Amazonian relationships:
An example of a complex area and a complex problem

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Amazonia is a rich and diverse ecosystem. It comprises the Amazon basin and the lowlands of southern Colombia, southern Venezuela, eastern Ecuador, northern and eastern Peru, 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 its biogeographic history is recent (Amorim 2001). Just a few years ago the first quantitative approaches using phylogenetic hypotheses were generated. Cracraft & Prum's (1988) study gave the first steps to resolve the question about Amazonia's origin, but Amorim's (2001) work was the first to challenge the traditional view of Amazonia as a single unit (Cabrera & Willink 1973, Hooghiemstra 1997).

The earliest attempts to reconstruct the Amazonian biogeographic history were non-quantitative approaches based on narrative descriptions of those events that contributed to today's diversity of species. These are known as the Amazonian diversification hypotheses (Wallace 1852, Haffer 1969, for a revision see Haffer 1997 and Nores 2000). 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 for two main reasons. First, because they are based on explicit or implicit *a priori* assumptions (Amorim 2001), and secondly 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 analyzes 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) was 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 (Cracraft, 1991) to generate their hypotheses of area relationships. Amorim (2001) and Hall & Harvey (2002) have proposed the latest and most recent area relationship hypotheses using phylogenetic and distributional data, using "cladistic biogeography" and BPA, respectively.

In spite of all these efforts, the origin and the biogeographic history of the Amazonian diversity is still in 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). From the biogeographic framework, however, these area relationship hypotheses have failed to document explicit historical events, like those events resulting from cladogenetic events, since seven of the 16 area cladograms were developed without phylogenetic information of the Amazonian taxa (Table 1). For example, Racheli (2004) has criticized the use of the Matrix Parsimony Representation technique used by Hall & Harvey (2002) to produce their combined area cladogram, questioning the use of the competing topologies as source data. Additionally most of these hypotheses have been formulated from a single taxonomic group. It is obvious that the history of the area had to have affected all the Amazonian taxa that coexisted over the region, producing their speciation, extinction, or dispersion pattern(s).

The diversification hypotheses:
The non-quantitative approaches

There have been proposed more than 16 diversification hypotheses (Nores 2000), these hypotheses formulated a causation perspective for the Amazonian diversity - lacking any approach to quantitative analysis and therefore these hypotheses have had a strong narrative tradition. Nores (2000) presented an extensive review of these hypotheses. One of the first to highlight 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".

Table 1. Main hypotheses of area relationship proposed for Amazonia. For each pattern the author's name, taxa used, method and explanation suggested are shown. Be, Belem; BPA, Brooks parsimony analysis; CAT, Caatinga; CB, "cladistic biogeography", no method specified; GU, Guiana; IM, Imeri; IN, Inambari; IV, implicit vicariance; MRP, matrix parsimony representation; NP, Napo; PA, Para; PAE, parsimony analysis of endemicity; PH, phylogeography; RO, Rondonia; SD, Serra do Mar.

Author	Taxa	Method	Area cladogram	Process invoked
Prum (1988)	Birds	BPA	((GU,(PA, BE)),(RO, IM, IN, NP))	IV*
Prum (1988)	Birds	BPA	(GU,((RO,(BE,PA)),(IM,(IN,NP))))	IV*
Cracraft & Prum (1988)	Birds	BPA	(SD,((CH,CA),(GU,((SD,BE_PA),(IM,(IN,NP))))))	Vicariance
da Silva & Oren (1996)	Primates	PAE	(GU, (PA, BE)), ((RO, IN1), (IM, IN2, NP))	Vicariance
Bates et al. (1998)	Birds	PAE	(GU, (IM, (IN, NP)), (BE, (PA1, (PA2, (RO))))	IV*
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)	Insects and primates	CB	(((IM,(GU,BE)),(NP,IN)),(PA,(SD,CAT)))	Vicariance
Hall & Harvey (2002)	Butterflies	PH	(GU,((RO,(BE,PA)),(IM,(IN,NP))))	Vicariance
Hall & Harvey (2002)	Vertebrates and butterflies	MRP	((RO,(BE,PA)),(GU,(IM,(IN,NP))))	Vicariance
Marks (2002)	Birds	PH	((GU,(IN,(NP,(CH,(CA,IM))))),(RO,(PA,SD)))	none explicit**
Marks (2002)	Birds	PH	(RO,((GU,(IN,(NP,(CH,(CA,IM))))),(PA,SD)))	none explicit**
Racheli & Racheli (2003)	Birds	PAE	((IM,(NP,IN)),(GU,((BE,PA2),(PA1,RO))))	IV*
Racheli & Racheli (2004)	Butterflies	PAE	((GU,(BE,(PA2,(RO,PA1)))),(IM,(IN,NP)))	IV*
Racheli & Racheli (2004)	Butterflies	PAE	(GU,((BE,(PA2,(RO,PA1))),(IM,(IN,NP))))	IV*

* 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 product basically of dispersal, but there is no explicit reference about the process involved.

The principal argument is that the current biodiversity is the result of the vicariant events depicted from the formation of the Amazon River and its tributaries. All of the diversification hypotheses have presented a vicariance perspective of the Amazonian history; clearly the speciation is given by allopatric events caused by a variety of barriers to 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 diversification hypotheses: the Pleistocene refuge hypothesis (Haffer 1969), the riverine hypothesis (Wallace 1852, Sick 1967), and the gradient hypothesis (Endler 1977).

The quantitative approaches

Quantitative analyses gained ground during the last few years since the impact and acceptance of the phylogeography research program (Lougheed et al. 1999, Ditchfield 2000, Patton et al. 2000, Marks et al. 2002, Costa 2003). Population genetics analyses, undoubtedly, have 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 analyses have been developed to answer the speciation history of one or two particular taxonomic groups and not to explore the relationship between the areas.

Under an explicit biogeography framework, the area relationship for the Amazonia has been reconstructed eleven times (Table 1), but since some authors presented more than one, there are 16 proposed area cladograms. All these biogeographic studies stated that the history of Amazonia was driven mainly by vicariance events that have produced a hierarchical pattern (Moritz et al. 2000, Ron 2000, Amorim 2001, Bates 2001, Hall & Harvey 2002). Ron (2000) and Hall & Harvey (2002), based on the congruence between the history of the areas 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. The Guiana position, however, continues to be uncertain, its relationship with the so-called upper (Imeri and Napo) and lower (Inambari, Rondonia, Para, and Belem) Amazonia is inconsistent among the hypotheses and sometimes appears to be an independent unit. Additionally, 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, and several 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 accepted for some groups of animals and within the neontologists, to explain the diversification patterns (Brower 1994, Hall & Harvey 2002). One major problem that involves all of the above mentioned hypotheses of area relationship is that they were formulated to account for events of the late Pleistocene period, leaving out earlier periods (Cretaceous or late Tertiary) which molecular phylogenies of frogs, lizards, birds, and mammals suggest to be a critical time for the main events of speciation (Moritz et al. 2000, Ron 2000).

The most important contributions about the origin of the Amazonian biota probably 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 to be common within the Amazonian birds (Marks et al. 2002, p. 164). Costa's (2003) analysis of small mammals in Amazonia and the Brazilian Atlantic forest showed that these two regions are not exclusive in their fauna composition, and that the genetic similarity exhibited between the mammals in 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 repeats when new taxa are studied, and how wrong was the idea of two different units (provinces or domains) that now appear 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 general area cladogram for the history 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 birds and mammals, they have produced new insights about the origin of the Amazonian biota and have placed new challenges to the biogeography research program. Given this scenario if we want to understand the biotic diversity of the Amazonia, and the reasons to explain why it supports that diversity we have to search for a reconstruction of the Amazonian history using all the distributional and phylogenetic information available, using an explicit cladistic method to account all the possible events that have taken place in Amazonia.

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