

INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA - INPA
PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA (ECOLOGIA)

O papel da escala nas estimativas de sobreposição de nicho e de efeitos ambientais sobre duas espécies irmãs de serpentes Neotropicais

THAIS DE ALMEIDA CORRÊA NOGUEIRA

Manaus, Amazonas

Julho, 2018

THAIS DE ALMEIDA CORRÊA NOGUEIRA

O papel da escala nas estimativas de sobreposição de nicho e de efeitos ambientais sobre duas espécies irmãs de serpentes Neotropicais

Orientador: Dr. Igor Luis Kaefer

Coorientador: Dr. Rafael de Fraga

Dissertação apresentada ao Instituto Nacional de Pesquisas da Amazônia como parte dos requisitos para obtenção do título de Mestre em Biologia (Ecologia).

Manaus, Amazonas

Julho, 2018

N778 Almeida-Correa, Thais

O papel da escala nas estimativas de sobreposição de nicho e de efeitos ambientais sobre duas espécies irmãs de serpentes neotropicais/ Thais de Almeida Corrêa Nogueira. --- Manaus : [sem editor.], 2018.
51 f.: il.

Dissertação (Mestrado) --- INPA, Manaus, 2018.
Orientador: Igor Luis Kaefer .
Coorientador: Rafael de Fraga.
Área de concentração: Ecologia.

1. Philodryas. 2. RAPELD. 3. Species distribution model.
I. Título.

CDD 597.96

Sinopse:

Estudamos a influência de variáveis ambientais sobre a distribuição das serpentes *Philodryas argentea* e *Philodryas georgeboulengeri*, e a sobreposição de nicho entre as espécies. Elaboramos modelo de distribuição ecológica com análises de regressão e o algoritmo de Máxima Entropia. Compilamos dados de ocorrência de ambas espécies com registros de coleções herpetológicas, bancos de dados e artigos formalmente publicados.

Palavras-chave: Amazônia, Modelo de Distribuição de espécies, Squamata

Dedico este trabalho à toda minha família,
ao meu noivo Andrew e amigos.

AGRADECIMENTOS

Agradeço ao Igor L. Kaefer não apenas pela orientação e apoio, mas pelo incentivo na carreira científica, sua paciência e dedicação ao longo da construção deste trabalho. Por ser mais que um orientador, um exemplo de cientista a ser seguido.

Ao Rafael de Fraga por todas as valiosas contribuições desde a concepção do projeto até à redação final do nosso artigo.

Ao Wellyngton Ayala que, além de amigo e colega, auxiliou em análises de dados fundamentais para a execução do trabalho.

Ao Instituto Nacional de Pesquisas da Amazônia (INPA), pela infraestrutura e apoio logístico, especialmente à coleção herpetológica do INPA-H, assim como o Museu Emílio Goeldi e a Fundação de Medicina Tropical pela disponibilização de dados.

Ao Programa de Pós-Graduação (PPG) em Biologia (Ecologia) do INPA. Por exímios professores que nos transmitem não só conhecimento mas são inspirações profissionais.

Aos amigos do PPG Ecologia, que estiveram sempre apoiando uns aos outros durante cada fase que passamos juntos, principalmente nos momentos mais difíceis.

Sou grata à Universidade Federal do Amazonas (UFAM) através do Kaefer Lab, um lugar de aprendizado, companheirismo e apoio. Especialmente aos amigos de laboratório pelo apoio emocional, receptividade e estímulo.

Aos órgãos de fomento que permitiram a execução do trabalho. À CAPES pela bolsa de mestrado. À FAPEAM e CNPq que financiaram as coletas nos módulos de amostragem (PRONEX, processo 653/2009). Ao Programa de Pesquisas em Biodiversidade (PPBio), ao Centro de Estudos Integrados da Biodiversidade Amazônica (INCT-CENBAM) e ao Instituto

Nacional de Pesquisas da Amazônia (INPA) que planejaram, instalaram e mantiveram os módulos de amostragem RAPELD e disponibilizaram publicamente os dados.

Principalmente agradeço ainda a Deus, e à minha família que sempre me apoiou e me incentivou a percorrer meus sonhos, vibrando comigo a cada conquista, me aconselhando em momentos de dúvidas. Ao meu noivo Andrew Ramos que acreditou em mim e me estimulou em cada etapa da minha evolução, demonstrando sempre o seu orgulho em cada avanço.

Aos amigos de longa data que sempre acreditaram no meu potencial, que leram meu trabalho ou me ouviram falar sobre ele incansavelmente, ainda que não entendendo por completo continuaram a me apoiar.

"Eventually, we'll realize that
If we destroy the ecosystem,
we destroy ourselves."

Jonas Salk, 1984

O papel da escala nas estimativas de sobreposição de nicho e de efeitos ambientais sobre duas espécies irmãs de serpentes Neotropicais

Resumo

A detecção de padrões ecológicos é altamente dependente da escala espacial. No entanto, o fator escala é pouco explorado em testes da influência do ambiente e em estimativas do grau de similaridade ecológica entre espécies. Neste estudo, testamos as hipóteses de que 1) a influência de variáveis ambientais sobre a distribuição de duas espécies irmãs difere entre duas escalas geográficas distintas, e 2) a sobreposição de nichos limita a coocorrência local. Como modelo utilizamos duas espécies irmãs de serpentes arborícolas com distribuição majoritariamente amazônica. Modelamos a distribuição ecológica de *Philodryas argentea* e *P. georgeboulengeri* em duas diferentes escalas espaciais: local, por meio de análise de regressão *stepwise* ao longo de um transecto de 880 km, com unidades amostrais uniformemente distribuídas; e ampla (bacia Amazônica), utilizando modelos baseados no algoritmo de Máxima Entropia. Para *P. argentea*, as variáveis que mais contribuíram para o modelo em escala local foram cobertura arbórea e altitude, enquanto amplitude anual de temperatura foi predominante em escala ampla. Para *P. georgeboulengeri*, as variáveis mais importantes em escalas local e ampla foram cobertura arbórea e altitude, respectivamente. A sobreposição de nicho entre as duas espécies foi estimada em 23%, e os nichos não foram considerados similares nem equivalentes. Concluímos que 1) a detecção das variáveis mais relevantes para a distribuição de ambas as espécies é dependente da escala espacial da abordagem; e que 2) embora limitada, a coocorrência das duas espécies em escala local é permitida pela elevada dissimilaridade entre os nichos aferida em macroescala.

Palavras-chave: Amazônia, Dipsadidae, *Philodryas*, modelo de distribuição de espécies, RAPELD.

Scale-dependent estimates of niche overlap and environmental effects on two sister species of Neotropical snakes

Abstract

Detecting ecological patterns is highly dependent on spatial scale. However, scale has been poorly explored when testing environmental influences and estimating niche overlap between species. In this study, we tested the hypotheses that 1) environmental filtering acting on species distribution differs between two different geographic scales, and 2) niche overlap limits species occurrence at local scale. As study model we used two sister-species of arboreal snakes mostly distributed in the Amazon. We modelled ecological distribution of *Philodryas argentea* and *P. georgeboulengeri* on different spatial scales: local, using stepwise regression analysis along an 880 km transect with evenly distributed sampling plots; and wide (Amazon basin), using Maximum Entropy algorithm. Variables that contributed to *P. argentea* occurrence were tree cover at local scale, and elevation for wide scale. For *P. georgeboulengeri*, the most important variable in local and wide scales were tree cover and elevation, respectively. Niche overlap was estimated at 23% and niches were not similar or equivalent. We conclude that 1) detection of the most relevant variables for distribution of both species is dependent on spatial scale approached; and 2) although limited, cooccurrence of both species at local scale seems to be allowed by the high niche dissimilarity observed in macro-scale.

Keywords: Amazonia, Dipsadidae, *Philodryas*, RAPELD, species distribution model.

Sumário

Introdução	11
1. Introduction	16
2. Methods	19
Field Sampling	16
Environmental Heterogeneity	21
Niche Overlap Analyses	24
3. Results	25
Field Sampling	25
Environmental Heterogeneity	26
Niche Overlap Analyses	28
4. Discussion	30
Acknowledgements	33
5. Literature Cited	33
Conclusão	46
Referência	47
Apendix I	53
Apendix II	55

Introdução Geral

Processos ecológicos têm sido descritos em uma variedade de escalas espaciais, e diferentes escalas potencialmente geram padrões de distribuição de espécies distintos (Chave, 2013). Proporções dos limites de distribuição espacial tendem a refletir os limites do nicho, visto que espécies podem ter densidades reduzidas ou estarem ausentes onde há redução do *fitness* causada por restrições bióticas e abióticas em diferentes escalas (Holt, 2003; Sexton *et al.*, 2009). A competição interespecífica é uma das interações bióticas que podem limitar a distribuição, porque a exclusão competitiva tende a reduzir a sobreposição de nichos entre espécies similares, por meio de segregação espacial (Elton, 1946; Normand *et al.*, 2009). Já interações abióticas podem influenciar a distribuição de espécies (e.g. Di-Bernardo *et al.*, 2007; Fraga *et al.*, 2013; Chefaoui *et al.*, 2018) por meio de filtragem ambiental. Por exemplo, ectotérmicos como serpentes e algumas de suas presas (e.g. lagartos, anfíbios) podem não tolerar certas condições de temperatura e precipitação, e por isso são filtradas ou têm fluxo gênico reduzido entre manchas de habitats (Gibbons & Semlitsch, 1987; Lillywhite, 1987; Yanosky *et al.*, 1996; Fraga *et al.*, 2017).

Em escala local, o efeito de variáveis ambientais sobre a distribuição de espécies de serpentes é pouco compreendido, devido à baixa detectabilidade das espécies mesmo com combinações entre delineamentos amostrais padronizados e grande esforço de amostragem (Fraga *et al.*, 2014). Embora seja plausível que a cobertura arbórea seja relevante para serpentes arborícolas, e que fatores edáficos sejam relevantes para espécies fossoriais, essas relações raramente são recuperadas em estudos de ecologia de comunidades (Fraga *et al.*, 2011). Até o momento, a distância de corpos d'água tem sido demonstrada como relevante na estruturação de assembleias de serpentes amazônicas (Fraga *et al.*, 2011) e uso de habitats por espécies individuais (Fraga *et al.*, 2013), provavelmente devido à sua influência na distribuição de presas potenciais como aves (Bueno *et al.*, 2012), anfíbios anuros (Rojas-Ahumada, 2012) e lagartos (Oliveira, 2017). Em escalas maiores, ainda que fatores climáticos como pluviosidade não tenham sido demonstrados como relevantes para a distribuição de espécies de serpentes, existe uma relação positiva com a disponibilidade de anuros (Parris, 2004), resultando em uma possível relação indireta de fatores climáticos com a ocorrência de serpentes (Henderson *et al.*, 1978; Gibbons & Semlitsch, 1987). Em escalas amplas, estudos sobre o efeito de variáveis ambientais em serpentes são escassos devido à histórica

dificuldade em se compilar pontos de ocorrência, especialmente em áreas de difícil acesso, como florestas tropicais (Guedes *et al.*, 2018). De fato, têm sido proposto que o uso de modelos de distribuição de espécies (SDM) em regiões pobremente amostradas pode gerar resultados pouco confiáveis, e que esses modelos deveriam ser validados por amostragens em campo (Carneiro *et al.*, 2016).

Espécies irmãs são excelentes modelos para testes de hipóteses envolvendo sobreposição e segregação de nicho, bem como de processos de competição interespecífica (Pianka, 1973; Duré & Kehr, 2004; Duré *et al.*, 2009). O compartilhamento de recursos por mais de uma espécie configura sobreposição de nichos, o que pode levar à competição interespecífica (Pianka, 1981). Nesse cenário, é necessário que as espécies difiram minimamente em seus requerimentos e tolerâncias ecológicas, a fim de possibilitar a coexistência (Pianka, 1974; Abrams, 1980; Schoener, 1983). Por exemplo, serpentes simpátricas do gênero *Philodryas* podem ter períodos de atividade e substratos de forrageio diferentes, o que tem sido sugerido como compensação adaptativa à competição (Hartmann & Marques, 2005).

O gênero *Philodryas* Wagler 1830 (Dipsadidae, Squamata) é composto por 23 espécies endêmicas da região Neotropical. São normalmente diurnas e exploram uma extensa variedade de presas, incluindo aracnídeos, peixes, tetrápodes terrestres, e até mesmo indivíduos coespecíficos (e.g., Hartmann & Marques, 2005; Laspiur *et al.*, 2012; Machado-Filho, 2015). O gênero apresenta espécies com diversos hábitos de vida, como terrestres, arborícolas e aquáticas. *Philodryas argentea* (Daudin, 1803) e *Philodryas georgeboulengeri* Grazziotin *et al.*, 2012, espécies-modelo deste estudo, são consideradas filogeneticamente irmãs, e agrupadas em um clado irmão à *Philodryas viridissima* (Linnaeus 1758) (Pyron *et al.*, 2015). Há sobreposição na distribuição geográfica das duas espécies em escala de bioma, mas não sabemos se o padrão é recuperado em escalas menores (locais e regionais), uma vez que *P. argentea* é amplamente distribuída na Amazônia e *P. georgeboulengeri* tem distribuição restrita às regiões oeste e sudoeste do bioma (Prudente *et al.*, 2008). Quanto ao uso do ambiente pelas duas espécies, observou-se que utilizam tanto o solo quanto a vegetação, sendo classificadas como arborícolas (Martins & Oliveira, 1998; Cunha & Nascimento, 1978).

Nesse estudo, procuramos adotar uma abordagem integrativa para investigar a influência de variáveis ambientais e grau de sobreposição de nicho sobre *Philodryas argentea*

e *Philodryas georgeboulengeri*, avaliando uso do hábitat e/ou efeito da heterogeneidade ambiental sobre a abundância e ocorrência das espécies, em diferentes escalas. Utilizamos tanto o método de amostragem ecológica RAPELD (Magnusson *et al.*, 2013) quanto o de distribuição potencial de espécies usando algoritmo de Entropia Máxima. Em escala espacial ampla, esperamos encontrar um padrão de sobreposição na distribuição espacial das espécies, indicando alta sobreposição de nicho. Diferentemente, em escalas regional e local, esperamos encontrar segregação tanto espacial quanto ecológica, demonstrando que a detecção de possíveis reflexos de competição depende da escala espacial de análise.

Capítulo 1

Almeida-Corrêa, T., Ayala, W.E., Fraga, R. & Kaefer, I.L. 2018.
Scale-dependent estimates of niche overlap and
environmental effects on two sister species of
Neotropical snakes. *Journal of tropical ecology*.

Scale-dependent estimates of niche overlap and environmental effects on two sister species of Neotropical snakes

Keywords: Amazon, Dipsadidae, *Philodryas*, species distribution model, RAPELD.

Thaís de Almeida Corrêa Nogueira*¹, Wellyngton Espíndola Ayala¹, Rafael de Fraga², Igor Luis Kaefer^{1,3}

¹ Programa de Pós-Graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia. Av. André Araújo 2936, Petrópolis, 69060-001, Manaus, Brazil.

² Instituto de Ciências e Tecnologia das Águas, Universidade Federal do Oeste do Pará, Av. Mendonça Furtado, Aldeia, 68040-050, Santarém, Brazil.

³ Instituto de Ciências Biológicas, Universidade Federal do Amazonas, Av. Rodrigo Octávio, 6200, Coroado I, Manaus, Brazil.

*e-mail: thais.laredo@gmail.com

Abstract

Detecting ecological patterns is highly dependent on the spatial scale of the analysis. However, the importance of scale has been poorly explored when testing environmental influences and estimating niche overlap between animal species. In this study, we tested the hypotheses that: 1) environmental influences on species distribution in two different geographic scales will be distinct, and 2) niche overlap limits species local occurrence. As a study model we used two sister species of arboreal snakes, with primarily Amazonian distributions. We modelled ecological distributions of *Philodryas argentea* and *P. georgeboulengeri* on different spatial scales: local, using regression analysis along an 880 km transect with evenly distributed sampling plots; and broad, modelling occurrence data with a Maximum Entropy algorithm. Variables that contributed to *P. argentea* occurrence were tree cover at the local scale, and elevation for broad scale. For *P. georgeboulengeri*, the most important variable at local and broad scales were tree cover and elevation, respectively. Niche overlap was estimated at 23% and niches were not similar. We conclude that: 1) detection of the most relevant variables for distribution of both species is dependent on spatial scale used; 2) although limited, cooccurrence of both species at local scale seems to be allowed by the high niche dissimilarity observed in macro-scale.

INTRODUCTION

Ecological processes have been described at a variety of spatial scales, and different scales potentially generate distinct species distribution patterns (Chave 2013). Geographic distribution limits tend to reflect niche boundaries, since species may have reduced density or be absent where there is fitness reduction due to biotic and abiotic restrictions at different scales (Holt 2003, Sexton et al. 2009). Interspecific competition is a biotic interaction that may limit distribution, because competitive exclusion tends to reduce niche overlap between similar species due to spatial segregation (Elton 1946, Normand et al. 2009). Abiotic

interactions may also influence species' distributions (e.g. Chefaoui et al. 2018, Di-Bernardo et al. 2007, Fraga et al. 2013) through environmental filters. For ectothermic forms, such as snakes, may be subject of certain environmental conditions related to the thermal environment that may filter their distributions or reduce their dispersal capacities and, consequently, restrict gene flow between populations (Fraga et al. 2017, Gibbons & Semlitsch 1987, Lillywhite 1987, Yanosky et al. 1996).

At the local scale, effects of environmental variables on snake distributions are poorly understood due to low detectability of species, even when standardized sample design is combined with substantial sampling effort (Fraga et al. 2014). Although it is likely that tree cover might be relevant to arboreal snakes, while edaphic factors might be so for fossorial species, such inter-relations are rarely recovered by community ecology studies (Fraga et al. 2011). Distance from streams has been shown to be relevant to spatial structuring of snake assemblages in Amazonia (Fraga et al. 2013), probably due to its influence on the distribution of potential prey, such as birds (Bueno et al. 2012), anuran amphibians (Rojas-Ahumada 2012) and lizards (Oliveira 2017). At the larger scale, even though climatic factors such as rainfall have not been shown to be relevant for snake species distributions, there is a positive relation between rainfall and anuran richness and density (Parris 2004), leading to a possible indirect relationship between climatic factors and snake species occurrences (Gibbons & Semlitsch 1987, Henderson et al. 1978). At the broad scale, studies of how environmental variables effect snakes are scarce, due to the historical difficulty of compiling occurrence data, especially in remote areas such as tropical forests (Guedes et al. 2018). Indeed, it has been proposed that species distribution models (SDM) based on data from poorly sampled areas can generate unreliable results, and that such models should be validated by field sampling (Carneiro et al. 2016).

Sister species are excellent models for testing hypothesis regarding niche overlap and segregation, as well as interspecific competitive interactions (Duré & Kehr 2004, Duré et al. 2009, Pianka 1973). Resource sharing by more than one species indicates niche overlap, which might lead to interspecific competition (Pianka 1981). In consequence, for species to coexist, it is necessary that they differ at least minimally in their physiological requirements and ecological tolerances (Abrams 1980, Pianka 1974, Schoener 1983). For example, sympatric snakes of genus *Philodryas* can have different activity periods and foraging substrate, which has been suggested as an adaptive response to competition minimization (Hartmann & Marques 2005).

The snake genus *Philodryas* Wagler 1830 (Dipsadidae, Squamata) consists of 23 species, all endemic to the Neotropical region. They are mostly diurnal and exploit an extensive variety of prey, including arachnids, fish, terrestrial tetrapods and even smaller conspecifics (e.g., Hartmann & Marques 2005, Laspiur et al. 2012, Machado-Filho 2015). Species of this genus may have different lifestyles, such as terrestrial, arboreal and aquatic. *Philodryas argentea* (Daudin 1803) and *Philodryas georgeboulengeri* Grazziotin et al. 2012, model-species for this study, are considered phylogenetically sister taxa, grouped in a sister clade to *Philodryas viridissima* (Linnaeus 1758) (Pyrón et al. 2015). There is an overlap in the geographic distribution of the two species at the biome scale (Amazon basin). However, we do not know whether this pattern is repeated at smaller scales (e.g., local and regional), since *P. argentea* is widely distributed in the Amazonia and *P. georgeboulengeri* has a restricted distribution in the west and southwestern regions of the biome (Prudente et al. 2008). In terms of habitat use, both species use the ground and vegetation, though they are classified as arboreal (Cunha & Nascimento 1978, Martins & Oliveira 1998).

In this study, we aimed to investigate the influence of environmental variables on *Philodryas argentea* and *Philodryas georgeboulengeri* distribution, and on the extent of niche overlap between the species. We used stepwise regressions and maximum entropy algorithms to investigate species distributions at two distinct spatial scales. We compiled occurrence data of both species with an unprecedented effort along a transect of some 880 km in the Amazon region. For both species, we expected to find that scale had an influence in determining the most relevant environmental variables affecting distribution. Additionally, we expected to find restrictions imposed by niche similarity on species co-occurrence at the local scale.

METHODS

Field Sampling

Data from *P. argentea* and *P. georgeboulengeri* were sampled between 2006 and 2015 at 21 spatially standardized sampling units (modules) that were set-up following the RAPELD method (Magnusson et al. 2013). Sampling units were located along a transect of about 880 km from Manaus (Amazonas) to Porto Velho (Rondônia), in the interfluvium between Purus and Madeira rivers (hereafter PMRI; Fig.1). The average distance between neighboring sampling units was 40 km. In total there were 298 sampling plots at 21 modules positioned along the transect.

The RAPELD sampling modules consist of two parallel trails each of 5 km length, separated by 1 km. Each trail contains seven plots, 250 m long and 10 m wide, which follow local altitudinal contours and so avoid environmental variation within the plot in such factors as soil texture and water table depth. We used modules as sampling units because of the low

detection probabilities of most of snake species in Amazonia (Fraga et al. 2014). Standardization of sampling units permits comparisons between different sampling sites, since the number of observers and observation time are standardized (Magnusson et al. 2013).

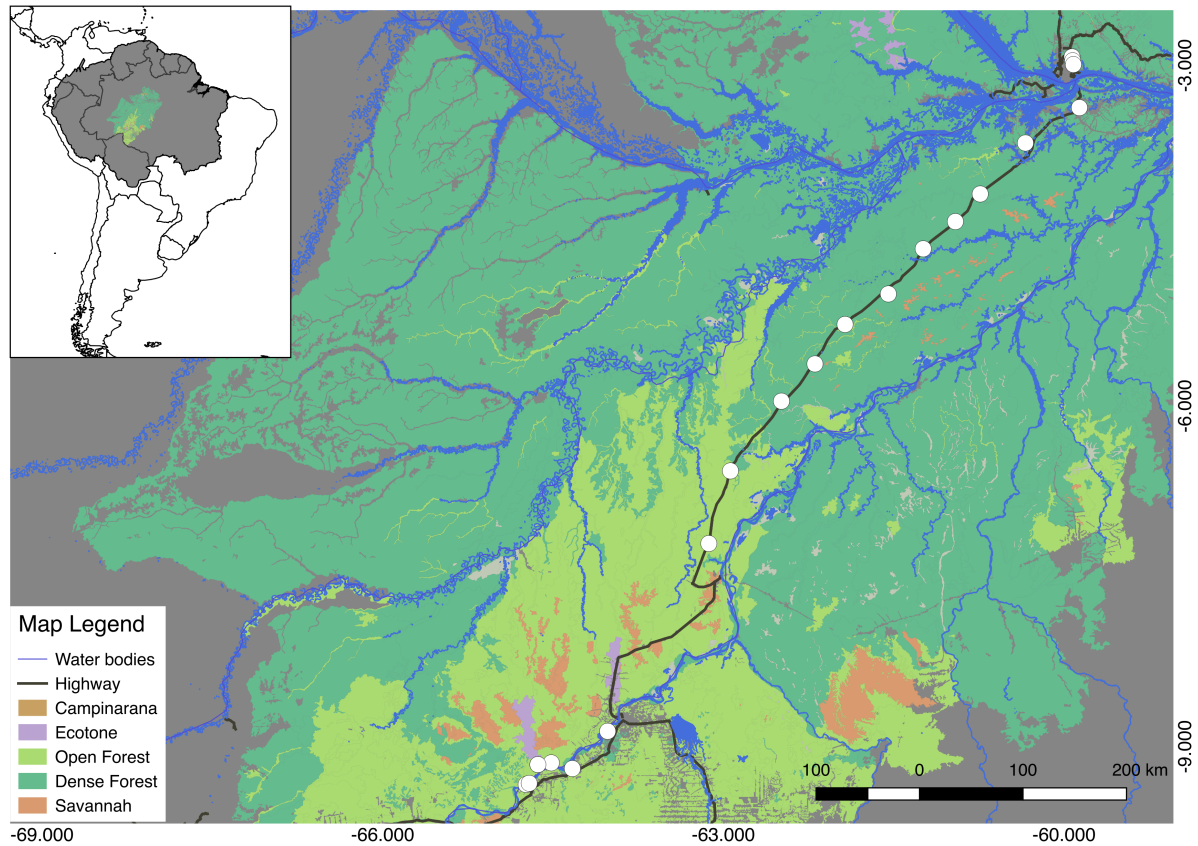


Figure 1. Sampling area with modules following the RAPELD system. White points represent sampling units (modules) with 10 to 14 plots each. Different background colors indicate vegetation types and, consequently, environmental heterogeneity in the Purus-Madeira interfluvium.

The study area is covered by primary and secondary tropical rainforest and seasonally flooded forests (IBGE 1997). The PMRI covers approximately 15.4 million hectares, and it is relatively flat at the local scale, with an elevation of 25 to 80 m (Ferrão et al. 2018, Maldonado et al. 2012).

Each plot was surveyed for 1h, with two observers simultaneously using nocturnal visual sampling (Fraga et al. 2014). Expeditions occurred at all times of the year to reduce the

influence of seasonality on species detection. We complemented our field sampling with occurrence data for both species from the herpetological collections in the Museu Paraense Emilio Goeldi (MPEG), Museu de Zoologia da Universidade de São Paulo (USP), Instituto Nacional de Pesquisas da Amazônia (INPA), Gerência de Animais Peçonhentos from Fundação de Medicina Tropical do Amazonas (FMT) and Universidade Federal de Rondônia (UNIR). Additionally, occurrence data for each species were obtained from digital public repositories SpeciesLink (<http://www.specieslink.org.br>) and Global Biodiversity Information Facility – GBIF (<http://www.gbif.org>). Geographical coordinates of each species were grouped in 5 km² quadrants in order to compare data with the RAPELD modules. Additionally, we searched for occurrence data from published article with both species coordinates. Using all the available data (field sampling, collections, digital databases and scientific articles) we constructed a map illustrating the currently known range of each species using QGis (QGis Development Team 2017).

Environmental Heterogeneity

To test for possible effects of environmental variables on the niche width and distributions of two species, we considered 19 bioclimatic variables, all known to directly affect ectothermic animals. Data were extracted from the public repository AMBDATA (<http://www.dpi.inpe.br/Ambdata>). Additionally we obtained elevation and tree cover data through Global Land Cover Facility (<http://glcf.umd.edu>), since these predictors may influence, both directly and indirectly, the availability of habitat for arboreal species. We therefore used 21 variables to represent environmental heterogeneity across the distribution of the target-species. The original resolution of the variables was 1 km², which was adjusted to

the size of the RAPELD modules (5 km²) using the *raster* package in the R computational environment (Hijmans & van Etten 2014). Variables were analysed using the Spearman Station Correlation matrix in R, and for variables with more than 80% correlation, only one was retained in the models.

For wide scale analyses, final models were composed of tree cover, elevation, annual temperature range, annual precipitation seasonality, annual precipitation and annual temperature seasonality as independent variables, and occurrence data of each species as the dependent variable. For the local scale we used the same set of independent and dependent variables for comparative purposes. Selected variables after collinearity analysis were: tree cover, elevation and annual temperature seasonality. Environmental variables selected may reflect habitat preferences and resource availability, since: 1) tree cover in turn acts directly on those arboreal species that use vertical strata for resting and foraging; 2) elevation indirectly influences vegetation structure; 3) temperature directly influences the distribution of ectothermic animals via thermoregulation, therefore potentially affects both snakes and their potential prey.

Relationships between predictor variables and species occurrence were tested with stepwise regression with both forward and backward model selection. Models were built using per species binary occurrence data (presence or absence) as response variables. Since detection probabilities for most Amazonian snakes are low, abundance data may not accurately reflect population size (Fraga et al. 2014). In the stepwise regression with bidirectional elimination, independent variables are sequentially added or removed from the model, and the best fitted model is that with the lowest AIC (Akaike Information Criterion) value. Lower AIC indicates the most relevant variables affecting species distribution, because they generate less information loss through unfitted data. We chose a statistical method based

on model selection and variables ranking because it is a similar approach to that used by the maximum entropy algorithm. This, therefore, allowed us to compare results obtained by the two spatial scales investigated here.

Habitat suitability maps were produced for each species from species distribution modeling (SDM; Vasconcelos & Nascimento 2016, Soares de Oliveira et al. 2016). Among different available approaches, the Maximum Entropy algorithm (MaxEnt) is the one that has the best performance (Hijmans & Graham 2006). MaxEnt is a machine-learning technique, which considers the presence/absence of a species in a given area as response to environmental predictors. Thus, the method reflects species occurrence as a result of environmental filtering. Samples were derived from subgroups composed of geographic coordinates with distances greater than 5 km between them, and the environmental layers. Bioclimatic data used were those from the geographical area covered by the input data.

We used the ENMeval package (Muscarella et al 2014) to automate parameter selection for use in the MaxEnt package. Model selection was made from the highest mean value of Area Under the Curve (AUC; Warren & Seifert 2011). To evaluate model accuracy, we used the Receiver Operator Characteristic (ROC) statistic, deploying the AUC of ROC with standard characteristics, except the maximum number of interactions (moved to 10,000), and cross-validation replications (10 replications used), replications mean, where 10% of the data were randomized as test data and the rest was randomized for model training in each replication (Elith et al 2010, Kearney et al 2010, Phillips & Dudík 2008). AUC values equal or greater than 0.75 indicated that the species distribution was not random but influenced by the environmental layers. The use of such results refined the model to produce one with the best predictive power (Elith et al 2006). The use of minimum AUC values, as adopted here, is considered a valid measure for species distribution estimates, whereas models reflect the

ecological niche (Jiménez-Valverde 2012). We used a Jackknife test to evaluate the importance of each variable to the model fit, with variables successively deleted to quantify increase or decrease in AUC values. We evaluated model efficiency with both absence and presence of each variable (Garcia-Callejas & Araujo 2016).

Niche Overlap Analyses

Using the suitability map obtained for each species through MaxEnt, we compared and quantified the niche of each species using the R-ecospat package (Cola et al. 2017), which allows direct comparisons of species-environment interactions (Broennimann et al. 2012). This package also allows evaluation of niche equivalency and similarity, as well as quantifying niche overlap (Warren et al. 2008). We summarized the environmental variables using Principal Components Analysis (PCA), to produce scores representing the distribution of the two species and projected them into a grid of cells delimited by the minimum and maximum values of the scores obtained to the entire study area. Niche overlap was calculated using Schoener's metric (D), which reflects relative use of particular resources (microhabitats in the current instance), so allowing direct comparison to traditional measures, as this is a very widely used niche-measure metric. Statistical significance was obtained via a randomization test, where pseudoreplicate datasets were created by randomly partitioning and then compared using similar D values (Broennimann et al. 2012). For Schoener's metric 0 indicates total niche divergence, while 1 indicates identical niches, considering that all environmental requirements are adequate for the occurrence of the two species (Godsoe & Case 2015). This method was used to test hypotheses regarding niche conservatism, this being the alternative hypotheses for niche equivalency which predicts no statistically significant

differences between alternative niche modules. For niche similarity between species it addresses whether the environmental niches occupied are more similar than would be expected by chance under a specific null model (Broennimann et al. 2012, Graham et al. 2004, Peterson et al. 1999, Warren et al. 2008). This method provides comparative information on niche dynamics between sister species or between native and invasive species (Cola et al. 2017, Guisan et al. 2014, Petitpierre et al. 2012).

RESULTS

Field Sampling

At the local scale we found 25 individuals of *P. argentea* and 47 of *P. georgeboulengeri*. *Philodryas argentea* was encountered in six field sampling modules, and *P. georgeboulengeri* in 14. Species co-occurrence was low, with the species mutually present in only two sampling modules (9.52%).

Input data for wide-scale models were set by 95 occurrence points for *P. argentea* and 22 for *P. georgeboulengeri* (Fig. 4). Adding records from public databases, herpetological collections and published papers, we produced an updated map showing the known ranges for both species (Fig. 2). *P. argentea* is widely distributed across the Amazon basin, as expected, while *P. georgeboulengeri* has distribution restricted to the central and southwest portions of the Amazon biome.

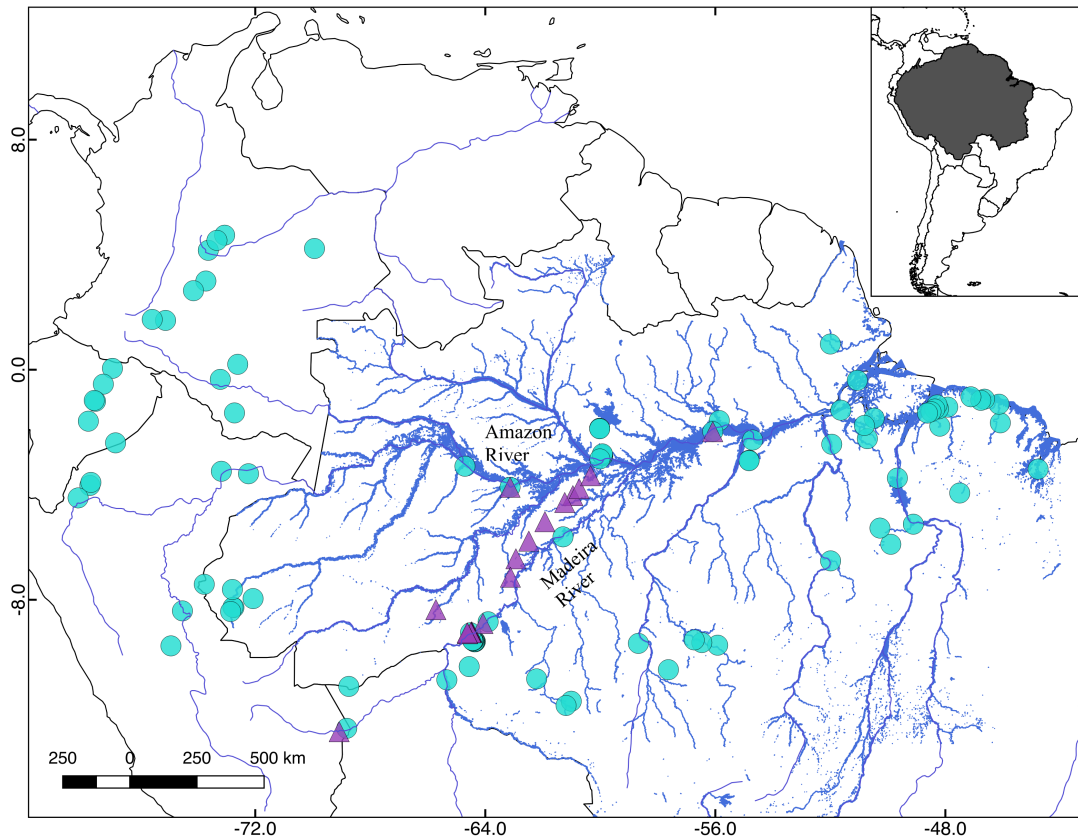


Figure 2. Geographic range of *Philodryas argentea* (blue circles) and *Philodryas georgeboulengeri* (purple triangle) based on data from scientific collections, online databases, filed surveys and published papers.

Environmental Heterogeneity

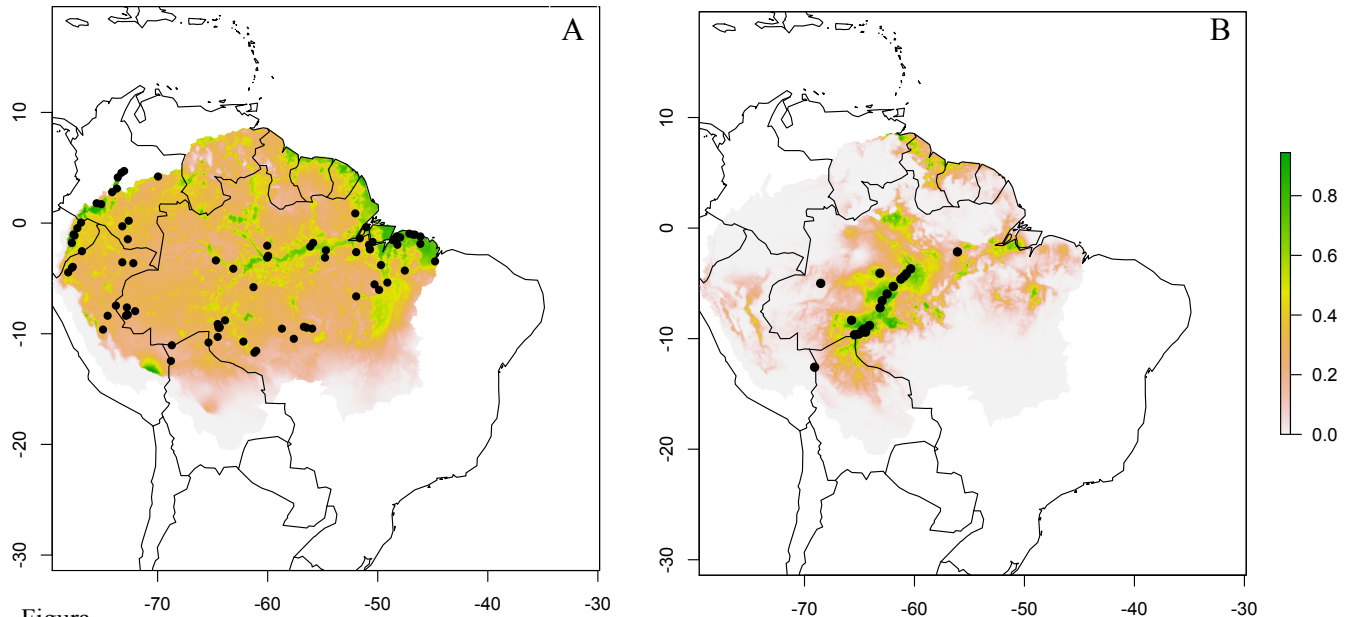
Stepwise regressions indicated that local scale distribution of *P. argentea* is best explained by tree cover and elevation ($p = 0.02$), while the best model for *P. georgeboulengeri* comprised of tree cover only ($p = 0.01$). AIC values for each stepwise model are summarized in Table 1.

Table 1. AIC values for Stepwise regressions, used to ranking environmental variables as predictors of occurrence (occur) of *Philodryas argentea* (Parg) and *P. georgeboulengeri* (Pgeo). Values in bold indicate final model for each species. The symbol ~ denotes “as a function of”.

Step	Stepwise model	Parg	Pgeo
1	occur ~ elevation + tree cover + temp. seasonality	- 41.93	-31.60
2	occur ~ elevation + tree cover	- 42.49	-33.56
3	occur ~ tree cover		- 33.68

The habitat suitability map for *P. argentea* (Fig. 3, A) suggested a wide region with medium suitability (40–60%), and multiple small and dispersed regions with high suitability (above 60%). The model returned low suitability (30–50%) for most of the PMRI, which is consistent with absence of *P. argentea* in this region. The model was mainly fitted by annual temperature range (Table 2).

In the PMRI central region, where *P. argentea* had lowest suitability, we recorded higher suitability (above 60%) for *P. georgeboulengeri*. This region extends into the sampling modules near to the Madeira river, where there is species co-occurrence (Fig. 3, A; B). The proportions of habitats suitable for *P. georgeboulengeri* were more restricted than for *P. argentea* (Fig. 3; B), and mainly associated with variation in elevation (Fig. 3; B). Habitat suitability for *P. georgeboulengeri* was low (below 20%) across a large part of the Amazon (Fig. 3; B).



Figura

3. Environmental habitat suitability for occurrence of *Philodryas argentea* (A) and *Philodryas georgeboulengeri* (B), based on 21 environmental layers. Black points represent occurrence data obtained from field-based samples.

Table 2. Percent-based contribution of each variable for species distribution models obtained by Maximum Entropy algorithm, for the tree snakes *Philodryas argentea* (Parg) and *P. georgeboulengeri* (Pgeo). Values in bold represent variables with the highest percentage of contribution to the model.

Variable	Parg	Pgeo
Annual temp. range	27.4	12.3
Tree cover	21.6	7.7
Elevation	16.9	45.6
Annual prec.	15.9	11.2
Prec. seasonal.	9.4	16.6
Temp. seasonal.	8.8	6.6

Niche Overlap Analyses

Niche overlap between species was estimated as $D = 0.23$. This finding suggests niche partitioning, which was supported by the equivalence ($p = 1$) and similarity analyses ($1 \leftarrow 2$, $p = 0.13$; $1 \rightarrow 2$, $p = 0.30$; see Appendix 2). Both alternative hypothesis were rejected in this study, indicating that the niches of the two sister species are statistically significantly different, and that the observed niche differentiation between species is result of habitat selection/suitability (Peterson et al. 1999, Warren et al. 2008). We found that *P. georgeboulengeri* has a narrower niche than *P. argentea*, because suitable habitats for this species have lower amplitudes of environmental variation. Tree cover influenced both species occurrence positively. However, only *P. argentea* was also positively influenced by annual precipitation and temperature. Elevation negatively influenced the ecological niche of *P. georgeboulengeri* (Fig. 3). For PCA correlation circle and similarity analyses, see appendix S2.

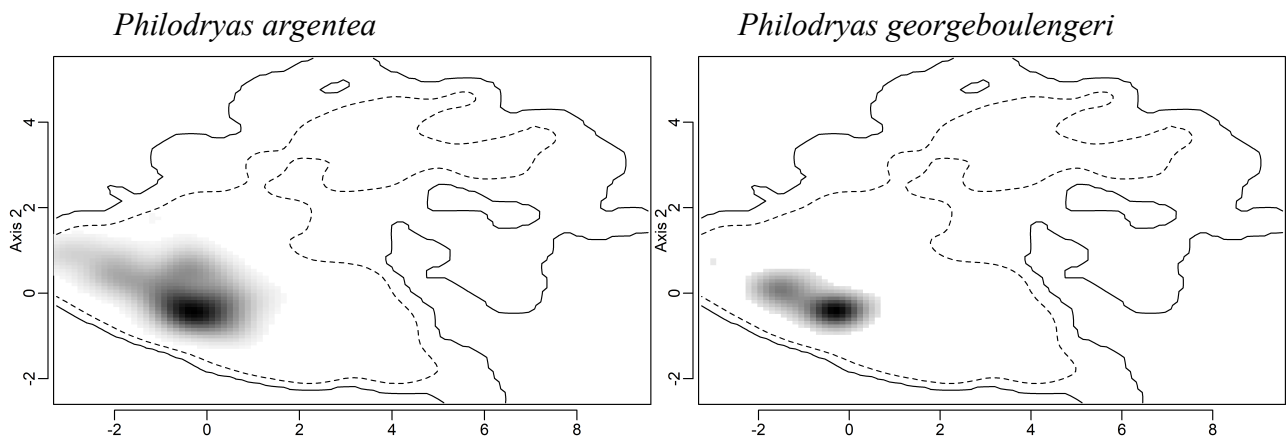


Figure 3. Results of the “within-environment” PCA niche equivalency analyses between sister-taxa *Philodryas argentea* (a) and *Philodryas georgeboulengeri* (b). Shading reflects density/per cell of each species occurrences. Solid and dashed contour lines reflect, respectively, 100% and 50% of available environment.

DISCUSSION

We found spatial segregation, determined by environmental heterogeneity, to be present between the two species of *Philodryas* studied here. These were present at both the local (RAPELD modules) and broad scales (Amazon basin). At the local scale, tree cover percentage determined distribution of both species, although *P. argentea* was also influenced by elevation. At the broad scale, habitat suitability for *P. argentea* was mainly defined by annual temperature amplitude, while elevation was the variable that mostly contributed to the *P. georgeboulengeri* model. These findings were associated with the fact that there is 77% niche partitioning between the species, although they are sympatric in a small region of the upper Rio Madeira. Niche partitioning has been suggested as one of the main factors segregating distributions of phylogenetically closely-related species, mainly through resources competition (Cahill et al. 2008, Darwin 1859, Mayfield & Levine 2010, Webb et al. 2002), although levels of ancestral niche conservatism might also be expected (Wiens & Graham 2005).

Local variation in tree cover percentage is expected to indirectly affect biodiversity, because it causes variation in such factors as light intensity and prey availability (Foley et al. 2005, Mayaux et al. 2005, Sala et al. 2000). Specifically for the *Philodryas* species studied here, tree cover is expected to determine availability of foraging and resting sites (Machado-Filho 2015, Martins & Oliveira 1998), and so affect snake populations positively and directly. The pronounced effect of elevation on local occurrence of *P. argentea* is mainly due to its restricted distribution at local scale, isolated to extremities of the transect sampled, where elevation is higher (Bertani et al. 2013, Ferrão et al. 2018). This species is absent from the PMRI lowlands, where habitat suitability is low for *P. argentea* but high for *P.*

georgeboulengeri at the broad scale. These findings suggest that elevation is the determining factor distribution at different spatial scales for these sister-species, because the absence of *P. argentea* in certain regions of the gradient coincident with the niche occupied *P. georgeboulengeri*.

At broad scale, the large contribution of extent of annual temperature variation to the model of *P. argentea* distribution seems to be related to the species wide distribution throughout the Amazon basin. This finding reflects the high sensitivity to temperature variation-that characterizes ectothermic animals (Shine & Lambeck 1990, Tattersall & Cadena 2010). A similar pattern was not recovered at the local scale probably because temperature variation is low at the sampled area. On the other hand, the distribution model for *P. georgeboulengeri* is more influenced by elevation, possibly because the species distribution is restricted to the lowlands of southwestern Amazonia.

Modelled niches were neither equivalent nor similar between species, which was supported by low niche overlap. These results were consistent with the fact that, despite their phylogenetic proximity (Pyron et al. 2015), different environmental variables were associated with the distribution of each species. Since the phylogenetic niche conservatism theory (Wiens & Graham 2005) indicates that sister species will share characteristics from the common ancestor, a high between-niche similarity was expected for the two *Philodryas* analysed (Machado-Filho 2015). However, the species are spatially segregated at both broad and local scales, even though they were sympatric in some sampling modules. Co-occurrence might be related to relaxation of a possible competition provided by a combination of high local abundance and diversity of prey (Machado-Filho 2015, Martins & Oliveira 1998).

Exclusive occurrence of *P. georgeboulengeri* along a large portion of the sampled transect indicates that this species might be a superior competitor under conditions of low

elevation and other related characteristics that were not evaluated in this study, such as resources availability. Under such circumstances, our hypothesis is that *P. argentea* was locally excluded or forced to emigrate from PMRI, by competition in the past. Such a hypothesis is supported by the fact that *P. georgeboulengeri* is more recent phylogenetically (Pyron et al. 2015), and more specialized in habitat use (this study) than *P. argentea* although there is no information on diet. Alternatively, environmental filtering may have influenced the distribution of both species through different levels of physiological tolerance to habitat conditions. The wide distribution of *P. argentea* across a series of widely-different habitats indicates that this species is highly tolerant of the form and extent of environmental variation that occurs in the complex rainforests of the Amazon basin. However, a high sensitivity to environmental variation for *P. georgeboulengeri* restricts its distribution to a relatively small area with low elevations.

Our results are relevant for conservation, especially for *P. georgeboulengeri*. Tree cover determines the distribution of this species, and suitable habitats are restricted to an area threatened by current anthropic actions. Although the PMRI region currently has 28 protected areas (Gordo & Santos Pereira 2015, Waldez et al. 2013, Graça et al. 2014), and has one of the highest incidences of endemism in Amazonia (Graça et al. 2014), the region is being severely deforested for hydroelectric production and highway construction (Fearnside & Graça 2006, Fearnside 2014). Projected estimates are that more than 5.4 millions hectares of forest in the region will be removed by 2050 (Maldonado et al. 2012). Additionally, because of global climate change, the potential effects of temperature on distribution is also a concern. In both scenarios we expect that *P. georgeboulengeri* may experience population decline due to habitat loss, which is critical for a species with narrow geographic and environmental ranges.

We have shown that combining different spatial scales can be a promising and complementary approach when refining our knowledge of biodiversity distribution. This is especially relevant for such neglected taxa as snakes, where knowledge is still highly deficient in tropical regions (Guedes et al. 2018). The recent availability of large amounts of species occurrence data (e.g. GBIF, SpeciesLink), allied to a regular distribution of standardized sampling units in remote regions (Magnusson et al. 2013), should allow a much more extensive and applied use of models testing extension and contraction of ecological niches and allow this to be applied as a framework for decision-making in conservation.

ACKNOWLEDGEMENTS

We are grateful to M. Ferrão, J. Dayrell, E. Farias, M.C. Araújo, P.I. Simões, M. Antunes, D. Bower, Pinduca, Neneco, Rubico, Joãozinho and Philip Gleason for fieldwork assistance. Fieldwork was supported by FAPEAM/CNPq - PRONEX-processo 653/2009. For logistical and institutional support we thank Programa de Pesquisa em Biodiversidade (PPBio), the National Institute for Science, Technology and Innovation for Amazonian Biodiversity (INCT-CENBAM), National Institute of Amazonian Research (INPA) and Programa de Grande Escala da Biosfera - Atmosfera na Amazônia (LBA). Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – CAPES provided a scholarship to T. A. Corrêa-Almeida. Adrian Barnett helped with the English.

Literature Cited

ABRAMS, P. 1980. Some comments on measuring niche overlap. *Ecology*. 61(1):44-49.

BERTANI, C. T., ROSSETTI, F. D. & ALBUQUERQUE, P. C. G. 2013. Object-based classification of vegetation and terrain topography in Southwestern Amazonia (Brazil) as a tool for detecting ancient fluvial geomorphic features. *Computers & Geosciences*. 60:41-50.

BROENNIMANN, O., FITZPATRICK, M. C., PEARMAN, P. B., PETIPIERRE, B., PELLISSIER, L., YOCCOZ, N. G., THUILLER, W., FORTIN, M. J., RANDIN, C., ZIMMERMANN, N. E. & GRAHAM, C. H. 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography*. 21(4):481-497.

BUENO, A. S., BRUNO, R. S., PIMENTEL, T. P., SANAIOTTI, T. M. & MAGNUSSON, W. E. 2012. The width of riparian habitats for understory birds in an Amazonian forest. *Ecological Applications*. 22(2):722-734.

CAHILL J. F., KEMBEL S. W., LAMB E. G. & KEDDY P. 2008. Does phylogenetic relatedness influence the strength of competition among vascular plants? *Perspectives in Plant Ecology, Evolution and Systematics*. 10: 41–50.

CARNEIRO, L. R. D. A., LIMA, A. P., MACHADO, R. B. & MAGNUSSON, W. E. 2016. Limitations to the use of species-distribution models for environmental-impact assessments in the Amazon. *PloS one*. 11(1):p.e0146543.

CHAVE, J. 2013. The problem of pattern and scale in ecology: what have we learned in 20 years? *Ecology Letters*. 16(s1):4-16.

CHEFAOUI, R. M., HOSSEINZADEH, M. S., MASHAYEKHI, M., SAFAEI-MAHROO, B. & KAZEMI, S. M. 2018. Identifying suitable habitats and current conservation status of a rare and elusive reptile in Iran. *Amphibia-Reptilia*. 39(3): 355-362. doi: 10.1163/15685381-17000185.

DI COLA, V., BROENNIMANN, O., PETITPIERRE, B., BREINER, F. T., D'AMEN, M., RANDIN, C., ENGLER, R., POTTIER, J., PIO, D., DUBUIS, A. & PELLISSIER, L. 2017. ecospat: an R package to support spatial analyses and modeling of species niches and distributions. *Ecography*. 40(6):774-787.

CUNHA, O. R. & NASCIMENTO, F .P. 1978. Ofídios da Amazônia X - As cobras da região leste do Pará. *Publicação Avulsa do Museu Paraense Emílio Goeldi*. 31:1-218.

DARWIN, C. 1859. *The Origin of Species*. Modern Library. New York.

DI-BERNARDO, M., BORGES-MARTINS, M., OLIVEIRA, R. B. & PONTES, G. M. F. 2007. Taxocenoses de serpentes de regiões temperadas do Brasil. In: L. B. NASCIMENTO & M. E. OLIVEIRA (Eds.). *Herpetologia no Brasil II*. Belo Horizonte: Sociedade Brasileira de Herpetologia. PUC Minas & Conservação Internacional. 222-263.

- DURÉ, M. I. & KEHR, A. I. 2004. Influence of microhabitat on the trophic ecology of two leptodactylids from northeastern Argentina. *Herpetologica*. 60(3):295-303.
- DURÉ, M. I., KEHR, A. I. & SCHAEFER, E. F. 2009. Niche overlap and resource partitioning among five sympatric bufonids (Anura, Bufonidae) from northeastern Argentina. *Phyllomedusa: Journal of Herpetology*. 8(1):27-39.
- ELITH, J., GRAHAM, C. H., ANDERSON, R. P., DUDÍK, M., FERRIER, S., GUISAN, A., HIJMANS, R. J., HUETTMANN, F., LEATHWICK, J. R., LEHMANN, A. & LI, J. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography*. 129-151.
- ELITH, J., KEARNEY, M. & PHILIPS, S. 2010. The art of modelling range-shifting species. *Methods in Ecology and Evolution*. 1(4):330-342.
- ELTON, C. 1946. Competition and the structure of ecological communities. *The Journal of Animal Ecology*. 54-68.
- FEARNSIDE, P. M. 2014. Impacts of Brazil's Madeira River Dams: Unlearned lessons for hydroelectric development in Amazonia. *Environmental Science & Policy*, 38: 164-172.
- FEARNSIDE, P. M. & GRAÇA, P. M. L. 2006. BR-319: Brazil's Manaus-Porto Velho Highway and the potential impact of linking the arc of deforestation to central Amazonia. *Environmental Management*. 38(5): 705-716

FERRÃO, M., FRAGA, R., MORAVEC, J., KAEFER, I. L. & LIMA, A. P. 2018. A new species of Amazonian snouted treefrog (Hylidae: *Scinax*) with description of a novel species-habitat association for an aquatic breeding frog. PeerJ. 6:p.e4321.

FOLEY, J. A., DEFRIES, R., ASNER, G. P., BARFORD, C., BONAN, G., CARPENTER, S. R., CHAPIN, F. S., COE, M. T., DAILY, G. C., GIBBS, H. K. & HELKOWSKI, J. H. 2005. Global consequences of land use. Science. 309(5734): 570-574.

FRAGA, R., LIMA, A. P. & MAGNUSSON, W. E. 2011. Mesoscale spatial ecology in a tropical snake assemblage: the width of riparian corridors in central Amazon. Herpetological Journal. 21:51-57.

FRAGA, R., MAGNUSSON, W. E., ABRAHÃO, C. R., TANIA, S. & LIMA, A. P. 2013. Habitat Selection by *Bothrops atrox* (Serpentes: Viperidae) in Central Amazonia, Brazil. Copeia. 4:684-690.

FRAGA, R., STOW, A. J., MAGNUSSON, W. E. & LIMA, A. P. 2014. The costs of evaluating species densities and composition of snakes to assess development impacts in Amazonia. PloS one. 9(8):e105453.

FRAGA, R. 2016. Diversidade regional de serpentes na Amazônia: uma abordagem multidimensional com implicações para conservação. Tese de Doutorado. Instituto Nacional de Pesquisas da Amazônia.

FRAGA, R., LIMA, A. P., MAGNUSSON, W. E., FERRÃO, M. & STOW, A. J. 2017. Contrasting Patterns of Gene Flow for Amazonian Snakes That Actively Forage and Those That Wait in Ambush. *Journal of Heredity*. 108(5): 524-534.

GARCÍA-CALLEJAS, D. & ARAÚJO, M. B. 2016. The effects of model and data complexity on predictions from species distributions models. *Ecological Modelling*. 326:4-12.

GIBBONS, J., SEMLITSCH, R. 1987. Activity patterns. 396–421. In: SEIGEL, R. A., J. T. COLLINS, & S. NOVAK, editors. (Eds.). *Snakes: ecology and evolutionary biology*. MacMillan Publishing Company, New York.

GODSOE, W. & CASE, B. S. 2015. Accounting for shifts in the frequency of suitable environments when testing for niche overlap. *Methods in Ecology and Evolution*. 6(1):59-66.

GORDO, M. & SANTOS PEREIRA, H. 2015. *Unidades de Conservação do Amazonas no Interflúvio Purus-Madeira: Diagnóstico Biológico*.

GRAÇA, P. M. L. A., SANTOS JR., M. A., ROCHA, V. M., FEARNSIDE, P. M., EMILIO, T., MENGER, J. S., MARCIENTE, R., BOBROWIEC, P. E. D., VENTICINQUE, E. M., ANTUNES, A. P., BASTOS, A. N. & ROHE, F. 2014. Cenários de desmatamento para região de influência da rodovia BR-319: perda potencial de habitats, status de proteção e ameaça para a biodiversidade. pp. 91-101 In: T. Emilio & F. Luizão (eds.). *Cenários para a*

Amazônia: Clima, Biodiversidade e Uso da Terra. Editora INPA, Manaus, Amazonas, Brasil.

194 pp.

GRAHAM, C. H., RON, S. R., SANTOS, J. C., SCHNEIDER, C. J. & MORITZ, C. 2004.

Integrating phylogenetics and environmental niche models to explore speciation mechanisms in dendrobatid frogs. *Evolution*. 58(8):1781-1793.

GUEDES, T. B., BARBO, F. E., FRANCA, D. & ZAHER, H. 2018. Morphological variation of the rare psammophilous species *Apostolepis gaboi* (Serpentes, Dipsadidae, Elapomorhini). *Zootaxa*. 4418(5):469-480.

GUISAN, A., PETITPIERRE, B., BROENNIMANN, O., DAEHLER, C. & KUEFFER, C. 2014. Unifying niche shift studies: insights from biological invasions. *Trends in Ecology & Evolution*. 29(5):260-269.

HARTMANN, P. A. & MARQUES, O. A. V. 2005. Diet and Habitat use of two sympatric species of *Philodryas* (Colubridae), in south Brazil. *Amphibia-Reptilia*. 26:25-31.

HENDERSON, R. W., DIXON, J. R. & SOINI, P. 1978. On the seasonal incidence of tropical snakes. *Milwaukee Public Museum Contribution in Biology and Geology*. 17(1):1-15.

HIJMANS, R. J. & GRAHAM, C. H. 2006. The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology*. 12(12):2272-2281.

HIJMANS, R. J. & VAN ETTEN, J. 2014. raster: Geographic data analysis and modeling. R package version. 2. 15.

HOLT, R. D. 2003. On the evolutionary ecology of species' ranges. *Evolutionary ecology research*. 5(2):159-178.

IBGE, 1997. Recursos naturais e meio ambiente: uma visão do Brasil. Instituto Brasileiro de Geografia e Estatística. 2:208.

JIMÉNEZ-VALVERDE, A. 2012. Insights into the area under the receiver operating characteristic curve (AUC) as a discrimination measure in species distribution modelling. *Global Ecology and Biogeography*. 21(4):498-507.

KEARNEY, M. R., WINTLE, B. A. & PORTER, W. P. 2010. Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conservation Letters*. 3(3):203-213.

LASPIUR, A., ACOSTA, J. C. & FAVA, G. A. 2012. *Philodryas trilineata* argentine mousehole snake diet. *Herpetological Review*. 43(1):151-152.

LILLYWHITE, H. B. 1987. Temperature, energetics and physiological ecology. In: SEIGEL, R. A., COLLINS, J. T. & NOVAK S. S. eds. *Snakes: Ecology and Evolutionary Biology*. New York. McGraw-Hill. 422-477.

MACHADO-FILHO, P. R. 2015. Evolução do hábito alimentar e utilização do substrato pelo gênero *Philodryas* Wagler, 1830. Dissertação de Mestrado. UNESP. São José do Rio Preto. São Paulo. 98.

MAGNUSSON, W. E., PEZZINI, R. B. N., BACCARO, F. B., BERGALLO, F., PENHA, H., RODRIGUES, J., et al. 2013. Biodiversidade e Monitoramento Ambiental Integrado: O Sistema RAPELD na Amazônia.

MALDONADO, F. D., KEIZER, E. W. H., GRAÇA, P. M. L. D. A., FEARNSIDE, P. M. & VITEL, C. S. 2012. Previsão temporal da distribuição espacial do desmatamento no interflúvio Purus-Madeira até o ano 2050. Junior, WCDS, AV WAICHMAN, et al. Rio Purus: Águas, Território e Sociedade na Amazônia Sul Ocidental. 183-196.

MARTINS, M. & OLIVEIRA, M. E. 1998. Natural History of Snakes in Forests of the Manaus Region, Central Amazonia, Brazil. Herpetological Natural History. 6(2):78-150.

MAYAUX, P., HOLMGREN, P., ACHARD, F., EVA, H., STIBIG, H. J. & BRANTHOMME, A. 2005. Tropical forest cover change in the 1990s and options for future monitoring. Philosophical Transactions of the Royal Society of London B: Biological Sciences. 360(1454):373-384.

MAYFIELD, M. M. & LEVINE, J. M. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*. 13:1085–1093. doi: 10.1111/j.1461-0248.2010.01509.x

MUSCARELLA, R., GALANTE, P. J., SOLEY-GUARDIA, M., BORJA, R. A., KASS, J. M., URIARTE, M. & ANDERSON, R. P. 2014. ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. *Methods in Ecology and Evolution*. 5(11):1198-1205.

NORMAND, S., TREIER, U. A., RANDIN, C., VITTOZ, P., GUISAN, A. & SVENNING, J. C. 2009. Importance of abiotic stress as a range-limit determinant for European plants: insights from species responses to climatic gradients. *Global Ecology and Biogeography*. 18(4):437-449.

OLIVEIRA, A. S. F. D. 2017. Uso da zona ripária como fator determinante da estrutura de uma assembleia de lagartos em área de terra-firme na Amazônia Central.

PARRIS, K. M. 2004. Environmental and spatial variables influence the composition of frog assemblages in sub-tropical eastern Australia. *Ecography*. 27:392-400. doi:[10.1111/j.0906-7590.2004.03711.x](https://doi.org/10.1111/j.0906-7590.2004.03711.x)

PETERSON, A. T., SOBERÓN, J. & SÁNCHEZ-CORDERO, V. 1999. Conservatism of ecological niches in evolutionary time. *Science*. 285(5431):1265-1267.

PETITPIERRE, B., KUEFFER, C., BROENNIMANN, O., RANDIN, C., DAEHLER, C. &

GUISAN, A. 2012. Climatic niche shifts are rare among terrestrial plant invaders. *Science*. 335(6074):1344-1348.

PHILLIPS, S. J. & DUDÍK, M. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*. 31:161-75.

PIANKA, E. R. 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics*. 4:53-74.

PIANKA, E. R. 1974. Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences*. 71(5):2141-2145.

PIANKA, E. R. 1981. Competition and niche theory. *Ariel*. 128:205-172.

PRUDENTE, A. L. C., SILVA, M. A. A., ROCHA, W. A. & FRANCO, F. L. 2008. Morphological variation in *Xenoxybelis boulengeri* (Procter, 1923)(Serpentes, Xenodontinae, Philodryadini). *Zootaxa*. 1743:53-61.

PYRON, R. A., GUAYASAMIN, J. M., PEÑAFIEL, N., BUSTAMANTE, L. & ARTEAGA, A. 2015. Systematics of *Nothopsini* (Serpentes, Dipsadidae), with a new species of *Synophis* from the Pacific Andean slopes of southwestern Ecuador. *ZooKeys*. 541:109-147. <http://doi.org/10.3897/zookeys.541.6058>

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: <https://www.R-project.org/>.

ROJAS-AHUMADA, D. P., MAGNUSSON, W. E. & MENIN, M. 2012. Role of environmental and spatial processes in structuring anuran communities across a tropical rain forest. *Austral Ecology*. 37:865-873.

SALA, O. E., CHAPIN, F. S., ARMESTO, J. J., BERLOW, E., BLOOMFIELD, J., DIRZO, R., HUBER-SANWALD, E., HUENNEKE, L. F., JACKSON, R. B., KINZIG, A. & LEEMANS, R. 2000. Global biodiversity scenarios for the year 2100. *Science*. 287(5459): 1770-1774.

SCHOENER, T. W. 1983. Field experiments on interspecific competition. *American Naturalist*. 240-285.

SEXTON, J. P., MCINTYRE, P. J., ANGERT, A. L. & RICE, K. J. 2009. Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics*. 40:415-436.

SHINE, R. & LAMBECK, R. 1990. Seasonal shifts in the thermoregulatory behaviour of Australian blacksnakes, *Pseudechis porphyriacus* (Serpentes: Elapidae). *Journal of Thermal Biology*. 15(3-4):301-305.

SOARES DE OLIVEIRA, I., RÖDDER, D., CAPINHA, C., AHMADZADEH, F., KARLOKOSKI CUNHA DE OLIVEIRA, A. & TOLEDO, L. F. 2016. Assessing future habitat availability for coastal lowland anurans in the Brazilian Atlantic rainforest. *Studies on neotropical fauna and environment*. 51(1):45-55.

TATTERSALL, G. J. & CADENA, V. 2010. Insights into animal temperature adaptations revealed through thermal imaging. *The Imaging Science Journal*. 58(5):261-268.

VASCONCELOS, T. S. & NASCIMENTO, B. T. 2016. Potential climate-driven impacts on the distribution of generalist treefrogs in South America. *Herpetologica*. 72(1):23–31. DOI:10.1655/HERPETOLOGICA-D-14-00064

WALDEZ, F., MENIN, M. & VOGT, R. C. 2013. Diversidade de anfíbios e répteis Squamata na região do baixo rio Purus, Amazônia Central, Brasil. *Biota Neotropica*, 13(1).

WARREN, D. L., GLOR, R. E. & TURELLI, M. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution*. 62(11):2868-2883.

WARREN, D. L. & SEIFERT, S. N. 2011. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological Applications*. 21(2):335-342.

WEBB, C. O., ACKERLY, D. D., MCPEEK, M. A. & DONOGHUE, M. J. (2002).

Phylogenies and community ecology. *Ann. Rev. Ecol. Evol. Syst.* 33: 475–505.

WIENS, J. J. & GRAHAM, C. H. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution and Systematics.* 36:519-539.

YANOSKY, A. A., DIXON, J. R. & MERCOLLI, C. 1996. Ecology of the snake community at El Bagual Ecological Reserve, northeastern Argentina. *Herpetological Natural History.* 4(2):97-110.

Conclusão geral

Modelar a distribuição de espécies em regiões tropicais de difícil acesso na Amazônia representa um grande desafio, especialmente quando se leva em consideração a baixa detectabilidade de serpentes como as duas espécies de *Philodryas* estudadas. No entanto, nós mostramos que combinar dados provenientes de amostragem padronizada e pontos de ocorrência das espécies obtidos em bancos de dados, é útil e eficiente para investigar fatores que determinam a distribuição de espécies em escala local e ampla, bem como diferenças nos requerimentos e tolerâncias ecológicas que compõem os nichos de cada espécie. Em relação aos objetivos da pesquisa, concluímos que: 1) a detecção das variáveis mais relevantes para a distribuição de ambas as espécies é dependente da escala espacial da abordagem; e que 2) embora limitada, a coocorrência das duas espécies em escala local é permitida pela elevada dissimilaridade entre os nichos aferida em macroescala.

Philodryas argentea é amplamente distribuída por florestas densas da Amazônia, o que sugere que é uma espécie generalista em relação à grande proporções de heterogeneidade ambiental. Entretanto, interações competitivas no passado ou filtragem ambiental provavelmente excluíram essa espécie da região de baixas altitudes do PMRI, onde foi

substituída por *P. georgeboulengeri*. Por sua vez, essa espécie têm distribuição restrita pela variação na cobertura arbórea dentro do PMRI, o que causa preocupação em relação à conservação. A intensidade alta do desmatamento previsto para as próximas décadas no PMRI provavelmente causará declínio populacional por perda de habitats. Estudos futuros devem focar em modelagens evolutivas de nichos para estimar o impacto de alterações antropogênicas de habitats sobre as estruturas populacionais das duas espécies.

Referências

ABRAMS, P. 1980. Some comments on measuring niche overlap. *Ecology*, 61(1):44-49.

BUENO, A. S., BRUNO, R. S., PIMENTEL, T. P., SANAIOTTI, T. M. & MAGNUSSON, W. E. 2012. The width of riparian habitats for understory birds in an Amazonian forest. *Ecological Applications*, 22(2):722-734.

CARNEIRO, L. R. D. A., LIMA, A. P., MACHADO, R. B. & MAGNUSSON, W. E. 2016. Limitations to the use of species-distribution models for environmental-impact assessments in the Amazon. *PloS one*, 11(1):p.e0146543.

CHAVE, J. 2013. The problem of pattern and scale in ecology: what have we learned in 20 years? *Ecology Letters*, 16(s1):4-16.

CHEFAOUI, R. M., HOSSEINZADEH, M. S., MASHAYEKHI, M., SAFAEI-MAHROO, B. & KAZEMI, S. M. 2018. Identifying suitable habitats and current conservation status of a rare and elusive reptile in Iran. *Amphibia-Reptilia*, 39(3): 355-362. doi: 10.1163/15685381-17000185.

- CUNHA, O. R. & NASCIMENTO, F. P. 1978. Ofídios da Amazônia X - As cobras da região leste do Pará. *Publicação Avulsa do Museu Paraense Emílio Goeldi*, 31:1-218.
- DI-BERNARDO, M., BORGES-MARTINS, M., OLIVEIRA, R. B. & PONTES, G. M. F. 2007. Taxocenoses de serpentes de regiões temperadas do Brasil. In: L. B. NASCIMENTO & M. E. OLIVEIRA (Eds.). *Herpetologia no Brasil II*. Belo Horizonte: Sociedade Brasileira de Herpetologia. *PUC Minas & Conservação Internacional*, 222-263.
- DURÉ, M. I. & KEHR, A. I. 2004. Influence of microhabitat on the trophic ecology of two leptodactylids from northeastern Argentina. *Herpetologica*, 60(3):295-303.
- DURÉ, M. I., KEHR, A. I. & SCHAEFER, E. F. 2009. Niche overlap and resource partitioning among five sympatric bufonids (Anura, Bufonidae) from northeastern Argentina. *Phyllomedusa: Journal of Herpetology*, 8(1):27-39.
- ELTON, C. 1946. Competition and the structure of ecological communities. *The Journal of Animal Ecology*, 54-68.
- FRAGA, R., LIMA, A. P. & MAGNUSSON, W. E. 2011. Mesoscale spatial ecology in a tropical snake assemblage: the width of riparian corridors in central Amazon. *Herpetological Journal*, 21:51-57.

- FRAGA, R., MAGNUSSON, W. E., ABRAHÃO, C. R., TANIA, S. & LIMA, A. P. 2013. Habitat Selection by *Bothrops atrox* (Serpentes: Viperidae) in Central Amazonia, Brazil. *Copeia*, 4:684-690.
- FRAGA, R., STOW, A. J., MAGNUSSON, W. E. & LIMA, A. P. 2014. The costs of evaluating species densities and composition of snakes to assess development impacts in Amazonia. *PloS one*, 9(8):e105453.
- FRAGA, R., LIMA, A. P., MAGNUSSON, W. E., FERRÃO, M. & STOW, A. J. 2017. Contrasting Patterns of Gene Flow for Amazonian Snakes That Actively Forage and Those That Wait in Ambush. *Journal of Heredity*, 108(5): 524-534.
- GIBBONS, J., SEMLITSCH, R. 1987. Activity patterns. 396–421. In: SEIGEL, R. A., J. T. COLLINS, & S. NOVAK, editors. (Eds.). Snakes: ecology and evolutionary biology. *MacMillan Publishing Company*, New York.
- GUEDES, T. B., BARBO, F. E., FRANCA, D. & ZAHER, H. 2018. Morphological variation of the rare psammophilous species *Apostolepis gaboi* (Serpentes, Dipsadidae, Elapomorhini). *Zootaxa*, 4418(5):469-480.
- HARTMANN, P. A. & MARQUES, O. A. V. 2005. Diet and Habitat use of two sympatric species of *Philodryas* (Colubridae), in south Brazil. *Amphibia-Reptilia*, 26:25-31.

HENDERSON, R. W., DIXON, J. R. & SOINI, P. 1978. On the seasonal incidence of tropical snakes. *Milwaukee Public Museum Contribution in Biology and Geology*, 17(1):1-15.

HOLT, R. D. 2003. On the evolutionary ecology of species' ranges. *Evolutionary ecology research*, 5(2):159-178.

LASPIUR, A., ACOSTA, J. C. & FAVA, G. A. 2012. *Philodryas trilineata* argentine mousehole snake diet. *Herpetological Review*, 43(1):151-152.

LILLYWHITE, H. B. 1987. Temperature, energetics and physiological ecology. In: SEIGEL, R. A., COLLINS, J. T. & NOVAK S. S. eds. *Snakes: Ecology and Evolutionary Biology*, New York. McGraw-Hill. 422-477.

MACHADO-FILHO, P. R. 2015. Evolução do hábito alimentar e utilização do substrato pelo gênero *Philodryas* Wagler, 1830. Dissertação de Mestrado. UNESP. São José do Rio Preto. São Paulo. 98.

MAGNUSSON, W. E., PEZZINI, R. B. N., BACCARO, F. B., BERGALLO, F., PENHA, H., RODRIGUES, J., et al. 2013. Biodiversidade e Monitoramento Ambiental Integrado: O Sistema RAPELD na Amazônia.

MARTINS, M. & OLIVEIRA, M. E. 1998. Natural History of Snakes in Forests of the Manaus Region, Central Amazonia, Brazil. *Herpetological Natural History*. 6(2):78-150.

NORMAND, S., TREIER, U. A., RANDIN, C., VITTOZ, P., GUISAN, A. & SVENNING, J. C. 2009. Importance of abiotic stress as a range-limit determinant for European plants: insights from species responses to climatic gradients. *Global Ecology and Biogeography*, 18(4):437-449.

OLIVEIRA, A. S. F. D. 2017. Uso da zona ripária como fator determinante da estrutura de uma assembleia de lagartos em área de terra-firme na Amazônia Central.

PARRIS, K. M. 2004. Environmental and spatial variables influence the composition of frog assemblages in sub-tropical eastern Australia. *Ecography*, 27:392-400. doi:[10.1111/j.0906-7590.2004.03711.x](https://doi.org/10.1111/j.0906-7590.2004.03711.x)

PIANKA, E. R. 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics*. 4:53-74.

PIANKA, E. R. 1974. Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences*. 71(5):2141-2145.

PIANKA, E. R. 1981. Competition and niche theory. *Ariel*. 128:205-172.

PRUDENTE, A. L. C., SILVA, M. A. A., ROCHA, W. A. & FRANCO, F. L. 2008. Morphological variation in *Xenoxybelis boulengeri* (Procter, 1923)(Serpentes, Xenodontinae, Philodryadini). *Zootaxa*. 1743:53-61.

PYRON, R. A., GUAYASAMIN, J. M., PEÑAFIEL, N., BUSTAMANTE, L. & ARTEAGA, A. 2015. Systematics of *Nothopsini* (Serpentes, Dipsadidae), with a new species of *Synophis* from the Pacific Andean slopes of southwestern Ecuador. *ZooKeys*. 541:109-147. <http://doi.org/10.3897/zookeys.541.6058>

ROJAS-AHUMADA, D. P., MAGNUSSON, W. E. & MENIN, M. 2012. Role of environmental and spatial processes in structuring anuran communities across a tropical rain forest. *Austral Ecology*. 37:865-873.

SCHOENER, T. W. 1983. Field experiments on interspecific competition. *American Naturalist*. 240-285.

SEXTON, J. P., MCINTYRE, P. J., ANGERT, A. L. & RICE, K. J. 2009. Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics*. 40:415-436.

YANOSKY, A. A., DIXON, J. R. & MERCOLLI, C. 1996. Ecology of the snake community at El Bagual Ecological Reserve, northeastern Argentina. *Herpetological Natural History*. 4(2):97-110.

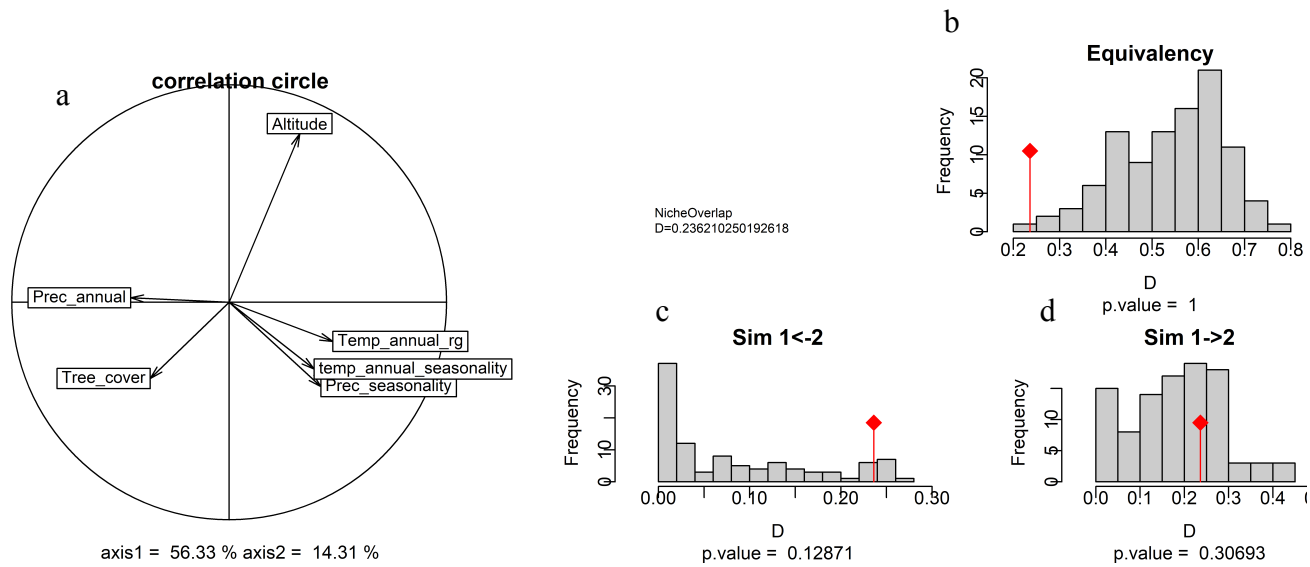
Apendices

Apendix I

Brief name	Full name	Correlated Variables
BIO1	*Annual Mean Temperature	Elevation, BIO 5, BIO6, BIO8, BIO9, BIO10, BIO11, BIO12, BIO15
BIO2	Mean Diurnal Range	BIO7
BIO3	*Isothermality (BIO2/BIO7)(*100)	BIO4
BIO4	Temperature Seasonality	BIO3
BIO5	Max Temperature of Warmest Month	BIO1, BIO8, BIO9, BIO10, BIO11
BIO6	Min Temperature of Coldest Month	BIO1, BIO8, BIO9, BIO10, BIO11
BIO7	Temperature Annual Range	BIO2
BIO8	Mean Temperature of Wettest Quarter	BIO1, BIO5, BIO6, BIO9, BIO10 BIO11
BIO9	Mean Temperature of Driest Quarter	BIO1, BIO5, BIO6, BIO8, BIO10 BIO11
BIO10	Mean Temperature of Warmest Quarter	BIO1, BIO5, BIO6,

BIO11	Mean Temperature of Coldest Quarter	BIO8, BIO9, BIO11 BIO1, BIO5, BIO6, BIO8, BIO9, BIO10
BIO12	*Annual Precipitation	Elevation, Precipitation Seasonality, BIO1, BIO13, BIO16
BIO13	Precipitation of Wettest Month	BIO12, BIO16
BIO14	Precipitation of Driest Month	BIO17
BIO15	*Precipitation Seasonality	Elevation, BIO1, Annual Precipitation, BIO17
BIO16	Precipitation of Wettest Quarter	BIO12, BIO13
BIO17	Precipitation of Driest Quarter	BIO15
BIO18	Precipitation of Warmest Quarter	
BIO19	Precipitation of Coldest Quarter	
	*Elevation	Annual Temperature, Annual Precipitation, Precipitation Seasonality
	*Tree Cover	

Appendix II



Niche of two *Philodryas* in bioclimatic variables - exemple of a principal component analysis. a) Contribution of environmental variables on two axes of the PCA and the percentage of inertia explained by the two axes. (b-d) Histograms show the observed niche overlap (D) between the two species and represents the simulated overlap between the two species where the red flag indicates the empirical niche overlap (D=0.23). Tests of niche similarity of *P. argentea* to *P. georgeboulengeri* (c), and similarity of *P. georgeboulengeri* to *P. argentea* (d), calculated from 100 iterations.