juan J. Morrone, Jim Patton, Paula Posadas, André Freitas, and Keith Brown Jr. for their constructive comments. The first author is much indebted with Isabel Sanmartin for her constant incentive and encouragement. Our thanks are extended to Salvador Arias and Mario Quijano for their concern in the compilation of the data set, and entertain discussions. All the members of the Laboratorio de Sistemática & Biogeografía are acknowledged for their individual efforts.

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Table 1: Main hypotheses of area relationship proposed to Amazonia. For each pattern the author's name, the taxa used, the method and the explanation suggested to the pattern are shown. Area acronyms as follows: Belem (Be), Catinga (CAT), Guiana (GU), Imeri (IM), Inambari (IN), Napo (NP), Para (PA), Rondonia (RO), Serra do Mar (SD).

* We assume implicit vicariance since the hypothesis was produced using pattern methods that recognize only vicariance events.
** Marks (2002) found low genetic divergence between Imeri and Central America populations produced basically by dispersal, but there is not an explicit reference about the process involved in the history of Amazonia.

AUTHOR / YEAR	**TAXA**	**METHOD**	**AREA CLADOGRAM**	**PROCESS INVOKED**
Prum (1988)	Aves (Toucans)	“Maximum Parsimony” (BPA)	((GU,(PA, BE)), (RO, IM, IN, NP))	Implicit vicariance*
Prum (1988)	Aves (Toucans, Carpenters, Coatings)	BPA	(GU,((RO,(BE,PA)),(IM,(IN,NP))))	Implicit vicariance*
Cracraft & Prum (1988)	Aves (Toucans and Parrots)	BPA	(SD,((CH,CA),(GU,((SD,BE_PA),(IM,(IN,NP))))))	Vicariance
da Silva & Oren (1996)	Primates	Parsimony Aanalysis of Endemicity (PAE)	(GU, (PA, BE)), ((RO, IN1), (IM, IN2, NP))	Vicariance
Bates *et al.* (1998)	Aves (Passerine)	PAE	(GU, (IM, (IN, NP)), (BE, (PA1, (PA2, (RO))))	Implicit vicariance*
Patton *et al.* (2000)	Rodents and Marsupials	BPA	(GU, (IM, (IN, NP))), (RO, PA, BE)	Vicariance
Ron (2000)	Squamata	PAE	((PA,(RO,(BE,GU))),(IN,NP))	Vicariance
Ron (2000)	Anura	PAE	(BE,(RO,(GU,(IN,NP))))	Vicariance
Amorin (2001)	Diptera, Hemiptera, Primates	“cladistic biogeography” no method was specified	(((IM,(GU,BE)),(NP,IN)),(PA,(SD,CAT)))	Vicariance
Hall & Harvey (2002)	Lepidoptera (Riodinidae)	Phylogeography	(GU,((RO,(BE,PA)),(IM,(IN,NP))))	Vicariance
Hall & Harvey (2002)	Anura, Squamata, Birds, Primates, Rodents, Marsupials, Lepidoptera	Combination using MRP	((RO,(BE,PA)),(GU,(IM,(IN,NP))))	Vicariance
Marks (2002)	Aves	Phylogeography	((GU,(IN,(NP,(CH,(CA,IM))))),(RO,(PA,SD)))	not explicit **
Marks (2002)	Aves	Phylogeography	(RO,((GU,(IN,(NP,(CH,(CA,IM))))),(PA,SD)))	not explicit **
Racheli & Racheli (2003)	Aves (Psittacidae)	PAE	((IM,(NP,IN)),(GU,((BE,PA2),(PA1,RO))))	Implicit vicariance*
Racheli & Racheli (2004)	Lepidoptera (Papilionidae)	PAE	((GU,(BE,(PA2,(RO,PA1)))),(IM,(IN,NP)))	Implicit vicariance*
Racheli & Racheli (2004)	Lepidoptera (Papilionidae)	PAE	(GU,((BE,(PA2,(RO,PA1))),(IM,(IN,NP))))	Implicit vicariance*

Table 2. The three explicit model of costs used in TREEFITTER (Ronquist 2001). The acronyms of the process are presenting as appears in TREEFITTER: ccost (codivergence cost), ucost (duplication cost), scost (sorting cost), and icost (switches cost).

Model	ccost	ucost	scost	icost
MV	-1	0	0	0
Reconciliation	0	1	0	20000
Ronquist's model	0,01	0,01	1	2

Table 3. Data set used in the analysis, number of terminals and references. The phylogenetic method used in the original study is represented by MP to maximum parsimony, ML to maximal likelihood, BI to bayesian inference and distance to all the methods that used distances, taxonomic rank of the terminals when them correspond to haplotypes (Hp), species (Sp) is also showed.

	Terminals		**Number of**	**Phylogenetic**	
Taxon	**Sp**	**Hp**	**Terminals**	**Analysis**	**Source**
Hyla (Anura)	X		17	MP	Chek *et al*., 2001
Epidobates (Anura)	X		9	MP	Clough & Summers, 2000
Phyllobates (Anura)	X		3	MP	Clough & Summers, 2000
Dendrobates (Anura)	X		12	MP	Clough & Summers, 2000
Bufo (Anura)	X		7	Distances	Maxson, 1984
Bolitoglossa (Urodela)	X		21	MP	Parra-olea *et al.,* 2004
Anolis (Squamata)		X	16	MP	Glor *et al*., 2001
Mabuya (Squamata)	X		5	MP	Mausfield *et al*., 2002
Lachesis (Squamata)		X	9	MP	Zamudio & Greene, 1997
Xyphorhynchus (Aves)		X	43	MP	Alexio, 2002
Pionopsitta (Aves)	X		8	MP	Cracraft & Prum, 1988
Selenidera (Aves)	X		7	MP	Cracraft & Prum, 1988
Pteroglossus viridis group (Aves)	X		3	MP	Cracraft & Prum, 1988
Pteroglossus bitorquatus group (Aves)	X		6	MP	Cracraft & Prum, 1988
Glyphorynchus spirurus (Aves)		X	41	MP	Marks *et al.,* 2002
Tangara (Aves)	X		62	MP	Burns & Naoki, 2004
Amazona ochrocephala (Aves)		X	15	BI	Eberhard & Bermingham, 2004
Thamnophilidae (Aves)	X		15	MP	Bates *et al.,* 1999
Leptopogon amaurocephalus (Aves)		X	5	MP	Bates, 2002
Hypocnemis hypoxantha (Aves)		X	6	MP	Bates, 2002
Hylophylax poecilinota (Aves)		X	4	MP	Bates, 2002
Myrmeciza hemimelaena (Aves)		X	5	MP	Bates, 2002
Rodnius prolixux , *Rodnius robustus* (Hemiptera)		X	29	MP	Monteiro *et al.,* 2003
Chimarra (Trichoptera)	X		30	MP	Blahnik, 2002
Charis cleonus species complex (Lepidoptera)	X		19	MP	Hall & Harvey, 2002
Juditha (Lepidoptera)	X		8	MP	Hall & Harvey, 2001; 2002
Charis gynea species complex (Lepidoptera)	X		8	MP	Hall & Harvey, 2001; 2002
Thisbe (Lepidoptera)	X		6	MP	Hall & Harvey, 2001; 2002
Aricoris (Lepidoptera)	X		23	MP	Hall & Harvey, 2001; 2002
Synargis (Lepidoptera)	X		24	MP	Hall & Harvey, 2001; 2002
Lemonias (Lepidoptera)	X		8	MP	Hall & Harvey, 2001
Heliconiiti (Lepidoptera)	X		61	MP	Brower & Egan, 1997
Morphidae (Lepidoptera)	X		30	MP	Penz & De vries, 2002
Anthomyiidae (Diptera)	X		12	MP	Shigueo & de Carvalho, 2004
Lutzomyia longipalpis (Diptera)		X	12	MP	Arrivillaga *et al.,* 2002
Rutela (Coleoptera)	X		14	MP	Jameson, 1997
Augochlorella (Hymenoptera)	X		15	MP	Coelho, 2004
Rhipidomys (Mamalia)	X		5	MP	Costa, 2003
Marmosa murina (Mamalia)		X	3	MP	Costa, 2003
Metachirus nudicaudatus (Mamalia)		X	6	MP	Costa, 2003
Oryzomys megacephalus species complex (Mamalia)	X		3	MP	Costa, 2003
Oryzomys macconelli species complex (Mamalia)	X		5	MP	Patton *et al.,* 2000
Isotrix (Mamalia)	X		4	MP	Patton *et al.,* 2000
Micoureus (Mamalia)	X		4	MP	Patton *et al.,* 2000
Philander (Mamalia)	X		6	MP	Patton *et al.,* 2000
Marmosops (Mamalia)	X		4	MP	Patton *et al.,* 2000
Proechimys goeldii species complex (Mamalia)	X		3	MP	Patton *et al.,* 2000
Mesomys (Mamalia)	X		3	MP	Patton *et al.,* 2000
Thrichomys (Mamalia)	X		4	ML	Braggio & Bonvicino, 2004
Oecomys (Mamalia)	X		28	ML	Belchior & Rodrigues, 2003
Lonchophylla (Chiroptera)	X		22	MP	Davalos & Janza, 2004
Cyanomops (Chiroptera)	X		8	MP	Peters *et al.,* 2002
Vampyressa (Chiroptera)	X		14	MP	Porter & Baker, 2004
Pteronotus (Chiroptera)	X		15	MP	Simmons & Conway, 2001
Callitrichidae (Primates)	X		16	ML	Sena *et al.,* 2002
Sanguinus (Primates)	X		23	MP	Jacobs *et al.,* 1999
Alouatta (Primates)	X		6	MP	Cortéz *et al.,* 2002
Ateles (Primates)		X	22	MP	Dubach & Collins, 2000
Leopardus tigrinus (Felidae)		X	9	Distances	Johnson *et al.,* 1999

Table 4. Twenty general area cladograms fitted to the data set. Hypotheses' source and the acronyms used to facility the discussions are presented. Hypotheses denoted with a number are the product of resolve in all the possibilities, the politomic nodes presented in the original hypothesis, since the programs require it.

Acronym	**Author/year**	**General Area Cladogram**
H1	Prum (1988) And Harvey & Hall (2002) Riodinidae	(GU,((RO,(BE,PA)),(IM,(IN,NP))))
H2	Cracraft&prum (1988) 1	(SD,((CH,CA),(GU,((BE,PA),(IM,(IN,NP))))))
H3	Cracraft&prum (1988) 2	((GU,((SD,(BE,PA)),(IM,(IN,NP)))),(CH,CA))
H4	da Silva & Oren (1996) 1	(((BE,PA),GU),((IN,RO),(IM,NP)))
H5	da Silva & Oren (1996) 2	((GU,(BE,PA)),(RO,(IN,(IM,NP))))
H6	da Silva & Oren (1996) 3	((GU,(BE,PA)),(RO,(IM,(IN,NP))))
H7	da Silva & Oren (1996) 4	((GU,(BE,PA)),(RO,(NP,(IM,IN))))
H8	Bates et al. (1998)	((((GU,(IM,(NP,IN))),(BE,(PA2,(PA1,RO)))),SD),(CA,CH))
H9	Patton et al. (2000) 1	((GU,(IM,(IN,NP))),((RO,BE),PA))
H10	Patton et al. (2000) 2	((GU,(IM,(IN,NP))),(RO,(BE,PA)))
H11	Patton et al. (2000) 3	((GU,(IM,(IN,NP))),(BE,(RO,PA)))
H12	Ron (2000) Reptiles	((PA,(RO,(BE,GU))),(IN,NP))
H13	Ron (2000) "Amphibia"	(BE,(RO,(GU,(IN,NP))))
H14	Amorin (2001)	(((IM,(GU,BE)),(NP,IN)),(PA,(SD,CAT)))
H15	Harvey & Hall (2002) combined	((RO,(BE,PA)),(GU,(IM,(IN,NP))))
H16	Marks (2002) 1	((GU,(IN,(NP,(CH,(CA,IM))))),(RO,(PA,SD)))
H17	Marks (2002) 2	(RO,((GU,(IN,(NP,(CH,(CA,IM))))),(PA,SD)))
H18	Racheli & Racheli (2003)	((IM,(NP,IN)),(GU,((BE,PA2),(PA1,RO))))
H19	Racheli & Racheli (2004) 1	((GU,(BE,(PA2,(RO,PA1)))),(IM,(IN,NP)))
H20	Racheli & Racheli (2004) 2	(GU,((BE,(PA2,(RO,PA1))),(IM,(IN,NP))))

Table 5. Fit of the 20 hypotheses previously proposed to the Amazonia under the three explicit models of cost offered in TREEFITTER to each data set partition. The fit was evaluated by calculation the p-value as the number of randomizations with an equal or lower cost than the observed; the statistical significance was tested against 1000 times permutation of organisms and areas terminals. For simplicity NS (non significant) S (significant), all cases we used 0.05 as the limit of the significance level.

* Hypothesis with Para area divided
** Significant value at 0,05 level
*** Significant value <=0,01

Hypothesis	**Random cost<=Obs**								
	MV			**Reconciliation**			**Ronquist**		
	all data set	haplotypes	species	all data set	haplotypes	species	all data set	haplotypes	species
H1	NS	NS	NS	NS	NS	NS	S***	S***	S**
H2	NS	NS	NS	NS	NS	NS	S***	S***	S***
H3	NS	NS	NS	NS	NS	NS	S***	S***	S***
H4	NS	NS	NS	NS	NS	NS	S**	S***	NS
H5	NS	NS	NS	NS	NS	NS	S***	S***	NS
H6	NS	NS	NS	NS	NS	NS	S***	S***	S***
H7	NS	NS	NS	NS	NS	NS	S***	S***	NS
H8*	NS	NS	NS	NS	NS	NS	S***	S***	S***
H9	NS	NS	NS	NS	NS	NS	S***	S***	S**
H10	NS	NS	NS	NS	NS	NS	S***	S***	S**
H11	NS	NS	NS	NS	NS	NS	S***	S***	S***
H12	NS	NS	NS	NS	NS	NS	S***	S***	S**
H13	NS	NS	NS	NS	NS	NS	S***	S***	S***
H14	NS	NS	NS	NS	NS	NS	S***	S***	S***
H15	NS	NS	NS	NS	NS	NS	S***	S***	S**
H16	NS	NS	NS	NS	NS	NS	S***	S***	S***
H17	NS	NS	NS	NS	NS	NS	S***	S***	S***
H18*	NS	NS	NS	NS	NS	NS	S***	S***	S**
H19*	NS	NS	NS	NS	NS	NS	S***	S***	S***
H20*	NS	NS	NS	NS	NS	NS	S***	S***	S***

Table 6. Fit of the 20 previously proposed hypotheses to each of the Amazonia data set partitions. The fit was evaluated as the number of vicariance events predicted by the hypotheses; the statistical significance of the events recovered was tested against 1000 permutated terminals in the organism phylogenies, calculating the p-value. For simplicity NS (no significant) S (significant), all cases we used 0.05 as the limit of the significance level.

* Hypothesis with Para area divided
** Significant value = 0,05
*** Significant value <=0,01

Hypothesis	**Number of vicariance events**			**Vicariance Events Random>=Obs**		
	all data set	**haplotypes**	**species**	**all data set**	**haplotypes**	**species**
H1	136	33	106	NS	NS	NS
H2	203	39	168	S***	S**	S***
H3	206	40	171	S***	S**	S***
H4	135	31	109	NS	NS	NS
H5	134	31	108	NS	NS	NS
H6	135	31	109	NS	NS	NS
H7	134	31	108	NS	NS	NS
H8*	216	41	172	NS	S**	NS
H9	129	30	102	NS	NS	NS
H10	129	30	102	NS	NS	NS
H11	130	30	103	NS	NS	NS
H12	131	33	102	NS	NS	NS
H13	108	23	87	NS	NS	NS
H14	152	28	128	S**	NS	S**
H15	129	30	102	NS	NS	NS
H16	209	43	171	NS	NS	NS
H17	207	42	172	NS	NS	NS
H18*	148	30	114	S***	NS	S***
H19*	147	30	113	S***	NS	S***
H20*	142	30	108	NS	S**	NS

Table 7. Fit of each model to the data set give 1000 randomizations of pterminals. The fit was obtained by calculation of the p-value. For simplicity NS (non significant) S (significant), all cases we used 0.05 as the limit of the significance level.

** Significant value = 0,05
*** Significant value <=0,01

Partition	**Permutation**	**Random cost<=Observ**		
		mv	**reconciliation**	**Ronquist**
All data	pterm	NS	NS	S***
Species set	pterm	NS	NS	S***
Haplotypes set	pterm	NS	NS	S***

Table 8. Evaluation of the vicariance events recovered by the cladograms of each partition. The fit of the cladograms to the data set was calculated as the number of randomizations with a higher number of vicariance events than the found by the cladograms. For simplicity NS (non-significant) S (significant), all cases we used 0.05 as the limit of the significance level.

** Significant value = 0,05
*** Significant value <=0,01

Hypothesis	**Number of vicariance events**			**Vicariance Events Random>=Obs**		
	all data set	**haplotypes**	**species**	**all data set**	**haplotypes**	**species**
H tree 1	95	35	66	S***	S***	NS
H tree 2	95	35	NA	S***	S***	NA
H tree 3	95	35	NA	S**	S***	NA

Table 9. Nodes shared with general pattern after the exclusion of the taxa found to be the main promoters of the general pattern.

Group eliminated	Nodes shared	Codivergence	Duplication	Switches	Sortings	Total events
Xiphorhynchus	3	4	7	11	6	28
Amazona	4	3	3	2	2	10
Mico	5	1	3	5	0	9
Juditha	6	4	2	1	1	8
Pteroglossus bitorquatus group	6	4	0	10	3	17
Morphinae	6	3	6	11	5	25
Charis gynea	6	3	1	19	2	25
Pteroglossus viridis group	7	1	0	2	0	3
all eight taxa	3					
all groups except these taxa	5					

Table 10. Number of nodes shared by the previous hypotheses and with the patterns obtained from this study. The value was rescaled by the smallest number of nodes present in each pair of trees. The general pattern is denoted as GAC.

	h1	h2	h3	h4	h5	h6	h7	h8	h9	h10	h11	h12	h13	h14	h15	h16	h17	h18	h19	h20
h2	0,33																			
h3	0,50	0,63																		
h4	0,33	0,17	0																	
h5	0,50	0,17	0	0,83																
h6	0,67	0,33	0,17	0,67	0,83															
h7	0,50	0,17	0	0,67	0,83	0,83														
h8	0,33	0,38	0,38	0	0,17	0,33	0,17													
h9	0,67	0,33	0,33	0,17	0,33	0,50	0,33	0,50												
h10	0,83	0,33	0,50	0,33	0,50	0,67	0,50	0,50	0,83											
h11	0,67	0,33	0,33	0,17	0,33	0,50	0,33	0,50	0,83	0,83										
h12	0	0	0	0	0	0	0	0	0	0	0									
h13	0	0	0	0	0	0	0	0	0	0	0	0,25								
h14	0,17	0,14	0,14	0	0	0,17	0	0,14	0,17	0,17	0,17	0,40	0,25							
h15	0,83	0,33	0,50	0,33	0,50	0,67	0,50	0,50	0,83	1,00	0,83	0	0	0,17						
h16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0					
h17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,88				
h18	0,33	0,29	0,29	0	0,17	0,33	0,17	0,57	0,33	0,33	0,33	0	0	0,14	0,33	0	0			
h19	0,33	0,29	0,29	0	0,17	0,33	0,17	0,71	0,33	0,33	0,33	0	0	0,14	0,33	0	0	0,86		
h20	0,33	0,29	0,29	0	0,17	0,33	0,17	0,71	0,33	0,33	0,33	0	0	0,14	0,33	0	0	0,71	0,86	
GAC	0,17	0	0	0	0	0,17	0	0,20	0,17	0,17	0,17	0,20	0,25	0	0,17	0	0	0,14	0,14	0,14
Haplotypes	0,17	0,25	0,25	0	0	0,17	0	0,30	0,17	0,17	0,17	0,20	0,25	0,14	0,17	0	0	0,14	0,14	0,14
Especies	0	0	0	0	0	0	0	0,20	0	0	0	0	0	0	0	0	0	0,14	0,14	0,14

Figures Caption

Figure 1.
Pie charts showing the distribution of the data set. A. Taxonomic composition given in number of terminals. B. Number of terminals distributed in each of Haffer’s Amazonian areas.

Figure 2.
Dispersal/vicariance rate for each group of taxa used in the analyses.

Figure 3.
Most frequents dispersal routes between single areas. The thickness of the arrows is proportional to the number of groups that support the route.

Figure 4.
General area cladograms produced under Ronquist’s model of costs and using the whole data set.

Figure 5.
General area cladograms produced under Ronquist’s model of costs and using haplotypes data set.

Figure 6.
General area cladogram produced under Ronquist’s model of cost and using species data set.

Figure 7.
Strict consensus of the eleven most parsimonious trees found by PAE. The nodes recovered are the most common within previous hypothesis.

Figure 1A.

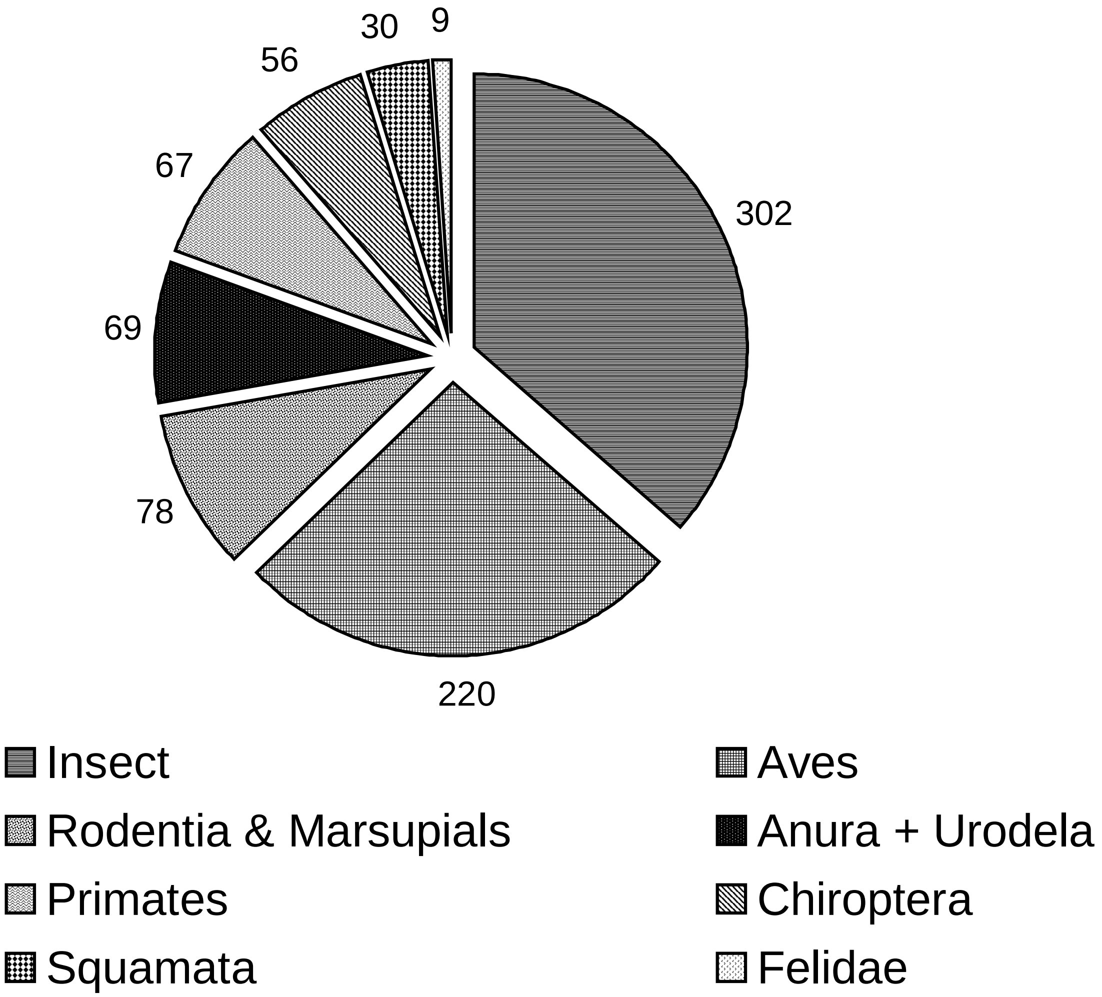
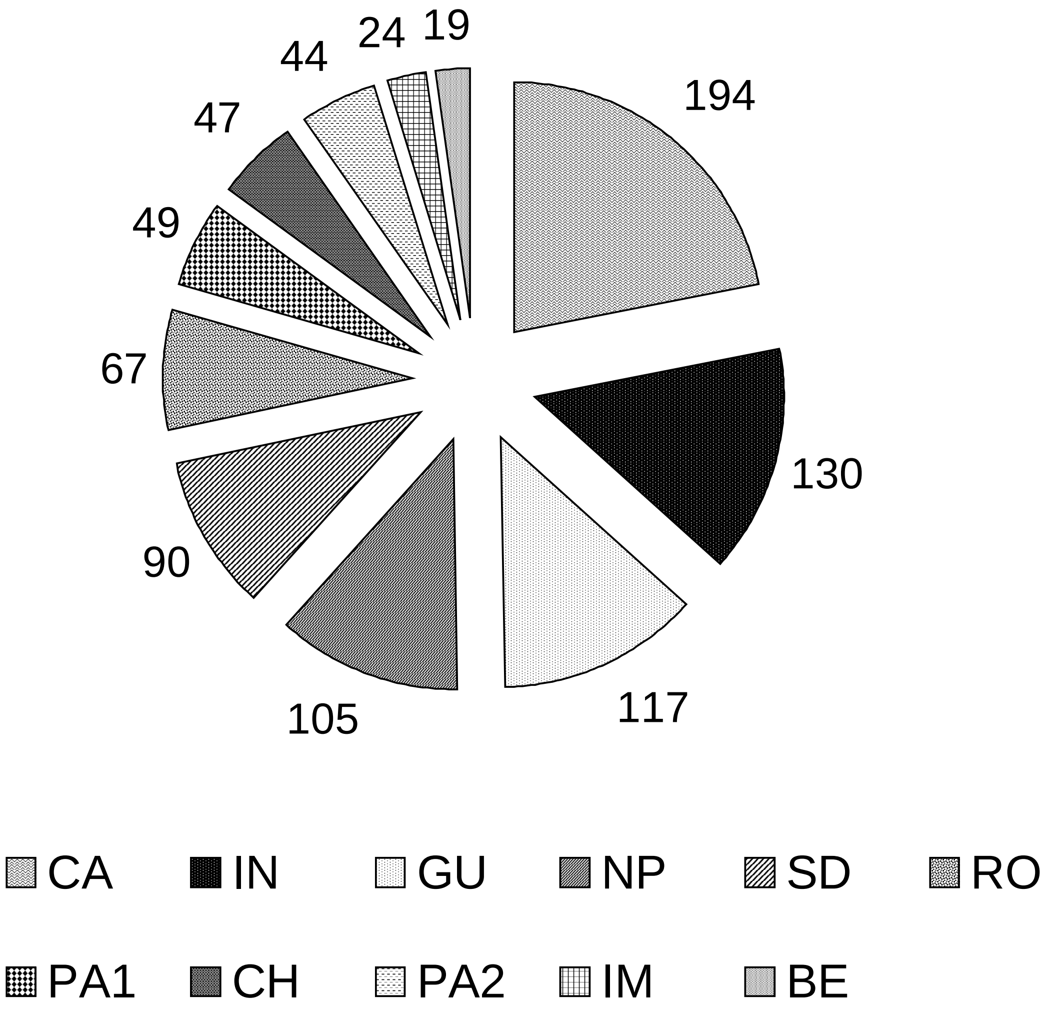

302
220
78
69
67
56
30
9
Insect
Aves
Rodentia & Marsupials
Anura + Urodela
Primates
Chiroptera
Squamata
Felidae

Figure 1B.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117
105
90
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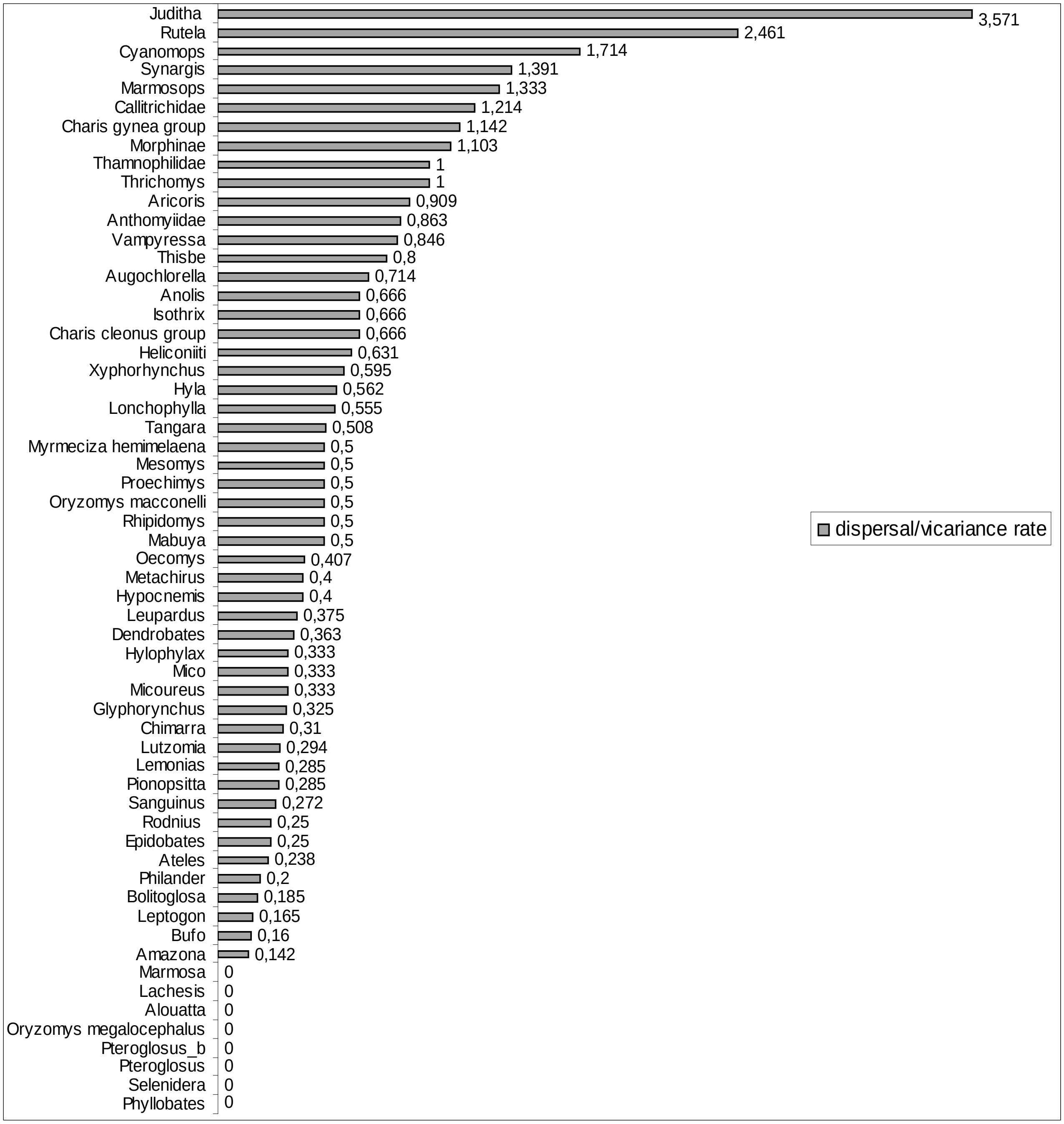
CA
IN
GU
NP
SD
RO
PA1
CH
PA2
IM
BE

Figure 2.


Juditha 3,571
Rutela 2,461
Cyanomops 1,714
Synargis 1,391
Marmosops 1,333
Callitrichidae 1,214
Charis gynea group 1,142
Morphinae 1,103
Thamnophilidae 1
Thrichomys 1
Aricoris 0,909
Anthomyiidae 0,863
Vampyressa 0,846
Thisbe 0,8
Augochlorella 0,714
Anolis 0,666
Isothrix 0,666
Charis cleonus group 0,666
Heliconiiti 0,631
Xyphorhynchus 0,595
Hyla 0,562
Lonchophylla 0,555
Tangara 0,508
Myrmeciza hemimelaena 0,5
Mesomys 0,5
Proechimys 0,5
Oryzomys macconelli 0,5
Rhipidomys 0,5
Mabuya 0,5
Oecomys 0,407
Metachirus 0,4
Hypocnemis 0,4
Leupardus 0,375
Dendrobates 0,363
Hylophylax 0,333
Mico 0,333
Micoureus 0,333
Glyphorynchus 0,325
Chimarra 0,31
Lutzomia 0,294
Lemonias 0,285
Pionopsitta 0,285
Sanguinus 0,272
Rodnius 0,25
Epidobates 0,25
Ateles 0,238
Philander 0,2
Bolitoglosa 0,185
Leptogon 0,165
Bufo 0,16
Amazona 0,142
Marmosa 0
Lachesis 0
Alouatta 0
Oryzomys megalocephalus 0
Pteroglosus_b 0
Pteroglosus 0
Selenidera 0
Phyllobates 0
dispersal/vicariance rate

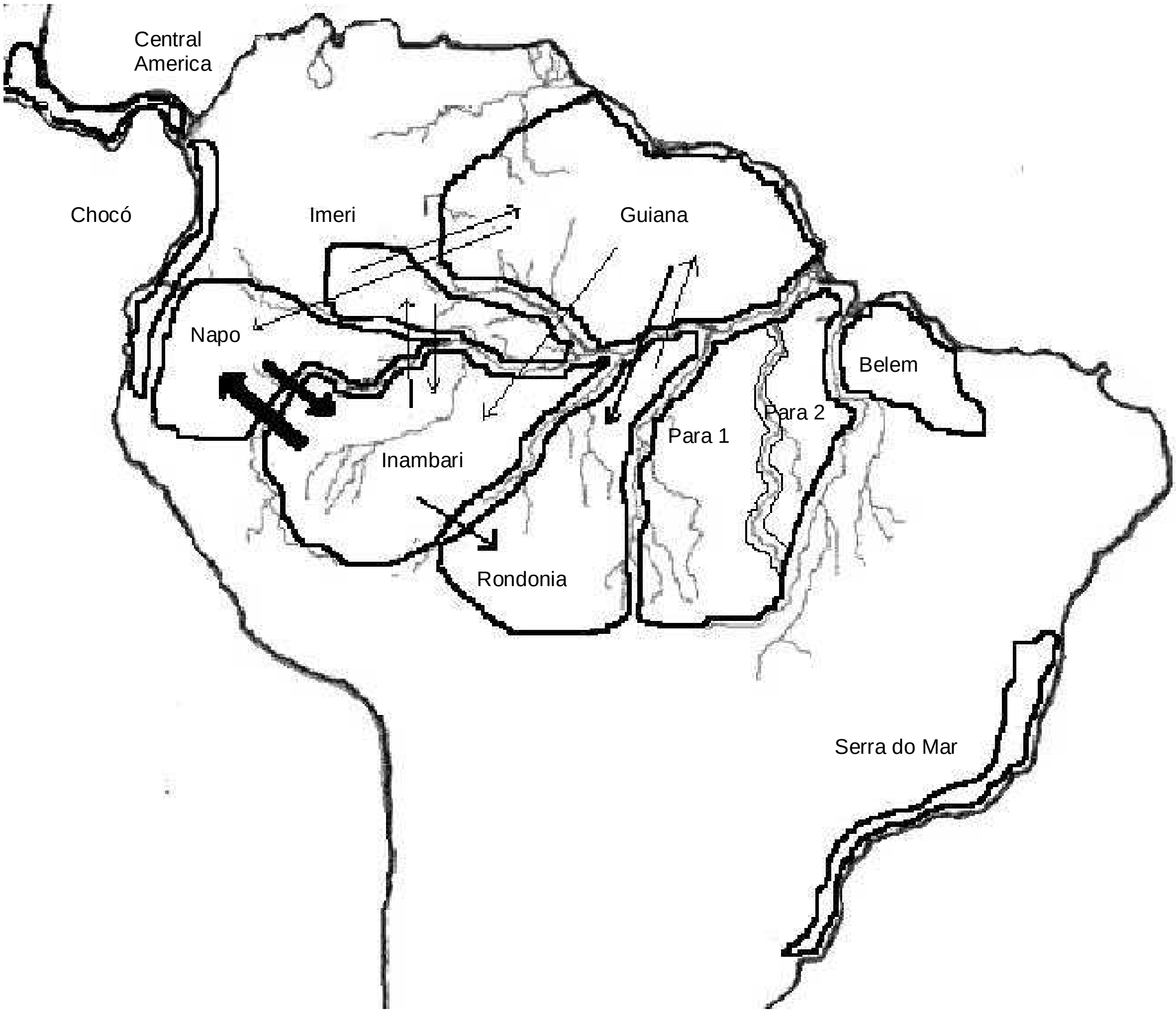
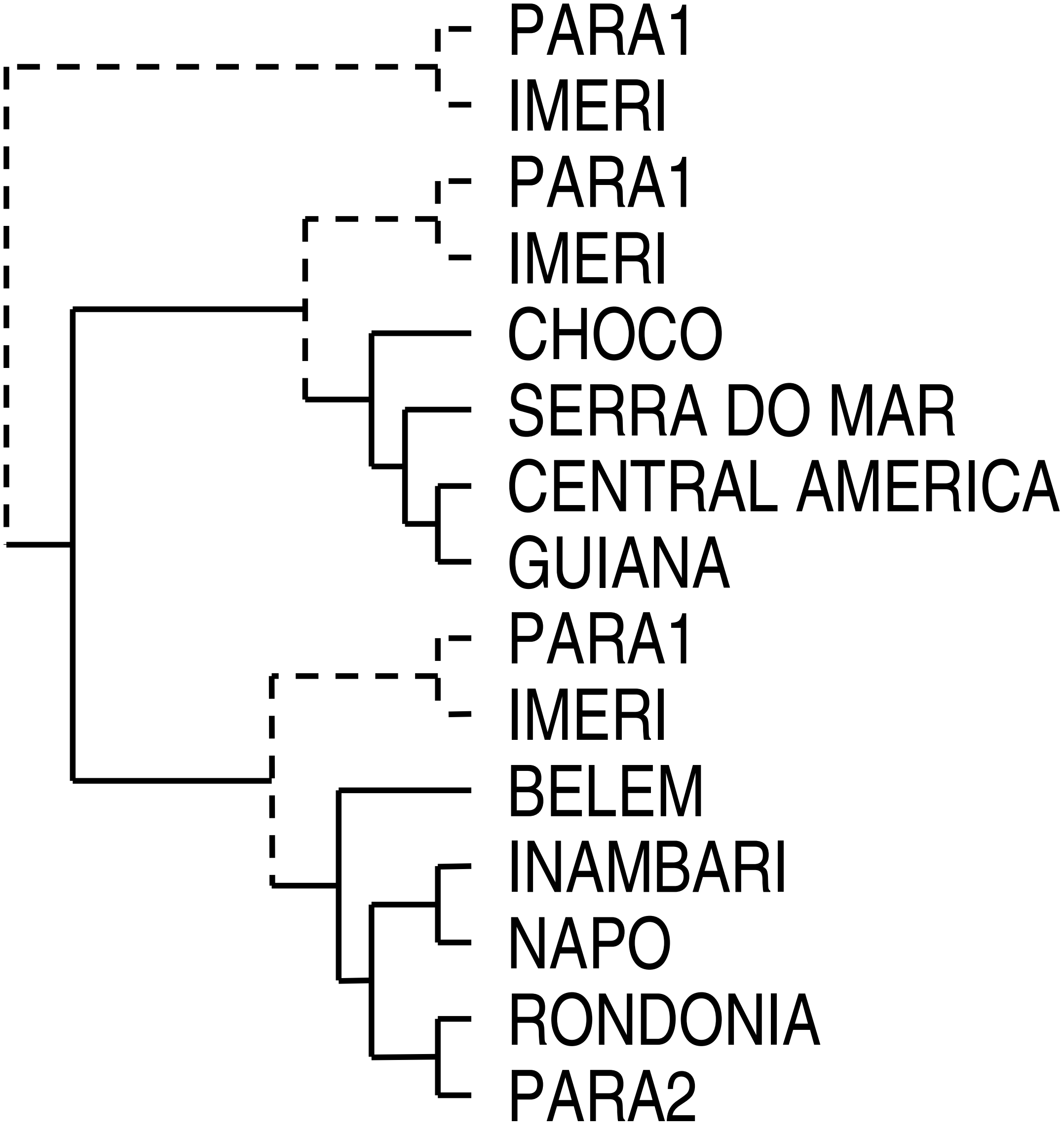

Central
America
Chocó
Imeri
Guiana
Napo
Belem
Para 2
Para 1
Inambari
Rondonia
Serra do Mar

Figure 3.

Figure 4.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IMERI
PARA1
IMERI
CHOCO
SERRA DO MAR
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GUIANA
PARA1
IMERI
BELEM
INAMBARI
NAPO
RONDONIA
PARA2

Figure 5.

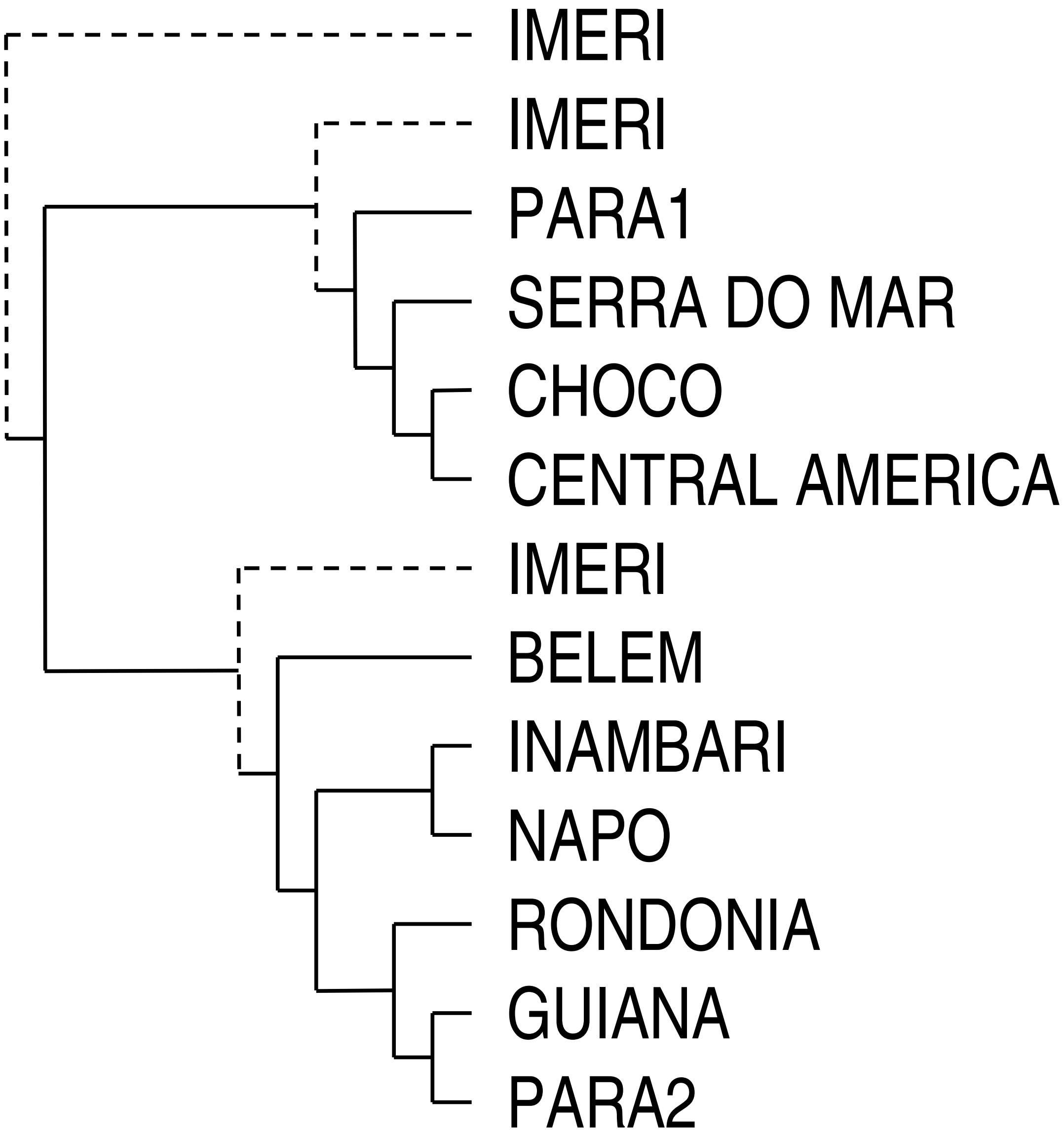

IMERI
IMERI
PARA1
SERRA DO MAR
CHOCO
CENTRAL AMERICA
IMERI
BELEM
INAMBARI
NAPO
RONDONIA
GUIANA
PARA2

Figure 6.

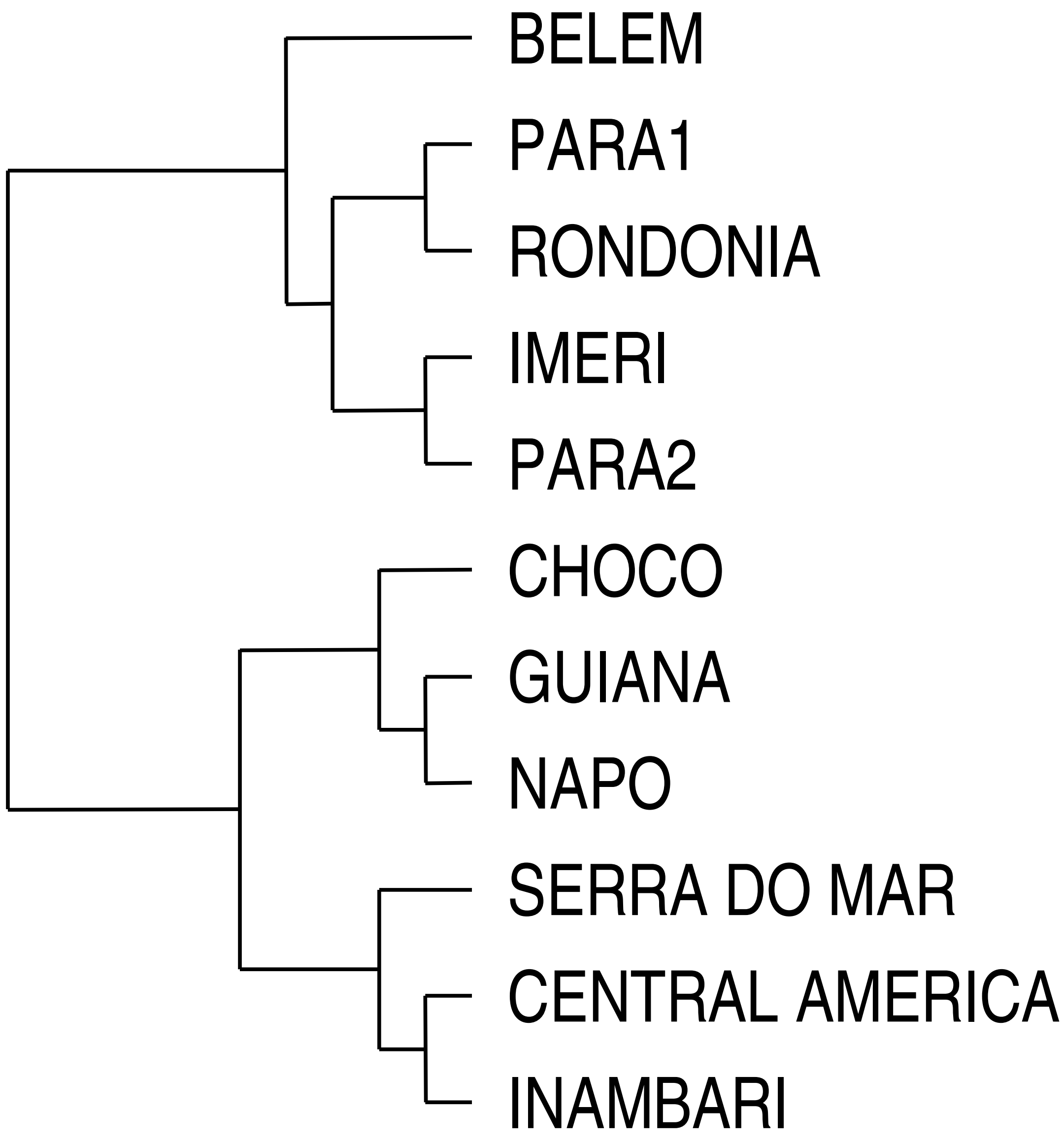
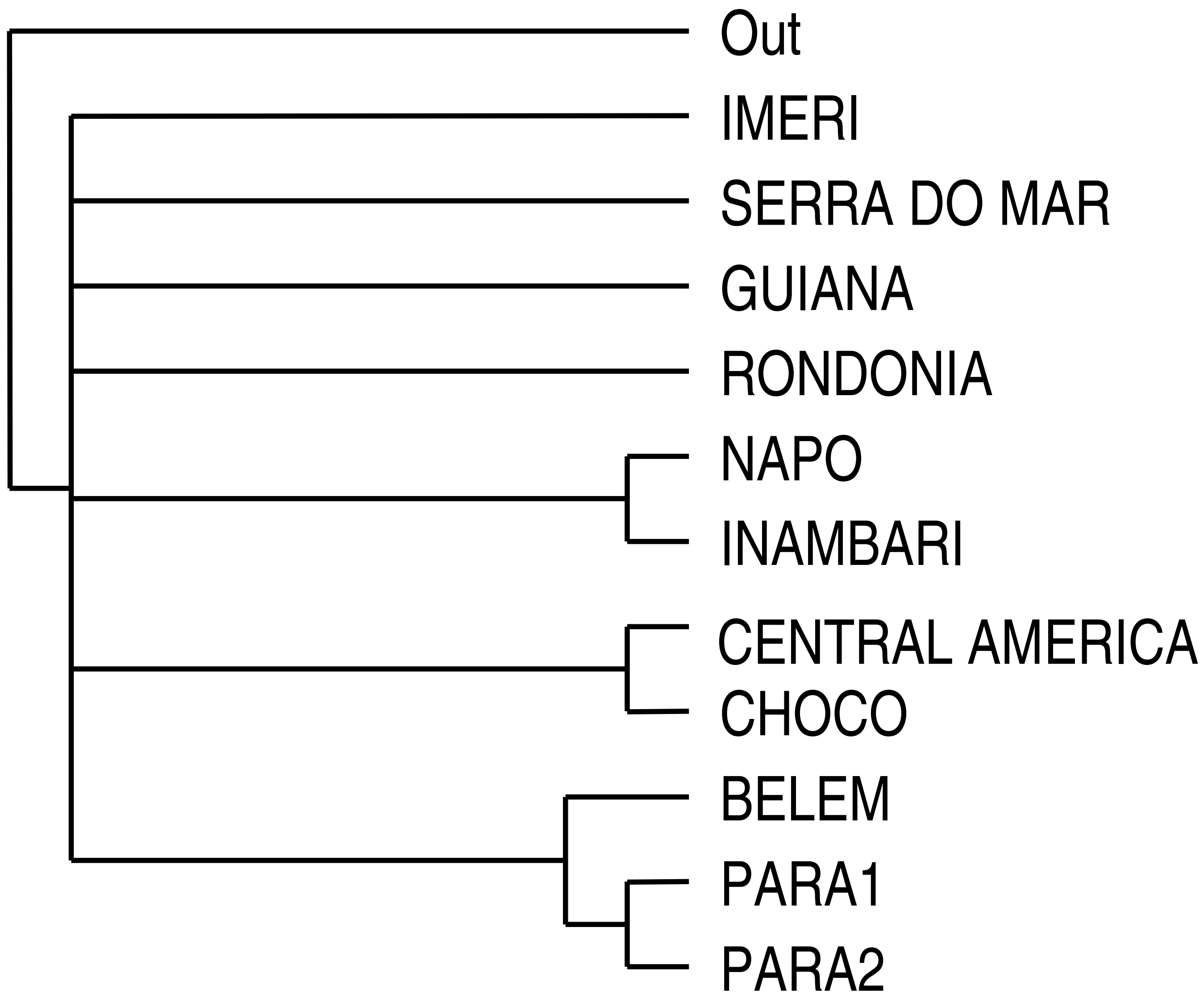

BELEM
PARA1
RONDONIA
IMERI
PARA2
CHOCO
GUIANA
NAPO
SERRA DO MAR
CENTRAL AMERICA
INAMBARI

Figure 7.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SERRA DO MAR
GUIANA
RONDONIA
NAPO
INAMBARI
CENTRAL AMERICA
CHOCO
BELEM
PARA1
PARA2