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Diversidade Filogenética, Distribuição Geográfica e Prioridades de Conservação em Jararacas Sulamericanas (Serpentes: Viperidae: *Bothrops* e *Bothrocophias*)

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“There is a theory which states that if ever anyone discovers exactly what the Universe is for and why it is here, it will instantly disappear and be replaced by something even more bizarre and inexplicable.

There is another theory which states that this has already happened”.

Douglas Adams

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Resumo

A crise da biodiversidade impõe a necessidade urgente de avaliar de modo mais criterioso padrões de distribuição e ameaças à riqueza biológica do planeta. No entanto, há poucos estudos quantificando os efeitos da perda de hábitat sobre padrões de diversidade filogenética, uma importante medida de diversidade que incorpora informações sobre parentesco entre as espécies. Este trabalho visa estudar esta relação na linhagem de serpentes endêmicas Neotropicais incluídas em *Bothrops* e *Bothrocophias*, testando medidas usuais de diversidade biológica como substitutos para conservar a diversidade filogenética neste bem estudado e amplamente distribuído clado de serpentes. Nós buscamos registros de ocorrência dos 40 táxons terminais da filogenia utilizada como hipótese de trabalho. Em seguida, geramos modelos de distribuição potencial para todos estes táxons, calculando tamanho de distribuição e porcentagem de perda de habitat. Nós estimamos valores de diversidade evolutiva (ED) para todos os táxons terminais. Estes valores foram ponderados por dados de perda de habitat (EDHL) e categorias de ameaça da IUCN (EDGE). Testamos a presença de sinal filogenético em tamanho de área, porcentagem de perda de habitat e categorias de ameaça, e fizemos regressões destas variáveis com valores de ED para cada táxon terminal. Em seguida, mapeamos áreas de alta riqueza e alta diversidade filogenética (PD) na América do Sul. Finalmente, testamos medidas usuais de biodiversidade como indicadores da diversidade evolutiva, comparando distâncias filogenéticas obtidas ao acaso com distâncias obtidas em conjuntos de espécies selecionados de acordo com endemismo, riqueza, grau de ameaça, presença em biomas abertos ou florestais ou em *hotspots*. Diferentes táxons prioritários foram obtidos nas diferentes formas de ponderação de medidas de diversidade evolutiva (ED, EDHL ou EDGE). Houve relação positiva e significativa entre ED e EDHL, mas não entre EDGE e as demais medidas. Não foi encontrado sinal filogenético significativo para tamanho de área, percentagem de perda de habitat e categoria de ameaça, e nenhuma regressão entre estas variáveis e ED foi significativa. Foram encontradas três grandes regiões continentais com altos índices de PD, sendo em geral coincidentes com regiões de alta riqueza. Conjuntos de espécies reunidos de acordo com endemismo, tipos de biomas e *hotspots* não apresentaram valores de distância filogenética diferentes do esperado ao acaso, indicando que métricas usuais não representam bem a diversidade filogenética. Conjuntos de espécies ameaçadas ou presentes nas áreas de maior riqueza apresentaram distâncias filogenéticas menores do que esperado ao acaso, indicando que tais medidas protegem uma parcela pequena de diversidade evolutiva no grupo. Uma abordagem de priorização levando em conta a perda de habitat e diversidade evolutiva pode ser a melhor maneira para preservar a história deste grupo de serpentes, e poderá ajudar na conservação de outros organismos menos conhecidos quanto à distribuição e filogenia.

Palavras-chave: Padrões de distribuição, biodiversidade, diversidade evolutiva, serpentes, perda de habitat, status da IUCN.

Abstract

The current extinction crisis requires an urgent and detailed evaluation of the distribution of biological diversity. However, the effects of habitat loss on patterns of phylogenetic diversity, an important measure of diversity that incorporates information about relation between species, are still poorly understood. The aim of our study is understand the effects of habitat loss on phylogenetic diversity and test widely used metrics of biological diversity as surrogates for conserving evolutionary diversity in a well studied, wide ranging Neotropical endemic snakes lineage. We compiled species occurrence records for the 40 terminal taxa in a recent pitviper phylogeny. We then generated species distribution models (SDMs) for all terminal taxa and calculated range sizes and percentage of habitat loss. We estimated evolutionary distinctiveness (ED) values, and weighted this index with data on habitat loss (EDHL) and threat status (EDGE). We tested the phylogenetic signal in range size, percentage of habitat loss and IUCN threat status, and then regressed these values with ED scores. We mapped areas of high richness and high phylogenetic diversity (PD). Finally, we tested the performance of widely used biodiversity metrics for capturing phylogenetic distinctiveness of pitviper faunas, selected according to endemism, richness, threat, presence in forest or open biomes or in biodiversity hotspots. Taxonomic priority ranks differed according to different weighs applied to evolutionary diversity, with EDGE categories showing wider differences from other metrics. We found no phylogenetic signal in range sizes, threat and percentages of habitat loss, and no significant correlations between ED values and these variables. The spatial distribution of PD is concentrated in three large main areas, being generally coincident with spatial variations in richness. Pitviper faunas assembled according to endemism, open and forest biomes and biodiversity hotspots were not significantly clustered or overdispersed in the phylogeny (not different from random assemblages). However, the species subset included in the IUCN redlist showed significant phylogenetic clustering, as did the species subset found in the richest areas. Usual biodiversity metrics are poor surrogates for representing the evolutionary diversity in the group. An approach taking into account habitat loss and phylogenetic diversity would be the best way to preserve the history of this group of Neotropical snakes, and could aid in the conservation of other organisms for which phylogenetic or spatial data are not available.

Introdução Geral

A crise atual da biodiversidade exige a detecção urgente de prioridades para a conservação (Myers & Knoll, 2001; Brooks *et al.*, 2006). Esforços para medir e mapear a biodiversidade de maneira eficaz representam um grande desafio para a ciência da conservação, que devem fornecer descrições da diversidade biológica da melhor maneira possível em um curto prazo necessário para ações eficientes (Faith, 1992; Mace & Purvis, 2008; Evans *et al.*, 2009). Dado o limitado número de recursos e tempo, planejamentos no âmbito da conservação são forçados a enfrentar a "agonia da escolha" (Vane-Wright *et al.*, 1991; Crozier, 1992). Como resposta, a disciplina emergente da biogeografia da conservação tenta responder questões urgentes, como o que devemos conservar da biodiversidade, e em que áreas? (Cadotte & Davies, 2010).

A diversidade biológica pode ser medida de diversas maneiras. A abordagem mais comum é simplesmente contar o número de espécies presentes em uma área, utilizando a riqueza de espécies como parâmetro básico de comparação (Gaston, 2000), ou utilizar os diversos índices de diversidade que consideram riqueza, dominância e abundância de espécies (ver Magurran, 2004). Entretanto, espécies são componentes de grupos hierárquicos mais inclusivos, vinculados por relações de parentesco, e não representam unidades independentes em análises de biodiversidade, ecologia ou evolução; assim, espécies filogeneticamente próximas tendem a ser intrinsecamente parecidas, e não podem ser comparadas adequadamente sem que sejam levadas em conta relações de parentesco (Queiroz & Donoghue, 1990; Maddock & Du-Plessis, 1999; Mace *et al.*, 2003; Agapow *et al.*, 2004).

Estudos recentes têm adotado informações sobre diversidade filogenética, aliadas a bons dados de distribuição geográfica, como importantes ferramentas para a detecção de espécies e áreas prioritárias para a conservação (Jones *et al.*, 2005; Mooers *et al.*, 2005; Rodrigues *et al.*, 2005; Smith *et al.*, 2005). No começo dos anos 90, vários grupos de pesquisa, principalmente da Austrália (Faith, 1992), sugeriram argumentos consistentes para considerar a diversidade filogenética (*Phylogenetic diversity*, PD) como unidade de medida de diversidade biológica (Crozier, 1992). Visto que diversidade é o produto da descendência com modificações, as informações de parentesco, sintetizadas em uma árvore filogenética, podem prever a variação morfológica, genética ou ecológica contida em um conjunto de espécies (Faith, 1992).

Além disso, é sabido que a diversidade biológica não está distribuída de forma homogênea no planeta (Brooks *et al.*, 2004; Whittaker *et al.*, 2005). Portanto, estratégias de conservação dependem de uma compreensão detalhada dos padrões de distribuição geográfica das espécies e linhagens, componentes essenciais da biodiversidade. Uma das abordagens principais para priorizar regiões para a conservação da biodiversidade tem sido a detecção de áreas onde coincidem alto endemismo e altas taxas de perdas de hábitat. Esta abordagem detectou 34 regiões prioritárias para a conservação biológica ao redor do globo, denominadas *hotspots* de biodiversidade (Myers *et al.*, 2000; Myers, 2003), incluindo oito na região Neotropical. Entretanto, análises que incorporam não apenas informações sobre endemismo e pressões antrópicas, mas também informações sobre relações históricas entre espécies, são ainda pouco comuns como subsídio à conservação (ver Crisci, 2001).

Um exemplo de trabalho utilizando filogenias e distribuição geográfica foi realizado por Sechrest *et al.* (2002), concluindo que 70% de toda a história evolutiva dos primatas e carnívoros está contida em 25 *hotspots* globais de biodiversidade. No entanto, não há análises similares para a região Neotropical, sendo difícil avaliar a congruência entre altos valores de endemismo, perdas de hábitat e seus efeitos sobre a diversidade filogenética.

Embora a extinção de espécies endêmicas reflita a perda de componentes únicos da biodiversidade, uma abordagem filogenética permite avaliar se as perdas em número de espécies correspondem ou não à perdas proporcionais em termos de diversidade evolutiva, ou de diferentes linhagens componentes da biodiversidade (Vázquez & Gittleman, 1998; Mooers *et al.*, 2005). Em casos onde existe ampla redundância evolutiva, ou seja, quando há várias espécies proximamente relacionadas, os impactos sobre uma determinada espécie podem ser relativamente menos deletérios ao grupo, se houver proteção de espécies filogeneticamente próximas. Ao contrário, quando são ameaçadas espécies evolutivamente distintas, a perda e os impactos são maiores do que simplesmente a perda de uma unidade taxonômica do nível da espécie (Faith, 1992; Linder, 1995).

Um caso clássico de espécies contendo alta diversidade evolutiva são as duas espécies de Tuatara (*Sphenodon punctatus* e *S. guntheri*), únicos membros atuais da ordem Rhinchocephalia (Daugherty *et al.*, 1990). Em contraste, qualquer espécie de *Anolis* representa uma das 386 espécies em seu gênero, uma entre 391 espécies da família Polychrotidae e uma entre mais de 8 mil espécies da ordem Squamata (Uetz, 2012). Assim, um conjunto de espécies formado por um lagarto do gênero *Anolis* e um *Sphenodon* é mais filogeneticamente diverso do que um conjunto de cinco espécies de *Anolis*. Portanto, pode ser necessário conservar conjuntos de espécies que incluam tanta história evolutiva quanto possível (Linder, 1995; Purvis *et al.*, 2005), e não simplesmente o maior número de espécies.

São reconhecidos vários fatores globais de ameaça aos répteis, incluindo perda e degradação de habitat, introdução de espécies exóticas, poluição, parasitismo, superexploração humana e mudanças climáticas (Gibbons *et al.,* 2000). Mas, não só para os répteis (Gibbons *et al.,* 2000) mas para organismos melhor avaliados como aves e mamíferos, a destruição do habitat é a ameaça principal (Hilton-Taylor & Stuart, 2009). Os impactos da perda de hábitat sobre os organismos terrestres, como lagartos e serpentes, são observados mais diretamente (Dodd, 1993; Ballinger & Congdon, 1996; Gibbons *et al.*, 2000), podendo ser quantificados de modo objetivo. No entanto, mesmo para os répteis, ainda há necessidade de avaliar de modo quantitativo o efeito das perdas de hábitat em diferentes partes do planeta (Gibbons *et al*., 2000).

A fauna de répteis Neotropicais está entre as mais ricas e diversificadas do mundo, gerando boas oportunidades de investigação sobre o efeito dos impactos humanos na biodiversidade. No entanto, a maioria das informações sobre riqueza, composição faunística, distribuição geográfica e conservação de répteis Neotropicais é ainda incompleta (Rodrigues, 2005). Embora haja um relativo acúmulo de informações sobre relações de parentesco para diferentes linhagens, há poucos estudos que integrem aspectos filogenéticos a análises de ameaça ou de pressão de perdas de hábitat na fauna Neotropical. Esperamos que o presente estudo, utilizando informações sobre distribuição geográfica e filogenia de *Bothrops* e *Bothrocophias,* uma das linhagens de serpentes mais bem estudadas e amplamente distribuídas da região Neotropical (Campbell & Lamar, 2004; Fenwick *et al.*, 2009), possa gerar informações relevantes para a conservação de outros grupos de organismos, distribuídos ao longo das mesmas regiões, porém ainda pouco conhecidos do ponto de vista de filogenia, taxonomia e distribuição. Pretendemos, portanto, fornecer dados inéditos e testar uma abordagem inovadora para gerar informações relevantes para ações de conservação mais eficazes contra a perda de biodiversidade na fauna de répteis Neotropicais.

Organismos de estudo

Entre as várias linhagens de répteis endêmicas da região Neotropical, destacam-se as serpentes viperídeas incluídas tradicionalmente no gênero *Bothrops* Wagler, 1824 ou em gêneros afins (*Bothrops sensu lato*, ver Fenwick *et al.,* 2009). Este grupo de serpentes, conhecidas informalmente como jararacas, representa uma das linhagens de répteis Neotropicais mais bem estudadas em termos de história natural, distribuição, taxonomia e relações de parentesco (Hoge, 1953; Hoge & Romano-Hoge, 1981; Borges & Araujo, 1998; Andrade & Abe, 1999; Gutberlet & Campbell, 2001; Martins *et al.*, 2001; Marques *et al.*, 2002; Harvey *et al.*, 2005; Cisneros-Heredia *et al.*, 2006; Araújo & Martins, 2007; Carrasco *et al.*, 2009, 2010; Wasko & Sasa, 2010, entre outros). O monofiletismo deste grupo de serpentes vem sendo corroborado em um grande número de estudos (Gutberlet & Campbell, 2001; Parkinson *et al.*, 2002; Castoe & Parkinson, 2006).

A hipótese filogenética utilizada em nosso trabalho (Fenwick *et al.,* 2009) incluiu 90% das espécies descritas para o grupo e detalhou as relações entre seus componentes por meio de análises moleculares e morfológicas, corroborando o monofiletismo do grupo, e, de modo geral, recuperando as principais linhagens supraespecíficas propostas em estudos anteriores (Salomão *et al.*, 1999; Wuster *et al.*,2002; Castoe & Parkinson, 2006). O estudo de Fenwick e colaboradores propôs a divisão de *Bothrops sensu lato* em *Bothrops* Wagler, 1824; *Bothropoides* Fenwick *et al*. 2009; *Rhinocerophis* Garman, 1881; *Bothriopsis* Peters, 1861; e *Bothrocophias* Gutberlet e Campbell, 2001. Entretanto, no início de 2012, na fase final de nosso trabalho, Carrasco *et al.* (2012) publicaram uma nova hipótese filogenética e uma nova proposta taxonômica para o grupo, mantendo apenas os gêneros *Bothrops* e *Bothrocophias,* e sinonimizando *Bothriopsis*, *Bothropoides* e *Bothriopsis* à *Bothrops*. Esta proposta taxonômica mais recente (Carrasco *et al.* 2012) e mais simples é adotada em nosso estudo, favorecendo a estabilidade da nomenclatura neste grupo de serpentes. De modo geral, a topologia obtida em Fenwick *et al*. (2009), e aqui utilizada como hipótese de trabalho, é corroborada por Carrasco *et al.* (2012), indicando a relativa robustez do conhecimento filogenético no grupo.

A linhagem das jararacas inclui pelo menos 40 espécies distribuídas desde a América Central e Antilhas até a Patagônia (Campbell e Lamar, 2004). Nesta ampla área de distribuição, as serpentes do grupo ocupam um grande conjunto de ambientes e tipos de vegetação, que variam desde florestas úmidas de baixa altitude até áreas abertas montanhosas, como as cadeias andinas (Campbell e Lamar, 2004; Fenwick *et al.*, 2009). As serpentes do grupo apresentam uma grande variação na forma do corpo, associada a diferentes estratégias de uso dos ambientes disponíveis, variando desde espécies exclusivamente terrícolas, que predominam em ambientes tipicamente abertos ou desérticos, até espécies quase estritamente arborícolas, frequentes em áreas dominadas por florestas (Campbell & Lamar, 1989; Sazima & Haddad, 1992; Martins *et al.*, 2001). Entre essas espécies há ainda uma grande variação quanto à extensão da distribuição geográfica, uma vez que existem espécies com distribuição muito ampla (*Bothrops atrox e B. asper*, por exemplo) até espécies endêmicas insulares (*Bothrops insularis e B. alcatraz*). Deste modo, os componentes deste grupo de viperídeos estão sujeitos a diferentes pressões seletivas e a diferentes níveis de impactos antrópicos.

Embora haja um bom conhecimento acumulado sobre diversidade e distribuição geográfica sobre o grupo, são raros os estudos de síntese sobre padrões de distribuição geográfica e conservação nesta linhagem de serpentes. Consequentemente, sabe-se pouco a respeito dos efeitos da destruição de hábitats sobre a linhagem das jararacas, tanto em nível de espécies quanto sobre grupos mais inclusivos.

Objetivo Geral

Avaliar a perda de diversidade filogenética imposta pelas perdas de hábitat natural sobre as jararacas (gêneros *Bothrops e Bothrocophias,* Carrasco *et al.*, 2012), e propor prioridades espaciais e taxonômicas para a conservação desta linhagem de serpentes.

Metas Específicas

- Mapear a distribuição geográfica das espécies incluídas em hipótese filogenética recente e abrangente sobre o grupo (Fenwick *et al*., 2009);
- Cruzar os mapas de distribuição das espécies com os dados de perda de hábitat;
- Avaliar as relações entre filogenia, tamanho de distribuição, grau de ameaça e percentagem de perdas de hábitat, testando a presença de sinal filogenético nestas características;
- Calcular porcentagens de perda de habitat para cada espécie, com base em porcentagem de remanescentes de vegetação nativa na América do Sul (Eva *et al.*, 2002);
- Classificar espécies e áreas prioritárias para a conservação utilizando informações da filogenia e dados de perda de habitat;
- Testar e relatar se medidas de diversidade biológica mais usuais, como riqueza, endemismo e categorias de ameaça de extinção da IUCN são boas representantes para conservar a diversidade evolutiva neste grupo de serpentes.

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Phylogenetic diversity, habitat loss and conservation priorities in Neotropical pitvipers (Serpentes: Viperidae: *Bothrops* and *Bothrocophias*)

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Running Head: Phylogenetic diversity of Neotropical pitvipers

ABSTRACT

Aim To study the effect of habitat loss on phylogenetic diversity of Neotropical pitvipers and to test widely used metrics of biological diversity as surrogates for conserving evolutionary diversity in a well studied, wide ranging Neotropical endemic snake lineage.

Location South America and adjacent islands occupied by pitvipers.

Methods We compiled species occurrence records for the 40 terminal taxa in a recent and comprehensive phylogeny of Neotropical pitvipers. We then generated species distribution models (SDMs) for all terminal taxa, except insular species, using Maxent, and compared to known records and inferred absences, to reduce comission errors. We calculated range sizes and percentage of habitat loss for each terminal taxon. We estimated evolutionary distinctiveness (ED) values for each terminal taxon, and weighted these values with percentages of habitat loss (EDHL) and extinction probabilities applied to IUCN threat status (EDGE), using the *Tuatara* package in Mesquite. We tested for phylogenetic signal in range size, percentage of habitat loss and IUCN threat status, and then regressed these values with ED scores. We mapped species richness and phylogenetic diversity (PD) in the *Biodiverse* software. Finally, we tested the performance of widely used biodiversity metrics selected according to endemism, richness, threat, presence in major biomes or biodiversity hotspots for capturing phylogenetic distinctiveness, by comparing random values of mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) to values obtained in these pitviper faunas, using *Picante* package in R software.

Results. Taxonomic conservation priority ranks differed according to the metric of evolutionary diversity, with EDGE values showing the widest differences from ED and EDHL. We found no phylogenetic signal in range size, threat and habitat loss, and no significant relations between ED and these variables. We recognized three areas of high levels of PD, generally coincident with spatial variations in richness. Values of MPD and MNTD for pitviper faunas assembled according to endemism, open and forest biomes and biodiversity hotspots were not significantly different from random. However, the species subset included in the IUCN redlist showed significant phylogenetic clustering in both metrics (MPD and MNTD), as did the species subset found in the richest areas in MNTD.

Main conclusions Usual biodiversity metrics as endemism, richness and IUCN status are not good surrogates for evolutionary history of Neotropical pitvipers. Although spatial conservation priorities are generally congruent with biodiversity hotspots, distribution of phylogentic diversity is highly variable even within hotspots, indicating the need for refined targeted approaches for conserving evolutionary diversity. Taxonomic priorities based on habitat loss and phylogenetic diversity are seen as the best way to preserve the history of this clade of Neotropical snakes

Keywords Distribution patterns, biodiversity, evolutionary diversity, snakes, habitat loss, IUCN status, conservation biogeography.

INTRODUCTION

The current biodiversity crisis requires the urgent detection of conservation priorities (Myers & Knoll, 2001; Brooks *et al.*, 2006). Efforts to effectively measure and map biodiversity represent a major challenge to conservation science, which must provide the best possible descriptions of biological diversity in the short term required for efficient action (Faith, 1992; Mace & Purvis, 2008; Evans *et al.*, 2009). Given limited resources and time, conservation planning is forced to solve the “triage dilemma”, and face the “agony of choice” (Vane-Wright *et al.*, 1991; Crozier, 1992). As a response, the emerging discipline of conservation biogeography tries to answer the urgent questions: what to conserve of biodiversity, and in what areas? (Cadotte & Davies, 2010).

The most straightforward measures of biological diversity rely on richness as a basic parameter (Gaston, 2000a; Cianciaruso *et al.*, 2009), or use a combination of richness, dominance and abundance to provide quantitative indices (e.q. Shannon’s and Simpson’s index- see Magurran, 2004). Another common form of biodiversity measure is based on patterns of endemism, which indicate concentrations of geographically unique species or biological assemblages (Myers *et al.*, 2000; Myers, 2003). However, species diversity and distribution patterns must be interpreted as a result of evolutionary relationships (Vane-Wright *et al.*, 1991; Faith, 1992; Mace *et al.*, 2003; Purvis *et al.*, 2005; Cadotte & Davies, 2010). Extant species, fundamental and usual units in most biodiversity studies, are parts of more inclusive evolutionary groups (Felsenstein, 1985; Agapow, 2005; Avise, 2005). For example, the two Tuatara species (*Sphenodon punctatus* and *S. guntheri*) are the sole extant members of the Order Rhinchocephalia (Daugherty *et al.*, 1990), while any member of the Neotropical genus *Anolis* is one of the 386 species in its genus, one of 391 species in the family Polychrotidae and one of the more than

8.000 species in the order Squamata (Uetz, 2012). So, a group of species consisting of a lizard of the genus *Anolis* and a *Sphenodon* is phylogenetically more diverse than a set of five (or even more) species of *Anolis*. As closely related taxa share unique evolutionary histories, they tend to resemble each other in basic biological attributes, and must not be interpreted as independent data sources for most biodiversity comparisons (Maddock & Du-Plessis, 1999; Mace *et al.*, 2003; Agapow *et al.*, 2004).

Recent advances in rapid molecular DNA-sequencing, combined with the increased availability of distribution data and geographic information system (GIS) mapping techniques (Kozak *et al.*, 2008) have favoured the application of phylogenetic relationships for comparative studies, including those aimed at detecting conservation priorities (Faith, 1992; Mooers *et al.*, 2005; Rodrigues *et al.*, 2005; Redding & Mooers, 2006; Cadotte & Davies, 2010; Cadotte *et al.*, 2010; Collen *et al.*, 2011). The information summarized in a phylogeny can be used for interpreting and conserving evolutionary processes of morphological, genetic and ecological diversification (Felsenstein, 1985; Faith, 1992; Mace *et al.*, 2003). Measures of evolutionary history can either be spatial, mapping geographical variation of phylogenetic diversity (PD, Faith, 1992; Faith & Baker, 2006) or taxonomic, comparing species or lineages according to evolutionary distinctiveness (ED) metrics (Isaac *et al.* 2007).

However, despite the current biodiversity crisis and the recent advances in mapping phylogenies (Myers & Knoll, 2001; Laffan *et al.*, 2010), the impact of human activities on the evolutionary legacy of most biological lineages has never been properly assessed (Gaston, 2000b). Although habitat loss is seen as the major cause of biodiversity loss on the planet (Hilton-Taylor & Stuart, 2009), very little is known about the impact of the loss of natural habitats on phylogenetic and evolutionary patters and processes (Gaston, 2000b; Purvis *et al*., 2005). In the megadiverse Neotropical realm, one of the most biologically complex portions of Earth, the impact of human activities on evolutionary patterns remains virtually unstudied (Rodrigues, 2005), since no study taking into account the evolutionary diversity and extinction probabilities was carried out to this date in that region.

One of the most studied and widely distributed monophyletic group of snakes in the Neotropical region are the pitvipers, referred here as members of *Bothrops* and *Bothrocophias* (Carrasco *et al.*, 2012). This Neotropical endemic lineage occupies a wide range of environments and vegetation types, from lowland rainforests to open areas in the Andean chains and Patagonia (Campbell & Lamar, 2004). Even with extensive accumulated knowledge on natural history, taxonomy and phylogenetic relationships of pitvipers (Hoge, 1953; Hoge & Romano-Hoge, 1981; Borges & Araujo, 1998; Andrade & Abe, 1999; Martins *et al.*, 2001; Marques *et al.*, 2002; Campbell & Lamar, 2004; Harvey *et al.*, 2005; Cisneros-Heredia *et al.*, 2006; Carrasco *et al.*, 2009, 2010; Wasko & Sasa, 2010, among others), patterns of endemism, geographic distribution or phylogenetic diversity in this monophyletic group of snakes have never been thoroughly assessed, hampering effective and informed conservation action.

Herein we provide a study on the effects of habitat loss on phylogenetic diversity of a well studied clade of Neotropical snakes. The first objective of our study is to rank extant species according to conservation priorities, using information on phylogeny and habitat loss. Further, we evaluate if current threat categories retain appropriately patterns of phylogenetic diversity and habitat loss within the clade. A second part of our study aims to evaluate the effect of phylogeny on range sizes, habitat loss and threat levels. Then, we test if geographical patterns of 1) threat, 2) endemism and 3) richness are good surrogates for representing and conserving evolutionary diversity within Neotropical pitvipers, and also test if pitviper faunas found in major biomes or in biodiversity hotspots include larger amounts of phylogenetic diversity than expected by chance.

METHODS

Distribution records

We collected distribution data for the 40 terminal taxa present in a recent phylogeny of Neotropical pitvipers (Fenwick *et al.* 2009). All data were georeferenced and mapped in ArcView 9.0 (ESRI, 2009), according to usual geographic information system (GIS) techniques. Distribution records were obtained mostly in taxonomic or faunistic studies (e.g. Gutberlet & Campbell, 2001; Campbell & Lamar, 2004; Harvey *et al.*, 2005; Xavier & Rodrigues, 2008; Carrasco *et al.*, 2009, 2010). In early 2012, Carrasco *et al.* (2012) published a new phylogeny for the genus, which is basically congruent with the topology presented in Fenwick *et al.* (2009), but reverts the taxonomy to the traditional use of *Bothrops* (including *Bothropoides*, *Rhinocerophis* and *Bothriopsis*) and *Bothrocophias* as the only two genera of Neotropical pitvipers. Although this simpler taxonomic arrangement has been adopted in our study, we use the phylogeny of Fenwick *et al* (2009) as a working hypothesis for our analyses.

After collecting and revising point locality databases, we generated maps of potential distribution according to species distribution models (SDMs) techniques, using Maxent (Phillips *et al.*, 2004, 2006; Elith *et al.*, 2010), in order to minimize sampling gaps and avoid errors of comission. We mapped potential ocurrences using the following uncorrelated environmental 1km resolution variables from the Worldclim project (Hijmans *et al.*, 2005), the same used by Costa *et al.* (2010): altitude, annual precipitation, isothermality, maximum temperature of warmest month, mean diurnal range, mean temperature of warmest quarter, mean temperature of wettest quarter, minimum temperature of coldest month, precipitation of coldest quarter, precipitation of driest month, precipitation of warmest quarter, precipitation of wettest month, precipitation seasonality, temperature annual range and temperature seasonality. As our climatic data layers are confined to continental South America, records for insular species and for *Bothrops asper* in Central America were not included in SDMs.. For species with at least 30 point locality records we divided the occurrences into training and test points (70% e 30%, respectively). For species with less than 30 localities we used only training points. To evaluate the performance of the models we used the area under the curve (AUC) metric, which compares model outputs with null expectations using a threshold-independent measure (Fielding & Bell, 1997). A value of 0.5 indicates that the model is no better than random, and AUC = 1 indicates that the model discriminates perfectly between presence and absence records (Graham & Hijmans, 2006). Resulting models with AUC of at least 0.75 (considered the minimum value indicating adequate models, Fielding & Bell, 1997) were transformed in presence-absence polygons by adopting the LPT (Lower Presence Thresholds method, Pearson *et al.*, 2007). In this procedure, we defined an *E* parameter (Peterson *et al.*, 2008) according to the number of points for each taxon: *E* was set to 5% for taxa known from more than 30 point records; 10% for taxa known from 29 to 10 points, and 15% for taxa known from less than 10 points (i.e., for this taxon we eliminated the lowest 15% values of occurrence probabilities at known locality records, and used this new value as threshold for considering potential presence). Finally, in order to reduce omission of known presence localities, and to avoid commission errors common in ENM techniques (Corsi *et al.*, 2000), we adjusted model outputs to known ranges of each species, comparing Maxent outputs to published range maps and reliable point locality records obtained in the taxonomic literature (e. q. Gutberlet & Campbell, 2001; Marques *et al.*, 2002; Campbell & Lamar, 2004; Cisneros-Heredia & Touzet, 2004; Harvey *et al.*, 2005; Cisneros-Heredia *et al.*, 2006; Silva & Rodrigues, 2008; Carrasco *et al.*, 2009, 2010). This step is necessary because species distribution models are based only on environmental factors and are ignorant of dispersal limitations and species interactions, usually indicating the presence of species in areas of known absence (Pulliam, 2000; Graham & Hijmans, 2006). Thus, modeled distributions falling outside the expected range (according to published maps and reliable records) were interpreted as model overprediction, and eliminated (see discussion and similar procedures in Graham & Hijmans, 2006).

After obtaining the final distribution maps we calculated the total distribution area and percentage of habitat loss for each terminal taxon. Habitat loss was measured by clipping final range maps with data in Global Land Cover 2000 (Eva *et al.*, 2002). For the insular species *Bothrops insularis* we calculated remaining habitat as the ratio between extant forests and secondary grassland areas in Queimada Grande island, using data presented in Martins *et al.* (2008). Due to lack of detailed data on habitat loss for other insular areas, we used the mean percentage of habitat loss for these species. Detailed data on resilience to habitat loss in pitvipers is scarce. Thus, although the capacity to persist in degraded habitats is expected to vary across pitviper species, we considered the loss of natural habitat as equally deleterious to all studied taxa.

Evolutionary scores for taxonomic conservation priorities

To estimate the unique evolutionary contribution of each species we used ED (evolutionary distinctiveness) scores, a measure based on the sum of all branch lengths from which the species is descended, including the terminal branch, the length of the branches and the number of ramifications (Isaac *et al.*, 2007). ED values represent the amount of unique evolutionary history represented by each terminal taxon (Isaac *et al.*, 2007). This measure was weighted for each terminal taxon with measures of suspected extinction risk, generating 1) EDGE index (see Isaac *et al.*, 2007; Collen *et al.*, 2011), representing the combination of ED values and IUCN redlist status (IUCN, 2011) and 2) EDHL, representing ED values weighted according to percentage of habitat loss within inferred ranges, using the gross percentage obtained for each species in a scale of 1 to 0, where 1 indicate a 100% habitat loss (e.q. specie with 90% habitat loss has 0.9 score). For weighting using IUCN categories we adopted the 'IUCN 100' approach presented in Mooers *et al.* (2008), translating IUCN categories to extinction probabilities in the next 100 years, in a scale of 1 to 0 (with 1 indicating 100% probability of extinction in 100 years). In this scoring approach there is a strong contrast among categories, with Critically Endangered (CR) species receiving the value of 0.9 (90% probability of extinction in 100 years), Endangered (EN) species receiving 0.6, Vulnerable (VU) species 0.1, Near Threatened (NT) receiving 0.01 and species in Least Concern (LC) a value near zero (0.001). Although the real status of species not included in redlist assessments (NE, Not Evaluated) is probably highly variable, no conservation action is in place or recommended for these species. So, in this scheme, NE taxa are considered as relatively safe, and receive the same value of taxa in Least Concern (for more details, see Mooers *et al.*, 2008). Finally, we analyzed if these measures (ED, EDHL and EDGE) are correlated, using R (R Development Team, 2010). All taxonomic conservation priority analyses were performed in the *Tuatara* package (Maddison & Mooers, 2007) of the *Mesquite* software (Maddison & Maddison, 2008).

Since closely related species share most of their evolutionary histories, and must not be considered as independent units in comparative analyses (Blomberg *et al.*, 2003), we tested for phylogenetic signal in range size, percentage of habitat loss and IUCN threat status using the *Picante* package (Kembel *et al.*, 2010) in R (R Development Team, 2010). If no significant phylogenetic signal was observed, we tested the correlation between ED and range size, percentage of habitat loss and IUCN threat status of each terminal taxon in R (R Development Team, 2010).

Spatial conservation priorities: phylogenetic diversity, richness and endemism

We used final distribution maps and the pitviper phylogeny to map areas of high richness and high phylogenetic diversity (PD) in South America and the Antilles, using the *Biodiverse* software (Laffan *et al.*, 2010). PD has been defined as the minimum total length of all the phylogenetic branches required to span a given set of data on the phylogenetic tree (Faith, 1992). For this analysis we transformed our distribution polygons to points, by overlapping range maps to the centroids of a 0.25 degree square grid covering the study area. We generated 100 random points in our study area and correlated values of richness and PD, transformed in the same scale, found in these points to study the relationship between these two variables. We compared variations in richness and phylogenetic diversity following discrepancy maps presented in Pio *et al.* (2011), by subtracting values of PD from richness values, after standardizing both variables as percentages. Positive values in the map indicate sites where PD was greater than species richness, and negative values indicate sites where richness is higher than PD.

We tested the surrogacy between different biodiversity measures by comparing mean pairwise distance (MPD) and mean nearest taxon distance (MNTD, see Kembel *et al.*, 2010) of pitviper faunas assembled according to the following criteria: a) endemism, selecting areas containing the ten taxa (25% of total terminal taxa) with the smallest ranges; b) richness, selecting the 25% richest regions, with species occurrence in these regions (according to richness maps produced in *Biodiverse*) and c) threat, selecting threatened pitviper species in the IUCN redlist (IUCN, 2011). In order to assess the effect of major habitat types on measures of evolutionary diversity, we also compared MPD and MNTD of pitviper faunas found in open or forest biomes. Finally, we used MPD and MNTD values to test if biodiversity hotspots (Myers *et al.*, 2000; Myers, 2003) harbour pitviper faunas with higher phylogenetic diversity than expected by chance. For all these analyses we randomized observed pitiviper assemblages 1000 times, using "shuffle distance matrix labels" and "randomize community data matrix abundances" within *Picante* package (Kembel *et al.*, 2010) in R (R Development Team, 2010).

RESULTS

Distribution records, range size and habitat loss

We gathered and georeferenced at least 2.400 records, each one a unique combination of species per locality. The mean value of AUC was 0.97, and no model presented AUC below 0.75, indicating good overall model performance (Table 1). Just six species presented range sizes smaller than 100.000 km², including four island endemics. The species with the widest distribution is *Bothrops atrox* (Table 1), with an area of 6,249,435 km². Mean value of habitat loss for all species is 33.63%. The species most severely affected by habitat loss is *Bothrops itapetiningae* (75%), followed by *B. fonsecai* (71%) and *B. leucurus* (69%)*;* the taxa with larger percentages of remaining original habitat are *Bothrops pictus* (3%), *B. bilineatus smaragdinus* (5%) and *B. brazili* (6%) (Table 01).

No phylogenetic signal was observed in habitat loss (p = 0.49), range size (p = 0.91) and IUCN threat status (p = 0.90). No significant correlation was found between ED and range size (*t*

= -0.9419, df = 38, *p* = 0.352), habitat loss (*t* = -1.5066, df = 38, *p* = 0.140) and IUCN threat status (*t* = -1.3705, df = 38, *p* = 0.179).

Taxonomic conservation priorities

ED values ranked *Bothrops jonathani*, *B. barnetti* and *B. ammodytoides* as taxa with most unique evolutionary histories (Figure 1; Table 2). EDHL values (using habitat loss as proxy for extinction risk) listed *Bothrops itapetiningae*, *B. alternatus*, and *B. jonathani* as the three top priority species, combining high ED and high percentages of habitat loss (Figure 2; Table 2). Using the IUCN threat status as measure of extinction risk (EDGE) ranks *Bothrops insularis* and *B. alcatraz* (both threatened insular species) as highest priorities for conservation, with much higher values than all remaining taxa (see Figure 3, Table 2).

Ranks of conservation priority for each terminal taxa obtained using ED and EDHL were positively correlated (*t* = 2.758, df = 38, p= 0.009; Figure 4). However, no significant correlation was found between ranks using EDGE and ED (*t* = 0.3349, df = 38, *p* = 0.739) or EDGE and EDHL (*t* = -0.2663, df = 38, *p* = 0.792).

Spatial conservation priorities

Species richness and PD are highly correlated (*t* = 21.6914, df = 98, *p* = < 0.001; Figure 5). Distribution of phylogenetic diversity (PD) is highly variable across continental South America, reaching peak concentrations in three main areas (Figure 6A). A large area of high concentration of PD is found along the eastern versant of the Andes, mainly in its the northern and central portion (Area 1); another large area of high PD is the southeastern portion of the Brazilian shield, along the contact between the southern parts of the Atlantic forest and Cerrado hotspots (Area 2);

and a third, smaller area is found at the center of the continent, in the northwestern portion of the Cerrado and southern Amazonian headwaters (Area 3). Variations in richness levels show similar results (Figure 6B), but highlights only northern to central Andes as areas of extraordinary richness. Southern Andes and the northwestern portion of the Cerrado, harbouring high PD values, show only moderate richness values. Overlap between richness and PD is concentrated along the Andes and in the southern portions of the Brazilian shield (Figure 6C). A discrepancy map indicates that PD values exceed richness values in most South America, with richness tending to exceed PD towards northern portions of the Andes and southeastern Brazil (Figure 6D). The percentage of grid cells where phylogenetic diversity is higher than richness is 96,13%.

Areas with high PD are characterized by the sympatric occurrence of different pitviper lineages: Area 1 (eastern versant of the Andes) harbours most clades within *Bothrops*, except species included in the traditional *jararaca* and *neuwiedi* species groups (*Bothropoides* in Fenwick *et al.*, 2009), and represents the southern limits of the range of both the traditional *Bothrops bilineatus* group (*Bothriopsis* in Fenwick *et al.*, 2009) and of *Bothrocophias.* Area 2 (Brazilian shield) harbours most species of the *alternatus, jararaca* and *neuwiedi* species groups, but lacks *Bothrocophias* and species of the *Bothrops bilineatus* group (*Bothriopsis* in Fenwick *et al.*, 2009). Finally, Area 3 harbors one species *Bothrocophias* and six species from different clades within *Bothrops,* but lacks species of the *Bothrops alternatus* species group (*Rhinocerophis* of Fenwick *et al.*, 2009).

Values of MPD and MNTD for pitviper faunas assembled according to 1) endemism, 2) presence in forested or open biomes or in 3) hotspots were not significantly different from values obtained in random assemblages (Table 3). However, the species subset formed by pitvipers included in the IUCN redlist showed significant phylogenetic clustering (i.e, phylogenetic distances smaller than in random species subsets of the same richness) in both metrics: MPD (Z = -2.700; *P* = 0.008, Table 3) and MNTD (Z = -2.724; *P* = 0.007, Table 3). The species subset found in the richest areas also showed significant phylogenetic clustering in the MNTD metric (Z = -1.999, *p* = 0.019; see Table 03). Although not differing from random, positive or negatives values of Z show are also informative. Positive values found in forest biomes (MPD) and hotspots (MNTD) indicate a tendency for greater phylogenetic distance (phylogenetic overdispersion) in these pitviper faunas (see Table 3). Meanwhile, all other variables showed negative signals, indicating an overall tendency for phylogenetic clustering (see Table 3).

DISCUSSION

Distribution records, range size and habitat loss

Pitvipers occupy a wide range or regions and habitats in South America, and this is reflected in the wide differences in range sizes observed; this also reflects in a wide variation in percentages of habitat loss across the clade. Overall, species and lineages under less severe impact of habitat loss (more than 90% remaining habitats) are concentrated in the Amazon or in specific portions of the Andes, mainly in its central region. By contrast, most species under high impact of habitat loss are found in biodiversity hotspots (sensu Myers *et al.*, 2000; Myers, 2003), especially in the southern portion of the Cerrado and in most of the Atlantic Forest.

The lack of significant correlations between ED and range sizes indicates that range size varies independently of phylogeny, or lineage age, in *Bothrops* and *Bothrocophias*. However, this trend is not observed in other studied lineages (Webb & Gaston, 2000; Jones *et al.*, 2005).

Studies with primates and carnivores suggest a linear and negative relationship, with range sizes decreasing in older lineages (Jones *et al.*, 2005). This same trend is verified in vascular plants (Ricklefs & Latham, 1992) and birds (Webb & Gaston, 2000). Range sizes are known to be affected by many factors, being determined by interactions between recent ecological or climatic changes and long term, historical-geological shifts (Brown & Lomolino, 1998). Significant negative relationships between ED and range size (i.e. older lineages, larger ranges) could indicate that recent lineages are not being able to fully disperse to expected ranges; conversely, significant positive relationships (older lineages, smaller ranges) could indicate that ancient lineages represent geographical relicts, and tend to be more prone to extinction, being susceptible even to relatively localized human impacts (Jones *et al.*, 2005). Thus, in our study, a significant positive relationship between ED and habitat loss, or between ED and IUCN categories, could indicate that ancient lineages, already isolated in small areas, are being disproportionally affected by human disturbance (Webb & Gaston, 2000). Although we detected some clades with high relative ED values under high levels habitat loss, especially the *alternatus* species group (*Rhinocerophis* of Fenwick *et al.*, 2009), this trend does not apply to the lineage as a whole. Except for the highly impacted *alternatus* group, variations in percentages of habitat loss are randomly scattered among lineages, being interpreted as a result of geographical location and independent of clade age or range size.

Taxonomic conservation priorities

Taxonomic conservation ranks using ED values tend to species of the traditional *B. alternatus* group (*Rhinocerophis* of Fenwick *et al.*, 2009) as top priorities. This distinctive pitiviper lineage harbors two of the three top priority species, all found in open habitats on the Southern or Central portions of South America: *Bothrops jonathani* is found in Andean open areas*; B. ammodytoides* is found in semi-arid Patagonian steppes and *B. barnetti,* found in arid deserts along the Pacific versant of the Andes. When ED values are weighted according to percentage of habitat loss (EDHL), this overall pattern is retained, with four of five species of this linage receiving the highest scores. These results indicate that species in this lineage should receive more careful attention in conservation initiatives, due to the coincidence of high ED and serious impact of habitat loss. At least three species in this clade (*B. alternatus, B. itapetiningae* and *B. ammodytoides*) are typical of open, grassland habitats, which tend to be overlooked in conservation initiatives (Bond & Parr, 2010), and have been heavily impacted by agricultural activities (Eva *et al.*, 2002); two other species (*B. cotiara* and *B. fonsecai*) are found in mixed, semi-open, and highly impacted Araucaria Forests; actions to conserve the habitats of these species must be seen as highly urgent, as threats to these species may pose serious challenges to the conservation of evolutionary diversity in Neotropical pitvipers.

The lack of significant correlations between ED values and range size, habitat loss and IUCN threat status indicates that neither of these measures are good surrogates for the conservation of evolutionary diversity in Neotropical pitvipers. EDHL values are significantly correlated to ED values, but since EDHL is weighted by a quantifiable, continuous measure of potential threat, which also informs on urgency of action, we consider EDHL as a better measure of conservation priority than the raw ED values. Moreover, EDGE as not a reliable measure of conservation priority in the studied clade. Given the lack of detailed threat assessment for the majority of studied species (only six species of 40 are evaluated, 25%), only two, phylogenetically close insular species included as terminal taxa in Fenwick *et al*. (2009) are included in global redlists (IUCN, 2011). Another species, *Bothrops pirajai* is considered

Vulnerable (IUCN, 2011), but was not included in the phylogeny. The fact that the assemblage formed by the two threatened showed significant phylogenetic clustering (i.e, values of phylogenetic distance smaller than expected by chance) indicates that conservation strategies aiming at these species alone will probably fail to conserve the overall evolutionary history in the studied clade. If current global threatened status is considered as the sole measure of conservation priority, a very large portion of the phylogenetic diversity in the clade would not be properly represented in conservation actions. Although the inclusion of *Bothrops pirajai* could change the results of the MNTD and MPD tests, these would probably not differ from random, indicating that PD would not be properly captured in the subset of threatened species. Currently, species included under Least Concern or Not Evaluated may be under serious threat, including top priority species under ED and EDHL values. The comprehensive evaluation of threat status in Neotropical pitvipers is mandatory, as slight changes in threat categories can be decisive in the results of the EDGE priority status (Collen *et al.*, 2011). Given these limitations, we suggest that conservation priorities and urgent action should be directed to species showing high EDHL values (high ED combined with extensive habitat loss) in order to conserve the largest amount of imperiled evolutionary diversity in this clade. This is a clear indication that the taxonomic coverage of threat assessments should be urgently expanded, as only mammals, birds and amphibians have been subject to comprehensive global threat assessments (Collen *et al.*, 2011; Mooers *et al.*, 2008; Hilton-Taylor & Stuart, 2009).

Although many ecological of natural history traits are correlated with phylogeny (Magnuson-Ford *et al.*, 2010), the lack of phylogenetic signal in range sizes and habitat loss in our results indicates that geographical location determines most of the variation in range sizes and habitat loss in Neotropical pitvipers. Moreover, the lack of significant phylogenetic signal for IUCN 100 scores (obtained according to redlist status) indicates that current threat categories of

Neotropical pitvipers are defined more by species-specific characters than by evolutionary relationships. Although two insular species of the same clade are included in redlists, many other species, in different clades and showing widely different range sizes and levels of habitat loss, receive similar scores in the IUCN 100 ranking system (all LC or NE).

Spatial conservation priorities

Knowing the amount of phylogenetic diversity (PD) contained within a given area, based on a well studied group, can provide a general prediction of the entire PD in that area (Faith & Baker, 2006). Moreover, PD measures are not defined arbitrarily and are free from predefined thresholds for detecting spatial priorities (Faith & Baker, 2006). Although our results show that correlation between PD and species richness is high, in accordance with previous studies (Rodrigues & Gaston, 2002; Cadotte & Davies, 2010; Rodrigues *et al.*, 2011), PD and richness are based on different concepts. Taxonomic approaches such as richness are not based on evolutionary history, and so cannot capture variation in higher taxonomic or evolutionary levels (Mace *et al.*, 2003; Crozier *et al.*, 2005). Moreover, PD tends to be less sensitive to taxonomic changes and different species concepts, that have high impact on richness measures (Isaac *et al.*, 2004). Phylogenetic diversity might be important to maintaining ecosystem services, where related species tends to share similar ecologies (Cadotte *et al*., 2008) and might maximizing options in an uncertain future (Avise, 2005).

Despite a general coincidence between richness and PD, our results highlight that the richest areas are not totally congruent with areas of high PD, with a tendency of higher PD values (exceeding richness) towards southern portions of the continent (see Figure 6D). Moreover, the species subset included in the richest areas did not include PD values larger than random assemblages. A study on the cape floristic province, a biodiversity hotspot in South Africa (Forest *et al.* 2007), found that conventional taxon measures misses areas with large gains in PD. Although previous studies indicate that conservation strategies based on richness capture great levels of PD (Rodrigues *et al.*, 2011), in our results, at least part of two of the three main concentrations of phylogenetic diversity were not covered by areas of highest richness levels (see Figure 6C). Thus, including spatially explicit and refined PD measures into conservation planning favors the detection of fine grained PD variations within large, global priority areas, and may effectively aid in the spatial protection of evolutionary history.

The tendency of great phylogenetic distance found in hotspots agrees with results in Sechrest *et al.* (2002) for primate and carnivores, which indicates that hotspots contained significantly more PD than expected by chance. However, much of this unique history for these groups was found to be present in only one hotspot, Madagascar (Spathelf & Waite, 2007). So, instead of focusing all efforts in these large areas, at the risk of losing overlooking other important areas, we must provide more spatially refined analyses, supplementing the hotspots analyses with additional detailed maps of priority areas for the conservation of evolutionary diversity (Purvis *et al.*, 2005; Spathelf & Waite, 2007).

As expected and in accordance with these results, species subsets formed by narrow endemics, species in IUCN redlists or species forming the richest assemblages all failed to capture phylogenetic diversity levels higher than expected by random (see Table 3), indicating that conservation strategies must be specifically aimed at maximizing PD, in order to adequately represent non-random, targeted portions of evolutionary patterns and processes.

A better understanding of the distribution of imperiled and phylogenetically distinct species is highly desirable (Faith *et al.*, 2006; Erwin, 2010; Collen *et al.*, 2011). Given the intense levels of habitat loss and large knowledge gaps for many taxonomic groups, this kind of data is essential for conservation initiatives in the Neotropics. The loss of evolutionary diversity will alter not only current patterns of biological diversity, but also affect the evolutionary process which generates current and future diversity (Myers & Knoll, 2001). Our results indicate that usual metrics of threat to biodiversity seem unable to capture the actual risk to evolutionary diversity. We highlight the importance of including spatially refined measures of phylogenetic diversity, coupled with spatial measures of threat (Faith, 2007), as new and necessary tools for conservation assessments in megadiverse and poorly studied faunas.

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BIOSKETCHES

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TABLES

Table 1- Values of the area under the curve (AUC) obtained for species distribution models, total inferred range area in km², percentage of habitat loss, IUCN status and presence/absence in Neotropical Hotspots (0 = absence; 1 = presence, Myers *et al.*, 2003) for Neotropical pitvipers. IUCN status: NE - Not Evaluated; LC - Least Concern; and CR - Critically Endangered.

Species	AUC	Area (km²)	% Habitat loss	IUCN	Hotspots
Bothrocophias andianus	0.98	164.832	9.44	NE	1
Bothrocophias campbelli	0.99	172.777	33.75	NE	1
Bothrocophias hyoprora	0.95	3.821.280	8	NE	0
Bothrocophias microphthalmus	0.97	931.918	15.35	NE	1
Bothrocophias myersi	0.99	156.557	34.08	LC	1
Bothrops alcatraz	NA	1,96	33.63	CR	1
Bothrops alternatus	0.96	2.415.980	52.45	NE	1
Bothrops ammodytoides	0.97	1.509.761	29.41	NE	0
Bothrops asper	0.98	1.232.493	36.13	NE	1
Bothrops atrox	0.94	6.249.435	8.98	NE	0
Bothrops barnetti	0.98	251.591	19.94	NE	1
Bothrops b. bilineatus	0.95	2.863.787	24.75	NE	1
Bothrops b. smaragdinus	0.94	2.581.771	4.76	NE	1
Bothrops brazili	0.91	5.094.521	5.73	NE	0
Bothrops caribbaeus	NA	539	33.63	NE	1
Bothrops chloromelas	0.98	279.450	11.07	NE	1
Bothrops cotiara	0.99	267.710	48.89	NE	1
Bothrops diporus	0.96	1.834.600	35.42	NE	1

Table 1 continued:

Bothrops erythromelas	0.98	966.159	58.49	LC	0
Bothrops fonsecai	1	164.877	71.15	NE	1
Bothrops insularis	NA	0,43	26.05	CR	1
Bothrops isabelae	0.98	249.269	36.84	NE	0
Bothrops itapetiningae	0.99	499.319	75.19	LC	1
Bothrops jararaca	0.97	1.213.601	59.57	NE	1
Bothrops jararacussu	0.98	1.137.415	60.46	LC	1
Bothrops jonathani	0.94	467.805	20.36	NE	1
Bothrops lanceolatus	NA	1.100	33.63	NE	1
Bothrops leucurus	0.99	371.851	68.83	NE	1
Bothrops marajoensis	1	167.652	17.35	NE	0
Bothrops mattogrossensis	0.93	3.321.849	32.84	NE	1
Bothrops moojeni	0.97	2.416.344	51.12	NE	1
Bothrops neuwiedi	0.99	859.704	65.96	NE	1
Bothrops osbornei	0.99	99.073	31.23	NE	1
Bothrops pauloensis	0.98	1.494.463	58.10	NE	1
Bothrops pictus	0.98	89.083	3.21	NE	0
Bothrops pulcher	0.99	263.483	20.85	NE	1
Bothrops punctatus	0.98	189.550	30.16	NE	1
Bothrops sanctaecrucis	0.99	246.569	9.97	NE	1
Bothrops taeniatus	0.88	5248.006	10.58	NE	0
Bothrops venezuelensis	0.96	143.968	26.07	NE	1

Table 2- Evolutionary distinctiveness metrics in values and ranks (in parentheses) for Neotropical pitvipers. EDHL = ED values calibrated with percentage of habitat loss as probability of extinction. EDGE = ED values calibrated with IUCN threat categories as probability of extinction. The ten highest ranked taxa in each metric are marked with an asterisk.

Species	ED	EDHL	EDGE
Bothrocophias andianus	0.174 (11)	0.016 (33)	0.002 (13)
Bothrocophias campbelli	0.173 (12)	0.059 (11)	0.002 (14)
Bothrocophias hyoprora	0.194 (9*)	0.016 (34)	0.002 (11)
Bothrocophias microphthalmus	0.111 (26)	0.017 (32)	0.001 (28)
Bothrocophias myersi	0.243 (6*)	0.083 (7*)	0.002 (8*)
Bothrops alcatraz	0.058 (37)	0.020 (29)	0.052 (2*)
Bothrops alternatus	0.217 (8*)	0.113 (2*)	0.002 (10*)
Bothrops ammodytoides	0.286 (3*)	0.083 (5*)	0.003 (5*)
Bothrops asper	0.052 (38)	0.019 (30)	<0.001 (38)
Bothrops atrox	0.052 (39)	0.005 (39)	<0.001 (39)
Bothrops barnetti	0.287 (2*)	0.057 (12)	0.003 (4*)
Bothrops b. bilineatus	0.133 (21)	0.033 (23)	0.001 (23)
Bothrops b. smaragdinus	0.112 (25)	0.004 (40)	0.001 (27)
Bothrops brazili	0.114 (24)	0.007 (38)	0.001 (26)
Bothrops caribbaeus	0.110 (28)	0.037 (22)	0.001 (30)
Bothrops chloromelas	0.097 (29)	0.011 (36)	<0.001 (31)
Bothrops cotiara	0.115 (23)	0.056 (14)	0.001 (25)
Bothrops diporus	0.124 (22)	0.044 (19)	0.001 (24)

Table 2 continued:

Bothrops erythromelas	0.142 (19)	0.083 (6*)	0.001 (21)
Bothrops fonsecai	0.096 (30)	0.069 (9*)	<0.001 (32)
Bothrops insularis	0.082 (32)	0.022 (28)	0.075 (1*)
Bothrops isabelae	0.079 (34)	0.029 (26)	<0.001 (35)
Bothrops itapetiningae	0.189 (10*)	0.142 (1*)	0.002 (12)
Bothrops jararaca	0.050 (40)	0.030 (25)	<0.001 (40)
Bothrops jararacussu	0.148 (17)	0.089 (4*)	0.001 (19)
Bothrops jonathani	0.497 (1*)	0.099 (3*)	0.005 (3*)
Bothrops lanceolatus	0.110 (27)	0.038 (21)	0.001 (29)
Bothrops leucurus	0.081 (33)	0.056 (15)	<0.001 (34)
Bothrops marajoensis	0.079 (35)	0.013 (35)	<0.001 (36)
Bothrops mattogrossensis	0.148 (16)	0.049 (16)	0.001 (18)
Bothrops moojeni	0.075 (36)	0.038 (20)	<0.001 (37)
Bothrops neuwiedi	0.092 (31)	0.061 (10*)	<0.001 (33)
Bothrops osbornei	0.156 (13)	0.048 (17)	0.002 (15)
Bothrops pauloensis	0.134 (20)	0.078 (8*)	0.001 (22)
Bothrops pictus	0.268 (4*)	0.008 (37)	0.003 (6*)
Bothrops pulcher	0.147 (18)	0.031 (24)	0.001 (20)
Bothrops punctatus	0.155 (14)	0.047 (18)	0.002 (16)
Bothrops sanctaecrucis	0.259 (5*)	0.026 (27)	0.003 (7*)
Bothrops taeniatus	0.152 (15)	0.017 (31)	0.002 (17)
Bothrops venezuelensis	0.219 (7*)	0.057 (13)	0.002 (9*)

Table 3- Values of phylogenetic dispersion (mean pairwise distance - MPD; and mean nearest taxon distance - MNTD) calculated in *Picante* software (Kembel *et al.*, 2010) for pitviper assemblages selected according to different biodiversity measures (endemism, richness and threat), presence in major biomes or presence in biodiversity hotspots. Z values represent the standardized effect size observed vs. null assemblages and P values the quantile observed vs. null communities. Significant results in bold.

	MPD		MNTD	
	Z value	P value	Z value	P value
Endemism	-0.276	0.397	-0.852	0.196
Richness	-1.284	0.100	-1.999	**0.019**
IUCN	-2.700	**0.008**	-2.724	**0.007**
Open Biomes	-0.601	0.296	-1.137	0.130
Forest Biomes	0.475	0.656	-0.375	0.363
Hotspots	-0.062	0.435	0.728	0.753

FIGURES

Figure 1- Evolutionary distinctiveness (ED) values mapped on the phylogenetic tree (Fenwick *et al.,* 2009) of neotropical pitvipers, with branches proportional to lengths.

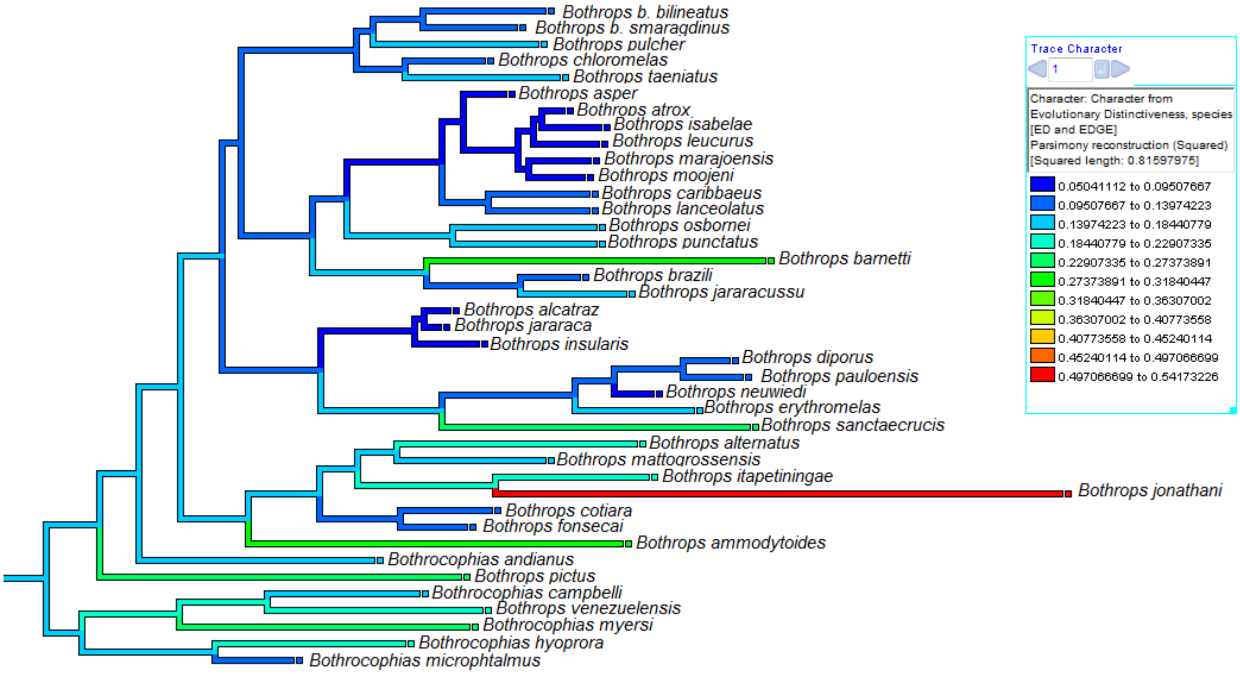
Figure 2- Evolutionary distinctiveness weighted by habitat loss (EDHL, see text for more information) mapped on the phylogenetic tree (Fenwick *et al.,* 2009) of neotropical pitvipers, with branches proportional to lengths.

Figure 3- Evolutionary distinctiveness weighted with IUCN status (EDGE) (see text for more information) mapped on the phylogenetic tree (Fenwick *et al.,* 2009) of neotropical pitvipers, with branches proportional to lengths.

Figure 4- Relationship between ranks of evolutionary distinctiveness (ED) and evolutionary distinctiveness weighted by habitat loss (EDHL) of neotropical pitvipers.

Figure 5- Regression between normalized and rescaled values of species richness and phylogenetic diversity (PD), in 100 random sites across continental South America.

Figure 6- Map of pitvipers in 0.25 degree grid cells in South America and the Antilles, in Albers projection. A-Map of phylogenetic diversity of pitvipers. The numbers (1, 2 and 3) represent areas with high phylogenetic diversity; B- Map of species richness of pitvipers. C- Map of overlap of richest and with most phylogenetic diversity areas; D- Discrepancy map resulting from the substraction of standardized (%) species richness and phylogenetic diversity (PD). Areas where PD is higher than species richness are indicated by red, with blue areas indicating sites where richness exceeds PD. The percentage of grid cells where phylogenetic diversity is higher than species richness is indicated.



Character: Character from Evolutionary Distinctiveness, species [ED and EDGE]
Parsimony reconstruction (Squared)
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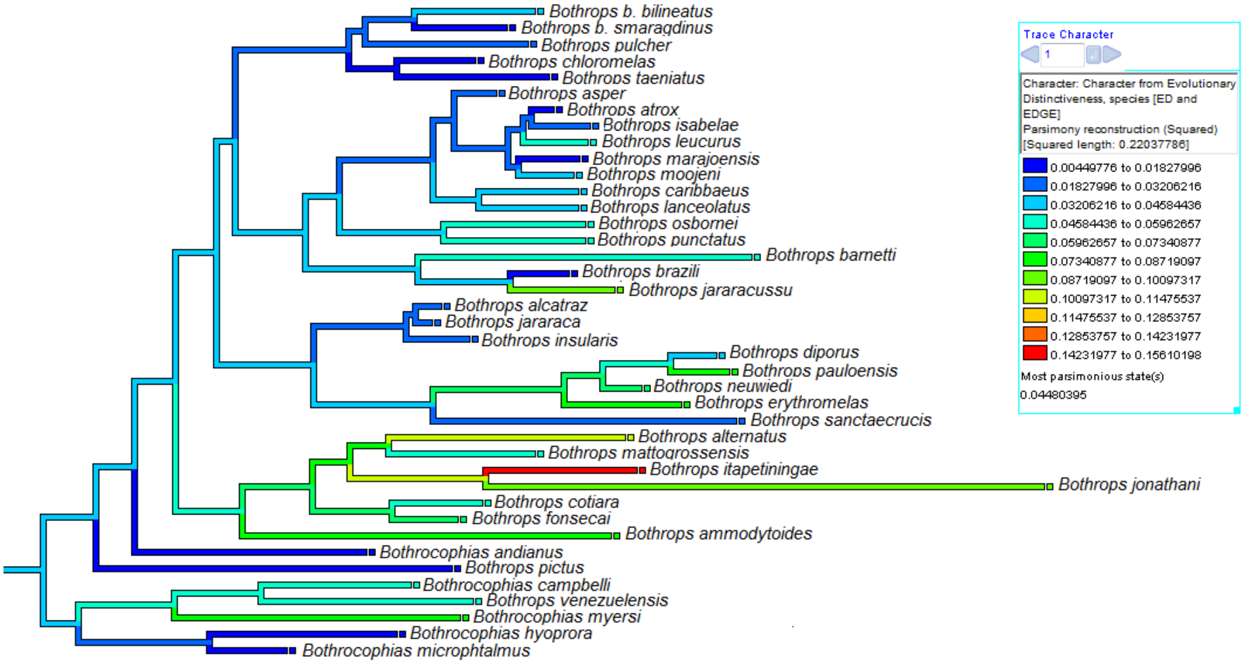
Fig1



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Most parsimonious state(s)
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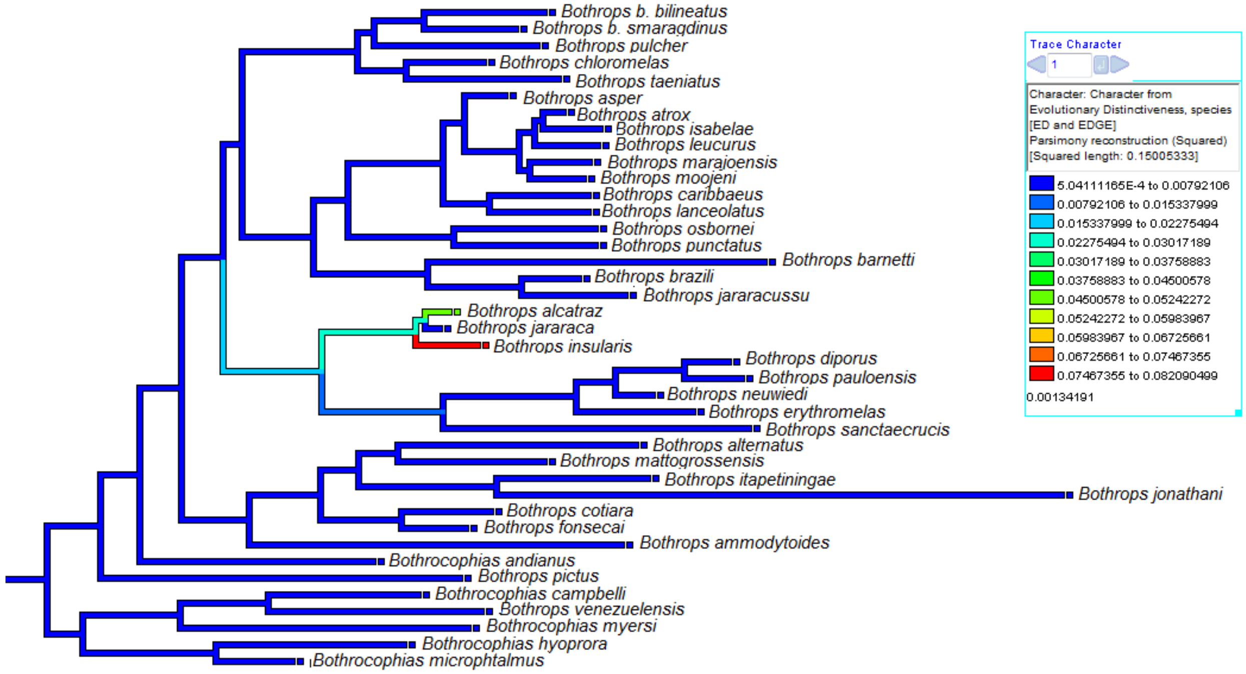
Fig 2.


Bothrops b. bilineatus
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Bothrops asper
Bothrops atrox
Bothrops isabelae
Bothrops leucurus
Bothrops marajoensis
Bothrops moojeni
Bothrops caribbaeus
Bothrops lanceolatus
Bothrops osbornei
Bothrops punctatus
Bothrops barnetti
Bothrops brazili
Bothrops jararacussu
Bothrops alcatraz
Bothrops jararaca
Bothrops insularis
Bothrops diporus
Bothrops pauloensis
Bothrops neuwiedi
Bothrops erythromelas
Bothrops sanctaecrucis
Bothrops alternatus
Bothrops mattogrossensis
Bothrops itapetiningae
Bothrops jonathani
Bothrops cotiara
Bothrops fonsecai
Bothrops ammodytoides
Bothrocophias andianus
Bothrops pictus
Bothrocophias campbelli
Bothrops venezuelensis
Bothrocophias myersi
Bothrocophias hyoprora
Bothrocophias microphtalmus
Trace Character
1
Character: Character from Evolutionary Distinctiveness, species [ED and EDGE]
Parsimony reconstruction (Squared)
[Squared length: 0.15005333]
5.04111165E-4 to 0.00792106
0.00792106 to 0.015337999
0.015337999 to 0.02275494
0.02275494 to 0.03017189
0.03017189 to 0.03758883
0.03758883 to 0.04500578
0.04500578 to 0.05242272
0.05242272 to 0.05983967
0.05983967 to 0.06725661
0.06725661 to 0.07467355
0.07467355 to 0.082090499
0.00134191

Fig 3

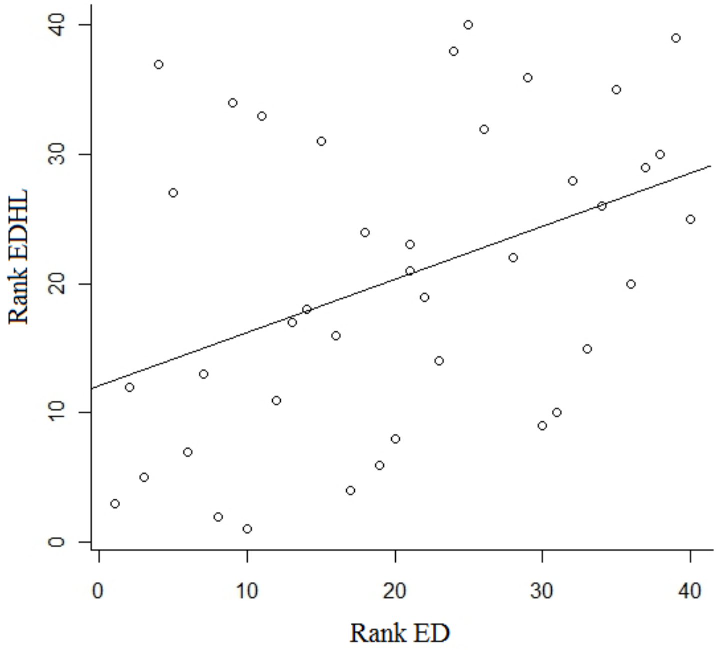
Rank EDHL
Rank ED
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Fig. 4

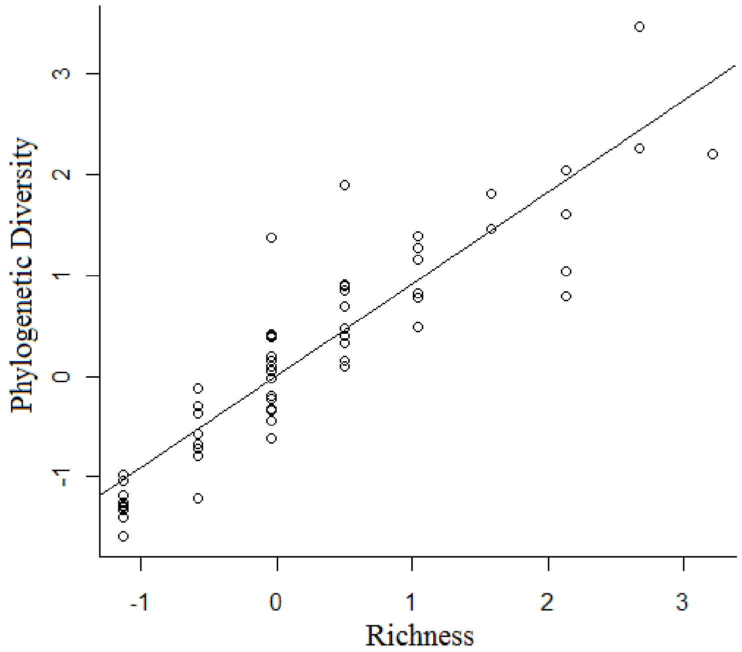

Fig.5

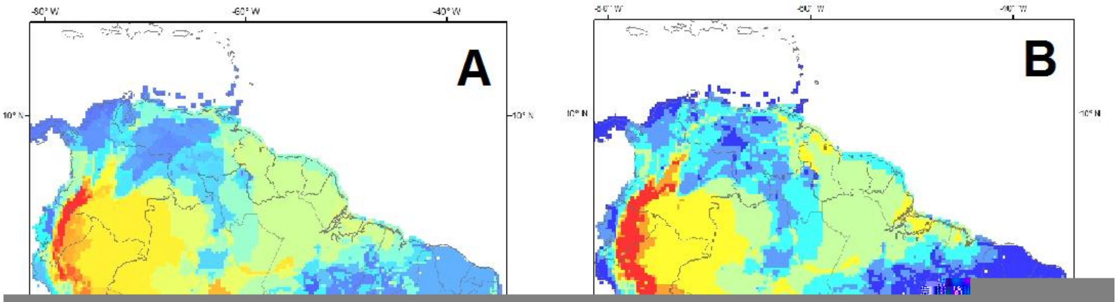

Fig. 6

Conclusões Gerais

- Métricas usuais de priorização de áreas, tais como concentrações de riqueza, endemismo, *hotspots* de biodiversidade, presença em biomas abertos ou florestais não protegem mais diversidade filogenética que o acaso na linhagem das jararacas;
- Métricas de seleção de espécies prioritárias para a conservação utilizando as atuais listas globais de espécies ameaçadas (IUCN) não protegem mais diversidade filogenética que o acaso na linhagem das jararacas;
- A baixa performance das métricas usuais (não filogenéticas) de seleção de áreas e táxons como substitutos da diversidade evolutiva indica que são necessários métodos que incluam diretamente as informações de parentesco em estratégias de conservação;
- São necessárias novas, mais detalhadas e mais abrangentes avaliações de ameaça dos répteis Neotropicais. Mesmo nas jararacas, um grupo bem conhecido em vários aspectos de biologia e história natural, a maioria das espécies nunca foi objeto de avaliações de ameaça usando critérios da IUCN;
- A falta de relação entre diversidade evolutiva (ED) e tamanho de distribuição, grau de perda de habitat e grau ameaça na IUCN mostra que estas categorias variam independente da filogenia. Assim, fatores geográficos parecem afetar mais diretamente as variações em tamanho de distribuição e exposição a ameaças no grupo estudado.
- Regiões de alta concentração de diversidade filogenética são geralmente congruentes com *hotspots* de biodiversidade, mas os padrões de riqueza, perda de habitat e diversidade filogenética são altamente variáveis mesmo dentro destas áreas, indicando a necessidade

de maior detalhamento espacial e inclusão direta de informações filogenéticas em análises de conservação;

- Priorizar a conservação de espécies com altos valores de ED ponderados por altas taxas de perdas de hábitat pode ser uma estratégia eficiente para direcionar ações urgentes para a conservação no grupo, potencialmente auxiliando na conservação de outros organismos para os quais dados filogenéticos ou espaciais não estão disponíveis.

Apêndice

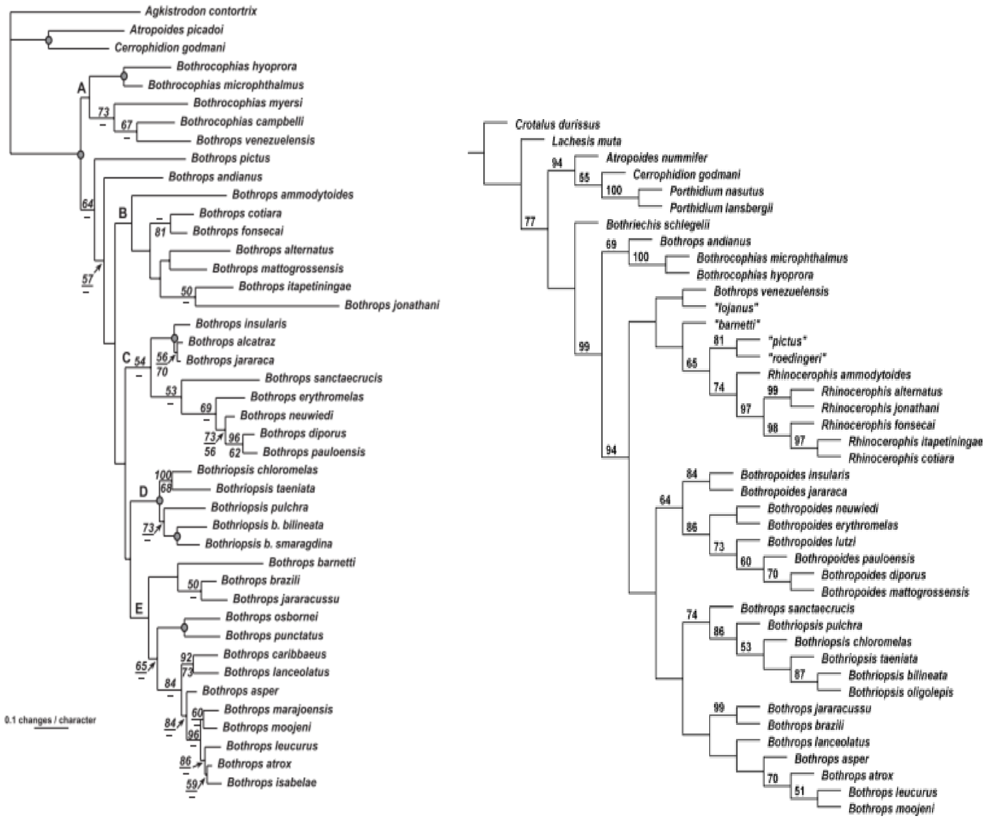

Figura 1. À esquerda, filogenia das jararacas neotropicais (Fenwick *et al*., 2009), utilizada como hipótese de trabalho no presente estudo. À direita filogenia mais recente do grupo (Carrasco *et al*., 2012). Ambos os estudos utilizam dados morfológicos e moleculares combinados.

Figura 2- Fotos de alguns exemplares representantes dos gêneros *Bothrops* e *Bothrocophias,* sendo: 1- *Bothrocophias campbelli* (Foto: James Shristensen); 2- *Bothrops bilineatus* (Foto: Ivan Sazima); 3- *Bothrops alcatraz* (Foto: Otávio Marques); 4- *Bothrops pauloensis* (Foto: Cristiano Nogueira); 5- *Bothrops atrox* (Foto: John White); e 6- *Bothrops itapetiningae* (Foto: Cristiano Nogueira).

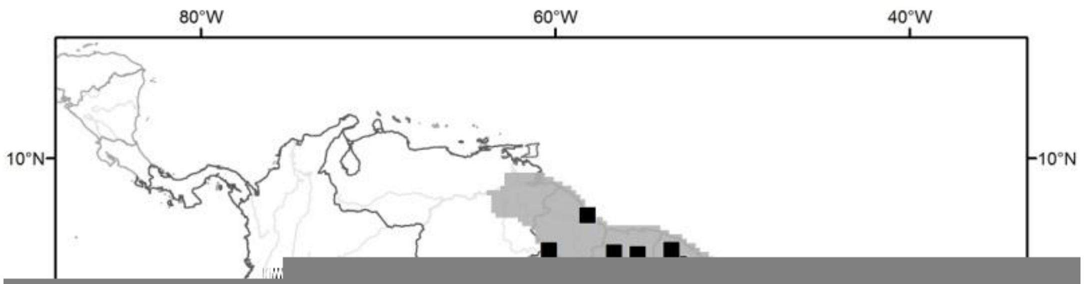

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Figura 3- Mapa da distribuição das espécies *Bothrops b. bilineatus, B.b. smaragdinus* e *B. pulcher*, mostrando pontos de ocorrência e área de distribuição potencial, de acordo com modelos de distribuição das espécies (SDMs)..

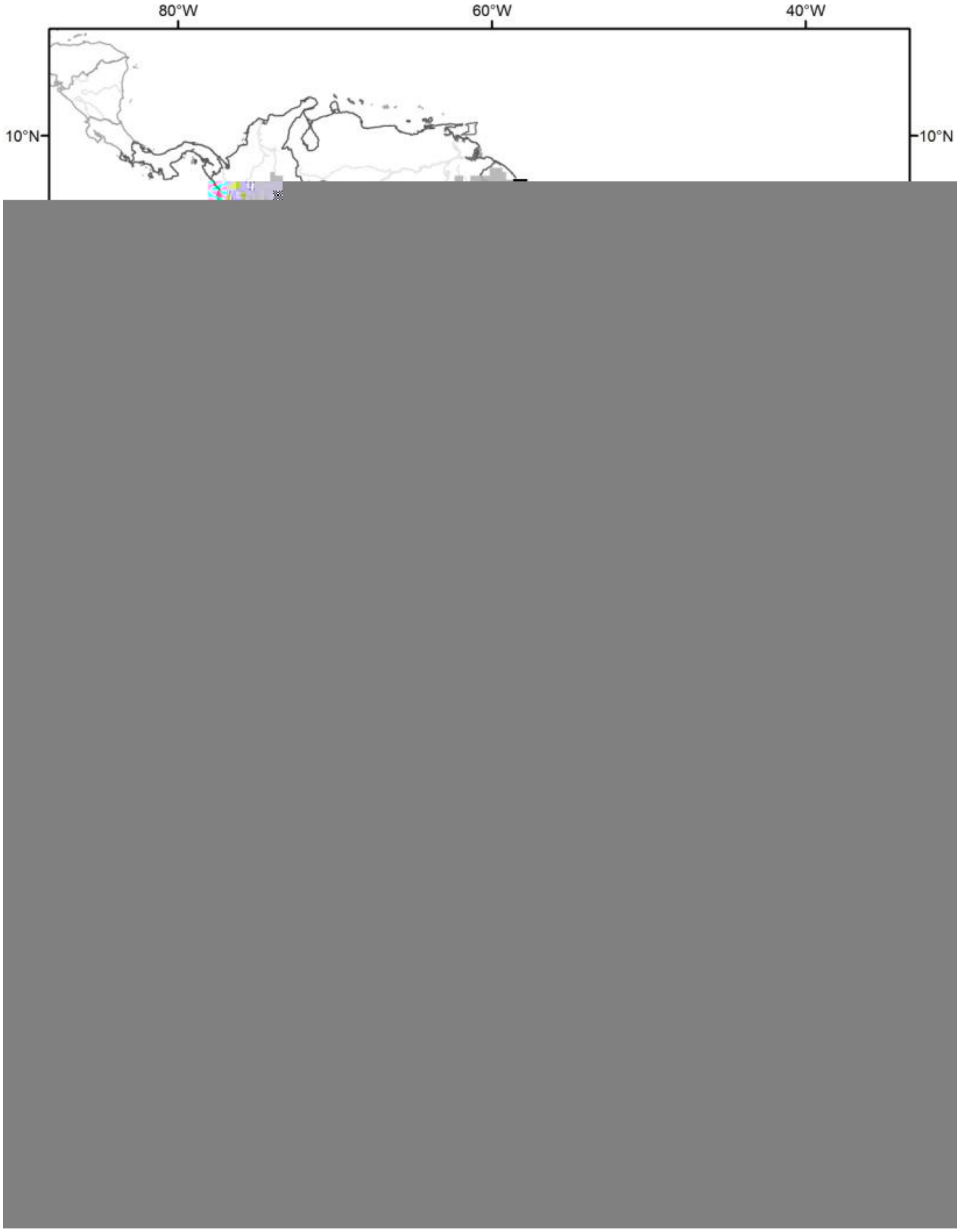

Figura 4- Mapa da distribuição das espécies *Bothrops chloromelas e B. taeniatus,* mostrando pontos de ocorrência e área de distribuição potencial, de acordo com modelos de distribuição das espécies.

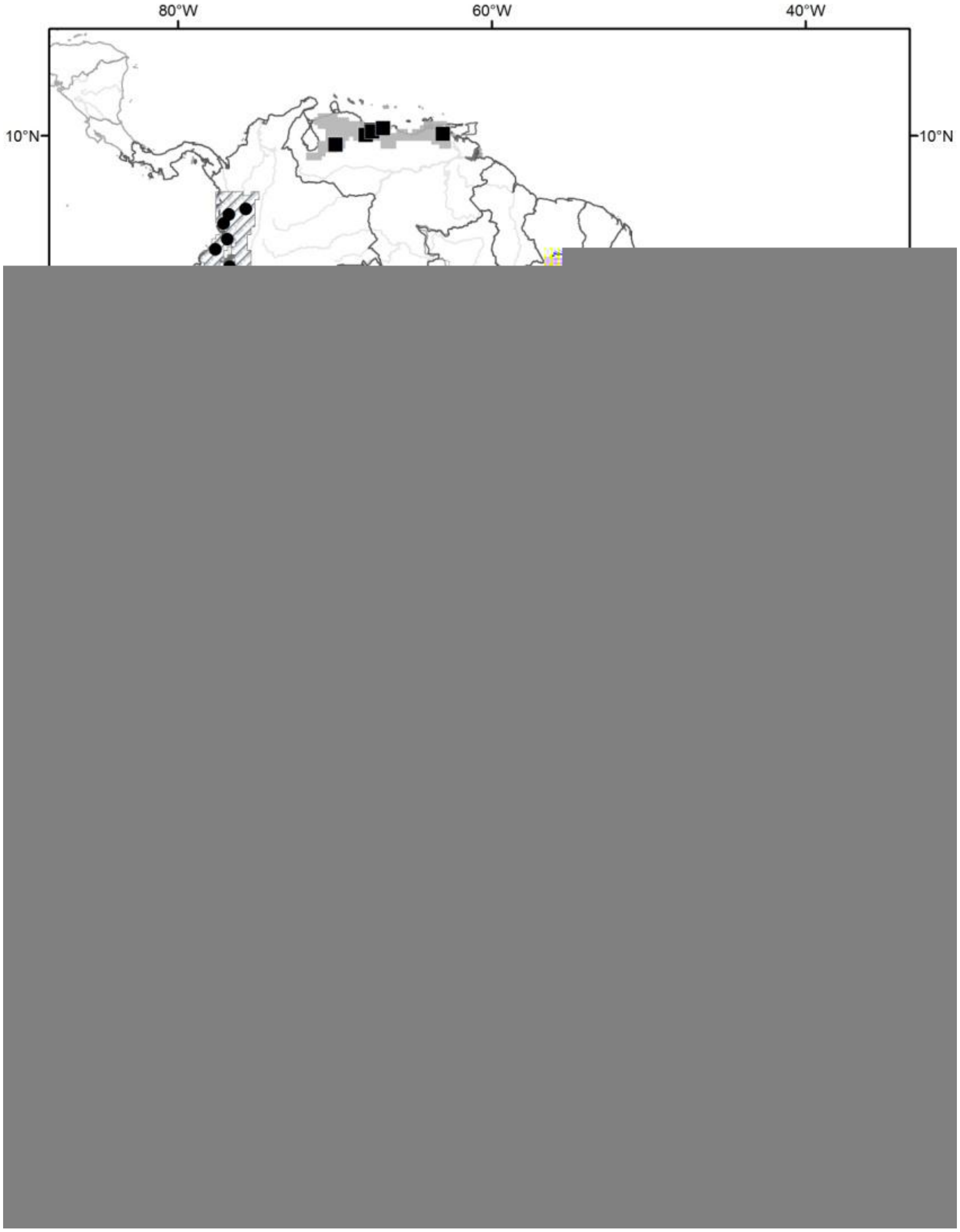

Figura 5- Mapa da distribuição das espécies *Bothrocophias campbelli*, *B. myersi* e *Bothrops venezuelensis*, mostrando pontos de ocorrência e área de distribuição potencial, de acordo com modelos de distribuição das espécies.

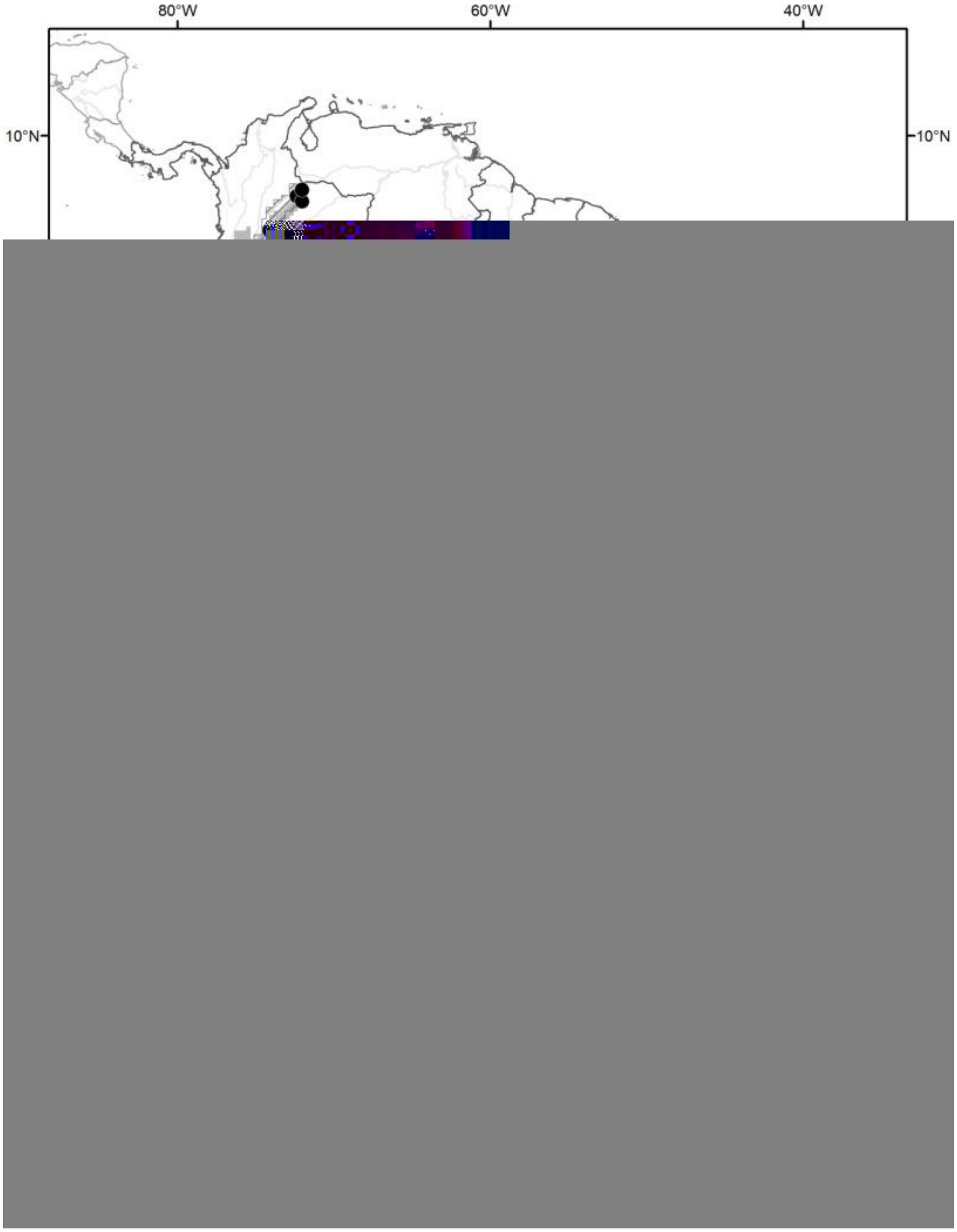

Figura 6- Mapa da distribuição das espécies *Bothrocophias hyoprora* e *B. microphthalmus,* mostrando pontos de ocorrência e área de distribuição potencial, de acordo com modelos de distribuição das espécies.

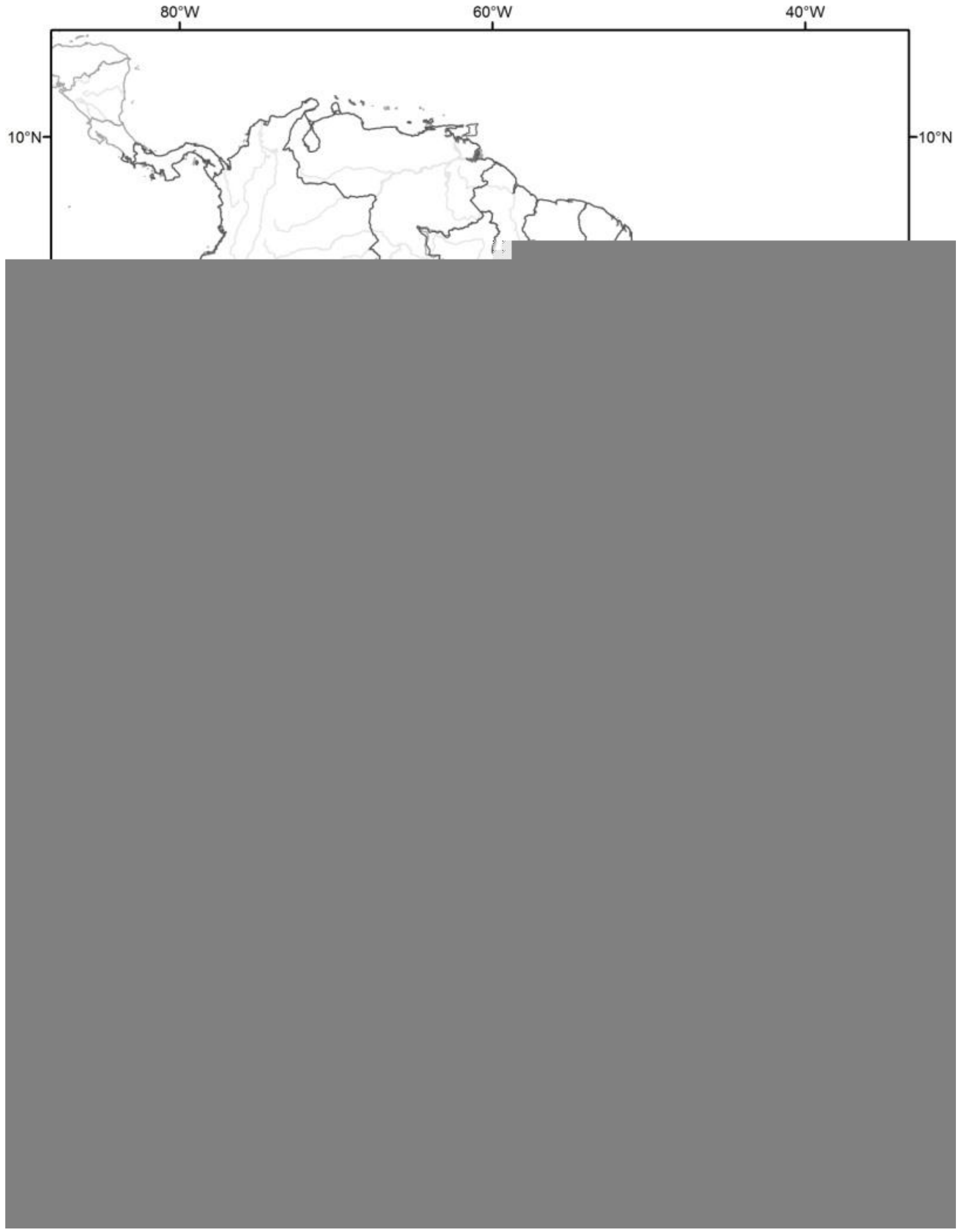

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Figura 7- Mapa da distribuição das espécies *Bothrops alcatraz, B. insularis* e *B. jararaca,* mostrando pontos de ocorrência e área de distribuição potencial, de acordo com modelos de distribuição das espécies.

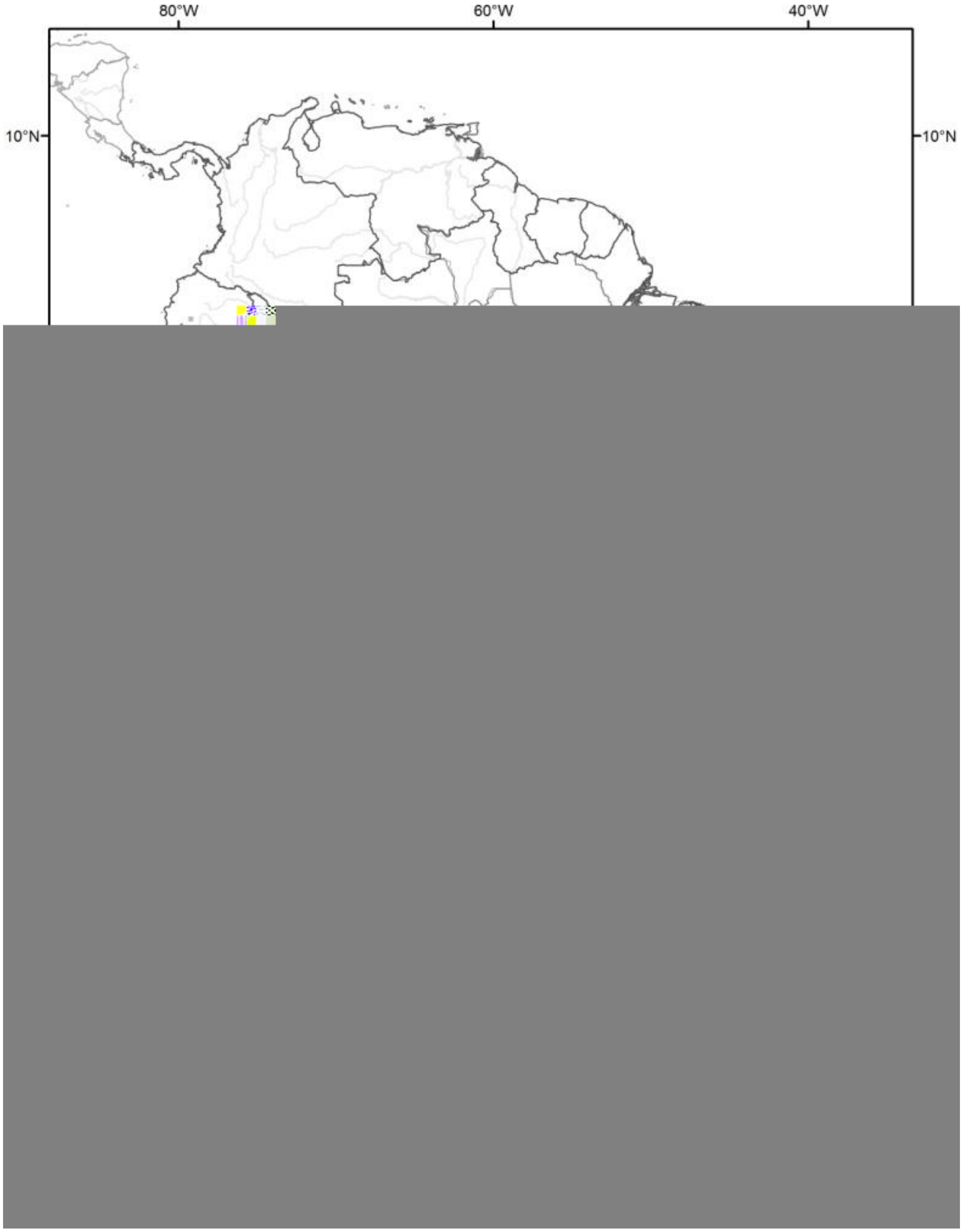

Figura 8- Mapa da distribuição das espécies *Bothrops diporus* e *B. pauloensis,* mostrando pontos de ocorrência e área de distribuição potencial, de acordo com model os de distribuição das espécies.

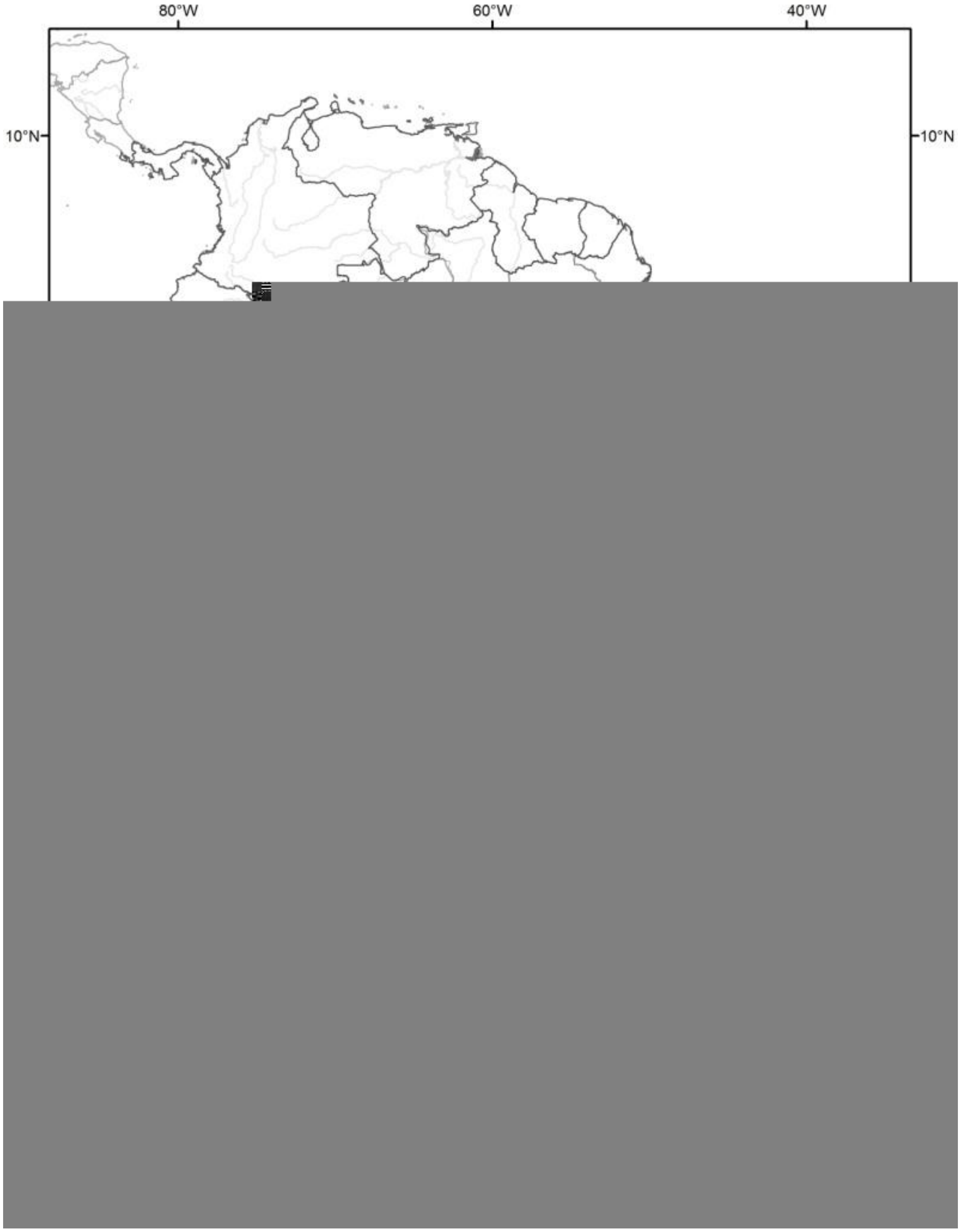

Figura 9- Mapa da distribuição das espécies *Bothrops erythromelas*, *B. neuwiedi* e *B. sanctaecrucis,* mostrando pontos de ocorrência e área de distribuição potencial, de acordo com modelos de distribuição das espécies.

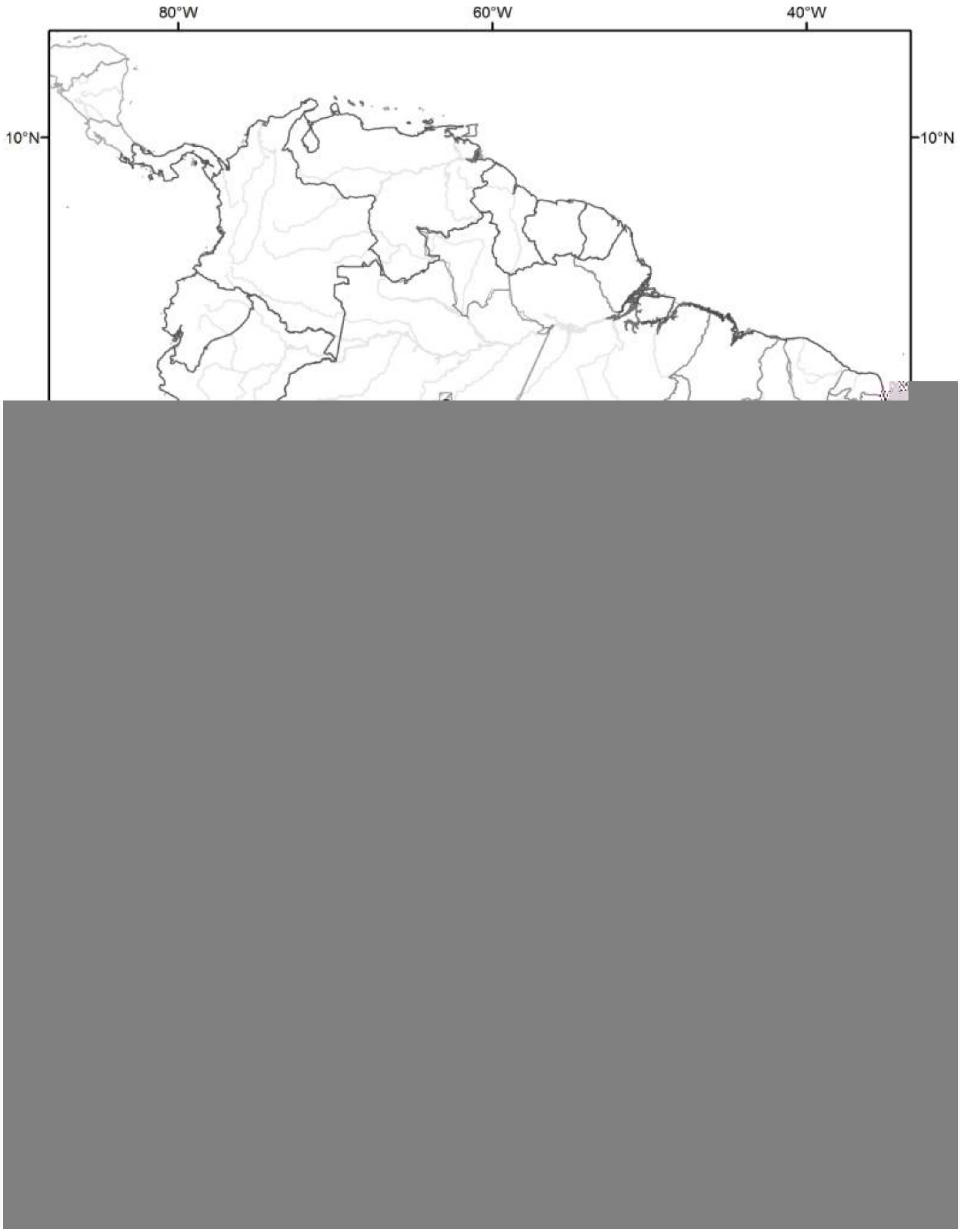

Figura 10- Mapa da distribuição das espécies *Bothrops mattogrossensis* e *B. alternatus,* mostrando pontos de ocorrência e área de distribuição potencial, de acordo com modelos de distribuição das espécies.

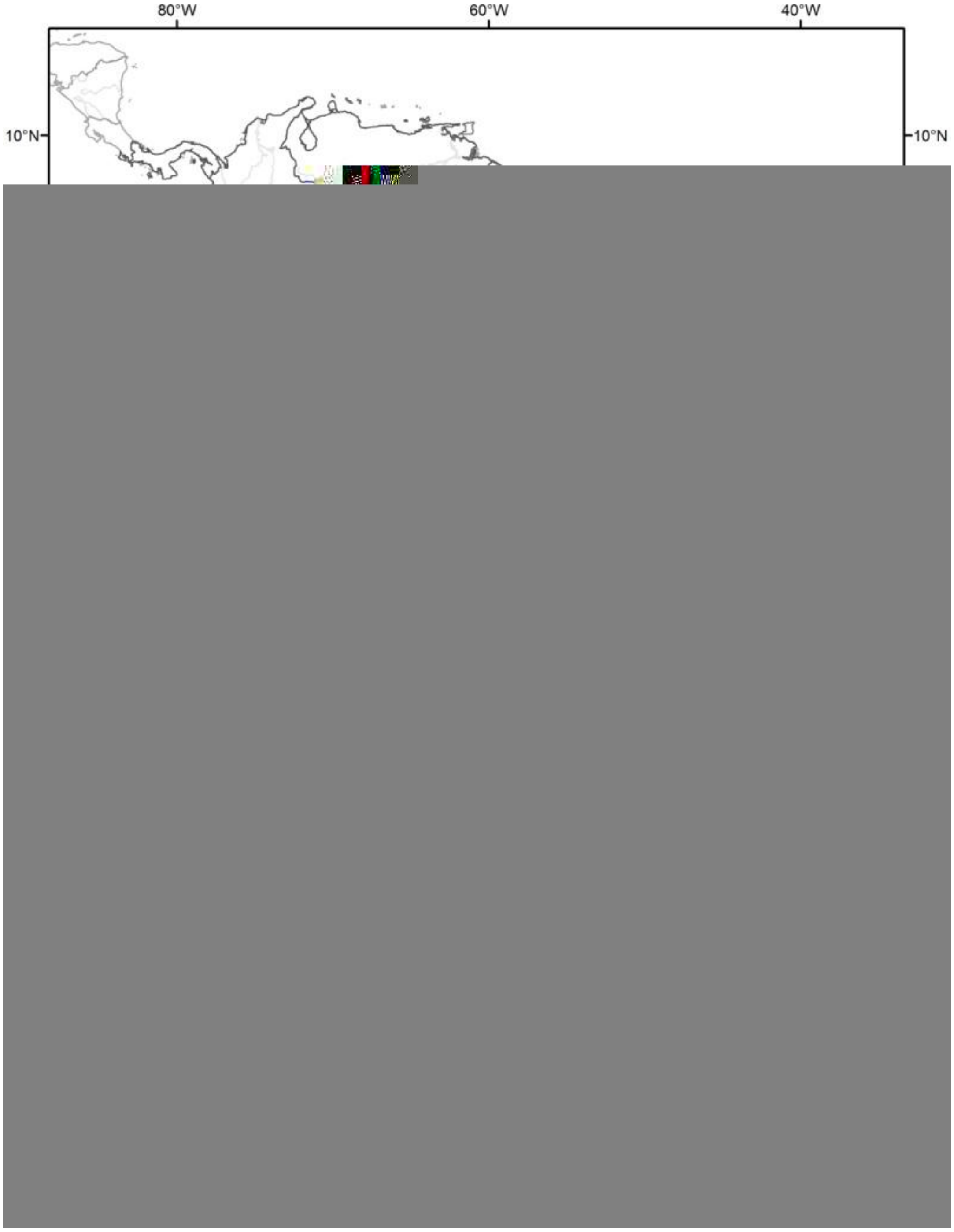

Figura 11- Mapa da distribuição das espécies *Bothrocophias andianus* e *Bothrops pictus,* mostrando pontos de ocorrência e área de distribuição potencial, de acordo com modelos de distribuição das espécies.

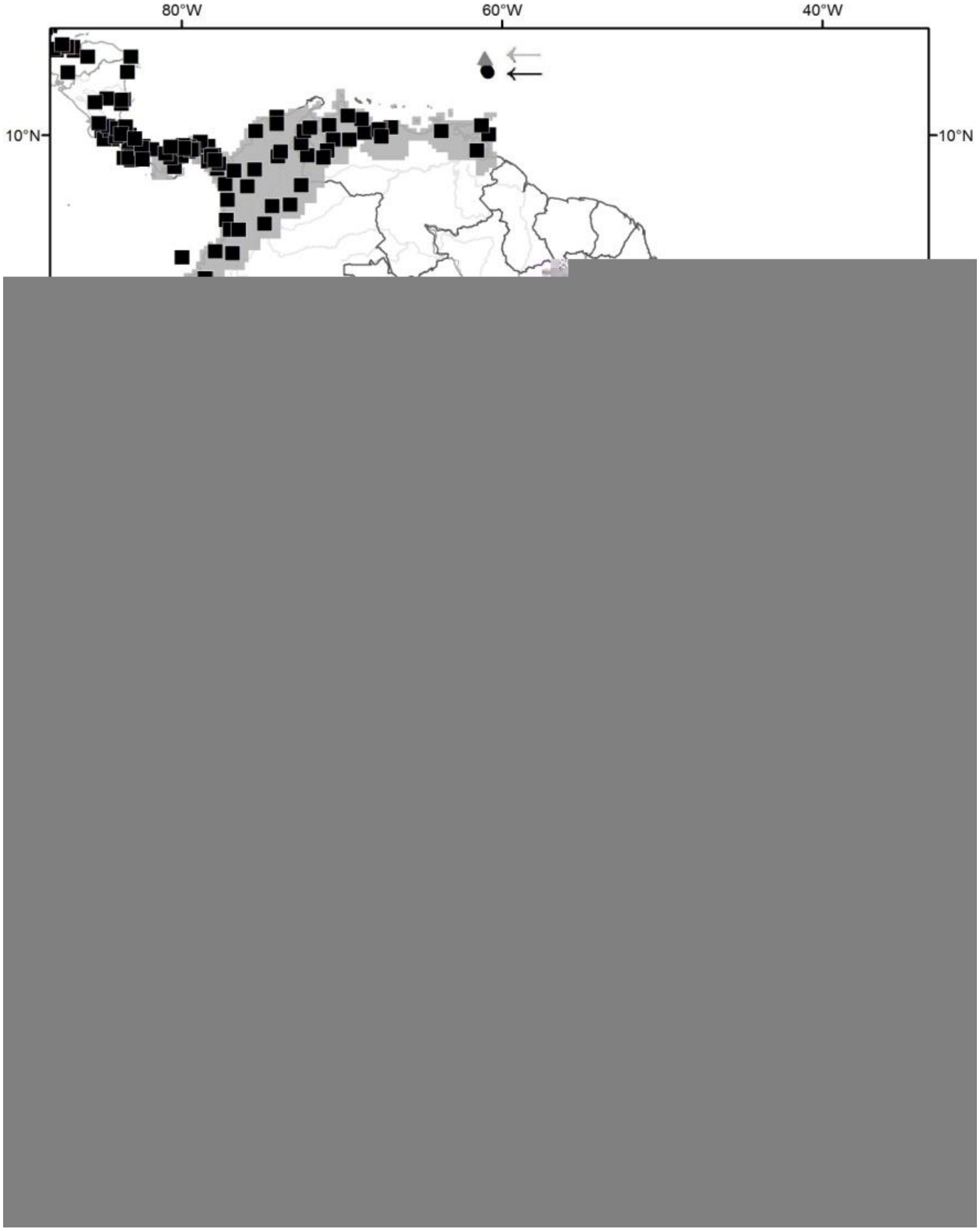

Figura 12- Mapa da distribuição das espécies *Bothrops asper*, *B. caribbaeus* e *B. lanceolatus*, mostrando pontos de ocorrência e área de distribuição potencial, de acordo com modelos de distribuição das espécies.

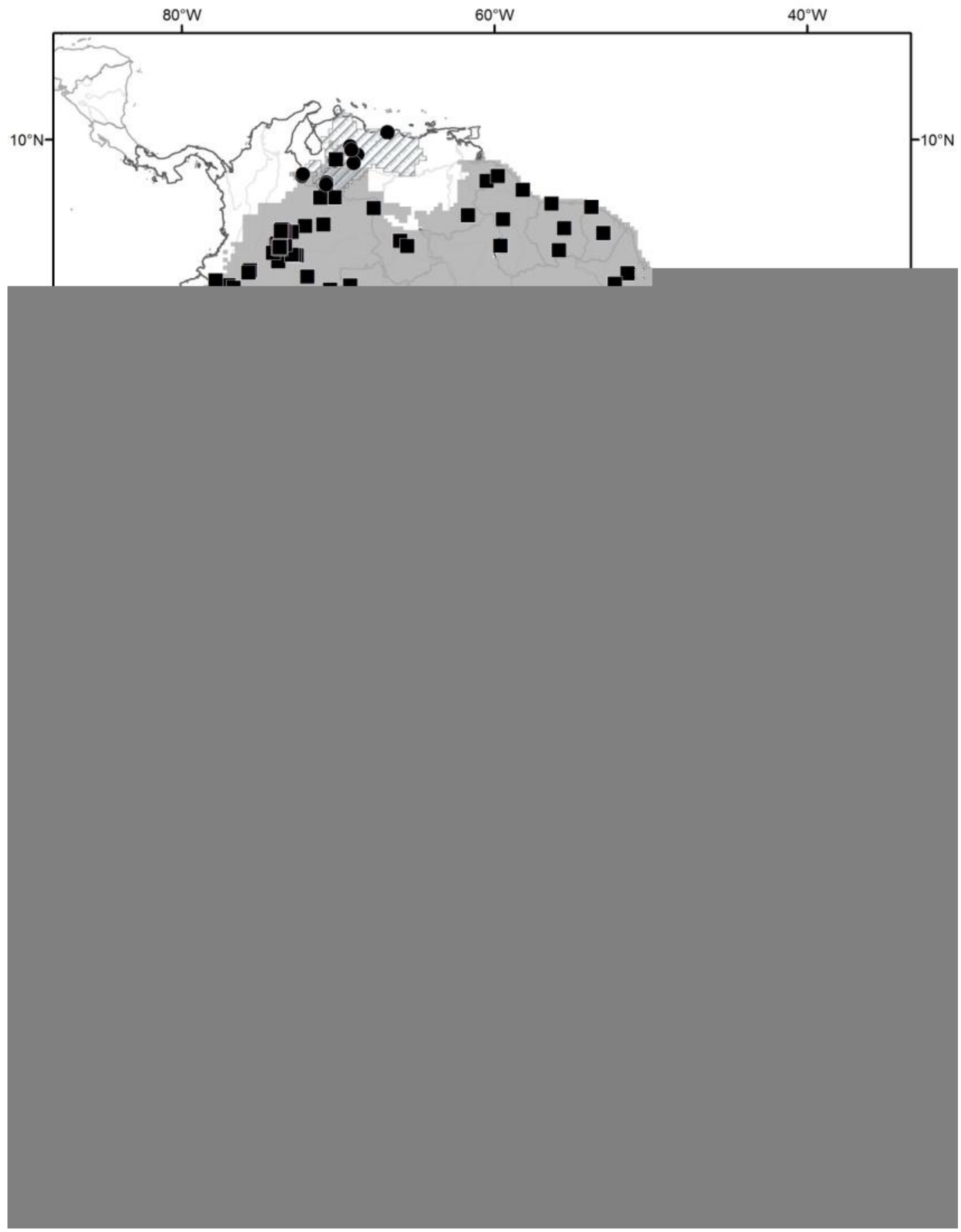

Figura 13- Mapa da distribuição das espécies *Bothrops atrox, B. isabelae* e *B. leucurus,* mostrando pontos de ocorrência e área de distribuição potencial, de acordo com modelos de distribuição das espécies.

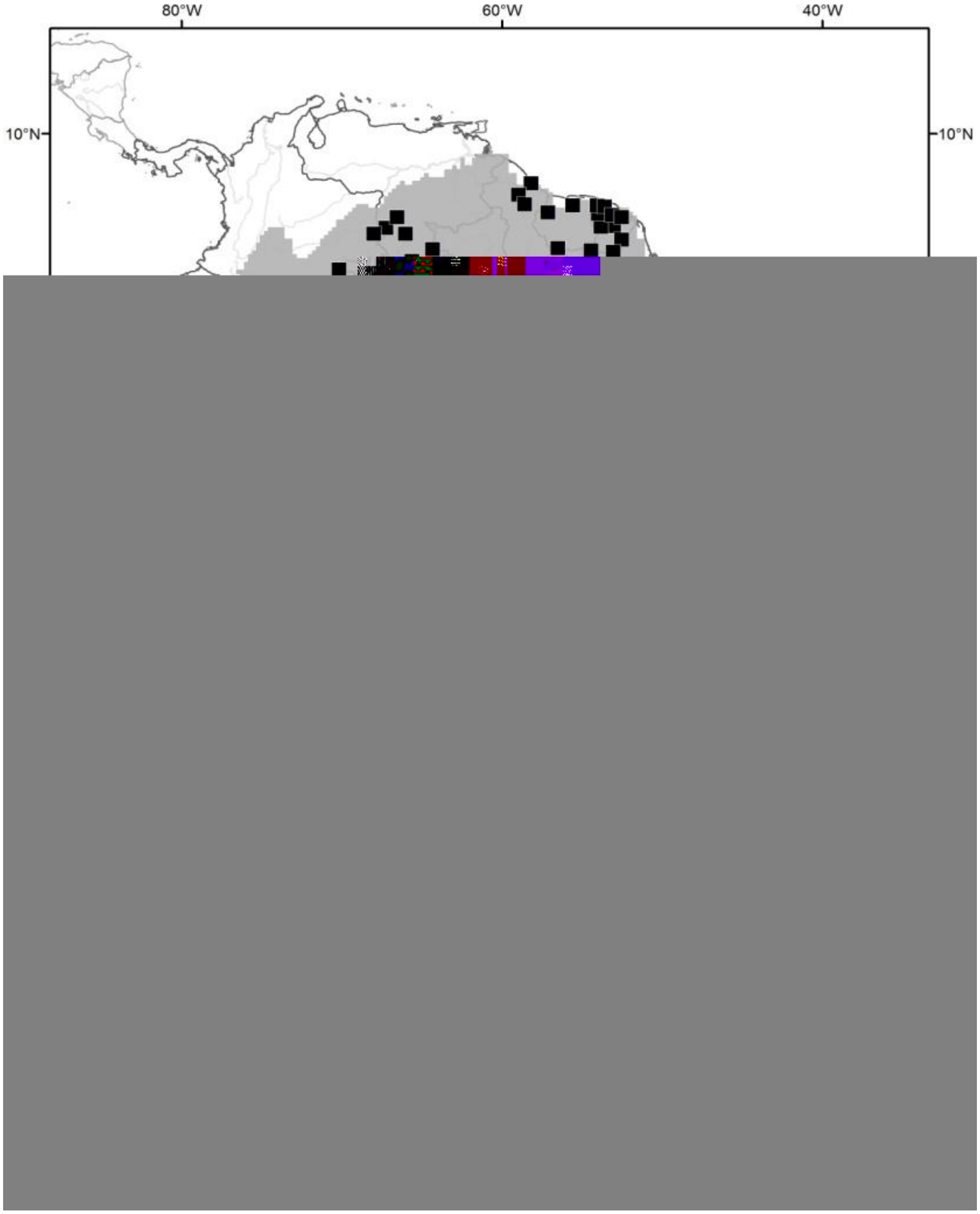

Figura 14- Mapa da distribuição das espécies *Bothrops barnetti, B. brazili* e *B. jararacussu*, mostrando pontos de ocorrência e área de distribuição potencial, de acordo com modelos de distribuição das espécies.

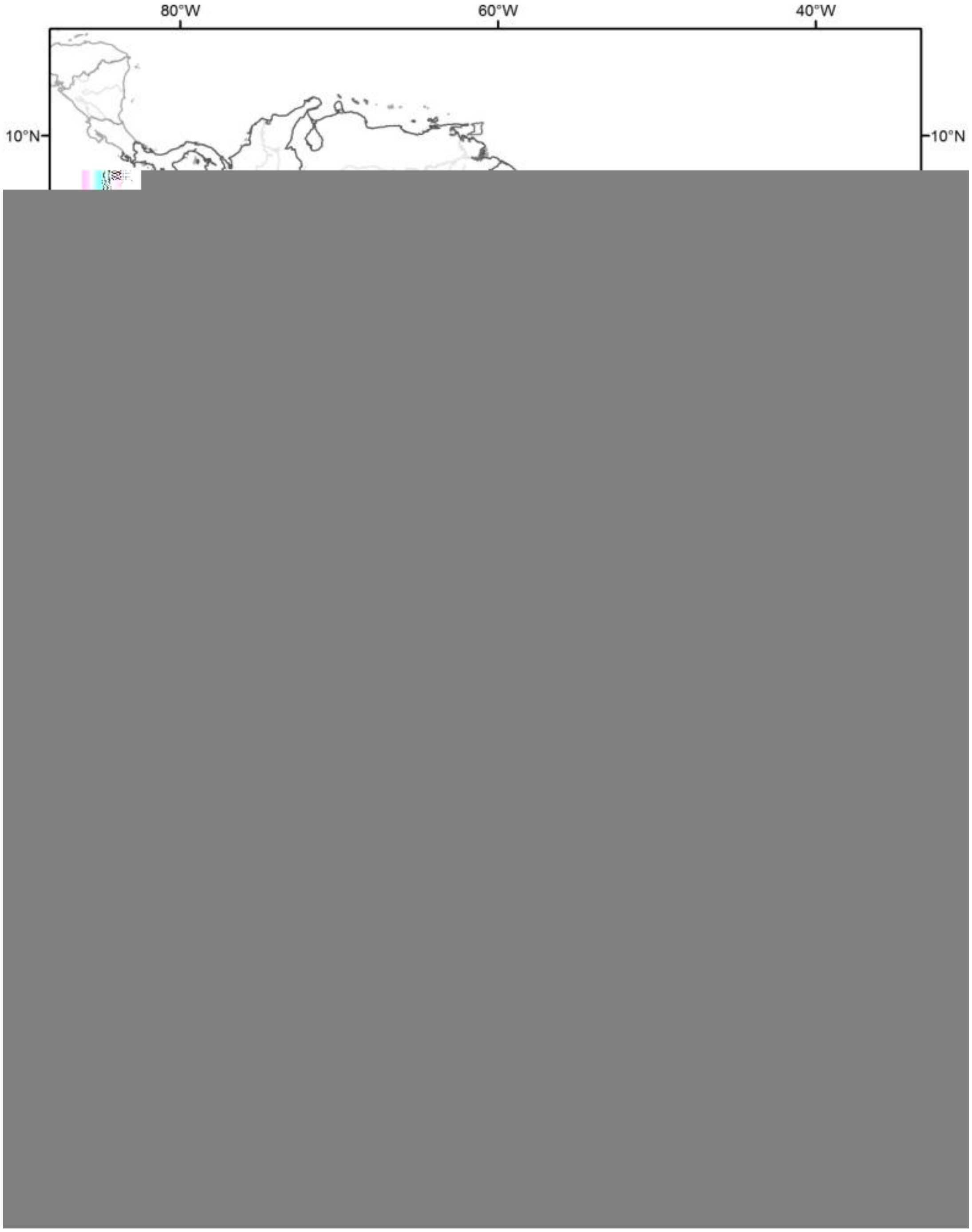

Figura 15- Mapa da distribuição das espécies *Bothrops marajoensis* e *B. moojeni,* mostrando pontos de ocorrência e área de distribuição potencial, de acordo com modelos de distribuição das espécies.

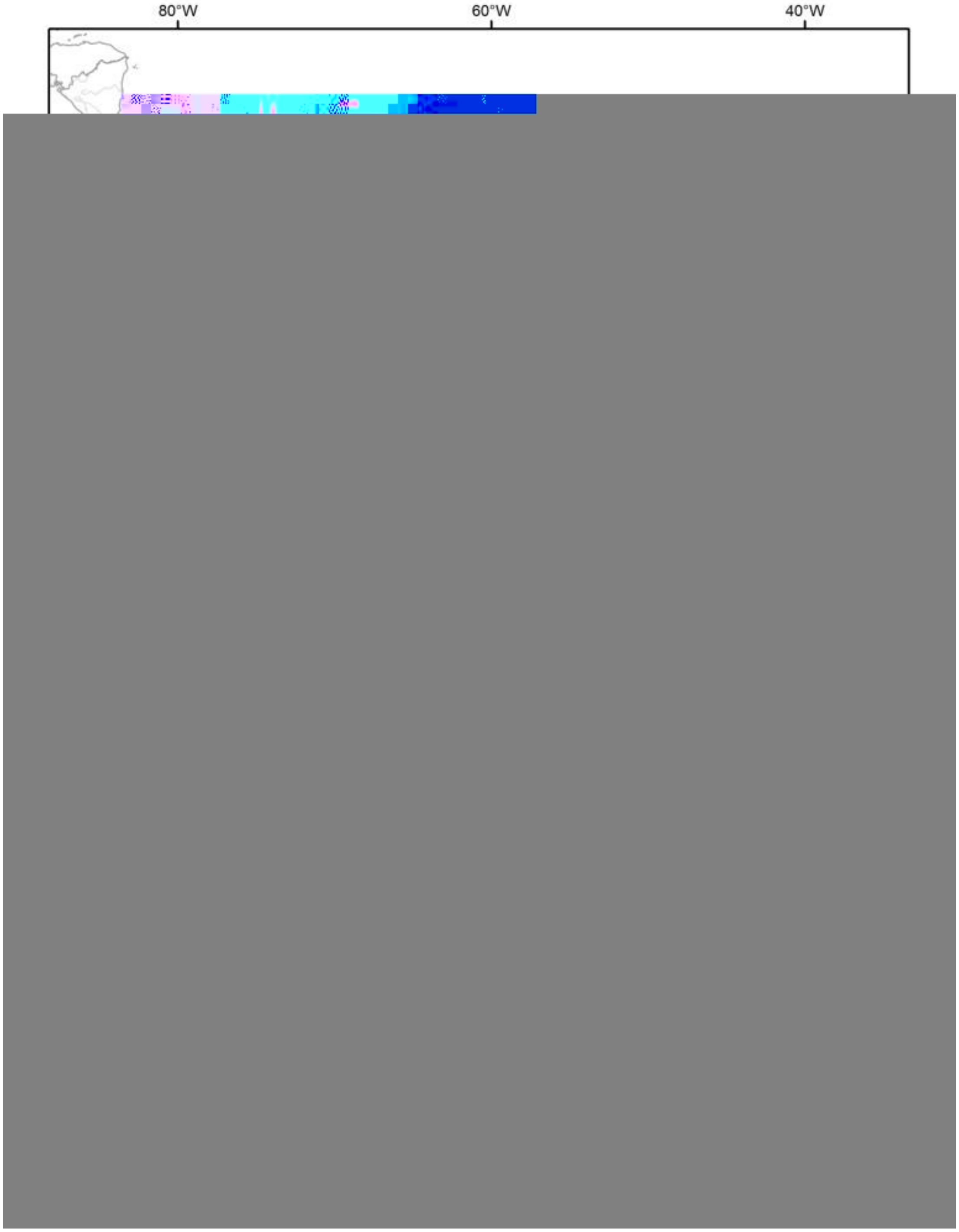

Figura 16- Mapa da distribuição das espécies *Bothrops osbornei* e *B. punctatus*, mostrando pontos de ocorrência e área de distribuição potencial, de acordo com modelos de distribuição das espécies.

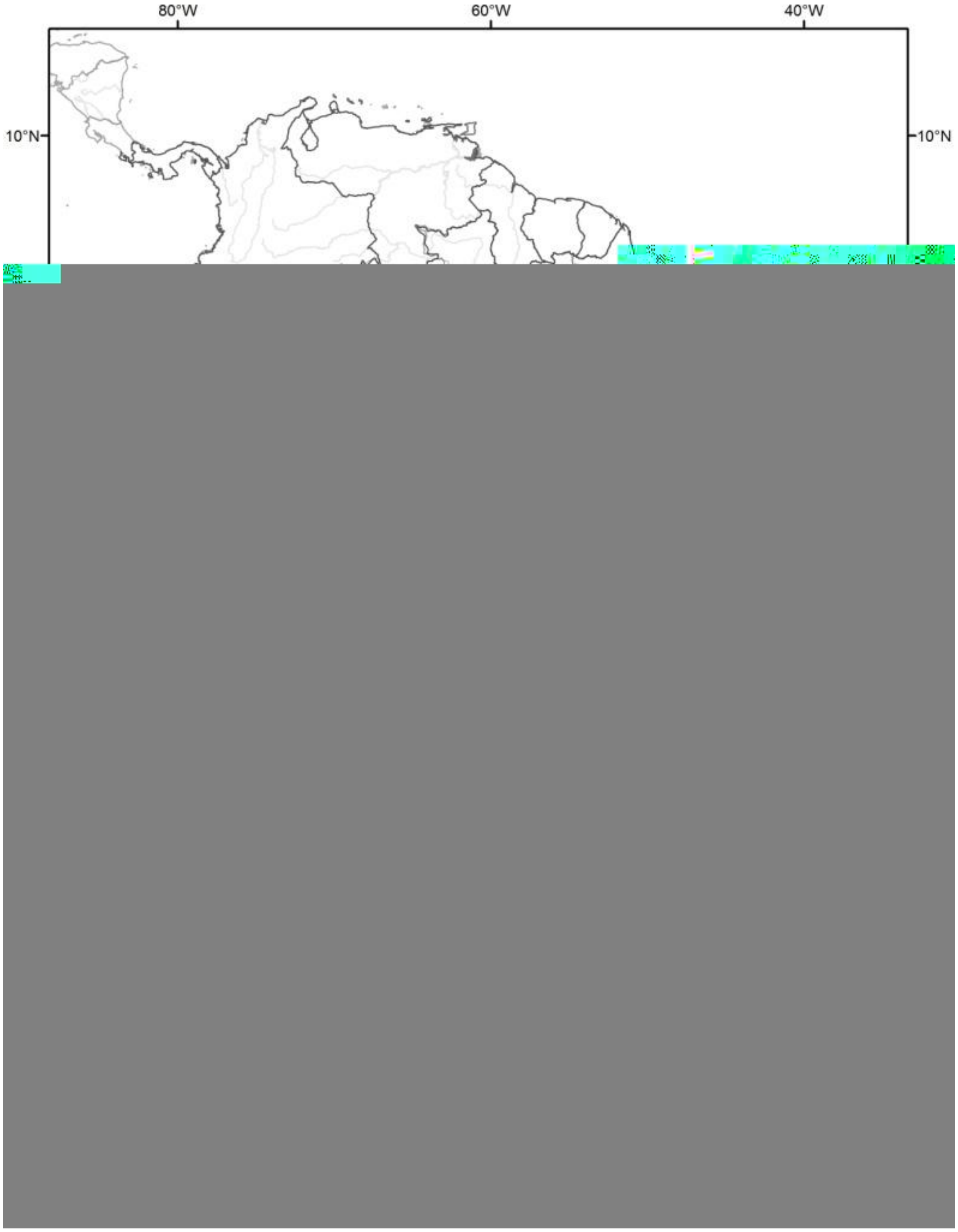

Figura 17- Mapa da distribuição das espécies *Bothrops ammodytoides, B. cotiara* e *B. fonsecai*, mostrando pontos de ocorrência e área de distribuição potencial, de acordo com modelos de distribuição das espécies.

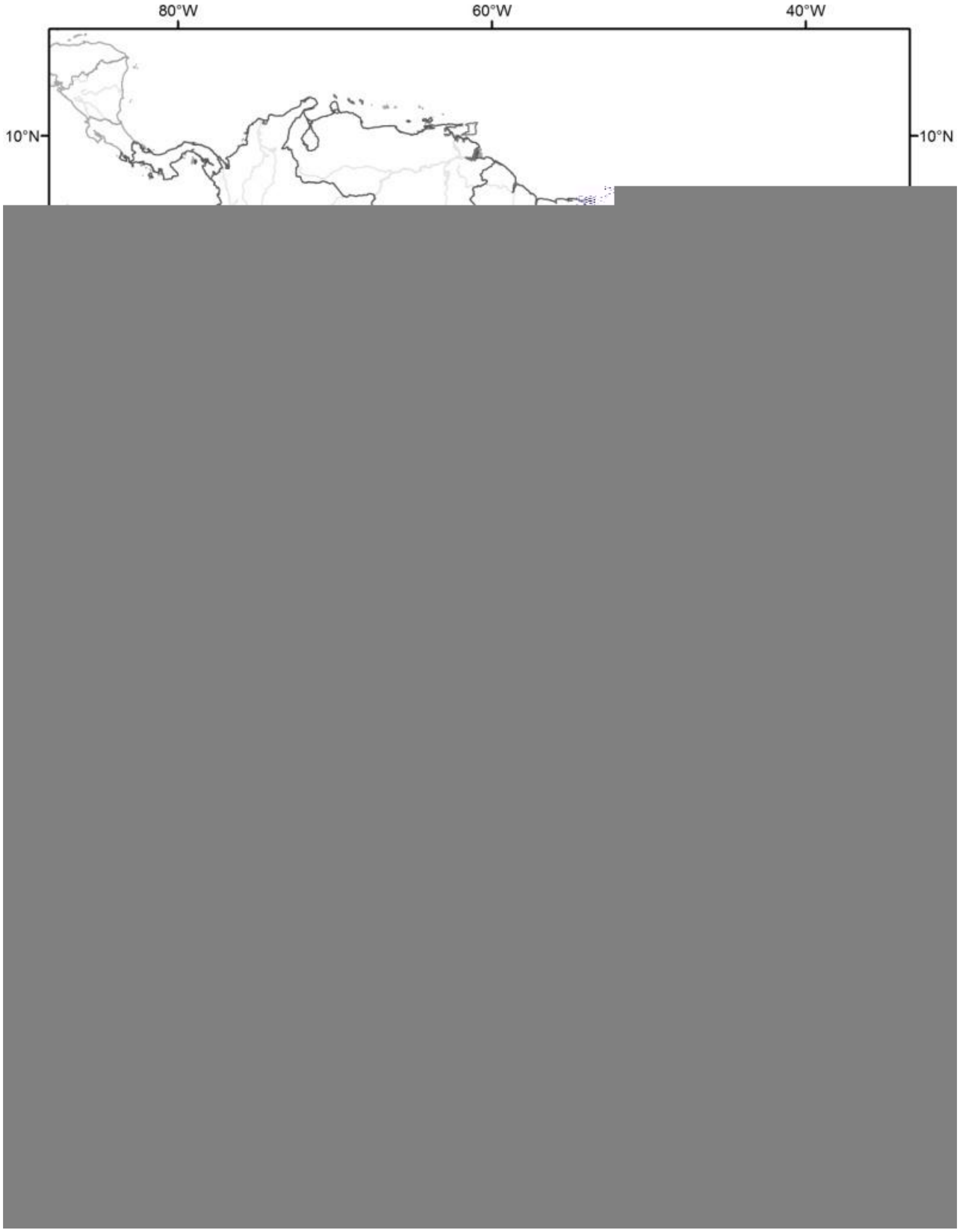

Figura 18- Mapa da distribuição das espécies *Bothrops itapetiningae* e *B. jonathani*, mostrando pontos de ocorrência e área de distribuição potencial, de acordo com modelos de distribuição das espécies.