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ANIMAL SCIENCE

Co-occurrence patterns between false coral snake *Atractus latifrons* (Günther, 1868) (Serpentes: Dipsadidae) and venomous coral snakes from the Amazon

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Abstract: Batesian mimicry may result in remarkable cases of phenotypic convergence that represent classic examples of evolution through natural selection. The existence of mimicry systems among coral snakes, however, remains controversial because of contradictions between the predictions of mimetic theory and the empirical patterns of co-occurrence and species abundance. Here, we analyze the geographic distribution of coral snake species of the genus *Micrurus* and populations of the false coral snake *Atractus latifrons* in Amazonia, and perform ecological niche modeling (ENM) analyzes to generate potential geographic distributions of species of *Micrurus* and *A. latifrons*, identify patterns of co-occurrence and assess whether the distribution of *A. latifrons* coincides with the distribution of *Micrurus* species, which could suggest the existence of a possible mimetic relationship between the species. We identified six *Micrurus* species that may represent mimetic models for *A. latifrons*. The results of the co-occurrence analysis corroborates the results from ENM, indicating that chromatic patterns of *A. latifrons* and their respective model species are aggregated. Our study suggests that all color patterns of *A. latifrons* – including the tricolor monads, and the more common tricolor dyads and tricolor tetrads – may benefit from the resemblance with other *Micrurus* species as perfect and imperfect mimics.

Key words: Co-occurrence, ecological niche modeling, models, mimics, color variation.

INTRODUCTION

The selection of adaptive similarities involving mimics and models represents a classic problem in evolutionary biology (Kikuchi & Pfennig 2012). The term Batesian mimicry refers to a phenomenon in which a non-noxious species replicates a visual, acoustic or chemical signal emitted by a venomous species (model), resulting in adaptive advantages against predation (Ruxton et al. 2004, Hossie & Sherratt 2013, Rabosky et al. 2016). In such systems – Batesian mimicry complexes – Ruxton et al. (2004) claim that imitators should occur only in sympatry with their models. However, Pfennig & Mullen (2010) mentioned exceptions in which Batesian mimics exist in areas lacking their putative models, or where distributions of mimics are not totally included in the models' range. Nonetheless, the precise distributional relationships (full sympatry or allopatry) of potential models and their respective presumed mimics are largely unknown for many groups potentially involved in Batesian mimetic associations.

Several studies suggest that the co-occurrence of mimics and models may affect the abundance of perfect and imperfect mimics (Huheey 1976, Brodie III & Janzen 1995, Pfennig et al. 2001, Caley & Schluter 2003, Harper & Pfennig 2007, Kikuchi & Pfennig 2013). In areas where models are scarce or absent, the chances of predation on mimics would tend to increase (Huheey 1976, Pfennig et al. 2001, Harper & Pfennig 2007); alternatively, in areas where the model is relatively common, the odds of the predator finding it will be higher, promoting avoidance (i.e., lower predation rates) of any perfect or imperfect mimics (Brodie III & Janzen 1995, Caley & Schluter 2003, Kikuchi & Pfennig 2013).

Mimicry evolved in different snake lineages, with vipers (Viperidae) and coral snakes (Elapidae) frequently serving as models. Coral snakes advertise their danger with aposematic red, black, and white (or yellow) rings (Roze 1996). In the Neotropical region, coral snakes of the genera *Micrurus*, *Leptomicrurus,* and *Micruroides* are often associated with mimetic complexes involving non-venomous (aglyphous) or mildly-venomous (opisthoglyphous) species, known as false coral snakes, belonging mostly to the genera *Atractus, Lampropeltis, Tantilla, Oxyrhopus, Erythrolamprus, Pliocercus* and *Simophis* (Greene & McDiarmid 1981, Campbell & Lamar 1989, 2004, Savage & Slowinski 1992, Roze 1996, Almeida et al. 2016).

The vast majority of assumptions about mimicry systems involving coral snakes rely on sympatric distribution and similarities in chromatic patterns between venomous and non-venomous species (Greene & McDiarmid 1981, Marques & Puorto 1991, Brodie III & Janzen 1995, Torre-Loranza et al. 2006, Almeida et al. 2014, Bosque et al. 2016). Combining phylogenetic techniques, distributional comparisons, and general similarity, Rabosky et al. (2016) demonstrated a high correlation between the occurrence of red and black band patterns (RBB, sensu Rabosky et al. 2016) of venomous and non-venomous coral snakes in space and time. Thus, RBB patterns would only have appeared in non-venomous coral snakes after its emergence in venomous coral snakes, and only in areas of sympatry between both forms. However, according to Brattstrom (1955), the color similarities between such species may have resulted from evolutionary convergence around a cryptic pattern that provides protection, while the fixation of the color pattern resulted from the selection of a disruptive effect.

Recently, Akcali & Pfennig (2017) showed that resemblance level of mimics depends on their degree of sympatry (deep, edge, and allopatry) with the model, since each species exhibits different responses to selective pressures. For instance, the polychromatism of the false coral snake *Atractus latifrons* and its geographic congruence with species of *Micrurus* in Amazonia (*M. albicinctus* Amaral 1925, *M. averyi* Schmidt 1939, *M. filiformis* (Günther 1859), *M. langsdorffi* Wagler 1824, *M. lemniscatus* (Linnaeus 1758) and *M. diutius* Burger 1955) indicated a high distributional correspondence between mimics and models (Almeida et al. 2014). Furthermore some authors have already been suggested a possible mimetic relationships between *A. latifrons* and *Micrurus* in the Amazon (Cunha & Nascimento 1983, Savage & Slowinski 1992, Martins & Oliveira 1993, Silva 2004, Almeida et al. 2014).

The assessment of congruent geographic patterns among mimics and models may be limited by low rates of abundance, precluding trustworthy analyses about patterns of geographic overlap. In this sense, ecological niche modeling (ENM) has been broadly used in recent decades to infer the potential geographic distribution of species from incomplete empirical information about their distributions. ENM associates known occurrences of species throughout the geographic space with environmental conditions of evaluated sites (Rangel & Loyola 2012). From such associations, one can identify and map new locations where viable populations of species are likely to occur (Peterson et al. 2011). An important point of using ENMs to estimate geographic distributions is that they often predict broader ranges because they do not consider biotic interaction and dispersal constraints which limits the species distributions at local scales (Peterson et al. 2011, Uribe-Rivera et al. 2017). Despite this, if some aspects are taken into account in the modeling process, such as the accessible area for species occurrence, the quality of species occurrence records, and the niche-modeling method used (Jiménez-Valverde et al. 2008, Peterson et al. 2011), the distributional area estimated by ENM could provide a good approximation of the occupied distributional area at large scales (Peterson et al. 2011). Therefore, ENM represents an important tool for overcoming Wallacean shortfalls (Lomolino 2004, Hortal et al. 2015) and testing ecological and biogeographical hypotheses.

In this study, we evaluated the congruence between the geographic distributions of different color patterns of the false coral snake *A. latifrons* and the true coral snakes of the genus *Micrurus* in Amazonia to suggest, based on the co-occurrence between the species and the similarity between the color patterns, the existence of a possible mimetic relationship between the tested species. In order to reduce the effects of sampling gaps in the accurate assessment of distributions, we use ENM to generate potential geographic distributions of *Micrurus* and *A. latifrons* species to test species correlation, assuming sympatry as evidence of the Batesian mimetic complexes.

MATERIALS AND METHODS

We examined 157 specimens of *Atractus latifrons* and 402 specimens of coral snakes of the genus *Micrurus*: *M. albicinctus* (n= 7), *M. averyi* (n= 19), *M. filiformis* (n= 74); *M. langsdorffi* (n= 24), *M. lemniscatus* (n= 325), and *M. diutius* (n= 109) with an Amazonian distribution, housed in 21 institutions (Supplementary Material – Appendix S1); institutional abbreviations followed Sabaj (2016), except for Centro de Estudos e Pesquisas Biológicas (CEPB) and Coleção Herpetológica da Universidade Federal do Ceará (CHUFC), not listed there). Nomenclature of the color patterns of *A. latifrons* followed Almeida et al. (2014). However, to perform the co-occurrence test of chromatic patterns of *A. latifrons* and *Micrurus* species, we recognize here the variations described as “tricolor dyads” defined by Almeida et al. (2014) as actually variations of the pattern “Tricolor monads”, which we designate as “Tricolor monads 1” (similar to *Micrurus averyi*) and “Tricolor monads 2” (similar to *Micrurus langsdorffi*).

To select *Micrurus* species acting as potential models for *Atractus latifrons,* we followed two parameters: (1) the potential model of a mimetic species should occur in sympatry with *A. latifrons*; (2) the potential model should exhibit a typical coral pattern (black, white and/or red rings), forming monads or triads on the body and tail, as well as a black dorsal cephalic cap similar to the mimic patterns. The species-level identification of most of the *Micrurus* taxa followed Roze (1996), except the for *M. lemniscatus* species group, in which we followed Pires et al. (2014).

Ecological niche modeling and geographic distributions

We used ecological niche models to predict geographic distributions for species from known occurrence records. For niche modeling analyses, we used longitude and latitude data associated with specimens having clear and unproblematic occurrence records (Appendix S2). The models were generated considering the extent of the Neotropical region as the historically accessible area since both genera, *Atractus* and *Micrurus,* have a Neotropical distribution. We followed the recommendation by Araújo & New (2007) to generate consensus predictions by combining outputs from different niche modeling methods (weighted by individual model accuracy) and climatic models (Rangel & Loyola 2012). We obtained a set of bioclimatic variables at 0.5° resolution from the ecoClimate database (http://ecoclimate.org, Lima-Ribeiro et al. 2015), representing pre-industrial climatic conditions, for five coupled atmosphere-ocean general circulation models (AOGCM): CCSM4, CNRM, GISS-E2-R, MIROC-ESM, and MRI-CGCM3. To minimize collinearity among bioclimatic variables, we used a varimax-rotated factor analysis to select the set of variables with the highest loadings in the first five factors (Terribile et al. 2012). Thus, we chose the following five orthogonal variables: annual mean temperature, annual temperature range, precipitation of the wettest month, precipitation of the driest month, and precipitation of the warmest quarter. We performed factor analysis based only on CCSM bioclimatic variables, as these variables were highly correlated across all AOGCMs (i.e., the loadings across all AOGCMs provided quite similar results, with shifts usually below 0.05 of difference in the highest loadings).

We used 11 modeling algorithms, including presence-only and presence-absence methods, ranging from simple bioclimatic envelope models (BIOCLIM) and distance-based methods (Euclidian distance and Gower distance), multivariate methods (ecological niche factor analysis – ENFA and Mahalanobis distance), as well as more complex methods such as regression models (Generalized linear model – GLM, Multivariate adaptive regression splines - MARS and Generalized additive model) and machine learning-based methods (Maxent, Artificial Neural Networks, and Randon forest). For a general description of niche models, see Franklin (2009) and Peterson et al. (2011).

For the modeling process, we mapped occurrence records at the same resolution as climate data. To evaluate the congruence between model and mimic species distribution, we modeled each chromatic pattern of *Atractus latifrons* separately (Figure S1, Table SI). The species presence records (and pseudo-absences for those methods that use presence and pseudo-absence) were allocated randomly into 75% for calibration and 25% for evaluation, and we repeated this process 50 times. Pseudo-absences were randomly selected in the background region (excluding cells with occurrence records) with the same proportion as species records (prevalence of 0.5). The 50 repetitions in each method were converted into presence-absence maps based on thresholds established by the area under the ROC curve (AUC). All 300 models (50 repetitions x 6 modeling methods) were included in the consensus maps of each AOGCM, weighted by their model fit according to the True Skill Statistics (TSS, Allouche et al. 2006, Diniz-Filho et al. 2009). The average across the ensemble outputs of each AOGCM resulted in the final consensus map of habitat suitability (varying from 0 to 1) for each *Micrurus* species and chromatic pattern of *A. latifrons*. Final accuracy of ensemble models is presented in the Appendix S2. We generated all models using the computational platform BioEnsembles (Diniz-Filho et al. 2009, Terribile et al. 2012).

We used habitat suitability predictions to map the potential geographic distribution of each *Micrurus* species and chromatic patterns of *A. latifrons*. Because ENM analyses do not consider biotic interactions and other local factors limiting species ranges (e.g. geographic barriers), their transferability (extrapolation in geographic space) may include areas that are inaccessible for the species. Since we are dealing with species with poor dispersal, we adopted conservative parameters to delimitate more realistic, easily interpreted distributions. Thus, we applied a decision threshold of 0.5, and considered areas (or cells) suitable if they had suitability values higher than 0.5. We assessed the final maps based on expert background knowledge (P.A. and D.T.) to ensure the predictions reflected the real potential distribution of each form.

Testing for co-occurrence patterns

From the geographic distributions obtained from ENM, we tested for non-random patterns of co-occurrence as evidence of positive relationships between *Micrurus* species and *A. latifrons* chromatic population coexistence. We performed the co-occurrence analysis using the co-occurrence module of EcoSim (Gotelli & Entsminger 2004). We used the matrix of presence (1) and absence (0) generated by ENM, and set each species and chromatic pattern in rows and the localities (or cells) in columns. We used the C-score index (number of “checkboard units”) (Stone & Roberts 1990) as a quantitative co-occurrence index (the higher the C-score, the less co-occurrence, on average, between all of the species’ pairs in the matrix). We estimate C-score through 5,000 simulations by reshuffling elements within each row of the matrix to test the probability that each species pair is significantly aggregated (observed C-score lower than simulations) or segregated (observed C-score higher than simulations). We also generate polygonal geographic distributions for each *Micrurus* model and mimetic *Atractus* by generating a convex hull around the occurrence locations (Figure S2), while removing raster cells within these polygons that the ENMs identified as unsuitable. Then, we repeated the co-occurrence analysis with these polygons and compare it with that from ENM to evaluate if the results could be influenced by overprediction in ENM distributions.

To assess a positive relationship between the distributions of mimics and models, we replicated the procedure of niche modeling and included the vector of habitat suitability of each model species of *Micrurus* as a predictor variable (together with the five climatic predictors described above) in the modeling process of each corresponding *Atractus latifrons* mimic chromatic pattern. Then, we adjusted a multiple regression model between habitat suitability of each chromatic pattern of *A. latifrons* (the dependent response variable) and the set of six independent variables (habitat suitability of the corresponding *Micrurus* sp. Model plus the five climatic variables), and noted the standardized regression coefficients for each independent variable. We used these standardized regression coefficients to evaluate the correlation between habitat suitability (i.e., the geographic distribution) of each mimic with the habitat suitability of its corresponding model. Although we are aware that the significance of these coefficients cannot be considered due to the implicit collinearity between suitability and the climatic variables used in the ENM process, this approach was useful to assess a possible association of the geographic distribution of mimics with the distribution of the corresponding model (each standardized coefficient has partial importance regarding the other predictor variables in the regression model).

Finally, to evaluate if the geographic distribution of mimics could be constrained by the distribution of *Micrurus* models, we modeled the geographic distribution of *A. latifrons* as a whole (i.e., using all records of all mimics) following the same protocol as above. From this modeled distribution (see Figure S3), we re-sampled 1000 times geographic ranges (i.e. null ranges) for each chromatic pattern and calculated the proportion that each of these null ranges overlapped with the respective *Micrurus* model distribution. The size of these null ranges for each *A. latifrons* chromatic pattern was equal to the ENM distribution, and we also set for these null ranges to be continuous (thus approximating the modeled ranges). We then compare if the observed overlapping proportion for each model *Micrurus* and respective *A. latifrons* chromatic pattern was frequently higher (or not) than the proportion from the null ranges.

RESULTS

Morphological analyses

Based on the correspondence of color pattern among *Atractus latifrons* and *Micrurus* species, we recognized six species of *Micrurus* as potential mimetic models for *A. latifrons*: *M. albicinctus*, *M. averyi*, *M. filiformis*, *M. langsdorffi*, *M. lemniscatus* and *M. diutius* (Figure 1). Therefore, based on similarities of general color patterns, we assumed the following associations: the bicolor monads pattern of *Atractus latifrons* resembles *Micrurus albicinctus* (Figure 2a–b); the tricolor monads pattern 1 of *A. latifrons* resembles *M. averyi* (Figure 2c–d); the tricolor monads pattern 2 resembles *M. langsdorffi* (Figure 2e–f); the tricolor dyads pattern of *A. latifrons* resembles

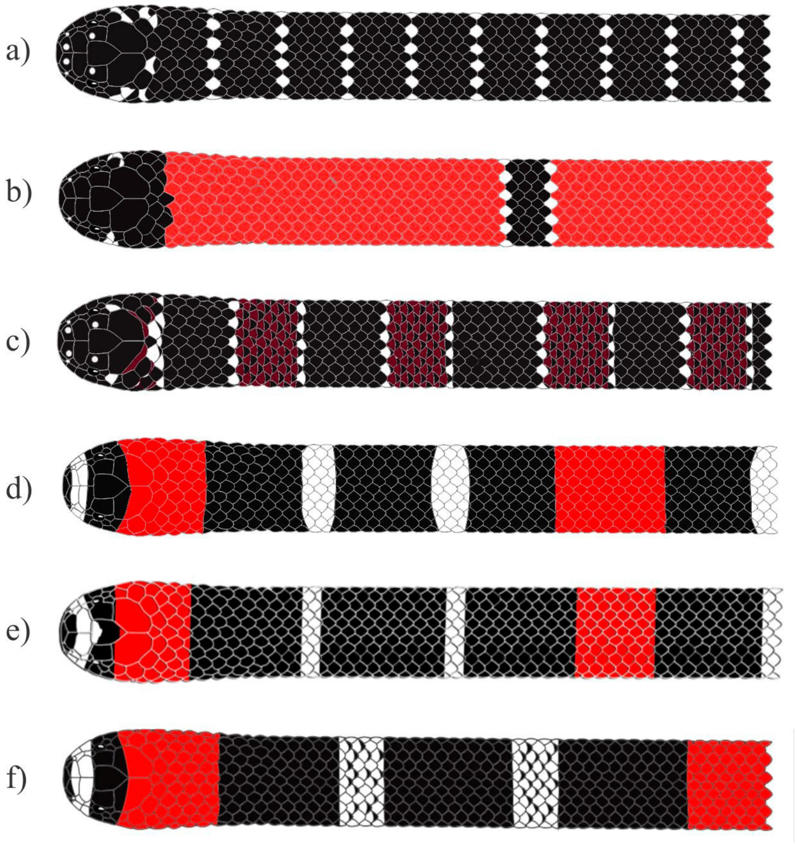

Figure 1. Color patterns of possible mimetic models of genus *Micrurus*: a) *Micrurus albicinctus;* b) *Micrurus averyi;* c) *Micrurus langsdorffi;* d) *Micrurus filiformis;* e) *Micrurus lemniscatus;* and f) *Micrurus diutius.*

the tricolor triads pattern of *M. lemniscatus* and *M. diutius* species (Figure 3a–c) and the tricolor tetrads pattern of *A. latifrons* resembles the tricolor triads pattern of *M. filiformis* (Figure 4a–b), although with a few number of triads along the body *M. diutius* and *M. lemniscatus* can also serve a models for *A. latifrons* (Figure 3a-c).

Geographical analyses

Considering only the chromatic patterns of mimics and models, we observed a strong association between venomous coral snakes and the different forms already described for *Atractus latifrons*. However, in addition to this chromatic association, the distribution analyzes also indicated the existence of sympatry between supposed models and mimics (Figure 5).

The distributions generated by niche modeling showed a clear pattern of range overlap between the tricolor dyads (TD), tricolor tetrads (TT), tricolor monads (TM) and bicolor monads (BM) chromatic patterns of *Atractus latifrons*. The analysis of potential species distribution indicated (1) the co-occurrence of the bicolor monads pattern of *A. latifrons* and *M. albicinctus* in a restricted region of Amazonia, specifically the states of Rondônia and Amazonas; (2) the tricolor dyads pattern of *A. latifrons* co-occurs with *M. lemniscatus* and *M. diutius* as potential models in Amazonia, specifically in the states of Pará and Amazonas; (3) the tricolor tetrads pattern of *A. latifrons* co-occurs with *M. filiformis* and *M. lemniscatus* in central Amazonia, and (4) the tricolor monads pattern of *A. latifrons* co-occurs with the potential models *M. langsdorffi*

Figure 2. Chromatic bicolor monads patterns of mimic *Atractus latifrons* (a) and model *Micrurus albicinctus* (b); tricolor monads pattern *morph* 1 of *A. latifrons* (c) and model *Micrurus averyi* (d); and the tricolor monads pattern morph 2 of *A. latifrons* (e) and model *Micrurus langsdorffi* (f). Scale: 10mm.

and *M. averyi* in part of the Colombian Amazon, in the Peruvian Amazon and in the Brazilian Amazon, specifically in the states of Amazonas and Roraima (Figure 5).

The results of the co-occurrence test for *Atractus latifrons* color pattern and their respective models indicated positive relationships (i.e., the probability of the observed C-score index ≤ the simulated index was 0.999) for all associations, indicating that chromatic patterns of *A. latifrons* and their respective model species are aggregated. The co-occurrence test corroborated the association involving patterns of bicolor monads, tricolor

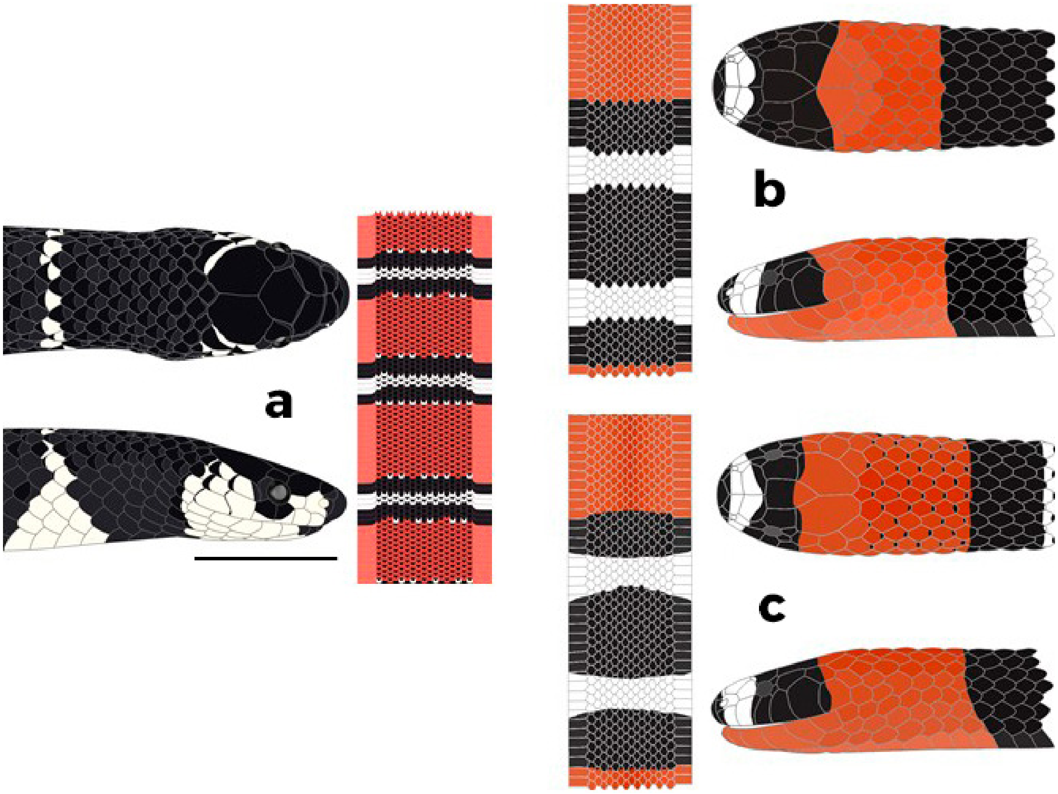

Figure 3. Chromatic tricolor dyads patterns of mimic *Atractus latifrons* (a) and model *Micrurus lemniscatus* (b); and *Micrurus diutius* (c). Scale: 10mm.

Figure 4. Chromatic tricolor tetrads patterns of mimic *Atractus latifrons* (a) and model *Micrurus filiformis* (b) Scale: 10mm.

monads, tricolor dyads, and tricolor tetrads, suggesting that the distributions of chromatic patterns of the mimic *A. latifrons* and of the different models of *Micrurus* do not occur randomly. The results were the same for the co-occurrence test from the polygons obtained by convex hulls, except for the pattern *A. latifrons* TM vs *M. averyi*, which was non-significant (i.e.,

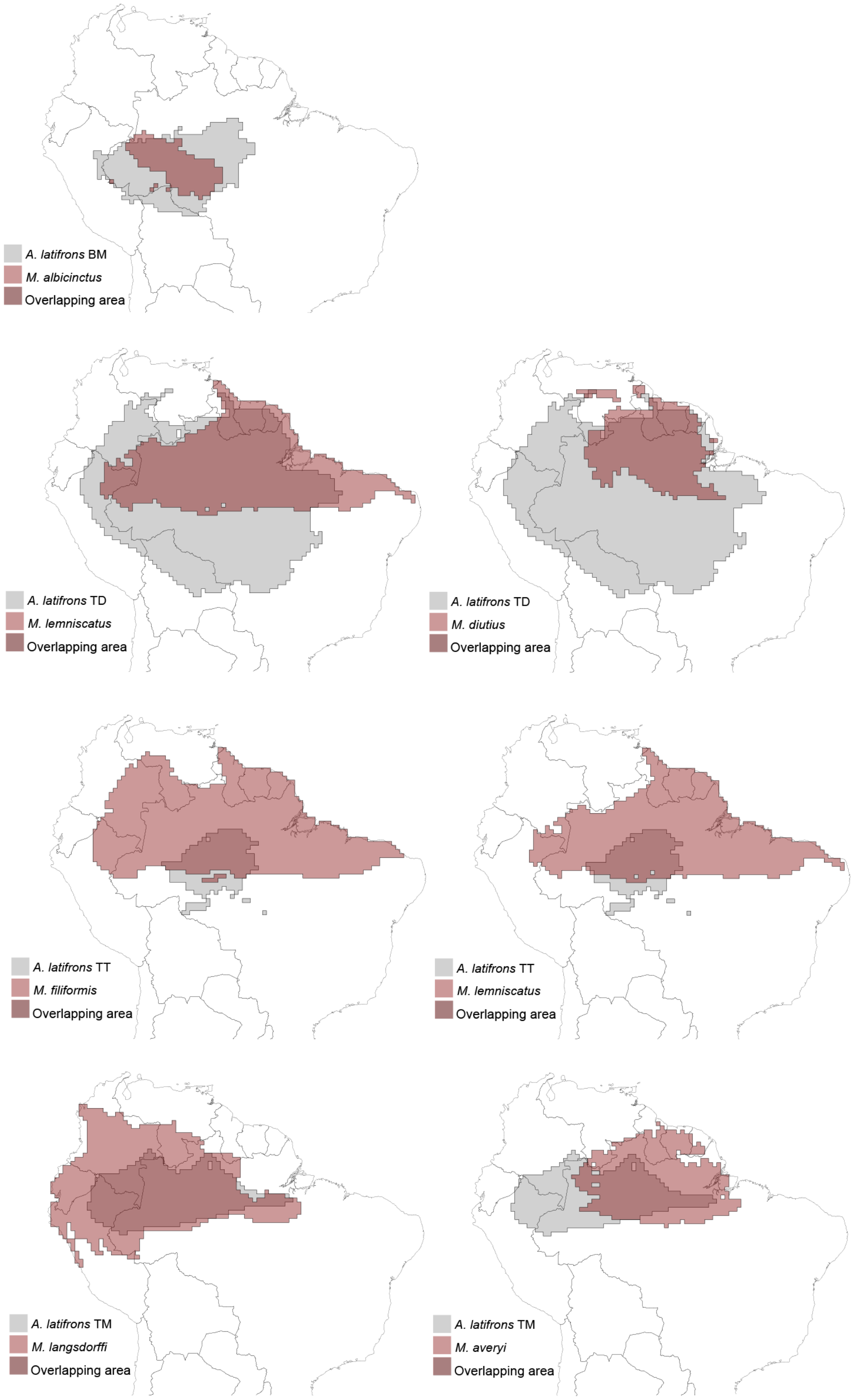

Figure 5. Geographic distribution from ENM for chromatic patterns of *Atractus latifrons* and correspondent coralsnake mimetic model.

the probability of the observed C-score index ≤ the simulated index was 0.389). This probably occurred because the convex hull for both *A. latifrons* TM and *M. averyi* were smaller than the distributions estimated by ENM and thus, the overlap between them was minimal (Figure S2).

We found that the spatial distribution of *A. latifrons* exhibiting bicolor monads and *M. albicinctus* (measured as habitat suitability) had the highest standardized coefficient, indicating that the distribution of this chromatic pattern of *A. latifrons* has a strong correlation with the distribution of *M. albicinctus* (Table I; Figure 6), corroborating the co-occurrence test. For the chromatic tricolor dyads pattern, the models *M. lemniscatus* and *M. diutius* exhibited the lowest correlations. For the other chromatic patterns, correlations were high for the associations between the tricolor monads pattern vs. *M. langsdorffi* and intermediary correlations for the tricolor monads pattern vs. *M. averyi*. Similar results were obtained in the comparison of the observed and null proportions of ranges overlapping (Table II, Figure 6), in which the observed proportion for *A. latifrons* TD vs. *M. diutius* and *M. lemniscatus* were lower than most of the null proportions. For all other mimetic relationship, but *A. latifrons* TT vs. *M. filiformis*, the observed overlapping proportion was higher than null proportions. This result for *A. latifrons* TT vs. *M. filiformis* is expected since the observed proportion was rather low (only 11%, Table II; see also Figure 5).

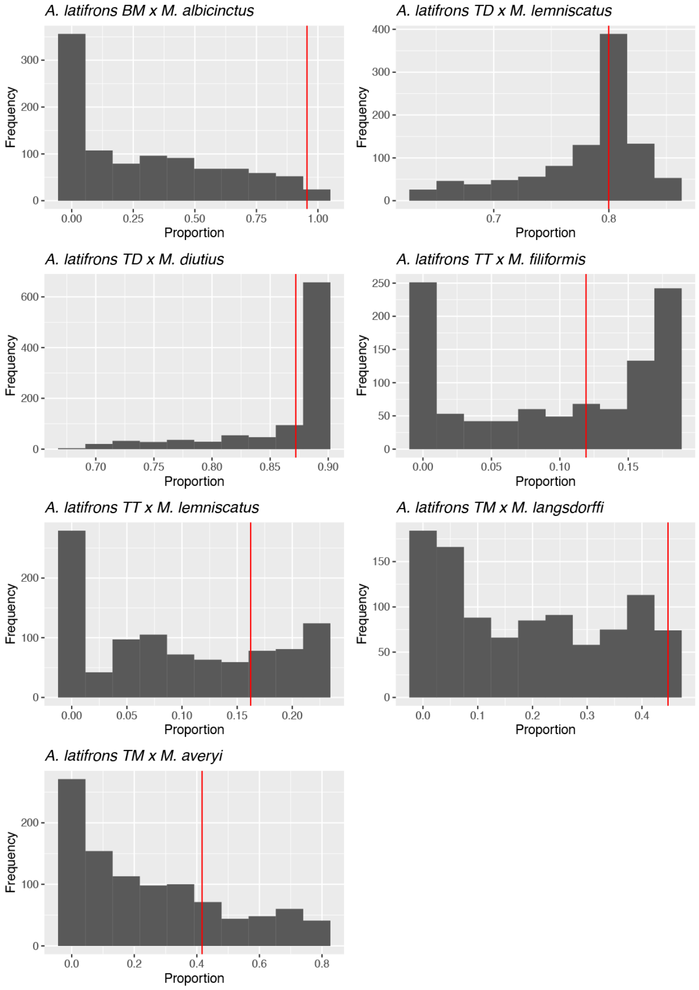

Figure 6. Histograms of simulated proportions of range overlapping derived from the 1000 resampled geographic distributions for each chromatic pattern. The red line indicates the observed proportion of range overlapping between each *A. latifrons* chromatic pattern and the respective *Micrurus* species.

Table I. **Beta coefficients (β) from multiple regression analysis between habitat suitability of chromatic patterns of *Atractus latifrons* (response variable) and bioclimatic variables plus habitat suitability of each *Micrurus* species (predictor variables). TD - tricolor dyads; TT - tricolor tetrads; TM - tricolor monads, and BM – bicolor monads. Bio1 – annual mean temperature, Bio7 – annual temperature range, Bio13 - precipitation of the wettest month, Bio14 - precipitation of the driest month, Bio18 - precipitation of the warmest quarter. [1]*Micrurus lemniscatus*, [2]*Micrurus diutius*, [3]*Micrurus filiformis*, [4]*Micrurus langsdorffi*, [5]*Micrurus averyi*, and [6]*Micrurus albicinctus*.**

Variables	Atractus TD	Atractus TT	Atractus TM	Atractus BM
Bio1	0.43	0.23	0.04	0.07
Bio7	0.06	0.18	0.24	0.05
Bio13	-0.01	0.11	-0.13	-0.07
Bio14	-0.13	-0.13	0.07	0.10
Bio18	0.20	0.10	0.04	0.06
Suitability	0.25[1]; 0.25[2]	0.61[3]	0.73[4]; 0.49[5]	0.956

Table II. **Comparison between the observed and simulated proportions of range overlapping among *A. latifrons* chromatic patterns and *Micrurus* species. Simulated proportions derived from the 1000 resampled geographic distributions for each chromatic pattern.**

Mimic x Model species	Observed proportion	N. of simulations < observed
A. latifrons BM x *M. albicinctus*	0.955	986
A. latifrons TD x *M. lemniscatus*	0.799	546
A. latifrons TD x *M. diutius*	0.872	298
A. latifrons TT x *M. filiformis*	0.119	531
A. latifrons TT x *M. lemniscatus*	0.162	723
A. latifrons TM x *M. langsdorffi*	0.447	1000
A. latifrons TM x *M. averyi*	0.416	758

DISCUSSION

Reports of mimicry involving snakes in the Amazonia usually suggest the relationship between a species of non-venomous coral snake imitating a single venomous coral snake species (1 *vs*. 1). Here we report on a mimetic complex involving a single polychromatic species of non-venomous coral snake (Almeida et al. 2014) and several sympatric species of *Micrurus*, with associations that include different color patterns and different levels of similarity, representing perfect and imperfect instances of mimicry. In Brazil, the only comparable instance of potential mimicry already tested in the literature involves the false coral snake *Erythrolamprus aesculapii*, for which populations from the Atlantic Forest appear to represent mimics of the monad patterned species *M. corallinus*, while populations from the Cerrado biome resemble the triad patterned species *Micrurus frontalis* and *M. lemniscatus* (Marques & Puorto 1991).

The mimicry assumptions in this study rely strictly on similarities of color patterns and distributional congruence based on objective data of localities of occurrence, without any additional analytical support. Experimental studies by Smith (1975) and Brodie III & Moore (1995) revealed an innate avoidance by birds of all ring color patterns, regardless of width and color. Nevertheless, we based our mimetic associations on a more recent study work by Akcali & Pfennig (2017) who suggest that the greater the geographic overlap between models and mimics, the greater their similarity.

Several studies have tested the similarity of chromatic patterns between models and mimics with respect to levels of geographic congruence (Harper 2006, Harper & Pfennig 2007, 2008, Pfennig et al. 2007, Kikuchi & Pfennig 2010, Akcali & Pfennig 2017). All of them agree that the relationship between geographical variation and mimetic precision supports the assumption that the mimic's accuracy increases as the model becomes rare (Pfennig et al. 2001, Ruxton et al. 2004, Harper & Pfennig 2007, Iserbyt et al. 2011). Our results regarding a positive mimetic relationship between *A. latifrons* as a perfect mimic of the apparently rare model *M. albicinctus* corroborate this tendency. On the other hand, the abundance and wide distribution of imperfect chromatic patterns, such as tricolor dyads in *A. latifrons*, may favor mimics through co-occurrence with a greater number of models, such as *M. lemniscatus*, *M. diutius* and *M. filiformis* (see Edmunds 2000, Kikuchi & Pfennig 2013). Indeed, we observed that the distribution of the pattern tricolor dyads of *A. latifrons* largely overlaps with areas of greatest *Micrurus* species richness (see Figure S4).

Among the proposed mimetic relationships involving *Atractus latifrons* and sympatric species of *Micrurus* in Amazonia (Cunha & Nascimento 1983, Savage & Slowinski 1992, Martins & Oliveira 1993, Silva 2004, Almeida et al. 2014), we were unable to assess the presumed mimetic relationship with *M. hemprichii ortoni* suggested by Silva (2004) due to the absence of the tricolor triads pattern in our sample of *A. latifrons*. Our distributional data corroborate previous evidence of perfect mimicry among some populations of *A. latifrons* and *M. albicinctus* by ecological niche modeling, the co-occurrence test and the strong similarity of color. Some populations of *A. latifrons* may also represent imperfect mimics, considering the relationships established among tricolor monads, tricolor dyads and tricolor tetrads of mimics and their models *M. averyi*, *M. langsdorffi*, *M. lemniscatus*, *M. diutius,* and *M. filiformis*, respectively. The combination of ENM methods promotes additional support to the assumption of non-random co-occurrence of color patterns for at least one mimetic system involving species with bicolor monads. Additional effects combining niche modeling techniques and distributional patterns of model and mimics of other systems may improve the accuracy of mimicry studies based on indirect data such as sympatry of color patterns and behavioral repertoire.

Finally, we note that for some *Micrurus* species and particular chromatic patterns of *A. latifrons*, the niche models that estimated potential geographic distributions relied on a limited number of occurrence records (e.g. *M. albicinctus*, *M. averyi*, bicolor patterns in monads and tetrads of *Atractus latifrons*), despite our exhaustive efforts at gleaning all information available in museum collections. Several studies point out that model performance generally decreases with sample size (Stockwell & Peterson 2002, Wisz et al. 2008), however this does not necessarily mean that the predicted distribution is inaccurate (e.g. Kadmon et al. 2003). For instance, a few records may suffice to characterize distributions of species with narrow environmental tolerances (Kadmon et al. 2003), certainly the case for the species analyzed here. Also, although niche modeling is expected to overpredict geographic distributions, our approach indicated it can be useful to investigate the patterns of species co-occurrence. Nevertheless, our results can only be considered as indications of the existence of a mimicry complex between these species, since it was not possible to indicate precisely which species acted as model or mimic. Further studies focused on these relationships would be required to confirm the mimicry complexes. We hope that new records from future sampling will provide additional support for our results, especially regarding the chromatic patterns of *A. latifrons*.

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SUPPLEMENTARY MATERIAL

Appendix S1. Examined specimens of the *Atractus latifrons* and *Micrurus*.Countries are identified with capital letters and bold, states are only capitalized, counties in italics, and locations in simple text.

Appendix S2. Number of spatially unique occurrence records used in the niche modelling for each Micrurus species and Atractus latifrons chromatic pattern.
Table SI. Spatially unique occurrence records used in the niche modelling for each *Micrurus* species and *Atractus latifrons* chromatic pattern.

Table SII. Accuracy of ENM models for the ensemble suitability among modeling methods for each climatic model, and overall mean accuracy for the ensemble among modeling methods and climatic models.

Figure S1. Modeled geographic distributions and occurrence records for *Atractus latifrons* chromatic patterns.
Figure S2. Polygons generated by a convex hull for each combination of mimic *A. latifrons* and *Micrurus* model species.
Figure S3. Modeled geographic distribution of *Atractus latifrons*, based on all occurrence records for this species.
Figure S4. Richness pattern of Micrurus mimetic models in the Amazonia, resulting from stacking the geographic ranges from ENM.

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