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Effects of climate and geography on spatial patterns of genetic structure in tropical skinks

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ABSTRACT

Knowledge of how contemporary and historical factors drive patterns of genetic structure across geographic space can shed light on the processes underlying diversification. This approach is especially fruitful in studies of widespread species or species clades that occur across multiple environmental conditions and biomes. In the Neotropics, specifically, molecular data from widespread vertebrate species have revealed high levels of lineage diversity and spatial genetic structure – yet studies that explore the possible correlates of local structure patterns are lacking. We investigate the distribution of lineage diversity within two widespread South American skink species complexes of the genus *Mabuya*. We characterize genetic structure and diversity in these widely ranged lizards, and identify potential geographic and environmental correlates, to shed light on the processes that promote lineage diversification across the heterogeneous landscapes which they occupy. In both groups, we found mitochondrial lineages to be spatially structured along the coastal forests and the savannas of Brazil. These mtDNA patterns are, however, not shared with those inferred from nuclear DNA markers. The geographic location of major mitochondrial genetic breaks is consistent with those of other taxa, suggesting common responses to former landscape change in eastern South America, particularly along geological faults. Genetic differentiation is correlated with environmental turnover and geographic separation in one, but not in the other, group of skinks. Compared to other studies of similarly widely distributed organisms, the link between spatial environmental gradients and genetic differentiation is not as strong or consistent, suggesting a more complex history underlying current phylogeographic patterns. Our genetic data indicate the existence of yet undescribed diversity in wide-ranging lizards, and the value of phylogenetic and phylogeographic studies of similarly understudied species.

1. Introduction

Uncovering how contemporary and historical abiotic factors affect patterns of genetic structure across geographic space can help us to understand the processes that underlie lineage divergence and species diversification (Wang et al., 2013; Carnaval et al., 2014). To achieve this goal, evolutionary studies have greatly benefited from the integration of genetic and environmental data. For instance, molecular analyses have revealed an expanse of deeply divergent, sometimes morphologically cryptic lineages whose range limits show strong correlation with geographic and environmental breaks (Gamble et al., 2012; Gehara et al., 2014). It has been suggested that this pattern is a result of constraints imposed by environmental gradients on species dispersal (e.g., Prates et al., 2016a, 2018) and population gene flow (e.g., Sexton et al., 2014), leading to spatial genetic structure. Additionally, it has been shown that environmental variation across regions may lead to genetic divergence among populations due to local adaptation (Manthey and Moyle, 2015; Wang, 2013). Integrating genetic and ecological data from widespread species or species complexes can therefore inform studies aiming to uncover the drivers of lineage

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diversity and speciation.

In South America, molecular data from morphologically conserved, widespread vertebrate species have revealed high levels of lineage diversity and spatial genetic structure, which may be related to pronounced landscape heterogeneity in this region (Gamble et al., 2012; Gehara et al., 2014; Geurgas et al., 2008; Nunes et al., 2012; Omland et al., 2000; Werneck et al., 2015). This is the case of several species whose ranges span contrasting habitats, including wet forests (e.g., Amazonia and the Atlantic Forest) and open savannas (e.g., Cerrado) or xeric shrublands (e.g., Caatinga and Chaco) (e.g., Batalha-Filho et al., 2012; Carnaval et al., 2014; Gehara et al., 2014; Iganci et al., 2011; Ribeiro-Júnior and Amaral, 2017, 2016). While numerous biogeographic studies in South America have focused on narrowly distributed wet forest taxa (e.g., Amaro et al., 2012; Fouquet et al., 2015, 2012; Rodrigues et al., 2014; Turchetto-Zolet et al., 2013), much less emphasis has been given to widespread, ecologically diverse species (Recoder et al., 2014; Werneck, 2011; Werneck et al., 2015; Wynn and Heyer, 2001). While it is often difficult to sample the entire range of widely distributed species, this bias is unfortunate given that broadly distributed organisms represent an opportunity to study mechanisms of diversification and adaptation across complex environmental boundaries (Gamble et al., 2012; Gehara et al., 2014; Geurgas et al., 2008; Nunes et al., 2012; Werneck et al., 2015).

Here we investigate the presence and distribution of lineage diversity within two widespread South American skink taxa that likely represent species complexes: *Mabuya dorsivittata* and *Mabuya macrorhyncha*. We use the *Mabuya* classifications in lieu of more recent taxonomic changes (*Aspronema dorsivittatum*, *Psychosaura agmosticha*, and *P. macrorhyncha*; Hedges and Conn, 2012) to avoid disruptive taxonomic instability due to the lack of continental sampling and unclear relationships within *Mabuya* (Karin et al., 2016; Miralles et al., 2017). To date, the range of *M. dorsivittata* has been poorly characterized; this taxon is distributed from the Chaco of northeastern Argentina through the Pampas, Atlantic Forest, and eastern Cerrado in Brazil (Carranza and Arnold, 2003; Hedges and Conn, 2012; Williams and Kacoliris, 2011). Additionally, color and body size variation has been detected in populations of *M. dorsivittata* from a variety of elevations across southeastern Brazil (MTR, personal observation); yet, no recent formal morphological assessment has been performed. Our second target group consists of *Mabuya agmosticha* and of several populations assigned to *M. macrorhyncha*, some of which may represent undescribed forms. Within this group, hereafter referred to as the *M. macrorhyncha* species complex, the name *M. macrorhyncha* has been attributed to populations from the Atlantic Forest, while the name *M. agmosticha* has been assigned to populations from the arid Caatinga in northeastern Brazil (Couto-Ferreira et al., 2011; de Freitas, 2014; Garda et al., 2013; Rodrigues, 2000). *Mabuya agmosticha* has been diagnosed from *M. macrorhyncha* based on morphological characters and mitochondrial sequence data, but the taxonomic boundaries between these two closely related forms are not entirely clear (Pinto-Sánchez et al., 2015; Rodrigues, 2000). Importantly, although *Mabuya* species are abundant in the Neotropics, historical relationships and species ranges within this group are poorly known (Miralles et al., 2009; Miralles and Carranza, 2010; Pinto-Sánchez et al., 2015). Based on several nuclear and mitochondrial DNA markers, we examine cryptic diversity and infer historical relationships among lineages and explore the role that environmental heterogeneity may have played in shaping the observed patterns of spatial genetic structure.

Our approach is two-fold. First, to identify cryptic lineages and outline their distributions, we generate mitochondrial and nuclear DNA sequences from throughout the ranges of the target taxa and apply phylogenetic (Bayesian inference and Maximum Likelihood) and population genetic methods (STRUCTURE analyses) to characterize and compare patterns of genetic structure within these two widespread species complexes. Second, to investigate the relative roles of geography and environment as potential drivers of lineage diversity and distribution, we compare levels of genetic structure across the many ecoregions occupied by these species and test whether and how environmental shifts better predict levels of population genetic structure relative to geography alone. If ecological gradients contribute to genetic divergence, we expect environmental differences between sampled sites to predict genetic distances, independent of geographic separation. To quantify these environmental differences, we use measures of climate differences across sampled sites (i.e., isolation by environment) as well as measures of habitat suitability along the paths that connect them (i.e., isolation by resistance; Wang, 2013). By characterizing genetic diversity and structure in these widely ranged lizard taxa, as well as identifying their potential geographic and environmental correlates, we hope to shed light on the processes that promote lineage diversification across heterogeneous landscapes.

2. Materials & methods

2.1. Sampling and molecular data

Individuals from the *Mabuya dorsivittata* complex were collected from across the majority of the known species range, including a number of localities where no previous genetic data have been generated. Individuals from the *M. macrorhyncha* complex, including *M. macrorhyncha* and *M. agmosticha* species, were collected from across their respective ranges (See Appendix A, Table S1 for specimen and locality information).

We generated new genetic data for 89 samples of *M. dorsivittata* and 56 samples representing the *M. macrorhyncha* species complex. For *M. dorsivittata*, three mitochondrial and seven nuclear genes were sequenced on an ABI 3730xl DNA Sequencer with Macrogen (New York, NY, USA). They include the mitochondrial 12S, 16S, *cytochrome b* (cyt*b*), and the nuclear markers *btb and cnc homology 1* (BACH1), *oocyte stimulating factor oocyte maturation factor* (CMOS), *dynein axonemal heavy chain 3* (DNAH3), *recombination activating gene 1* (RAG1), *ribosomal protein L35* (RPL35), *synuclein alpha interacting protein* (SNCAIP), and *myosin heavy chain* (MYH). For the *M. macrorhyncha* complex, we sequenced the 12S, CMOS, cyt*b*, DNAH3, RAG1, and MYH genes. Other *M. dorsivittata* sequences available in Genbank were used to complement the sequence panel (Appendix A, Table S2). Primers and PCR profiles follow previous studies of lizard taxa (Gartner, et al., 2013; Miralles et al., 2009; Pellegrino, 2001; Townsend et al., 2008; Whiting et al., 2006), and are available in Appendix A (Table S3). DNA sequences were edited and aligned in Geneious vR6 (http://www.geneious.com, Kearse et al., 2012) using the Geneious algorithm, and submitted to Genbank (Accession numbers in Appendix A, Table S2). Summary statistics for each gene (e.g. base pair length, number of haplotypes, haplotype diversity, and nucleotide diversity) were calculated with DNAsp (Librado and Rozas, 2009) and are available in Appendix A (Table S4).

2.2. Inferring evolutionary lineages

To characterize mitochondrial phylogenetic structure within our target taxa, we inferred phylogenetic relationships among sampled individuals using both Bayesian (BI) and Maximum Likelihood (ML) methods, using MrBayes (BI) v3.2.1 (Ronquist et al., 2012) and Garli (ML) v2.0 (Zwickl, 2008). Alignment partition schemes, as well as best-fitting models of evolution, were inferred per gene based on Bayesian information criterion (BIC) scores using PartitionFinder v1.1.1 (Lanfear et al., 2012). For the nuclear genes, the haplotypic phase of heterozygotes was estimated using PHASE 2.1.1 (Flot, 2010; Stephens and Donnelly, 2003). Exact partitions and models of evolution used are available in Appendix A (Table S5). The entire mitochondrial dataset was concatenated and analyzed in MrBayes, which was run four times independently, each for 20 million generations, discarding the first 25% of trees as burn-in. The Garli analysis included 1000 bootstrap

replicates. Stationarity of Bayesian analyses was assessed in Tracer v1.6 to ensure convergence of model parameters (effective sample sizes (ESS) > 200) (Rambaut et al., 2014).

2.3. Examining spatial genetic structure

To examine population genetic structure, as well as to examine whether the distribution of resulting genetic groups correlates with environmental variation, we implemented genetic clustering analyses based on the bi-allelic phased nuclear loci using the Bayesian Markov Chain Monte Carlo (MCMC) program STRUCTURE V2.3.4 (Pritchard et al., 2000). STRUCTURE was run with 20 iterations of each K (for K = 1–10) using the admixture model of ancestry and correlated allele frequencies for 200,000 generations as burn-in, followed by 500,000 generations. Results were analyzed with the Cluster Markov Packager Across K server (CLUMPAK; Kopelman et al., 2015) to identify an optimal K value based on the ΔK method (Evanno et al., 2005), as well as to summarize and visualize the results from multiple runs (Earl and vonHoldt, 2011; Pritchard et al., 2000). Although some nuclear datasets lacked resolution (Appendix A, Table S4; Figs. S6–7), we tested different combinations of nuclear data in STRUCTURE, including using only a subset of nuclear data that displayed more comparative genetic diversity (e.g. genes DNAH3, MYH, RAG1, and RPL35), which resulted in the same or very similar results; we therefore show results from the inclusion of all data obtained.

2.4. Quantifying genetic differentiation across habitats

To assess whether genetic differentiation across geographic space correlates with environmental breaks, we first outlined habitats in South America by adapting the ecoregions in Olson et al. (2001) to define the humid Atlantic Forest, the semi-arid Caatinga, the savannas of the Cerrado, the dry, lowland areas of the Chaco, and the grasslands of the Pampas. Then, we implemented a hierarchical analysis of molecular variance (AMOVA) using mitochondrial haplotype frequencies in Arlequin v3.5.2.1 (Excoffier and Lischer, 2010) to assess the relative partition of genetic variation within sampled localities, across localities within ecoregions (i.e., habitat), and across ecoregions occupied by each species complex. In this analysis, the Chaco was excluded due to a low number of sampled individuals in this ecoregion.

2.5. Testing correlations between genetic, environmental, and geographic distances

Tests of Isolation by Distance (IBD) and Isolation by Resistance (IBR, which incorporates measurements of resistance to dispersal between points across a landscape) have been widely applied to assess the influence of geographic separation on levels of gene flow across natural populations (McRae, 2006; Slatkin, 1993; Spear et al., 2010; Wright, 1943). In addition, the role of Isolation by Environment (IBE) has been studied in systems where differing climatic conditions are thought to have a strong imprint on the distribution of genetic variation (McRae and Beier, 2007; Wang and Bradburd, 2014). Under IBE, ecologically associated mechanisms such as adaptation to local environments are assumed to reduce gene flow and promote genetic divergence between populations, independent of geographic distance (Edelaar and Bolnick, 2012; Nosil et al., 2008; Nosil et al., 2005; Rundle and Nosil, 2005; Wang and Bradburd, 2014; Wang and Summers, 2010). To assess the influence of environmental vs. geographic-based variables on spatial genetic structure – more specifically, to test for the contributions of IBD, IBR, and IBE in explaining genetic distances within each taxa (Wang and Bradburd, 2014; Wang et al., 2013) – we utilized the Multiple Matrix Regression with Randomization (MMRR) function in R (Wang, 2013). We ran the MMRR analyses separately for each species complex and molecular dataset (mtDNA and nuDNA), with 10,000 permutations. In each comparison, we used a matrix of Juke's Cantor (JC) corrected genetic distances across all pairs of localities as a response variable matrix. Genetic distances and metrics were estimated in MEGA v6 (Tamura et al., 2013) based on either the concatenated mitochondrial data, or the concatenated nuclear sequences. To evaluate whether geographic distance, resistance, or environment best explain the levels of genetic divergence observed, we built three variable matrices, each representing a possible predictor, to evaluate the influences of IBD, IBE, and IBR on overall genetic diversity through three independent MMRR analyses.

2.6. Estimating matrices of isolation by distance, resistance, and environment

To estimate a matrix of isolation by distance (IBD), we calculated pairwise Euclidean distances (in kilometers) between each sampled individual using the R package *fossil* (Vavrek, 2011). To estimate a matrix of isolation by environment (IBE), we used the first four principal components extracted from a Principal Component Analysis (PCA) based on climatic data to build a pairwise environmental distance matrix across all individuals (points used, Appendix A, Fig. S1). A PCA was performed by including point-extracted values from 19 WorldClim bioclimatic variables (Hijmans et al., 2005), which describe aspects of local temperature and precipitation, using the *prcomp* function in R. Though these species complexes are distributed across a range of altitudes, elevation was ultimately excluded due to its high correlation to both environmental and geographic distances. Lastly, to estimate a matrix of isolation by resistance (IBR), we developed an Ecological Niche Model (ENM) for each species complex, 84 distinct localities for the *M. dorsivittata* complex and 53 distinct localities from the *M. macrohyncha* complex, and used it to generate a friction layer wherein grid cells with higher suitability scores were assigned lower friction values (ENMs: Appendix A, Fig. S2). We then employed these friction layers to estimate circuit distances across each pair of individuals while accounting for multiple pathways with Circuitscape (McRae and Beier, 2007). Finally, we plotted each geographic or environmental distance matrix against mitochondrial and nuclear distances to ensure linearity, hence verifying that the data were appropriate for use in a MMRR framework (Appendix A, Fig. S3).

To build ENMs for estimation of friction layers, we obtained occurrence data of *M. dorsivittata* and *M. macrorhyncha* from tissue-sampled individuals used in this study, and vetted occurrence records downloaded from VertNet (http://www.vertnet.org), *species*Link (http://splink.cria.org.br/), GBIF (gbif.org), and literature records which allowed no more than a 10 km error (occurrence record citations in Appendix A). All ENMs were built with the 19 bioclimatic layers from Worldclim.org (Hijmans et al., 2005) using MaxEnt (Phillips et al., 2006) implemented in SDMToolbox v1.1c (Brown, 2014). Combinations of model parameters, including a range of regularization multipliers and different feature classes, were tested following the methods detailed in Portik et al. (2017). Optimal model parameters were defined as having the lowest test omission rate, high discrimination ability, and low complexity (Brown, 2014; Shcheglovitova and Anderson, 2013). A minimum convex polygon defined by a 100 km buffer around each occurrence record was used, occurrence records were spatially rarefied (10 km distance), and then partitioned into three random subsets of data and background for testing and training to reduce the effects of spatial auto-correlation and over-fitting (Boria, et al., 2014; Hijmans, 2012; Veloz, 2009).

3. Results

3.1. Phylogenetic patterns and lineage diversity

Across individuals in both species complex datasets, we were able to amplify > 90% of the molecular markers targeted (Appendix A, Table S2). Phylogenetic analyses based on mitochondrial genes recovered

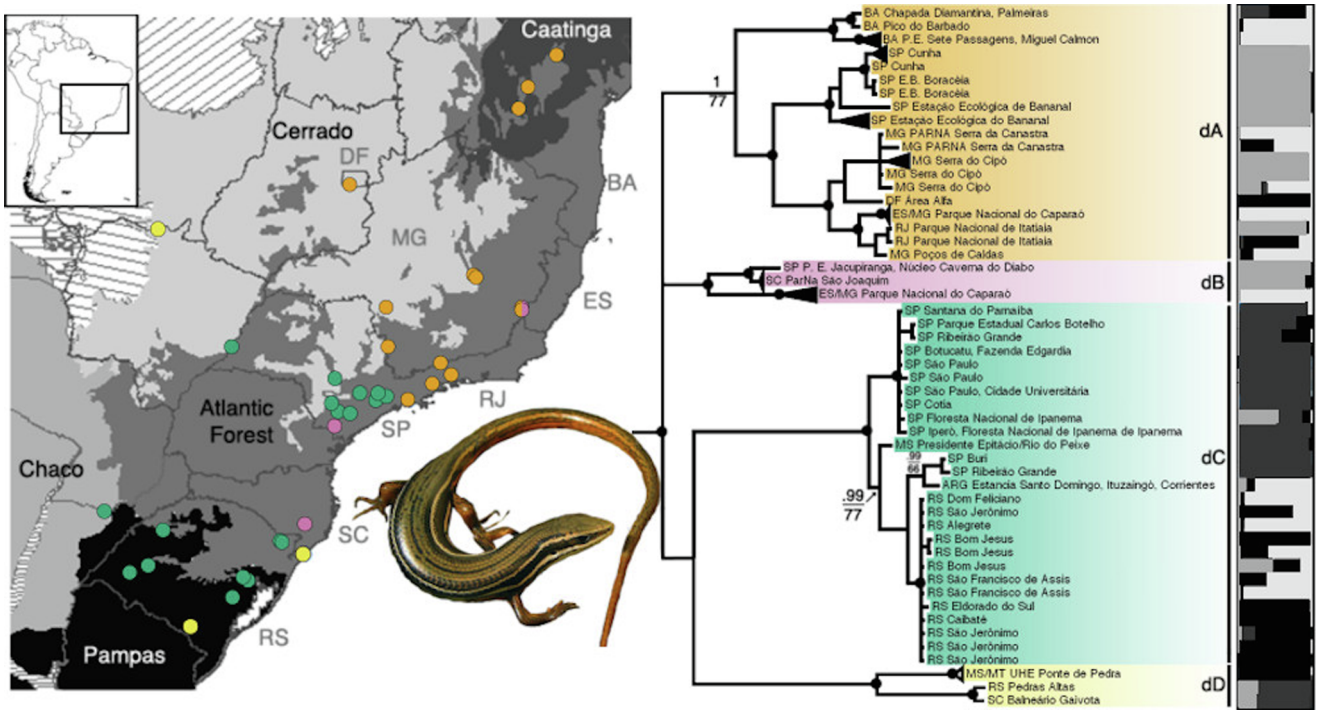

Fig. 1. Sampled localities and phylogenetic reconstruction of the *Mabuya dorsivittata* complex based on mtDNA. Black circles: posterior probability (PP)/maximum likelihood (ML) support > 0.90/85. No label: PP/ML < 0.90/85. Colors denote mitochondrial haplogroups (dA – orange; dB – purple; dC – green; dD – yellow) and STRUCTURE clusters (d1 – white; d2 – light grey; d3 – dark grey; d4 – black). Ecoregions adapted from World Wildlife Fund (Olson et al., 2001). Abbreviations: BA – Bahia; DF – Distrito Federal; ES – Espírito Santos; MG – Minas Gerais; RJ – Rio de Janeiro; RS – Rio Grande do Sul; SC – Santa Catarina; SP – São Paulo. Photo: *M. dorsivittata*, by M. Teixeira, Jr. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

multiple clades in both species complexes, as described below (Figs. 1 and 2). ML and BI analyses of both species complexes yielded similar topologies and comparable node support. The mitochondrial trees are structured, but lack support at deeper nodes, rendering relationships across groups within each species complex unresolved (Figs. 1 and 2). For the *M. dorsivittata* complex, mtDNA is structured into four well-supported haplogroups, with average divergence of 4.7% between haplogroups. The mitochondrial haplogroups (dA-dD) do not clearly segregate in physical space. Instead, the ranges of multiple groups overlap (Fig. 1).

In the *M. macrorhyncha* complex, phylogenetic analyses recovered five well-supported mitochondrial haplogroups (mA-mE), with an average divergence of 3.8% between groups. Haplogroups show some spatial structure across the range of the complex (Fig. 2). Groups mA-mC (yellow, orange, green) occur in the Caatinga and in the open mountain habitats of the northern tip of the Atlantic Forest ("campos rupestres"), while groups mD (purple) and mE (blue) occur along the coastal and montane ranges of the Atlantic Forest, including the type locality of *M. macrorhyncha* at Ilha da Queimada Grande, in the state of São Paulo (Fig. 2). The monophyletic haplogroup mB includes all *M. agmosticha* samples, and is nested phylogenetically within *M. macrorhyncha*. While sampling specimens of the *M. macrorhyncha* complex, we observed unique dorsal and tail coloring in two specimens: one individual in the mC group (from Pico do Barbado, Bahia) displayed a distinct spotted dorsal pattern (Fig. 2), and a few individuals from group mD (in Serra do Cipó, Minas Gerais) had a black, instead of the characteristic olive, tail color (no picture). These phenotypically divergent samples were recovered in two different structured and well-supported clades with other individuals exhibiting the typical phenotype for the species (Fig. 2).

3.2. Patterns of nuclear genetic structure

STRUCTURE analyses of *M. dorsivittata* based on phased diploid nuclear data identified four genetic clusters (d1-4), which do not correspond to the mitochondrial haplogroups (Fig. 1). All genetic clusters are distributed across ecoregion boundaries and/or ecotones (Appendix A, Fig. S4). Those individuals belonging to genetic cluster d1 (white in Fig. 1) are found in four montane localities in the mid and northern Atlantic Forest, as well as in the southern Brazilian grasslands and Chaco. Samples in the cluster d2 (light grey) are distributed across the montane and coastal Atlantic Forest. Genetic cluster d3 (dark grey) ranges across the southern Atlantic Forest and into the Cerrado. Cluster d4 (black) is widely distributed across the northern mountains of the Atlantic Forest, through the Cerrado, and the southern Brazilian Highlands.

STRUCTURE analyses based on nuclear data of the *M. macrorhyncha* complex identified four genetic clusters (m1-4), which do not correspond to mitochondrial genetic haplogroups, yet are somewhat geographically structured (Fig. 2). Cluster m1 (white in Fig. 2) is distributed across the Caatinga, and is comprised of samples identified as *M. macrorhyncha* and *M. agmosticha*; cluster m2 (light grey) occurs in the mountains and coastal *restingas* in the Atlantic Forest; cluster m3 (dark grey) ranges the northern to mid-Atlantic Forest; and cluster m4 (black) includes coastal southern Atlantic Forest localities as well as one montane locality in the northern Atlantic Forest *campos rupestres*. STRUCTURE suggests some admixture between genetic clusters within the *M. macrorhyncha* species complex, with admixed individuals occurring in coastal and northern montane Atlantic Forest localities (Fig. S5).

3.3. Genetic breaks across ecoregion boundaries

Ecoregion boundaries had little effect on the partitioning of genetic variation in both species groups. For the *M. dorsivittata* complex, the AMOVA showed that most of the genetic partitioning (61.43%) is observed within ecoregions; genetic differentiation between ecoregions and within sites explains only 24.60% and 13.97%, respectively, of the

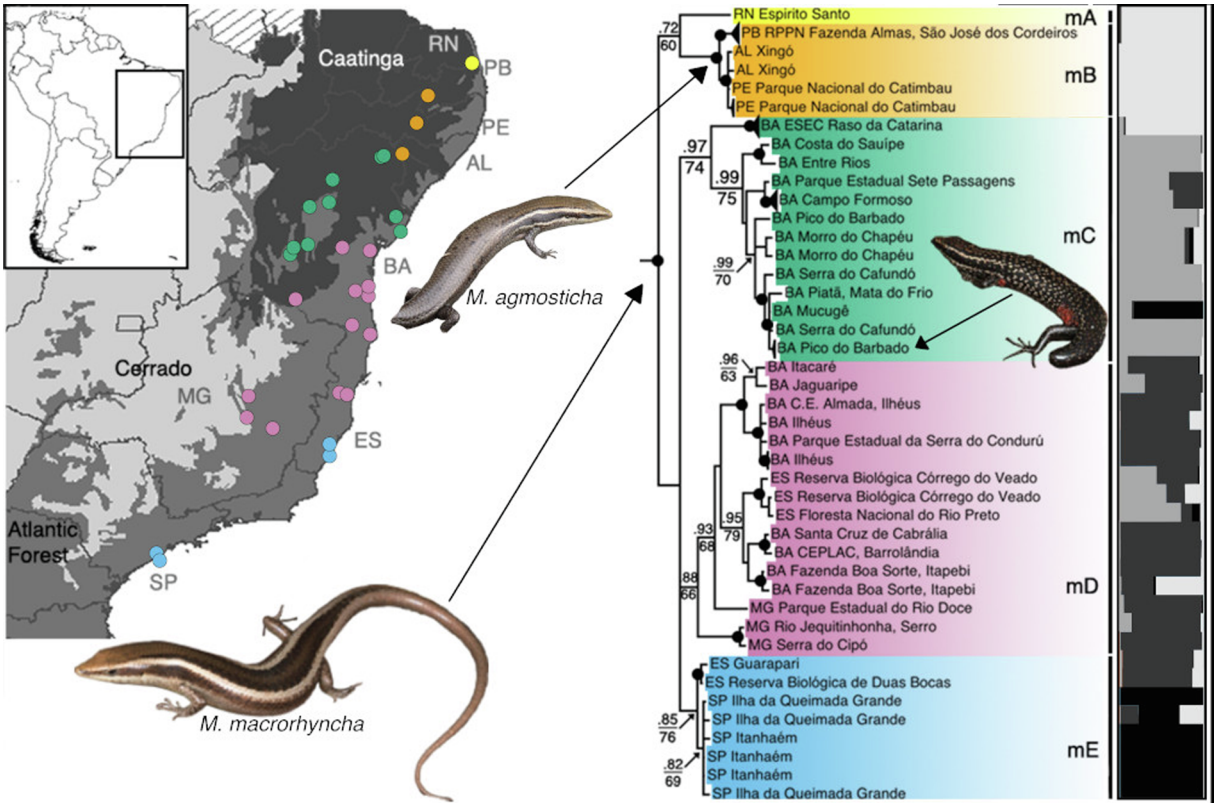

Fig. 2. Sampled localities and phylogenetic reconstruction of the *Mabuya macrorhyncha* complex based on mtDNA. Black circles: posterior probability (PP)/maximum likelihood (ML) support > 0.90/85. No label indicates: PP/ML < 0.90/85. Colors denote mitochondrial haplogroups (mA – yellow; mB – orange; mC – green; mD – purple; mE – blue) and STRUCTURE clusters (m1 – white; m2 – light grey; m3 – dark grey; m4 – black). Ecoregions adapted from World Wildlife Fund (Olson et al., 2001). Abbreviations: AL – Alagoas; BA – Bahia; ES – Espírito Santos; MG – Minas Gerais; PB – Paraíba; PE – Pernambuco; RN – Rio Grande do Norte; SP – São Paulo. Photos: *M. macrorhyncha*, by A. Garda; *M. macrorhyncha* sp. (from Pico do Barbado, BA), by M.T. Rodrigues; *M. agmosticha*, by E. Dias (Dias and Rocha, 2013) (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

Table 1
AMOVA results (based on mtDNA distances) for the (A) *Mabuya dorsivittata* complex and the (B) *M. macrorhyncha* complex.

(A) *M. dorsivittata* complex		**(B) *M. macrorhyncha* complex**	
Source of variation	% of variation	Source of variation	% of variation
Among ecoregion	**24.6**	Among ecoregion	5.21
Among sites within ecoregion	**61.43**	Among sites within ecoregion	**90.62**
Within sites	**13.97**	Within sites	**4.17**

Samples are grouped by ecoregion. Significant values are bolded.

total variation (Table 1). The AMOVA analyses of the *M. macrorhyncha* complex are similar, with 90.62% of genetic diversity within this species found within ecoregions (4.17% within sites, and 5.21% between ecoregions; Table 1).

3.4. Environmental correlates of genetic distance across sites

In the *M. dorsivittata* complex, MMRR analyses demonstrate that environmental (IBE), resistance (IBR), and geographic (IBD) distance contribute significantly to mitochondrial and nuclear genetic distances (Table 2). Resistance distance (mtDNA: $R^2 = 0.24$, $\beta_{CIR} = 0.49$; $p < 0.001$; nuDNA: $R^2 = 0.11$, $\beta_{CIR} = 0.34$; $p < 0.001$) was a slightly better predictor than geographic distance (mtDNA: $R^2 = 0.19$, $\beta_{Euclid} = 0.44$, $p < 0.001$; nuDNA: $R^2 = 0.10$, $\beta_{Euclid} = 0.31$, $p < 0.001$). Furthermore, environmental distance variables had significant but weaker contributions to mitochondrial sequence variation relative to geographic and resistance distance (mtDNA: $R^2 = 0.11$, $p < 0.001$; $p_{PC1} = 0.051$, $p_{PC2} = 0.91$, $p_{PC3} = 0.02$, $p_{PC4} = 0.01$), yet stronger comparative contributions relative to geographic and resistance distances in the analysis of the nuclear data (nuDNA: $R^2 = 0.19$, $p < 0.001$, $p_{PC1} = 0.92$, $p_{PC2} = 0.74$, $p_{PC3} = 0.41$, $p_{PC4} < 0.001$).

In the case of the *M. macrorhyncha* complex, MMRR analyses shows that IBD, IDR and IBE explain very little or none of the genetic variation in mitochondrial or nuclear sequence data (Table 2). Geographic distance was the only significant explanatory variable for mtDNA distance (mtDNA: $R^2 = 0.04$, $\beta_{Euclid} = 0.20$, $p < 0.05$; nuDNA: $R^2 = 0.02$, $\beta_{Euclid} = 0.16$, ns), however its contribution was very small. Neither resistance nor environmental distances were significant explanatory variables (Table 2).

4. Discussion

4.1. Phylogenetic and phylogeographic structure

Both the *M. dorsivittata* and *M. macrorhyncha* complexes show considerable mitochondrial spatial structure across their ranges. However, as observed in other similarly widespread taxa, deeper nodes had low support (Barley et al., 2013; Hedges and Conn, 2012; Miralles and Carranza, 2010; Pinto-Sánchez et al., 2015; Potter et al., 2016; Prates et al., 2016b). Increased geographic and genetic sampling may be necessary to resolve the relationships between haplogroups within both species complexes. This could be especially illuminating for the *M. dorsivittata* complex haplogroup dD, which is found across three sites located 1500 km apart but at no intermediate localities – a geographical pattern also shared with other (*Tropidurus*) lizards (Sena, 2015). It is plausible that improved sampling in intermediate areas could reveal

Table 2
Multiple Matrix Regression with Randomization (MMRR) results for *Mabuya* species complexes.

***M. dorsivittata* complex**	**IBE R^2**	**β_{PC1}**	**β_{PC2}**	**β_{PC3}**	**β_{PC4}**
mtDNA	**0.11**	0.16	-0.008	**0.14**	**0.17**
nuDNA	**0.19**	0.008	-0.02	-0.05	**0.45**
	IBR R^2	**β_{CIR}**		**IBD R^2**	**β_{Euclid}**
mtDNA	**0.24**	**0.49**		**0.19**	**0.44**
nuDNA	**0.11**	**0.34**		**0.10**	**0.31**
***M. macrorhyncha* complex**	**IBE R^2**	**β_{PC1}**	**β_{PC2}**	**β_{PC3}**	**β_{PC4}**
mtDNA	0.03	0.11	0.04	0.09	0.06
nuDNA	0.05	0.10	-0.10	0.15	0.09
	IBR R^2	**β_{CIR}**		**IBD R^2**	**β_{Euclid}**
mtDNA	0.01	-0.08		**0.04**	**0.20**
nuDNA	0.02	0.15		0.02	0.16

Included are the fit of the model (R^2) and regression coefficients (β) for each matrix used to explain Isolation by Environment (IBE), Isolation by Resistance (IBR), and Isolation by Distance (IBD). Significant values are in bold.

this group to be more widespread than presently known, as well as elucidate unique spatial patterns of genetic structure across this region. Alternatively, this pattern may be explained by human mediated dispersal: local logging and wood transport across this highly disturbed area is common, leading to confounding phylogeographic patterns across taxa (MTR, personal observation).

Some of the structure patterns observed in the target species are shared with other local taxa. For instance, we detected considerable mitochondrial divergence between *M. dorsivittata* haplogroups dA and dC in the mid-Atlantic Forest, near the Rio Tietê in São Paulo state (Fig. 1). This area is known to harbor phylogeographic breaks within other species (Amaro et al., 2012; Batalha-Filho et al., 2012, 2010; Bragagnolo et al., 2015; Cabanne et al., 2008; Grazziotin et al., 2006), and it has been posited that a major geological event during the Miocene caused an uplift of at least 160 m, referred to as the Serra do Mar Rift System within the Taubaté basin, and promoted initial and continuing genetic divergence in the area (Amaro et al., 2012; Bragagnolo et al., 2015; Ribeiro, 2006; Riccomini et al., 2010). Future investigations will test for congruence in the timing of this divergence across co-distributed taxa.

Mitochondrial and nuclear discordance was observed within both species complexes, a pattern also detected in other widely ranged taxa (Bryson et al., 2014; Moritz et al., 2015; Vences et al., 2014). Nuclear genetic clusters show admixture across both complexes, and do not correspond to mitochondrial clades (Figs. 1 and 2). Within the *M. dorsivitatta* complex, three of the four nuclear clusters are distributed across ecoregions (d1: Atlantic Forest, Pampas, Chaco; d3: Atlantic Forest, Cerrado; d4: Atlantic Forest, Cerrado, Pampas), in patterns dissimilar to those seen in mitochondrial DNA (Fig. 1). Most notably, the mitochondrial genetic split within the Atlantic Forest (clades dA & dC) is observed within the nuclear data directly around the mid-Atlantic Forest barrier (near the Rio Tietê; nuclear groups d2 & d3). However the level of admixture detected in the nuclear markers increases with the amount of geographic distance among samples belonging to the same mitochondrial haplogroup. The *M. macrorhyncha* complex does exhibit comparatively more mitochondrial genetic structure within ecoregions, while nuclear genetic clusters m2-4 are largely admixed within the Atlantic Forest and m1 is confined to the Caatinga (Fig. 2). Though both species complex datasets only have ~ 10% missing data, it is possible that uneven sampling and/or lack of sampling of existing populations may have led to the underestimation of STRUCTURE clusters in both species complexes. This phenomenon has recently been scrutinized, and illustrates the need for further testing or refined clustering methods (Gilbert, 2016; Janes et al., 2017; Puechmaille, 2016).

4.2. Phylogenetic and phenotypic diversity within the M. macrorhyncha complex

Our results suggest that *M. agmosticha* is more closely related to *M. macrorhyncha* than previously recognized (Hedges and Conn, 2012). Although there are morphological differences described between *M. macrorhyncha* and *M. agmosticha* (Dias and Rocha, 2013; Júnior et al., 2014; Rodrigues, 2000; Sales et al., 2015; Vrcibradic and Rocha, 2005), our improved genetic and geographic sampling, and the clustering of members of the two species into one distinct genetic cluster in the STRUCTURE analysis, suggest that these species require further taxonomic attention. For instance, individuals in the Caatinga identified morphologically as *M. macrorhyncha* (mitochondrial clades mA and mC) and *M. agmosticha* (mB) are in a single nuclear cluster (m1). Furthermore, unique phenotypes identified during collection (spotted dorsum and black tail) were recovered within well-supported mitochondrial clades, along with individuals exhibiting the typical phenotype described for the species. Species within *Mabuya*, as well as related skink genera, have been known to be relatively morphologically conserved, with a number of species often difficult to identify without close inspection of minute characteristics (Barley et al., 2013; Hedges and Conn, 2012; Miralles and Carranza, 2010). Our results reinforce the need to revise the taxonomy of this group under the light of targeted and carefully collected phenotypic data that can be contrasted with the molecular information analyzed here.

4.3. Differing drivers of genetic structure

Environmental differences were previously found to have an underestimated amount of influence on the genetic diversity of widespread taxa through locally adaptive genetic divergence (Wang, 2013). Though most of the genetic variation within *M. dorsivittata* occurs within ecoregions (Table 1), environmental and geographic distances significantly explain some of the genetic divergence (Table 2). Conversely, distance poorly predicted genetic divergence within the *M. macrorhyncha* complex ($R^2 = 0.04$), although this was a significant predictor. These differences between skink groups may be related to their occurrence in different parts of South America, their distinct ranges, as well as to different ecological preferences: *M. dorsivittata* is able to explore forest edges and open settings from low to high elevation areas in southern Brazil, while *M. macrorhyncha* is predominantly associated with ground bromeliads in open areas adjacent to forest habitats, from sea level to high elevations in lower latitudes (Rodrigues, 2000; Williams and Kacoliris, 2011). The fact that both skink complexes are active thermoregulators, vagile, and widely ecologically tolerant can account for the poor correlation between genetic differentiation,

geography, and climate (Strangas et al., 2019). Previous studies have shown that paleoclimatic distribution of lizard species has had a significant influence on contemporary phylogenetic structure (Oliveira et al., 2018; Werneck et al., 2012). That being, preliminary correlative models of the *Mabuya* species analyzed here, when projected into former climates, suggest that former distributions were not significantly restricted enough to promote deme isolation and lineage differentiation (Rivera, unpublished data).

The levels of IBD observed in these skink complexes are weak when compared to other studies of widely distributed species of reptiles (Guarnizo et al., 2016; Moussalli et al., 2009), amphibians (Robertson et al., 2009; Wang, 2013), mammals (McRae and Beier, 2007), and plants (Cornille et al., 2016; Ortego et al., 2015; Wu et al., 2016), where genetic distance was strongly correlated to geographic distance. This may result from complex histories as well as phylogeographic patterns across this topographically heterogeneous region. Unlike the *M.dorsivittata* complex, widely distributed amphibians (Robertson et al., 2009; Wang, 2013), fish (Jørgensen et al., 2005), and plants (Mayol et al., 2015; Wu et al., 2016) have had genetic differences much more strongly tied to environmental similarity. These results imply that historical processes not described by current climate and topography may hold the key to understanding genetic divergence within the species complexes described here. This lends further support for the growing need to describe genetic structure and diversification within similarly widespread species in complex and biodiverse habitats.

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Appendix A

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