MARÍLIA PALUMBO GAIARSA

Definindo prioridades de conservação em grupos monofiléticos: um estudo de caso com uma linhagem de serpentes neotropicais

Setting conservation priorities within monophyletic groups: a case study with a Neotropical snake lineage

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... “You have to trust in something - your gut, destiny, life, karma, whatever - because believing that the dots will connect down the road will give you the confidence to follow **your heart**, even when it leads you off the well-worn path, and that will make all the difference.”

... “If you haven't found it yet, keep looking, and don't settle. As with all matters of the heart, you'll know when you find it, and like any great relationship it just gets better and better as the years roll on. So keep looking. **Don't settle**”.

... “Your time is limited, so don't be trapped by dogma, which is living with the results of other people's thinking. Don't let the noise of others' opinions drown out your own inner voice, heart and intuition. They somehow already know what you truly want to become. **Everything else is secondary**”.

“Stay hungry, stay foolish”

Steve Jobs

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RESUMO

Devido à atual crise da biodiversidade e à falta de recursos destinados à conservação, as espécies ameaçadas devem ser diferenciadas umas das outras para que aquelas sob maior risco possam receber atenção antes. Dentro de uma mesma linhagem, as espécies terão diferentes importâncias relativas para a conservação da diversidade evolutiva e ecológica, atual e passada. Propomos aqui uma nova abordagem ao criar um índice de priorização (PI) que possa ser utilizado em grupos monofiléticos, e que considere conjuntamente características de história de vida, singularidade ecológica e grau de distinção filogenética. Nossa linhagem modelo foi a tribo Pseudoboini, um grupo de serpentes neotropicais para o qual compilamos informações disponíveis na literatura, informações fornecidas por outros pesquisadores e dados originais coletados em coleções científicas. Para criar o PI combinamos três diferentes índices: vulnerabilidade à extinção (IVE), singularidade ecológica (EO) e grau de distinção filogenética (PD). O IVE foi calculado a partir da média do ranqueamento das espécies de acordo com sete fatores que afetam a sobrevivência das populações de serpentes (tamanho corporal, fecundidade média, amplitude alimentar, distribuição geográfica, amplitude de utilização de habitats, amplitude altitudinal e habilidade de persistir em ambientes alterados). O EO considera a distância absoluta do fenótipo de uma determinada espécie em relação ao fenótipo mais comum na linhagem (calculado para tamanho corporal, fecundidade média, amplitude alimentar e amplitude de utilização de habitats). Já o PD considera o quão relictual uma determinada espécie é. Houve uma grande variação em relação aos dados biológicos dos pseudoboíneos. O IVE foi uniformemente distribuído por toda a Tribo e *Oxyrhopus petola* apresentou o menor IVE. As espécies com maior IVE foram: *Clelia langeri*, *Pseudoboa martinsi*, *Siphlophis compressus*, *Clelia hussami* e *Clelia scytalina*. *Phimophis iglesi*, que parece ser a espécie irmã de todos os pseudo-boíneos, apresentou o maior PD. Exceto por *Clelia errabunda*, *Oxyrhopus dolia*, e *Phimophis chui*, a maior parte das espécies apresentou valores baixos de EO. O menor PI foi apresentado pela espécie *Oxyrhopus melanogenys* e encontramos os maiores valores de PI para as espécies *Phimophis iglesi*, *Clelia hussami*, *P. chui*, *C. langeri*, e *C. scytalina*. Apenas duas espécies que apresentaram altos valores de IVE neste estudo estão presentes em listas vermelhas (*Clelia langeri* e *Siphlophis longicaudatus*), além de outras cinco espécies de pseudo-boíneos. Desta forma, futuras avaliações de risco de extinção devem prestar especial atenção a todas estas espécies. Além disso, espécies que apresentaram altos valores de IVE também apresentaram alto grau de distinção filogenética, o que reforça a necessidade de conservação de espécies mais relictuais. Representantes de quase todos os clados dos pseudo-boíneos estão presentes entre as 10 espécies com maiores valores de PI, maximizando a diversidade filogenética dos táxons priorizados. Apesar de não ser possível comparar valores obtidos em estudos com diferentes linhagens (os índices gerados são clado-específicos), quando esta abordagem for aplicada a grupos mais inclusivos de organismos (e.g., famílias e subfamílias), poderá haver uma melhora na qualidade dos processos de priorização.

Palavras-chave: Pseudoboini, índice de priorização, singularidade ecológica, distinção filogenética.

ABSTRACT

Given the present biodiversity crisis and the lack of available resources, threatened species must be differentiated from each other so that those at higher risk can be attended first. Within lineages, species differ in their need for conservation action and in their relative importance for conserving current and ancient ecological and evolutionary diversity. We here propose a new approach to create a priority index (PI) for species within monophyletic groups, by combining life history traits, ecological singularity, and phylogenetic distinctness. Our model lineage was the tribe Pseudoboini, a group of Neotropical snakes for which we gathered literature data, unpublished observations provided by other researchers, as well as original data from museums specimens. To create the PI, we combined three different indices: vulnerability to extinction (IVE), ecological oddity (EO) and phylogenetic distinctness (PD). IVE was calculated by ranking species according to a combination of six factors known to affect snake population survival (body size, mean fecundity, dietary breadth, geographic distribution, altitudinal range, and ability to persist in altered habitats). Ecological oddity, which takes into account the distance of a given trait of a given species in relation to the lineage mean for that trait, was calculated for four characters (body size, mean fecundity, habitat breadth, and dietary breadth), and PD takes into account how relictual a given species is. There was a great amount of variation in the biological variables among pseudoboines. IVE was evenly distributed across the Tribe. *Oxyrhopus petola* presented the lowest IVE and *Clelia langeri* the highest. Besides the latter, five additional species showed high IVEs: *Pseudoboa serrana*, *Clelia scytalina*, *Clelia hussami*, *Siphlophis compressus*, and *Pseudoboa martinsi*. *Phimophis iglesi*, which seems to be the sister species of all pseudoboines, showed the highest PD. Except for *Clelia errabunda*, *Oxyrhopus doliatus*, and *Phimophis chui*, most species presented low EO values. The lowest PI was obtained for *Oxyrhopus melanogenys* and the highest for *Phimophis iglesi*. Besides the latter, *Clelia hussami*, *P. chui*, *C. langeri*, and *C. scytalina* also presented high PIs. Only two species with high IVE in our study are included in red lists (*Clelia langeri* and *Siphlophis longicaudatus*), and five additional species appeared with high IVEs; thus, all these species should receive special attention in future assessments of extinction risk. Species with higher vulnerability to extinction were also those with higher phylogenetic distinctness, reinforcing the importance of conserving relictual species. Representatives from almost all clades within the pseudoboines are listed amongst the ten higher PI values, what maximizes the phylogenetic diversity of the prioritized taxa. Although it is not possible to compare values obtained in studies with different lineages (the indices generated are clade-specific), when extended to more inclusive lineages within a group of organisms (e.g., subfamilies, families) this approach might enhance the quality of future prioritization processes.

Keywords: Pseudoboini, priority index, ecological oddity, phylogenetic distinctness.

INTRODUÇÃO GERAL

Um dos principais desafios para a conservação da biodiversidade consiste em prever o declínio de uma espécie com base em sua vulnerabilidade à extinção, buscando aumentar suas perspectivas de sobrevivência (Caughley 1994, Regan et al. 2004). A partir de informações sobre a biologia das espécies, bem como das ameaças às quais estão sujeitas, são criadas as listas de espécies ameaçadas, cujos objetivos incluem chamar a atenção para espécies com maior risco de extinção, ressaltar os fatores que podem levar as populações ao declínio e fornecer subsídios para direcionar programas de conservação (Mace & Lande 1991, Collar 1996).

Devido à atual crise da biodiversidade e à falta de recursos destinados à conservação (Brooks et al. 2002), as espécies ameaçadas devem ser diferenciadas umas das outras para que aquelas sob maior risco possam receber atenção antes. Desta forma, é necessário priorizar os esforços de conservação (Pimm et al. 1998, Wilson et al. 2006), o que Vane-Wright e colaboradores (1991) chamaram de “a agonia da escolha” (“agony of choice”). A partir de informações sobre níveis de ameaça, endemismo e riqueza de espécies já foram identificadas algumas áreas prioritárias para a conservação (e.g. *Hotspots* da Biodiversidade, Mittermeier et al. 1998, Myers et al. 2000; áreas prioritárias para conservação, MMA 2007), e há uma crescente preocupação em relação às espécies (e.g. Stattersfield et al. 1998, Redding et al. 2010, Machado et al. 2008).

As espécies enfrentam diferentes riscos de extinção em vista de seus atributos, tais como distribuição geográfica, necessidades em relação à qualidade de seu habitat e tamanho populacional. A destruição dos habitats é a principal causa da extinção de espécies (Pimm et al. 1995, IUCN 2009), mas a vulnerabilidade destas à extinção pode também estar relacionada a características próprias de sua história natural (e.g., McKinney 1997, Purvis et al. 2000). Os fatores intrínsecos mais frequentemente considerados incluem especializações ecológicas (e.g., em dieta ou habitats; McKinney 1997), distribuição geográfica restrita (Rabinowitz et al. 1986, Dodd 1993, Purvis et al. 2000, Cardillo et al. 2008) e atributos de história de vida que diminuem a taxa com a qual novos indivíduos são recrutados nas populações (e.g., maturação sexual tardia, pequeno tamanho da ninhada, grande tamanho do corpo, entre outros; para revisões veja McKinney 1997, Purvis et al. 2000).

O sistema de classificação de vulnerabilidade à extinção de espécies mais utilizado é o da IUCN. Este sistema se baseia em regras e utiliza critérios quantitativos que têm

como base princípios da biologia de populações, como tamanho e crescimento populacional, qualidade do habitat e estimativas do risco de extinção em tempo definido (IUCN 2001). Além do sistema da IUCN, índices baseados em pontuações criados com base em características intrínsecas e extrínsecas que afetam a vulnerabilidade à extinção das espécies também podem ser utilizados para avaliar o risco à extinção de uma espécie. A partir de pontuações atribuídas a cada espécie podem ser criados rankings de prioridade para a conservação (e.g., Millsap et al. 1990, Filippi & Luiselli 2000, França & Araújo 2006, Santos et al. 2007). Tais rankings podem ser úteis pois além de permitir que os táxons sejam comparados de forma mais objetiva (Millsap et al. 1990, Todd & Burgman 1998), as variáveis podem ser facilmente definidas e os resultados são fáceis de interpretar (Beissinger et al. 2000).

Quando consideramos espécies de uma mesma linhagem, podemos quantificar a biodiversidade a partir da diversidade de caracteres (Faith 1992, Purvis & Hector 2000), por meio de sua “singularidade ecológica” (*ecological oddity*), sendo o grau de singularidade definido como a distância absoluta do fenótipo de uma determinada espécie em relação ao fenótipo mais comum na linhagem (Redding et al. 2010). Desta forma, quanto mais distinta uma espécie é em relação às outras espécies de uma linhagem, maior sua singularidade ecológica.

Já foi também proposto que o cálculo da biodiversidade (May 1990) deveria considerar a representação da história evolutiva de um grupo (Faith 1992, 2002), supondo que esta medida representaria a diversidade de características relictuais. Assim, o grau de distinção de uma espécie seria inversamente proporcional à sua proximidade às demais espécies de uma linhagem e ao número relativo de espécies próximas (Owens & Bennett 2000; para diferentes abordagens veja May 1990, Vane-Wright et al. 1991, Heard & Mooers 2000, Mace et al. 2003, Forest et al. 2007, Steel et al. 2007). O grau de “distinção filogenética” é uma das métricas desenvolvidas para quantificar a história evolutiva de um grupo (PD do inglês *phylogenetic distinctness*; May 1990, Vane-Wright et al. 1991): quanto mais relictual é uma espécie, maior seu PD.

Em virtude das serpentes serem pouco evidentes na natureza (Santos et al. 2006) e da escassez de estudos populacionais de longo prazo para a grande maioria das espécies (Parker & Plummer 1987), seus declínios são difíceis de serem observados, tornando métodos de determinação do estado de conservação e estratégias de manejo difíceis de serem colocados em prática (Dodd 1993). Já foram identificadas algumas características que tendem a tornar as serpentes mais vulneráveis à extinção. Por exemplo, espécies

que apresentam caça por espreita e ausência de combate entre machos (Reed & Shine 2002, Webb et al. 2002), espécies com distribuições geográficas restritas (Filippi & Luiselli 2000, França & Araújo 2006, Reading et al. 2010), espécies visadas pelo tráfico ilegal (Filippi & Luiselli 2000) e aquelas com algum grau de especialização ecológica e/ou baixa fecundidade (Foufopoulos & Ives 1999, Santos et al. 2007, Segura et al. 2007). Alguns autores sugerem ainda que os répteis seriam mais sensíveis a mudanças no habitat quando comparados a outros grupos de vertebrados (Reed & Shine 2002, Santos et al. 2006, 2007).

OBJETIVOS

Em virtude das diferenças morfológicas e de história de vida entre as espécies de uma mesma linhagem, esperamos que estas difiram em relação às ameaças às quais estão sujeitas, bem como em sua vulnerabilidade à extinção, sua singularidade ecológica e distinção filogenética. Assim, dentro de uma mesma linhagem, certamente existem diferenças na necessidade de conservação das diferentes espécies. De forma semelhante, diferentes espécies de uma mesma linhagem terão diferentes importâncias relativas para a conservação da diversidade evolutiva e ecológica, atual e passada. Esta dissertação é composta por um artigo a ser submetido a uma revista da área de conservação no qual criamos um índice de priorização para ser utilizado dentro de grupos monofiléticos, considerando conjuntamente a vulnerabilidade à extinção das espécies, sua singularidade ecológica e seu grau de distinção filogenética. Para tanto, utilizamos uma linhagem neotropical de serpentes (a tribo Pseudoboini) que apresenta grande diversidade biológica (ver abaixo). Esperamos que esta nova abordagem auxilie os esforços de conservação de grupos monofiléticos, diminuindo a “agonia da escolha” (Vane-Wright et al. 1991). Ao final da dissertação, apresentamos uma conclusão geral com as implicações dos resultados obtidos e direcionamentos para estudos futuros.

GRUPO DE ESTUDO

A tribo Pseudoboini (família Dipsadidae, subfamília Xenodontinae, *sensu* Zaher et al. 2009) é composta por serpentes de médio a grande porte (Pizzatto & Marques 2002, Scott Jr. et al. 2006) e compreende 47 espécies distribuídas em nove gêneros (*Boiruna*, *Clelia*, *Drepanoides*, *Mussurana*, *Oxyrhopus*, *Phimophis*, *Pseudoboa*, *Rhachidelus* e *Siphlophis*). Ocorre em grande parte dos neotrópicos, desde o México até a Argentina (Jenner & Downling 1985, Ferrarezi 1994, Uetz 2007), com 34 espécies no Brasil (SBH

2009). A maior parte dos pseudoboie se alimenta de lagartos e pequenos mamíferos, mas também existem espécies especialistas em diferentes itens alimentares (e.g., lagartos, *Siphlophis* spp., *Pseudoboa nigra*; ovos de squamata, *Drepanoides anomalus*; e ovos de aves, *Rhachidelus brazili*; Cunha & Nascimento 1978, 1993, Vitt & Vangilder 1983, Andrade & Silvano 1996, Martins & Oliveira, 1998, Prudente et al. 1998, Marques et al. 2001, Lema & Pinto 2002, Marques et al. 2005, Orofino et al. 2010, O.A.V. Marques, com. pess.). Além disso, a Tribo é composta por espécies predominantemente terrestres (e.g., *Clelia* spp. e *Boiruna* spp.), mas também existem espécies semi arborícolas (e.g., *Drepanoides anomalus* e *Siphlophis cervinus*) e semi fossoriais (e.g., *Phimophis* spp.; Cunha & Nascimento 1978, 1993, Martins & Oliveira 1998, Marques et al. 2001, Argôlo 2004, Marques et al. 2005). Esta diversidade ecológica encontrada no grupo faz com que este seja um bom modelo de estudo para o objetivo aqui proposto.

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Setting conservation priorities within monophyletic groups: a case study with a Neotropical snake lineage

Marília P. Gaiarsa^{1,2}, Laura R. V. Alencar¹, Paula H. Vadujo¹ and Marcio Martins¹

¹Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, Travessa 14, Cidade Universitária, São Paulo, SP, Brasil, CEP 05508-090

²Correspondence author: magaiarsa@yahoo.com.br

Introduction

Given the biodiversity crisis and the lack of available resources (Brooks et al. 2006) threatened species and areas must be differentiated from each other so that those at higher risk can be attended first. Thus, a major challenge for conservation biology is to set priorities for conservation efforts (Pimm et al. 2001, Wilson et al. 2006), what Vane-Wright et al. (1991) addressed as the “agony of choice”. Some areas have already been identified as priorities for conservation using levels of threat, endemism and species richness (e.g. Biodiversity Hotspots, Mittermeier et al. 1998, Myers et al. 2000), and there is a growing concern regarding species (e.g. Stattersfield et al. 1998, Redding et al. 2010).

The prediction of extinction risk helps to predict the outcomes of different future scenarios, facilitating conservation prioritization (Pimm et al. 1988, Primack 1993, Caughley 1994, Webb et al. 2002, Jones et al. 2003, Wilson et al. 2006). Habitat destruction is the main extinction promoting process (Pimm et al. 1995, IUCN 2009), but species vulnerability can also be affected by intrinsic traits such as ecological specializations (e.g., in diet and in habitat requirements; McKinney 1997), restricted geographic range (Rabinowitz et al. 1986, Dodd 1993, Purvis et al. 2000, Cardillo et al. 2008), and life histories attributes which decreases the rate at which new individuals are incorporated in the populations (e.g., late maturation, small litter size, large body size; for revisions see McKinney 1997, Purvis et al. 2000).

Regarding species, biodiversity can be quantified within a phenotypic framework (Owens & Bennet 2000). In this sense, character diversity is also an important measure of biodiversity (Faith 1992, Purvis & Hector 2000). One way to assess character

diversity is through ecological oddity, where *odd* is defined as “absolute distance from the average phenotype” (Redding et al. 2010). Therefore, the more distinct a species is in relation to the other species within a clade, the higher its ecological oddity. Redding et al. (2010) used this metrics to measure how the protection of evolutionarily distinct and globally endangered species (EDGE) would capture the biological diversity of a lineage.

It has also been proposed that the calculus of biodiversity (May 1990) should take into account the representation of evolutionary history (Faith 1992, 2002), assuming that such a measure would provide a representation of the ancient feature diversity of organisms. In essence, the relative distinctness of a taxon is inversely proportional to the relative number and closeness of its relatives (Owens & Bennett 2000; for a range of approaches see May 1990, Vane- Wright et al. 1991, Heard & Mooers 2000, Mace et al. 2003, Forest et al. 2007, Steel et al. 2007). Phylogenetic distinctiveness is one of the metrics developed to measure the evolutionary history of a group (PD; May 1990, Vane-Wright et al. 1991): the more relictual a species is, the higher its PD.

Species are expected to differ regarding the threats to which they are subject, their intrinsic vulnerability, their ecological oddity, and their phylogenetic distinctiveness. Thus, even within a lineage, species differ in their need for conservation action and in their relative importance for conserving current and ancient ecological and evolutionary diversity. Here we consider all these aspects in association as a way to set conservation priorities within a monophyletic group, a Neotropical clade of snakes. We hope this new approach can help to alleviate the “agony of choice” (Vane-Wright et al. 1991) when closely related species are assessed.

Methods

The lineage

The tribe Pseudoboini (family Dipsadidae, subfamily Xenodontinae, *sensu* Zaher et al. 2009) is composed by moderate-sized snakes (Pizzatto & Marques 2002, Scott Jr. et al. 2006) and encompasses 47 species and nine genera (*Boiruna*, *Clelia*, *Drepanoides*, *Mussurana*, *Oxyrhopus*, *Phimophis*, *Pseudoboa*, *Rhachidelus* and *Siphlophis*). The tribe is distributed throughout the Neotropics (Jenner & Downling 1985, Ferrarezi 1994), from Mexico to Argentina (Uetz 2007). Most pseudoboines feed on lizards and small mammals, but there are also species which are specialized in different prey types

(lizards, *Siphlophis* spp., *Pseudoboa nigra*; squamate eggs, *Drepanoides anomalus*; and bird eggs, *Rhachidelus brazili*; Cunha & Nascimento 1978, 1993, Vitt & Vangilder 1983, Martins & Oliveira 1998, Prudente et al. 1998, Marques et al. 2001, Lema & Pinto 2002, Marques et al. 2005, Orofino et al. 2010, O.A.V. Marques, pers. com.). Additionally, the tribe is composed predominantly by terrestrial species (e.g., *Clelia* spp. and *Boiruna* spp.), but there are also semi-arboreal (e.g., *Drepanoides anomalus* and *Siphlophis cervinus*) and semi-fossorial species (*Phimophis* spp.; Cunha & Nascimento 1978, 1993, Martins & Oliveira 1998, Marques et al. 2001, Argôlo 2004, Marques et al. 2005).

Data gathering

For each species we used literature data, unpublished observations provided by other researchers, as well as original data gathered from preserved specimens in collections. The following Brazilian scientific collections were visited: Instituto Butantan (IB, São Paulo, SP), Museu de História Natural Capão da Imbuia (MHNCI, Curitiba, PR), Museu de Zoologia da Universidade de São Paulo (MZUSP, São Paulo, SP), Museu Paraense Emílio Goeldi (GOELDI, Belém, PA), Pontifícia Universidade Católica do Rio Grande do Sul (PUCRS, Porto Alegre, RS), Coleção Herpetológica da Universidade de Brasília (CHUNB, Brasília, DF) and Universidade Federal do Mato Grosso (UFMT, Cuiabá, MT). We followed the taxonomy of Zaher et al. (2009) and made no distinction among subspecies. We were able to gather more than half of the explanatory variables for 34 (72%) of the 47 species of pseudoboines. For the species *Oxyrhopus erdisii*, *O. fitzingeri* and *O. marcapatae* we were unable to find any information (Tables 1 and 3).

Index of vulnerability to extinction

We adapted the method of Millsap et al. (1990) along with data on seven intrinsic factors known to affect snake population survival, to create an index of vulnerability to extinction (IVE; see below). We only included in the analysis species for which data was available for at least 50% of the factors. Factors were as follows:

1. *Body size* (BS): larger species tend to be more vulnerable to extinction since they tend to be less abundant, present greater home ranges, and have later sexual maturity (i.e., more long-living), characteristics that tend to decrease their ability to cope with negative interventions in their habitats (e.g., McKinney 1997, Foufopoulos &

Ives 1999, Purvis et al. 2000, Dulvy & Reynolds 2002; but see Luiselli et al. 2005). Because the tail length of snakes is affected by microhabitat use (Lillywhite & Henderson 1993, Martins et al. 2001, Pizzatto et al. 2007), and among pseudoboines there are both terrestrial (e.g. *Clelia clelia*) and semi-arboreal species (e.g. *Siphlophis longicaudatus*), we considered snout to vent length (SVL) instead of total length. The maximum known SVL for each species was used, regardless of the sex.

2. *Mean fecundity* (MF): species with low fecundity tend to be more prone to extinction because low fecundity populations take longer to recover when reduced to a small size than do high fecundity populations (e.g., Pimm et al. 1988, Bennet & Owens 1997, McKinney 1997, Purvis et al. 2000). Mean litter size was used regardless of the number of litters available, considering eggs or vitellogenic follicles larger than 10 mm (Shine 1977a, 1977b).

3. *Dietary breadth* (DB): animals that are specialists in resource use tend to be more vulnerable to extinction due to their probably lower ability to cope with the negative interventions in their habitats (e.g., McKinney 1997, Purvis et al. 2000). To characterize the degree of diet specialization we used the percentage of the most important prey item in the diet. Prey items considered were: amphibians, birds, bird eggs, lizards, lizard eggs, mammals and snakes. We used every record, regardless of the number of individual prey available for each species.

4. *Geographic distribution* (GD): animals that have a small geographic distribution tend to be more vulnerable to extinction due to their probably reduced capacity to cope with negative interventions in their habitats (e.g., Diamond 1984, Purvis et al. 2000, Fisher & Owens 2004, Cardillo et al. 2008). We estimated distribution areas by calculating 100% minimum convex polygons (MCP) using occurrence points from collection records and literature data. Thus, our geographic distribution corresponds to the extent of occurrence of the IUCN criteria (IUCN 2001). MCPs were calculated using the Home Range extension for Arcview 3.3 (Rodgers & Carr 1998). We considered the exact capture location when available; otherwise we used the main urban area of the municipality in which the specimen was captured.

5. *Habitat breadth* (HB): animals that use habitats in a more specialized way tend to be more vulnerable to extinction due to their probably reduced capacity to cope with negative interventions in their habitats (e.g., Purvis et al. 2000, 2005, Norris & Harper 2004). Terrestrial Ecoregions of the World (Olson et al. 2001) were used as habitat

types. To access this factor the species geographic distribution map was superimposed to a map of the Terrestrial Ecoregions.

6. *Altitudinal range* (ALT): animals occurring in a restricted vertical distribution tend to be stenothermics and stenobaries, therefore being more vulnerable to extinction due to their probably reduced capacity to cope with negative interventions in their habitats (e.g., McKinney 1997). The data for this factor was obtained from the species geographic ranges.

7. *Ability to persist in altered habitats* (AAH; adapted from Filippi & Luiselli 2000): animals that are less able to persist in altered habitats tend to be more vulnerable to extinction (e.g., Purvis et al. 2000, Fisher & Owens 2004). This factor was assessed based on the personal experience of researchers. Experienced researchers were asked to assign values for each species as follows: 0-5 for species which are extremely able to persist in disturbed habitats (occurring even in urban areas); 6-11 for those which may eventually persist in disturbed habitats (found in rural areas where small patches of natural vegetation are available); 12-17 for species which rarely persist in disturbed habitats (may be found in natural habitat patches); and 18-23 for species which do not persist in disturbed habitats (found only in large extensions of natural habitat). We employed the mean of the scores given by each researcher for each species. Even though in some cases the opinion of researchers varied considerably (most probably due to the subjectivity involved, see Keith et al. 2004, Regan et al. 2004), we believe this metric is still informative of the sensibility of different species to human disturbances.

We are aware that the use of population parameters such as maximum age and frequency of reproduction (e.g., Filippi & Luiselli 2000) would enhance our ability to predict extinction risk. However, there is virtually no population studies on snakes (Dodd 1987, 1993, Gibbons et al. 2000). For this reason, we used fecundity and geographic range as surrogates for demographic parameters.

For each factor we ranked the species and assigned their ranking number, such that the higher the score, the higher the importance of that factor to vulnerability to extinction. When ties occurred, we employed the mean ranking score, as usual in ranking statistical procedures. Afterwards, we used a mean of the factors to create the index of vulnerability to extinction (IVE) for the 39 species for which data was available. To evaluate the correlation degree among factors we performed a Spearman rank correlation analysis using the program XLSTAT version 7.5.2 (Addinsoft 2004). Habitat breadth was highly correlated with geographic distribution ($r = 0.94$, $p < 0.001$)

and was discarded in the calculation of the IVE. The remaining factors were not strongly correlated ($r < 0.52$ in all cases; Table 2) and were thus considered as independent and kept in the analysis. We opted to use a linear ranking system to build the IVE because in our case (in which a diverse set of biological data is used and complete data sets are available for many species) this system provides a great resolution among taxa (Millsap et al. 1990, Todd & Burgman 1998). Furthermore, in linear ranking schemes, variables can be easily defined and the results are very straightforward (Beissinger et al. 2000).

Ecological Oddity

We used the ecological oddity index (EO) proposed by Redding et al. (2010), which takes into account the distance of a given trait of a given species in relation to the lineage mean for that trait. We calculated EO for four traits: three continuous (body size, mean fecundity and habitat breadth) and one categorical (dietary breadth). We calculated habitat breadth as described above. We only included in the analysis species for which data was available for at least 50% of the factors. We are aware that the use of more variables like population density, home range, body mass, and maximum age (Redding et al. 2010) would result in a better representation of EO, but these data were not available for pseudoboines.

For the continuous factors we log transformed the values to remove the effect of outliers and then calculated the absolute distance of each species score to the mean score of that variable (c.f. Redding et al. 2010). For the categorical variable dietary breadth, the value assigned to a species was the frequency of the prey category in the entire data set (c.f. Redding et al. 2010). Therefore, the more a snake species feeds upon a food item that a great number of other species also feed, the smaller its EO value for dietary breadth. We only considered prey items representing over 20% of the diet. The mean of these four factors was used as the EO index, which was calculated for 43 species.

Phylogenetic distinctness

Using the available phylogeny of the tribe (Fig. 1; H. Zaher & F.G. Grazziotin, unpublished data) and considering all branch lengths as one, we calculated the phylogenetic distinctness (PD) for the 29 species present in the phylogeny. We calculated the PD scores through May's distinctness measure (May 1990) on Tuatara

module (Madison & Mooers 2007) of the Mesquite package (Madison & Madison 2007).

Priority index

By associating all the indexes above (IVE, EO and PD), we generated a priority index (PI). Since each index is different in magnitude, we performed a standardization of the values using Z-scores in order to render them comparable. The priority index was then calculated from mean Z-scores of all indices (IVE, EO and PD). We only included in the analysis species for which at least two of the indices were available.

Results

There was a great amount of variation in the biological features considered among pseudoboines (Table 1). Mean adult snout-vent length varied from 246 mm (*Phimophis scriptorcibatus*) to 2790 mm (*Clelia plumbea*), with a mean 1087 mm (SD = 502 mm). Clutch size ranged from 2.0 (*Phimophis iglesiassi*) to 15.0 eggs (*Oxyrhopus occipitalis*) with a mean 7.6 (SD = 3.3). Regarding dietary breadth, the tribe Pseudoboini include a large number of highly specialized species in different items (Table 1), like bird eggs (*Rhachidelus brazili*), squamate eggs (*Drepanoides anomalus*), and lizards (*Phimophis guerini*, *P. iglesiassi*, *P. scriptorcibatus* and *Pseudoboa nigra*). Geographic distributions of pseudoboines are in general very wide and varied considerably among species (mean = 3,086,886 km²; SD = 3,493,432 km²). The tribe includes several species with very large geographic distributions (over 5,000,000 km² in 11 species), and also an island endemic (560 km² in *Clelia errabunda* from Saint Lucia, West Indies; Table 1). Habitat breadth also presented considerable variation (mean = 26.0 ± 26.5 habitat types): from species which occur in a single habitat type (e.g., *Clelia hussami*, known to occur only in Araucaria Moist Forests in southern Brazil) to some which occur in over 100 habitat types (e.g., *Clelia clelia*). Altitudinal range also varied considerably among pseudoboines (1123 ± 867 m), from species with narrow ranges of elevations (e.g., *Phimophis scriptorcibatus*, 295-473 m above sea level) to some with a very wide range of elevations (e.g., *Siphlophis longicaudatus*, 3-1333 m above sea level).

On the other hand, the factor ability to persist in altered habitats did not present a great variation among pseudoboines (mean = 16.0 ± 5.7). Most species lie around the second and third quartiles of this factor (between 7.3 and 17.8; Table 1) and two

particular species, *Oxyrhopus guibei* and *Pseudoboa newwiedi*, are extremely tolerant to habitat disturbances (values of 2.13 and 3.0, respectively). However, 12 species are present in the fourth quartile (with values greater than 17.9), being extremely sensitive to habitat disturbance (e.g. *Boiruna sertaneja*, *Mussurana montana*, and *Phimophis scriptorcibatus*).

The index of vulnerability to extinction (IVE) was calculated for 39 species and ranged from 13.6 (*Oxyrhopus petola*) to 27.4 (*Clelia langeri*), with a mean of 19.2 ± 3.7 . Besides *C. langeri*, five additional species appeared in the upper quartile of IVE (i.e., higher vulnerability to extinction): *Pseudoboa serrana*, *Clelia scytalina*, *Clelia hussami*, *Siphlophis compressus*, and *Pseudoboa martinsi*.

Ecological oddity (EO) was calculated for 43 species and ranged from 0.06 (*Siphlophis worontzowi*) to 0.83 (*Phimophis chui*; Table 3), with a mean of 0.25 ± 0.18 . Only three species appeared in the upper quartile (0.64 to 0.83; i.e., higher oddity): *Clelia errabunda*, *Oxyrhopus doliatus*, and *Phimophis chui*.

Phylogenetic distinctness (PD) was obtained for 29 species. *Phimophis iglesiassi*, which seems to be the sister species of all pseudoboines (Fig. 1), had the highest PD (10.0), whereas all other species in the tribe had PDs from 1.0 to 2.5 (Table 4). High PDs among the latter species were obtained by *Siphlophis compressus*, *S. cervinus* and *Oxyrhopus formosus* (all with 2.5; Table 4).

Priority index (PI) was calculated for 39 species and ranged from -0.90 (very low priority for *Oxyrhopus melanogenys*) to 2.05 (very high priority for *Phimophis iglesiassi*; Table 4). Besides *P. iglesiassi*, the species *Clelia hussami* (1.64), *P. chui* (1.34), *C. langeri* (0.84), and *C. scytalina* (0.76) also presented high PIs (Table 4). All other species presented PIs below 0.8 (Table 4).

Discussion

Our results indicate that pseudoboine snakes comprise an ecologically diverse assemblage of snake taxa (Table 1). Most species are moderate-sized snakes, with relatively low fecundity, high degree of feeding specialization, and large geographic ranges. The diet of pseudoboines is mainly composed by lizards and small mammals, with larger species (genera *Clelia* and *Pseudoboa*) also feeding on snakes. In addition, two species seem to be egg specialists (*Drepanoides anomalus* in squamate eggs and *Rhachidelus brazili* in bird eggs).

Of the species evaluated herein, five are present in red lists (all of them prepared using the IUCN categories and criteria; IUCN 2001): three in the Rio Grande do Sul State (southern Brazil) red list (*Clelia plumbea*, Vulnerable; *Pseudoboa haasi*, Vulnerable, and *Siphlophis longicaudatus*, Endangered; Marques et al. 2002), one in the São Paulo State (southeastern Brazil) red list (*Mussurana montana*, Vulnerable; São Paulo 2008), and one in the Bolivian national red list (*Clelia langeri*, Vulnerable; Baudoin 2010). In our study, only *C. langeri* and *S. longicaudatus* appeared with high IVEs (27.4 and 23.1, respectively). Thus, these two species and the remaining species which appeared with high IVEs in our study (e.g., *Pseudoboa serrana*, *Clelia scytalina*, *Clelia hussami*, *Siphlophis compressus*, and *Pseudoboa martinsi*) should receive special attention in future assessments of extinction risk both regionally and globally.

Although we used only intrinsic factors in the composition of our vulnerability index (IVE), the use of extrinsic factors would make this index a better indicator of the actual risk pseudoboinae are facing. Given that the main factor of endangerment for reptiles is habitat loss and fragmentation (IUCN 2009), examples of extrinsic factors that could be used are the amount of protected areas within the geographic distribution, the proportion of natural habitat remaining within the geographic distribution, the quality of the remaining fragments, as well as the expected change in habitat quality in the next decade (cf. criterion B of IUCN, 2001). On the other hand, we decided not to include the extrinsic factors illegal trade and road mortality (Filippi & Luiselli 2000, França & Araújo 2006, Santos et al. 2007), since there is no evidence that these factors are important for Neotropical snakes (RENTAS 2001, 2007, CITES 2009; P.A. Hartmann, pers. comm.).

A critical step and one of the main issues in assessing conservation priorities is how data deficient species are treated (O'Grady et al. 2004), since it is difficult to have complete information about all species being assessed (Sattler 2007). For example, the five species with greater EO (*Phimophis chui*, *Oxyrhopus doliatus*, *Clelia errabunda*, *Clelia hussami* and *Phimophis scriptorhibatus*) did not have their PIs calculated because of lack of data on their biology (see Table 3). We decided not to evaluate these data deficient species in order to avoid wrong estimates, since discrepancies in risk assessments can erode confidence in conservation decision (Mrosovsky 1997). Furthermore, a species misclassification can lead to resource misdirection, especially when the error accumulates over criteria (Todd & Burgman 1998).

Despite the remarkable variation in the life history traits included in the EO calculation (body size, fecundity, dietary breadth, and habitat breadth), these factors seem to be conserved in most of the tribe representatives, resulting in high EO values for few species that differ from the average morphological and/or ecological phenotype. Thus, two thirds of the 43 pseudoboines evaluated for ecological oddity (EO) had relatively low values for this index, while only three species had very high EOs. Unlike expected (Cadotte et al. 2009, Redding et al. 2010), EO and PD were not correlated (Spearman $r = 0.148$; $p = 0.445$), since among pseudoboines higher singularity in ecological or morphological features were not necessarily found in more relictual species. Higher PD values were, though, found in species presenting higher IVE values, indicating that more intrinsically vulnerable species are also those with higher phylogenetic distinctiveness. This reinforces the need for conservation initiatives towards relictual species.

Other aspects may be taken into account when evolutionary information is incorporated into conservation policies. Some authors have proposed that speciation rate is an important trait for prioritization (Heard & Mooers 2000), aiming to maintain a high evolutionary potential. Since speciation results in the production of biodiversity (Brooks et al. 1992), successful taxa might act as species dynamos for the production of future forms (e.g. Erwin 1991, Brooks et al. 1992, Heard & Mooers 2000). We believe that a good alternative would be to compromise, i.e., to consider both ancient evolutionary history and speciation rate, in such a way that representatives of all major clades within a given lineage are satisfactorily protected and/or included in conservation policies. Representatives from almost all pseudoboine lineages are listed amongst the ten higher PI values, maximizing the phylogenetic diversity (*sensu* Faith 1992) of the prioritized taxa. The only genera that did not present high PIs was *Oxyrhopus*, comprised mostly by widespread, generalist and disturbance-tolerant species.

In the present “age of extinction” we are faced by the agony of choice (Vane-Wright et al. 1991) and have to decide which species are saved and which are lost (Heard & Mooers 2000, Posadas et al. 2001). In order to help species prioritization, the approach used herein considers not only the vulnerability to extinction of species (e.g. Filippi & Luiselli 2000; França & Araújo 2006), but also the evolutionary history of the lineage studied (e.g. May 1990, Vane-Wright et al. 1991), as well as the degree of ecological uniqueness of species within the lineage (c.f. Redding et al. 2010). Although it is not possible to compare values obtained in studies with different clades (the indices

generated are clade-specific), when extended to more inclusive lineages within a group of organisms (e.g., subfamilies, families) this approach might enhance the quality of future prioritization processes.

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Table 1. Data gathered for species of the Tribe Pseudoboini to create the priority index. BS: body size (maximum snout-vent length, in millimeters). MF: mean fecundity (mean, range and number of litters). DB: dietary breadth (categories and frequency of prey; we only considered frequencies above 20% of the diet; total number of records in brackets; A = amphibian; B = bird; EgB = bird eggs; EgS = Squamate eggs; L = lizard; M = mammal; S = snake). GD: geographic distribution (x 1000 Km²). HB: habitat breadth (number of Terrestrial Ecorregions covered by the geographic distribution). ALT: altitudinal range (lower limit and upper limit). AAH: ability to persist in altered habitats (mean of the scores assigned by experienced researchers). We did not include in this table species for which all data was missing (*Oxyrhopus erdisii*, *Oxyrhopus fitzingeri* and *Oxyrhopus marcapatae*). Species ranked by alphabetical order.

Species	BS	MF	DB	GD	HB	ALT	AAH
<i>Boiruna maculata</i>	1919	7.94 (4-15; N=13)	S (0.58); O (0.33) [N=31]	5,561.02	34	1211 (0-1211)	13.17 ± 9.12 (5-23; N=3)
<i>Boiruna sertaneja</i>	1940	9.25 (4-14; N=8)	L (0.29); S (0.71) [N=14]	1,010.96	12	820 (5-825)	23 (N=1)
<i>Clelia equatoriana</i>	1400	-	-	323.87	22	1861 (9-1870)	-
<i>Clelia errabunda</i>	1380	-	-	0.56	1	-	-
<i>Clelia clelia</i>	2398	12.6 (9-22; N=6)	L (0.27); S (0.49) [N=41]	13,906.61	117	2756 (1-2757)	22.5 ± 0.71 (22-23; N=2)
<i>Clelia hussami</i>	1080	-	-	6.02	1	295 (753-1048)	-
<i>Clelia langeri</i>	1295	-	M (1) [N=1]	61.45	7	783 (681-1464)	-
<i>Clelia plumbea</i>	2790	12.6 (4-29; N=14)	S (0.76) [N=17]	5,593.80	28	1133 (2-1135)	20 ± 2.94 (17-23; N=4)
<i>Clelia rustica</i>	1850	8.88 (7-13; N=12)	M (0.5); S (0.4) [N=10]	3,379.38	22	4586 (0-4586)	16.75 ± 6.01 (12.5-21; N=2)
<i>Clelia scytalina</i>	1190	-	-	824.31	41	1667 (15-1682)	-
<i>Drepanoides anomalus</i>	662	2.33 (2-4; N=9)	L (0.22); EgS (0.78) [N=9]	4,074.13	27	307 (1-308)	21.5 (N=1)
<i>Mussurana bicolor</i>	825	9 (7-15; N=8)	A (0.5) [N=6]	1,772.31	13	709 (21-730)	14.5 (N=1)
<i>Mussurana montana</i>	940	9 (7-11; N=2)	L (0.5); S (0.5) [N=2]	40.47	5	1089 (539-1628)	23 (N=1)
<i>Mussurana quimi</i>	1054	11.27 (7-16; N=8)	M (0.75) [N=8]	1,502.16	12	1097 (74-1171)	-
<i>Oxyrhopus clathratus</i>	1132	7.78 (3-16; N=37)	M (0.82) [N=34]	843.79	11	1053 (0-1053)	13 ± 7.62 (5-23; N=4)

<i>Oxyrhopus doliatus</i>	365	-	-	-	1	2283 (67-2350)	-
<i>Oxyrhopus formosus</i>	846	4 (N=1)	L (1) [N=3]	2,525.24	18	614 (12-626)	22 ± 1.41 (21-23; N=2)
<i>Oxyrhopus guibei</i>	1080	12.34 (3-20; N=105)	M (0.77); L (0.21) [N=43]	4,018.27	24	1196 (7-1203)	2.13 ± 2.95 (0.01-6.5; N=4)
<i>Oxyrhopus leucomelas</i>	-	-	-	175.75	11	1894 (155-2049)	-
<i>Oxyrhopus melanogenys</i>	901	9.75 (7-13; N=8)	M (0.46); L (0.46) [N=52]	3,125.71	24	805 (1-806)	10.51 ± 14.84 (0-21; N=2)
<i>Oxyrhopus occipitalis</i>	834.9	15 (13-17; N=2)	L (1) [N=1]	3,723.35	33	1142 (47-1189)	-
<i>Oxyrhopus petola</i>	1104	7.14 (2-12; N=25)	M (0.3); L (0.35); B (0.25) [N=20]	13,125.56	126	3487 (2-3489)	9.33 ± 9.71 (1-20; N=3)
<i>Oxyrhopus rhombifer</i>	958	8.27 (4-17; N=12)	M (0.49); L (0.49) [N=41]	7,149.87	37	1196 (0-1196)	15.8 ± 8.58 (5-23; N=5)
<i>Oxyrhopus trigeminus</i>	860	7.94 (2-12; N=14)	M (0.33); L (0.56) [N=36]	7,462.51	41	1193 (1-1194)	12.5 (N=1)
<i>Oxyrhopus vanidicus</i>	906	12.5 (12-13; N=2)	M (0.5); L (0.5) [N=6]	1,604.80	23	931 (21-952)	-
<i>Phimophis chui</i>	300	-	-	-	1	475 (N=1)	22.5 (N=1)
<i>Phimophis guerini</i>	1038	4.75 (3-7; N=3)	L (0.92) [N=12]	5,375.62	32	1133 (19-1152)	14.6 ± 6.5 (8-21; N=5)
<i>Phimophis guianensis</i>	649	-	-	2,142.97	36	157 (1-158)	-
<i>Phimophis iglesiassi</i>	444	2 (2-2; N=2)	L (1) [N=3]	692.62	6	535 (181-716)	21 (N=1)
<i>Phimophis scriptorcibatus</i>	246	-	L (1) [N=2]	-	2	178 (295-473)	23 (N=1)
<i>Phimophis vittatus</i>	651	5 (N=1)	-	414.46	6	1037 (79-1116)	-
<i>Pseudoboa coronata</i>	1093	4.58 (3-6; N=5)	M (0.38); L (0.38); O (0.33) [N=8]	7,909.62	52	761 (9-770)	12.5 ± 14.85 (2-23; N=2)
<i>Pseudoboa haasi</i>	1293	5.36 (3-10; N=11)	M (0.6); S (0.2) [N=15]	404.74	7	1041 (3-1044)	14.33 ± 9.02 (5-23; N=3)
<i>Pseudoboa martinsi</i>	1090	6 (N=1)	S (1) [N=1]	928.50	12	103 (20-123)	22 ± 1.41 (21-23; N=2)
<i>Pseudoboa neuwiedii</i>	972	5.63 (3-12; N=5)	M (0.25); L (0.5); S (0.25) [N=4]	2,647.73	47	826 (6-832)	3 (N=1)
<i>Pseudoboa nigra</i>	1261	9.5 (3-24; N=18)	L (0.67) [N=21]	5,451.47	29	1190 (2-1192)	10.75 ± 8.29 (2-22; N=4)
<i>Pseudoboa serrana</i>	1243	-	-	31.93	5	586 (618-1204)	15.5 (N=1)
<i>Rhachidelus brazili</i>	1372	4.5 (2-7; N=6)	B (0.2); EgB (0.8) [N=15]	837.74	5	817 (318-1135)	14.25 ± 7.09 (8-23; N=4)
<i>Siphlophis cervinus</i>	990	4.88 (3-6; N=5)	L (0.82) [N=38]	6,463.12	48	405 (4-409)	16.5 ± 7.78 (11-22; N=2)
<i>Siphlophis compressus</i>	1229	6.2 (3-12; N=12)	L (0.96) [N=26]	8,876.16	57	333 (1-334)	19.17 ± 2.75 (16-21; N=3)

<i>Siphlophis leucocephalus</i>	708	-	L (1) [N=1]	73.77	5	367 (34-401)	-
<i>Siphlophis longicaudatus</i>	931	6 (5-7; N=6)	L (0.75); S (0.25) [N=12]	434.86	9	1330 (3-1333)	11 (N=1)
<i>Siphlophis pulcher</i>	803	4 (2-7; N=4)	L (0.83) [N=30]	196.63	8	1005 (0-1005)	15 ± 9.85 (4-23; N=3)
<i>Siphlophis worontzowi</i>	746	-	L (0.83) [N=6]	1,868.49	15	1273 (51-1324)	22.5 ± 0.71 (22-23; N=2)

Table 2. Spearman rank correlation coefficient of the six factors used to generate the index of vulnerability to extinction. BS: body size, MF: mean fecundity, DB: dietary breadth, GD: geographic distribution, ALT: altitudinal range and AAH: ability to persist in altered habitats.

	BS	MF	DB	GD	ALT
MF	-0.4654				
DB	-0.1813	0.5023			
GD	-0.3040	0.2788	0.3596		
ALT	-0.3861	0.5122	0.5089	0.2299	
AAH	0.0469	0.0788	0.3483	0.1372	0.3368

Table 3. Ranking scores of factors used to build the index of vulnerability to extinction and values for ecological oddity for the species of the tribe Pseudoboini (see text for further details). Species tanked by alphabetical order. BS: body size, MF: mean fecundity, DB: dietary breadth, GD: geographic distribution, HB: habitat breadth, ALT: altitudinal range, and AAH: ability to persist in altered habitats. We did not include in this table species for which all data was missing (*Oxyrhopus erdisii*, *Oxyrhopus fitzingeri* and *Oxyrhopus marcapatae*).

Species	Vulnerability index							Ecologica Oddity			
	BS	MF	DB	GD	HB	ALT	AAH	BSeo	MFeo	HBeo	DBeo
<i>Boiruna maculata</i>	36	14.5	12	9	34	7	10	0.2919	0.0628	0.3925	0.2312
<i>Boiruna sertaneja</i>	37	9	15	24	19	23	29.5	0.2966	0.1291	0.0598	0.0913
<i>Clelia clelia</i>	38	2.5	4	1	43	3	27	0.3887	0.2634	0.9292	0.0654
<i>Clelia equatoriana</i>	-	-	-	-	24.5	-	-	0.1550	-	0.2035	-
<i>Clelia errabunda</i>	-	-	-	-	2.5	-	-	0.1487	-	1.1389	-
<i>Clelia hussami</i>	22.5	-	-	38	2.5	35	-	0.0423	-	1.1389	-
<i>Clelia langeri</i>	33	-	30.5	35	12.5	26	-	0.1211	-	0.2938	0.0769
<i>Clelia plumbea</i>	39	2.5	18	8	30	13.5	21	0.4544	0.2635	0.3082	0.0850
<i>Clelia rustica</i>	35	12	8	15	24.5	1	19	0.2760	0.1116	0.2035	0.0829
<i>Clelia scytalina</i>	28	-	-	28	37.5	4	-	0.0844	-	0.4738	-
<i>Drepanoides anomalus</i>	5	30	20	12	29	34	23	0.1703	0.4690	0.2924	0.7870
<i>Mussurana bicolor</i>	9	10.5	8	21	21	28	13	0.0747	0.1172	0.0250	0.5000
<i>Mussurana montana</i>	16	10.5	8	36	7.5	16	29.5	0.0180	0.1172	0.4400	0.0764

<i>Mussurana quimi</i>	21	6	16.5	23	19	15	-	0.0317	0.2148	0.0598	0.0577
<i>Oxyrhopus clathratus</i>	27	16	23	26	16.5	17	9	0.0627	0.0539	0.0975	0.0633
<i>Oxyrhopus doliatus</i>	-	-	-	-	2.5	-	-	0.4289	-	1.1389	-
<i>Oxyrhopus formosus</i>	11	28.5	30.5	18	23	29	24.5	0.0638	0.2350	0.1163	0.0417
<i>Oxyrhopus guibei</i>	22.5	5	19	13	27.5	8.5	1	0.0423	0.2543	0.2413	0.0678
<i>Oxyrhopus leucomelas</i>	-	-	-	-	16.5	-	-	-	-	0.0975	-
<i>Oxyrhopus melanogenys</i>	13	7	3	16	27.5	25	4	0.0364	0.1520	0.2413	0.0547
<i>Oxyrhopus occipitalis</i>	10	1	30.5	14	33	12	-	0.0695	0.3391	0.3796	0.0417
<i>Oxyrhopus petola</i>	26	17	1	2	44	2	3	0.0518	0.0164	0.9614	0.2877
<i>Oxyrhopus rhombifer</i>	17	13	5	6	36	8.5	17	0.0098	0.0806	0.4293	0.0578
<i>Oxyrhopus trigeminus</i>	12	14.5	11	5	37.5	10	7.5	0.0567	0.0627	0.4738	0.0488
<i>Oxyrhopus vanidicus</i>	14	4	8	22	26	21	-	0.0340	0.2599	0.2228	0.0593
<i>Phimophis chui</i>	1	-	-	39	2.5	-	27	0.5140	-	1.1389	-
<i>Phimophis guerini</i>	20	25	26	11	32	13.5	14	0.0250	0.1603	0.3662	0.0382
<i>Phimophis guianensis</i>	3	-	-	19	35	36	-	0.1789	-	0.4174	-
<i>Phimophis iglesiasi</i>	2	31	30.5	29	10.5	31	22	0.3438	0.5360	0.3608	0.0417
<i>Phimophis scriptorcibatus</i>	-	-	-	-	5	-	-	0.6002	-	0.8379	0.0417
<i>Phimophis vittatus</i>	4	23	-	31	10.5	19	-	0.1776	0.1380	0.3608	-
<i>Pseudoboa coronata</i>	25	26	2	4	41	27	7.5	0.0475	0.1758	0.5771	0.2111
<i>Pseudoboa haasi</i>	32	22	13	32	12.5	18	12	0.1204	0.1081	0.2938	0.0462

<i>Pseudoboa martinsi</i>	24	19.5	30.5	25	19	37	24.5	0.0463	0.0589	0.0598	0.1111
<i>Pseudoboa neuwiedii</i>	18	21	8	17	39	22	2	0.0035	0.0869	0.5332	0.0678
<i>Pseudoboa nigra</i>	31	8	14	10	31	11	5	0.1095	0.1407	0.3235	0.0278
<i>Pseudoboa serrana</i>	30	-	-	37	7.5	30	16	0.1033	-	0.4400	-
<i>Rhachidelus brazili</i>	34	27	21	27	7.5	24	11	0.1462	0.1838	0.4400	0.8000
<i>Siphlophis cervinus</i>	19	24	22	7	40	32	18	0.0045	0.1486	0.5423	0.0340
<i>Siphlophis compressus</i>	29	18	27	3	42	33	20	0.0984	0.0449	0.6169	0.0401
<i>Siphlophis leucocephalus</i>	6	-	30.5	34	7.5	-	-	0.1411	-	0.4400	0.0417
<i>Siphlophis longicaudatus</i>	15	19.5	16.5	30	15	5	6	0.0222	0.0589	0.1847	0.0590
<i>Siphlophis pulcher</i>	8	28.5	24.5	33	14	20	15	0.0865	0.2350	0.2358	0.0347
<i>Siphlophis worontzowi</i>	7	-	24.5	20	22	6	27	0.1184	-	0.0372	0.0347

Table 4. Mean ranking scores (with Z-scores indicated in parenthesis) for the index of vulnerability to extinction (IVE), mean ecological oddity, phylogenetic distinctiveness and priority index for the species of the tribe Pseudoboini. Species are ranked in descending order of priority index. We only included in the analysis species for which at least two of the indices were available (*Oxyrhopus erdisii*, *Oxyrhopus fitzingeri*, *Oxyrhopus leucomelas* and *Oxyrhopus marcapatae* are not presented).

Species	Mean IVE	Mean Ecological Oddity	Phylogenetic distinctiveness	Priority index
<i>Phimophis iglesiasi</i>	22.29 (0.8089)	0.3206 (0.3789)	10 (4.976)	2.0546
<i>Clelia hussami</i>	24.5 (1.3996)	0.5906 (1.8721)	-	1.6358
<i>Phimophis chui</i>	17.38 (-0.501)	0.8265 (3.1765)	-	1.3378
<i>Clelia langeri</i>	27.4 (2.1731)	0.164 (-0.487)	-	0.8431
<i>Clelia scytalina</i>	24.38 (1.3662)	0.2791 (0.1498)	-	0.7580
<i>Pseudoboa serrana</i>	24.1 (1.2929)	0.2716 (0.1084)	-	0.7006
<i>Drepanoides anomalus</i>	21.86 (0.6946)	0.4297 (0.9824)	1.66 (-0.1354)	0.5139
<i>Siphlophis compressus</i>	24.57 (1.4186)	0.2001 (-0.2873)	2.5 (0.3794)	0.5036
<i>Phimophis guianensis</i>	23.25 (1.0662)	0.2981 (0.255)	1.66 (-0.1354)	0.3952
<i>Rhachidelus brazili</i>	21.64 (0.6375)	0.3925 (0.7767)	1.43 (-0.2776)	0.3788
<i>Pseudoboa martinsi</i>	25.64 (1.7044)	0.069 (-1.0121)	-	0.3462
<i>Siphlophis cervinus</i>	23.14 (1.0376)	0.1823 (-0.3853)	2.5 (0.3794)	0.3439
<i>Oxyrhopus formosus</i>	23.5 (1.1328)	0.1142 (-0.7622)	2.5 (0.3794)	0.2500
<i>Siphlophis pulcher</i>	20.43 (0.3136)	0.148 (-0.5753)	2.22 (0.209)	-0.0176

<i>Clelia clelia</i>	16.93 (-0.62)	0.4117 (0.8827)	1.25 (-0.3867)	-0.0413
<i>Boiruna sertaneja</i>	22.36 (0.828)	0.1442 (-0.5962)	1.25 (-0.3867)	-0.0516
<i>Siphlophis leucocephalus</i>	19.5 (0.0659)	0.2076 (-0.2457)	-	-0.0899
<i>Clelia plumbea</i>	18.86 (-0.1056)	0.2778 (0.1424)	1.25 (-0.3867)	-0.1166
<i>Phimophis guerini</i>	20.21 (0.2564)	0.1474 (-0.5783)	1.66 (-0.1354)	-0.1524
<i>Pseudoboa coronata</i>	18.93 (-0.0866)	0.2529 (0.0047)	1.11 (-0.4719)	-0.1846
<i>Pseudoboa haasi</i>	20.21 (0.2564)	0.1421 (-0.6077)	1 (-0.5399)	-0.2971
<i>Boiruna maculata</i>	17.5 (-0.4676)	0.2446 (-0.041)	1.25 (-0.3867)	-0.2984
<i>Phimophis vittatus</i>	17.5 (-0.4676)	0.2255 (-0.1468)	-	-0.3072
<i>Oxyrhopus clathratus</i>	19.21 (-0.0103)	0.0694 (-1.0101)	2 (0.073)	-0.3158
<i>Pseudoboa neuwiedii</i>	18.14 (-0.2961)	0.1728 (-0.4378)	1.25 (-0.3867)	-0.3735
<i>Clelia rustica</i>	16.36 (-0.7725)	0.1685 (-0.4619)	2 (0.073)	-0.3871
<i>Siphlophis worontzowi</i>	17.75 (-0.4009)	0.0634 (-1.0428)	2.22 (0.209)	-0.4169
<i>Oxyrhopus occipitalis</i>	16.75 (-0.6677)	0.2075 (-0.2464)	-	-0.4570
<i>Mussurana montana</i>	17.64 (-0.4295)	0.1629 (-0.4928)	-	-0.4612
<i>Oxyrhopus petola</i>	13.57 (-1.5155)	0.3293 (0.4274)	1.25 (-0.3867)	-0.4916
<i>Mussurana bicolor</i>	15.79 (-0.9249)	0.1792 (-0.4025)	1.43 (-0.2776)	-0.5350
<i>Siphlophis longicaudatus</i>	15.29 (-1.0583)	0.0812 (-0.9446)	2.22 (0.209)	-0.5979
<i>Mussurana quimi</i>	16.75 (-0.6677)	0.091 (-0.8905)	1.43 (-0.2776)	-0.6119
<i>Oxyrhopus vanidicus</i>	15.83 (-0.9122)	0.144 (-0.5973)	1.11 (-0.4719)	-0.6605

<i>Pseudoboa nira</i>	15.71 (-0.9439)	0.1504 (-0.5621)	1 (-0.5399)	-0.6820
<i>Oxyrhopus rhombifer</i>	14.64 (-1.2297)	0.1444 (-0.5953)	1.43 (-0.2776)	-0.7009
<i>Oxyrhopus trigeminus</i>	13.93 (-1.4203)	0.1605 (-0.5061)	1.43 (-0.2776)	-0.7346
<i>Oxyrhopus guibei</i>	13.79 (-1.4584)	0.1514 (-0.5564)	1.43 (-0.2776)	-0.7641
<i>Oxyrhopus melanogenys</i>	13.64 (-1.4965)	0.1211 (-0.7239)	1.11 (-0.4719)	-0.8974
<i>Clelia equatoriana</i>	-	0.1792 (-0.4026)	-	-
<i>Clelia errabunda</i>	-	0.6438 (2.1664)	-	-
<i>Oxyrhopus doliatus</i>	-	0.7839 (2.941)	-	-
<i>Phimophis scriptorcibatus</i>	-	0.4933 (1.3339)	-	-

Figure 1. Consensus of ten trees (9.237 steps) obtained from maximum linear parsimony using molecular characters (sub units 12S and 16S from mitochondrial rDNA e C-mos), with a total of 1278 bases pairs (H. Zaher and F.G. Grazziotin, data not published).

CONCLUSÃO GERAL

Embora tenhamos acumulado uma grande quantidade de informações sobre os pseudoboíneos (por meio de exame de exemplares de coleções, levantamento bibliográfico e consulta a especialistas), ainda existem espécies praticamente desconhecidas. Por exemplo, não foi possível encontrar informações sobre a biologia de três espécies (*Oxyrhopus erdisii*, *O. fitzingeri* e *O. marcapatae*) e os dados disponíveis para outras (*Clelia equatoriana*, *C. errabunda*, *Oxyrhopus doliatus* e *Phimophis scriptorcibatus*) são ainda muito escassos, o que praticamente inviabiliza avaliações de risco de extinção.

Nossos resultados indicam que a tribo Pseudoboini compreende de fato um grupo ecologicamente diverso, com espécies de pequeno a grande porte, fecundidade relativamente baixa, alto grau de especialização em diferentes itens alimentares e ampla distribuição geográfica. Apenas cinco espécies estão presentes em listas vermelhas: três no Rio Grande do Sul (*Clelia plumbea*, Vulnerável; *Pseudoboa haasi*, Vulnerável, e *Siphlophis longicaudatus*, Ameaçada; Marques et al. 2002), uma em São Paulo (*Mussurana montana*, Vulnerável; São Paulo 2008), e uma na lista vermelha nacional da Bolívia (*Clelia langeri*, Vulnerável; Baudoin 2010).

Ainda que tenhamos encontrado uma grande diversidade de características de história de vida na Tribo estudada, dois terços das espécies apresentaram valores relativamente baixos de singularidade ecológica. Apenas as espécies *Clelia errabunda*, *Oxyrhopus doliatus* e *Phimophis chui* apresentaram alto grau de singularidade ecológica. No entanto, o índice de vulnerabilidade à extinção (IVE) e o grau de distinção filogenética (PD) foram mais uniformemente distribuídos (exceto pelas espécies *Clelia langeri*, IVE = 27.4, e *Phimophis iglesiassi*, PD = 10.0). Além disso, as espécies que apresentaram altos valores de PD também apresentaram altos valores de IVE, o que reforça a importância da conservação de espécies mais relictuais. As espécies que apresentaram maiores índices de priorização (PI) foram: *Phimophis iglesiassi*, *Clelia hussami*, *P. chui*, *C. langeri* e *C. scytalina*.

Na atual “era da extinção” somos confrontados com a agonia da escolha (Vane-Wright et al. 1991), tendo que decidir quais espécies serão salvas e quais serão perdidas (Heard & Mooers 2000, Posadas et al. 2001). Visando auxiliar na priorização de espécies, a abordagem aqui utilizada considera não só a vulnerabilidade à extinção das espécies da linhagem estudada (e.g., Filippi & Luiselli 2000, França & Araújo 2006),

como também sua história evolutiva (e.g., May 1990, Vane-Wright et al. 1991) e seu grau de singularidade ecológica (c.f. Redding et al. 2010). Apesar de não ser possível comparar valores entre estudos com diferentes linhagens (os índices gerados são específicos a cada linhagem), quando for aplicada a grupos mais inclusivos de organismos (e.g., famílias e subfamílias), esta abordagem poderá melhorar a qualidade dos processos de priorização.

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ANEXO

Mapas de distribuição das espécies de serpentes da Tribo Pseudoboini

Geographic distribution (shaded area) and localities for *Boiruna sertaneja*.

Geographic distribution (shaded area) and localities for *Boiruna maculata*. The "x" corresponds to a known record for a state or province without precise data.

Geographic distribution (shaded area) and localities for *Clelia langeri* and *C. errabunda* (star).

Geographic distribution (shaded area) and localities for *Clelia hussami*.

Geographic distribution (shaded area) and localities for *Mussurana montana*. The “x” corresponds to a known record for a state or province without precise data.

Geographic distribution (shaded area) and localities for *Mussurana bicolor*. The “x” corresponds to a known record for a state or province without precise data.

Geographic distribution (shaded area) and localities for *Mussurana quimi*. The “x” corresponds to a known record for a state or province without precise data.

Geographic distribution (shaded area) and localities for *Oxyrhopus clathratus*. The “x” corresponds to a known record for a state or province without precise data.

Geographic distribution (shaded area) and localities for *Oxyrhopus guibei*. The "x" corresponds to a known record for a state or province without precise data.

Geographic distribution (shaded area) and localities for *Oxyrhopus formosus*, *O. doliiatus* (star), *O. erdisii* (triangle) and *O. fizingeri* (darker shaded area). The "x" corresponds to a known record for a state or province without precise data.

Geographic distribution (shaded area) and localities for *Oxyrhopus occidentalis*. The "x" corresponds to a known record for a state or province without precise data.

Geographic distribution (shaded area) and localities for *Oxyrhopus petola*. The "x" corresponds to a known record for a state or province without precise data.

Geographic distribution (shaded area) and localities for *Phimophis guerini*. The "x" corresponds to a known record for a state or province without precise data.

Geographic distribution (shaded area) and localities for *Oxyrhopus variidicus* and *Phimophis chui* (star). The "x" corresponds to a known record for a state or province without precise data.

Geographic distribution (shaded area) and localities for *Phimophis iglesiasi*. The "x" corresponds to a known record for a state or province without precise data.

Geographic distribution (shaded area) and localities for *Phimophis guianensis*. The "x" corresponds to a known record for a state or province without precise data.

Geographic distribution (shaded area) and localities for *Phimophis vittatus* and *P. script-oricibatus* (star). The "x" corresponds to a known record for a state or province without precise data.

Geographic distribution (shaded area) and localities for *Pseudoboa coronata*. The "x" corresponds to a known record for a state or province without precise data.

Geographic distribution (shaded area) and localities for *Pseudoboa nigræ*. The "x" corresponds to a known record for a state or province without precise data.

Geographic distribution (shaded area) and localities for *Pseudoboa newwiedii*. The "x" corresponds to a known record for a state or province without precise data.

Geographic distribution (shaded area) and localities for *Siphlophis cervinus*. The “x” corresponds to a known record for a state or province without precise data.

Geographic distribution (shaded area) and localities for *Siphlophis compressus*. The “x” corresponds to a known record for a state or province without precise data.

Geographic distribution (shaded area) and localities for *Siphlophis longicaudatus*. The "x" corresponds to a known record for a state or province without precise data.

Geographic distribution (shaded area) and localities for *Siphlophis leucocephalus*.

Geographic distribution (shaded area) and localities for *Siphlophis worontzowi*.

Geographic distribution (shaded area) and localities for *Siphlophis pulcher*. The "x" corresponds to a known record for a state or province without precise data.