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

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#### 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 at different geographic scales will be distinct, 2) niche overlap limits species local occurrence. We modeled ecological distributions of *Philodryas argentea* (n = 319) and *P. georgeboulengeri* (n = 61) in the Amazonian biome at different spatial scales: local, using regression analysis along 880 km transect with evenly distributed plots; and broad, modeling occurrence data with a Maximum Entropy algorithm. Variables that contributed to *P. argentea* occurrence were tree cover and elevation at local scale and annual temperature range for broad scale. For *P. georgeboulengeri*, the most important variables at local and broad scales were tree cover and elevation of the most relevant variables for distribution of both species is dependent on spatial scale used; 2) although limited, co-occurrence of species at local scale scale.

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## Introduction

Ecological processes have been described at a variety of spatial scales, and 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). Spatial, trophic and temporal niche dimensions are the ones that mainly cause interspecific segregation (Pianka 1974). Abiotic interactions may also influence species' distributions (e.g. Di-Bernardo et al. 2007; Fraga et al. 2013; Chefaoui et al. 2018) through environmental filters. Ectothermic animals, such as snakes, may be subject of certain environmental conditions (e.g. thermal environment, precipitation regime) that may filter their distributions or reduce their dispersal capacities and, consequently, restrict gene flow between populations (Gibbons & Semlitsch 1987; Lillywhite 1987; Yanosky et al. 1996; Fraga et al. 2017).

At the local scale, effects of environmental variables (both climatic and structural) on snake distributions are poorly understood due to low detectability of species, even when standardized sampling design is combined with substantial sampling effort (Fraga et al. 2014; Fraga 2016). Although it is likely that tree cover might be relevant to arboreal snakes, while edaphic factors might be so for fossorial species, such interrelations 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 et al. 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 richness and density of potential prey such as anurans (Parris 2004).

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At the broad scale, studies of how environmental variables affect 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 the tes of hypothesis regarding niche overlap and segregation, as well as interspecific competitive interactions (Pianka 1973; Duré & Kehr 2004; Luiselli 2006; Duré et al. 2009). 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 (Pianka 1974; Abrams 1980; Schoener 1983). For example, sympatric snakes of the 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 con-specifics (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) (Pyron 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). These species are both diurnal and consume lizards and possibly frogs (Martins & Oliveira 1998; Machado-Filho 2015). 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 21 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 sampled both species from 2006-2015, consisting of an unprecedented effort along a transect of around 880 km along the interfluve between the Madeira and Purus rivers in the Amazon region. In addition, we compiled broad-scale occurrence data from online repositories and published literature. 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.

# **Materials and 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 interfluve between Purus and Madeira rivers (Figure 1). The average distance between neighbouring 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 the 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).

The Purus-Madeira interfluve covers approximately 15.4 million ha, and it is relatively flat at the local scale, with an elevation of 25 to 80 m (Maldonado et al. 2012; Ferrão et al. 2018). Soils are classified mostly as plinthosols, with poor drainage characteristic, with a predominant texture of silt and sand (Cintra et al. 2013; Martins et al. 2014), and podzolic soils with clay and sand as predominant texture (IBGE 1997). The study area is covered by primary and secondary tropical rainforest and seasonally flooded forests (IBGE 1997).



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 interfluve.

Each plot was surveyed for 1 h, 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 Emílio Goeldi, Belém (MPEG), Museu de Zoologia da Universidade de São Paulo, São Paulo (MZUSP), Instituto Nacional de Pesquisas da Amazônia, Manaus (INPA), Gerência de Animais Peçonhentos from Fundação de Medicina Tropical do Amazonas, Manaus (FMT) and Universidade Federal de Rondônia, Porto Velho (UNIR). Additionally, occurrence data for each species were obtained from digital public repositories SpeciesLink (http://www.specie slink.org.br) and Global Biodiversity Information Facility - GBIF (http://www.gbif.org), including its synonym. Geographical coordinates of each species were grouped in 5 km<sup>2</sup> quadrats in order to compare data with the RAPELD modules. Additionally, we searched for occurrence data from the literature 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 distribution of each species using QGis (QGis Development Team 2017). Here we considered the Purus-Madeira interfluve region and data collected at RAPELD modules as local scale and the Amazon basin and all occurrence points as broad scale.

# **Environmental heterogeneity**

To test for possible effects of environmental variables on the niche width and distributions of two species, we considered 19 bioclimatic variables (Appendix 1), all known to directly affect ectothermic animals. Data were extracted from the public repository World Clim (http://www.worldclim.org). 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 (Appendix 1) to represent environmental heterogeneity across the distribution of the target species. The original resolution of the variables was 1 km<sup>2</sup>, which was adjusted to the size of the RAPELD modules (5 km<sup>2</sup>) using the *raster* package in the R computational environment (Hijmans & van Etten 2014; R Core Team, 2017). Variables were analyzed using the Spearman Station Correlation matrix in R, and for variables with more than 80% correlation, only one was retained in the models.

For broad-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; Soares de Oliveira et al. 2016; Vasconcelos & Nascimento 2016). Among different available approaches, the Maximum Entropy algorithm (MaxEnt) is the one that has the best performance (Hijmans & Graham 2006). MaxEnt is a machinelearning 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 (Phillips & Dudík 2008; Elith et al. 2010; Kearney et al. 2010). AUC values equal to 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 (García-Callejas & Araújo 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 (Di 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 environmental variables the 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 (Peterson et al. 1999; Graham et al. 2004; Warren et al. 2008; Broennimann et al. 2012). This method provides comparative information on niche dynamics between sister species or between native and invasive species (Petitpierre et al. 2012; Guisan et al. 2014; Di Cola et al. 2017).

# Results

# Field sampling

At local scale (throughout the RAPELD modules) we found 25 individuals of *P. argentea* and 47 of *P. georgeboulengeri. Philodryas argentea* was encountered in 6 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 broad-scale models (considering data from repositories) were set by 95 occurrence points for *P. argentea* and 22 for *P. georgeboulengeri* (Figure 2). Adding records from public databases, herpetological collections, and published papers, we produced an updated map showing the known ranges for the two species (Figure 2). *Philodryas argentea* is widely distributed across the Amazon basin, as expected, while



Figure 2. Geographic range of *Philodryas argentea* (blue circles) and *Philodryas georgeboulengeri* (purple triangles), based on data from scientific collections, online databases, field surveys and published papers. Black dots represent occurrences from RAPELD modules.

**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.	- 41.93	-31.60
2	occur ~ elevation + tree cover	- 42.49	-33.56
3	occur ~ tree cover		- 33.68

*P. georgeboulengeri* has a distribution restricted to the central and southwest portions of the Amazon biome.

# **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.

The habitat suitability map for *P. argentea* (Figure 3a) 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 Purus-Madeira interfluve, which is consistent with the absence of *P. argentea* in this region. The model was mainly fitted by an annual temperature range (Table 2).

In the Purus-Madeira interfluve, 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 both species co-occur (Figure 3a, b). The proportions of habitats suitable for *P. georgeboulengeri* were more restricted than for *P. argentea* (Figure 3b), and mainly associated with variation in elevation (Figure 3b). Habitat suitability for *P. georgeboulengeri* was low (below 20%) across a large part of the Amazon (Figure 3b).

#### 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<-2, p = 0.13; 1->2, p = 0.30; see Appendix 2). 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* (Figure 4). For PCA correlation circle and similarity analyses, see Appendix 2.

#### 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



Figure 3. Environmental habitat suitability for the occurrence of (a) *Philodryas argentea* and (b) *Philodryas georgeboulengeri*, 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 two snakes *Philodryas argentea* (Parg) and *P. georgeboulengeri* (Pgeo). Values in bold represent variables with the highest percentage 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

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 (Darwin 1859; Webb et al. 2002; Luiselli 2006; Cahill et al. 2008; Mayfield & Levine 2010), 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 (Sala et al. 2000; Mayaux et al. 2005; Foley et al. 2005). Specifically for the *Philodryas* species studied here, tree cover is expected to determine the availability of foraging and resting sites (Martins & Oliveira 1998; Machado-Filho 2015), and so affect snake populations positively and directly. Additionally, elevation was the determining variable affecting distribution at different spatial scales for these sister-species, because the absence of *P. argentea* in certain regions of the elevation gradient is coincident with the niche occupied *P. georgeboulengeri*.

At a broad scale, the large contribution of the 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.

Modeled 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 analyzed (Machado-Filho 2015). Both alternative hypotheses 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 the result of habitat selection/ suitability (Peterson et al. 1999; Luiselli 2006; Warren et al. 2008). 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 the relaxation of a possible competition provided by



Figure 4. Results of the 'within-environment' PCA niche equivalency analyses between the sister-taxa (a) *Philodryas argentea* and (b) *Philodryas georgeboulengeri*. Shading reflects density/per cell of each species occurrences. Solid and dashed contour lines reflect, respectively, 100% and 50% of available environment.

a combination of high local abundance and diversity of prey (Martins & Oliveira 1998; Luiselli 2006; Machado-Filho 2015).

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 Purus-Madeira interfluve, by competition in the past. 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 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 Purus-Madeira interfluve region currently has 28 protected areas (Waldez et al. 2013; Graça et al. 2014; Gordo & Santos Pereira 2015), 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 & Graca 2006; Fearnside 2014). Projected estimates are that more than 5.4 million ha 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 are 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.

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# **Disclosure statement**

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# Apendix 1. Correlated bioclimatic variables using Spearman Station Correlation matrix

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, BIO8, BIO9, BIO11
BIO11	Mean Temperature of Coldest Quarter	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	

# Apendix 2.



The niche of two *Philodryas* in bioclimatic variables. (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 represent 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.