CONSERVING AMAZONIA: A PHYLOGENETIC APPROACH
Conservando la biodiversidad de la Amazonia: una aproximación filogenética

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RESUMEN

TITULO: CONSERVANDO LA BIODIVERSIDAD DE LA AMAZONIA: UNA APROXIMACIÓN FILOGENÉTICA.*

FEDERICO LÓPEZ OSORIO**

PALABRAS CLAVE: CONSERVACIÓN, AMAZONIA, PARTICULARIDAD EVOLUTIVA, JERARQUÍA DE ÁREAS, ENDEMISMO, FILOGENIA, BIOGEOGRAFÍA

La Amazonia es un bosque tropical lluvioso gravemente amenazado, por lo que requiere ser estudiado desde diferentes puntos de vista. En este trabajo nuestro objetivo principal fue establecer prioridades de conservación para las áreas de endemismo de la Amazonia utilizando medidas de particularidad evolutiva. Consideramos dos conjuntos de áreas de endemismo. El primero consistió de ocho áreas grandes que han sido usadas tradicionalmente en estudios biogeográficos, dichas áreas son: Belém, Tapajós, Xingú, Guyana, Rondônia, Imeri, Inambari y Napo. El segundo conjunto consistió de 16 áreas que corresponden a subdivisiones de las áreas grandes. Reunimos 50 filogenias de la literatura y 1715 registros distribucionales. Establecimos prioridades de conservación para las áreas de endemismo mencionadas anteriormente utilizando medidas de particularidad evolutiva basadas en el conteo de nodos y contrastamos con prioridades basadas en riqueza y endemicidad de especies. En el primer análisis, identificamos a Guyana como el área más importante para conservación, seguida de Inambari y Napo. En el segundo análisis, las áreas más importantes fueron: una subdivisión de Guyana que corresponde a Guyana y al oriente y nor-oriente de los estados de Roraima y Amazonas en Brasil, respectivamente; una subdivisión de Inambari que corresponde al nor-occidente del estado de Amazonas en Brasil; y finalmente, otra subdivisión de Guyana que corresponde a Suriname, Guyana Francesa, y el estado de Amapá en Brasil. Las jerarquías de áreas según particularidad evolutiva estuvieron directamente correlacionadas con aquellas basadas en riqueza y endemicidad de especies. Las estrategias actuales de conservación en la Amazonia, aunque diseñadas de acuerdo a otros criterios no filogenéticos, parecen estar enfocándose en las áreas más importantes para conservación según nuestro estudio.

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ABSTRACT

TITLE: CONSERVING AMAZONIA: A PHYLOGENETIC APPROACH

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KEYWORDS: EVOLUTIONARY DISTINCTIVENESS, AMAZONIA, CONSERVATION, PRIORITIZATION RANKING, ENDEMISM, BIOGEOGRAPHY

Amazonia is a heavily threatened rainforest that encompasses a major proportion of Earth’s biological diversity; therefore, conservation of Amazonia demands immediate study, ideally, from a multiplicity of points of view. In this study, our main goal was to establish conservation priorities for Amazonia's areas of endemism based on measures of evolutionary distinctiveness. We considered two previously suggested approaches to areas of endemism in Amazonia. The first approach consisted of eight large areas traditionally used in biogeographical studies: Belém, Tapajós, Xingu, Guiana, Rondônia, Imeri, Inambari, and Napo. The second approach comprised sixteen smaller areas congruent with the larger areas. We assembled a data set of fifty phylogenies representing various taxonomic groups and 1715 distributional records. We identified priorities for the aforementioned areas of endemism according to node-based metrics of evolutionary distinctiveness and contrasted these results with priorities based on raw species richness and species endemicity. In the first analysis, we identified Guiana as the most important area for conservation, followed by Inambari. The remaining areas in this first ranking decreased by a half (e.g. Napo) or less for all indexes' values. In the second analysis, a subdivision of Guiana corresponding to Guyana, and the east and north-east of the Brazilian states of Roraima and Amazonas respectively, was at the top of the ranking; followed by a subdivision of Inambari corresponding to the north-west of the Brazilian state of Amazonas, at the left bank of Rio Juruá; the third position was occupied by yet another subdivision of Guiana corresponding to Suriname, French Guiana, and the Brazilian state of Amapá. The distinctiveness-based rankings were directly correlated with those based on species richness and species endemicity. Current conservation strategies in Amazonia, although relying on many other criteria apart from phylogeny, are focusing on the most important areas for conservation identified in this study.

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* BACHELOR'S THESIS

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INTRODUCTION

A BRIEF OVERVIEW OF AMAZONIA'S BIODIVERSITY AND ITS CONSERVATION VALUE

Amazonia is the largest Tropical rainforest on Earth. The Amazon basin harbors a highly diverse biota distributed from the Northern Andes in the west to the Northern Brazil Atlantic coast in the east, and extends to the north and south onto the Guianan and Brazilian shields respectively (Haffer 1969). According to recent reports, the numbers of species inhabiting Amazonia are at least one million insects, 40.000 plants, 3000 fishes, 1294 birds, 427 mammals, 427 amphibians, and 378 reptiles (WWF 2003; Silva et al. 2005a). Amazonian species are not randomly distributed. Previous studies have identified congruent distributional limits (i.e. areas of endemism) for birds (Haffer 1978; Cracraft 1985; Bates et al. 1998; Silva et al. 2002; Silva et al. 2005a), mammals (Silva & Oren 1996; Pires-Costa et al. 2000), frogs (Ron 2000), butterflies (Brown 1979; Hall & Harvey 2002), and taxa from various taxonomic groups in a combined analysis (Kress et al. 1998).

Amazonia's species diversity and patterns of endemism have been critically endangered by rampant deforestation (Laurance et al. 2001; Laurance et al. 2004; Fearnside 2005; Laurance 2007). From 1990 to 2003 the rate of forest clearance ranged from 1.1 to 2.9 million ha per year, where the highest peak was observed in 1995 (Laurance 1998; Laurance et al. 2004). Currently, the rate of deforestation is roughly 1.1 million ha per year (INPE 2007; Fearnside 2008); however, deforestation in Amazonia has been considerably underestimated (Nepstad et al.1999). Predominantly, the causes of deforestation in Amazonia have been large-scale development projects, industrial logging, road networks, extensive cattle ranching, high rates of population growth, and fires (Nepstad et al. 1999; Cochrane 2001; Laurance & Williamson 2001; Laurance et al 2001; Fearnside 2005; Kirby et al. 2006; Laurance 2007; Laurance & Luizão 2007). Another preeminent motive of deforestation is the globally increasing demand for biofuels; land in Amazonia has been altered due to soy-farming and oil palm plantations for ethanol production (Bush & Lovejoy 2007; Laurance 2007). Altogether, the most important consequences of deforestation in Amazonia have been substantial loss of biodiversity, habitat disruption, and global warming (Sioli 1985; Bush 1996; Laurance et al. 2001; Fearnside 2005; Chazdon et al. 2009). Consequently, preserving Amazonia is paramount in conservation planning.

PHYLOGENETICS AND BIODIVERSITY CONSERVATION

To guide conservation efforts, an essential issue is how biodiversity is measured (Witting & Loeschcke 1995). Purvis and Hector (2000) categorized commonly used measures of biodiversity as follows: 1) number of species in a site or habitat (i.e. species richness); 2) distributional evenness of individuals among species; and 3) estimates of difference (e.g. molecular, morphological) among species. The basic problem with species richness and evenness is that they are driven by species which are common, widespread, and therefore less vulnerable (Lamoreux et al. 2006; Brooks et al. 2006). Using phylogenies as a general frame, the third category has been approached for conservation purposes from two perspectives, evolutionary distinctiveness and phylogenetic diversity.

Evolutionary distinctiveness (ED henceforth) refers to species-specific measures developed to assign scores of evolutionary value according to tree topology only (e.g. May 1990; Vane-Wright et al. 1991; Williams et al. 1991), or topology and branch lengths (e.g. Pavoine et al. 2005; Redding & Mooers 2006; Isaac et al. 2007). On the other hand, the phylogenetic diversity or PD is generally measured for a *subset* of species as the sum of the branch lengths of a tree spanning that subset and the root (Faith 1992a, 1992b, 2008; Barker 2002; Steel et al. 2005; Faith & Baker 2006). As identified by Reading et al. (2008), some of the major differences between ED and PD are: PD is effective only if *all* the species within the optimal subset are protected (a very resource demanding task in some cases), otherwise new optimal subsets are possible; unlike ED, PD is not species-specific and thus does not offer priority species rankings, which are important to conservation approaches like the IUCN Red List of Threatened Species; and finally, PD is uninformative on an ultrametric tree.

Although in recent years major advances in phylogeny-based conservation metrics have been achieved (e.g. Witting et al. 2000; Pavoine et al. 2005; Redding & Mooers 2006; Crozier et al. 2005; Steel et al. 2005; Isaac et al. 2007; Pardi & Goldman 2007; Steel et al. 2007; Faith 2008; Borderwich et al. 2009), most of these measures have neglected the role of biotic distribution and biogeography in the problem of conserving biodiversity (see, however, Moritz & Faith 1998; Rodrigues & Gaston 2002; Forest et al. 2007). Vane-Wright et al. (1991; see also Williams et al. 1991) were probably the first authors to couple measures of ED with the biogeographic concept of complementarity of biotas. More recently, Posadas et al. (2001) modified Vane-Wright et al. (1991) approach to consider not only distinctiveness and complementarity, but also species endemicity. Including distributional and biogeographical information allow to, for example, decrease the conservation value of widespread species, and to maximize the amount of preserved biodiversity using as few areas as possible (Posadas et al. 2001).

Previous conservation studies in Amazonia have focused on identifying multiple taxonomic groups adequately sampled (Heyer et al.1999) or sites of high species diversity and endemism (Nelson et al. 1990; Kress et al.1998), and on ranking Amazonian areas of endemism according to species richness, generic richness, time-based PD measures, and species endemicity (Silva et al. 2005b). Other studies have centered in exploring and predicting the loss of the Amazonian rainforest based on environmental data or development schemes (Laurance et al. 2001; Maslin et al. 2005; Malhi et al. 2008; Aragao et al. 2008; Malhi et al. 2009). Here, our main goal was to establish conservation priorities for Amazonia’s areas of endemism using Vane-Wright et al. (1991) and Posadas et al. (2001) ED measures, along with more traditional biodiversity measures such as raw species richness, species endemicity, and complementarity of biotas.

MATERIALS AND METHODS

AREAS OF ENDEMISM

Regardless of the scientific need to discover areas of endemism directly from the data, many biogeographic and conservation studies proceed in the opposite direction: they contrast areas that are already defined and examine the properties of those areas. For our analyses, we considered two appraisals of Amazonia's areas of endemism with the purpose of evaluating area size and geographic limits as likely influences on prioritization and complementarity. First, we used eight wide-ranging areas defined by Bates et al. (1998) and Silva et al. (2005a) (see Fig. 1). These areas are essentially those suggested by Haffer (1978) and Cracraft (1985); however, the Pará area has been divided into Tapajós (or Pará 1) and Xingú (or Pará 2). The basis for such splitting is the role of the Xingú river as a putative barrier, at least for birds, between eastern and western Pará. Thus, we initially partitioned Amazonia as follows (see Fig. 1): Belém, Xingú, Tapajós, Rondônia, Guiana, Imeri, Inambari, and Napo. Second, we also considered sixteen smaller regions which are congruent with the eight larger areas and correspond to a large extent to those defined by Silva and Oren (1996) (see Fig. 2). We labeled this second set of areas with the first three letters of the names of the larger areas followed by a number (e.g. Gui1, Gui2, and Gui3, where each is a subdivision of Guiana).

TAXA

We assembled fifty phylogenetic trees from the literature with species or “subespecies” as terminals (see Table 1); unintenionally, plant taxa was poorly represented (one phylogeny). If a paper had trees result of partitioned and combined data sets, we only considered the latter. We selected phylogenies according to the following rules, which rely on the strict concordance between monophyly and the area inhabited. In all cases, for a given tree, *t* is a subset of terminal nodes that belong to the same species or subspecies. First, if *t* was a fully resolved monophyletic group, and all of its terminals inhabited the same area of endemism, *t* was collapsed (i.e. reduced) into a single terminal node. For example, for the tree (a((b(bb))(c(cc)))), where a, b, and c are three different species (or subspecies) present in areas 1, 2, and 3 respectively, the tree was treated as (a(bc)). If *t* fulfilled the initial condition from this first rule but not the latter (i.e. each of its terminals was present in a different area), it was not collapsed. Second, if *t* was a monophyletic but fully unresolved group, it was collapsed into a single terminal node; therefore, if all terminals of *t* were present in the same area the outcome was that from the first rule, or else a widespread terminal node. Third, if *t* was not monophyletic it was not collapsed.

After we applied these rules, we omitted those trees with more than one tetratomy or more than two trichotomies (Sanmartín et al. 2001). In addition to the distributional data from the original papers, we included records from the Global Biodiversity Information Facility (GBIF) for those trees with no instraspecific relationships. The total amount of records was 1715. If not presented as such, we converted the records into decimal degrees; then transformed all records into Keyhole Markup Language (KML), and visualized them in a three-dimensional Earth browser to decide presence or absence in a given area of endemism.

PRIORITIZATION RANKING

To set conservation priorities, we initially used more traditional measures of biodiversity, namely, raw species richness and species endemicity; the latter measured as the quotient between endemic and total species. Subsequently, we applied the ranking protocol suggested by Posadas et al. (2001; see also Posadas et al. 2004). The foundation of this approach is the *W* index proposed by Vane-Wright et al. (1991). For any fully bifurcating tree, each branch-point results in two sister lineages which are the same age and have undergone equivalent evolutionary change (Krell & Cranston 2004). Commonly, one of the two lineages originating from a node has fewer species than does the other (Crisp & Cook 2005). The *W* index considers taxa in such species-poor lineages to be more unique and vulnerable to lineage extinction, and therefore of higher conservation value. A caveat worth mentioning is that a tree may be unbalanced – that is, have unequal number of species on either side of each node – because misinformative characters or biased taxon sampling (Mooers et al. 1995; Stam 2002), among other causes. Vane-Wright et al. (1991) node-based *W* index, although not suitable to capture PD, is reliable at selecting the most relictual species (Redding et al. 2008), and thus offer a valuable approximation to preserve biodiversity.

Posadas et al. (2001) proposed the following modifications to the *W* index. To avoid bias due to different numbers of taxa when summing the index values obtained from different trees, the *W* index value of each taxon is scale by the total, this is W_s index. To include the degree of endemicity of a taxon, the *W* index value of each taxon is divided among the number of areas where such taxon is present, this yields the W_e index. The outcome of combining these two modifications is the W_{es} index. We ranked Amazonian areas of endemism according to the basic *W* index and its modifications outlined above. This area ranking procedure is briefly explained in an example illustrated in Fig. 3. To evaluate the relationship between distinctiveness and species richness, we correlated the W_{es} index to raw species richness.

Finally, we calculated complementarity (measured as the complement of the Jaccard index of similarity) among pairs of areas with the aim of evaluating distinctiveness in species composition. It should be stressed, however, that these estimates of richness, endemicity, and complementarity are restricted to taxa for which we have available phylogenetic information, and for that reason may not accurately represent the actual features of Amazonia. For all calculations we used the software Richness (Miranda-Esquivel 2001).

RESULTS

RICHNESS, ENDEMICITY, AND DISTINCTIVENESS ACCORDING TO BATES ET AL. (1998) AND SILVA ET AL. (2005A) AREAS

The richest area was Inambari with 103 species, followed by Guiana and Napo with 95 and 76 species, respectively (see Table 2, Fig. 1). In the case of species endemicity, raw *W*, and its modifications, W_s, W_e, and W_{es}, the three most important areas were Guiana, Inambari, and Napo (see Table 2, Fig. 1); the following position in these rankings was characterized by a major value decrease. The pair of areas with the highest number of species in common were Napo and Xingú, whereas Napo and Inambari had the fewest (Table 4).

RICHNESS, ENDEMICITY, AND DISTINCTIVENESS ACCORDING TO SILVA AND OREN'S (1996) AREAS

The three richest areas were Gui2 with 58 species, Ina4 with 54, and Ron1 with 51 (see Table 3, Fig. 2). For endemicity, we observed ties between Gui2 and Ron1 for the first position and between Gui3 and Tap1 for the second position; Ina4 occupied the third place. Raw *W* index ranked Gui2, Ron1, and Nap1 as top priorities (see Table 3, Fig. 2). Taking endemicity into account (W_e index) changed this ranking to Ron1, Gui2, and Gui3. For the W_s and W_{es} measures, their rankings encompassed the same areas in the first positions, however, for W_s the listing order was Gui2, Gui3, and Ina2 and for W_{es} it was Gui2, Ina2, and Gui3.

COMPLEMENTARITY

Preferably, once we have identified the area of highest priority based on any attribute – in our case, distinctiveness – the second most important area should be selected according to complementarity to maximize the number of species protected (Vane-Wright et al.1991; Posadas et al. 2001). In this case, complementarity offered less resolution among areas because close complementarity values suggest that more than one area could be selected to properly supplement the biota of another area. For example, for the set of larger areas (Table 4) the area of highest priority according to distinctiveness was Guiana, if we consider complementarity, the second area to prioritize could be Xingú, Rondônia, or Tapajós instead of Inambari, which was the second most important area in the distinctiveness rankings. Likewise, for the set of smaller areas (Table 5), the first area in the majority of distinctiveness rankings, Gui2, could be followed by Ime2, Ron1, Xin1, or Ina2 according to complementarity. If two or more areas have similar or equal complementarity values, one of such areas could be preferred as second priority on the basis of ED, gamma-diversity, and proportion of endemic species (Roig-Juñent & Debandi 2004).

DISCUSSION

Regardless of the set of areas of endemism used, the distinctiveness indexes identified congruent conservation priorities. If we consider, for example, the W_{es} area rankings, the two areas of highest priority for the set of smaller areas, Gui2 and Ina2, are located within the two most important, larger areas, Guiana and Inambari. The area labeled as Gui2 is a subdivision of Guiana corresponding to Guyana, and east and north-east of the Brazilian states of Roraima and Amazonas respectively; while area Ina2 is a subdivision of Inambari that comprises the north-west of the Brazilian state of Amazonas, at the left bank of Rio Jurua. The finding that the ED measures considered in this study seem partly resilient to changes in area size is particularly important for conservation planning because smaller areas may represent more feasible strategies, whether from a conceptual or financial perspective.

For the set of larger areas, the endemicity and distinctiveness rankings remained completely stable; Guiana, Inambari, and Napo were always the three most valuable areas for conservation. For raw species richness such ranking changed its order to Inambari, Guiana, and Napo. So, distinctiveness showed a fair reflection of raw species richness and endemicity. W_{es} was strongly correlated to raw species richness ($r = 0.965$, p-value = 0.0001). Taking into account that Guiana and Inambari are the largest Amazonian areas of endemism, distinctiveness values could be directly related to area size.

For the set of smaller areas, the distinctiveness indexes did not yield stable rankings. However, the majority of measures, with the exception of W_e, ranked area Gui2 as that of highest priority. Richness and endemicity rankings were in agreement with distinctiveness for the most important area for conservation, Gui2, but in disagreement for the other areas. The relationship between W_{es} and richness ($r = 0.803$, p-value = 0.0002) was also a strong correlation.

Although considerably large reserves (at least 1 million ha) are imperative for the future of Amazonian biodiversity (Peres 2005; Laurance 2005), an obvious drawback of our study is that it is unlikely to protect the whole extent of any of the areas considered; instead, our results should constitute a frame of reference for further inquiry using smaller geographical units. For example, grid-cell-based studies focusing on those areas of endemism identified here as conservation priorities. Unfortunately, such studies, which may yield more attainable priority areas, currently would be even more hampered than our approach by the need for an exhaustive survey of the Amazonian biota, quality distributional data (i.e. geographical coordinates) for all taxa, and, if to be based on evolutionary information, well-resolved and complete phylogenies (Mace et al. 2003).

Nevertheless, grid-cell-based studies to set conservation priorities in Amazonia have been conducted. Kress et al. (1998) divided Amazonia into 472 1 x 1° grid cells, and measured species diversity and species endemism using 3991 records representing various taxonomic groups. Kress et al. (1998) included nine of those cells into the highest species diversity category (43-67 species), and nine into the highest concentrations of endemism category (4-13 endemic species); the vast majority of these cells are located within the three most important areas for conservation according to our results: Guiana, Inambari, and Napo (see Fig. 4 and Fig. 5). However, Kress et al. (1998) stress that grids with the highest species richness in their study also correspond to many of the most intensively collected areas, and few areas in Amazonia have been thoroughly sampled for most groups (see also Heyer et al. 1999). Therefore, our results, as other biodiversity studies in Amazonia, could also be influenced by sampling efforts (see Appendix 1. for an overview of our distributional data).

In comparison to previous case studies based on phylogenetic information, our results were consistent with those of Silva et al. (2005b); these authors applied two measures proposed by Sechrest et al. (2002) to a phylogeny of all New World primate genera (Schneider 2000). The first measure was clade evolutionary history, a measure equivalent to PD calculated using time units, while the second was species evolutionary history, measured as the time from present to the time of last divergence. Silva et al (2005b) ranked Inambari and Napo as the areas of highest priority with equal values for both measures, and these areas were followed by Guiana and Rondônia. The fact that ED and PD identified alike priority areas suggests that such areas are adequately prioritized from two different evolutionary perspectives and measures.

Concerning the current state of conservation planning in Amazonia, two groups of areas, discernible in terms of protected coverage (Silva et al. 2005b), are of our concern. The first group includes Napo, Imeri, and Guiana, all with more than 40% of their lands acknowledged as protected, while the second group comprises Inambari, Rondônia, Tapajós, and Xingu, all with 20% to 40% protected coverage. Additionally, the Brazilian portions of Napo, Imeri, Guiana, and Inambari have the lowest percentages of area deforested and could be considered the least vulnerable (Silva et al. 2005a). Therefore, in spite of being based on other criteria apart from phylogeny, current conservation efforts in Amazonia are aiming at the most important areas for conservation identified in this study.

To conclude, the Amazonian rainforest has been heavily threatened, and hence constitutes an obvious target for conservation planning. Measures which include evolutionary and biogeographic information provide an effective framework to set conservation priorities. Guiana, Inambari, and Napo are the most important areas for conservation according to node counting measures of distinctiveness. The measures used here prioritized congruent areas when the set of geographic units used changed, reflected the behavior of species richness and endemicity, and yielded results in accordance with previous studies. Conservation planning in Amazonia requires research from different disciplines, and would highly benefit from additional evolutionary, taxonomic, ecological, and environmental studies.

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TABLES

Table 1.

Author(s)	Order	Year
I. Agnarsson et al.	Araneae	2007
A. Aleixo	Passeriformes	2002
S. R. Andena et al.	Hymenoptera	2007
A. W. Brower et al.	Lepidoptera	2006
D. C. Canatella et al.	Anura	1998
A. A. Chek et al.	Anura	2001
Z. A. Cheviron et al.	Passeriformes	2005
L. Cortés-Ortiz et al.	Primates	2003
L. P. Costa	Rodentia/Didelphimorphia	2003
S. S. Denham et al.	Poales	2002
J. R. Eberhard & E. Bermingham	Psittaciformes/Piciformes	2005
J. Faivovich et al.	Anura	2005
A. A. Garda & D. C. Canatella	Anura	2007
L. G. Giugliano et al.	Squamata	2006
L. G. Giugliano et al.	Squamata	2007
M. Gómez-Laverde et al.	Rodentia	2004
D. J. Harvey & J. P. W. Hall	Lepidoptera	2002
F. G. Hoffman & R. J. Baker	Chiroptera	2003
I. J. Lovette	Passeriformes	2004
R. Mallarino et al.	Lepidoptera	2005
B. D. Marks et al.	Passeriformes	2002
J. L. Patton et al.	Rodentia/Didelphimorphia	2000
K. C. M Pellegrino et al.	Squamata	2001
S. L. Pereira & A. J. Baker	Galliformes	2004
K. M. Pickett & J. W. Wenzel	Hymenoptera	2007
T. W. Reeder et al.	Squamata	2002
C. C. Ribas et al.	Psittaciformes	2005
C. C. Ribas et al.	Psittaciformes	2006
A. Silva de Paula et al.	Hemiptera	2007
M. N. F. da Silva & J. L. Patton	Didelphimorphia	1998
C. Steiner & F. M. Catzeflis	Didelphimorphia	2004
R. Symula et al.	Anura	2003
N. Wahlberg & A. V. L. Freitas	Lepidoptera	2007
N. Wahlberg et al.	Lepidoptera	2005
J. D. Weckstein	Piciformes	2004
M. Weksler	Rodentia	2006

Table 2.

	W	We	Ws	Wes	Richness	Endemicity
Belém	29.06	12.91	4.08	1.67	21	5
Guiana	**168.87**	**114.76**	**24.57**	**16.16**	**95**	**53**
Tapajós	67.26	43.50	8.63	4.85	40	22
Xingú	38.78	22.12	4.97	2.75	23	9
Rondônia	94.05	59.39	7.93	4.28	50	22
Inambari	**166.84**	**97.43**	**23.70**	**14.79**	**103**	**48**
Imeri	53.31	19.38	5.80	2.71	33	8
Napo	**130.75**	**65.52**	**16.69**	**8.58**	**76**	**28**

Table 3.

	W	We	Ws	Wes	Richness	Endemicity
NAP1	**90.65**	35.11	10.85	4.81	50	10
NAP2	88.71	33.05	10.46	3.58	46	12
NAP3	30.64	5.16	5.01	0.93	16	0
IME1	48.37	15.86	4.80	2.02	30	7
IME2	9.32	2.79	0.86	0.33	6	1
GUI1	62.27	27.12	6.37	2.36	35	10
GUI2	**105.64**	**54.63**	**18.73**	**8.96**	**58**	**23**
GUI3	84.03	**46.51**	**14.90**	**7.10**	48	**21**
INA1	36.07	14.24	4.02	1.17	26	6
INA2	67.22	38.42	**11.68**	**7.92**	40	17
INA3	25.45	13.49	4.79	3.31	19	7
INA4	84.48	39.21	11.60	5.41	**54**	19
RON1	**95.05**	**59.72**	8.14	4.30	**51**	**23**
TAP1	67.28	42.52	8.71	4.68	40	**21**
XIN1	43.13	23.69	5.56	3.00	24	10
BEL1	27.72	10.58	4.14	1.17	20	4

Table 4.

	Belém	Guiana	Tapajós	Xingú	Rondônia	Inambari	Imeri
Guiana	0.916						
Tapajós	0.849	0.937					
Xingú	0.952	0.965	0.875				
Rondônia	0.908	0.957	0.941	0.957			
Inambari	0.949	0.894	0.956	0.984	0.891		
Imeri	0.941	0.877	0.942	0.963	0.908	0.876	
Napo	0.922	0.890	0.964	0.990	0.895	0.807	0.853

Table 5.

	NAP2	NAP3	IME1	GUI2	GUI3	NAP1	INA1	INA2	INA3	INA4	RON1	TAP1	XIN1	BEL1	IME2
NAP3	0.808														
IME1	0.866	0.757													
GUI2	0.917	0.928	0.886												
GUI3	0.944	0.933	0.917	0.767											
NAP1	0.685	0.842	0.904	0.920	0.946										
INA1	0.839	0.865	0.880	0.937	0.943	0.866									
INA2	0.897	0.923	0.906	0.957	0.989	0.902	0.862								
INA3	0.934	0.971	0.886	0.900	0.953	0.970	0.929	0.843							
INA4	0.864	0.906	0.880	0.913	0.915	0.818	0.904	0.881	0.942						
RON1	0.934	0.953	0.905	0.962	0.979	0.902	0.915	0.917	0.971	0.859					
TAP1	0.951	0.963	0.939	0.957	0.900	0.966	0.952	0.961	0.983	0.932	0.942				
XIN1	1.000	0.974	0.962	0.962	0.971	0.986	0.980	0.984	1.000	1.000	0.973	0.897			
BEL1	0.918	0.941	0.958	0.901	0.867	0.939	0.930	0.983	0.917	0.928	0.924	0.846	0.977		
IME2	0.960	0.842	0.941	0.968	0.962	0.963	0.968	0.955	0.958	0.966	0.982	0.978	1.000	0.960	
GUI1	0.920	0.891	0.818	0.792	0.831	0.924	0.983	0.944	0.920	0.940	0.964	0.958	0.946	0.900	0.921

FIGURES

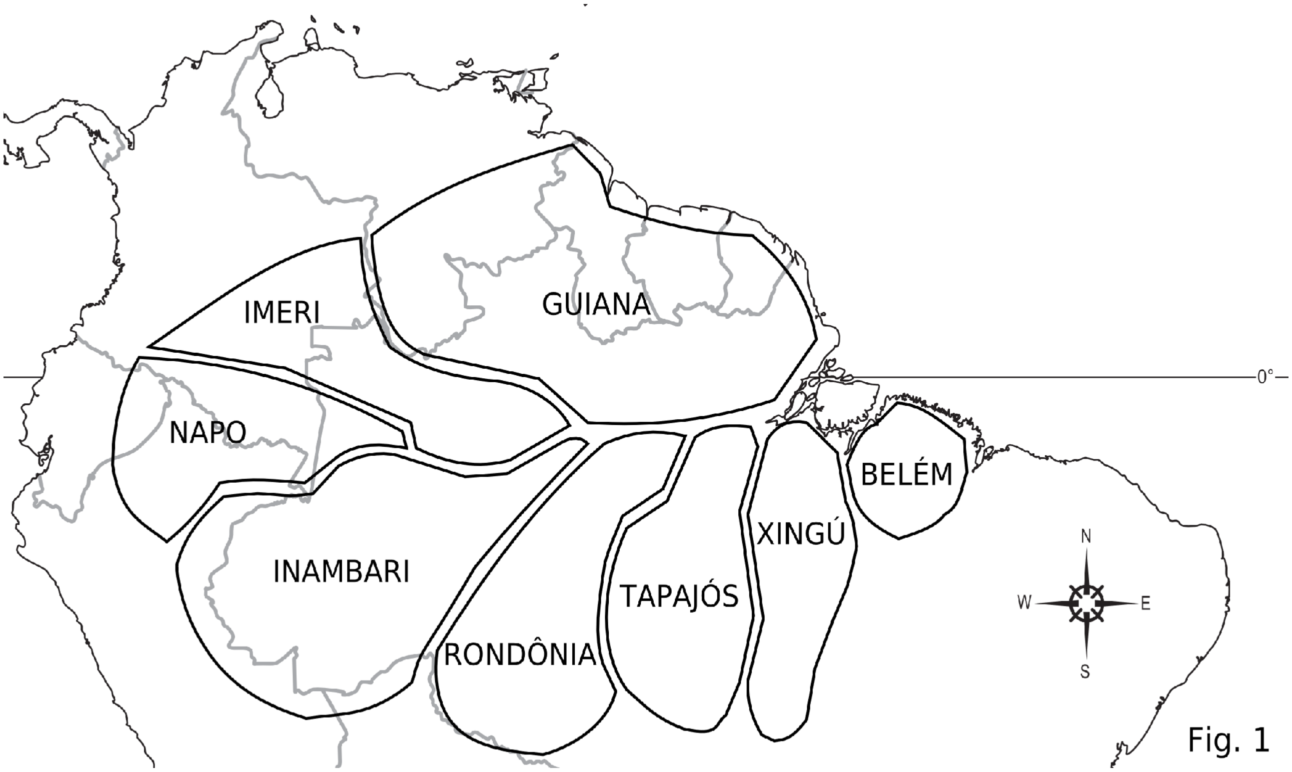
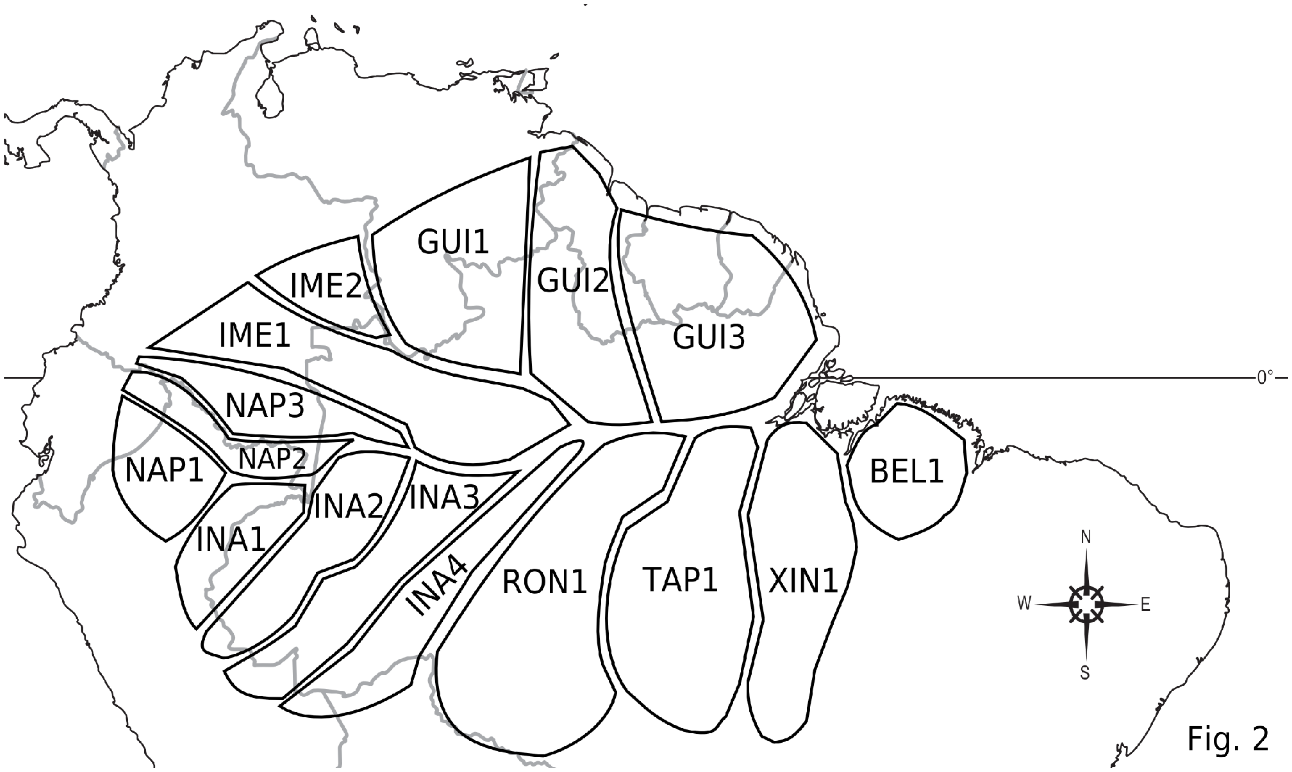


Fig. 1


GUI1
GUI2
GUI3
IME2
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INA4
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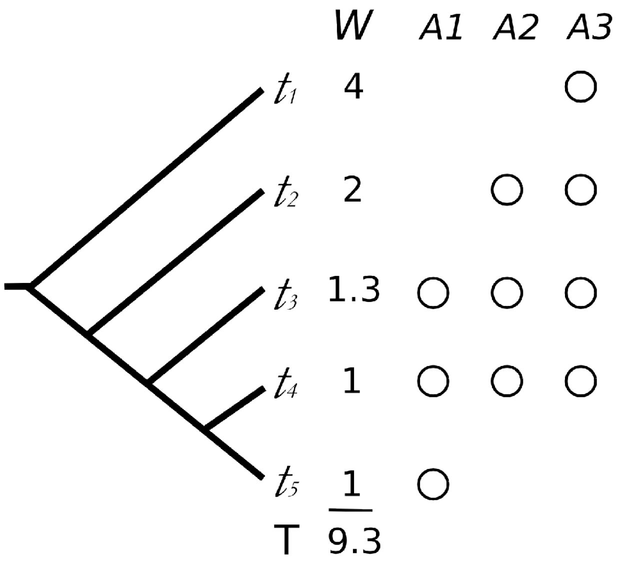
Fig. 2



	W	W_e	W_s	W_{es}
A1	3.3	1.8	0.4	0.2
A2	4.3	1.8	0.5	0.2
A3	8.3	5.8	0.9	0.6

Fig. 3

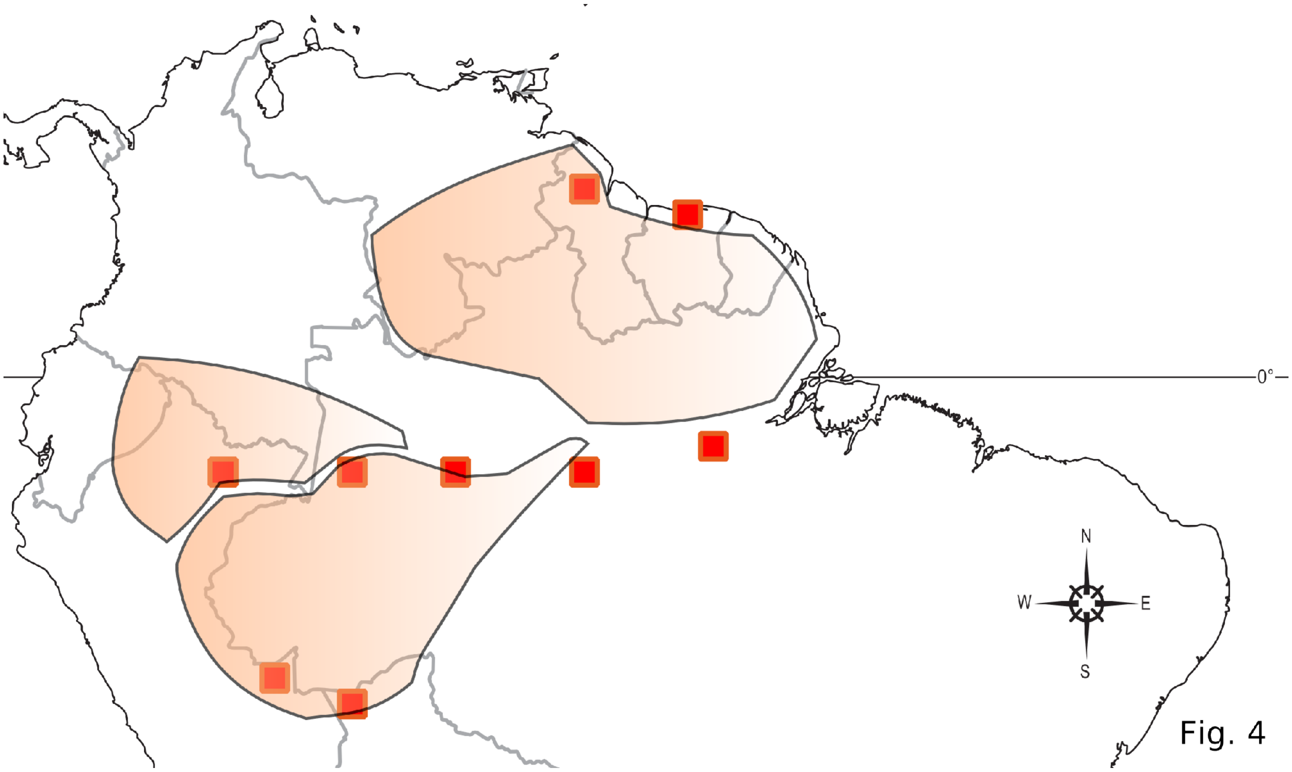


Fig. 4

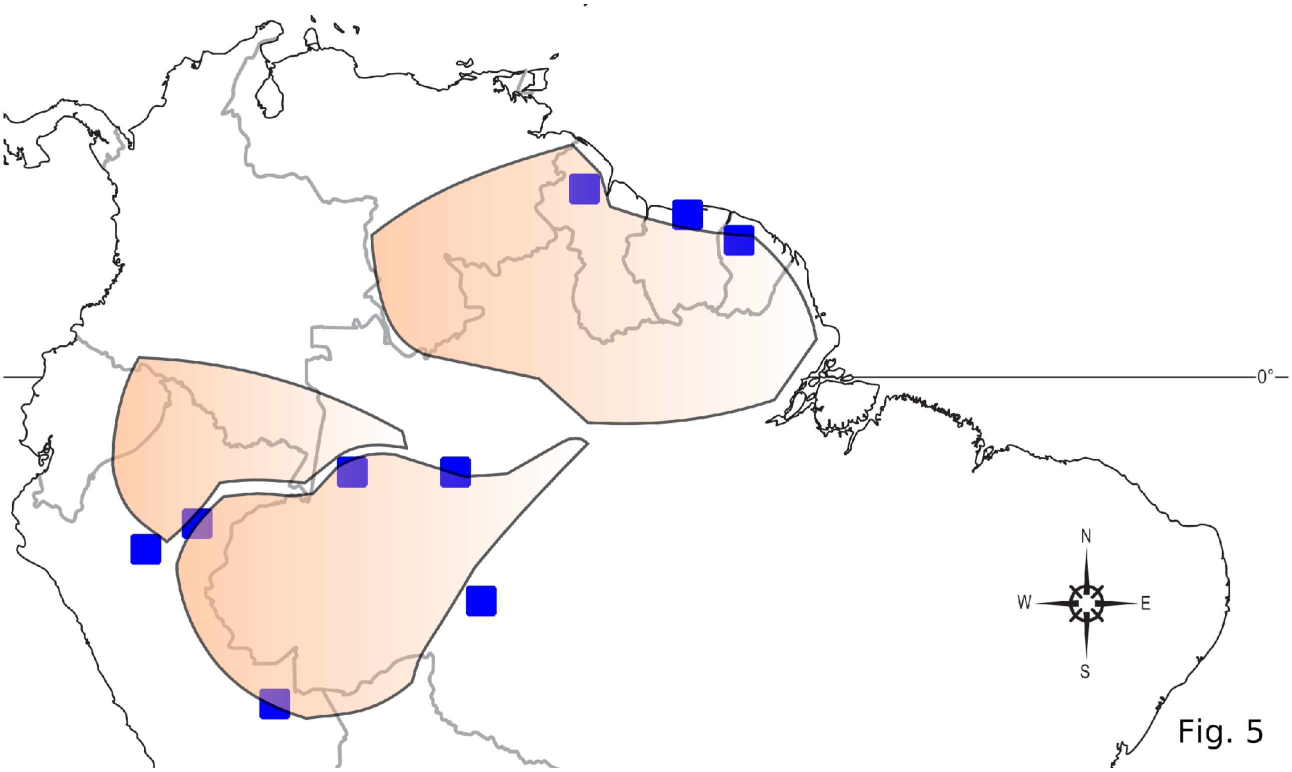


Fig. 5

SUPPLEMENTARY MATERIAL

1.