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BIOGEOGRAFIA DOS POLISTÍNEOS NEOTROPICAIS: UMA ABORDAGEM ECOLÓGICA E EVOLUTIVA

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SÃO CARLOS – SÃO PAULO – BRASIL

Dezembro de 2014

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BIOGEOGRAFIA DOS POLISTÍNEOS NEOTROPICAIS: UMA ABORDAGEM ECOLÓGICA E EVOLUTIVA

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“Quando eu vim lá da Bahia
Rumo a São Paulo eu meti os peito
Baiano veio de pau-de-arara
Ser pobre não é defeito
Eu vim pra ganhar dinheiro
Serviço eu não enjeito

Só que eu tô com uma vontade
De comer côco que não tem jeito

(...)

Quero rever a Bahia
Porque tenho esse direito
Nosso Senhor do Bonfim
Trago dentro do meu peito
Eu sonho com a Bahia
Mas São Paulo é meu leito

Só que eu tô com uma vontade
De comer côco que não tem jeito”

Tião Carreiro e Pardinho

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SUMÁRIO

EXTRATO...7

ABSTRACT...9

1. INTRODUÇÃO...11

2. CAPÍTULO 1 (Polistinae biogeography in the Neotropics: history and prospects) 16

3. CAPÍTULO 2 (Progression rules and Neotropical Polistinae: the Round-trip hypothesis) 37

4. CAPÍTULO 3 (Witnesses of the broadest Neotropical disjunction and their idiosyncratic responses to climate change) 66

5. CONSIDERAÇÕES FINAIS 144

5. REFERÊNCIAS BIBLIOGRÁFICAS 148

EXTRATO

Carvalho, Antônio Freire. D.S. Universidade Federal de São Carlos, São Carlos, dezembro de 2014. Biogeografia dos polistíneos Neotropicais: uma abordagem ecológica e evolutiva. **Orientador: Dr Marco Antonio Del Lama. Co-orientadora: Drª Ana Carolina Carnaval.**

Apesar da ampla diversidade na região Neotropical, pouco se sabe a respeito da biogeografia das vespas sociais da subfamília Polistinae. Esta tese divide-se em três capítulos que, apesar de possuírem objetivos específicos distintos, têm como objetivo central a discussão da influência de processos ambientais, ecológicos e evolutivos na distribuição da diversidade genética e de espécies (i.e., riqueza biológica) de polistíneos. Para tanto, no primeiro capítulo é fornecida uma ampla revisão acerca das origens da subfamília Polistinae e processos causadores de diversidade na região Neotropical. No segundo capítulo são propostas possíveis rotas de colonização utilizadas pela subfamília nas Américas seguindo o modelo proposto pela hipótese “Round-trip”. Esta hipótese sustenta-se na recorrência de regras de progressão, inferidas por relações filogenéticas e de distribuição, apontando clados mais basais de diversos gêneros da subfamília ocorrendo na região Amazônica e clados mais derivados no leste da América do Sul. A ocorrência de uma regra de progressão contrária para *Polistes* sustenta uma segunda rota mais rara e, provavelmente, mais antiga, do leste para o oeste. O terceiro capítulo foca na disjunção das florestas Amazônica e Atlântica e nas espécies que, devido às alterações na distribuição das florestas, tiveram suas populações fragmentadas. Neste estudo é fornecida uma lista ampla com 127 táxons Neotropicais com linhagens disjuntas entre as duas florestas, modelos de estabilidade climática para oito espécies (dois polistíneos e seis vertebrados) e análises filogeográficas para as vespas *Angiopolybia pallens* e *Synoeca surinama*. As espécies de vespa foram escolhidas por apresentarem características ecológicas distintas, mas por ocorrerem em simpatria nas florestas Amazônica e Atlântica. Visou-se com isto testar a hipótese original deste projeto: a disjunção afetou de forma idiossincrática a diversidade genética de espécies com populações amplamente fragmentadas. As informações apresentadas nos três trabalhos podem servir como suporte em futuros estudos acerca da biogeografia da subfamília, principalmente aqueles que foquem na integração de eventos ambientais para explicar processos evolutivos e ecológicos.

ABSTRACT

Carvalho, Antônio Freire. D.S. Universidade Federal de São Carlos, São Carlos, December 2014. Biogeography of the Neotropical Polistinae: an ecological and evolutionary approach. **Advisor: Dr Marco Antonio Del Lama. Co-advisor: Dr Ana Carolina Carnaval.**

Despite the huge diversity in the Neotropical region, little is known about the biogeography of the subfamily Polistinae. This thesis is divided into three chapters which, despite their distinct specific aims, have as central target the discussion of the influence of environmental, ecological and evolutionary processes on the distribution of genetic diversity and species richness of polistines. For this end, in the first chapter is provided a wide review on the origins of Polistinae and change-promoter processes in the Neotropics. In the second chapter, possible colonization routes used by the subfamily in the Americas are proposed based on the Round-trip hypothesis. Such a hypothesis is corroborated by the recurrence of progression rules, inferred by phylogeny-distribution relationships, pointing more basal clades of several genera occurring in the Amazonian rainforest and more derived clades in eastern South America. The occurrence of an inverse progression rule for *Polistes* sustains a second rarer and older route from east to west. The third chapter focuses on the disjunction between Amazonia and Atlantic Forest and on the species that, due to changes in forest distributions, had their populations fragmented. It is provided in this study a wide list with 127 Neotropical taxa with disjunct lineages between both forests, climate stability models for eight species (two paper wasps and six vertebrates) and extensive phylogeographies for the wasps *Angiopolybia pallens* and *Synoeca surinama*. Such wasp species were used as genetic models to test spatially-esplicit hypotheses of climate stability and were chosen by present distinct ecological characteristics, but occur in sympatry in Amazonia and Atlantic Forest. It was aimed with this to test the following hypothesis: the disjunction affected idiosyncratically the genetic diversity of species with populations widely fragmented. The information presented in the three studies might serve as support in future works on Polistinae biogeography, mainly those that focus on the integration of environmental events to explain both evolutionary and ecological processes.

INTRODUÇÃO

Analisando o estado atual da biogeografia da subfamília Polistinae pode-se perceber que processos históricos interferindo na distribuição das espécies Neotropicais foram raramente recorridos para explicar a imensa diversidade do grupo na região. Eventos ambientais como a expansão e retração de refúgios ecológicos, surgimento de rios e montanhas, amplamente discutidos utilizando anfíbios, mamíferos, répteis ou outros insetos como modelos, são possivelmente os principais mecanismos contribuindo para a separação de linhagens na maior floresta tropical do planeta, a Amazônia (HOORN *et al.*, 2010), por exemplo. Tais eventos são considerados como de alto impacto na formação de novas espécies em diferentes escalas de tempo (HAFFER, 1997; 2008). Outrossim, propostas referentes a rotas de colonização e associações de dados de genética de populações, filogenia e filogeografia com estes eventos são pouco frequentes para membros da subfamília.

Os avanços atuais de análises integrativas como o uso de modelagem de nicho climático aliado a métodos moleculares (HUGALL *et al.*, 2002; CARNAVAL *et al.*, 2009) têm facilitado a compreensão de questões fundamentais como “por que tal espécie não ocupa determinada área?” ou “como determinado clado passou a ocupar determinada área?”. Estes avanços têm mostrado que inferências poderosas em biogeografia necessitam de mais do que esforços isolados utilizando métodos de análise ecológicos ou filogenéticos, mas sim da integração entre estes dois campos (WIENS & DONOGHUE, 2004). Sob esta perspectiva, o estudo de diferentes fatores influenciando a distribuição de linhagens e, consequentemente, a história evolutiva dos polistíneos, deveria ser tratado como o principal desafio em biogeografia e especiação da subfamília.

Com o objetivo de contribuir para o avanço da biogeografia de Polistinae, esta tese foca em algumas lacunas no conhecimento da área e está organizada na forma de três capítulos, os quais contemplam: Capítulo 1 – estado da arte, possíveis mecanismos ambientais influenciando na distribuição e especiação de Polistinae e perspectivas no estudo biogeográfico da subfamília; Capítulo 2 – rotas de colonização utilizadas pelos polistíneos na região Neotropical; e Capítulo 3 – o uso de duas espécies de Polistinae como modelos genéticos (filogeografia), bem como outras espécies de vertebrados como modelos ecológicos, para entender o maior evento vicariante da América do Sul, a disjunção entre as Florestas Amazônica e Atlântica. As duas espécies de vespas *Angiopolybia pallens* (Lepeletier) e *Synoeca surinama* (Linnaeus) foram escolhidas por apresentarem-se distribuídas em simpatria na Amazônia e na Floresta Atlântica e por a segunda também ocorrer em ambientes mais secos do cerrado brasileiro. Além disso, visto que *A*. *pallens* é uma espécie de raio de voo curto (CRUZ *et al.*, 2006) e de pequeno porte (±1,0 cm) e que *S*. *surinama* é uma espécie de grande porte (±2,0 cm), o que pode influenciar em um raio de voo mais amplo, esperava-se encontrar padrões distintos de resposta destas espécies à disjunção. Os testes desta hipótese foram realizados mediante análises de modelagem histórica de nicho climático e filogeografia.

Vale ressaltar que os três capítulos estão em forma de artigo e que a estrutura de cada um segue normas pré-estabelecidas pelas revistas às quais serão ou foram submetidos para publicação. Segue abaixo um resumo simples das ideias discutidas em cada capítulo.

Histórico e perspectivas da Biogeografia de Polistinae nos Neotrópicos (Capítulo 1)

Visando organizar o estado atual do conhecimento biogeográfico a respeito da subfamília e apontar caminhos para a solução de problemas não resolvidos, uma ampla revisão acerca das origens da subfamília Polistinae e dos processos causadores de diversidade na região Neotropical é incluída neste trabalho. Além disso, baseando-se em avanços recentes em biogeografia, principalmente na integração de informações ecológicas e evolutivas, são propostas direções para pesquisas futuras com o grupo. Este estudo foi submetido para publicação na revista Journal of Hymenoptera Research, está em processo de revisão e algumas das modificações solicitadas pelos revisores já estão incluídas no texto aqui apresentado.

Inferência de rotas de colonização (Capítulo 2)

Neste trabalho faz-se o uso do conceito de Regras de Progressão (HENNIG, 1966) como hipótese nula. O pressuposto se baseia na ideia de que linhagens basais estão restritas aos centros de origem e linhagens derivadas ocupam regiões de colonização mais recente. Para testar a hipótese foi revisada a distribuição de espécies de oito gêneros de Polistinae cujas relações filogenéticas são conhecidas, totalizando 104 espécies. Ao associar os resultados de filogenia com as informações de distribuição foram traçadas prováveis rotas de colonização para os polistíneos na região Neotropical.

O trabalho fornece uma ideia ampla acerca dos processos de colonização por polistíneos nos Neotrópicos, corroborando a hipótese de que a subfamília chegou no Novo Mundo em um cenário Gonduânico e que a Amazônia é o principal centro de diversidade de linhagens basais para o grupo. Tais informações criam um dilema: se o grupo colonizou as Américas vindo da África, por que a maioria das linhagens basais estão na Amazônia? A resposta, embora em forma de hipótese, é proposta ao retratar as relações de filogenia e distribuição do grupo mais basal da subfamília: o gênero *Polistes*. Somente neste gênero são encontradas linhagens basais no leste brasileiro e linhagens derivadas no Caribe e na América do Norte; algo que suporta a hipótese de que a colonização de Polistinae nas Américas se deu por um processo composto por duas etapas, uma rota rara do leste para o oeste e uma rota mais comum do oeste, principalmente Amazônia, para o leste. A hipótese é nomeada como “Round-trip”, ou seja, uma viagem de ida e volta. Pretende-se submeter este trabalho à revista Neotropical Entomology.

Respostas idiossincráticas das testemunhas da maior disjunção Neotropical a alterações climáticas (Capítulo 3)

Neste capítulo são incluídos todos os resultados genéticos oriundos do projeto de pesquisa de Doutorado bem como os resultados de paleomodelagem de *A*. *pallens* e *S*. *surinama* para toda a América do Sul. Este trabalho é o mais ambicioso dos três. Nele são revisadas as distribuições de 6.419 espécies Neotropicais incluindo mamíferos, répteis, aves, vespas sociais e abelhas sem ferrão. Destas, somente 127 linhagens apresentam uma distribuição disjunta entre a Amazônia e a Floresta Atlântica.

Analisando o status de conservação destas espécies vê-se frequentemente que as mesmas são, na grande maioria dos casos, consideradas como minimamente ameaçadas de extinção. Contudo, a IUCN não leva em consideração que estas espécies apresentam pequenas populações isoladas a centenas de quilômetros e que os menores distúrbios, sejam eles causados pelo homem ou não, podem levar à extinção de linhagens exclusivas destas espécies consideradas no trabalho como testemunhas da maior disjunção da região Neotropical.

A partir da análise conjunta de modelagem histórica de nicho climático e filogeografia comparada de *A*. *pallens* e *S*. *surinama*, é proposto que os refúgios ecológicos evidenciados são, de fato, mantenedores de populações variáveis desde o Último Período Interglacial, há pelo menos 120 mil anos, e que populações residentes nestas áreas apresentam maiores níveis de diversidade genética do que aquelas oriundas de regiões de expansão populacional recente. Realizando a paleomodelagem para alguns destes grupos (dois mamíferos, dois répteis, duas aves e as duas vespas) pode-se apontar regiões comuns de estabilidade entre todas as espécies mediante paleomodelagem combinada, uma metodologia desenvolvida em um trabalho que foi submetido para publicação na revista Journal of Insect Conservation (CARVALHO & DEL LAMA, subm.). Estes resultados deram ensejo à hipótese de que estas são regiões de extrema importância para a conservação de diferentes grupos, muitos deles carismáticos e potenciais alvos de programas de conservação como o papagaio moleiro *Amazona farinosa* (Boddaert), o tamanduá-anão *Cyclopes didactylus* (Linnaeus) e o surucuá-de-coleira *Trogon collaris* Vieillot. Pretende-se submeter este trabalho à revista Molecular Ecology.

CAPÍTULO 1

POLISTINAE BIOGEOGRAPHY IN THE NEOTROPICS: HISTORY AND PROSPECTS

(Submetido para publicação: Journal of Hymenoptera Research)

Polistinae biogeography in the Neotropics: history and prospects

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Abstract

There has been a paucity of discussions regarding Polistinae biogeography in the last two decades. This well-known and very diverse group of insects is highly endemic in the Neotropics, but environmental factors influencing the enormous biological diversity in the region are not well established. Exploring evidence on the two main hypotheses concerning the origins and early colonization processes of paper wasps we position in favor of the Gondwanan hypothesis and discuss change-promoter processes in the Neotropics whose effects might have altered the distributions and facilitated the speciation of Polistinae in the region. Furthermore, based on recent advances in biogeography, mostly in the integration of ecological and evolutionary information, we highlight directions for future biogeographical research within the group.

Keywords Biological richness, ecology, evolution, paper wasps, speciation, species distribution

Introduction

It is surprising how young the biogeography of Polistinae is. Many questions remain unsolved or have never been posed for this subfamily. This gap in our knowledge is partially due to the absence of discussions linking variations (e.g., morphological, molecular and physiological) with historical processes. Exciting themes such as colonization routes, population genetics and phylogeography have not been featured in discussions of paper wasps' biology, thereby seriously limiting our ability to draw evolutionary conclusions. Furthermore, many recent advances in science have not been applied to the study of these insects. For example, it is not known how distributions of Polistinae species have changed during the Late Cenozoic or if existed and where refuges were located for forest-dwelling species during periods of extreme cold (i.e., the ice ages). These issues have already been explored and explanations have been proposed for some amphibians (Carnaval et al. 2009), birds (Batalha-Filho et al. 2012; Maldonado-Coelho 2012), ants (Resende et al. 2010) and plants (Pinheiro et al. 2013). Also, population relationships and historical demography are unknown for the Polistinae subfamily.

Compared with Africa, Europe and Asia, regions where paper wasps are abundant, an endemism of nearly 70% (~630 species) is recorded in the Americas (Richards 1978, Jeanne 1991, Silveira 2008) and most of the species are restricted to the Neotropics. In fact, these insects constitute a well-represented group in the Neotropical region, both in terms of abundance and richness. In addition, differences regarding both nest and body morphological traits and behavioral strategies (e.g., necrophilia, cyclic oligogyny) indicate that the region is the main hotspot for Polistinae or, using the words of O. W. Richards, is “the metropolis of social wasps” (Evans and West-Eberhard 1970).

Despite this richness, there is a paucity of biogeographic studies related to Polistinae. In fact, discussions regarding the origins and distribution patterns of this subfamily were not discussed by almost two decades; the last study on this subject before Silva and Noll (2014) was published by Carpenter (1996). However, factors related to the current distribution and success of paper wasps are typically associated with environmental conditions (e.g., Dejean et al. 2011). In addition, the historical reasons regarding the irradiation of these insects in the Neotropics – i.e., the explosion of species richness, likely during the Cenozoic – have not been discussed.

Many unanswered questions regarding the biogeography of these interesting insects can be posed: (1) what evidence exists supporting the biogeographical hypotheses on the origins of Polistinae and colonization of the New World?, (2) what are the primary ecological and environmental constraints shifting the distributions of the wasps and promoting changes in the Neotropics that make it “the metropolis of social wasps”? and (3) how did these wasps proceed while colonizing the New World? In this work we focus on the first two questions; the later is the theme of another ongoing study. In order to address these questions, we provide a brief review of the two main hypotheses regarding Polistinae biogeography (i.e., the Beringian and Gondwanan hypotheses) and associate historical processes such as climatic-vegetational changes, orogeny and global temperature oscillations with the promotion of changes in Polistinae diversity and distribution in the Neotropics. In the last section of the text, we highlight some perspectives that are, in our opinion, critical for a deeper understanding of Polistinae biogeography. We maintain that these perspectives will drive future knowledge in this field. If we are able to influence ecological and evolutionary integrative discussions about these wasps, our goals in this work will certainly be achieved.

Biogeographical hypotheses: origins of Polistinae and colonization of the Neotropics

Early biogeographical hypotheses stated that paper wasps originated in the tropics based on the high diversity of such insects in the region (Wheeler 1922, Richards and Richards 1951). The sympatric and restricted occurrence in the oriental tropics of the three social subfamilies of Vespidae (Stenogastrinae, Vespinae and Polistinae) and the presence of ancestral forms in nest architecture (West-Eberhard 1969) and basal morphological traits (Van der Vecht 1965) support assumptions that the Vespinae/Polistinae split likely occurred in southeastern Asia (Van der Vecht 1965, Richards 1971). According to these assumptions, the dispersion of paper wasps into the New World occurred twice through the Bering Strait in the Middle Tertiary and the current distribution therein was likely reached after the last ice age (Richards 1978).

Carpenter (1981) criticized the relation between center of diversity and center of origin and suggested that the distribution pattern of paper wasps is “widely Gondwanan.” It was also suggested by Carpenter (1993) that the separation between Africa and South America in the Early Cretaceous (120–100 million years ago; Mya) was an important event in the evolutionary history of the group. Carpenter (1996) also reviewed the two main hypotheses of Polistinae biogeography and performed Component Analyses for *Polistes* Latreille subgenera. Area cladograms presented in that work supported the Gondwanan distribution of subgenera and rejected the expected dispersion through the Bering Strait (as defended by Van der Vecht 1965, Richards 1971, 1978).

Other data also support the Gondwanan distribution of paper wasps and we reviewed some of these studies, focusing on paleontological, phylogenetic and divergence time evidence.

Fossil records

There are few data related to the paleodistribution of paper wasps based on fossil records. Despite this fact, important evidence that permits inferences about the biogeographic hypotheses was obtained by Brown (1941a) with a specimen from the Upper Cretaceous: a wasp nest comb of *Brownichnus favosites* (previously treated as genus *Celliforma*) from Utah, United States. The specimen shows traits comparable to papery nests, just like those of *Polistes*. This finding defined the presence of social behavior in insects earlier than that predicted in that time, from the Eocene to the Cretaceous, but Brown (1941a) was unable to determine the relationships of the specimen with today's social wasps.

After some discussions regarding the classification of such a comb in Bequaert and Carpenter (1941) and Brown (1941b), Wenzel (1990) confirmed that the comb is indeed from a social wasp. Despite the fact that Wenzel (1990) has not been conclusive about the relationships of *B*. *favosites* with present-day groups, the author advocated that the comb is certainly from a Vespinae or a Polistinae. Moreover, he defended that if *B*. *favosites* is an ancient *Polistes*, the vicariance hypothesis (i.e., Gondwanan) "should remain intact."

Phylogeny

Phylogenetic inferences have provided important information about the evolutionary history of Polistinae. Carpenter (1991) carried out the first cladistic analysis of the relationships among the genera of subfamily based on morphological and nest architecture characters. This analysis placed the cosmopolitan Polistini as the sister group to the other tribes. Ropalidiini (Old World), Mischocyttarini and Epiponini were grouped in a polytomy. Wenzel and Carpenter (1994) solved the polytomy by placing Mischocyttarini as an intermediate group and Ropalidiini and Epiponini as more derived groups. Pickett and Carpenter (2010), however, reviewed several molecular and morphological characters of Vespidae and placed Ropalidiini as the most basal group, followed by Mischocyttarini and Polistini + Epiponini as sister tribes.

The evolutionary history of *Polistes* has been the most thoroughly studied by phylogenetic assessments. We reviewed five of the main studies (Carpenter 1996, Zhu et al. 2000, Arévalo et al. 2004, Pickett and Wenzel 2004, Pickett et al. 2006) and noted that the Old World subgenera are invariably those at the base of the trees and that the New World subgenera are derived. We consider this settlement as a strong evidence for a more recent colonization in the western tropics. Likewise, considering that Mischocyttarini and Epiponini only occur in the Neotropics, and that no fossils of these groups were recorded outside of this region [following the suggestion of Carpenter and Grimaldi (1997) in not considering the misidentifications of two *Polybia* Lepeletier found in Burnham (1978) from England] and if genus *Paleopolistes* from France is not an Epiponini (Perrard and Carpenter 2014) we are tempted to give credit to the hypothesis that both tribes arose in the New World after the separation of Africa and South America (120 Mya).

Divergence time estimates

Ezenwa et al. (1998) raised assumptions that even though the oldest known paper wasp fossil dates from the Cretaceous (Brown 1941a), the Vespinae/Polistinae split likely occurred in the Middle Jurassic (about 175 Mya) and the four tribes arose between 175 and

80 Mya. These assumptions, although not tested empirically, strengthen the hypothesis of a possible colonization of the Americas in a Gondwanan scenario due the exclusivity of Mischocyttarini and Epiponini in this region.

Based on these data, we tend to give credence to the Gondwanan hypothesis as a reasonable and convincing assumption able to explain the origins and colonization processes of the worldwide Polistinae distribution, as well as early colonization routes.

The life in the metropolis

Distinct from other regions of the globe, the Neotropics are composed of large, humid forests that have undergone several changes (Hoorn et al. 2010). These forests harbor most of the paper wasp fauna in the region (Richards 1978). The causes for the high biodiversity levels in these rainforests have been recurrently associated with environmental changes and hypotheses regarding extrinsic processes (non-genetic mechanisms) that facilitate speciation in the biota, mostly in the Amazonian region, have also been explored in previous studies. Haffer (1997, 2008) provided extensive reviews concerning these hypotheses and argued that several of them are relevant to speciation processes in different geological periods of the Cenozoic.

Although environmental processes have not been commonly explored to explain the diversity of paper wasps in the Neotropics, historical and recurrent events have certainly provided evolutionary scenarios for adaptive irradiation of this group in the region. Richards (1978) recognized that climate and vegetation changes in South America have mixed the distribution of paper wasps during the geologically recent past of Brazil. Dejean et al. (2011) associated the fluctuation of species richness to climatic phenomena such as El Niño and La

Niña in French Guiana. However, empirical analyses and theoretical assumptions regarding environmental factors able to induce putative alterations in populations of paper wasps have not been sufficiently discussed. Here, we provide a quick review of the main hypotheses concerning speciation processes in the Neotropics. We aim to highlight the major environmental events that we consider to have been involved in the Neotropical irradiation of Polistinae during the Cenozoic. Other proposals can be found in the reviews of Haffer (1997, 2008), including the Gradient, Canopy-density and Museum hypotheses; we opted not to include these hypotheses in this work because the arguments used to explain speciation processes are less general in these hypotheses than in those presented here.

Climatic-vegetational changes: the Refuge hypothesis

The Refuge hypothesis predicts the occurrence of putative forest refuges – regions where forests remain unaltered irrespective of global temperature oscillations – during the Cenozoic and before, i.e., more than 60 Mya (Haffer 1997, 2008). Even so, Haffer (1969) proposed initially that climatic-vegetational changes during the Pleistocene (1.8–0.1 Mya) were the main causes for novelties and speciation processes to arise in the Amazonian rainforest. This idea suffered criticisms (e.g., Bush and Oliveira 2006) and was not supported by many studies that contested the short timespan for speciation events predicted initially by the author since most of the Neotropical groups likely arose before the Pleistocene (e.g., Zink and Slowinski 1995, Costa 2003, Geurgas et al. 2008).

Haffer modified his earlier ideas based mainly on Bennett's (1990) assumptions regarding the influences of Milankovitch cycles on communities over a time scale of 20–100 thousand years, or ky. These cycles, caused by alterations in the Earth's orbit, would have affected population structures and caused disruptive events in the Neotropical communities and might be the main factors responsible for oscillating the climate of the planet due to its influence on glacial/interglacial cycles (see Bennett (1990) for complete explanations on the Milankovitch cycles). In summary, the Refuge hypothesis (Haffer 1997, 2008) is particularly based on the effects of dry/humid periods of the Cenozoic on the speciation events in the Amazonian rainforest.

Some refuges have also been proposed for the Brazilian Atlantic Forest (e.g., Carnaval and Moritz 2008, Carnaval et al. 2009), suggesting that these areas might have indeed served as stable forest patches for many forest-dwelling taxa throughout climatic-vegetational changes. Moreover, because each species has its own ecological niche, idiosyncratic responses to alterations as well as different distribution of refuges are expected for different species.

Richards (1978) considered that climatic-vegetational changes could have affected the distribution of species but pointed out that paper wasps had not showed clear evidence for refuge areas. Indeed, there are no empirical data concerning this matter, but distribution of some species denote that the retraction of South American rainforests during dry periods disrupted populations of *Epipona media* Cooper, *Synoeca septentrionalis* Richards and *Angiopolybia pallens* (Lepeletier) (Menezes et al. 2010, 2011, Carvalho et al. 2014).

Phylogeographic analyses carried out with the extinction-threatened ant *Dinoponera lucida* Emery (Resende et al. 2010) and with orchid bees (López-Uribe et al. 2014) indicated that, in fact, different size refuges were important for the creation and maintenance of hymenopterans' diversity in the Neotropical rainforests. For paper wasps, however, there are no studies on this matter.

Paleogeography and River hypotheses

According to these hypotheses, different models are expected to have caused geographic separation and speciation of the animal populations in the Amazonian rainforest that are related to worldwide sea level changes, uplifts of plateaus and flooding of plains. The emergence of islands (Island Model (Emsley 1965, Croizat 1976)), archs (Arch Model (Morell 1996)), lagoons (Lagoon Model (Marroig and Cerqueira 1997)) and rivers (River hypothesis (Sick 1967)) in the Amazonian basin were recognized as historical events that putatively shifted species' distribution ranges, facilitating their differentiation.

Despite Haffer (2008) arguing that some of these inferences are highly speculative and contain several missing links, it is possible that such alterations in the geography of the Amazonian region, if they occurred during the Cenozoic, would have provided a great variety of environments for diversification of paper wasps. Furthermore, it is not surprising that large bodies of water might act as barriers to the flow between disrupted populations of land species. For wasps, that would not be different. Indeed, swarms have great difficulty in dispersing across water. This fact possibly affected the decline of paper wasps in the Caribbean, for example, due to limitations of the chemical trail system, but might not be a very convincing overall explanation since the tribe is present throughout Southeast Asia, the Philippines, and Australia (Jeanne 1981, Carpenter and Grimaldi 1997), for example.

Mainland species in turn might also have had their distributions altered during landscape changes in the Cenozoic caused by both water barriers and land uplifts. Unfortunately, although these alterations have influenced substantially the distribution of some land organisms (Croizat 1976, Hershkovitz 1977), it is not possible to our knowledge to quantify precisely how much these changes have contributed to extinction, disruptions and speciation events of paper wasps.

Disturbance-Vicariance hypothesis

This hypothesis regards the influence of cold/warm cycles (not dry/humid, as proposed by the Refuge hypothesis) as selecting Amazonian lineages throughout temperature oscillations during the Pleistocene (Colinvaux 1993, Bush 1994). Invasion, counter-invasion and competitive interactions are seen in this model as events affecting distributions and abundances of species. According to these assumptions, the presence of invading and cold-adapted taxa could have resulted in local extinctions, favoring isolation of genotypes and allopatric speciation of some taxa.

There is a regional focus of this hypothesis on the peripheral areas of the Amazonian rainforest due to the high faunal endemism in such areas. Such regions are recognized by the model as being rich in endemic taxa due to their supposed environmental instability. Indeed, temperature oscillations during the Pleistocene might have influenced the distribution of taxa and genotypes, but speciation events are mostly expected to have occurred before 1.8 Mya (Zink and Slowinski 1995, Costa 2003).

The Quaternary is undoubtedly a short time to explain the huge diversity of paper wasp species in the Neotropics. Both temperature oscillations and the short period, however, are apparently sufficient for population structuring mainly of widely disrupted taxa. Polistinae species might have undergone their distribution to optimal locations during such changes in the temperature and environmentally related genotypes might have been frequently selected. Such alterations might also have influenced both behavioral and physiologic traits, including feeding habits, defense, nest building, resistance to diseases and predators and adaptive strategies against cold or warm climate. Future researches are undoubtedly needed for accurate detailing.

Future directions

Since ecological and phylogenetic information can comprise very useful frameworks for raising hypotheses on historical biogeography in scenarios constantly in change, to explore the different impact of variables on the distribution of Polistinae is an important subject to be discussed. Furthermore, the knowledge of environmental and geological constraints that affect distribution of species can help predictions about extrinsic mechanisms shifting large-scale distributional patterns. In addition, to resolve important questions like the causes of some clades disperse to some areas but not to others is the major challenge in historical biogeography (Wiens and Graham, 2005) and define the favorable and unfavorable conditions that unbalance population density over time figures as a crucial factor to describe distribution of any group (Haldane 1956). However, understanding how extrinsic factors alter distribution we can determine environmental and ecological constraints that species can tolerate or not and, likewise, which regions these species might occupy by dispersal events.

A very promising group of paper wasps for start this kind of research is that composed by forest-dwelling species. Using data regarding current distribution, one can propose past and present distributions of acceptable conditions for a clade to occur, based on ecological niche modelling, for example (e.g., Hugall et al. 2002, Carnaval et al. 2009). Since the bioclimatic conditions that maintain the distribution of humid forests have changed in the Neotropics during ice ages and since forest-dwelling species depend on forest coverage to nest and forage, the distribution of these wasps has likely responded in a convergent manner to these alterations. Thinking about the biogeographic research of paper wasps in the next years, the formulation of potential paleodistribution models might be considered a cornerstone that will drive population genetics hypotheses, mostly based on phylogeographic frameworks, in studies of these insects.

Specialized literature related to the distribution or phylogenetics is very common for different clades of paper wasps. However, a fine-scale distribution pattern of Neotropical Polistinae could be more precisely understood by reviewing specialized literature; i.e., species by species. Also, tests of hypotheses using these data for making inferences about the ecological and evolutionary causes of the success or failure of Polistinae in colonizing certain regions have been rarely done. For example, the Tropical Niche Conservatism hypothesis (Wiens and Graham 2005) could explain the tendency of paper wasps to inhabit tropical areas instead of temperate regions since the subfamily was originated in a similar environment (i.e., tropical Asia). A strategy for testing such a hypothesis could be based on the integration of physiological responses, such as thermoregulation, and population relationships in the study of dry-adapted lineages of paper wasps. Since niche conservatism predicts that unaltered lineages are not likely to habit areas characterized by conditions different from fundamental niches, lineages of a clade showing thermoregulatory responses different from their ancestral populations would be expected to be adapted to local climatic alterations as a result of niche expansion.

Many recent studies have shown that integrative approaches linking climatic and phylogeny-based information to explain biogeographical patterns might be very useful for testing explicit hypotheses of causation by particular, mostly environmental, events (Hugall et al. 2002, Waltari et al. 2007, Carnaval et al. 2009). Moreover, recent discussions have drawn attention to the strong connection between evolutionary processes (e.g., ecological specialization) and environmental events such as climatic-vegetational changes in shaping the distribution of organisms over time (Wiens 2004, Hoorn et al. 2010). Quantifying the different impacts of each of these factors in the evolutionary history of Polistinae should be regarded as the main challenge in the future of biogeography and speciation research of the subfamily. The study of biogeographical processes using such wasps as models can also aid in our understanding of significant events that have influenced the distribution, historical demography and extinctions of the Neotropical biota, including the disjunction between Amazonia and Atlantic Forest and the demographic retraction of populations adapted to rainforest conditions during glacial periods, for example.

Despite Ezenwa et al. (1998) have proposed possible periods for the arising of the Polistinae tribes, current techniques are more precise for inferring divergence times. Based on a molecular clock model, which permits dating putative splits between lineages using fossil-calibrated phylogenetic trees, the proposal of the geological periods in which the subfamily Polistinae and its four tribes arose, as well as temporal concentration of speciation events, would be more convincing. Such research could also be conducted to test hypotheses regarding the influence of geological events such as river formation and land uplifts on the separation of lineages since the periods in which these events occurred are known.

In light of the differences regarding life histories, occupied niches, huge diversity, etc., the Neotropical paper wasps represent an interesting group to be used as model in a wide range of studies. However, in almost 20 years of apparent inertia, biogeographic patterns as colonization routes and causes behind alterations on the distribution were not explored using advanced analyses. We expect that by focusing on some of the challenges presented in this work, the study of biogeography with these wasps will progress in the forthcoming years.

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CAPÍTULO 2

PROGRESSION RULES AND NEOTROPICAL POLISTINAE: THE ROUND-TRIP HYPOTHESIS

(Periódico pretendido: Neotropical Entomology)

Progression rules and Neotropical Polistinae: the Round-trip hypothesis

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Abstract

Biogeographic studies with the subfamily Polistinae are rare. Using the wide concept of progression rules as null hypothesis we test if intuitive predictions of this model are confirmed in these wasps. Such concept is based on the relations between centers of origin and basal forms and, conversely, recently colonized areas as those where novelties are commonly seen. Our analyses consisted in carefully review distribution of several social wasps (Polistinae) whose phylogenies are available and associate this information (i.e., phylogeny-distribution relationships) to colonization routes. This procedure permitted us to find a two-step colonization fashion in the Neotropical region, based on the progression rules principle, which we propose as the Round-trip hypothesis. First route (east to west) is rare, being seen in a small group of *Polistes* and second (west to east) is remarkably repeated in several other lineages. So, we propose northwestern Neotropics (mainly

Amazonia basin) as the major center of origins of Neotropical Polistinae and conclude that Round-trip hypothesis might explain both earlier and later colonization routes of paper wasps analyzed.

Key-words

Biogeography, colonization routes, distribution range, phylogeny, social wasps, Vespidae.

Introduction

"Within a continuous range of different species of a monophyletic group, the transformation series of characters run parallel with their progression in space" – Hennig's progression rule [as seen in Morrone and Crisci (1995)]. In other words, Hennig's (1966) prediction assumes that more geographically displaced taxa in a lineage should show the more derived character states, while the clades that remained nearer the center of taxon origins should exhibit basal characteristics.

At first glance this concept might sound ingenuous due the natural idiosyncrasy of each taxon against environmental, ecological and genetic constraints. Centers of origin might be those in which apomorphic traits are seen today as well and both explanations might be true for different taxa. The substitution of certain form by another depends on how lineages were formed, dispersed and interacted with their biotic and abiotic environments (Brown and Lomolino 1998). Progression rules, however, might be seen as a noteworthy null hypothesis for predictions on the distribution of clades due to the inherent reasonability and possibility of test over phylogenetic and distribution integrative models. Doing such procedure, the remarked phylogenetic predictability registered for islands (Rundell et al. 2004, Gillespie

2005, Parent et al. 2008, Rubinoff 2008) could also be tested, maybe confirmed, within continental areas.

We use paper wasps (Hymenoptera: Polistinae) to test if the predictions of progression rules explain satisfactorily colonization routes in the Neotropics. These interesting social insects, whose distribution of four tribes (Polistini, Mischocyttarini, Ropalidiini and Epiponini) is mostly tropical, have well-established phylogenies of both high and low taxonomic levels, but biogeographic patterns within the Neotropical region are not well-known so far. Two analogous hypotheses have figured in the center of biogeographical discussions during the last century (i.e., Beringian and Gondwanan hypotheses) and the understanding of large-scale distribution patterns regarding these wasps remain uncertain due the limited attempts of explaining such patterns. The absence of both refined and strongly supported proposals concerning colonization routes limits the raising of biogeographical hypotheses and the clear understanding concerning the historical reasons behind the success of these insects, mainly in the Neotropics.

In this work we review the distribution of 104 Neotropical species belonging to eight genera of Polistinae whose phylogenetic relationships are available aiming to clarify probable routes used by such insects during the colonization of the Neotropics. For this, we use phylogenetic and distributional data to propose colonization routes based on progression rules principle (Hennig 1966). We defend that early colonization of Americas by paper wasps happened over a Gondwanan scenario (as proposed by Carpenter 1981, 1993, 1996) and that Neotropical biogeography of Polistinae might be explained, in wide-terms, by a two-step colonization fashion, as suggested by the proposed Round-trip hypothesis.

Methods

Aiming to test if progression rules predict colonization routes of paper wasps in the Neotropics, we integrate phylogenetic and distribution data of 104 species belonging to *Polistes* Latreille, *Mischocyttarus* de Saussure and six genera of Epiponini. For this, we reviewed the positioning of such species in recent phylogenies and associate information to distribution data present in Richards' (1978) catalogue and surveying works. After building such dataset, information was used to infer colonization routes, as shown in Figure 1.

Our predicted colonization routes of Polistinae in the Neotropics are tested through integrated analyses of phylogeny and distribution of basal, intermediate and derived groups within *Polistes* (phylogeny seen in Pickett et al. 2006 and Pickett and Carpenter 2010), *Mischocyttarus* (Silveira 2008), *Angiopolybia* Araujo (Andena et al. 2007a), *Pseudopolybia* de Saussure (Andena et al. 2007b), *Chartergellus* Bequaert (Andena, 2007), *Synoeca* de Saussure (Andena et al. 2009a), *Epipona* Latreille (Andena et al. 2009b) and *Apoica* Lepeletier (Pickett and Wenzel 2007).

More diverse genera as *Polistes* and *Mischocyttarus*, for example, are divided into several subgenera and phylogenies of such groups follow this classification. Also, many groups have more than one monophyletic clade (e.g., subgenus *Aphanilopterus*). Due this, we carried out the analyses for each subgenus (and/or lineage) whose useful phylogenetic information (i.e., those well-resolved lineages – i.e., nonpolytomic – that permit to associate phylogeny to a spatial progression) is available. After this, we raise a hypothesis that might explain in wide-terms both early and late colonization routes of Polistinae in the Neotropics.

We did not evaluate relationships within *Charterginus* Fox (phylogeny seen in Andena et al. 2009c) due the exclusivity of this genus in Amazonia and *Polybia* Lepeletier once the phylogeny proposed by Carpenter et al. (2000) analyzed phylogenetic relationships among subgenera and species relationships are not completely resolved so far. Relationships within *Brachygastra* Perty (Andena and Carpenter 2012) did not provide associations with progression rules. Because phylogenetic reconstruction of genetic and morphological data can be very time-consuming and are not likely to provide new insights, we decided not to reconstruct the phylogenies and, instead, only discuss the results previously published. Although the results of Pickett and Carpenter (2010) cover significantly the within-genus relationships discussed here, we opted to use information mostly from single taxa studies (e.g., Pickett et al. 2006, Silveira 2008, Andena et al. 2007a) because of the amount of incongruences seen in the first work relative to the others (as, for example, the positioning of Polistini as derived in relation to Ropalidiini as well as Mischocyttarini as sister group of Epiponini). Adapted schemes and references of each phylogeny used by us are shown in Figure SM1.

Results

Polistini (*Polistes*)

The evolutionary history of *Polistes* has been issue of several recent phylogenetic reconstructions and both morphologic and molecular analyses have been carried out since Carpenter’s (1996) subgenera phylogeny. These analyses stated the basal positioning of Old World subgenera but did not resolve entirely the relationships among derived New World groups. Pickett et al. (2006) carried out a meta-analysis using both previously available and new data to propose a robust phylogeny for this group. Such study set *Polistes sensu stricto* as the sister group of New World subgenera which are arranged into five subgenera disposed in three main clades (*Aphanilopterus* + ((*Palisotius* + *Epicnemius*) + (*Onerarius* + *Fuscopolistes*))).

In the subgenus *Aphanilopterus* three clades are separated and exhibit two phylogeny-distribution patterns. Firstly, the group that apparently tracked the colonization route from eastern South America towards Amazonia, Central and North America. This group is represented by a clade in which *P*. *simillimus* Zikán (eastern Brazil to Argentina) is determined as basal (see the distribution of this and the other species discussed in this study in Table 1). In this clade is also present *P*. *crinitus* (Felton) (three subspecies) that belongs to a Caribbean group, whereas *P*. *exclamans* Vierek (seven subspecies) and *P*. *instabilis* de Saussure might be found from Costa Rica to USA. These later species compose the derived lineages (see Pickett et al. 2006). Phylogeny-distribution relationships of such clade reveal a progression rule that support a route from east to west, but this route is very rare, being accessed by us only in this lineage.

Secondly, the clade whose relationships reveal a spatial progression from North America towards eastern South America. This route is supported by the exclusivity of basal species *P*. *goeldii* Ducke, *P*. *apicalis* de Saussure, *P*. *annularis* (Linnaeus) and *P*. *commanchus* de Saussure in northwestern Neotropics (NN) and Nearctic Region and the distribution of more derived species *P*. *canadensis* (Linnaeus) and *P*. *lanio* (Fabricius) from the Nearctics to eastern Brazil, as well as the exclusivity of *P*. *cavapyta* de Saussure in southern South America.

In the clade composed by the subgenera *Palisotius* and *Epicnemius* is seen mostly widespread species which are not far informative under the perspective of progression rules. *Onerarius* and *Fuscopolistes* are composed by, mostly, North and Central America (NCA) species.

Mischocyttarini (*Mischocyttarus*)

Mischocyttarus is a highly diverse genus, composed by several species with endemic and very restrict distribution, divided by Silveira (2008) into eleven subgenera. Silveira's (2008) phylogeny set a basal node that separates the genus into two major clades: *Clypeopolybia* and *Mischocyttarus sensu stricto* branch and a second branch joining remainder groups. *Clypeopolybia* presented polytomies and is not far informative. *Mischocyttarus sensu stricto*, however, presents *M*. *acunai* Alayo (NCA) and northwestern species *M*. *tomentosus* Zikán and *M*. *smithii* (de Saussure) and the derived *M*. *drewseni* de Saussure which is widespread.

Second major branch presents subgenus *Monogynoecus* as the most basal. We reviewed distribution of species included in this subgenus and noticed that eight of the ten species are restrict to northwestern Neotropics. However, there is not a progression of species relationships in the phylogeny which permit us to propose ancestral or more recent areas for this lineage. Phylogeny-distribution inferences are evident in this branch, in turn, for the subgenera *Kappa* and *Omega*. All the basal species included in the phylogeny of both subgenera are those from northwestern and/or central Neotropics whereas more derived species *M*. (*Kappa*) *funerulus* Zikán and *M*. (*Omega*) *buyssoni* (Ducke) are only found in eastern Neotropics and discretely in central Brazil.

Epiponini

Angiopolybia

Phylogenetics of the mostly Amazonian genus *Angiopolybia* (Andena et al. 2007a) separates the four species into two clades: [*A*. *obidensis* (Ducke) + *A*. *paraensis* (Spinola)] + [*A*. *pallens* (Lepeletier) + *A*. *zischkai* Richards]. *A*. *pallens* is the species that presents the widest distribution, ranging from Panama to eastern South America. Such species shows a disjoint distribution between Neotropical rainforests Amazonia and Atlantic Forests and Carvalho et al. (2014) proposed western lineages as ancestral of Atlantic populations. Other three species are exclusive to the northwestern Neotropics.

Pseudopolybia

Andena et al. (2007b) presented phylogenetic relationships among the four species of *Pseudopolybia*. This genus is distributed in the Amazonian region, central Brazil and Atlantic rainforest. *P*. *langi* Bequaert and *P*. *difficilis* (Ducke) are endemic in northwestern Neotropics while *P*. *vespiceps* (de Saussure) and *P. compressa* (de Saussure) are the only species which occur in eastern South America. The later two species are stated within the more derived grouping by Andena et al. (2007b).

Chartergellus

Chartergellus is a small genus occurring in Central and South America, ranging from Costa Rica to southern Brazil. Andena (2007) presented phylogenetic relationships among the eight species of this genus and set *C*. *zonatus* Spinola + (*C*. *nigerrimus* Richards + *C*. *sanctus* Richards) as the more derived clade. *C. zonatus* occurs in both Amazonia and Atlantic Forest and *C*. *sanctus* is endemic to the eastern portion of South America (Brazilian state Espírito Santo). All the other species are restricted to northwestern Neotropics. *C*.

communis Richards and *C*. *atectus* Richards also occurs discretely in central Brazil and NCA, respectively.

Synoeca

The genus *Synoeca* is composed by five species. *S*. *septentrionalis* Richards shows a disjoint distribution in the western and eastern rainforests (Menezes et al. 2011) whereas *S*. *surinama* (Linnaeus) is easily found in Amazonia and Atlantic Forest and, discretely, in the Brazilian savannah associated with gallery forests. *S*. *cyanea* (Fabricius), in turn, is the only species endemic to the eastern portion of South America. The other two species *S*. *virginea* (Fabricius) and *S*. *chalibea* de Saussure are basal and restricted to the western rainforests.

The genus is focus of recent discussions concerning phylogenetic relationships and taxonomic characters (Andena et al. 2009a, Cely and Sarmiento 2011, Carpenter et al. 2013). Phylogenetic inferences presented by Andena et al. (2009a) and Carpenter et al. (2013) showed that the clade *S*. *cyanea* + *S*. *surinama* is the more derived of this genus and support a common ancestry with *S*. *septentrionalis*. The remarkable intraspecific variation of the genus observed by Cely and Sarmiento (2011) and Menezes et al. (2011) show the importance of population studies with the group.

Epipona

Phylogenetic relationships of genus *Epipona* were determined by Andena et al. (2009b). This five species genus is mostly Amazonian. However, *E*. *tatua* (Cuvier) is also found in the Brazilian states Bahia, Espírito Santo and São Paulo and *E*. *media* Cooper was recently sampled in the rainforests of Bahia (Menezes et al. 2010). These two species are settled as close by Andena et al. (2009b). All the other species *E*. *niger* Brèthes, *E*. *guerini* (de Saussure) and *E*. *quadrituberculata* (Gribodo) are endemic in northwestern Neotropics.

Apoica

Apoica is a nocturnal genus with broad distribution in the Neotropics. It is composed by ten species and the only phylogenetic study regarding this genus (Pickett and Wenzel 2007) did not solve entirely the relationships among the species. However, *A*. (*Deuterapoica*) *arborea* de Saussure is stated as the most basal (statement also seen in Pickett and Carpenter 2010) and only occurs in the northwestern Neotropics and central Brazil. Four of the other nine species have wide distribution and might be found both in dry (savannah and caatinga) and in humid forests (Amazonia and Atlantic) of South America. *Ap*. *pallens* (Fabricius) and *A*. *thoracica* du Buysson, particularly, are those with broader occurrence in the Atlantic rainforest.

Discussion

Achieving the Neotropics

Carpenter (1996) indicated present-day Indian Ocean (Indomalayan region) as the best candidate for the place where paper wasps arose (*Polistes*' center of origin). Two conclusions might be drawn about colonization of the Neotropics using this statement due to the location of this region in Asia since Early Eocene [~50 Mya (Rowley 1996)] and the contiguous Gondwanan location of India and Africa. These two analogous conclusions denote that polistine expansion towards New World might have followed the route (1) Indomalayan region – Eastern Asia – Beringia – New World (Figure 2a) or the route (2) Indomalayan region – Africa – New World (Figure 2b), respectively.

Richards (1971) advocated the first route as the path used by paper wasps to achieve New World and that this track was performed twice: firstly by an ancestral polistine and secondly by *Polistes*. This route would imply a late colonization of the Americas in the mid Tertiary such as Richards (1978) suggested and, intuitively, the emergence of paper wasps in South America via Isthmus of Panama. This route was accepted during a long time (see Van der Vecht 1965, Richards 1971, 1978, Reeve 1991) as the more plausible in explaining colonization of the Neotropics due the suggested origins of Vespidae in Late Cretaceous and social wasps in Tertiary [see comments in Carpenter (1996)], data which are not empirically sustained.

Second route in turn proposes that the colonization process did not track over the Nearctic region to achieve Neotropics. This route is associated to an earlier origin of Polistinae and to a vicariant event which disrupted South American/African biota during a late stage of Gondwana breakup (Carpenter 1993). This route is supported by findings regarding an American fossil vespid from Upper Cretaceous (Brown 1941a, Wenzel 1990), Component Analyses carried out by Carpenter (1993, 1996), phylogenetic inferences (Carpenter 1991, Wenzel and Carpenter 1994) and supposed divergence times concerning the origins of Polistinae (Ezenwa et al. 1998).

This later route suggests an early colonization of eastern South America and a late colonization of Central and North America. However, there are no empirical assessments validating these intuitive observations. Aiming to test such hypothesis (i.e., origins of Neotropical Polistinae in eastern South America) one might argue that the diversity and high level of endemism found in Amazonia (Richards 1978) is pointing to a contrary pattern. In addition, Amazonia figures as the probable center of origin of many paper wasps (e.g., Carvalho et al. 2014). Trying to solve this dilemma we reviewed the distribution of 104

Neotropical Polistinae whose evolutionary relationships are known. As our comparisons showed, the predictions concerning the hypothesis that we raise here (see below) might be able in explain large-scale distribution patterns of these wasps by two routes. We expect that this hypothesis might be tested afterwards by the use of other lines of evidence, as well as by studying other clades.

The Round-trip hypothesis

Using both phylogenetic information and distributional data provided by Richards (1978) and several other works (Table 1) we reviewed carefully the current distribution of 104 paper wasps and assume herein that the members of subfamily Polistinae have mostly followed a two-step colonization fashion in the New World. First, the route used by *Polistes* towards North America (Figure 3a) and second the route from west to eastern coast of South America used by other *Polistes*, *Mischocyttarus* and Epiponini (Figure 3b).

Most of the basal clades within these groups are those whose distribution is restricted to Amazonian rainforest whereas intermediate and derived species are widely distributed (i.e., widespread species) or uniquely seen in the Atlantic rainforest. In a small portion of the basal subgenus *Polistes* (*Aphanilopterus*), however, the opposite is detected. As our parsing shows, each monophyletic clade (be it a genus, a subgenus or a group within a subgenus) exhibits its own progression rule, with multiple colonization waves from ancestral areas towards newer ones.

In sum, the Round-trip hypothesis states that each monophyletic group of paper wasp shows its own progression rule, with an early colonization wave from eastern South America towards west and multiple waves from Amazonia towards east.

Biogeographical implications of the Round-trip hypothesis

Biogeographic inferences using phylogenetic relationships have not been raised for most of these groups so far. We reviewed distribution of each species whose phylogenetic relationships are available and noted that the basal positioning of the exclusively Amazonian species figures as a constant topology seen in the phylogenies. Widespread and exclusively Atlantic rainforest species in turn are commonly those more derived; a fact that evidences a model of recent colonization of eastern South America. However, a different and rare progression rule is seen in the basal genus *Polistes* which demonstrate the opposite direction of colonization. The analyses of distribution of several species prompted us to raise a hypothesis that explains this pattern, the Round-trip hypothesis.

Our inferences concerning distribution patterns of paper wasps in the Neotropics are tested here through association of phylogenetic and distributional information. These associations indicate that ‘east to west’ route was used by a small portion of living groups whereas ‘west to east’ route is highly representative. Such appraisals indicated a two-step colonization fashion and provided information to propose that northwestern Neotropics (especially Amazonia basin) are the major center of origins for Polistinae.

We are inclined to believe that current diversity was probably reached during Cenozoic (Tertiary and Quaternary) landscape changes, mainly due to glaciation events as defended by Richards (1978), and that environmental conditions during analogous environmental conditions (i.e., glacial and interglacial periods) selected different and efficient adaptive strategies for the establishment of most of paper wasps in the Neotropics. Amazonian and Atlantic rainforests might have sheltered many forest-dwelling species during dry periods which, in humid periods, scattered and occupied their recent distribution areas. Disjoint distributions between Amazonia and Atlantic rainforests are commonly recorded for some polistines (see Menezes et al. 2010, 2011, Carvalho et al. 2014) and denote that expansion through a rainforest corridor was used as a route by forest-dwelling species before long-term glacial events (Figure 3b). Generalists and dry-adapted lineages, in turn, might have suffered several speciation events within Amazonian region and had their distribution ranges enhanced since Middle Tertiary at least; achieving savannah and caatinga, for example.

Our inferences about colonization of the Neotropics by paper wasps through a two-step colonization fashion are based on the distribution data allied to morphological and molecular phylogenetics. Further analysis might obviously be drawn in order to test these assumptions and we encourage those evaluations especially based on phylogeographical approaches.

Final Remarks

Area cladograms presented by Carpenter (1996) indicate that dispersion across Beringia towards New World is not supported in a phylogenetic context and that colonization of paper wasps in New World must be more parsimonious over a Gondwanan scenario. Moreover, fossil records, phylogenetics and divergence times are evidences that strengthen the intuitive assumption that polistine colonized firstly Africa and later scattered through Americas. Distributional data, however, denote that northwestern Neotropics, especially Amazonia, are the probable center of origin of several lineages. Interestingly, this broadly repeated pattern is not the only. We reviewed carefully the distribution of several species of the three Neotropical Polistinae tribes and found a reverse pattern exclusive to a small group within the basal genus *Polistes*.

This first evaluation concerning the Round-trip hypothesis based on phylogeny and current distribution would not be treated as conclusive. We acknowledge further appraisals following phylogeographic approaches mainly within the group *Polistes* (*Aphanilopterus*) for deeper conclusions. Furthermore, particular analyses concerning widespread distributed species might clarify important issues on the colonization routes used by Polistinae in the Neotropical region.

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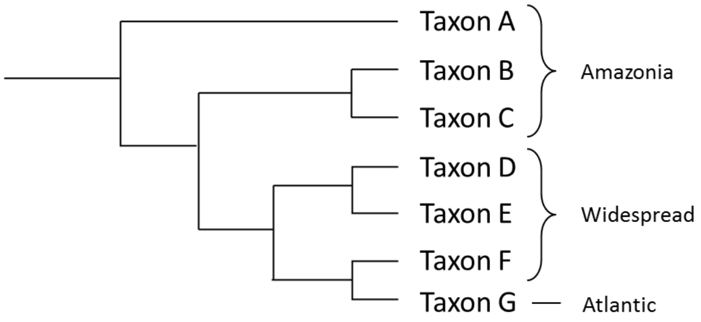


Figure 1: Schematic example showing how the associations between phylogenetics and distribution data were used to infer expansion of distribution range of a given lineage in the Neotropical forests. This example refers to ‘west to east’ route, the most common. The inverse pattern (i.e., Atlantic species in the basal positioning) is omitted of the scheme. Widespread distribution refers to the occurrence in Amazonia and other biomes (including dry forests as savannah and/or caatinga) and this is followed in the entire text.

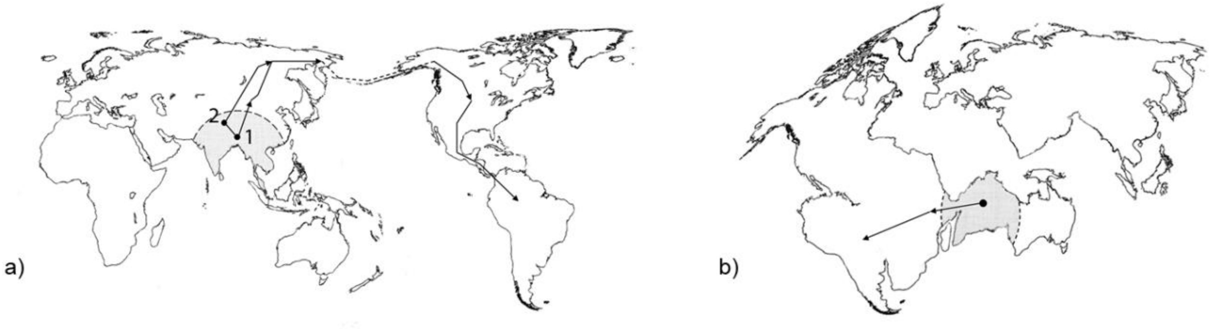


Figure 2: Current hypotheses regarding Polistinae biogeography: a) Beringian hypothesis; 1 and 2 refer to the two Polistinae lineages which have independently achieved Neotropics. b) Gondwanan hypothesis. Shadowed areas refer to probable centers of origin of Polistinae in the Indomalayan region, as proposed by different works (see text for references).

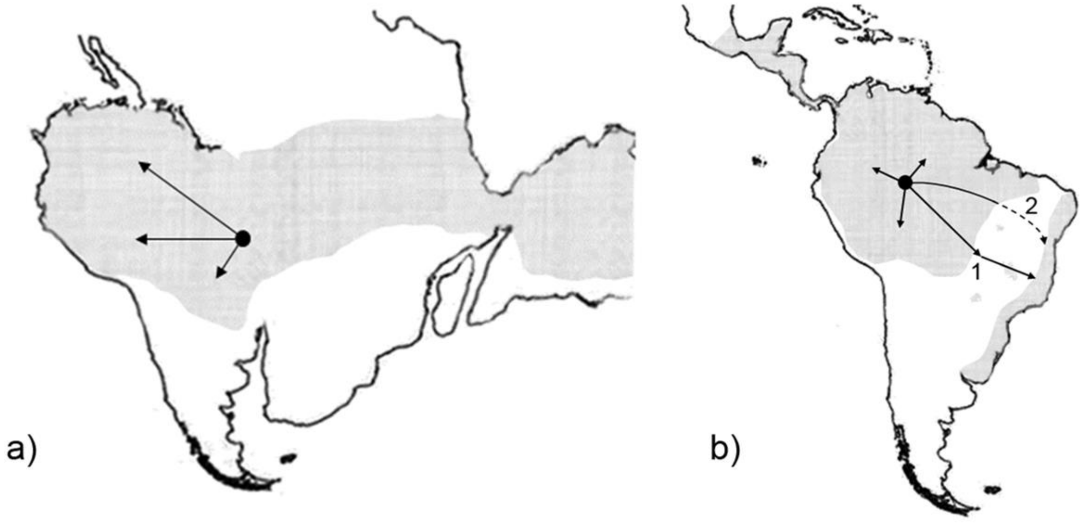


Figure 3: Predictable colonization routes of Polistinae in South America as predicted by the Round-trip hypothesis. a) Early colonization route ‘east to west’, predicted as a route used by ancestral groups (e.g., *Polistes*); b) late colonization routes ‘west to east’: 1 – generalists and dry-adapted species; and 2 – rainforest-dependent species (colonization happened through former connections between Amazonia and Atlantic Forest; this route explains the current disjoint patterns seen in *Angiopolybia pallens*, for example). Shadowed areas roughly correspond to tropical, rainforest-like in b, forests.

	Taxa	Distribution			
		NCA	**NN**	**CN**	**S+E**
***Polistes* (*Aphanilopterus*)**	*annularis* (Linnaeus)	■			
	apicalis de Saussure	■	■		
	biguttatus Haliday				■
	brevifissus Richards			■	■
	buyssoni Brèthes		■	■	
	canadensis (Linnaeus)		■	■	■
	cavapyta de Saussure				■
	cavapytiformis Richards				■
	commanchus navajoe Cresson	■			
	commanchus commanchus de Saussure	■			
	consobrinus de Saussure				■
	crinitus crinitus (Felton)	■			
	crinitus americanus (Fabricius)	■			
	crinitus multicolor (Olivier)	■			
	erythrocephalus Latreille	■	■	■	■
	exclamans exclamans Viereck	■			
	exclamans bahamensis Bequaert and Salt	■			
	exclamans picturatus Bequaert and Salt	■			
	exclamans bilineolatus Bequaert and Salt	■			
	exclamans arizonensis Snelling	■			
	exclamans lineonotus Bohart	■			
	exclamans durangoensis Snelling	■			
	ferreri de Saussure			■	
	goeldii Ducke	■	■	■	
	instabilis instabilis de Saussure	■			
	instabilis coahuilae Richards	■			
	lanio lanio (Fabricius)*		■	■	■
	melanotus Richards		■		
	satan Bequaert			■	
	simillimus Zikán		■		■
	versicolor (Olivier)		■	■	■
	versicolor kaieteurensis Bequaert		■		
	versicolor versicolor (Olivier)	■		■	
***Mischocyttarus* (*Kappa*)**	*adolphi* Zikán		■		
	atramentarius Zikán			■	
	bertonii Ducke				■
	funerulus Zikán			■	■
	goyanus Zikán			■	

	granadaensis Zikán		■		
	immarginatus Richards	■			
	injucundus Cameron		■	■	
	latior (Fox)			■	■
	socialis (de Saussure)		■		■
M. (*Mischocyttarus*)	*drewseni de Saussure*		■	■	■
	labiatus (Fabricius)		■	■	
	mattogrossoensis Zikán			■	
	metathoracicus (de Saussure)		■	■	
	rotundicollis (Cameron)		■	■	■
	smithii (de Saussure)		■		
	acunai Alayo	■			
	tomentosus Zikán		■		
M. (*Monogynoecus*)	*foveatus* Richards		■		
	lecointei (Ducke)		■		
	montei Zikán				■
	fraudulentus Richards		■		
	moralesi Zikán		■		
	carinulatus Zikán				■
	metoecus Richards		■		
	insolitus Zikán		■		
	lecointei lecointei (Ducke)		■		
	lecointei guianensis Richards		■		
M. (*Omega*)	*filiformis* (de Saussure)		■		
	surinamensis gr	■	■		
	elegantulus gr		■		
	silvicola Zikán		■		
	alboringer gr		■		
	punctatus gr	■	■		
	buyssoni gr				■
Angiopolybia	*obidensis* (Ducke)		■		
	paraensis (Spinola)*	■	■		
	zischkai Richards		■		
	pallens (Lepeletier)*	■	■		■
Pseudopolybia	*langi* Bequaert		■		
	difficilis (Ducke)		■		
	vespiceps (de Saussure)*		■	■	■
	compressa (de Saussure)*		■	■	
Chartergellus	*afoveatus* Cooper		■		
	amazonicus Richards		■		
	atectus Richards	■	■		
	chartarius (Olivier)		■		
	communis Richards		■	■	
	nigerrimus Richards		■		

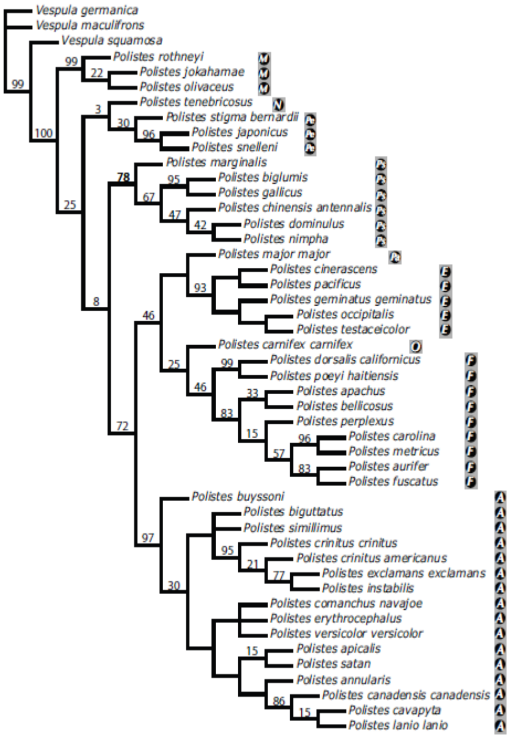
	punctatior Richards		▨		
	sanctus Richards				▨
	zonatus Spinola		▨		
Synoeca	*virginea* (Fabricius)		▨		
	chalibea de Saussure	▨	▨		
	septentrionalis Richards	▨	▨		▨
	surinama (Linnaeus)		▨	▨	▨
	cyanea (Fabricius)			▨	▨
Epipona	*quadrituberculata* (Gribodo)		▨	▨	
	guerini (de Saussure)	▨	▨		
	media Cooper			▨	▨
	tatua (Cuvier)	▨	▨	▨	▨
	niger Brèthes		▨		
***Apoica* (*Apoica*)**	*albimacula* (Fabricius)		▨		
	ambracarina Pickett		▨		
	pallens (Fabricius)	▨	▨	▨	▨
	thoracica du Buysson	▨	▨	▨	▨
	flavissima Van der Vecht		▨		
	gelida Van der Vecht	▨	▨	▨	
	pallida (Olivier)	▨	▨		
	strigata Richards		▨		
***Ap*. (*Deuterapoica*)**	*arborea* de Saussure		▨	▨	

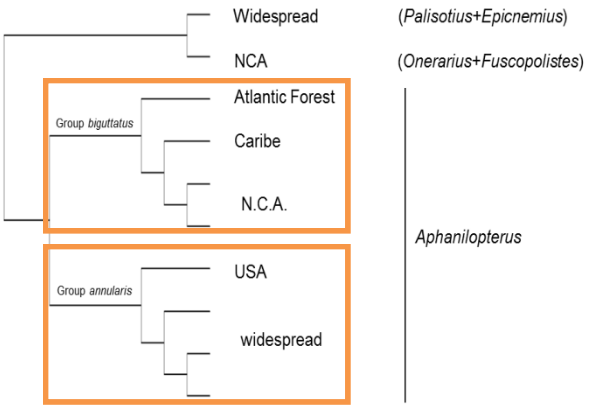
Table 1: Distribution of the 104 species of Polistinae studied in this work whose phylogenetic relationships are known in North and Central America (**NCA**), northwestern Neotropics (**NN**), central Neotropics (**CN**) and southern plus eastern Neotropics (**S+E**). *Presence of more than one morph.

Supplementary Material 1. Summarized phylogenies of the eight Polistinae genera studied in this work and source of information.

Authors' note: aiming to avoid license obtainment of original figures, we summarized those results into adapted schemes (right-side figures). We show here these data aiming to facilitate the work of reviewers and emphasize that these data, therefore, must be excluded in the final version.

Original **Adaptation**



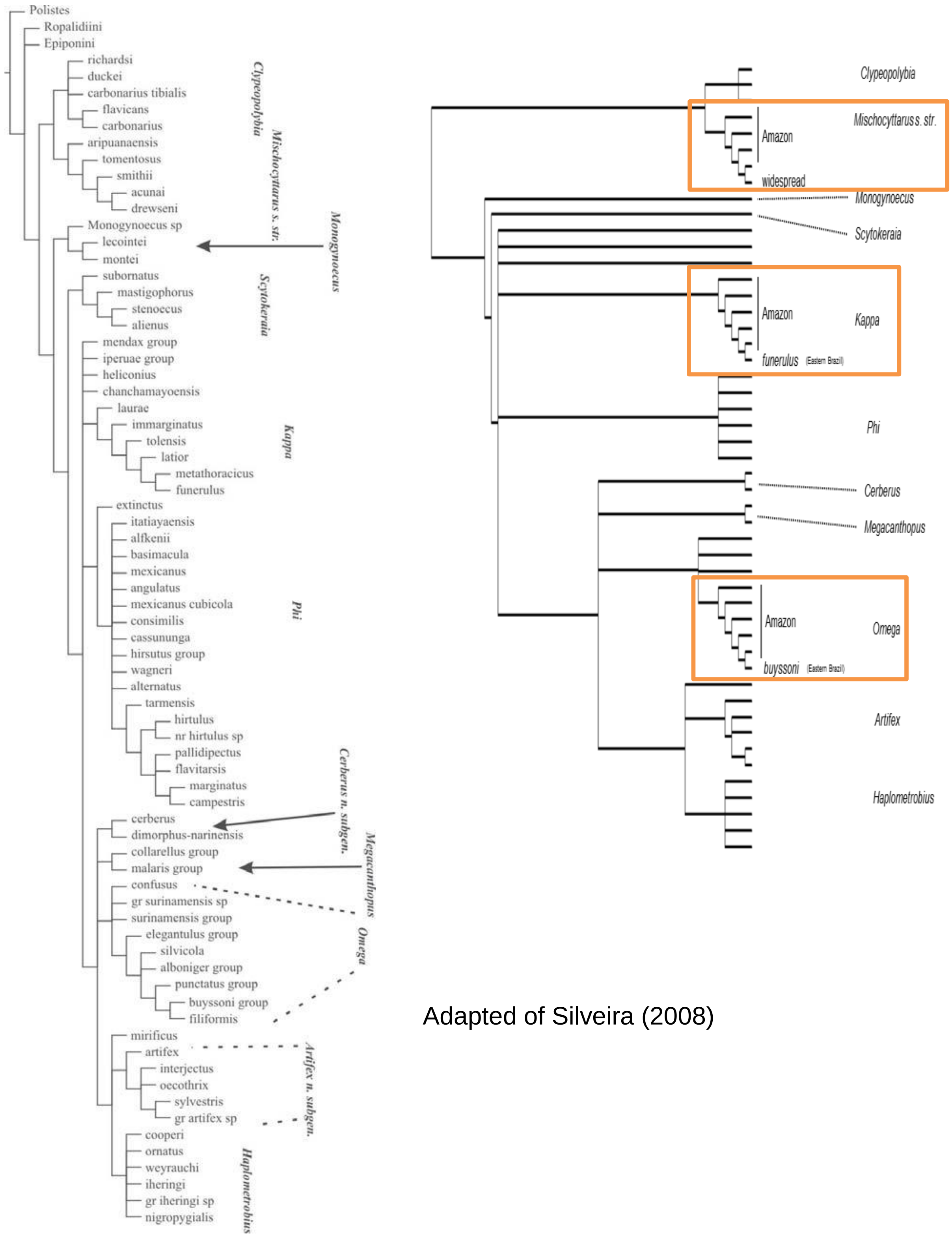


M *– Megapolistes*
Pe *– Polistella*
Pa *– Palisotius*
O *– Onerarius*
A *– Aphanilopterus*
N *– Nigmopolistes*
Ps *– Polistes s. stric.*
E *– Epicnemius*
F *– Fuscopolistes*

Polistes

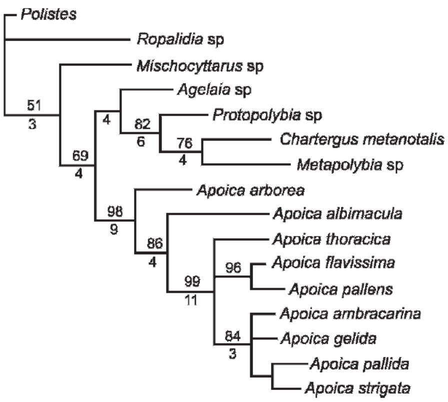
Adapted of Pickett et al. (2006)

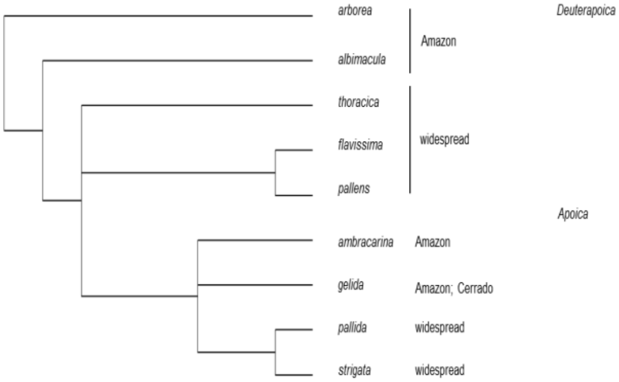
Mischocyttarus



Adapted of Silveira (2008)

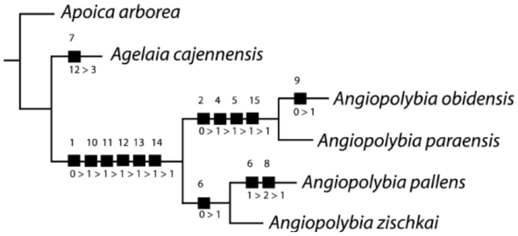
Apoica

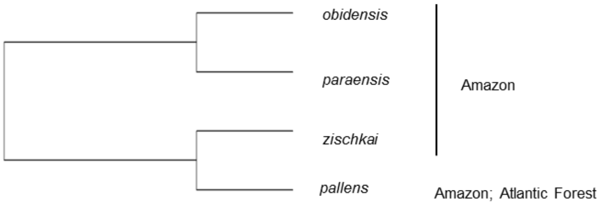




Adapted of Pickett and Wenzel (2007)

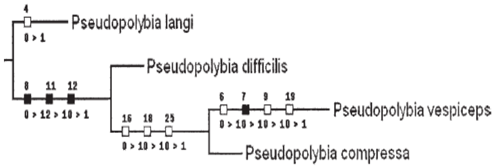
Angiopolybia

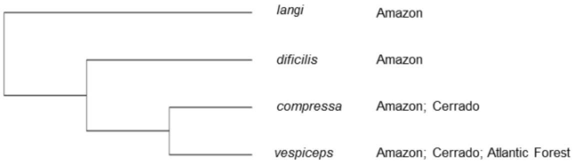




Adapted of Andena et al. (2007a)

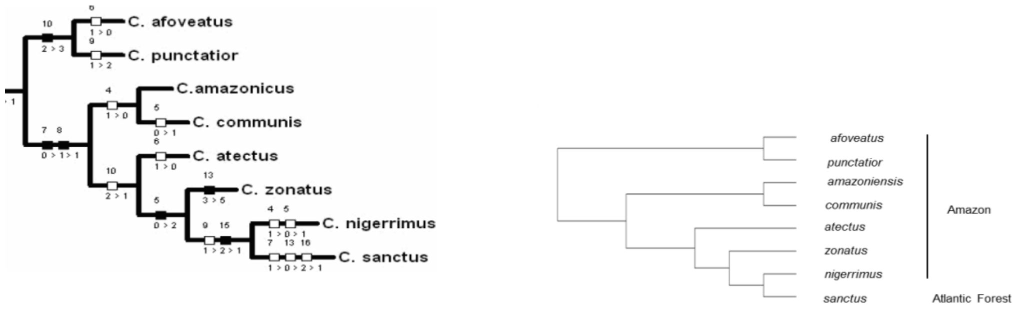
Pseudopolybia





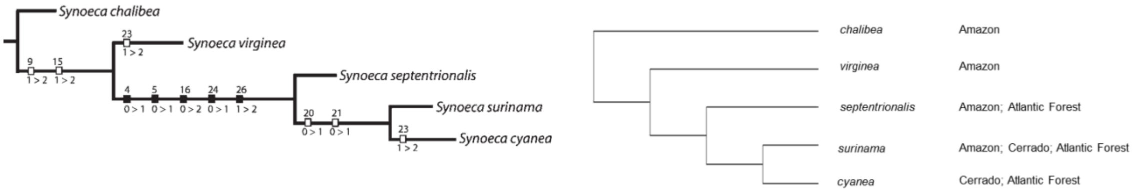
Adapted of Andena et al. (2007b)

Chartergellus



Adapted of Andena (2007)

Synoeca



Adapted of Andena et al. (2009a)

Epipona

Adapted of Andena et al. (2009b)

CAPÍTULO 3

WITNESSES OF THE BROADEST NEOTROPICAL DISJUNCTION AND THEIR IDIOSYNCRATIC RESPONSES TO CLIMATE CHANGE

(Periódico pretendido: Molecular Ecology)

Witnesses of the broadest Neotropical disjunction and their idiosyncratic responses to climate change

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Abstract

Biodiversity indexes and frequent loss of habitat in the Neotropics point to Amazonia and Atlantic Forest as hotspots to be preserved. The current disjunction faced by both forests displaces populations of dozens of species and has been target of phylogeographic studies in the last decades. However, such analyses have mostly focused on selected groups of vertebrates; little is known about the genetic effects of this event on allopatric populations of insects, for example. Also, the different threats imposed to species in these forests indicate that conservation status of broadly disjunct populations shall be reconsidered. We reviewed the distribution of 6,419 Neotropical animal species including mammals, reptiles, birds and insects aiming to compile information of clades whose distribution is disjunct between Amazonia and Atlantic Forest. This list contains 127 clades whose distributions are disjunct but only ten of these present morphological and/or distributional variants within drier forests. Exploring available paleoclimatic data relative to two periods of climatic extremes of the Late Cenozoic and the present days, we modelled the potential paleodistribution of eight of these broadly distributed, but disjunct, species to formulate hypotheses about past population demography and test such hypotheses by genetic comparisons with two social wasps. In face of so many nonrelated clades demonstrating distinct distribution patterns regarding the disjunction and to the differences in the genetic diversity among populations, we confirmed that (i) ecologically different taxa have responded idiosyncratically to the disjunction of the Neotropical rainforests and that (ii) disjunct distributions are extremely related to the dependency of forest-dwelling species to rainforest conditions.

Key-words: Allopatry, biodiversity prediction, composite paleomodelling, conservation status, genetic endemism, Neotropical rainforests, niche expansion, paper wasps, refuge.

Introduction

Studies about biodiversity patterns in the Neotropics have demonstrated that rainforests (Atlantic Forest and, especially, Amazonia) functioned both as cradles and museums of diversity: several clades presumably arose in these areas and remained occupying these environmental spaces over time. This pattern is ubiquitous, being observed in vertebrates, insects and plants (Richards, 1978; Stotz et al. 1996; Wilson, 2002; Silva et al. 2005). The causes of such huge number of species have been constantly discussed and associated with environmental aspects unique to rainforests, such as intense moisture and rainfall regimes, constant levels of temperature, as well as historical processes (Carnaval et al., 2009; Hoorn et al., 2010; 2013). The constant deforestation, pollution, inundation for energetic needs, etc., in both forests have lead governs to create conservation programs within such highly diverse but very threatened environments (Myers et al., 2000; Fearnside, 2003; Ribeiro et al., 2009). Moreover, in view of different pressures faced by the same taxon in both forests, conservation status of certain species should be carefully revisited.

A peculiar feature shared by the Neotropical rainforests is the co-distribution of certain taxa which show high habitat fidelity but low vagility (i.e., weak dispersal capacity under suboptimal conditions). This is the case of several tropical forest mammals, reptiles, birds and insects (Costa, 2003; Geurgas et al., 2008; Fouquet et al, 2012a; 2012b; Batalha-Filho et al., 2013). Because these forests are separated nowadays by a large corridor of dry vegetation composed by the Brazilian savannah and the caatinga, several questions have guided investigations: how did these species colonize such rainforests? Did they use former corridors and had their distribution disrupted by vicariant events or they colonized these rainforests by leaps through residual forests by dispersal events? Has the disjunction affected equally the genetic diversity of such taxa? Do populations share the same threats in both forests? The task of resolve these important questions requires at least the knowledge of (a) which taxa have allopatric populations in both rainforests, of course; (b) which taxa among those show evidences supporting long-distance penetrations under suboptimal conditions allowed by niche expansion, for example, since a vicariance model is more plausible for very specialized taxa; (c) which areas within the distribution ranges of disjoint taxa remained climatically stable (i.e., refuges) during disjunction events; how genetic diversity indexes vary (d) within each taxon and (e) between stable and unstable regions; and (f) how efficient the existent conservation programs are for fairly isolated populations. Answering these questions, ulterior strategies might be directed to specific areas where populations of low-vagility and very specialized taxa, presumably more subject to environmental changes than generalists, have occurred irrespective of time as well as to provide empirical evidences regarding genetic endemism for conservation programs under development.

We present in this work potential paleodistribution models of vertebrate and invertebrate species with disjunct distributions to build a composite, assemblage-scale, model of climatic stability in the two megadiverse Neotropical rainforests Amazonia and Atlantic Forest. Some of these taxa are used by us to show different patterns of disjoint distributions in order to pinpoint common areas of stability for nonrelated forest-dwelling taxa during the Late Cenozoic through composite paleomodelling (Carvalho and Del Lama, submitted to Journal of Insect Conservation). These species were chosen after we have reviewed the distribution of Neotropical species including mammals, reptiles, birds and insects whose distributions are disjunct between Amazonia and Atlantic Forest in the present days. Because genetic diversity is expected to be concentrated in the zones of stability (i.e., refuges) (Carnaval et al., 2009), these areas are predicted as of high importance for conservation of low-vagility, widely disjunct, species. In addition, we indicate the disjoint taxa for which niche expansion is a probable cause that explains their occurrences within dry biomes based on morphological and distributional evidences.

To test if spatiotemporal models of stability correctly predict genetic diversity, we use paper wasps (Vespidae, Polistinae, Epiponini) as indicators of both genetic endemism – the exclusivity of genetic lineages to an area – and environmental changes through time. The approach consists in the formulation of phylogeographic hypotheses based on paleomodelling and the test of the assumptions through historical demography (Hugall et al., 2002; Carnaval et al., 2009). Some of these wasps, a very diverse group in the Neotropics, might bear and overcome a variety of climatic alterations, but certain species can only be found under very specific environmental conditions (Richards, 1978; DeJean et al., 2010). Given the variety of occupied niches, these insects might be useful indicators of environmental changes through time and we focus on two widely distributed species:

Angiopolybia pallens (Lepeletier) and *Synoeca surinama* (Linnaeus). Whereas *A*. *pallens* is exclusive to Amazonia and Atlantic Forest, *S*. *surinama* occurs in both forests as well as, discretely, in dry vegetation of the Brazilian savannah, mostly associated with gallery forests. Such information leads us to treat the former as dependent on rainforests and the later as not dependent, or dry-adapted.

This work differs from previous analyses by present assemblage-scale spatially explicit hypotheses of stable areas for nonrelated taxa in the entire South Amrica and by point key-species that might have underestimated populations' conservation status due to disjunct distributions. Our ultimate goal in this work is indicate areas in which isolated relictual refuges have potentially kept populations irrespective of time during the Late Cenozoic. This work might be a useful reference for reevaluations regarding conservation status of very specialist key-species and environmental protection strategies in both rainforests as well as small-scale forest enclaves within drier environments.

Materials and Methods

Review of distributions

We investigated the distribution of 6,419 Neotropical species among mammals, birds, reptiles, paper wasps and stingless bees aiming to build a database of forest-dwelling disjoint species. This database includes possible cases of niche expansion based on morphological adaptations to or occurrence in suboptimal areas. Once we have selected probable taxa showing such distributional pattern, we confirmed taxon-by-taxon distributions through information contained in specialized studies for more precise information. Also, taxonomy and conservation status of each lineage were reviewed through consult of specialized studies and digital databases. Domesticated lineages were not included in the list. Besides disjoint species, we found taxa mostly from certain forest with few or only one congeneric lineage (or conspecific, in the case of clades with multiple subspecies) in the opposite forest. The review of distribution of each group was carried out as follows in Table 1.

Table 1: number of taxa consulted of each group studied in this work and the main references used to determine disjunct distributions in the Neotropics. Disjunct distributions were confirmed taxon by taxon in specialized literature (see **Table S4**).

Group	**Number of taxa consulted**	**Main References**
Mammals	652	Reis et al. (2006)
Reptiles	748	Database 1
Birds	3,751	Stotz et al. (1996); Sick (1997); Databases 2 and 3
Paper wasps	632	Richards (1978)
Stingless bees	636	Camargo and Pedro, 2012

DB1: http://reptile-database.reptarium.cz/; DB2: www.birdlife.org/; DB3: http://neotropical.birds.cornell.edu/portal/home; DB4: www.splink.org.br.

Occurrences data

A Maximum Entropy algorithm implemented in MaxEnt (Phillips et al., 2006) was used to build potential distribution maps. MaxEnt is a presence–background modelling technique that requires biological information (i.e., a list of sites in which the target species is known to occur) and has performed as well or better than alternative modelling methods in recent comparisons (Elith et al., 2006; Hernandez et al., 2006; Carnaval and Moritz, 2008; Wisz et al., 2008). The occurrence data for the vertebrates were obtained mostly through *species*Link network digital database (http://www.splink.org.br) but other studies such as Ávila-Pires (1995) and Miranda and Superina (2010) were also consulted. Because these data are not fairly available for paper wasp species *A*. *pallens* and *S*. *surinama*, occurrences were obtained through visits to entomological collections, donations of specimens and literature data. Surveying was also carried out in order to sample genetically specific populations.

Geo-located data used to generate niche models for all the species studied in this work are available in Table S1. Below is all the source of information consulted by us regarding the distribution of both wasps in South America.

Entomological collections visited

- Coleção Taxonômica do Departamento de Ecologia e Biologia Evolutiva da Universidade Federal de São Carlos (São Carlos, Brazil);
- Coleção Entomológica da Universidade Estadual Paulista Júlio de Mesquita Filho (São José do Rio Preto, Brazil);
- Museu Nacional, Universidade Federal do Rio de Janeiro (Rio de Janeiro, Brazil);
- Instituto Nacional de Pesquisas da Amazônia (Manaus, Brazil);
- British Museum, Natural History (London, United Kingdom);
- American Museum of Natural History (New York, USA);
- Smithsonian Institution (Washington, D.C., USA).

Literature

Available data in catalogues (e.g., Richards, 1978) and inventory studies citing the occurrence of *A*. *pallens* and *S*. *surinama* (e.g., Raw, 1998; Silveira, 2002; Silveira et al., 2005; 2008; Morato et al., 2008; Silva and Silveira, 2009; Tanaka-Jr and Noll, 2011) were consulted. To avoid the use of non geo-located information such as presence data in particular states or provinces, which are very frequent in catalogues and other published materials, only those data points that cited very precise locations were taken into account. In these cases, we sought for actual location of samples by consulting collectors and/or by the use of Google Earth.

Taxon sampling

Basing on previous information about the range of both species and before-sampling potential distribution models, some areas were chosen for inventory work. Field surveys were carried out in several Brazilian states, as follows: Acre, Amazonas, Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo, Sergipe, Pará, Paraíba, Pernambuco, Rondônia, Roraima and in the Distrito Federal. In addition, several collaborators donated specimens for our analyses. A list with all the samples obtained during these surveying expeditions and donations can be seen in the Table S2. We used active search by nests and individuals as well as attractive solutions (Noll and Gomes, 2009) during surveying. In the later two cases, we only sampled genetically those specimens obtained one kilometer of distance from each other.

Historical climate modelling

We modelled potential distributions using MaxEnt version 3.3.3k (Phillips et al., 2006; Phillips & Dudík, 2008) combining locality data and environmental descriptors based on 19 bioclimatic variables (Table S3). All the past and present bioclimatic data were obtained through the WorldClim database (www.worldclim.org). Stability models were built for *Cyclopes didactylus* (Linnaeus), *Mimon bennettii* (Gray), *Kentropyx calcarata* Spix, *Polychrus marmoratus* (Linnaeus), *Trogon collaris* Vieillot, *Amazona farinosa* (Boddaert), *A*.

pallens and *S*. *surinama* aiming to show putative patterns of response to Late Cenozoic climate change in different clades.

We used quadratic (Q), product (P), threshold (T) and hinge (H) features of MaxEnt, with regularization multiplier equal to 1, to build niche models since the Area Under the Curve values (AUC) found were higher than 0.9 (Giannini et al., 2012). Also, thirty percent of the occurrence data from each species were randomly chosen during the training of the data and used as information to test the models, following Rosauer et al. (2009).

For species that AUC was lower than 0.9 we implemented threshold-dependent tests (Pearson et al., 2007; Soley-Guardia et al., 2014) to evaluate how well the model of each species predicted its own localities, then selecting the logistic output format, which yields continuous values ranging from 0 to 1. These values indicate relative environmental suitability for the species; specifically, the probability of suitable environmental conditions to the species occur, or the probability of presence of the taxon if dispersal limitations and distributional restrictions due to biotic interactions are not relevant (Phillips & Dudík, 2008). Such tests were carried out by calibrating the models using different combinations of Q, P, T and H features and with levels of regularization ranging from 1, 1.5, …, 4. Aiming to diminish the influence of background choice on the model output (Anderson and Raza, 2010) we used environmentally independent training and test sets, using Amazonia (samples and layers) as training data for predictions on the Atlantic Forest, and vice-versa. In addition, we performed a third test with samples and layers from the full range of such species (i.e., using minimum convex area polygons to build the models). We carried out 84 different parameter combinations and used the following combination of features during such particular tests: QPTH, QPH, QTH and QPT.

Once contemporary models of potential distribution of species were generated, we projected them into past climatic conditions to predict species' potential distributions during the Late Pleistocene (21 thousand years, or ky) and the Last Interglacial (LIG, 120 ky). With this, we sought to identify predictable areas of stability (regions in which species were presumably present irrespective of time period) and unstable areas by superimposing potential distribution maps in a single model of stability (Hugall et al., 2002; Carnaval et al., 2009). The parameters used for paleomodelling followed those determined after the model evaluations under current conditions, as abovementioned.

Aiming to detect areas of stability for the eight abovementioned species, we combined the single species stability maps into a composite paleomodel. This allowed us to explore a model that predicts climate stability in assemblage-scale for such species in the entire South America.

Testing the predictability of niche models with paper wasps

Because it is expected that regions of stability concentrate more genetic diversity than areas of recent occupation (Carnaval et al., 2009), we carried out genetic analyses using phylogeographical frameworks based on historical demography as test of hypothesis. For this end, we estimated genetic diversity, phylogenetic and haplotype relationships, and historical demography of *A*. *pallens* and *S*. *surinama* populations using genetic data both separatedly and concatenated.

Laboratory procedures

Total genomic DNA was extracted from thorax and/or legs and antennae of individuals stored in ethanol 100%, by the Chelex® 100 protocol (Walsh et al. 1991). Approximately 485 bp of Cytochrome *b* (Cyt*b*), 438 bp of rDNA 12S and 416 bp of Cytochrome c oxidase I (Cox1) genes were amplified and sequenced in both directions with the primers and conditions presented in the Table 2. All PCR products were purified with Exonuclease I and Shrimp Alkaline Phosphatase (Fermentas). Automated sequencing was performed using BigDye Terminator v3.1 Cycle Sequencing kit (Applied Biosystems), followed by analysis on ABI Prism 3730 Genetic Analyzer Sequencers (Applied Biosystems) at the CREBIO (UNESP, Jaboticabal, SP, Brazil) according to the manufacturer's instructions. Sequences were edited in BioEdit (Hall, 1999) and initially aligned using the default parameters of ClustalW (Thompson et al., 1994).

Table 2: PCR conditions and sequence of the primers used in this study.

Gene region	**Sequences of the primers**	**PCR cycle (x40)**			**References**
		1	**2**	**3**	
Cyt*b*	**F:** TATGTACTACCATGAGGACAAATATC; **R:** ATTACACCTCCTAATTTATTAGGAAT	94°C, 30 seg	54°C, 20 seg	70°C, 60 seg	Crozier and Crozier (1993)
12S	**F:** TACTATGTTACGACTTAT; **R:** AAACTAGGATTAGATACCC	94°C, 30 seg	50°C, 60 seg	70°C, 60 seg	Kambhampati & Smith, (1995)
COX1	**F:** GGAGGATTTGGAAATTGRYTWRTTCC; **R:** GGTAAAATTAAAATATAAACTTC	95°C, 30 seg	45°C, 60 seg	72°C, 60 seg	Simon et al., (1994) (F); Kambhampati and Smith (1995) (R)

1. denaturation; 2. annealing; 3. extension.

Genetic analyses

Bayesian analyses were carried out in MrBayes (Huelsenbeck & Ronquist, 2001) using Markov chain Monte Carlo (MCMC) analyses with two independent runs, each with four chains sampled every 1,000 generations. After the run of 20 x 10^6 generations, the burn in was calculated in Tracer v1.5 (http://tree.bio.edu.ac.uk/software/tracer/). The majority-rule consensus was calculated from the remaining samples and trees were edited in FigTree 1.4 (http://tree.bio.ed.ac.uk/software/figtree). We used several polistine species as outgroups during such analyses. The choice of best fit-models of nucleotide substitution was conducted using Akaike Information Criteria (AIC) implemented in jModelTest v2.1.4 (Darriba et al., 2012) using default settings, but the best base tree search. When sample size was small compared to the number of parameters, AICc was used to infer best substitution models (Hurvich and Tsai 1989).

Haplotype relationships were accessed by the use of the median-joining algorithm implemented in Network (Bandelt et al. 1999). Nucleotide (π) and haplotype (Hd) diversities, as well as number of haplotypes (h), were calculated in Arlequin 3.5.1.2 (Excoffier et al. 2005). In order to test if there is any evidence of demographic expansion, the neutrality test indexes Tajima's D (Tajima, 1989), Fu's Fs (Fu, 1997) and the population size change test R_2 (Ramos-Onsins and Rozas, 2002) were calculated for each population subset in DnaSP 5.10.1 (Rozas et al., 2003). The significance of these tests were obtained based on 1,000 coalescent simulations. Signatures of genetic structure among clades, accessed by Φ statistics (Weir and Cockerham, 1984), were calculated in Arlequin 3.5.1.2 (Excoffier et al. 2005) through Analysis of Molecular Variance (AMOVA). Predictions of population size changes were priorly tested through mismatch distribution analyses using observed data to confront with an expected model of constant population size in DnaSP 5.10.1 (Rozas et al., 2003).

Spatiotemporal relationships among lineages were carried out aiming to test associations regarding climatic stability inferences and remarked genetic variation. These tests were conducted using a Bayesian framework implemented in BEAST v1.6.1 (Drummond & Rambaut 2007) based on a relaxed molecular clock model uncorrelated to lognormal with 10 x 10^6 generations, sampling one tree each 1,000 generation (burn in = 10%). In order to calibrate the molecular clock, we implemented the substitution rate calculated by Resende et al. (2010), equivalent to 1.455E-02 ± 1.25E-03 substitutions per My for Cox1 sequences of *A*. *pallens* and *S*. *surinama*.

Results

Witnesses of the disjunction

We found 127 clades whose distributions are disjunct between Amazonia and Atlantic Forest. Among them, twenty two lineages of mammals, twenty nine reptiles, fifty one birds and twenty five insects were registered (Fig. 1). The more representative groups of the list are the Phyllostomidae bats (14), the Colubridae snakes (14), the manakin birds of family Pipridae (7) and the paper wasps of family Vespidae (20) (Table S4). However, several groups (e.g., carnivores, primates, vireos, etc.) are represented by only one taxon. This is the case of the pygmy anteater *Cyclopes didactylus*, the howler monkey *Alouatta belzebul* (Linnaeus), the kinkajou *Potos flavus* Schreber and the Ariel toucan *Ramphastos vitellinus ariel* Vigors.

Thirty three clades present lineages whose taxonomical status point to more than one morphology, being indicated as subspecies or morph variants. Most of the groups have at least one representative with more than one conspecific lineage, indicating that special attention has been given to very disjoint lineages in the taxonomical classifications. Moreover, five of these taxa and other five clades apparently have adaptations to live in dry conditions (Table S4).

Interestingly, most of the analyzed taxa has conservation status indicated as ‘least concern’ in the International Union for Conservation of Nature Red List (http://www.iucnredlist.org/) but many of them are described as suffering decreasing on the population size in the same database (Table S4). We modelled the potential paleodistribution of eight species, including some of these taxa, and noticed that, as expected, the predicted stable areas are differently distributed in South America (Fig. 2a–h). While coastal portions of Atlantic Forest are predicted in most of the eight models as of high historical suitability for these taxa, the climatically stable regions in Amazonia vary considerably from one species to the other.

The composite paleomodel (Fig. 2j) revealed two wide stability zones in Amazonia. The first is distributed throughout northern South America, a region appointed here as the putative Guiana Refuge (GR), and the second ranges from Venezuela and Colombia boundaries to northeastern Bolivia, the Western Amazonia Refuge (WAR). This stable zone also covers part of the western Amazonia of Brazil. In the Atlantic Forest, on the other hand, three well-known refuges are indicated: the Pernambuco (PR), Bahia (BR) and São Paulo Refuges (SPR) (Fig. 2j).

It is worth stressing that even though species occurrences in the Atlantic Forest are less represented than in Amazonia, the composite paleomodel predicts that this region is the more probable to concentrate evolutionary history (Carvalho and Del Lama, submitted to Journal of Insect Conservation) for the eight species studied through ecological niche modelling (Fig. 2a–i). However, some of these clades possibly originated in Amazonia and therefore have older populations in the western rainforests than in the Atlantic Forest. This way, we tested the credibility of these climate stability models as predictors of genetic diversity through historical demography with the two paper wasps presented in the Fig. 2 taking into consideration the putative age of each lineage while testing the predictions through genetic frameworks (Figs. S1 and S2). The results of such tests are shown in the next section.

Spatial predictability of genetic diversity

We found potential refuges for *A*. *pallens* in both Atlantic Forest and Amazonia. They match areas previously identified as the Pernambuco (PR), Bahia (BR) and São Paulo (SPR) Refuges in the Atlantic Forest (Carnaval & Moritz, 2008; Carnaval et al., 2009), yet include two others in Amazonia: the Western Amazonia Refuge (WAR) and the Guiana Refuge (GR). Because higher genetic diversity is expected to be found in large stability areas relative to zones where colonization is likely to be more recent, or smaller in size, we used this hypothesis to guide the choice of target populations for population genetic analyses. The demographical tests were carried out with samples obtained in the WAR, BR and SPR.

Because we obtained sympatric samples of *A*. *pallens* belonging to two morphs (the more common yellow and the variant dark morph) in the WAR, and they are possibly genetically isolated from each other (Fig. 3), we also tested stability predictions for these clades separately (Tables S5 and S6). The dark morph is divided into northern (N) and southern (S) clades referent to Amazonas River and has considerable diversity, but genetic diversity is very lower than the more basal lineage, i.e., the yellow morph. Our Bayesian tree based on all the three sequenced gene regions (Fig. 3) indicates that the dark morph might be a new variant of Amazonian *A*. *pallens* and that the species shall be passing by speciation processes (see the monophyletic clade of dark morph in the Fig. 3). The more recent emergence of dark morph (~0.8 Myr, Fig. S1b) might be the cause of such unexpected values which shall not refute the spatially explicit hypotheses. This information led us to exclude such clade during the comparative analyses of population size changes (Fig. S3).

Additionaly, we used Cox1 sequences of *Angiopolybia zischkai* Richards during Bayesian analyses and this species was grouped with *A*. *pallens* yellow morph (Fig. S2b). This yet unresolved taxonomical problem led us to exclude a sample from Porto Velho, Rondônia, Brazil (see sample 001 previously pointed as dark morph in the Table S2.1) of the population analyses due to the genetic similarities with the refered species.

We also measured genetic diversity within the Western Amazonia Refuge (WAR) relative to the Atlantic lineages, regions of putative more recent colonization (Fig. S1), and the predictions are in agreement with the genetic data. Higher levels of diversity in Amazonia are detected when compared to Atlantic Forest refuges (Table S5). However, mismatch distributions in such refuge indicate population expansion for the three gene regions (Fig.

S3). Population expansion was also indicated in the BR with Cyt*b* and Cox1 sequences and discretely in the SPR with Cox1 sequences (Fig. S3).

Genetic data concerning populations of *A*. *pallens* (Table S5) support the existence of multiple and divergent clades within the Bahia Refuge (Fig. 3), agreeing with our model-based predictions of a large stability zone in this area. This also matches genetic patterns documented for vertebrate species, as seen in Carnaval et al. (2009). Also in agreement with the model, populations from southeastern Brazil (Rio de Janeiro and São Paulo states) have lower genetic diversity than the larger BR and agree with predictions that smaller refuges concentrate lower levels of genetic diversity than larger stable areas (Table S5).

Potential refuges for *S*. *surinama* were detected in the Atlantic Forest (PR and BR), in Amazonia (WAR), and in the potential southern connection between Amazonia and Atlantic Forest which we treat here as the Inland South America Refuge (ISAR, Fig. 3e). Also, the genetic data provided support for hypotheses of stability with this species. Genetic diversity in Amazonia is indeed higher than either savannah or Atlantic Forest populations (Table S5). On the other hand, populations from Bahia Refuge show lower genetic diversity but the relationships seen in the Bayesian trees indicate that Atlantic Forest populations are more derived and provide information that such low values are due to more recent colonization of eastern forests (~1.8 Myr, Fig. S2b). Also, there are multiple and divergent clades within the Amazonian region (Fig. 3), agreeing with our model-based predictions of a large refuge in this area. Mismatch distribution indicated considerable population expansion for *S*. *surinama* only in the ISAR for the gene regions Cyt*b* and Cox1.

Interestingly, savannah and some Amazonian samples were grouped in a monophyletic clade (Fig. 3f) that indicates multiple events of colonization from Amazonia to the Brazilian savannah, and vice-versa. This fact confirmed the expectative regarding the absence of genetic structure between ISAR and WAR. In contrast, populations from Atlantic Forest are apparently isolated of both forests because a manophyletic clade with little variation is detected as highly divergent from the remainder western refuges (Φ_{CT} = 89.85%, Fig S2a).

Discussion

The discontinuous distribution of dozens of forest-dwelling animal species (Fig. 1 and Table S4) supports the old idea of former connections between Amazonia and Atlantic Forest. Oliveira-Filho and Ratter (1995) suggested that this connection was facilitated by a huge net of gallery forests in the past of central Brazil. According to such study, this forest net used to be widely discontinuous due the existence of very dry areas inside Brazil, which set typical caatinga and savannah vegetation. Low-vagility disjoint species in both rainforests (Table S4) are evidences that such connections indeed occurred in the past but indicate that gallery forest nets actually are discrete residuals instead long-term connective facilitators of these former connections. In addition, as our paleodistribution models show (Fig. 2a–i), these potential corridors present noteworthy differences for ecologically different taxa at least from 120 ky to the present.

Forest dynamism in the Neotropics is marked by recurrent events of expansion and retraction of both dry and humid forests (Raven & Axelrod, 1974; Ab’Saber, 1990; Silva & Bates, 2002; Roig-Juñent et al., 2006). Such changes were associated by Haffer (1997; 2008) to millennial-scale cyclic orbital alterations (i.e., Milankovitch cycles) and suggest that rainforests might have been connected and disjoined repeatedly during the history of Earth (Ab’Saber, 1990; Bennett, 1990; Muller and MacDonald, 1995). Over this perspective, the wide disruption between Amazonia and Atlantic Forest in the present days is likely the result of several long-term changes in the central Brazil increased during glacial periods.

Biogeographical predictions concerning such broad disjunction have been posed for some groups. Vanzolini and Williams (1970), for example, proposed recent and rapid cycles of forest expansion and retraction as causes of the distribution patterns seen in *Anoles nitens* species group. Climatic alterations were predicted by the authors as the main causes governing such events which were treated as “the diversification model of South American biota” (see Geurgas et al., 2008). This model is based on both fragmentation and range expansion episodes: (i) northern/southern Amazonian fragmentation followed by (ii) range expansion of northernmost lineages across former connections between Amazonia and Atlantic Forest and (iii) separation of western and eastern rainforests. Geurgas et al. (2008) tested predictions raised by this model to explain biogeographic-phylogenetic responses of low-vagility leaf litter geckos (genus *Coleodactylus*) in face of the wide Amazonia-Atlantic disjunction. Although the results showed refuted some phylogenetic nuances raised by previous works (see discussion in Geurgas et al., 2008), the authors considered that the colonization may have been favored by forest expansion enhanced by both temperature and humidity increasing during Early Tertiary, as predicted by the model of Vanzolini and Williams (1970).

Current distribution, paleomodelling and phylogeography of forest-dwelling species indicate that populations suffered differently the effects of this disruption according to the inhabited region. Distribution of species in central Brazil, for example, apparently retracted to relictual populations within gallery forests of different magnitudes or became extinct. Such forest patches are remarkably inhabited by forest-dependent species (i.e., species not adapted to open vegetation conditions) and serve as small-scale refuges for widely-disjoint rainforest species within the Brazilian savannah (Eiten, 1972; Redford and Fonseca, 1986). Inland Atlantic populations in turn had their distribution reduced to humid highland forest enclaves (i.e., Brejos de Altitude) (Carnaval and Bates 2007) while coastal lineages were reduced to, at the least, two well-known refuges of different magnitudes, the Pernambuco and Bahia refuges (Carnaval and Moritz, 2008; Carnaval et al., 2009); both are recovered in the paleodistribution models of this work. Such disjunct patterns are recurrently associated with frequent climatic-vegetational changes during glaciation events (Costa, 2003; Carnaval and Bates, 2007; Resende et al. 2010; Thomé et al., 2010; Batalha-Filho et al., 2012) and the stability zones (i.e., refuges) have remarkable phylogeographical predictions (Carnaval et al., 2009). Besides historical differences among such areas, distinct responses of a same taxon are also expected due to idiosyncratic responses referent to degrees of habitat fidelity, vagility, niche conservatism and additive genetic variance to overcome ancestral limits which might distinguish populations from each other.

Biogeographical explanations for Amazonian lineages in turn are more complexes due the historical influence of rivers, mountain uplifts, sea-level alterations and climatic-vegetational changes (Hoorn et al. 2010). Da Silva and Patton (1998), for example, showed empirical evidences regarding the huge lineage diversity of mammals and noteworthy unexpected results concerning geographical placement and degree of lineage divisions within the Juruá Basin in western Amazonia, Brazil. Intraspecific variation of Amazonian herpetofauna in turn has shown an east/west diversification pattern pointing to vegetational changes during Oligocene glaciations as probable causes of the observed divergences (Vanzolini and Williams, 1970; Geurgas et al., 2008). Hoorn et al. (2010; 2013), on the other hand, associated Andean erosions as the cause of changing in the Amazonian basin from wetland to a fluvial environment which allowed the occurrence of a highly diverse range of species adapted to non-flooded areas.

Adapting to changes

We detected only 10 taxa with lineages adapted to dry-conditions. Gregorin et al. (2008) proposed a possible correlation between the length of forearm and the use of habitat by the Phyllostomidae bat *Mimon bennetti* (Gray), since the savannah populations of this species show longer structures than those from rainforests. According to the authors, such differences were enhanced due to open vegetation found in the savannah in which environmental pressures tend to select lineages with wider wingspans (Gregorin et al., 2008). Rodrigues (2003) associated drainage networks as explanation to the presence of *Helicops leopardinus* Schlegel in the caatinga since this water snake is typical in the northwestern rainforests. The occurrence of other species in gallery forests as the cocoa thrush, *Turdus fumigatus* Lichtenstein, for example, is linked to water resources commonly available in such regions (Stotz et al., 1996). On the other hand, the Amazonian barred-woodcreeper (*Dendrocolaptes certhia* Boddaert) might occurs in areas subject to seasonal inundation, white-sand forests like campinarana formations and savannas, as well as in rainforests (Stotz et al., 1996; Sick, 1997); however, the isolated small population in northeastern Brazil denotes that the wide use of drier environments is likely restricted to the northwestern subspecies. Conversely, the greenlet *Hylophilus thoracicus* Temminck, although disjunct, shows populations with distinct habitat preferences in northwestern, mostly rainforests, and eastern Neotropics, mostly scrubs and low open woodlands (Stotz et al., 1996). Since it is not known centers of origin for these groups for our knowledge, phylogeography-based proposals are necessary to link such adaptive traits to ancestral identity or more recent adaptations. Notwithstanding, we defend that the presence of disjoint taxa populations within dry areas might correspond to small-scale adaptations guided by niche expansion.

Adaptations to dry conditions or enhanced vagility within suboptimal areas might likely have permitted ancestral populations to colonize regions where these taxa are found today. Furthermore, variation preexistent to environmental changes might maintain populations within regions extremely impacted by climate alterations, as proposed by the Vanishing Refuge Model (Vanzolini and Williams, 1981; Damasceno et al. 2014). Phylogeography allied to historical climate modelling of such species might indicate where the taxa probably originated, possible directions of colonization routes and periods for such events have occurred in the Late Cenozoic as appointed with the paper wasps studied in this work.

Paleomodelling and phylogeography reveal idiosyncratic responses to the disjunction

In face of natural differences regarding origins, life histories, current distribution and use of habitat of each group listed in the Table S4, we naturally expected that the disjunction has affected differently each taxon. In addition, remarkable differences are expected in the potential paleodistribution models, population relationships and tree topologies. These assumptions prove to be true when, for example, clades sharing the same center of origin – but showing differences regarding colonization systems, habitat fidelity and niche expansion – are analyzed through both ecological and phylogeny-based approaches.

As our results show, the two wasps analyzed through historical demography present different responses to the disjunction. In addition, lower genetic diversity seen in *S.*

surinama reflects that ‘adaptation to different conditions’ shall not be always associated to ‘high genetic diversity’. Dry-adapted species might show high vagility, for example, and such unique trait might be able in promote population admixture, a fact that diminishes local structuration (Templeton 2006). Referred adaptations might be linked to ancestral variations in the traits which permit certain populations to bear new conditions imposed by the environment. In the case of these wasps, larger body size of *S*. *surinama* relative to *A*. *pallens*, thermoregulatory differences in the control of moisture and temperature levels inside nests and distinct colonization systems are putative characteristics influencing their distinct distribution both in large and small scale.

Remarkable differences are also seen in the genetic diversity of both species (Table S5). Such discrepancy might be attributed to flight capacity which is much differentiated between these wasps. While *A*. *pallens* shows low flight capacity (Cruz et al. 2006) *S*. *surinama* apparently has wider flight range and this fact, allied to the consequences of colonization system of new areas based on replication of nests, might homogenize small-scale diversity (i.e., population structure). This behavioral strategy is very efficient in terms of propagation but permit daughter colonies carry exclusively the same mitochondrial lineage of maternal nests. On the other hand, multiple events of colonization, rapid mutation levels and earlier origins of *A*. *pallens* might also be reasonable explanations for the higher genetic diversity seen in this species relative to *S*. *surinama*. Furthermore, niche conservatism might explain the absence of variation for overcome ancestral limits and the falling of populations while corridors between both forests became extinguished for *A*. *pallens*. Conversely, niche expansion is a reasonable explanation for the occurrence of *S*. *surinama* in different conditions.

Despite these differences, *A*. *pallens* and *S*. *surinama* show some congruencies regarding the potential distribution maps. Current distribution maps point the occurrence of suitable conditions for both species in the Neotropics mostly in Bahia, Pernambuco and Western Amazonia Refuges. In contrast, *A*. *pallens* past-distribution models indicate many and fast changes during Late Quaternary (see northern and southern connections between Amazonia and Atlantic Forest oscillating from one model to the other) whereas the paleomodels of *S*. *surinama* indicate that while new areas opened up for this species, the main location of contact zones between both rainforests did not change.

Interestingly is the higher diversity in Amazonia relative to other regions. The remarkable haplotype diversity and the basal positioning of the lineages on the trees give support to the idea that this biome is the center of origin of both species and might help the understanding of patterns of occupation by paper wasps in the Neotropics. This pattern is also noticed in *A*. *pallens* by Carvalho et al. (2014) using PCR-RFLP. Despite some studies have proposed that Polistinae achieved the Neotropics from Africa to South America over a Gondwanan scenario (Carpenter 1981, 1993, 1996), apparently, Amazonia is the center of origin of most of the Neotropical species (unpubl. information). Phylogeographical inferences raised here are unprecedented for the subfamily and will help the understanding of the different colonization processes by paper wasps.

Implications for conservation

Assuming the predictions of an extinction vortex related to the sex determination mechanism of Hymenoptera (Zayed and Packer 2005) and that genetically diverse populations are better able to avoid it and less likely to suffer the harmful effects of inbreeding, the identification of areas in which diversity is putatively concentrated should be focus of discussion (Carvalho and Del Lama, submitted to Journal of Insect Conservation). Locating such zones, efficient strategies might be directed in the sense of evaluate multi-species diversity, phylogenetic endemism and conservation management.

Composite paleomodelling in Fig. 3j indicates several common areas of stability for paper wasps and vertebrates. Because these refuges might concentrate independent evolutionary history in assemblage-scale, the conservation of such areas shall be priority for endemic lineages of species widely fragmented. Over this perspective, a plan of action is especially necessary for the Atlantic Forest Central Corridor, a hostspot widely embedded in the Bahia Refuge (BR) that has undergone critical impacts due to anthropic influence (Ribeiro et al., 2009; Sparovek et al., 2012). Moreover, such refuge is considered highly important for the historical maintaining of Atlantic populations, a fact sustained by both high genetic diversity and population structure recurrently reported for different taxa (e.g., Carnaval et al., 2009; Batalha-Filho et al. 2010; Resende et al., 2010).

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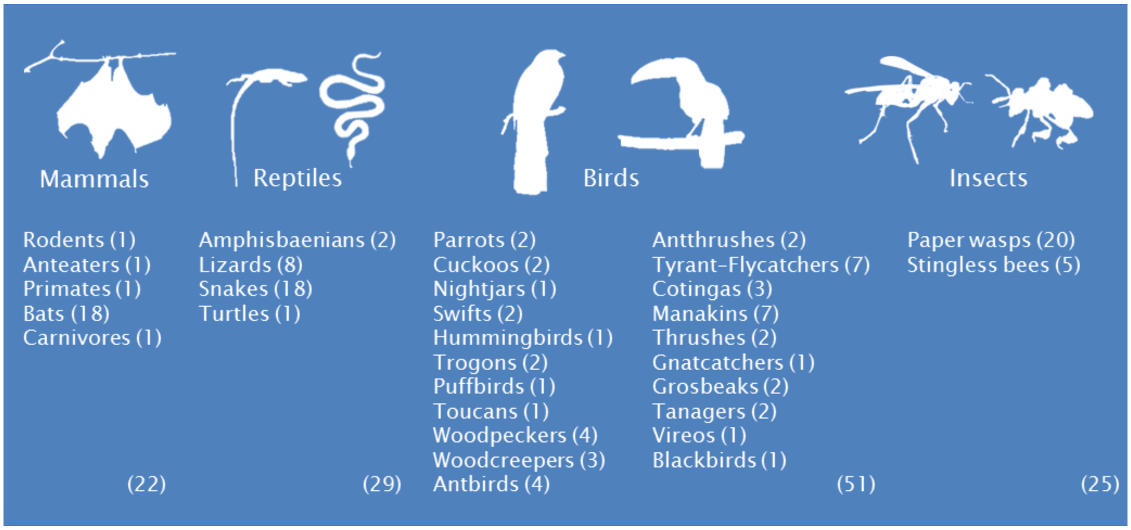


Fig. 1 Summarized list of the Neotropical groups with disjunct distributions between Amazonia and Atlantic Forest. A detailed list containing species names, conservation status and particularities of each lineage is provided in the Table S4.

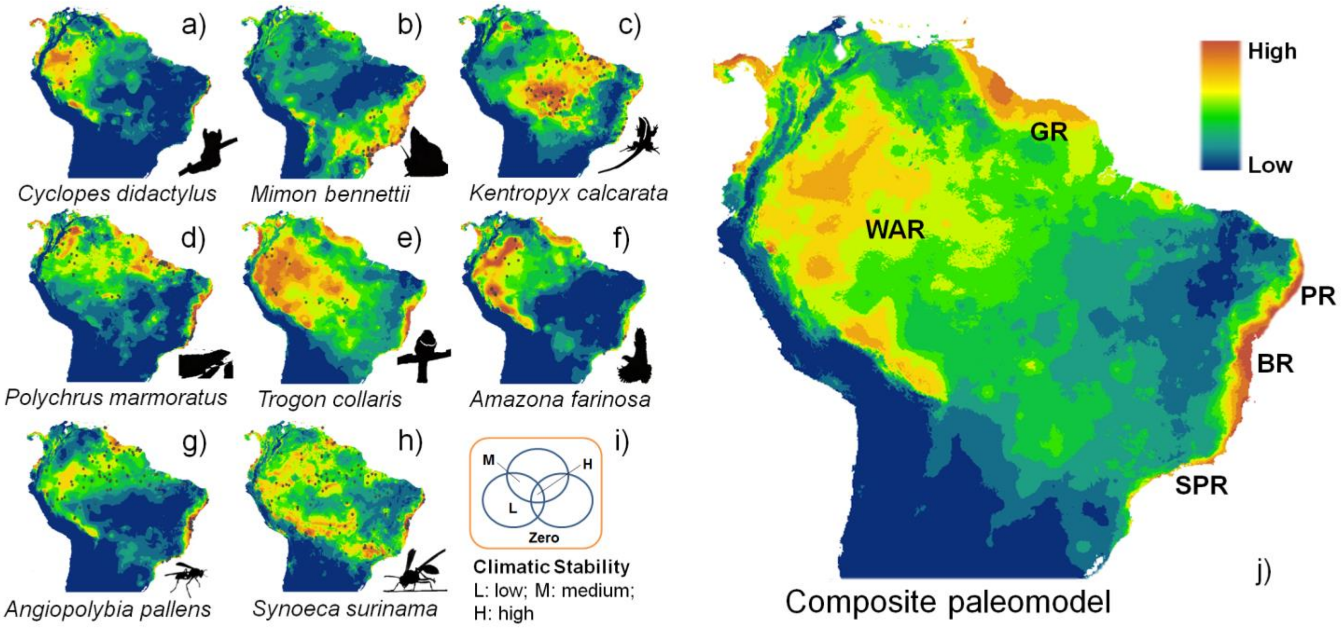


Fig. 2 Putative refuges of two mammals (a and b), two reptiles (c and d), two birds (e and f), two paper wasps (g and h) and the composite paleomodel (j) of these eight widely disjunct species in South America. In (i), climatic stability refers to the general procedure of overlaying for single species using the three potential distribution models (a-j) and for the composite paleomodel using all species stability models (j). Legend refers to historical climate stability. WAR: Western Amazonia Refuge; GR: Guiana Refuge; PR: Pernambuco Refuge; BR: Bahia Refuge and SPR: São Paulo Refuge.

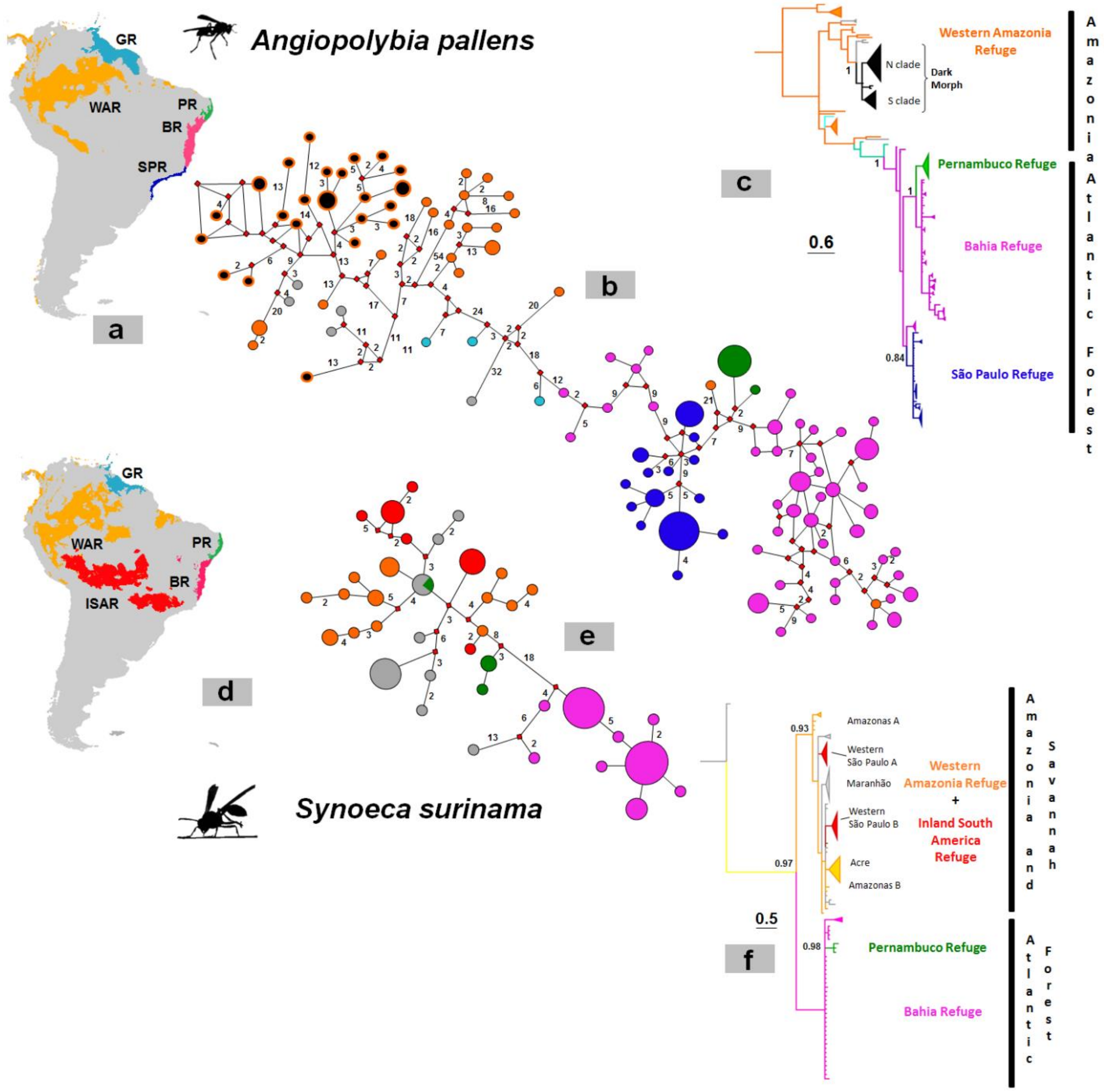


Fig. 3 Historical stability, median-joining networks and Bayesian inferences relative to *Angiopolybia pallens* (a – c) and *Synoeca surinama* (d – f), respectively. Colors in the networks and trees indicate stability zones of the respective species map. Stability zones in a and d refer to climatically stable regions obtained through paleomodelling; this is followed in the supplementary figures. Median-joining networks (b and e) are referent to the three mtDNA regions haplotypes for all the samples combined. Gray circles represent haplotypes from zones of putative recent population expansion. Haplotype size reflects relative frequency. Numbers on branchs and red diamonds refer to mutational steps, when >1, and missing intermediate haplotypes, respectively. Monophyletic clades whose samples were obtained in a same geographical region were collapsed in the concatenated Bayesian trees (d and f). Node values refer to posterior probabilities. For more details on these trees, check Figs S1 and S2.

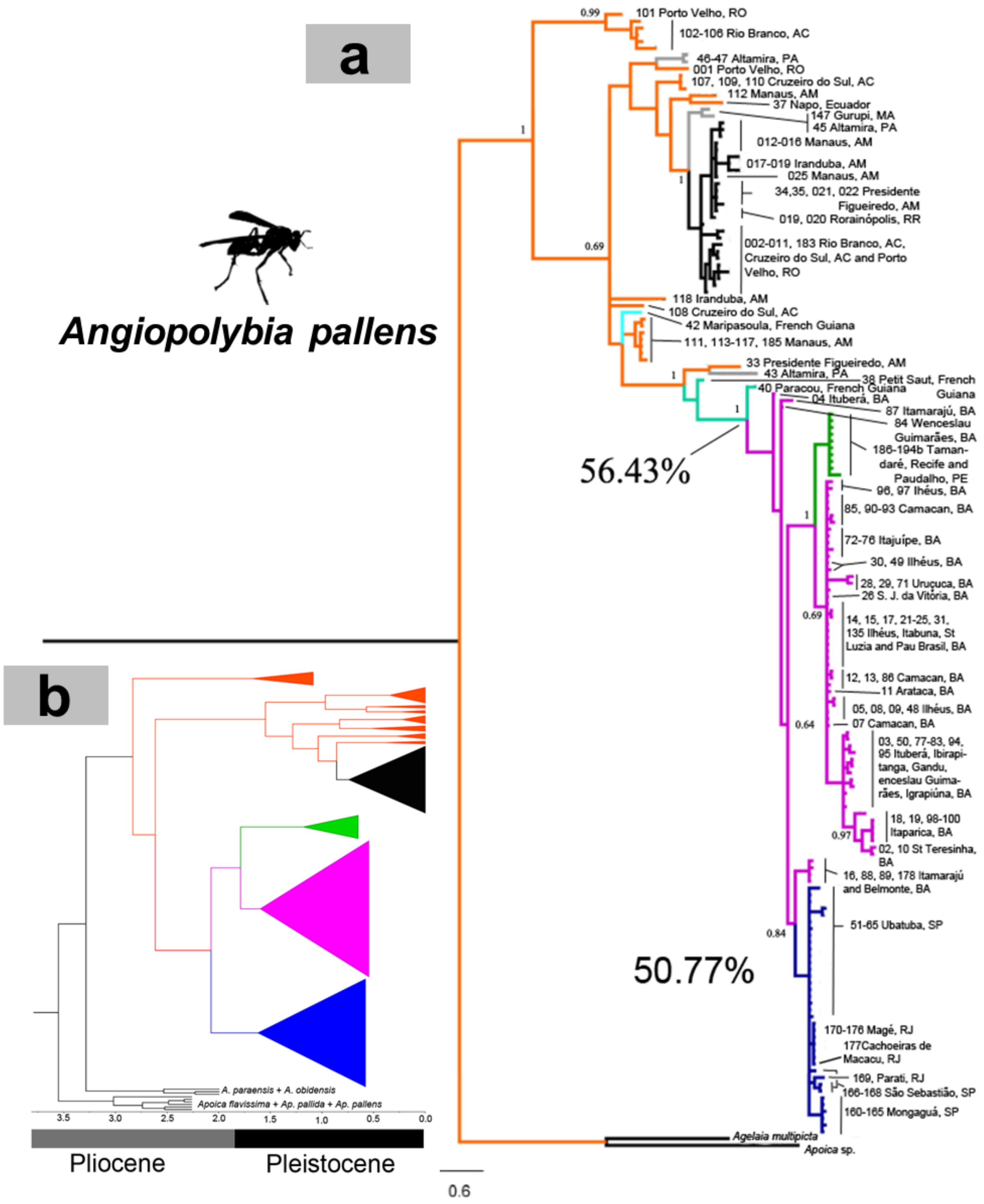


Fig. S1 Bayesian trees of (a) concatenated data (Cyt*b*, 12S and Cox1) and (b) exclusively Cox1 of *A*. *pallens*. Percentages and node values in (a) refer to molecular variances (Φ_{CT}) and posterior probabilities, respectively.

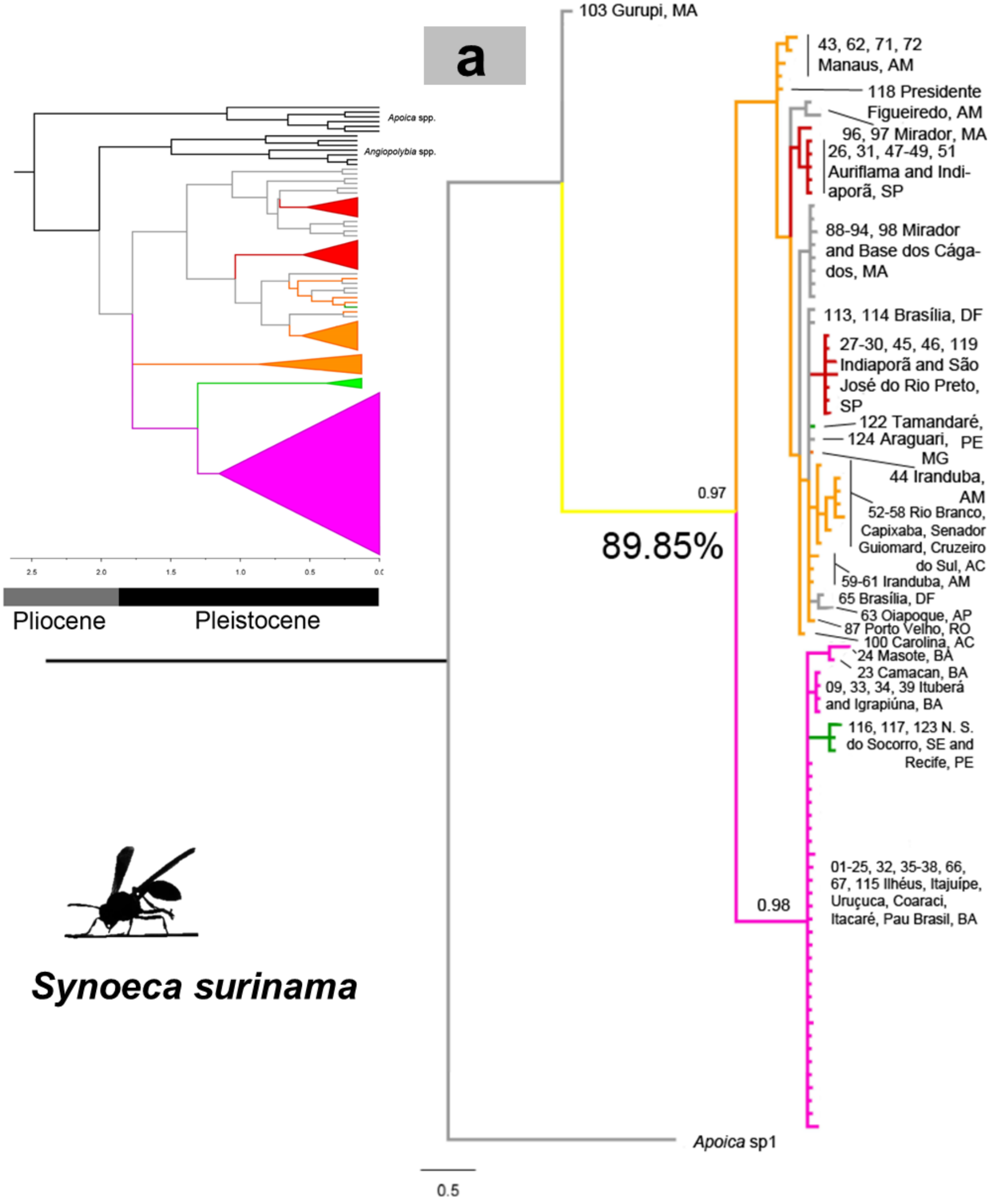
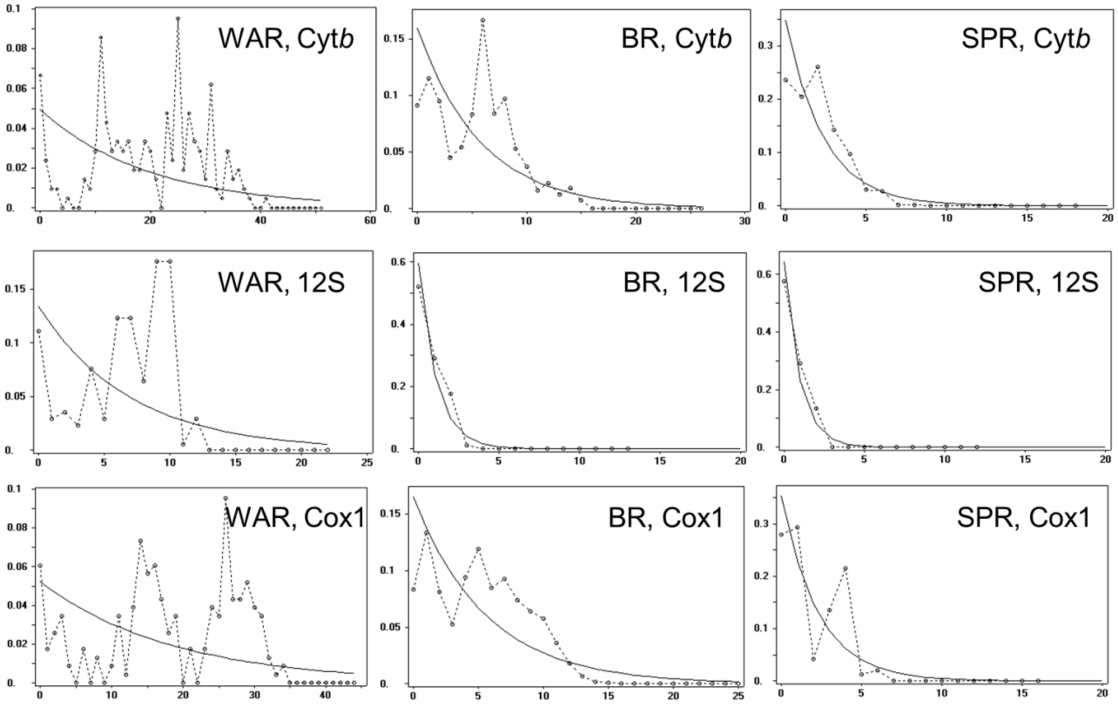


Fig. S2 Bayesian trees of (a) concatenated data (Cyt*b*, 12S and Cox1) and (b) exclusively Cox1 of *S*. *surinama*. Percentage and node values in (a) refer to molecular variance (Φ_{CT}) and posterior probabilities, respectively.

a) *Angiopolybia pallens*



a) *Synoeca surinama*

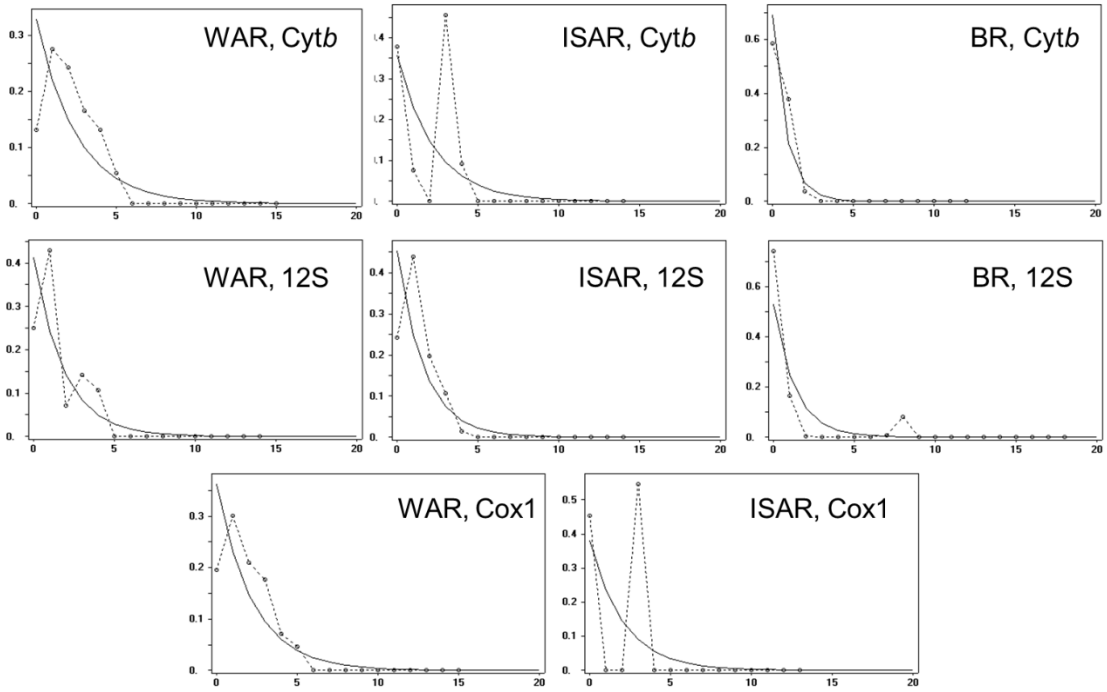


Fig. S3 Mismatch distributions referent to each putative refuge of *A*. *pallens* and *S*. *surinama*. Observed frequencies of pairwise differences (dotted line) are compared against expected frequencies under a scenario of expanding population sizes (continuous line).

Table S1 Geo-located data used to build niche models of *A*. *pallens* (Table S1.1), *S*. *surinama* (Table S1.2) and seven vertebrate species (Table S1.3).

Table S1.1 *Angiopolybia pallens*. D = dark morph; Y = yellow morph; and U = undetermined. Because more than one individual was consulted for the same locality, the sympatric occurrence of the morphs D and Y is referred as DY.

Table 1				
Country, Province	**Locality**	**Source of consult**	**Morph**	**dd long, dd lat**
Bolivia, Beni	Rurrenabaque	Smithsonian Institute	D	-67.5291734,-14.422468
Bolivia, La Paz	Alto Beni	AMNH	D	-67.18583333,-15.81568333
Bolivia, La Paz	Tumupasa	Smithsonian Institute	D	-67.8872252,-14.1466875
Brazil, Acre	Serra do Divisor	Morato et al. (2008)	U	-73.74,-7.83
Brazil, Acre	Cruzeiro do Sul	Surveying	DY	-72.59353638,-7.72119808
Brazil, Acre	Rio Branco	Surveying	DY	-67.87050962,-9.95488093
Brazil, Amazonas	Barcelos	INPA	U	-62.91389465,-0.64852283
Brazil, Amazonas	Parnajaú	INPA	D	-62.73880005,-2.01694780
Brazil, Amazonas	Carauari	INPA	Y	-66.92862511,-4.85537098
Brazil, Amazonas	Japurá	INPA	Y	-66.59951500,-1.82634090
Brazil, Amazonas	Novo Airão	INPA	Y	-60.96347809,-2.64230479
Brazil, Amazonas	São Gabriel da Cachoeira	INPA	Y	-67.04956055,0.03295898
Brazil, Amazonas	Ipixuna	INPA	D	-71.87049866,-7.36621226
Brazil, Amazonas	Barcelos	INPA	D	-61.56188965,-2.04576879
Brazil, Amazonas	Barcelos	INPA	D	-62.96813965,-1.57633919
Brazil, Amazonas	Novo Aripuanã	INPA	D	-60.01487732,-5.26634976
Brazil, Amazonas	Manicoré	INPA	Y	-60.82408905,-5.49638744
Brazil, Amazonas	Itacoatiara	INPA	D	-58.49018097,-3.11994747
Brazil, Amazonas	Tabatinga	INPA	D	-69.9196859,-4.2460755
Brazil, Amazonas	Lábrea	INPA	D	-64.8109436,-7.2706109

Brazil, Amazonas	Mamirauá	Silveira et al. (2008)	U	-64.86139,-3.039444
Brazil, Amazonas	Alvarães	Silveira et al. (2008)	U	-64.8042,-3.2208
Brazil, Amazonas	Presidente Figueiredo	Surveying	U	-60.0250,-2.0344
Brazil, Amazonas	Iranduba	Surveying	DY	-60.17572403,-3.22295794
Brazil, Amazonas	Manaus	Surveying	DY	-59.96543884,-2.94372665
Brazil, Amazonas	Presidente Figueiredo	Surveying	DY	-60.31459808,-1.44077373
Brazil, Bahia	Salvador	ZOBODAT	U	-38.5108,-12.9711
Brazil, Bahia	Ilhéus	Surveying	Y	-39.0494,-14.7889
Brazil, Bahia	Itabuna	Surveying	Y	-39.2803,-14.7856
Brazil, Bahia	Santa Luzia	Surveying	Y	-39.3342,-15.4294
Brazil, Bahia	Camacan	Surveying	Y	-39.4958,-15.4192
Brazil, Bahia	Belmonte	Surveying	Y	-38.8828,-15.8631
Brazil, Bahia	Ituberá	Surveying	Y	-39.1492,-13.7322
Brazil, Bahia	Itaparica	Surveying	Y	-38.6786,-12.8883
Brazil, Bahia	Santa Terezinha	Surveying	Y	-39.5233,-12.7719
Brazil, Bahia	Arataca	Surveying	Y	-39.4144,-15.2633
Brazil, Bahia	Itamarajú	Surveying	Y	-39.5311,-17.0392
Brazil, Bahia	Itajuípe	Surveying	Y	-39.3750,-14.6781
Brazil, Bahia	São José da Vitória	Surveying	Y	-39.3392,-15.0844
Brazil, Bahia	Uruçuca	Surveying	Y	-39.2844,-14.5931
Brazil, Bahia	Ibirapitanga	Surveying	Y	-39.3736,-14.1642
Brazil, Bahia	Gandu	Surveying	Y	-39.4867,-13.7439
Brazil, Bahia	Wenceslau Guimarães	Surveying	Y	-39.4794,-13.6869
Brazil, Bahia	Igrapiúna	Surveying	Y	-39.1422,-13.8264
Brazil, Bahia	Pau Brasil	Surveying	Y	-39.65019580,-15.46523300
Brazil, Ceará	Parque Nacional de Ubajara	INPA	Y	-40.9340,-3.8320
Brazil, Maranhão	Açailândia	INPA	Y	-47.03830719,-5.09145713
Brazil, Maranhão	Microrregião de Gurupi	INPA	Y	-46.70013428,-3.23444100

Brazil, Maranhão	Bom Jardim	INPA	Y	-46.49568558,-7.02090889
Brazil, Maranhão	São Pedro da Água Branca	INPA	Y	-48.26122284,-5.12206254
Brazil, Pará	Belém	AMNH	D	-48.43954444,-1.443472222
Brazil, Pará	Rio Trombetas	INPA	U	-56.82952881,0.28289680
Brazil, Pará	Oriximiná	INPA	D	-55.76660156,-1.65595837
Brazil, Pará	Tucuruí	INPA	Y	-49.73510742,-3.98413583
Brazil, Pará	Novo Repartimento	INPA	Y	-50.03019333,-4.36523949
Brazil, Pará	Apeú	INPA	Y	-47.98519135,-1.30451374
Brazil, Pará	Óbidos	INPA; AMNH	D	-55.47510278,-1.912855556
Brazil, Pará	Altamira	MPEG - Donation	U	-52.2064,-3.2033
Brazil, Pará	Caxiuanã	Silva and Silveira (2009)	U	-51.29516602,-1.82891297
Brazil, Pará	Mocajuba	Smithsonian Institute	Y	-49.5004285,-2.5895306,
Brazil, Pernambuco	Paudalho	Surveying	Y	-35.1673621,-7.9137218
Brazil, Pernambuco	Recife	Surveying	Y	-34.9652794,-8.0432485
Brazil, Pernambuco	Tamandaré	Surveying	Y	-35.1736914,-8.730033
Brazil, Piauí	Parque Nac. de Sete Cidades	INPA	Y	-41.6776,-4.1741
Brazil, Rio de Janeiro	Parati	Surveying	Y	-44.7636,-23.2197
Brazil, Rio de Janeiro	Magé	Surveying	Y	-43.0720,-22.5693
Brazil, Rio de Janeiro	Cachoeiras de Macacu	Surveying	Y	-42.6200,-22.4144
Brazil, Rondônia	Nova Mamoré	INPA	D	-65.28488159,-10.53304524
Brazil, Rondônia	Porto Velho	Surveying	DY	-63.94108415,-8.83062556
Brazil, Roraima	Pacaraima	INPA	Y	-61.13479614,4.41008295
Brazil, Roraima	Ilha de Maracá	INPA	Y	-61.50146484,3.39279087
Brazil, Roraima	Ilha de Maracá	Raw (1998)	U	-61.66,3.4166
Brazil, Roraima	Rorainópolis	Surveying	D	-60.47012329,0.42846280
Brazil, Roraima	Rorainópolis	Surveying	D	-60.46600342,0.76490037
Brazil, São Paulo	Ubatuba	Surveying	Y	-45.0711,-23.4339
Brazil, São Paulo	Mongaguá	Surveying	Y	-46.6233,-24.0857

Brazil, São Paulo	São Sebastião	Surveying	Y	-45.4621,-23.8016
British Guiana	Shudihar River	AMNH	D	Not found
British Guiana	Wismar	AMNH	D	Not found
British Guiana	Essequibo (Essequebor)	Smithsonian Institute	Y	Not found
British Guiana, Bartica	Kartabo	Smithsonian Institute	DY	Not found
British Guiana, Cuyuni-Mazaruni	Cuyuni River	BMNH	U	-60.09,6.63
British Guiana, Potaro-Siparuni	Kaieteur	AMNH	D	-59.47929167,5.172980556
British Guiana, Cuyuni-Mazaruni	Bartica	AMNH	DY	-58.63083611,6.391341667
British Guiana, Demerara-Mahaica	Georgetown, Tukeit	AMNH	DY	-58.14530278,6.784888889
British Guiana, Potaro-Siparuni	Tumatumari	AMNH	Y	-59.1439,5.259644444
British Guiana, Potaro-Siparuni	Kangaruma	AMNH	Y	-59.199498,5.3298451
British Guiana, Takutu-Essequibo	Kuyuwini River	AMNH	D	-58.47898333,2.210758333
Colombia	Caqueta	Smithsonian Institute	Y	Not found
Colombia, Amazonas	Leticia	AMNH	D	-69.93107778,-4.179127778
Colombia, Amazonas	PNN Amacayacu	Sharkey Lab	U	-70.14558050,-3.29275220
Colombia, Amazonas	Leticia	Smithsonian Institute	Y	-69.9198234,-4.2388429
Colombia, Caquetá	San José del Fragua	Sharkey Lab	U	-75.98830,1.361110
Colombia, Guapi	PNN Gorgona	Sharkey Lab	U	-77.8833333330,2.56666670
Colombia, Guaviare	PNN Serranía de Chiribiquete	Sharkey Lab	U	-72.89840698,0.71683921
Colombia, Narino	Barbacoas	BMNH	U	-78.1556443,1.6560377
Costa Rica, San José	San Carlos	Smithsonian Institute	D	-84.1160967,9.6174454
Ecuador, Napo	Jatún Sacha	AMNH	D	-77.6148499,-1.0872628
Ecuador, Napo	Napo	AMNH - Donation	U	-77.833333,-0.666667
Ecuador, Sucumbios	Limonocha	AMNH	DY	-76.62063333,-0.400363889
French Guiana	Bagne at Crique Anguille	AMNH	D	-52.51666667,4.833333333
French Guiana	Saul	AMNH	U	Not found
French Guiana	Sentier de Rorota, Montjoly	AMNH	D	-52.24636944,4.883461111
French Guiana	Matoury	AMNH	D	-52.33208889,4.850430556

French Guiana	Piste de St.-Elie	AMNH	D	-53.278525,4.822811111
French Guiana	Cacao	AMNH	Y	-52.46666667,4.566666667
French Guiana	Maripasoula	AMNH - Donation	U	-54.033333,3.65
French Guiana	Petit Saut	AMNH - Donation	U	-53.05,5.066667
French Guiana	Paracou	AMNH - Donation	U	-52.9,5.383333
French Guiana	Sinnamary	AMNH - Donation	U	-52.951859,5.372225
French Guiana	Grand Santi	ZOBODAT	U	-54.38,4.25
Guatemala	Sanarate	HOD	U	14.0667,-89.85
Guatemala, Gualan	Zacapa Dept.	HOD	U	15.1333,-89.3667
Panama	Alhajuelo	Smithsonian Institute	D	Not found
Peru	San Ramon	AMNH	D	-75.36069167,-11.116825
Peru	Middle Rio Ucayali	AMNH	D	Not found
Peru	Puerto Maldonado	AMNH	Y	-69.23287778,-12.56182222
Peru	Tambopata	AMNH	D	-69.28333333,-12.85
Peru	Iquitos	AMNH - Donation	U	-73.247222,-3.748056
Peru	62km f/Pucallpa t/Tingo Maria	Smithsonian Institute	Y	-74.9191925,-8.5962715
Peru	Panguana	ZOBODAT	U	-74.9333,-9.61667
Peru	San Antonia de Cumbaza	ZOBODAT	U	-76.40568700,-6.40727560
Peru	Picota, San Martin	ZOBODAT	U	-76.33034170,-6.9207056
Peru	Tarapoto	ZOBODAT	U	-76.36666670,-6.48333330
Peru, Loreto	Iquitos	AMNH	DY	-73.2833147,-3.7529196
Peru, Loreto	Pucalpa	BMNH	U	-74.6767983,-8.3559387
Suriname	Voltzberg	AMNH	D	-56.53336944,4.532763889
Suriname	Voltzberg	AMNH	D	Not found
Suriname	Brownsberg Natuurpark	AMNH	D	-55.2,4.966666667
Suriname	Suriname, Marowijne River	BMNH	U	-57.89,4.89
Suriname	Paramaribo	Smithsonian Institute	D	-55.1782015,5.8483248,
Suriname	Marowijne	Smithsonian Institute	D	Not found

Suriname	Copenname River	Smithsonian Institute	D	Not found
Trinidad and Tobago	Port of Spain	AMNH	D	-61.4856888,10.6786222
Trinidad and Tobago	Arima Valley	AMNH	D	-61.292275,10.65285833
Trinidad and Tobago	Caparo	AMNH	Y	-61.3259864,10.4505657
Trinidad and Tobago	Lalaja Rd	AMNH	D	Not found
Trinidad and Tobago	St George, Maracas Valley	BMNH	U	-61.472,10.711
Trinidad and Tobago	St Benedict	Smithsonian Institute	D	-61.394434,10.6617678
Trinidad and Tobago	Monteserrat	Smithsonian Institute	D	Not found
Trinidad and Tobago	Heights of Aripo	Smithsonian Institute	D	Not found
Trinidad and Tobago	Sangre Grande	Smithsonian Institute	D	-61.1281423,10.5812007
Trinidad and Tobago	Caracciola	Smithsonian Institute	D	Not found
Trinidad and Tobago	Maracas	Smithsonian Institute	D	-61.4324827,10.7549554
Venezuela	Caripito	AMNH	Y	-63.08993056,10.11123889
Venezuela	Amazonas	AMNH	D	-64.71623889,1.939572222
Venezuela	Mt. Duida	AMNH	D	-65.52617778,3.307661111

Table S1.2 *Synoeca surinama*.

Table 2			
Country	**Locality**	**Source of consult**	**dd long,dd lat**
Bolivia	Villa Tunari, Cochabamba	Discover Life	-65.4361,-17.0011
Bolivia	Arroyo Tuhiri, Mapiri, Prov. La Paz	ZOBODAT	-68.2628,-15.2906
Bolivia	Cochabamba	INPA	-65.5004,-16.8834
Bolivia	Chapare Cesarzama	AMNH	-65.6666694444,-16.7124611111
Bolivia	Chapare Locotal	AMNH	-65.61685,-17.1848722222
Bolivia	Santa Cruz	AMNH	-63.0006583333,-17.8664722222
Bolivia	Chapare Sajta	AMNH	Not found
Bolivia	Mapiri	AMNH	-68.2171777778,-15.3104388889

Bolivia	Ixiamas	Smithsonian Institution	-68.1264781,-13.7672714
Bolivia	Cavinas, Beni	Smithsonian Institution	Not found
Bolivia	Rio Mapiri	Smithsonian Institution	Not found
Bolivia	Huachi, Beni	Smithsonian Institution	Not found
Bolivia	Yungas Esp. Santo, Cochabamba	Smithsonian Institution	Not found
Bolivia, Beni	Riberalta	Smithsonian Institution	-66.0573148,-11.0179082
Brazil	Barra do Tapirape	AMNH	Not found
Brazil, Acre	Rio Branco	Surveying	-67.80756800,-9.97399890
Brazil, Acre	Senador Guiomard	Surveying	-67.69912720,-10.13280669
Brazil, Acre	Capixaba	Surveying	-67.69033660,-10.56094740
Brazil, Acre	Cruzeiro do Sul	Surveying	-72.65036110,-7.66490230
Brazil, Amapá	Oiapoque	Donation	-51.83544440,3.83148810
Brazil, Amapá	Porto Santana	INPA	-51.1846,-0.0274
Brazil, Amapá	Serra do Navio	MN-UFRJ	-52.0257,0.8668
Brazil, Amapá	Macapá	Silveira (2003)	-51.0882916,0.0222808
Brazil, Amazonas	Alvarães	Silveira et al. (2008)	-64.8042,-3.2208
Brazil, Amazonas	Mamirauá	Silveira et al. (2008)	-65.7077239,-2.2131887
Brazil, Amazonas	Benjamin Constant	INPA	-70.0311,-4.3831
Brazil, Amazonas	Novo Aripuanã	INPA	-60.3797,-5.1206
Brazil, Amazonas	Manaus	Surveying	-60.0250,-3.1019
Brazil, Amazonas	Iranduba	Surveying	-60.1861,-3.2847
Brazil, Amazonas	Rio Carabinani	INPA	-61.56188965,-2.04576879
Brazil, Amazonas	Presidente Figueiredo	INPA	-60.31459808,-1.44077373
Brazil, Amazonas	Parnajaú, Rio Papagaio	INPA	-62.5833333,-1.8833333
Brazil, Amazonas	Reserva Campinas	INPA	-60.03616333,-2.60423590
Brazil, Amazonas	Parna do Jaú, Vila Seringalzinho	INPA	-62.25952148,-3.33795396
Brazil, Amazonas	Itacoatiara	INPA	-58.44263500,-3.14198120
Brazil, Amazonas	Barcelos, Rio Negro	INPA	-62.9681,-1.5763

Brazil, Amazonas	Manicoré	MN-UFRJ	-61.3004,-5.8093
Brazil, Amazonas	Coari	MN-UFRJ	-63.1549,-4.0981
Brazil, Amazonas	Estirão do Equador	AMNH	-71.5665583333,-4.52476388889
Brazil, Bahia	Ilhéus	Surveying	-39.0494,-14.7889
Brazil, Bahia	Santa Luzia	Surveying	-39.3342,-15.4294
Brazil, Bahia	Itajuípe	Surveying	-39.3750,-14.6781
Brazil, Bahia	Uruçuca	Surveying	-39.2844,-14.5931
Brazil, Bahia	Itacaré	Surveying	-38.9967,-14.2775
Brazil, Bahia	Ituberá	Surveying	-39.1492,-13.7322
Brazil, Bahia	Coaraci	Surveying	-39.5511,-14.6408
Brazil, Bahia	Camacan	Surveying	-39.4958,-15.4192
Brazil, Bahia	Mascote	Surveying	-39.3025,-15.5631
Brazil, Bahia	Igrapiúna	Surveying	-39.1422,-13.8264
Brazil, Bahia	Palmeiras	Silva-Pereira&Santos2006	-41.5589,-12.5289
Brazil, Bahia	Riachão das Neves	Santos et al. (2009)	-44.9100,-11.7461
Brazil, Bahia	São Desidério	Santos et al. (2009)	-44.9733,-12.3633
Brazil, Bahia	Pau Brasil	Surveying	-39.65019580,-15.46523300
Brazil, Bahia	Água Preta	MN-UFRJ	-39.6137,-15.2349
Brazil, Bahia	Salvador	MN-UFRJ	-38.5108,-12.9711
Brazil, Distrito Federal	Brasília	Raw (1997; 1998); Surveying	-47.9297,-15.7797
Brazil, Goiás	L. de Pedra, 160 NE Brasília	Smithsonian Institution	Not found
Brazil, Goiás	São Miguel do Araguaia – Luís Alves	Surveying	-50.55425,-13.17555
Brazil, Goiás	Jataí	Surveying	-51.73577,-17.84749
Brazil, Goiás	Aragarças	Surveying	-52.25436,-15.91867
Brazil, Maranhão	Caxias	INPA	-43.34693520,-4.87466660
Brazil, Maranhão	Mirador	INPA	-44.34897420,-6.36195310
Brazil, Maranhão	Bom Jardim	INPA	-46.49568558,-7.02090889
Brazil, Maranhão	Carolina	INPA	-47.46261990,-7.33661800

Brazil, Maranhão	Urbano Santos	Silva et al. (2011)	-43.3952269,-3.2163406
Brazil, Maranhão	Barreirinhas	Silva et al. (2011)	-42.8236209,-2.7589999
Brazil, Mato Grosso	Rio Manso	Diniz and Kitayama (1994)	-55.4000,-14.9167
Brazil, Mato Grosso	Xavantina	Richards (1978)	-52.3500,-14.6667
Brazil, Mato Grosso	Pixaim	INPA	-56.8372,-16.7358
Brazil, Mato Grosso	BR 174, km 198	INPA	-59.32067871,-14.79347208
Brazil, Mato Grosso	Conf. dos Rios Xingu e Culuene	MN-UFRJ	-53.5466,-11.9385
Brazil, Mato Grosso	Cuiabá	Smithsonian Institution	-56.0414597,-15.6070359
Brazil, Mato Grosso	Nova Xavantina	Surveying	-52.3503337,-14.6961673
Brazil, Mato Grosso	Pontal do Araguaia	Surveying	-52.3159806,-15.9104771
Brazil, Mato Grosso do Sul	Paranaíba	Grandinete & Noll (2013)	-51.1870696,-19.6737683
Brazil, Minas Gerais	Barroso	Prezoto et al. (2009)	-43.9758,-21.1869
Brazil, Minas Gerais	Uberlândia	Elpino-Campos et al. (2007)	-48.2772,-18.9186
Brazil, Minas Gerais	Brasópolis, Córrego das Antas	INPA	-45.61094330,-22.47447520
Brazil, Minas Gerais	Sete Lagoas	DEBE-UFSCar	-44.2402361,-19.4557259
Brazil, Pará	Caxiuanã	Silva and Silveira (2009)	-51.4300,-1.7200
Brazil, Pará	Rio Tocantins, Ilha do Germoplasma	INPA	-49.40826416,-1.98812630
Brazil, Pará	Tucurui, Jatogal	INPA	-49.67410930,-3.76952760
Brazil, Pará	Alter do Chão	INPA	-54.95898100,-2.52307400
Brazil, Pará	Cachimbo	INPA	-54.90156200,-8.94894200
Brazil, Pará	Rio Trombetas, Lago Caetano	INPA	-57.00805664,-1.08758117
Brazil, Pará	Medicilândia	INPA	-52.88917140,-3.44864930
Brazil, Pará	Óbidos, 01°47'03"S/55°07'05"	INPA	-55.01781464,-1.79597047
Brazil, Pará	Rio Paru	MN-UFRJ	-53.6556,-0.4425
Brazil, Pará	Belém	MN-UFRJ	-48.4218,-1.4349
Brazil, Pará	Açari	MN-UFRJ	-47.5465,-1.5980
Brazil, Pará	Altamira, Cachimbo	MN-UFRJ	-54.9015,-8.9489
Brazil, Pará	Tucurui	AMNH	-49.6749555556,-3.76964166667

Brazil, Paraíba	Mamanguape	INPA	-35.1261,-6.8386
Brazil, Pernambuco	Tamandaré	Surveying	-35.1736914,-8.730033
Brazil, Pernambuco	Recife	Surveying	-34.9652794,-8.0432485
Brazil, Rondônia	Porto Velho	Surveying	-64.35791016,-9.38403211
Brazil, Roraima	Ilha de Maracá	Raw (1998)	-61.4975,2.8958
Brazil, Roraima	Rio Uraricoera	INPA	-61.50146484,3.39279087
Brazil, Roraima	Bonfim	INPA	-59.83315690,3.35701640
Brazil, São Paulo	Auriflama	UNESP, donation	-50.5547,-20.6856
Brazil, São Paulo	Indiaporã	UNESP, donation	-50.2897,-19.9800
Brazil, São Paulo	Magda	Tanaka-Jr and Noll (2011)	-50.2261,-20.6439
Brazil, São Paulo	Barretos	Tanaka-Jr and Noll (2011), donation	-48.5678,-20.5572
Brazil, São Paulo	São José do Rio Preto	UNESP, donation	-49.3823555,-20.8168139
Brazil, São Paulo	Pedregulho	Sidnei Mateus	-47.4778934,-20.2539423
Brazil, Sergipe	Nossa Senhora do Socorro	Surveying	-37.1408792,-10.8568173
British Guiana	Blairmont	Smithsonian Institution	-57.575291,6.2798695
British Guiana	Georgetown	Smithsonian Institution	-58.1515334,6.7875029
British Guiana	Waranama	AMNH	Not found
British Guiana	Georgetown	AMNH	-58.1443777778,6.80456666667
British Guiana	Arakaka	AMNH	-60.1806083333,7.50058611111
British Guiana	Bartica	AMNH	-58.6308361111,6.39134166667
British Guiana	Penal Settlement	AMNH	Not found
Colombia	Pto. Lopez, Lianos	ZOBODAT	-72.9167,4.15
Colombia	San Martin	AMNH	-73.75098611111,3.763275
Colombia	Caqueta, Rio Orteguaza	Smithsonian Institution	Not found
Colombia	Caqueta, Morelia, Rio Bodoquero	Smithsonian Institution	-75.7275612,1.4878073
Ecuador	Jatún Sacha, Prov. Napo	ZOBODAT	-77.6167,-10.6667
Ecuador	Morona Santiago Gualaquiza	INPA	-78.57176310,-3.40634920
Ecuador	Tena	AMNH	-77.8161277778,-0.9855472222

Ecuador	Zumbi, Zam-Chin. Prov.	Smithsonian Institution	-78.7808991,-3.8935414
Ecuador	Cumbaratza, Zam-Chin. Prov.	Smithsonian Institution	-78.8669015,-3.9926124
Ecuador	Limonocha, Napo	Smithsonian Institution	Not found
Ecuador, Pastaza	Puyo	Smithsonian Institution	-78.0001401,-1.4873644
Guiana	Georgetown	INPA	-58.16667,6.8
Guiana	Esseq. Plantain Is.	Smithsonian Institution	-58.4864464,6.9090205
Panamá	Isle Grande (Colon)	INPA	-79.56455850,9.6326757
Peru	Panguana	Discover Life	-74.9333,-9.61667
Peru	Pucallpa (Stadt)	INPA	-74.47837830,-8.38611032
Peru	Iquitos	AMNH	-73.2710361111,-3.75098611111
Peru	Upper R. Huallaga	AMNH	-76.2134888889,-9.89685
Peru	San Ramon	AMNH	-75.3643388889,-11.1165055556
Peru	Upper Rio Marañón	AMNH	-77.8782527778,-7.74543611111
Peru	Estirón, Rio Ampyiacu	AMNH	-70.7178138889,-4.16347222222
Peru	Satipo	Smithsonian Institution	Not found
Peru	Pucallpa	Smithsonian Institution	-74.5817184,-8.3751095
Peru, Junín	Valle Chanchamayo	MN-UFRJ; Smithsonian Institution	-75.3305,-11.0820
Peru, Junín	Satipo	MN-UFRJ	-74.6367,-11.2542
Peru, Rupa Rupa	Tingo Maria	Smithsonian Institution	-75.9978806,-9.2985227
Suriname	Paramaribo	MN-UFRJ	-55.2159,5.5859
Trinidad and Tobago	Arima Valley	AMNH	-61.292275,10.6528583333
Trinidad and Tobago	Porto of Spain	Smithsonian Institution	-61.5209241,10.6811408
Trinidad and Tobago	Aripo	Smithsonian Institution	Not found
Trinidad and Tobago	Tucuche	Smithsonian Institution	-61.4177371,10.7331925
Venezuela	Atures + Coromoto	AMNH	-66.7284722222,2.34126944444
Venezuela	Atabapo	AMNH	-66.8073111111,3.88856111111

Table S1.3 *Amazona farinosa, Cyclopes didactylus, Kentropyx calcarata*, *Mimon bennettii*, *Trogon collaris* and *Polychrus marmoratus*.

Table 3		
Species	**dd long**	**dd lat**
Amazona farinosa	-45.41	-23.76
Amazona farinosa	-40.6003	-19.9356
Amazona farinosa	-40.0722	-19.3911
Amazona farinosa	-61.9014	-11.1753
Amazona farinosa	-61.9517	-10.8853
Amazona farinosa	-65.3394	-10.7828
Amazona farinosa	-72.7819	-8.87528
Amazona farinosa	-72.8722	-8.86028
Amazona farinosa	-72.8833	-8.55833
Amazona farinosa	-72.8578	-8.40528
Amazona farinosa	-73.2536	-8.28083
Amazona farinosa	-73.7014	-7.50611
Amazona farinosa	-73.7744	-7.45889
Amazona farinosa	-73.6744	-7.44333
Amazona farinosa	-73.6611	-7.43167
Amazona farinosa	-69.95	-4.15
Amazona farinosa	-60.025	-3.10194
Amazona farinosa	-50.7122	-1.80444
Amazona farinosa	-69.5	-1.09333
Amazona farinosa	-67.0892	-0.13028
Amazona farinosa	-70.5	0.386111
Amazona farinosa	-76.5167	0.5
Amazona farinosa	-72.7333	0.574444
Amazona farinosa	-52.0022	0.895556
Amazona farinosa	-67.5	2.916667

Amazona farinosa	-73.4	3.683333
Amazona farinosa	-73.1625	4.635833
Amazona farinosa	-67.8	4.9
Amazona farinosa	-67.795	5.243889
Amazona farinosa	-61.9517	-10.8853
Amazona farinosa	-73.7242	-7.51444
Cyclopes didactylus	-69.75	-10
Cyclopes didactylus	-68.725	-9.25
Cyclopes didactylus	-72.7833	-8.66667
Cyclopes didactylus	-72.7833	-8.66667
Cyclopes didactylus	-72.8167	-8.36667
Cyclopes didactylus	-73.6611	-7.43167
Cyclopes didactylus	-73.2667	-7.38333
Cyclopes didactylus	-70.85	-6.75
Cyclopes didactylus	-69.95	-4.15
Cyclopes didactylus	-71.7369	-2.13333
Cyclopes didactylus	-48.4833	-1.45
Cyclopes didactylus	-69.5	-1.09333
Cyclopes didactylus	-71.0189	0.878611
Cyclopes didactylus	-66.6581	1.899444
Cyclopes didactylus	-65.1833	2.5
Cyclopes didactylus	-66.6167	3.383333
Cyclopes didactylus	-73.635	4.153333
Cyclopes didactylus	-73.5561	4.268611
Cyclopes didactylus	-65.5508	7.429444
Cyclopes didactylus	-35.2621	-5.80195
Cyclopes didactylus	-34.9511	-8.00194
Cyclopes didactylus	-34.8957	-7.83806
Cyclopes didactylus	-36.2003	-9.62091
Cyclopes didactylus	-35.8295	-9.7013
Cyclopes didactylus	-35.8852	-9.22375

Cyclopes didactylus	-35.7024	-9.44279
Kentropyx calcarata	-40.0978	-19.1969
Kentropyx calcarata	-39.8589	-18.7161
Kentropyx calcarata	-39.7322	-18.5933
Kentropyx calcarata	-39.0647	-16.4497
Kentropyx calcarata	-58.4572	-15.2558
Kentropyx calcarata	-58.5744	-15.0725
Kentropyx calcarata	-55.7856	-14.8717
Kentropyx calcarata	-56.8171	-14.0943
Kentropyx calcarata	-58.677	-13.0753
Kentropyx calcarata	-54.7664	-12.9931
Kentropyx calcarata	-38.8	-12.5544
Kentropyx calcarata	-64.2272	-12.445
Kentropyx calcarata	-57.995	-12.4251
Kentropyx calcarata	-55.8738	-11.8994
Kentropyx calcarata	-54.8914	-11.5153
Kentropyx calcarata	-55.0494	-11.4462
Kentropyx calcarata	-55.4545	-11.336
Kentropyx calcarata	-57.6248	-11.0586
Kentropyx calcarata	-59.4632	-10.2096
Kentropyx calcarata	-59.4594	-10.1667
Kentropyx calcarata	-59.4543	-10.1658
Kentropyx calcarata	-59.4476	-10.1625
Kentropyx calcarata	-59.4466	-10.1622
Kentropyx calcarata	-59.4271	-10.1439
Kentropyx calcarata	-60.2631	-9.8603
Kentropyx calcarata	-58.2196	-9.8454
Kentropyx calcarata	-39.4817	-9.84167
Kentropyx calcarata	-58.076	-9.7688
Kentropyx calcarata	-55.4028	-9.7516
Kentropyx calcarata	-51.5129	2.292762

Kentropyx calcarata	-56.7802	-2.06446
Kentropyx calcarata	-59.4298	-1.9201
Kentropyx calcarata	-59.9739	-2.92773
Kentropyx calcarata	-60.59	-7.71446
Kentropyx calcarata	-44.7622	-3.51448
Kentropyx calcarata	-45.0087	-3.59413
Kentropyx calcarata	-44.7477	-5.38577
Kentropyx calcarata	-45.7744	-2.59144
Kentropyx calcarata	-51.7641	-12.8501
Kentropyx calcarata	-57.2706	-15.0614
Kentropyx calcarata	-48.456	-1.39165
Kentropyx calcarata	-48.8705	-1.71693
Kentropyx calcarata	-49.6491	-3.80419
Kentropyx calcarata	-50.7218	-1.80881
Kentropyx calcarata	-55.8245	-1.83231
Kentropyx calcarata	-56.7013	-2.16583
Kentropyx calcarata	-63.1612	-9.36044
Kentropyx calcarata	-53.0501	5.071177
Kentropyx calcarata	-51.2815	-0.11515
Kentropyx calcarata	-59.8897	-2.73349
Kentropyx calcarata	-45.8952	-5.74115
Kentropyx calcarata	-49.5651	-0.12504
Kentropyx calcarata	-50.5338	-1.05825
Kentropyx calcarata	-50.4385	-1.61557
Kentropyx calcarata	-46.3876	-1.35646
Kentropyx calcarata	-46.6231	-1.03731
Kentropyx calcarata	-46.7703	-1.05418
Kentropyx calcarata	-1.75906	-47.0731
Kentropyx calcarata	-47.1719	-1.19165
Kentropyx calcarata	-47.3128	-1.19541
Kentropyx calcarata	-47.9845	-1.29772

Kentropyx calcarata	-47.8422	-0.72446
Kentropyx calcarata	-48.0279	-0.75632
Kentropyx calcarata	-48.0998	-0.86853
Kentropyx calcarata	-48.2438	-1.36219
Kentropyx calcarata	-48.3089	-1.22609
Kentropyx calcarata	-52.582	-1.52133
Kentropyx calcarata	-54.7295	-2.49321
Kentropyx calcarata	-50.0722	-6.0771
Kentropyx calcarata	-64.4091	-9.26098
Kentropyx calcarata	-63.8482	-8.76486
Kentropyx calcarata	-62.2298	-10.7158
Kentropyx calcarata	-61.9402	-10.8821
Mimon bennettii	-49.6356	-25.5839
Mimon bennettii	-49.6242	-25.4908
Mimon bennettii	-49.7147	-25.4717
Mimon bennettii	-48.3289	-25.3067
Mimon bennettii	-49.0858	-24.9744
Mimon bennettii	-49.34	-24.11
Mimon bennettii	-48.3653	-24.0992
Mimon bennettii	-48.3494	-24.0058
Mimon bennettii	-49.4897	-23.7078
Mimon bennettii	-47.06	-22.9
Mimon bennettii	-40.8	-20.7999
Mimon bennettii	-40.8111	-20.7931
Mimon bennettii	-41.1847	-20.6036
Mimon bennettii	-41.2124	-20.5067
Mimon bennettii	-40.47	-20.2833
Mimon bennettii	-40.42	-20.2639
Mimon bennettii	-40.379	-19.2673
Mimon bennettii	-40.379	-19.2665
Mimon bennettii	-40.8908	-18.755

Mimon bennettii	-40.8957	-18.6851
Mimon bennettii	-55.7497	-15.4606
Mimon bennettii	-73.9167	2.75
Mimon bennettii	-49.223	-26.424
Mimon bennettii	-48.7327	-27.6851
Mimon bennettii	-48.4698	-27.5444
Mimon bennettii	-49.1061	-26.9549
Mimon bennettii	-49.2949	-25.5872
Mimon bennettii	-48.336	-25.5119
Mimon bennettii	-50.6004	-24.3338
Mimon bennettii	-50.5808	-25.3879
Mimon bennettii	-48.8247	-25.4762
Mimon bennettii	-49.4033	-23.4511
Mimon bennettii	-47.02	-23.9704
Mimon bennettii	-46.9325	-22.8525
Mimon bennettii	-46.876	-23.0266
Mimon bennettii	-40.8093	-20.7852
Mimon bennettii	-41.111	-20.53
Mimon bennettii	-40.4216	-20.2727
Mimon bennettii	-43.394	-22.4483
Mimon bennettii	-43.469	-22.9641
Mimon bennettii	-44.2784	-19.4495
Mimon bennettii	-48.8223	-15.9159
Mimon bennettii	-46.1054	-14.4831
Mimon bennettii	-48.3734	-14.109
Mimon bennettii	-47.9644	-15.7361
Mimon bennettii	-55.6609	-15.4485
Mimon bennettii	-44.3618	-9.07977
Mimon bennettii	-42.6952	-9.01088
Mimon bennettii	-39.1691	-14.7947
Mimon bennettii	-38.3302	-12.8253

Mimon bennettii	-51.6496	1.34142
Mimon bennettii	-52.9239	5.274469
Mimon bennettii	-53.3659	3.965688
Mimon bennettii	-55.6455	5.695992
Mimon bennettii	-58.6902	4.672547
Mimon bennettii	-65.191	2.522258
Mimon bennettii	-72.3166	-0.3576
Mimon bennettii	-72.7326	0.618859
Mimon bennettii	-73.5594	2.588213
Mimon bennettii	-76.2842	7.853512
Mimon bennettii	-82.5389	9.490895
Trogon collaris	-39.7322	-18.5933
Trogon collaris	-39.7322	-18.5933
Trogon collaris	-55.7497	-15.4606
Trogon collaris	-61.9517	-10.8853
Trogon collaris	-55.4508	-10.8178
Trogon collaris	-65.3394	-10.7828
Trogon collaris	-54.9	-10.1667
Trogon collaris	-56.0861	-9.87556
Trogon collaris	-72.8722	-8.86028
Trogon collaris	-72.8578	-8.40528
Trogon collaris	-73.2536	-8.28083
Trogon collaris	-73.7242	-7.51444
Trogon collaris	-73.6611	-7.43167
Trogon collaris	-69.5	-1.09333
Trogon collaris	-70.5	0.386111
Trogon collaris	-75.2667	0.716667
Trogon collaris	-74	1
Trogon collaris	-75.725	1.4875
Trogon collaris	-73.9167	2.75
Polychrus marmoratus	-40.4975	-20.6667

Polychrus marmoratus	-40.3378	-20.3194
Polychrus marmoratus	-40.3078	-20.1286
Polychrus marmoratus	-40.0728	-19.8644
Polychrus marmoratus	-40.0725	-19.8642
Polychrus marmoratus	-40.0728	-19.8639
Polychrus marmoratus	-40.0717	-19.8631
Polychrus marmoratus	-40.0717	-19.8628
Polychrus marmoratus	-40.0711	-19.8628
Polychrus marmoratus	-40.0736	-19.8625
Polychrus marmoratus	-40.0711	-19.8622
Polychrus marmoratus	-40.0725	-19.8611
Polychrus marmoratus	-40.0717	-19.8608
Polychrus marmoratus	-40.0694	-19.8608
Polychrus marmoratus	-40.0714	-19.8594
Polychrus marmoratus	-40.0722	-19.3911
Polychrus marmoratus	-40.0722	-19.3911
Polychrus marmoratus	-39.8589	-18.7161
Polychrus marmoratus	-39.7322	-18.5933
Polychrus marmoratus	-39.7319	-18.5933
Polychrus marmoratus	-39.5508	-18.0864
Polychrus marmoratus	-39.0647	-16.4497
Polychrus marmoratus	-39.4958	-15.4192
Polychrus marmoratus	-60.2631	-9.8603
Polychrus marmoratus	-58.2568	-9.8235
Polychrus marmoratus	-58.6786	-9.5141
Polychrus marmoratus	-63.9501	-8.79729
Polychrus marmoratus	-69.95	-4.15
Polychrus marmoratus	-69.9333	-4.14667
Polychrus marmoratus	-69.7333	-1.32833
Polychrus marmoratus	-71	-1
Polychrus marmoratus	-76.9667	0.05

Polychrus marmoratus	-76.7	0.05
Polychrus marmoratus	-74	1
Polychrus marmoratus	-70.5	1
Polychrus marmoratus	-75.5183	1.62
Polychrus marmoratus	-69	2.5
Polychrus marmoratus	-74.15	2.75
Polychrus marmoratus	-72.75	3.5
Polychrus marmoratus	-73.635	4.153333
Polychrus marmoratus	-71.7389	6.462222
Polychrus marmoratus	-71.1106	6.989167
Polychrus marmoratus	-70.7656	7.1025
Polychrus marmoratus	-51.7395	0.417813
Polychrus marmoratus	-60.1577	-1.3331686
Polychrus marmoratus	-69.9821	-4.36824
Polychrus marmoratus	-46.4909	-1.1726
Polychrus marmoratus	-48.2349	-1.36465
Polychrus marmoratus	-48.393	-1.39089
Polychrus marmoratus	-50.1191	-6.06243
Polychrus marmoratus	-4.20517	-69.9438
Polychrus marmoratus	-75.7457	1.981744
Polychrus marmoratus	-55.173	5.863173
Polychrus marmoratus	-55.0816	5.443041
Polychrus marmoratus	-56.15	3.783306
Polychrus marmoratus	-52.3169	-0.72697
Polychrus marmoratus	-69.1858	0.61154
Polychrus marmoratus	-44.7416	-3.47166
Polychrus marmoratus	-45.2245	-5.49932
Polychrus marmoratus	-45.7731	-2.49891
Polychrus marmoratus	-44.6833	-4.01667
Polychrus marmoratus	-50.3408	-0.9604
Polychrus marmoratus	-46.3212	-1.80286

Polychrus marmoratus	-46.7679	-1.06646
Polychrus marmoratus	-47.0552	-1.85336
Polychrus marmoratus	-47.1349	-1.47203
Polychrus marmoratus	-47.3188	-1.19471
Polychrus marmoratus	-47.2931	-0.94502
Polychrus marmoratus	-47.5489	-1.59801
Polychrus marmoratus	-47.4483	-0.79751
Polychrus marmoratus	-47.888	-1.45058
Polychrus marmoratus	-48.1531	-1.15403
Polychrus marmoratus	-48.7679	-1.89041

Table S2 Sample sources of *Angiopolybia pallens* (**Table S2.1**) and *Synoeca surinama* (**Table S2.2**) analyzed genetically in this study.

Table S2.1							
Sample	**Total lenght**	**# of regions analyzed**	**12S**	**Cox1**	**Cyt*b***	**State/Country**	**Morphotype**
02 Santa Teresinha	900 bp	2	(No data)	416	484	Bahia/Brazil	Yellow Morph
03 Ituberá	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
04 Ituberá	1338 bp	3	438 (7 indels)	416	484	Bahia/Brazil	Yellow Morph
05 Ilhéus	1338 bp	3	438 (7 indels)	416	484	Bahia/Brazil	Yellow Morph
07 Camacan	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
08 Ilhéus	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
09 Ilhéus	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
10 Santa Teresinha	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
11 Arataca	1338 bp	3	438 (7 indels)	416	484	Bahia/Brazil	Yellow Morph
12 Camacan	1338 bp	3	438 (7 indels)	416	484	Bahia/Brazil	Yellow Morph
13 Camacan	1338 bp	3	438 (7 indels)	416	484	Bahia/Brazil	Yellow Morph
14 Ilhéus	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
15 Santa Luzia	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
16 Belmonte	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
17 Ilhéus	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
18 Vera Cruz	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
19 Vera Cruz	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
21 Ilhéus	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
22 Itabuna	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
23 Ilhéus	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
24 Ilhéus	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
25 Ilhéus	1338 bp	3	438 (7 indels)	416	484	Bahia/Brazil	Yellow Morph
26 São José da Vitoria	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
28 Uruçuca	922 bp	2	438 (8 indels)	(No data)	484	Bahia/Brazil	Yellow Morph
29 Uruçuca	1338 bp	3	438 (7 indels)	416	484	Bahia/Brazil	Yellow Morph
30 Ilhéus	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph

31 Ilhéus	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
33 Presdente Figueiredo	1338 bp	3	438 (10 indels)	416	484	Amazonas/Brazil	Yellow Morph
34 Presidente Figueiredo	1338 bp	3	438 (10 indels)	416	484	Amazonas/Brazil	Yellow Morph
35 Presidente Figueiredo	1338 bp	3	438 (10 indels)	416	484	Amazonas/Brazil	Yellow Morph
36 Iquitos	1338 bp	3	438 (8 indels)	416	484	Loreto/Peru	Yellow Morph
37 Napo	1338 bp	3	438 (10 indels)	416	484	Napo/Ecuador	Yellow Morph
38 Petit Saut	1338 bp	3	438 (10 indels)	416	484	French Guiana	Yellow Morph
40 Paracou	1281 bp	3	438 (10 indels)	359 (3 indels)	484	French Guiana	Yellow Morph
42 Maripasoula	1338 bp	3	438 (10 indels)	416	484	French Guiana	Yellow Morph
43 Altamira	1338 bp	3	438 (10 indels)	416	484	Pará/Brazil	Yellow Morph
45 Altamira	1338 bp	3	438 (10 indels)	416	484	Pará/Brazil	Yellow Morph
46 Altamira	1338 bp	3	438 (9 indels)	416	484	Pará/Brazil	Yellow Morph
47 Altamira	1338 bp	3	438 (9 indels)	416	484	Pará/Brazil	Yellow Morph
48 Ilhéus	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
49 Ilhéus	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
50 Ibirapitanga	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
51 Ubatuba	1338 bp	3	438 (7 indels)	416	484	São Paulo/Brazil	Yellow Morph
52 Ubatuba	922 bp	2	438 (7 indels)	(No data)	484	São Paulo/Brazil	Yellow Morph
53 Ubatuba	1338 bp	3	438 (7 indels)	416	484	São Paulo/Brazil	Yellow Morph
54 Ubatuba	1338 bp	3	438 (7 indels)	416	484	São Paulo/Brazil	Yellow Morph
55 Ubatuba	1338 bp	3	438 (7 indels)	416	484	São Paulo/Brazil	Yellow Morph
56 Ubatuba	1338 bp	3	438 (7 indels)	416	484	São Paulo/Brazil	Yellow Morph
57 Ubatuba	1338 bp	3	438 (7 indels)	416	484	São Paulo/Brazil	Yellow Morph
58 Ubatuba	1338 bp	3	438 (7 indels)	416	484	São Paulo/Brazil	Yellow Morph
59 Ubatuba	1338 bp	3	438 (8 indels)	416	484	São Paulo/Brazil	Yellow Morph
60 Ubatuba	1338 bp	3	438 (7 indels)	416	484	São Paulo/Brazil	Yellow Morph
61 Ubatuba	1338 bp	3	438 (7 indels)	416	484	São Paulo/Brazil	Yellow Morph
63 Ubatuba	1338 bp	3	438 (7 indels)	416	484	São Paulo/Brazil	Yellow Morph
64 Ubatuba	922 bp	2	438 (7 indels)	(No data)	484	São Paulo/Brazil	Yellow Morph
65 Ubatuba	1338 bp	3	438 (7 indels)	416	484	São Paulo/Brazil	Yellow Morph

66 Ubatuba	1338 bp	3	438 (7 indels)	416	484	São Paulo/Brazil	Yellow Morph
67 Ubatuba	1338 bp	3	438 (7 indels)	416	484	São Paulo/Brazil	Yellow Morph
68 Ubatuba	1338 bp	3	438 (7 indels)	416	484	São Paulo/Brazil	Yellow Morph
69 Ubatuba	900 bp	2	(No data)	416	484	São Paulo/Brazil	Yellow Morph
70 Ubatuba	1338 bp	3	438 (7 indels)	416	484	São Paulo/Brazil	Yellow Morph
71 Uruçuca	900 bp	2	(No data)	416	484	Bahia/Brazil	Yellow Morph
72 Itajuípe	900 bp	2	(No data)	416	484	Bahia/Brazil	Yellow Morph
73 Itajuípe	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
74 Itajuípe	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
75 Itajuípe	900 bp	2	(No data)	416	484	Bahia/Brazil	Yellow Morph
76 Itajuípe	900 bp	2	(No data)	416	484	Bahia/Brazil	Yellow Morph
77 Ibirapitanga	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
78 Gandu	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
79 Gandu	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
80 Gandu	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
81 Wenceslau Guimarães	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
82 Wenceslau Guimarães	1338 bp	3	438 (7 indels)	416	484	Bahia/Brazil	Yellow Morph
83 Wenceslau Guimarães	1338 bp	3	438 (7 indels)	416	484	Bahia/Brazil	Yellow Morph
84 Wenceslau Guimarães	1338 bp	3	438 (7 indels)	416	484	Bahia/Brazil	Yellow Morph
85 Camacan	1338 bp	3	438 (7 indels)	416	484	Bahia/Brazil	Yellow Morph
86 Camacan	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
87 Itamarajú	1338 bp	3	438 (7 indels)	416	484	Bahia/Brazil	Yellow Morph
88 Itamarajú	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
89 Itamarajú	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
90 Camacan	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
91 Camacan	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
92 Camacan	900 bp	2	(No data)	416	484	Bahia/Brazil	Yellow Morph
93 Camacan	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
94 Igrapiúna	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
95 Igrapiúna	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph

96 Ilhéus	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
97 Ilhéus	438 bp	1	438 (8 indels)	(No data)	(No data)	Bahia/Brazil	Yellow Morph
98 Itaparica	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
99 Itaparica	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
100 Itaparica	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
101 Porto Velho	1338 bp	3	438 (10 indels)	416	484	Rondônia/Brazil	Yellow Morph
102 Rio Branco	1338 bp	3	438 (9 indels)	416	484	Acre/Brazil	Yellow Morph
103 Rio Branco	1338 bp	3	438 (9 indels)	416	484	Acre/Brazil	Yellow Morph
104 Rio Branco	1338 bp	3	438 (8 indels)	416	484	Acre/Brazil	Yellow Morph
105 Rio Branco	1338 bp	3	438 (9 indels)	416	484	Acre/Brazil	Yellow Morph
106 Rio Branco	1338 bp	3	438 (9 indels)	416	484	Acre/Brazil	Yellow Morph
107 Cruzeiro do Sul	1338 bp	3	438 (10 indels)	416	484	Acre/Brazil	Yellow Morph
108 Cruzeiro do Sul	1338 bp	3	438 (10 indels)	416	484	Acre/Brazil	Yellow Morph
109 Cruzeiro do Sul	1338 bp	3	438 (10 indels)	416	484	Acre/Brazil	Yellow Morph
110 Cruzeiro do Sul	1338 bp	3	438 (10 indels)	416	484	Acre/Brazil	Yellow Morph
111 Manaus	1338 bp	3	438 (9 indels)	416	484	Amazonas/Brazil	Yellow Morph
112 Manaus	1338 bp	3	438 (10 indels)	416	484	Amazonas/Brazil	Yellow Morph
113 Manaus	1338 bp	3	438 (10 indels)	416	484	Amazonas/Brazil	Yellow Morph
114 Manaus	1338 bp	3	438 (9 indels)	416	484	Amazonas/Brazil	Yellow Morph
115 Manaus	1338 bp	3	438 (10 indels)	416	484	Amazonas/Brazil	Yellow Morph
116 Manaus	900 bp	2	(No data)	416	484	Amazonas/Brazil	Yellow Morph
117 Manaus	900 bp	2	(No data)	416	484	Amazonas/Brazil	Yellow Morph
118 Iranduba	1338 bp	3	438 (10 indels)	416	484	Amazonas/Brazil	Yellow Morph
119 Iranduba	1338 bp	3	438 (11 indels)	416	484	Amazonas/Brazil	Yellow Morph
135 Pau Brasil	1338 bp	3	438 (8 indels)	416	484	Bahia/Brazil	Yellow Morph
147 Gurupi	1338 bp	3	438 (10 indels)	416	484	Maranhão/Brazil	Yellow Morph
160 Mongaguá	1338 bp	3	438 (7 indels)	416	484	São Paulo/Brazil	Yellow Morph
161 Mongaguá	1338 bp	3	438 (7 indels)	416	484	São Paulo/Brazil	Yellow Morph
162 Mongaguá	1338 bp	3	438 (6 indels)	416	484	São Paulo/Brazil	Yellow Morph
163 Mongaguá	1338 bp	3	438 (7 indels)	416	484	São Paulo/Brazil	Yellow Morph

164 Mongaguá	1338 bp	3	438 (7 indels)	416	484	São Paulo/Brazil	Yellow Morph
165 Mongaguá	1338 bp	3	438 (7 indels)	416	484	São Paulo/Brazil	Yellow Morph
166 São Sebastião	900 bp	2	(No data)	416	484	São Paulo/Brazil	Yellow Morph
167 São Sebastião	900 bp	2	(No data)	416	484	São Paulo/Brazil	Yellow Morph
168 São Sebastião	900 bp	2	(No data)	416	484	São Paulo/Brazil	Yellow Morph
169 Parati	900 bp	2	(No data)	416	484	Rio de Janeiro/Brazil	Yellow Morph
170 Magé	900 bp	2	(No data)	416	484	Rio de Janeiro/Brazil	Yellow Morph
171 Magé	900 bp	2	(No data)	416	484	Rio de Janeiro/Brazil	Yellow Morph
172 Magé	900 bp	2	(No data)	416	484	Rio de Janeiro/Brazil	Yellow Morph
173 Magé	900 bp	2	(No data)	416	484	Rio de Janeiro/Brazil	Yellow Morph
174 Magé	900 bp	2	(No data)	416	484	Rio de Janeiro/Brazil	Yellow Morph
175 Magé	900 bp	2	(No data)	416	484	Rio de Janeiro/Brazil	Yellow Morph
176 Magé	900 bp	2	(No data)	416	484	Rio de Janeiro/Brazil	Yellow Morph
177 Cachoeiras de Macacu	900 bp	2	(No data)	416	484	Rio de Janeiro/Brazil	Yellow Morph
178 Itamarajú	900 bp	2	(No data)	416	484	Bahia/Brazil	Yellow Morph
183 Porto Velho	900 bp	2	(No data)	416	484	Rondônia/Brazil	Yellow Morph
185 Manaus	416 bp	1	(No data)	416	(No data)	Amazonas/Brazil	Yellow Morph
186 Tamandaré	416 bp	1	(No data)	416	(No data)	Pernambuco/Brazil	Yellow Morph
187 Tamandaré	416 bp	1	(No data)	416	(No data)	Pernambuco/Brazil	Yellow Morph
188 Tamandaré	416 bp	1	(No data)	416	(No data)	Pernambuco/Brazil	Yellow Morph
189 Tamandaré	416 bp	1	(No data)	416	(No data)	Pernambuco/Brazil	Yellow Morph
190 Tamandaré	416 bp	1	(No data)	416	(No data)	Pernambuco/Brazil	Yellow Morph
191 Tamandaré	416 bp	1	(No data)	416	(No data)	Pernambuco/Brazil	Yellow Morph
192 Recife	416 bp	1	(No data)	416	(No data)	Pernambuco/Brazil	Yellow Morph
193 Recife	416 bp	1	(No data)	416	(No data)	Pernambuco/Brazil	Yellow Morph
194a Paudalho	416 bp	1	(No data)	416	(No data)	Pernambuco/Brazil	Yellow Morph
194b Paudalho	416 bp	1	(No data)	416	(No data)	Pernambuco/Brazil	Yellow Morph
001 Porto Velho	1338 bp	3	438 (10 indels)	416	484	Rondônia/Brazil	Dark Morph
002 Rio Branco	922 bp	2	438 (10 indels)	(No data)	484	Acre/Brazil	Dark Morph
003 Rio Branco	1338 bp	3	438 (10 indels)	416	484	Acre/Brazil	Dark Morph

004 Rio Branco	1338 bp	3	438 (10 indels)	416	484	Acre/Brazil	Dark Morph
005 Rio Branco	1338 bp	3	438 (8 indels)	416	484	Acre/Brazil	Dark Morph
006 Rio Branco	1338 bp	3	438 (10 indels)	416	484	Acre/Brazil	Dark Morph
007 Cruzeiro do Sul	1338 bp	3	438 (10 indels)	416	484	Acre/Brazil	Dark Morph
008 Cruzeiro do Sul	922 bp	2	438 (10 indels)	(No data)	484	Acre/Brazil	Dark Morph
009 Cruzeiro do Sul	1338 bp	3	438 (10 indels)	416	484	Acre/Brazil	Dark Morph
010 Cruzeiro do Sul	1338 bp	3	438 (10 indels)	416	484	Acre/Brazil	Dark Morph
011 Cruzeiro do Sul	1338 bp	3	438 (10 indels)	416	484	Acre/Brazil	Dark Morph
012 Manaus	1338 bp	3	438 (10 indels)	416	484	Acre/Brazil	Dark Morph
013 Manaus	1338 bp	3	438 (9 indels)	416	484	Amazonas/Brazil	Dark Morph
014 Manaus	1338 bp	3	438 (9 indels)	416	484	Amazonas/Brazil	Dark Morph
015 Manaus	1338 bp	3	438 (10 indels)	416	484	Amazonas/Brazil	Dark Morph
016 Manaus	1338 bp	3	438 (10 indels)	416	484	Amazonas/Brazil	Dark Morph
017 Iranduba	1338 bp	3	438 (10 indels)	416	484	Amazonas/Brazil	Dark Morph
018 Iranduba	1338 bp	3	438 (10 indels)	416	484	Amazonas/Brazil	Dark Morph
019 RorainÓpolis	1338 bp	3	438 (10 indels)	416	484	Amazonas/Brazil	Dark Morph
020 Rorainópolis	1338 bp	3	438 (10 indels)	416	484	Roraima/Brazil	Dark Morph
021 Presidente Figueiredo	1338 bp	3	438 (10 indels)	416	484	Amazonas/Brazil	Dark Morph
022 Presidente Figueiredo	1338 bp	3	438 (10 indels)	416	484	Amazonas/Brazil	Dark Morph
025 Manaus	1338 bp	3	438 (10 indels)	416	484	Amazonas/Brazil	Dark Morph

Table S2.2

Sample	**Total lenght**	**# of regions analyzed**	**12S**	**Cox1**	**Cyt*b***	**State/Country**
01 Ilhéus	1338 bp	3	437 (6 indels)	416	485	Bahia/Brazil
02 Ilhéus	901 bp	2	(No data)	416	485	Bahia/Brazil
03 Ilhéus	1338 bp	3	437 (6 indels)	416	485	Bahia/Brazil
05 Itajuípe	901 bp	2	(No data)	416	485	Bahia/Brazil
06 Uruçuca	1338 bp	3	437 (6 indels)	416	485	Bahia/Brazil
07 Uruçuuca	1338 bp	3	437 (5 indels)	416	485	Bahia/Brazil

08 Itacaré	1338 bp	3	437 (6 indels)	416	485	Bahia/Brazil
09 Ituberá	1338 bp	3	437 (6 indels)	416	485	Bahia/Brazil
10 Coaraci	1338 bp	3	437 (6 indels)	416	485	Bahia/Brazil
11 Coaraci	1338 bp	3	437 (1 'N', 6 indels)	416	485	Bahia/Brazil
12 Coaraci	1338 bp	3	437 (6 indels)	416	485	Bahia/Brazil
13 Coaraci	1338 bp	3	437 (6 indels)	416	485	Bahia/Brazil
14 Coaraci	901 bp	2	(No data)	416	485	Bahia/Brazil
15 Coaraci	1338 bp	3	437 (6 indels)	416	485	Bahia/Brazil
16 Coaraci	901 bp	2	(No data)	416	485	Bahia/Brazil
17 Coaraci	901 bp	2	(No data)	416	485	Bahia/Brazil
18 Coaraci	901 bp	2	(No data)	416	485	Bahia/Brazil
19 Coaraci	901 bp	2	(No data)	416	485	Bahia/Brazil
20 Coaraci	901 bp	2	(No data)	416	485	Bahia/Brazil
21 Camacan	1338 bp	3	437 (6 indels)	416	485	Bahia/Brazil
22 Camacan	416 bp	2	(No data)	416	(No data)	Bahia/Brazil
23 Camacan	901 bp	2	(No data)	416	485	Bahia/Brazil
24 Mascote	1338 bp	3	437 (4 indels)	416	485	Bahia/Brazil
25 Ilhéus	1338 bp	3	437 (6 indels)	416	485	Bahia/Brazil
26 Auriflama	922 bp	3	437 (1 indels)	(No data)	485	São Paulo/Brazil
27 Indiaporã	1338 bp	3	437 (2 indels)	416	485	São Paulo/Brazil
28 Indiaporã	1338 bp	3	437 (2 indels)	416	485	São Paulo/Brazil
29 Indiaporã	1338 bp	3	437 (4 indels)	416 (2 'N')	485	São Paulo/Brazil
30 Indiaporã	1338 bp	3	437 (2 indels)	416	485	São Paulo/Brazil
31 Auriflama	1338 bp	3	437 (1 indels)	416	485	São Paulo/Brazil
32 Camacan	1338 bp	3	437 (6 indels)	416	485	Bahia/Brazil
33 Igrapiúna	1338 bp	3	437 (6 indels)	416	485	Bahia/Brazil
34 Ituberá	1338 bp	3	437 (6 indels)	416	485	Bahia/Brazil
35 Ilhéus	1338 bp	3	437 (6 indels)	416	485	Bahia/Brazil
36 Ilhéus	1338 bp	3	437 (6 indels)	416	485	Bahia/Brazil
37 Ilhéus	1338 bp	3	437 (6 indels)	416	485	Bahia/Brazil

38 Ilhéus	1338 bp	3	437 (6 indels)	416	485	Bahia/Brazil
39 Igrapiúna	1338 bp	3	437 (6 indels)	416	485	Bahia/Brazil
43 Manaus	901 bp	2	(No data)	416	485	Amazonas/Brazil
44 Iranduba	1338 bp	3	437 (4 indels)	416	485	Amazonas/Brazil
45 Indiaporã	1338 bp	3	437 (2 indels)	416	485	São Paulo/Brazil
46 Indiaporã	1338 bp	3	437 (2 indels)	416	485	São Paulo/Brazil
47 Indiaporã	1338 bp	3	437 (1 indels)	416	485	São Paulo/Brazil
48 Indiaporã	1338 bp	3	437 (1 indels)	416	485	São Paulo/Brazil
49 Indiaporã	1338 bp	3	437 (1 indels)	416	485	São Paulo/Brazil
51 Indiaporã	1338 bp	3	437 (1 indels)	416	485	São Paulo/Brazil
52 Rio Branco	1338 bp	3	437 (7 indels)	416	485	Acre/Brazil
53 Rio Branco	1338 bp	3	437 (7 indels)	416	485	Acre/Brazil
54 Senador Guiomard	1338 bp	3	437 (7 indels)	416	485	Acre/Brazil
55 Capixaba	1338 bp	3	437 (7 indels)	416	485	Acre/Brazil
56 Cruzeiro do Sul	901 bp	2	(No data)	416	485	Acre/Brazil
57 Cruzeiro do Sul	901 bp	2	(No data)	416	485	Acre/Brazil
58 Cruzeiro do Sul	901 bp	2	(No data)	416	485	Acre/Brazil
59 Iranduba	1338 bp	3	437 (4 indels)	416	485	Amazonas/Brazil
60 Iranduba	901 bp	2	(No data)	416	485	Amazonas/Brazil
61 Iranduba	901 bp	2	(No data)	416	485	Amazonas/Brazil
62 Manaus	901 bp	2	(No data)	416	485	Amazonas/Brazil
63 Oiapoque	901 bp	2	(No data)	416	485	Amapá/Brazil
65 Brasília	901 bp	2	(No data)	416	485	Distrito Federal/Brazil
66 Pau Brasil	901 bp	2	(No data)	416	485	Bahia/Brazil
67 Pau Brasil	901 bp	2	(No data)	416	485	Bahia/Brazil
71 Manaus	1338 bp	2	437 (3 indels)	416	485	Amazonas/Brazil
72 Manaus	901 bp	2	(No data)	416	485	Amazonas/Brazil
87 PortoVelho	922 bp	2	437 (7 indels)	(No data)	485	Rondônia/Brazil
88 Mirador	901 bp	2	(No data)	416	485	Maranhão/Brazil
89 Mirador	901 bp	2	(No data)	416	485	Maranhão/Brazil

90 Mirador	901 bp	2	(No data)	416	485	Maranhão/Brazil
91 Base dos Cágados	901 bp	2	(No data)	416	485	Maranhão/Brazil
92 Mirador	901 bp	2	(No data)	416	485	Maranhão/Brazil
93 Mirador	485 bp	1	(No data)	(No data)	485	Maranhão/Brazil
94 Mirador	901 bp	2	(No data)	416	485	Maranhão/Brazil
96 Mirador	901 bp	2	(No data)	416	485	Maranhão/Brazil
97 Mirador	901 bp	2	(No data)	416	485	Maranhão/Brazil
98 Mirador	901 bp	2	(No data)	416	485	Maranhão/Brazil
100 Carolina	901 bp	2	(No data)	416	485	Maranhão/Brazil
103 Gurupi	922 bp	2	437 (4 indels)	(No data)	485	Maranhão/Brazil
113 Brasilia	416 bp	1	(No data)	416	(No data)	Distrito Federal/Brazil
114 Brasilia	416 bp	1	(No data)	416	(No data)	Distrito Federal/Brazil
115 90kmN Itabuna	416 bp	1	(No data)	416	(No data)	Bahia/Brazil
116 Nossa Senhora do Socorro	416 bp	1	(No data)	416	(No data)	Sergipe/Brazil
117 Nossa Senhora do Socorro	416 bp	1	(No data)	416	(No data)	Sergipe/Brazil
118 Presidente Figueiredo	416 bp	1	(No data)	416	(No data)	Amazonas/Brazil
119 São José do Rio Preto	416 bp	1	(No data)	416	(No data)	São Paulo/Brazil
122 Tamandaré	416 bp	1	(No data)	416	(No data)	Pernambuco/Brazil
123 Recife	416 bp	1	(No data)	416	(No data)	Pernambuco/Brazil
124 Araguari	416 bp	1	(No data)	416	(No data)	Minas Gerais/Brazil

Table S3 Bioclimatic variables used to build ecological niche models of the eight species:

BIO1 = Annual Mean Temperature

BIO2 = Mean Diurnal Range (Mean of monthly (max temp - min temp))

BIO3 = Isothermality (BIO2/BIO7) (* 100)

BIO4 = Temperature Seasonality (standard deviation *100)

BIO5 = Max Temperature of Warmest Month

BIO6 = Min Temperature of Coldest Month

BIO7 = Temperature Annual Range (BIO5-BIO6)

BIO8 = Mean Temperature of Wettest Quarter

BIO9 = Mean Temperature of Driest Quarter

BIO10 = Mean Temperature of Warmest Quarter

BIO11 = Mean Temperature of Coldest Quarter

BIO12 = Annual Precipitation

BIO13 = Precipitation of Wettest Month

BIO14 = Precipitation of Driest Month

BIO15 = Precipitation Seasonality (Coefficient of Variation)

BIO16 = Precipitation of Wettest Quarter

BIO17 = Precipitation of Driest Quarter

BIO18 = Precipitation of Warmest Quarter

BIO19 = Precipitation of Coldest Quarter

Table S4 Witnesses of the disjunction, their conservation status, population size estimates and taxonomic validation references. ¤ = presence of populations adapted to dry conditions; ψ = more than one species, subspecies or morphotype in the same clade; ϕ = domesticated, only natural populations were considered. Names inside parentheses are referent to a disjoint lineage relative to its clade; the occurrence of a disjoint taxon is highlighted as **Am.** (endemic in Amazonia) or **At.** (endemic in the Atlantic Forest). For example: *Enyalius* (*E*. *leechii*, **Am.**), read as ‘*Enyalius* is a genus mostly from Atlantic Forest, but *E*. *leechii* is endemic in Amazonia’. [1]Conservation threat status of subspecies according to the system developed by the Brazilian Ministry of the Environment (Machado et al., 2008).

Taxa		**Conservation status (IUCN)**	**Population size estimates (IUCN)**	**Confirmation of distribution and taxonomic validation**
		Mammals		
Rodents				
Dasyproctidae	*Dasyprocta* aff. *leporina*	Least Concern	Stable	Moreiraetal.2008
Anteaters				
Cyclopedidae	*Cyclopes didactylus* ψ	Least Concern	Unknown	Miranda&Superina2010
Primates				
Atelidae	*Alouatta belzebul* ψ	Vulnerable	Decreasing	Nascimentoetal.2008
Bats				
Phyllostomidae	*Choeroniscus minor*	Least Concern	Unknown	Tavaresetal.2010
	Glyphonycteris daviesi	Least Concern	Unknown	Gregorin&Rossi2005
	Glyphonycteris sylvestris	Least Concern	Unknown	Diasetal.2003
	Lampronycteris brachyotis	Least Concern	Stable	Scultorietal.2009
	Lichonycteris obscura	Least Concern	Unknown	IUCN Red List
	Lophostoma carrikeri	Least Concern	Decreasing	Gregorinetal.2011
	Micronycteris brosseti	Data deficient	Unknown	IUCN Red List
	Micronycteris hirsuta	Least Concern	Unknown	Peracchi&Albuquerque1985
	Micronycteris microtis	Least Concern	Stable	Perachietal.2006
	Mimon bennettii ¤	Least Concern	Stable	Gregorinetal.2008a
	Tonatia saurophila	Least Concern	Stable	Williansetal.1995
	Trinycteris nicefori	Least Concern	Unknown	Fariaetal.2006
	Vampyrum spectrum ¤	Near threatened	Decreasing	Gregorinetal.2008b
	Vampyrodes caraccioli	Least Concern	Unknown	Velazcoetal.2010

Molossidae	*Eumops hansae*	Least Concern	Unknown	Fábian&Gregorin2006
	Molossops neglectus	Data deficient	Unknown	Gregorinetal.2004
Vespertilionidae	*Lasiurus egregius*	Data deficient	Unknown	Passosetal.2010
	Rhogeessa hussoni	Data deficient	Unknown	Mikalauskasetal.2011
Carnivores				
Procyonidae	*Potos flavus* ¤ψ	Least Concern	Decreasing	Ford&Hoffmann1988
Reptiles				
Amphisbaenians				
Amphisbaenidae	*Leposternon microcephalum* ¤ψ	Not assessed	Not assessed	Perez&Ribeiro2008
	Leposternon polystegum	Least Concern	Unknown	IUCN Red List
Lizards				
Gymnophthalmidae	*Cercosaura ocellata*	Not assessed	Not assessed	Rodrigues2003
Leiosauridae	*Enyalius* (*E. leechii*, **Am.**)	Not assessed	Not assessed	Bertolotto2006
Mabuyidae	*Copeoglossum nigropunctatum* ψ	Not assessed	Not assessed	Hedges&Conn2012
Polychrotidae	*Anolis fuscoauratus*	Not assessed	Not assessed	Sousa&Freire2010
	Anolis punctatus	Least Concern	Unknown	Wincketal.2011
	Polychrus marmoratus ψ	Not assessed	Not assessed	Ávila-Pires1995
Teiidae	*Kentropyx calcarata*	Not assessed	Not assessed	Rodrigues2003
	Kentropyx striata	Not assessed	Not assessed	Reptile-Database
Snakes				
Anomalepididae	*Liotyphlops albirostris*	Not assessed	Not assessed	Reptile-Database
Boidae	*Corallus hortulanus* ¤	Not assessed	Not assessed	Rodrigues2003
Colubridae	*Apostolepis pymi*	Not assessed	Not assessed	Lema&Albuquerque2010
	Atractus guentheri	Not assessed	Not assessed	Reptile-Database
	Atractus reticulatus	Not assessed	Not assessed	Reptile-Database
	Chironius carinatus	Data deficient	Decreasing	Reptile-Database
	Chironius fuscus	Not assessed	Not assessed	Souza-Filhoetal.2012
	Chironius scurrulus	Not assessed	Not assessed	Reptile-Database
	Dipsas catesbyi	Least Concern	Unknown	Argôlo2004
	Helicops carinicaudus	Not assessed	Not assessed	Reptile-Database
	Helicops leopardinus ¤	Not assessed	Not assessed	Hamdan&Lira-da-Silva2012
	Hydrodynastes bicinctus (*H. b. schultzi*, **At.**)	Not assessed	Not assessed	Reptile-Database

	Liophis taeniogaster	Not assessed	Not assessed	Fernandesetal.2002
	Mastigodryas boddaerti	Not assessed	Not assessed	Montingellietal.2011
	Pseustes sulphureus	Not assessed	Not assessed	Borges-Nojosaetal.2006
	Xenodon rabdocephalus	Not assessed	Not assessed	Reptile-Database
Leptotyphlopidae	*Epictia tenella*	Not assessed	Not assessed	Reptile-Database
Viperidae	*Bothriopsis bilineata bilineata*	Not assessed	Not assessed	Bernardeetal.2011
Turtles				
Emydidae	*Trachemys* (*T. dorbigni*, **At.**) ϕψ	Not assessed	Not assessed	Fritzetal.2011
Birds				
Parrots				
Psittacidae	*Pionus menstruus* ψ	Least Concern	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2
	Amazona farinosa ψ	Near threatened	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2
Cuckoos				
Cuculidae	*Dromococcyx pavoninus*	Least Concern	Stable	Stotzetal.1996;Sick,1997;DB1;DB2
	Neomorphus geoffroyi	Vulnerable	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2
Nightjars				
Caprimulgidae	*Lurocalis semitorquatus* ψ	Least Concern	Stable	Stotzetal.1996;Sick,1997;DB1;DB2
Swifts				
Apodidae	*Panyptila cayennensis*	Least Concern	Stable	Stotzetal.1996;Sick,1997;DB1;DB2
	Glaucis hirsuta	Least Concern	Decreasing	Stotzetal.1996
Hummingbirds				
Trochilidae	*Heliothryx aurita*	Least Concern	Decreasing	Stotzetal.1996
Trogons				
Trogonidae	*Trogon collaris* ψ	Least Concern	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2
	Trogon viridis ψ	Least Concern	Stable	Stotzetal.1996;Sick,1997;DB1;DB2
Puffbirds				
Bucconidae	*Monasa morphoeus* ψ	Least Concern	Stable	Stotzetal.1996;Sick,1997;DB1;DB2
Toucans				
Ramphastidae	*Ramphastos vitellinus ariel* ¤	Not assessed	Not assessed	Stotzetal.1996;Sick,1997;DB1;DB2
Woodpeckers				
Picidae	*Veniliornis affinis*	Least Concern	Stable	Stotzetal.1996;Sick,1997;DB1;DB2
	Piculus flavigula ψ	Least Concern	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2

	Celeus flavus ψ	Least Concern	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2
	Celeus torquatus ψ	Near threatened	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2
Woodcreepers				
Dendrocolaptidae	*Glyphorynchus spirurus* ψ	Least Concern	Unknown	Stotzetal.1996;Sick,1997;DB1;DB2
	Dendrocolaptes certhia ¤ψ	Least Concern	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2
	Xiphorhynchus guttatus	Least Concern	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2
Antbirds				
Thamnophilidae	*Thamnophilus aethiops* (*T. a. distans*, **At.**)	Endangered[1]	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2;Machadoetal.2005
	Thamnomanes caesius	Least Concern	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2
	Myrmotherula axillaris	Least Concern	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2
	Pyriglena leuconota	Least Concern	Unknown	Stotzetal.1996;Sick,1997;DB1;DB2
Antthrushes				
Formicariidae	*Chamaeza campanisona* ψ	Least Concern	Stable	Stotzetal.1996;Sick,1997;DB1;DB2
	Grallaria varia ψ	Least Concern	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2
Tyrant-Flycatchers				
Tyrannidae	*Ornithion inerme*	Least Concern	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2
	Mionectes oleagineus ψ	Least Concern	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2
	Ramphotrigon megacephalum	Least Concern	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2
	Rhynchocyclus olivaceus ψ	Least Concern	Stable	Stotzetal.1996;Sick,1997;DB1;DB2
	Attila spadiceus ψ	Least Concern	Stable	Stotzetal.1996;Sick,1997;DB1;DB2
	Rhytipterna simplex	Least Concern	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2
	Conopias trivirgatus	Least Concern	Stable	Stotzetal.1996;Sick,1997;DB1;DB2
Cotingas				
Cotingidae	*Laniocera hypopyrra*	Least Concern	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2
	Pachyramphus marginatus marginatus	Not assessed	Not assessed	Stotzetal.1996;Sick,1997;DB1;DB2
	Schiffornis turdina ψ	Least Concern	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2
Manakins				
Pipridae	*Piprites chloris* ψ	Least Concern	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2
	Machaeropterus regulus	Least Concern	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2
	Manacus manacus	Least Concern	Stable	Stotzetal.1996;Sick,1997;DB1;DB2
	Chiroxiphia pareola ψ	Least Concern	Stable	Stotzetal.1996;Sick,1997;DB1;DB2
	Pipra pipra ψ	Least Concern	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2

	Pipra rubrocapilla	Least Concern	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2
	Neochelidon tibialis	Least Concern	Decreasing	Stotzetal.1996;Sick,1997;DB2
Thrushes				
Turdidae	*Turdus albicollis*	Least Concern	Stable	Stotzetal.1996;Sick,1997;DB1;DB2
	Turdus fumigatus ¤ψ	Least Concern	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2
Gnatcatchers				
Polioptilidae	*Ramphocaenus melanurus* ψ	Least Concern	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2
Grosbeaks				
Cardinalidae	*Caryothraustes canadensis*	Least Concern	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2
	Habia rubica	Least Concern	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2; Weiretal.2009
Tanagers				
Thraupidae	*Tachyphonus cristatus* ψ	Least Concern	Stable	Stotzetal.1996;Sick,1997;DB1;DB2
	Chlorophanes spiza ψ	Least Concern	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2
Vireos				
Vireonidae	*Hylophilus thoracicus* ¤	Least Concern	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2
Blackbirds				
Icteridae	*Cacicus cela* ψ	Least Concern	Decreasing	Stotzetal.1996;Sick,1997;DB1;DB2
		Insects		
Paper Wasps				
Vespidae	*Agelaia angulata angulata*	Not assessed	Not assessed	Richards1978
	Agelaia angulata bertonii	Not assessed	Not assessed	Richards1978
	Agelaia cajennensis	Not assessed	Not assessed	Richards1978
	Angiopolybia pallens ψ	Not assessed	Not assessed	Richards1978, Carvalhoetal.2014, this work
	Brachygastra albula	Not assessed	Not assessed	Richards1978
	Brachygastra fistulosa	Not assessed	Not assessed	Richards1978
	Brachygastra myersi	Not assessed	Not assessed	Richards1978
	Brachygastra scutellaris	Not assessed	Not assessed	Richards1978
	Chartergellus (*C. sanctus*, **At.**)	Not assessed	Not assessed	Richards1978
	Epipona media	Not assessed	Not assessed	Richards1978
	Leipomeles dorsata	Not assessed	Not assessed	Richards1978
	Metapolybia decorata	Not assessed	Not assessed	Richards1978
	Metapolybia docilis	Not assessed	Not assessed	Richards1978

	Mischocyttarus punctatus	Not assessed	Not assessed	Richards1978
	Mischocyttarus tomentosus	Not assessed	Not assessed	Richards1978
	Parachartergus smithii	Not assessed	Not assessed	Richards1978
	Parachartergus wagneri	Not assessed	Not assessed	Richards1978
	Protopolybia chartergoides Morph *cinctellus*	Not assessed	Not assessed	Richards1978
	Protopolybia emortualis	Not assessed	Not assessed	Richards1978
	Synoeca septentrionalis ψ	Not assessed	Not assessed	Richards1978, Menezesetal.2011
	Synoeca surinama ¤	Not assessed	Not assessed	Richards1978, This work
Stingless Bees				
Apidae	*Cephalotrigona capitata* ¤	Not assessed	Not assessed	Camargo&Pedro2012
	Geotrigona (*G. subterranea*, **At.**)	Not assessed	Not assessed	Camargo&Moure1996; Camargo&Pedro2012
	Lestrimelitta limao ϕ	Not assessed	Not assessed	Camargo&Pedro2012
	Nannotrigona (*N. testaceicornis*, **At.**) ϕ	Not assessed	Not assessed	Camargo&Pedro2012
	Oxytrigona flaveola ψ	Not assessed	Not assessed	Camargo&Pedro2012

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Table S5 Genetic diversity referent to the three mitochondrial gene regions of *A*. *pallens* (yellow morph) and *S*. *surinama* analyzed in this study.

Taxon		**Gene region**	**Parameters**							
			N	**h**	**Hd ± SD**	**π ± SD**	**PS**	**D**	**Fs**	**R_2**
***Angiopolybia pallens,* Yellow morph**										
	Amazonia, WAR	**Cyt*b***	21	14	0.933±0.040	0.03987±0.00426	77	-0.70334	0.809	0.12844**
		12S	19	10	0.889±0.048	0.01517±0.00083	18	0.73498	-0.210	0.13334**
		Cox1	22	14	0.939±0.033	0.04368±0.00309	57	0.01401	0.947	0.12713**
	Atlantic Forest, BR	**Cyt*b***	61	28	0.909±0.029	0.01092±0.00110	33	-0.96269	-11.762**	0.10308**
		12S	55	6	0.480±0.077	0.00158±0.00029	4	-0.89438	-2.125	0.11680**
		Cox1	59	24	0.917±0.022	0.01218±0.00119	28	-0.51396	-7.754*	0.10167**
	Atlantic Forest, SPR	**Cyt*b***	37	10	0.764±0.055	0.00388±0.00064	14	-1.40989	-2.888	0.11927**
		12S	24	4	0.424±0.113	0.00130±0.00039	3	-0.76831	-1.151	0.15752**
		Cox1	35	6	0.721±0.048	0.00441±0.00073	9	-0.48130	0.360	0.12082**
Synoeca surinama										
	Amazonia, WAR	**Cyt*b***	14	7	0.868±0.059	0.00424±0.00084	7	-0.24512	-1.990	0.16339**
		12S	8	4	0.750±0.139	0.00332±0.00123	5	-1.17532	-0.519	0.22223**
		Cox1	18	7	0.804±0.069	0.00424±0.00068	5	0.67724	-1.822	0.14895**
	Atlantic Forest, BR	**Cyt*b***	33	4	0.415±0.099	0.00093±0.00025	3	-0.89432	-1.371	0.14366**
		12S	22	4	0.260±0.120	0.00208±0.00147	8	-1.94882**	-0.173	0.15234**
		Cox1	35	1	-	-	0	n.a.	n.a.	n.a.
	Savannah, ISAR	**Cyt*b***	12	3	0.621±0.087	0.00372±0.00047	4	1.27047	2.033	0.17562**
		12S	12	5	0.758±0.093	0.00281±0.00072	5	-0.98759	-1.418	0.19024**
		Cox1	11	2	0.545±0.072	0.00393±0.00052	3	2.04545	3.556	0.18498**

N = number of specimens; **h** = number of haplotypes; **Hd** = haplotype diversity; **π** = nucleotide diversity; **SD** = standard deviation; **PS** = polymorphic sites; **D** = Tajima's D; **Fs** = Fu's Fs; **R_2** = Ramos-Rozas population expansion test. Significance of P: *< 0.05; **< 0.01.

Table S6 Genetic diversity referent to the three mitochondrial gene regions analyzed in this study for the dark morph of *A*. *pallens*.

Clade	Parameters	N	h	Hd ± SD	π ± SD	PS
			Cyt*b* (484 bp)			
North		15	5	0.743±0.090	0.00338±0.00076	6
South		11	4	0.800±0.075	0.00346±0.00074	4
Total		**26**	**9**	**0.883±0.036**	**0.00640±0.00047**	**10**

Clade	Parameters	N	h	Hd ± SD	π ± SD	PS
			12S (438 bp)			
North		15	4	0.638±0.093	0.00264±0.00100	5
South		10	5	0.844±0.080	0.00385±0.00079	5
Total		**25**	**8**	**0.770±0.070**	**0.00369±0.00082**	**9**

Clade	Parameters	N	h	Hd ± SD	π ± SD	PS
			Cox1 (416 bp)			
North		15	8	0.895±0.053	0.00705±0.00153	12
South		9	5	0.806±0.120	0.00641±0.00192	9
Total		**24**	**13**	**0.935±0.027**	**0.00942±0.00119**	**18**

N = number of specimens; **h** = number of haplotypes; **Hd** = haplotype diversity; **π** = nucleotide diversity; **SD** = standard deviation; **PS** = polymorphic sites.

CONSIDERAÇÕES FINAIS

Uma vez que os polistíneos apresentam elevados níveis de diversidade e endemismo na região Neotropical, estes insetos compreendem modelos bastante interessantes tanto ecológicos como genéticos para estudar a influência de eventos ambientais na distribuição da biodiversidade. Contudo, pouco tem sido investido para testar a previsibilidade destes eventos como promotores de mudança com estas vespas.

Nos trabalhos apresentados nesta tese são discutidos processos ambientais facilitadores de diversificação (Capítulo 1), rotas de colonização baseadas em regras de progressão (Capítulo 2) e testes de hipótese de previsibilidade de diversidade genética construídas mediante modelagem climática histórica e analisadas por filogeografia comparativa (Capítulo 3). Ao considerar estes trabalhos em conjunto, nota-se que o primeiro é completado pelo segundo e que o terceiro se destaca pela complexidade de técnicas utilizadas e espécies, que não vespas, estudadas. Tal estratégia no último capítulo foi utilizada como forma de demonstrar a recorrência de distribuições disjuntas Amazônia–Floresta Atlântica em diversos grupos e para corroborar a hipótese de que cada espécie tem respondido de forma diferente às alterações que culminaram na separação destes biomas. Buscou-se com isso elevar o impacto do trabalho ao expandir a problemática para grupos com biologia totalmente diferente, mas que podem ser comparadas mediante análises de distribuição potencial.

Tais comparações são comuns em estudos recentes. Na verdade, biogeógrafos fazem uso de diversas técnicas (moleculares, ecológicas, etc.) para explicar padrões de distribuição. Além disso, demonstrar a recorrência de algum evento ambiental como promotor extrínsico de diversificação (i.e., não genético) em diferentes espécies é algo desejável, desafiador e tema central em biogeografia. A modelagem de nicho climático, por exemplo, mostrou ser uma boa ferramenta para previsão de diversidade genética e estruturação genética com *Angiopolybia pallens*. O teste de modelos construídos para outros polistíneos poderá indicar diferentes respostas destes insetos à fragmentação de florestas em futuros estudos populacionais. O pioneirismo em estudar espécies tão diferentes, contudo, forneceu respostas acerca dos extremos que podem ser encontrados em estudos de genética de populações com vespas, algo sem precedentes para a subfamília até então.

Mais importante que indicar algumas lacunas no conhecimento da biogeografia de Polistinae e propor soluções para alguns dos problemas apontados, a maior contribuição desta tese é a diferente abordagem imprimida nos estudos. Visto que pouco se conhecia a respeito da genética de populações, sistemas de colonização de áreas, rotas de colonização e filogeografia destas vespas, as publicações poderão levantar novos questionamentos na área.

Por exemplo, quais adaptações são comuns em populações de espécies originadas em florestas úmidas que habitam condições áridas? Estas adaptações influenciam eventos de especiação? As possíveis repostas a essas perguntas poderão ser obtidas, por exemplo, ao analisar de forma integrada a genética de populações e a fisiologia da termorregulação em áreas de colonização antiga, possivelmente onde se encontram as condições fundamentais para a ocorrência da espécie, e em áreas de colonização tardia onde as condições climáticas, por exemplo, são contrastantes. Tais análises compreendem testes de conservadorismo e expansão de nicho, uma linha de pesquisa em ascenção na biogeografia.

Outro questionamento que pode ser levantado é se existem diferenças em escala de refúgio para a concentração da diversidade de vespas. Ou seja, quais são as áreas onde, em escala de assembleia, estão concentrados maiores graus de endemismo genético dentro de um refúgio? A análise pode ser feita mediante o estudo genético de populações de diferentes espécies em diversas regiões de um mesmo refúgio. Ao construir um modelo de estabilidade combinada mediante paleomodelagem, poder-se-á testar as previsões do modelo mediante análises de filoendemismo (Rosauer et al., 2009) e propor áreas prioritárias para a conservação de espécies, por exemplo.

Tendo em vista as diferenças acerca das histórias de vida, nichos ocupados, ampla diversidade, etc., os polistíneos Neotropicais representam um interessante grupo para ser utilizado como modelo em uma ampla gama de estudos. Espera-se que tentativas futuras possam elucidar dúvidas acerca da biogeografia destes insetos que foram levantadas nesta tese. O cumprimento dos principais objetivos dos trabalhos realizados será claro se os artigos influenciarem discussões que integrem fatores ecológicos e evolutivos para explicar padrões de variação em Polistinae.

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