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DIVERSIDADE GENÉTICA E PADRÕES FILOGEOGRÁFICOS DO ESCORPIÃO *JAGUAJIR ROCHAE* (BORELLI, 1910) EM UM GRADIENTE DE ESTABILIDADE CLIMÁTICA DA CAATINGA

Recife

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STÊNIO ÍTALO ARAÚJO FOERSTER

Diversidade genética e padrões filogeográficos do escorpião *Jaguajir rochae* (Borelli, 1910) em um gradiente de estabilidade climática da Caatinga

Dissertação apresentada ao Programa de Pós-Graduação em Genética da Universidade Federal de Pernambuco como parte dos requisitos exigidos para obtenção do título de Mestre em Genética.

Orientador: Dr. Valdir de Queiroz Balbino

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RESUMO

O domínio das Caatingas representa o maior núcleo contínuo de florestas tropicais sazonalmente secas do novo mundo, entretanto, a história evolutiva da fauna destes ambientes tem sido pouco investigada. Assim, o presente estudo buscou avaliar a atuação de potenciais núcleos de estabilidade climática como refúgios e / ou centros de diversificação da Caatinga, utilizando como modelo, o escorpião *Jaguajir rochae*. Diferentes estratégias de agrupamento e datação molecular foram empregadas em busca de possíveis compatibilidades cronológicas entre os processos de diversificação de linhagens mitocondriais de *J. rochae*, e os principais eventos climáticos e geomorfológico que moldaram as paisagens da Caatinga. Em adição, nove modelos de migração foram aplicados para elucidar os padrões de fluxo gênico entre populações distribuídas ao redor do Planalto da Borborema, avaliando assim, o efeito desta formação geológica na diferenciação genética e isolamento geográfico de populações de *J. rochae*. Nossos resultados indicam altos níveis de diversidade genética em populações situadas em áreas de Caatinga historicamente estáveis, e que os processos de diversificação intrapopulacional ocorreram após o soerguimento do Planalto da Borborema. Ainda, foi demonstrado que o Planalto da Borborema constitui uma barreira semipermeável ao fluxo gênico de *J. rochae*, e um padrão dinâmico de migração é proposto para a referida espécie. Finalmente, os processos que levaram a atual distribuição espacial da diversidade genética em populações de *J. rochae* são discutidos sob a luz da Teoria dos Gradientes Ecológicos.

Palavras-chave: Filogeografia. Biogeografia. SDTF. Invertebrados. Modelagem ecológica.

ABSTRACT

The Caatinga domain represent the largest and continuous nucleus of Seasonally Dry Tropical Forest in the New World, however, the evolutive story of its fauna is poorly known. Thus, we use the scorpion *Jaguajir rochae* as a biological model to investigate the role of potential nuclei of climatic stability, as diversification hotspots within the Caatinga formations. Different clustering strategies and molecular dating were applied to infer possible chronological associations among the processes of mitochondrial lineage diversification in *J. rochae*, and the major geoclimatic events that shaped the Caatinga landscapes. In addition, nine migration models were tested to elucidate the patterns of gene flow among populations distributed around the Borborema Plateau, evaluating its effects on the genetic differentiation and geographic isolation among populations of *J. rochae*. Our results indicate high levels of genetic diversity in populations distributed in historically stable areas of Caatinga, with intraspecific diversification events occurring after the uplift of the Borborema Plateau. We also demonstrated that the Borborema Plateau is a semipermeable barrier to the gene flow of *J. rochae*, and a dynamic pattern of gene flow is proposed for this species. Finally, the processes behind the current distribution of the genetic diversity among populations of *J. rochae* are discussed under the light of the Ecological Gradient Theory.

Keywords: Phylogeography. Biogeography. Caatinga. SDTF. Invertebrates. Ecological modelling.

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Referencial Teórico

Item	Definição
FTSSs	Florestas Tropicais Sazonalmente Secas
HRP	Hipótese dos Refúgios Pleistocênicos
NC	Núcleo Caatinga
HAP	Hipótese do Arco-Pleistocênico
MDEs	Modelos de Distribuição de Espécies
mtDNA	DNA mitocondrial
nDNA	DNA nuclear
rnDNA	DNA ribossômico nuclear
COI	Citocromo c oxidase I
SDTFs	Seasonally Dry Tropical Forests
CD	Caatinga Domain
BOP	Borborema Plateau
ICMBio	Instituto Chico Mendes de Preservação da Biodiversidade
COI	Cytochrome c oxidase I
SER	Serra Talhada
h	Number of haplotypes
Hd	Haplotype diversity
π	Nucleotide diversity
AMOVA	Analysis of Molecular Variance
BIC	Bayesian Information Criterion
LBF	Log Bayes Factor
MCMC	Markov Chain Monte Carlo
ESS	Effective Sample Size
M	Mutation-scaled migration rate
Θ	Mutation-scaled effective population size
ENMs	Ecological Niche Models
LIG	Last Interglacial
LGM	Last Glacial Maximum
VIF	Variance Inflation Factor
AUC_{TEST}	Area under the receiver operating characteristic curve for the testing data
AUC_{DIFF}	The difference between the area under the receiver operating characteristic curve calculated for testing, and training data
TSS	True Skill Statistics

OR0	0% Omission Rate
OR10	10% Omission Rate
CAR	Caruaru
CUM	Cumaru
AGU	Água Branca
AFO	Afogados da Ingazeira
CAE	Caetés
PAR	Parnamirim
LIM	Limoeiro
HPD	Highest Posterior Density

SUMÁRIO

1 INTRODUÇÃO

A identificação de refúgios naturais é uma etapa fundamental para a preservação da biodiversidade. Esses refúgios são áreas que propiciam condições favoráveis de habitat, facilitando a permanência das espécies em escala de tempo evolutiva, ao mesmo tempo em que preservam a diversidade genética da biota, favorecendo os eventos de diversificação de espécies e/ou linhagens. Nesse contexto, análises filogeográficas e inferências de diversidade genética, podem auxiliar na identificação e delimitação de refúgios (áreas de estabilidade climática) e centros de diversificação de espécies, além de expor potenciais barreiras ao fluxo gênico de populações.

No presente estudo, nós buscamos compreender e utilizar os padrões filogeográficos do escorpião *Jaguajir rochae* (Borelli, 1910), como ferramenta para testar a atuação de áreas de alta estabilidade climática como refúgios históricos, importantes para promover diversificação da biodiversidade em ambientes de Caatinga. Nós também avaliamos a atuação do Planalto da Borborema como o principal elemento orográfico da paisagem que limita o fluxo gênico entre populações de *J. rochae* em escala regional. Sob um ponto de vista histórico, nós apresentamos novas perspectivas sobre as inter-relações entre a história geoclimática da Caatinga e os processos de diversificação e estruturação de populações que ocorrem nestes ambientes. A notória escassez de informações sobre os processos evolutivos responsáveis pelos padrões atuais de distribuição espacial da diversidade genética em táxons de Caatinga foi uma das principais motivações para a condução deste estudo. Em adição, a assertiva geral de que a Caatinga não apresenta barreiras orográficas suficientes para impor resistência ao fluxo gênico entre populações, nos motivou a testar a hipótese de que o Planalto

da Borborema constitui um importante elemento na estruturação genética de espécies com baixa capacidade de dispersão.

Com isso, nós acreditamos que o presente estudo agrega novas informações que são relevantes para o progressivo desenvolvimento do conhecimento acerca da história biogeográfica da Caatinga, gerando um conteúdo que certamente fomentará discussões em âmbito acadêmico. Do ponto de vista prático, o nosso estudo ilustra a evolução da diversidade genética em linhagens mitocondriais de *J. rochae* ao longo do tempo, provendo detalhes sobre como a distribuição espacial desta diversidade respondeu aos ciclos climáticos do Pleistoceno em escala regional. Como os eventos climáticos mencionados possuem um comportamento cíclico, os nossos resultados podem fornecer subsídios para possíveis previsões a respeito dos efeitos das mudanças climáticas sobre a diversidade genética de animais com baixa capacidade de dispersão. Em adição, uma outra implicação imediata é de que a estabilidade histórica da Caatinga deve ser levada em consideração durante o delineamento de estratégias de preservação da biodiversidade, como por exemplo, a criação de unidades de conservação.

1.1 Objetivo geral

Obter estimativas de diversidade genética e elucidar padrões filogeográficos em populações do escorpião *J. rochae* em escala regional, buscando identificar potenciais refúgios e/ou centros de diversificação em ambientes de Caatinga, bem como possíveis barreiras ao fluxo gênico da espécie, utilizando para isso, modelos de distribuição de espécies e análises moleculares do gene mitocondrial citocromo C oxidase I (COI).

1.2 Objetivos específicos

1 Verificar se populações de *J. rochae* distribuídas em áreas de Caatinga historicamente estáveis apresentam maiores níveis de diversidade genética e estabilidade demográfica quando comparadas às populações de áreas instáveis;

2 Avaliar a possível influência do Planalto da Borborema no fluxo gênico e estruturação genética de populações de *J. rochae*;

3 Investigar a existência de possíveis associações cronológicas entre os eventos de diversificação intraespecífica em *J. rochae*, e a história geoclimática da região do Planalto da Borborema;

4 Inferir potenciais mudanças espaciais no nicho climático de *J. rochae* na região do Planalto da Borborema, ocorridas a partir do último período interglacial.

2 REFERENCIAL TEÓRICO

2.1 Aspectos biogeográficos da Caatinga

As florestas tropicais sazonalmente secas (FTSSs), são caracterizadas pelo predomínio de vegetação decídua, ocorrendo em regiões com regimes pluviométricos irregulares, e inferiores a 1.800 mm por ano. (Pennington *et al.,* 2009). Durante muito tempo, as formações de vegetação aberta da América do Sul (Caatinga, Cerrado e Chaco) foram classificados em um único bloco, representando a diagonal (ou corredor) de vegetação aberta que se estende da região nordeste do Brasil, até a região centro-norte da Argentina (Vanzolini, 1974; Bucher, 1982; Werneck, 2011). Essa classificação foi sustentada por diversos estudos envolvendo vertebrados (Short, 1975; Mares *et al.,* 1985; Vitt, 1991) e invertebrados (Camargo & Becker, 1999).

Nos dias atuais a Caatinga, Cerrado e Chaco são regiões ecológicas distintas, resultantes de diferentes padrões geomorfológicos, climáticos e biogeográficos (Pennington *et al.,* 2000, 2009; Motta *et al.,* 2002; Spichiger *et al.,* 2004; Werneck, 2011; Queiroz *et al.,* 2018). Consequentemente, os diferentes processos biogeográficos ocorridos nas referidas regiões ecológicas foram responsáveis por moldar a distribuição da biodiversidade atual, influenciando a história demográfica das populações, e promovendo eventos de especiação e/ou diversificação de linhagens (Werneck *et al.,* 2011; Apgaua *et al.,* 2014; Oliveira *et al.,* 2015; Bartoleti *et al.,* 2017; Leal *et al.,* 2018).

Dentre as florestas sazonalmente secas da região Neotropical, a Caatinga é uma região ecológica situada, em sua maior parte, no semiárido Brasileiro, abrangendo uma área de 912.529 km^2 (Silva *et al.,* 2018). Trata-se, portanto, do maior núcleo continuo de FTSS do Novo Mundo (Queiroz *et al.,* 2018). Em termos

florísticos, os padrões de distribuição da vegetação da Caatinga são fortemente influenciados por fatores climáticos, edáficos e geomorfológicos da paisagem, que resultam na distinção de dois grupos fitofisionômicos da Caatinga – a Caatinga cristalina, e a Caatinga sedimentar (Moro *et al.,* 2015; Queiroz *et al.,* 2018).

As conformações do relevo e os diferentes tipos de solo estão entre os principais filtros ambientais que permitem, ou restringem, o estabelecimento de comunidades vegetais na Caatinga (Tabarelli *et al.,* 2003; Santos *et al.,* 2012; Moro *et al.,* 2016). A Caatinga cristalina, por exemplo, possui ampla distribuição, ocorrendo em solos rasos, porém ricos em nutrientes, originados a partir de rochas cristalinas, enquanto que a Caatinga sedimentar, restringe-se aos solos sedimentares, profundos, mas geralmente com baixo teor de nutrientes (Moro *et al.,* 2015, 2016; Queiroz *et al.,* 2018). Em adição, diversos estudos têm demonstrado as complexas relações de similaridade e divergência entre as comunidades vegetais da Caatinga cristalina e da Caatinga sedimentar, evidenciando padrões distintos de riqueza e distribuição de plantas nesses dois ambientes (Gomes *et al.,* 2006; Cardoso & Queiroz, 2007; Costa *et al.,* 2015).

De acordo com Ab'Sáber (1974), as fitofisionomias típicas de Caatinga, definidas pelo autor como "verdadeiros sertões", ocorrem nas depressões interplanalticas do nordeste do Brasil, originadas a partir de aplanações neogênicas, isto é, ocorridas na segunda metade do Cenozoico, que compreende o final do período Terciário e início do Quaternário. Ainda segundo o referido autor, as fitofisionomias da Caatinga não sofreram grandes alterações em decorrência das oscilações climáticas do Quaternário, a ponto de serem substituídas por outras floras. Ao invés disso, a Caatinga se expandiu durante as épocas mais secas do Quaternário, por meio de corredores formados entre a Bacia Amazônica e o

Planalto Central, alcançando áreas que atualmente são ocupadas pelo Cerrado (Tricart, 1958; Ab'Sáber, 1974, 1977). Os modelos de expansão da Caatinga durante os períodos secos do Quaternário foram elaborados em concordância com os ensaios paleoclimáticos formalmente propostos por Damuth & Fairbridge (1970), os quais, apontam a persistência de climas áridos e semiáridos na região Sul-Americana equatorial durante o Quaternário, mostrando ainda, que os padrões de deslocamento vertical da célula de alta pressão do Atlântico Sul foram responsáveis por controlar o clima do Brasil durante o Quaternário, propiciando o estabelecimento de períodos secos durante as glaciações, e períodos mais úmidos em intervalos interglaciais.

Após os estudos realizados pelo geógrafo Aziz Ab'Sáber na década de 1970, diversos autores buscaram avaliar as possíveis relações entre as oscilações históricas dos biomas Neotropicais de vegetação aberta, e os padrões atuais de distribuição da biodiversidade (Werneck, 2011), utilizando como modelo, diversas espécies de vertebrados (Mares *et al.,* 1985; Carnaval & Bates, 2007; Carnaval & Moritz, 2008; Werneck *et al.,* 2015; Thomé *et al.,* 2016; Lima *et al.,* 2017; Costa *et al.,* 2018; Castro *et al.,* 2019), e invertebrados (Brown *et al.,* 1974; Magalhães *et al.,* 2014; Miranda *et al.,* 2017; Peretolchina *et al.,* 2018), bem como elementos da flora (Prado & Gibbs, 1993; Oliveira *et al.,* 1999; Santos *et al.,* 2007; Werneck *et al.,* 2011; Menezes *et al.,* 2016; Souza *et al.,* 2018).

Considerando os potenciais efeitos das variações climáticas ocorridas na região Neotropical no final do Plioceno e durante o Pleistoceno, Haffer (1969), propôs a hipótese dos refúgios pleistocênicos (HRP), para elucidar as possíveis origens da diversidade de aves Amazônicas. A HRP prediz que a fragmentação e a substituição espaço-temporal das florestas úmidas neotropicais, por

fitofisionomias abertas (Savanas), promoveram eventos de especiação alopátrica (por vicariância) em diferentes táxons (Haffer *et al.,* 1969; Wüster *et al.,* 2005). Subsequentemente, a HRP tem sido debatida por muitos autores (Hoorn *et al.,* 2010; Werneck, 2011; Werneck *et al.,* 2011; Turchetto-Zolet *et al.,* 2013), gerando inúmeras controvérsias fundamentadas em inconsistências nas premissas postuladas pela HRP. Provavelmente, a extensão que os biomas de vegetação aberta da região Neotropical alcançaram em seu ápice de expansão durante o Quaternário, e o tempo de divergência entre espécies e linhagens de diversos táxons neotropicais, correspondem às principais fontes de controvérsias relacionadas à HRP (Moritz, 2000; Colinvaux *et al.,* 2001).

A partir de dados palinológicos, Colinvaux et al. (2001) enfatizaram que as oscilações climáticas do Quaternário não foram suficientes para promover a substituição da floresta Amazônica por outras fitofisionomias, implicando apenas em mudanças populacionais nas comunidades vegetais do referido bioma. Adicionalmente, Cheng et al. (2013), por meio de datação absoluta de isótopos de oxigênio em espeleotemas, forneceram indícios de maiores concentrações pluviométricas no oeste da Amazônia durante o último período glacial, enquanto que na face leste, o clima seco foi mais pronunciado. Ainda segundo os autores, a estabilidade climática foi responsável por manter a biodiversidade do oeste da Amazônia, contrariando o princípio da fragmentação predita pela HRP.

Um segundo aspecto controverso da HRP ainda muito discutido em estudos atuais, refere-se ao tempo de diversificação de linhagens e/ou espécies. Se consideramos estritamente as premissas da HRP estabelecidas por Haffer (1969), estamos assumindo que os eventos de especiação ocorreram em um intervalo de tempo que abrange o Terciário-Quaternário, que em outras palavras, significa que

a diversificação da fauna amazônica é um fenômeno relativamente recente. Há evidências, no entanto, de que a cladogênese em diversos grupos taxonômicos que ocorrem em florestas úmidas da América do Sul precede essa janela de tempo (Moritz *et al.,* 2000; Rull, 2006; Couvreur *et al.,* 2011; Fritz *et al.,* 2011; Patel *et al.,* 2011; Álvarez-Presas *et al.,* 2014; Kozak *et al.,* 2015; Gehara *et al.,* 2017). Provavelmente, os exemplos mais explícitos de incompatibilidade cronológica entre a diversificação da fauna neotropical e as premissas postuladas pela HRP, são ilustrados por Moritz et al. (2000), em que apenas 7 de 125 eventos de diversificação de pequenos mamíferos da América do Sul ocorreram em uma escala de tempo que coincide com Pleistoceno, o que também foi observado em 18 de 64 eventos de especiação em grupos de aves Sul-Americanas. Em adição, processos de diversificação ocorridos antes do período Quaternário também são reportados para grupos taxonômicos de florestas secas da América do Sul (ex. Pennington *et al.,* 2009; Pirie *et al.,* 2009; De-Nova *et al.,* 2012).

É importante lembrar, que a HRP apresentada por Haffer (1969), foi elaborada unicamente a partir de dados de populações atuais de aves, desconsiderando, portanto, informações paleoecológicas (Bush & Oliveira, 2006), e a atuação de rios e outros corpos d'água como potenciais barreiras ao fluxo gênico das populações distribuídas na região Amazônica (Connor, 1986). Assim, não existe uma harmonia consensual entre as premissas estabelecidas pela HRP (stricto sensu), e a história biogeográfica de diversos táxons distribuídos na região Neotropical (Knapp & Mallet, 2003).

2.2 Núcleos de estabilidade climática da Caatinga

As FTSSs presentes na América do Sul possuem um padrão de distribuição disjunta, em que as maiores unidades de vegetação contínua são representadas por três grandes blocos: o núcleo Caatinga (NC), situado majoritariamente no nordeste do Brasil; o núcleo Misiones, localizado ao longo das bacias hidrográficas dos rios Paraná-Paraguai; e o núcleo Piedmont, distribuído em uma região que compreende o noroeste da Argentina e sudoeste da Bolívia (Prado & Gibbs, 1993; Prado, 2000; Werneck *et al.,* 2011). O núcleo Caatinga representa o mais extenso bloco contínuo de FTSS da região Neotropical (Prado & Gibbs, 1993; Pennington *et al.,* 2000, 2009; Werneck *et al.,* 2011). Historicamente, modelos de distribuição de espécies e análises palinológicas, indicam um padrão dinâmico de distribuição da vegetação contida no NC, o que significa dizer que apesar de sua grande extensão contínua, existem subnúcleos dentro do NC que podem ser distinguidos entre si de acordo com diferentes níveis de estabilidade climática (Werneck *et al.,* 2011).

Apesar de ter sido formulada sob a perspectiva das florestas úmidas neotropicais, a HRP proposta por Haffer (1969) e discutida no tópico anterior, está indiretamente associada com dinâmica da distribuição das FTSSs. Esta associação torna-se evidente se consideramos que as oscilações climáticas ocorridas entre o final do período Terciário (atualmente dividido nos períodos Paleógeno e Neógeno) e o período Quaternário, foram fundamentais para os processos de alternância entre as florestas úmidas e as florestas de vegetação aberta na região Neotropical (Haffer, 1969, Webb, 1978; Behling, 1998; Prado *et al.,* 2012).

Partindo da premissa de que as mudanças climáticas ocorridas ao longo do Quaternário foram responsáveis por promover eventos de expansão e retração das

FTSSs da América do Sul, Werneck et al. (2011) puderam então definir áreas de estabilidade climática situadas no NC, a partir de predições de ocorrência de ambientes favoráveis para estabelecimento de FTSSs em diferentes épocas do período Quaternário, as quais, foram validadas por meio de dados palinológicos. As áreas de estabilidade climática do NC estabelecidas por Werneck et al. (2011), condizem com a classificação das ecorregiões da Caatinga propostas por Velloso et al. (2002) (Figura 1), situando-se, na maior parte da Depressão Sertaneja Setentrional, Complexo Ibiapaba-Araripe, e Complexo da Chapada Diamantina. Há também, duas grandes áreas de estabilidade climática na Depressão Sertaneja Meridional, intercaladas por uma área instável, representada por uma diagonal que se estende desde a região centro-leste da Depressão Sertaneja Meridional, até a região centro-sul do Planalto da Borborema (Figura 2).

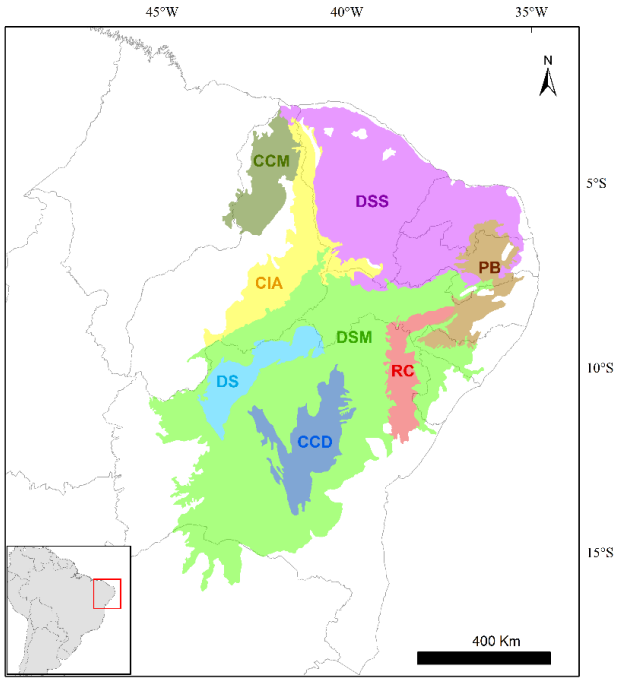

Figura 1. Ecorregiões propostas para a Caatinga: Complexo Campo Maior (CCM); Complexo da Chapada Diamantina (CCD); Complexo do Ibiapaba-Araripe (CIA); Depressão Sertaneja Meridional (DSM); Depressão Sertaneja Setentrional (DSS); Dunas do São Francisco (DS); Planalto da Borborema (PB); e Raso da Catarina (RC). Adaptado de Velloso et al. (2002).

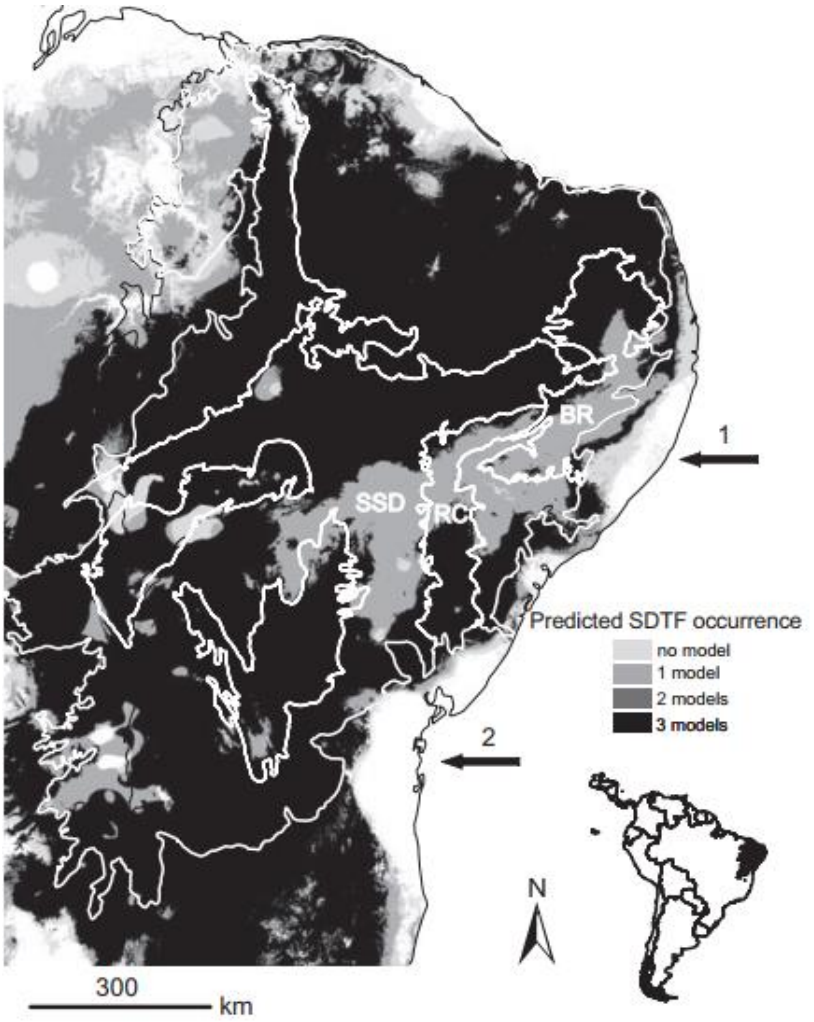

Figura 2. Representação das áreas de estabilidade (preto) e instabilidade (tons de cinza) climática da Caatinga gerada a partir de modelos de circulação atmosférica. As setas representam as áreas de alta estabilidade climática da Mata Atlântica, as quais, coincidem com os centros de diversidade Pernambuco (1), e Bahia (2). Nestas áreas, nenhum dos modelos indicaram a ocorrência de FTSSs. As linhas brancas delimitam as ecorregiões da Caatinga: Planalto da Borborema (BP), Raso da Catarina (RC), Depressão Sertaneja Meridional (SSD). Fonte: Werneck et al. (2011).

As inúmeras discussões sobre a origem e os padrões de distribuição da biodiversidade Sul-Americana no espaço e no tempo são comumente associadas a hipóteses formuladas sob a perspectiva das florestas úmidas (ex. Haffer, 1969; Nelson *et al.,* 1990; Fernandes *et al.,* 2012, 2013; Leite & Rogers, 2013). De fato, uma grande parcela do conhecimento sobre a biogeografia dos táxons da América

do Sul é oriunda de estudos com espécies típicas de florestas úmidas, como a floresta Amazônica (Morrone, 2000; Aleixo & Rossetti, 2007; Alfaro *et al.,* 2011; Dagosta & Pinna, 2017) e a mata Atlântica (Costa *et al.,* 2000; Cabanne *et al.,* 2008; Martins, 2011; Saraiva & da Silva, 2016) ou ainda, de remanescentes de florestas úmidas distribuídas dentro dos domínios das florestas de vegetação aberta, como os brejos de altitude (Costa, 2003). Por outro lado, a história biogeográfica da biota distribuída nas florestas de vegetação aberta da América do Sul tem recebido pouca atenção (Prado & Gibbs, 1993; Wüster *et al.,* 2005; Werneck *et al.,* 2011, 2012; Bueno *et al.,* 2016).

Uma das principais hipóteses biogeográficas referentes aos biomas de vegetação aberta da América do Sul é a hipóteses do arco pleistocênico (HAP), formulada por Prado & Gibbs (1993). A HAP assume que o padrão atual de distribuição disjunta das florestas de vegetação aberta da América do Sul, resulta da fragmentação de uma área ancestral contínua, que se estendeu, em sentido diagonal, do nordeste do Brasil, até o noroeste da Argentina (Prado & Gibbs, 1993). O ápice da expansão das florestas de vegetação aberta teria ocorrido durante o Pleistoceno, mais especificamente, em um intervalo de tempo que corresponde ao último máximo glacial (21.000 – 12.000 anos antes do presente), quando o clima frio e seco propiciou o a expansão das florestas de vegetação aberta, ao mesmo tempo em que as florestas úmidas se retraíram (Ab'Sáber, 1977; Prado & Gibbs, 1993).

Em casos específicos, a HAP tem sido adotada para explicar a distribuição de determinados táxons em diferentes escalas de tempo e espaço (ex. Werneck & Colli, 2006; Caetano *et al.,* 2008), porém, há também exemplos em que que a história biogeográfica de muitas espécies não condiz com as premissas

estabelecidas pela HAP (ex. Magalhães *et al.,* 2014; Côrtes *et al.,* 2015, Bueno *et al.,* 2016). Em nível de paisagem, diversos estudos florísticos têm refutado a HAP (Oliveira *et al.,* 1999; Pessenda *et al.,* 2010; Werneck *et al.,* 2011, 2012; Sobral-Souza *et al.,* 2015; Leite *et al.,* 2016; Arruda *et al.,* 2018). Por exemplo, Arruda *et al*. (2018), a partir de modelos de distribuição ecológica e uso de dados palinológicos, estimaram que durante o último máximo glacial, a expansão dos biomas de vegetação aberta do Brasil se restringiu às áreas ecotonais. Os modelos propostos por Arruda *et al*. (2018) apontam ainda um clima frio e úmido na maior parte do Brasil, refutando uma das asserções da HAP, que prediz um clima frio e seco na referida região (Ab'Sáber, 1977; Prado & Gibbs, 1993). Similarmente, Werneck *et al*. (2011) demonstraram que os modelos de distribuição das FTSSs neotropicais ao longo do Quaternário são incompatíveis com as premissas propostas pela HAP, denotando que as condições climáticas do último máximo glacial não foram favoráveis para a expansão das FTSSs, e que ao invés disso, a distribuição das FTSSs fora ainda mais disjunta nesse período. Um padrão semelhante foi também observado em áreas de Cerrado, que segundo Werneck *et al*. (2012), atingiu seu ápice de retração durante o último máximo glacial.

Como pode ser observado, a distribuição histórica dos biomas de vegetação aberta da América do Sul é um tema relativamente bem abordado na literatura (ex. Werneck, 2011; Werneck *et al.,* 2011; 2012; Arruda *et al.,* 2018). No entanto, o principal objetivo desses estudos tem sido a categorização e a delimitação dos referidos biomas neotropicais ao longo do espaço e do tempo. Enquanto isso, os efeitos da variação espaço-temporal desses biomas sobre a biota que os habitam ainda é um tema pouco explorado (Turchetto-Zolet *et al.,* 2013). Da mesma forma, são escassos os estudos que buscam validar as áreas de alta estabilidade climática

previamente preditas (ex. Werneck *et al.,* 2011, 2012; Arruda *et al.,* 2018) como refúgios históricos e/ou centros de diversificação em ambientes de vegetação aberta (Werneck *et al.,* 2011, 2012; Turchetto-Zolet *et al.,* 2013), sobre tudo em áreas de Caatinga (Werneck *et al.,* 2011, 2015).

2.3 A Filogeografia e os modelos de distribuição de espécies na identificação de centros de diversificação

Nas últimas décadas, o desenvolvimento de novas ferramentas computacionais contribuiu substancialmente para o progresso da biogeografia em escala global, especialmente quando se trata de modelos de distribuição de espécies (Guisan & Thuiller, 2005; Thuiller *et al.,* 2005; Dormann, 2007; Ficetola *et al.,* 2007; Sunday *et al.,* 2012; Mainali *et al.,* 2015). Conceitualmente, os modelos de distribuição de espécies (MDEs) correspondem ao conjunto de técnicas e algoritmos implementados para predizer a potencial distribuição de um táxon em diferentes escalas de tempo e espaço (Guisan & Thuiller, 2005; Elith & Leathwick, 2009).

Utilizando registros de ocorrência georreferenciados (presença de espécies) e um conjunto pré-selecionado de variáveis bióticas e abióticas, os MDEs são capazes de predizer a potencial distribuição de um determinado táxon em áreas não amostradas (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005). Esses modelos podem ser aplicados para elucidar inúmeras questões na biologia, como por exemplo, para predizer e / ou explicar padrões atuais de distribuição da biodiversidade (Pineda & Lobo, 2009; Raes *et al.,* 2009; Pérez & Font, 2012; Moraes *et al.,* 2014), estimar áreas de ocorrência de espécies raras (Williamns *et al.,* 2009; Marini *et al.,* 2010; Sousa-Silva *et al.,* 2014; Tronstad *et al.,* 2018),

ameaçadas (Crawford & Hoagland, 2010; Chunco *et al.,* 2013; Sousa-Silva *et al.,* 2014), e/ou invasoras (Young *et al.,* 2013); inferir possíveis respostas da biodiversidade frente às mudanças climáticas (Bond *et al.,* 2011; Padonou *et al.,* 2015), e delimitar ambientes prioritários para conservação (Syfert *et al.,* 2014; Padonou *et al.,* 2015; Angelieri *et al.,* 2016; Heuner *et al.,* 2016; Kaky & Gilbert, 2016; Fois *et al.,* 2018), dentre outras aplicações (uma revisão detalhada pode ser consultada em Guisan & Thuiller, 2005).

Um dos principais recursos dos MDEs é a possibilidade de projetar modelos de distribuição baseados em variáveis ambientais do período presente, sob condições ambientais de períodos passados ou futuros. Na literatura, essa técnica se chama transferabilidade (Randin *et al.,* 2006; Fitzpatrick & Hargrove, 2009), e tem sido utilizada principalmente em estudos de conservação, em que a intenção principal é estimar a distribuição de áreas favoráveis para a ocorrência de determinados táxons no presente, e também em cenários futuros hipotéticos (Franklin, 2013; Porfirio *et al.,* 2014), auxiliando na compreensão dos possíveis efeitos das mudanças climáticas sobre composição e distribuição espaço-temporal da biodiversidade (Sinclair *et al.,* 2010; Hamann & Aitken, 2012).

Os MDEs são ferramentas praticamente indispensáveis em estudos de biogeografia histórica, utilizados especialmente para formular hipóteses a priori (Werneck *et al.,* 2011, 2012, Sobral-Souza *et al.,* 2015; Arruda *et al.,* 2018), ou para testar hipóteses resultantes de outros tipos de análises (Porto *et al.,* 2012; Bryson Jr *et al.,* 2014; Oke *et al.,* 2014). Em ambos os casos, é extremamente importante incorporar aos MDEs, informações sobre a história natural e a ecologia das espécies-alvo, evitando assim, uma análise puramente matemática (“data-driven

analysis", Mellert *et al.,* 2011) e com pouco significado biológico (Dormann *et al.,* 2011).

Em estudos biogeográficos, os MDEs são comumente utilizados em paralelo com outros tipos de análises, como por exemplo, em inferências filogeográficas (Richards *et al.,* 2007), fundamentadas na teoria da coalescência (Kingman, 1982a, 1982b). A filogeografia é considerada uma disciplina intimamente vinculada à biogeografia, que integra métodos de disciplinas voltadas à microevolução (Etologia, Demografia, Genética de Populações), e macroevolução (Geografia Histórica, Peleontologia, Filogenia), para tratar dos princípios e processos que governam a distribuição geográfica de linhagens genealógicas no espaço e no tempo, especialmente em espécies filogeneticamente próximas (Avise, 2000, 2009; Templeton, 2004). Assim, a filogeografia permite o surgimento de novas perspectivas sobre a evolução das espécies, a partir da compreensão das interações entre a ecologia e a história natural das espécies-alvo, bem como dos eventos geológicos e influências ambientais e geográficas da paisagem (Knowles, 2009). Apesar de sua origem recente (meados da década de 1980), o número cada vez maior de publicações no decorrer dos anos é um reflexo fidedigno do notório interesse global pela filogeografia (Avise, 2009; Turchetto-Zolet *et al.,* 2013; Tu *et al.*, 2016).

Os fundamentos teóricos da filogeografia estão intrinsicamente entrelaçados com os princípios da teoria da coalescência. De forma simplificada, a teoria da coalescência assume que, em um modelo neutralista de evolução, é possível traçar a história genealógica de um conjunto de linhagens atuais, "retrocedendo" até o seu ancestral comum mais próximo (Nordborg, 2007). O processo de coalescência é a descoberta do ancestral comum mais próximo de um número qualquer de

linhagens. Em outras palavras, dizemos que um número n de linhagens coalesce, quando alcançamos o ancestral comum mais próximo dessas linhagens (Rosenberg & Nordborg, 2002).

O modelo neutro comumente adotado em simulações de coalescência é o de Wright-Fisher, amplamente utilizado em genética de populações e análises evolutivas de variações em loci gênicos ao longo do tempo (Gory *et al.,* 2018). Teoricamente, o tamanho constante das populações, a ausência de gerações sobrepostas, a panmixia e a ausência de seleção, constituem as principais conjecturas estabelecidas pelo modelo de Wright-Fisher (Hudson, 2002; Parida, 2010, 2012). Adicionalmente, ao adotar o referido modelo, assume-se que as novas gerações são formadas a partir de amostragens randômicas (com reposição) de um número qualquer de indivíduos parentais da geração atual (Nordborg, 2007). Considerando que as premissas propostas pelo modelo de Wright-Fisher podem parecer pouco realísticas quando aplicadas às comunidades reais, existem diversas derivações que se adequam às situações encontradas em populações naturais (Parida, 2012), incluindo modelos que consideram a ação de seleção balanceadora e direcional, a presença de gerações sobrepostas, e as flutuações no tamanho populacional ao longo do tempo, além de algoritmos capazes de operar com loci recombinantes (Hein *et al.,* 2005).

Por se tratar de linhagens genealógicas, o modelo de Wright-Fisher, e consequentemente, a teoria da coalescência, foram originalmente elaborados para analisar dados moleculares de natureza haplotípica (Kingman, 1982a). Por conta disso, os marcadores moleculares de linhagem podem ser vistos como o carro-chefe das análises filogeográficas (Avise, 2000, 2009). Dentre essa classe de marcadores, o DNA mitocondrial (mtDNA) é, sem dúvidas, um dos recursos mais

utilizados na filogeografia de espécies animais (Rahman *et al.,* 2010; Miraldo *et al.,* 2012; Turchetto-Zolet *et al.,* 2013). Na maioria dos animais, o mtDNA é uma molécula de estrutura circular, com tamanho médio de aproximadamente 16,5 kb (Bernt *et al.,* 2013), e de simples organização estrutural (Figura 3). Em artrópodes por exemplo, o mtDNA é organizado em uma molécula de DNA circular, usualmente contendo regiões que codificam 13 proteínas, 22 RNAs transportadores, dois RNAs ribossômicos, e uma região controladora (replicação/transcrição) rica em bases A+T (Chen *et al.,* 2011).

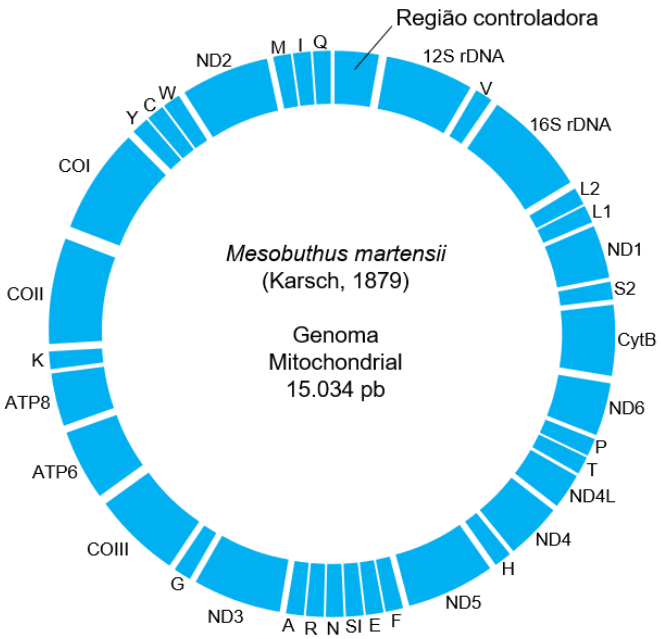

Figura 3. Representação esquemática da estrutura do genoma mitocondrial do escorpião *Mesobuthus martensii* (Karsch, 1879), mostrando a posição relativa de cada gene, e também da região controladora. Os genes que codificam as subunidades da NADH desidrogenase são indicados de maneira respectiva à cada subunidade (ND1-6, 4L), o mesmo foi feito para os genes responsáveis pelas subunidades da citocromo C oxidase (COI, COII, COIII), e para os genes das subunidades 6 e 8 da ATPase (ATP6, ATP8). Os genes de RNAs transportadores são indicados por letras referentes aos seus respectivos aminoácidos, seguindo o código da IUPAC; citocromo b (Cytb). Adaptado de Choi et al. (2007).

Além da estrutura simples, o mtDNA de animais possui algumas outras propriedades desejáveis em estudos de filogeografia. A transmissão uniparental do mtDNA assegura a natureza haplotípica da informação genética, requerida como input em análises filogeográficas (Avise, 2009). Uma vez que a genealogia das linhagens é comumente representada por árvores topológicas, marcadores haplotípicos são desejáveis para gerar tais topologias, isto porque, regiões autossômicas podem ser transmitidas por ambos os sexos, e as análises com essas sequências normalmente resultariam em um diagrama de rede, ao invés de uma topologia (Parida, 2012). A ausência de recombinação no mtDNA de animais (com raras exceções – ver Piganeau *et al.,* 2004; Tsaousis *et al.,* 2005) também é uma importante propriedade a ser considerada, garantindo que a origem da variação encontradas nas sequências do mtDNA decorre apenas de mutações acumuladas ao longo do tempo (Avise, 2009).

Com o uso adequado de modelos evolutivos e estimativas confiáveis de calibração (ex. registros fósseis, eventos geológicos, taxas de mutação), as variações no mtDNA podem ser aplicadas em simulações de relógio molecular, resultando em uma filogenia datada, que indica o tempo de divergência em cada nó presente na árvore (Rutschmann, 2006). Finalmente, a alta taxa de substituição de nucleotídeos presente no mtDNA possibilita a realização de inferências filogeográficas em nível intraespecífico, e o elevado número de cópias por célula (com raros casos de heteroplasmia) garante, do ponto de vista técnico, uma maior facilidade de obtenção do material genético (Avise, 2009).

Regiões informativas do DNA nuclear (nDNA) também podem ser incorporadas em análises filogeográficas. Normalmente, os *loci* de cópias únicas do nDNA são os mais desejáveis em inferências filogeográficas (Avise, 2009). No

entanto, por apresentar propriedades biológicas distintas, o nDNA não pode ser analisado sob a mesma perspectiva do mtDNA. Por exemplo, a taxa de substituição de nucleotídeos do nDNA é muito inferior à encontrada no mtDNA de animais (Hellberg, 2006; Fischer *et al.,* 2013). Há também, uma certa dificuldade em isolar haplótipos em regiões de nDNA de organismos diploides, além dos possíveis ruídos que a recombinação dessas regiões pode causar nas análises (Avise, 2009). Apesar disso, existem estratégias metodológicas para contornar a problemática dos marcadores de nDNA em inferências filogeográficas. Dentre elas está a própria seleção da região de interesse, e o uso de ferramentas adequadas de bioinformática para analisá-las. Nesse sentido, o DNA ribossômico nuclear (rnDNA) pode ser útil em estudos de filogeografia (Ji *et al.,* 2003). Em eucariotos, o rnDNA está organizado em blocos repetidos em tandem (Figura 4), compostos por uma região não transcrita, seguida de uma região externa transcrita, e dos genes ribossômicos 18S, 5.8S e 28S, intercalados pelas regiões internas transcritas 1 (entre os genes 18S e 5.8S) e 2 (entre os genes 5.8S e 28S) (Hillis & Dixon, 1991).

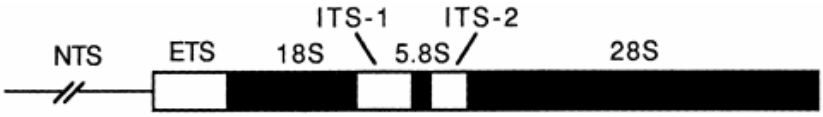

Figura 4. Estrutura do DNA ribossômico (rnDNA) comumente encontrado no genoma nuclear de eucariotos, mostrando uma unidade repetitiva composta pelas seguintes regiões: região não transcrita (NTS), espaçador externo transcrito (ETS), espaçadores internos transcritos 1 e 2 (ITS1, ITS2), e genes das subunidades ribossômicas 18S, 5.8S, e 28S. Fonte: Hillis & Dixon (1991).

Por se tratar de uma região repetitiva, o rnDNA ocorre com maior frequência no genoma, facilitando sua amplificação (Hwang *et al.,* 1998). Além disso, o rnDNA está sujeito a evolução em concerto, o que acaba levando à homogeneização

dessas regiões em nível intraespecífico ao mesmo tempo em que as divergências interpesecíficas se acentuam ao longo do tempo (Hillis & Dixon, 1991), tornando mais viável a identificação de haplótipos a partir de regiões do rnDNA.

Considerando que o rnDNA é herdado por ambos os sexos, a sua incorporação em análises filogeográficas pode reduzir o viés de uma possível dispersão assimétrica relacionada ao sexo, o que poderia levar a diferentes padrões filogeográficos entre machos e fêmeas de uma mesma espécie / população, se analisadas unicamente a partir de marcadores de mtDNA (Palumbi & Baker, 1994). Em adição, a implementação de marcadores de nDNA pode reduzir substancialmente os intervalos de confiança de inúmeros tipos de análises (ex. tamanho populacional, fluxo gênico, crescimento populacional, e tempo de divergência), levando a resultados mais fidedignos e com maior significado biológico (Zink *et al.,* 2005). Finalmente, quando usados em conjunto, as diferentes taxas de substituição de nucleotídeos encontradas em marcadores de mtDNA e rnDNA, permitem uma resolução mais refinada em filogenias datadas (Ojanguren-Affilastro *et al.,* 2017), assim como a construção de redes de haplótipos com diferentes padrões de aglomeração, que variam conforme o nível de conservação dos marcadores utilizados.

2.4 Seleção do organismo modelo

Eventos geológicos e ciclos climáticos são comumente interpretados como os motores que impulsionam as mudanças na paisagem ao longo do tempo, modelando os padrões de biodiversidade (Gillespie & Roderick, 2014). Em nível populacional, tanto os eventos geológicos quanto os ciclos climáticos deixam marcas no DNA dos indivíduos. Por exemplo, alterações de paisagem provocadas

pelos ciclos climáticos geralmente são rápidas (sob a perspectiva do tempo geológico), podendo deixar traços detectáveis de efeito gargalo ou efeito fundador, os quais, reduzem a diversidade genética das populações (Álvarez-Presas *et al.,* 2011). Por outro lado, as mudanças na paisagem ocorridas em decorrência de eventos geológicos, normalmente ocorrem ao longo de uma larga escala de tempo, permitindo a adaptação progressiva das espécies, a estabilização do tamanho populacional, e o acúmulo de variação genética intrapopulacional (Hewitt, 2004; Álvarez-Presas *et al.,* 2011). Essa série de fatores é frequentemente observada em populações que habitam áreas com alta estabilidade climática (ex. Hugall *et al.,* 2002; Carnaval *et al.,* 2009; Yannic *et al.,* 2013; Faye *et al.,* 2016).

Apesar das alterações da paisagem influenciarem efetivamente a dinâmica das populações, não existe um mecanismo único de resposta a essas alterações que englobe todas as espécies. Entretanto, espécies especialistas e com baixa capacidade de dispersão acabam sendo preferíveis em estudos de filogeografia, uma vez que os padrões de distribuição e diversidade desses táxons são fortemente correlacionados com a estabilidade histórica de seus habitats (Hewitt, 2004; Avise, 2009; Álvarez-Presas *et al.,* 2011; Silva *et al.,* 2017). Assim, sob condições desfavoráveis, espera-se que as espécies estenotópicas persistam apenas em áreas estáveis dentro de sua distribuição geográfica geral (refúgios), e que na ausência de mecanismos de longa dispersão, as populações de tais espécies estão mais propícias às flutuações demográficas (Silva *et al.,* 2017).

Em termos práticos, muitos escorpiões reúnem características ecológicas desejáveis em estudos de filogeografia, incluindo baixa capacidade de dispersão (Polis *et al.,* 1985; Habel *et al.,* 2012; Bryson Jr *et al.,* 2013a, 2016; Štundlová *et al.,* 2019), e significativa especificidade de micro-habitat (Bryson Jr *et al.,* 2013a,

2013b, Monod *et al.,* 2013; Ojanguren-Affilastro *et al.,* 2016; Esposito & Prendini, 2019). Em escorpiões da família Buthidae C.L. Koch, 1837 presume-se que a baixa capacidade de dispersão, e consequentemente, o limitado fluxo gênico entre as populações, atuem como mecanismos fundamentais em processos de especiação (Husemann *et al.,* 2012). Teoricamente, quanto mais limitada for a dispersão e mais generalista for o táxon ancestral (assumindo os escorpiões como exemplo), maior será a riqueza esperada de espécies em um ambiente mutável com barreiras geográficas recorrentes (Lourenço *et al.,* 2016).

Até 2014, eram registradas 28 espécies de escorpiões em áreas de Caatinga (Porto *et al.,* 2014). Com o avanço dos estudos sobre taxonomia dos escorpiões (Esposito *et al.,* 2017; Lira *et al.,* 2017; Santos-da-Silva *et al.,* 2017), a estimativa atual, é de que pelo menos 33 espécies de escorpiões ocorram na Caatinga. Dentre essas espécies, o gênero *Jaguajir* Esposito, Yamaguti, Souza, Pinto-da-Rocha & Prendini, 2017, reúne duas espécies com distribuição em áreas de Caatinga e Cerrado, e uma terceira, distribuída nas savanas do extremo norte do Brasil.

Os escorpiões do gênero *Jaguajir* são caracterizados pelo seu grande porte (5-11 cm), e pela presença de estruturas estridulatórias situadas nos pentes, e no terceiro esternito (detalhes em Esposito *et al.,* 2017). Estima-se que o gênero *Jagajir* tenha se originado na América do Sul (assim como o ancestral de todas as espécies da subfamília Centruroidinae Kraus, 1955) há cerca de 34,5 milhões de anos atrás, em um evento cladogenético que separou dois grandes clados, o primeiro contendo o ancestral dos atuais gêneros *Jaguajir*, *Troglorhopalurus* Lourenço, Baptista & Giupponi, 2004, *Rhopalurus* Thorell, 1876, *Physoctonus* Mello-Leitão, 1934, e *Ischnotelson* Esposito, Yamaguti, Souza, Pinto-da-Rocha & Prendini, 2017, todos com distribuição restrita à América do Sul; e o segundo clado,

que comporta os gêneros *Centruroides* Marx, 1890, e *Heteroctenus* Pocock, 1893, distribuídos na América Central e América do Norte (Esposito & Prendini, 2019). Embora não haja citação direta, os resultados apresentados por Esposito & Prendini (2019) sobre a história evolutiva da subfamília Centruroidinae, possivelmente corroboram a hipótese posotulada por Lourenço (1990, 1994), de que o Escudo Brasileiro representa um possível centro de dispersão para a família Buthidae.

O gênero *Jaguajir* ocorre unicamente em formações de vegetação aberta da América do Sul (Lourenço, 1986, 1994). A espécie *J. rochae* ocorre quase que exclusivamente em áreas de Caatinga, com registros também para áreas ecotonais (Caatinga-Cerrado, Caatinga-Mata Atlântica), ao passo em que *Jaguajir agamemnom* (C.L. Koch, 1839) se distribui majoritariamente em áreas de Cerrado. A distribuição geográfica da terceira espécie do gênero, *Jaguajir pintoi* (Mello-Leitão, 1932), está restrita às áreas de vegetação aberta situadas no extremo norte do Brasil, abrangendo ainda uma pequena parte do sudeste da Venezuela e oeste da Guiana (Figura 5) (Esposito *et al.,* 2017).

Dentre as espécies que ocorrem na Caatinga, *J. rochae* pode ser facilmente identificada pelo seu grande porte (60-72 mm), e também pela sua coloração característica, em tons de amarelo-claro (Lenarducci *et al.,* 2005; Esposito *et al.,* 2017) (Figura 6), além da presença de um aparelho estridulatório capaz de emitir sons audíveis (Prendini *et al.,* 2009).

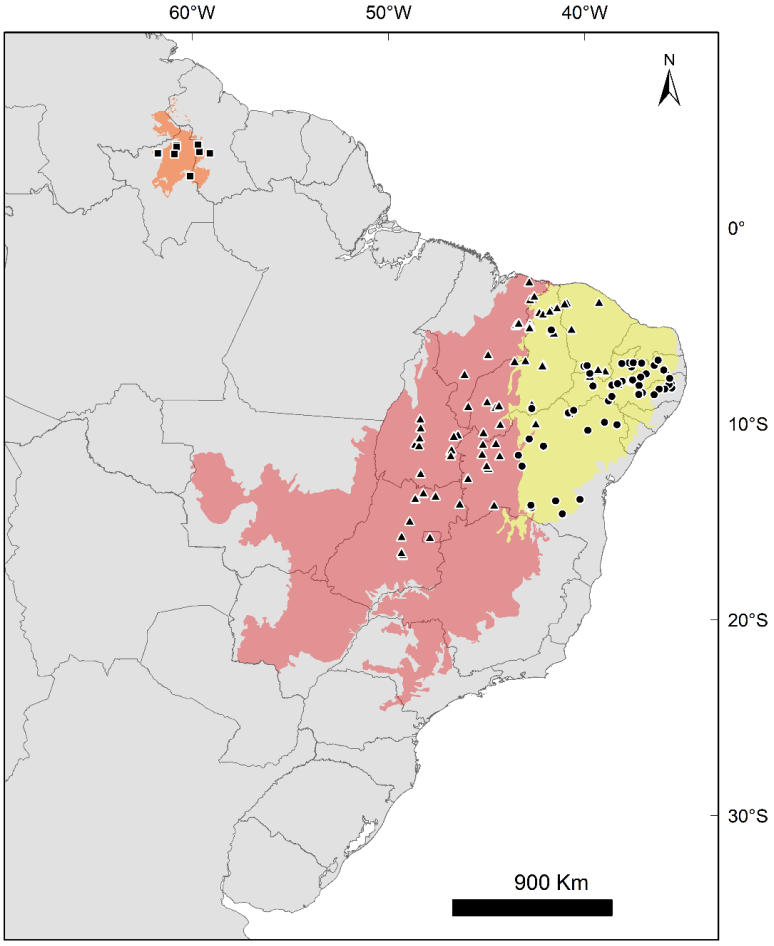

Figura 5. Distribuição geográfica das espécies do gênero *Jaguajir*: *J. rochae* (círculos), *J. agamemnom* (triângulos), e *J. pintoi* (quadrados). As áreas coloridas representam as delimitações da Caatinga (amarelo), e Cerrado (vermelho) de acordo com as projeções do Instituto Brasileiro de Geografia e Estatística (IBGE, 2004). A área em laranja, denota as formações abertas do tipo Savana, situadas no extremo norte do Brasil (Olson et al., 2001), em que são registradas ocorrências de *J. pintoi*. Adaptado de Esposito *et al*. (2017).

Do ponto de vista prático, a facilidade de identificação, a elevada abundância em inventários de fauna conduzidos na Caatinga (Carmo *et al.,* 2013; Lira *et al.,* 2018), e o porte robusto dos espécimes de *J. rochae*, facilitam o processo de obtenção e análise de material genético em análises filogeográficas. Além disso, a ampla distribuição de *J. rochae* em áreas de Caatinga (Figura 5) permite que esse táxon possa ser utilizado para inferir a atuação de áreas de estabilidade climática

da Caatinga como centros de diversificação de linhagens. Adicionalmente, a presença dessa espécie em áreas ecotonais, permite também, a comparação direta entre os padrões de história demográfica das populações que habitam a região central da distribuição da espécie, com as populações das áreas ecotonais, produzindo interpretações que podem ser relevantes no contexto da dinâmica das paisagens (ex. biomas, ecorregiões).

Figura 6. Espécime adulto de *Jaguajir rochae* (fêmea), fotografado no Parque Estadual Mata da Pimenteira, uma unidade de conservação da Caatinga situada na região central de Pernambuco (fevereiro, 2016).

Por fim, inúmeros estudos têm demonstrados que os escorpiões são excelentes modelos em estudos de biogeografia e filogeografia (Gantenbein & Largiadèr, 2003; Sousa *et al.,* 2012; Graham *et al.,* 2012, 2013a, 2013b, 2014; Bryson Jr *et al.,* 2013a, 2013b, 2014, 2016; Miller *et al.,* 2014; Ceccarelli *et al.,* 2016, 2017; Ojanguren-Affilastro *et al.,* 2017; Esposito & Prendini, 2019), contudo, os estudos dessa natureza são ainda incipientes na América do Sul, e restritos às espécies que ocorrem no sul e na costa oeste da América do Sul (ex. Ceccarelli *et al.,* 2016, 2017; Ojanguren-Affilastro *et al.,* 2017).

3 Insights on the role of historical habitat stability and geological barriers on lineage diversification processes in Caatinga environments revealed by landscape genetics of the scorpion *Jaguajir rochae* (Scorpiones: Buthidae)

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Abstract

Aim The Caatinga domain is the largest refugium of Seasonally Dry Tropical Forest (SDTF) on the Neotropics, and recent studies improved our knowledge on the historical biogeography of Caatinga taxa at broad scales. Although important, such conclusions may be masking deterministic processes related to the genesis and maintenance of genetic diversity at regional or local scales. We performed a series of phylogeographical analysis on the Caatinga scorpion *Jaguajir rochae*, to evaluate the potential role of geological barriers and SDTF stability of the genetic structuring processes at fine spatial scales.

Location Northeastern Brazil.

Taxon The Caatinga scorpion *Jaguajir rochae*.

Methods We sequenced a partial fragment of the mitochondrial gene cytochrome c oxidase I for 77 specimens from 11 sampling localities. Genetic diversity and historical demographic changes were accessed by several metrics. Bayesian methods were applied to infer genetic clusters, divergence dating, and migration models among populations, whereas niche suitability through the late-Quaternary was estimated by ecological niche models with optimized settings.

Results Populations from historically stable areas of SDTF display high levels of genetic diversity, whereas those from changeable environments are genetically undifferentiated. Most mitochondrial lineages diverged after the uplift of the Borborema Plateau (Pleistocene), but this massif persists as a prominent barrier to the gene flow of *J. rochae*. The climatic niche suitability of *J. rochae* remained relatively stable since the Last Interglacial, but spatial shifts were detected at local scale, agreeing with the proposed migration model.

Main conclusions For arid-adapted taxa with low dispersal capabilities, such as the scorpion *J. rochae*, historical refugia, and geomorphological features within the Caatinga domain are prominent forces acting under the genesis, and maintenance of genetic diversity.

Keywords SDTF, Phylogeography, Biogeography, invertebrates, Caatinga

Introduction

The historical stability of the South American open vegetation biomes becomes a convergence point among recent investigations (Werneck, Costa, Colli, Prado, & Sites, 2011; Werneck, Gamble, Colli, Rodrigues, & Sites, 2012; Sobral-Souza, Lima-Ribeiro, & Solferini, 2015; Costa et al., 2017; Arruda, Schafer, Fonseca, Solar, & Fernandes-Filho, 2018). In Seasonally Dry Tropical Forests (SDTFs) for example, paleoecological niche modelling and palynological data support the hypothesis of multiple stable nuclei of SDTFs on the neotropics (Werneck et al., 2011). Accordingly, many authors agree that most part of the spatial extent of neotropical SDTFs remained stable during the Quaternary (Sobral-Souza et al., 2015; Arruda et al., 2018, but see Costa et al., 2017), and a weak interplay with adjacent rainforests (Amazon forest and Atlantic forest) was proposed, but restricted to ecotonal zones (Arruda et al., 2018).

Behind the discussions concerning the dynamics of the spatial extent of SDTFs over time, which has been stressed in the literature (e.g. Pennington, Prado, & Pendry, 2000; Pennington, Lavin, & Oliveira-Filho, 2009; Werneck, 2011; Werneck et al., 2011), the impacts of these changes on the structure of communities and/or populations has received increasing attention in the last years (e.g. Bartoleti ,Peres, Fontes, da Silva, & Solferini, 2018; Oliveira et al., 2018; Foerster, Lira, & deSouza, 2019; Lanna et al., 2019). The expressive geographical extent of neotropical SDTFs, combined with its geomorphological features and habitat heterogeneity, certainly arouse the interest of naturalists to study the patterns and process behind the genesis of biodiversity in such environments. The Caatinga domain (CD) for example, offers a singular opportunity to explore the effects of niche and climate stability on the genetic structure of specific taxa, improving our knowledge on the historical modifications of the landscape promoted by cyclical climatic oscillations.

The CD is a geographically disjunct unity of SDTF, comprising a set of complex vegetation types – from cactus scrub to tall forests, but mostly represented by tree-dominated landscapes of (semi)deciduous species (Werneck et al., 2011). The strong seasonality of the rain season plays a pivotal role on the vegetation dynamics of the CD, impacting the aboveground net primary productivity (Moura & Lee, 2004; Menezes, Sampaio, Giongo, & Pérez-Marin, 2012; Salimon & Anderson,

2018), and the life cycles of its biodiversity (Vieira, Santana, & Arzabe, 2009; Rodrigues & Silva, 2014; Cavalcanti, Paiva, & França, 2016; Gonçalves, Cerqueira, Brasil, & Santos, 2017). The structure of biological communities of the CD derives from synergistic processes involving a strong niche conservatism and the effects of environmental conditions at local scale, resulting in complex landscapes marked by expressive levels of endemicity and β-diversity (Pennington et al., 2009; Queiroz, Cardoso, Fernandes, & Moro, 2018).

Werneck et al. (2011) have demonstrated the presence of historically unstable regions within the CD, matching the ecoregions of Borborema Plateau (BOP), Raso da Catarina, and the Southern Sertaneja Depression (Velloso, Sampaio, & Pareyn, 2002). More specifically, the study of Werneck et al. (2011) proposes that the BOP is one of the major divisors between stable and unstable areas of SDTF, which is predicted to occur at western and eastern sides of the BOP, respectively. This longitudinal gradient is geographically close to the Pernambuco Atlantic forest refugium (Carnaval & Moritz, 2008), and the climatic fluctuations of the Quaternary may be related to the possible interplay (vegetation shifts) between Caatinga and Atlantic forest (Werneck et al., 2011).

Considering that habitat stability is a predictor of demographic immutability, genetic and taxonomic diversity, and endemism (Carnaval, Hickerson, Haddad, Rodrigues, & Moritz, 2009; Faye et al., 2016; Gutiérrez-Rodríguez, Barbosa, & Martínez-Solano, 2017; Camps, Martínez-Meyer, Verga, Sérsic, & Cosacov, 2018; Noguerales, Cordero, & Ortego, 2018; Lima-Rezende et al., 2019), it is reasonable to think that historically stable areas within the CD act like a refugia, harboring demographically stable populations with high levels of genetic diversity (Werneck et al., 2011; Binks, Gibson, Ottewell, Macdonald, & Byrne, 2019) and several exclusive haplotypes. In this sense, phylogeographical structure of low-dispersal taxa can be a valuable resource to test hypotheses regarding the landscape evolution and its effects on geographical patterns of genetic diversity (Avise, 2009; Álvarez-Presas, Carbayo, Rozas, & Riutort, 2011; Silva et al., 2017). For such purposes, scorpions can be seen as a good biological model (Ceccarelli et al., 2016; Ceccarelli, Pizarro-Araya, & Ojanguren-Affilastro, 2017; Ojanguren-Affilastro, Adilardi, Mattoni, Ramírez, & Ceccarelli, 2017; Esposito & Prendini, 2019) because they are relatively stenotopic animals (Bryson Jr, Savary, & Prendini, 2013; Ojanguren-Affilastro et al., 2016), with low dispersal capabilities (Polis, McReynolds, & Ford, 1985; Bryson Jr,

Savary, Zellmer, Bury, & McCormack, 2016; Štundlová, Šmíd, Nguyen, & Šťáhlavský, 2019). Thus, it could be expected that the historical processes relating the evolution of bionomical traits in scorpions (i.e. physiological tolerances, population demography, geographical distribution, taxonomic and genetic diversity) can shed light on the biogeographic steps that shape the current biodiversity patterns at regional and local scales.

Among the 33 described species of scorpions that occur in the CD (Porto, Carvalho, de Souza, Oliveira, & Brescovit, 2014; Lira, Pordeus, & Albuquerque, 2017; Esposito, Yamaguti, Souza, Pinto-da-Rocha, & Prendini, 2017; Santos-da-Silva, Carvalho, & Brescovit, 2017), the genus *Jaguajir* comprises three species, of which, *Jaguajir rochae* (Borelli, 1910) is a typical element of Caatinga environments (Esposito et al., 2017), while the other two species, *Jaguajir agamemnom* (C.L. Koch, 1839) and *Jaguajir pintoi* (Mello-Leitão, 1932), are mainly distributed in Cerrado formations of central and northern regions of Brazil, respectively (Teruel & Tietz, 2008; Lourenço, 2008; Esposito et al., 2017). The geographical distribution of *J. rochae* extends across most part of the CD, comprising the entire extent of the longitudinal gradient of habitat stability mentioned above. In this study, therefore, we explore the genetic population structure of *J. rochae* under a phylogeographical framework, integrated with paleodistribution modelling, to test for genetic clustering of spatially structured haplogroups in historically stable and unstable areas within the CD.

We are motivated by the hypothesis that the BOP can be a physical barrier responsible for structuring populations of species adapted to dry climatic conditions, such as those present in Caatinga environments. We derive this main goal into five pertinent questions: I) are populations of *J. rochae* structured around the BOP? II) Are within-lineage diversification events occurred into the time slice comprising the late Quaternary climatic oscillations, or BOP uplift? III) Is the BOP a stringent barrier to the gene flow of *J. rochae* populations? IV) Are populations from historically stable areas (sensu Werneck et al., 2011) more genetically diverse and demographically stable than those from changeable environments? VI) Has niche suitability of *J. rochae* changed considerably around the BOP since the late-Quaternary climatic scenarios? We advocate that the answer for these questions will improve the knowledge on the biogeography and natural history of the CD, which, although recent advances, remains as one of least studied and most threatened

environments in South America (Santos, Leal, Almeida-Cortez, Fernandes, & Tabarelli, 2011; Silva, Barbosa, Leal, & Tabarelli, 2018).

Materials and Methods

Sample collection

Specimens of *J. rochae* were collected in 11 localities from both sides of the BOP (Fig. 1a), covering both historically stable and unstable areas of SDTF predicted by Werneck et al. (2011). Using tweezers and self-made ultraviolet light lanterns (wavelength = 395-400 nm), we sampled 77 specimens, with an average of seven individuals per locality (ranging from four to 10 specimens). Scorpions were collected at night (20h00min-23h00min), during random walks performed by at least two collectors, and kept alive until DNA extraction. Sample collection was authorized by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), under the process number 66699-1.

Molecular procedures

Absolute ethanol was used to fix specimens under laboratory conditions. One leg from the left side of all individuals was removed and preserved in absolute ethanol at -20°C as a tissue sample for DNA extraction. The remaining of each scorpion was stored as voucher specimens and deposited at the arachnological collection of Universidade Federal de Pernambuco (Recife, Brazil). Genomic DNA extraction was performed using the Chelex-100® resin (Bio-Rad Laboratories) protocol described in Casquet, Thebaud, & Gillespie (2012). Partial fragments of mitochondrial DNA were sequenced for the protein-coding gene cytochrome c oxidase I (COI), which was successfully used in several phylogeographical studies of scorpions and other arachnids (e.g. Bartoleti et al., 2017; Graham, Jaeger, Prendini, & Riddle, 2013; Graham, Wood, Henault, Valois, & Cushing, 2017; Graham, Myers, Kaiser, & Fet, 2019; Harms, Roberts, & Harvey, 2019; Peres, Benedeti, Hiruma, Sobral-Souza, & Pinto-da-Rocha, 2019; Pfingstl et al., 2019).

The targeted gene was amplified by polymerase chain reaction, in a 25 µl volume, containing 12.5 µl of GoTaq® Colorless Master Mix (Promega), 7.5 µl of ddH2O, 1.5 µl of each primer (forward and reverse), and 2 µl of undiluted DNA template. Forward and reverse primers are the same as described in Vink, Thomas,

Paquin, Hayashi, & Hedin (2005): C1-J-1718-spider and C1-N-2728-spider, respectively. The following thermal conditions were applied in PCR: an initial denaturation step of 5' at 95°C, 35 cycles of 95°C for 30", 52°C for 30" and 72°C for 45", and a final extension of 72°C for 10'. PCR products were checked for amplification in 1% agarose gel electrophoresis. Amplicons were purified using the Wizard® SV Gel and PCR Clean-Up System kit (Promega) and then sequenced in an automatic capillarity sequencer ABI PRISM 3500 Genetic Analyzer (Applied Biosystems).

Alignment and genetic diversity estimation

COI sequences were aligned in MAFFT 7 (Katoh & Standley, 2013) using parameter configurations for closely related DNA sequences with global homology (G-INS-i strategy as iterative refinement method, and 1PAM/k=2 for parameter matrix). We use the sequence KY982232.1 from GenBank as a directional reference to the alignment of the remaining sequences. This sequence was also included in our dataset as a member of Serra Talhada (SER) population. Poorly aligned regions in the multiple sequence alignment were automatically trimmed with Gblocks (Castresana, 2000) using the stringent criterion to remove contiguous nonconserved positions. We use the 'ape' (Paradis & Schliep, 2018) and 'pegas' packages (Paradis, 2010) on the R environment (R Core Team, 2019) to compute descriptive metrics of genetic diversity, including the number of haplotypes (h), the haplotype diversity (Hd), and the nucleotide diversity (π).

Genetic clusters and population differentiation

Genetic groups were designed using the Bayesian clustering approach implemented in BAPS 6.0 (Corander, Sirén, & Arjas, 2008). For this analysis, we chose the grouping method that accounts for linkage dependences among loci (Corander & Tang, 2007), and set the number of clusters to vary between 1 and 20. The algorithm implemented in BAPS uses a genetic mixture analysis to compute the optimal number of clusters from a set of DNA sequences, which is selected by the maximization of the log marginal likelihood (Corander et al., 2008).

Spatial patterns among genetic lineages were graphically analyzed using a median-joining haplotype network produced in PopArt 1.7 (Leigh & Bryant, 2015), with a prior identification of redundant haplotypes in R software with the 'haplotype'

library (Aktas, 2019). The degree of genetic differentiation among haplogroups defined in BAPS (see Results) was measured by the Φ_{ST} metric (Excoffier, Smouse, & Quattro, 1992; Holsinger & Weir, 2009), as implemented in the 'strataG' R package (Archer, Adams, & Schneiders, 2016).

A hierarchical analysis of molecular variance (AMOVA) implemented in 'pegas' R package was applied to disentangle the genetic variation at inter and intra-population level, as well as those shared between haplogroups inferred by BAPS (Excoffier et al., 1992) – just for practical purposes, we use the term "population" to design all individuals from the same sampling locality. Isolation by distance was measured for the whole data set, and for each haplogroup defined in BAPS through Mantel tests implemented in the R package 'ade4' (Dray & Dufour, 2007), using as input, pairwise interpopulation matrices of genetic differentiation (Φ_{ST}), and geographical distance (km). Significance was achieved under 10,000 permutations.

Demographic changes

Recognizable signatures of demographic changes were inferred by neutrality tests – Tajima's D (Tajima, 1989), Fu's Fs (Fu, 1997), and R2 statistic (Ramos-Onsins & Rozas, 2002) computed in Arlequin 3.5 (Excoffier & Lischer, 2010) and 'pegas' R library. To avoid misleading results due to technical limitations (i.e. sample size, DNA polymorphism), we calculated neutrality tests for the whole data set, and for each population with at least two haplotypes (Ramos-Onsins & Rozas, 2002; Grant, 2015). Statistical significance for each neutrality tests was achieved thought 10,000 replications.

Divergence dating

Split divergence times among *J. rochae* haplotypes were accessed from a dated gene tree estimated in BEAST 1.10.4 (Suchard et al., 2018) under a Bayesian inference. We include the species *Jaguajir agamemnom* (GenBank, accession KY982209.1) as the outgroup, based on the phylogenetic hypothesis proposed by Esposito, Yamaguti, Pinto-da-Rocha, & Prendini (2018). Redundant haplotypes were removed using the 'haplotypes' R package. We then partitioned the sequences alignment in codon positions 1+2, and position 3, once asymmetric mutation rates are expected to occur at the third codon position of mitochondrial genes (Oberski et

al., 2018), which can affect the fit of substitution models (Powell, Barker, & Lanyon, 2013).

Best substitution models for each partition were selected under a Bayesian Information Criterion (BIC), as implemented in 'phangorn' R package (Schliep, 2011). Clock and substitution models were unlinked for each DNA partition, but trees were linked and adjusted to follow a Yule speciation tree prior (Gernhard, 2008). Two separate runs were performed in BEAST to generate dated phylogenies under the strict molecular clock prior, and uncorrelated lognormal clock prior. For both simulations, we ran BEAST for 50 million generations, sampling every 5000 generation. The clock rate of 0.008125 substitution/site/million years was applied to both simulations (strict and uncorrelated clock models), but for the uncorrelated lognormal clock, we set this rate as a mean for a normal distribution with a standard deviation of 0.0005. This substitution rate was specifically developed for scorpions and used to date split divergences of several South American species (Gantenbein, Fet, Gantenbein-Ritter, & Balloux, 2005; Ojanguren-Affilastro et al., 2017).

We use two mathematically distinct methods to guide the choose of the most appropriate clock model: the former is a frequentist approach based on maximum likelihood theory implemented in MEGA X (Kumar, Stecher, Knyaz, & Tamura, 2018), and the latter is the log Bayes Factor (LBF), computed from the log marginal likelihood of each clock model simulation generated in BEAST using both path sampling, and stepping stone sampling framework (Baele, Li, Drummond, Suchard, & Lemey, 2012; Baele, et al., 2013). LBF was computed in R, using the 'mtraceR' package (Pacioni et al., 2015), applying the log marginal likelihood values of each clock model as input. Convergence of MCMC chains were inspected in Tracer 1.7 (Rambaut, Drummond, Xie, Baele, & Suchard, 2018) taking the Effective Sample Size values as reference (ESS > 200). Final tree topology was assembled in TreeAnnotator 1.10.4 (Suchard et al., 2018) using a maximum clade credibility tree approach after discarding the first 25% of sampled trees as burn-in.

Migration models

We use Migrate 4.3 (Beerli & Palczewski, 2010) to test for nine explicit migration models (Fig. 2), evaluating the effect of the BOP as a physical barrier to the gene flow of *J. rochae*. Migrate 4.3 estimates migration patterns among user-defined population groups under a Bayesian framework, applying a thermodynamic

integration method to approach the marginal likelihood of each scheme (Beerli & Palczewski, 2010). The output of the Migrate-n provides specific parameters for each migration model, such as the mutation-scaled values of migration rates (M), and effective population sizes (Θ), from which, the number of migrants per generation can be calculated. We set Migrate to run a single MCMC run of 200,000 steps, sampling every 100, with a final burn-in of five million steps; swap intervals for the thermodynamic static heating were kept in default mode, and convergence of MCMC chain parameters was accessed by ESS values (ESS > 200). Our migration models were designed to test two hypotheses: I) populations of *J. rochae* are geographically structured around the BOP, but migration occurs among them; and 2) there are a single panmictic population distributed along the sampling extent. We use a Python script provided by Peter Beerli (available at: http://peterbeerli.com/downloads/scripts/) to compute the LBF for each migration model tested in Migrate-n, prioritizing that with the greatest associated probability (Beerli & Palczewski, 2010; Graham et al., 2017). We then extract Θ and M values for the most likely migration model to obtain migration rates, in number of migrants per generation, as described in Gómez-Carballa et al. (2018).

Ecological niche modelling

We use ecological niche models (ENMs) to evaluate the niche stability of *J. rochae* though late Quaternary climatic oscillations, and also to predict the distance and direction of potential migration events from the last interglacial period (LIG, ~120-140 ka) to the Last Glacial Maximum (LGM, ~21 ka), and from the LGM to the present. ENMs were constructed with Maxent algorithm (Phillips, Anderson, & Schapire, 2006) implemented in 'dismo' R package (Hijmans, Phillips, Leathwick, & Elith, 2017). Maxent is a machine-learning tool that uses presence points and raster layers (explanatory variables) to predict the relative occupancy rate for a given species (Fithian & Hastie, 2013; Merow, Smith, & Silander, 2013; Merow, Allen, Aiello-Lammens, & Silander, 2016), outperforming others ENM methods, even working with few occurrence points (Elith et al., 2006; Merow et al., 2013). After a manual filtering process to remove records from non-natural environments (i.e. points within urban centers), we compiled 44 georeferenced presence points of *J. rochae*, obtained from several zoological collections (Tab. S1).

The spatial sampling extent for the modelling process was restricted to the latitudinal bounds of 2°20'-24°41'S, and longitudinal bounds of 60°6'-34°49'W, comprising the whole distribution of Caatinga and Cerrado formations (MMA, 2020), which is the typical habitat of scorpions from the genus *Jaguajir* (Esposito et al., 2017). As environmental predictors, we downloaded the 19 bioclimatic variables (2.5 arc-min resolution) from the WorldClim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), clipping it according to the spatial sampling extent cited above. To reduce model complexity and avoid multicollinearity problems, we use the 'usdm' R package (Naimi, Hamm, Groen, Skidmore, & Toxopeus, 2014) to retain only slightly autocorrelated bioclimatic variables ($r < 0.7$), with low contribution to the variance inflation factor ($VIF < 10$), following the recommendations of Guisan, Thuiller, & Zimmermann (2017), and Bond, Anderson, Henare, & Wehi (2019).

As a result, seven environmental predictors were used to generate the ENMs: maximum temperature of the warmest month (BIO5), temperature annual range (BIO7), mean temperature of warmest quarter (BIO10), mean temperature of coldest quarter (BIO11), annual precipitation (BIO12), precipitation of driest month (BIO14), and precipitation of warmest quarter (BIO18) (Hijmans et al., 2005). Presence points, and an additional of 10,000 random points generated in 'dismo' R package (background points), were partitioned in training and testing data using the 'checkerboard1' strategy, derived from the masked geographically structure approach described in Radosavljevic & Anderson (2014), and implemented on the 'ENMeval' R package (Muscarella et al., 2014). To minimize the spatial dependence of occurrence and background points, we scaled the checkerboard1 algorithm to partitioning the data set using 30 × 30 km grid cells. Optimal configuration for Maxent was estimated in 'ENMeval', allowing the regularization multiplier to vary between 0.5 and 4, and testing all feature classes available for Maxent (Fourcade, Besnard, & Secondi, 2017); best configuration scheme was chose by minimizing the associated AICc values, as recommended by Warren & Seifert (2011), and Radosavljevic & Anderson (2014). ENMs were constructed with current climate data, and then, projected to past climatic scenarios (LIG and LGM). For the LGM predictions, we assembled bioclimatic layers from the average values of three General Circulation Models: CCSM4 (Gent et al., 2011), MIROC (Watanabe et al., 2011), and MPI (Giorgetta et al., 2013). A complementary log-log transformation

was applied to the raw Maxent output, and the final predictions were interpreted as occurrence probability maps (Phillips, Anderson, Dudík, Schapire, & Blair 2017).

To assure reliable predictions, we use five metrics of model evaluation: the area under the receiver operating characteristic curve for the testing data (AUC_{TEST}), the difference between AUC_{TEST} and the AUC computed for the training data (AUC_{DIFF}), the true skill statistic (TSS), and omission rates based on minimum training presence threshold (OR0), and after excluding the 10% of the training localities with poorest predicted suitability (OR10). AUC_{TEST} ranges from 0 to 1, and estimates the ability of the model to differentiate predictions based on presence localities versus background points (Muscarella et al., 2014; Fourcade et al., 2017), while AUC_{DIFF} is expected to be positively correlated with model overfitting (Muscarella et al., 2014) and/or overparameterization (Warren & Seifert, 2011). The TSS is a threshold-dependent metric that take into account the balance between the true positive (i.e. sensibility) and negative (i.e. specificity) rates of the models (Allouche, Tsoar, & Kadmon, 2006; Liu, White, & Newell, 2011); accurate models are expected to have TSS near to 1 (Peres et al., 2019). OR0 and OR10 are threshold-dependent metrics used to measure model overfitting, with acceptable values near to 0 and 0.17, respectively (Wan, Wang, & Yu, 2011; Boria, Olson, Goodman, & Anderson, 2014; Muscarella et al., 2014; Wang, Wan, & Zhang, 2017).

Possible patters consistent with local migration were mapped based on the spatio-temporal changes in niche suitability of *J. rochae* though the late Quaternary. To do that, we transform the occurrence probability maps into binary maps, using a threshold value that maximize the sum of sensibility and specificity of each model (Liu, Berry, Dawson, & Pearson, 2005; Liu, Newell, & White, 2016). Then, we use Qgis 3.6 (QGIS Development Team, 2020) to obtain geographical centroids for every 30 × 30 km² grid cells in each predicted time (LIG, LGM, and current), estimating the hypothetical source of populations from one time slice to the next, by computing the length and direction between the centroid of the first time step to the nearest centroid of the following time step, that is, from the LIG to the LGM, and from the LGM to present (Gugger, Ikegami, & Sork, 2013). This analysis resulted in maps with vectors (arrows) representing possible migration distance and direction for each 30 × 30 km² grid cell.

Results

Genetic diversity

We obtained partial COI sequences for 77 specimens of *J. rochae*, that resulted in an alignment block of 685 bp with 73 variable sites, of which, 36 were parsimony-informative. Geographically restricted haplotypes accounts for 56.4% (n = 44) of the entire DNA data set, with a mean of 4.3 non-shared haplotypes per locality. CAR, and CUM were monomorphic populations in terms of haplotype composition, whereas AGU, AFO, and SER were the most diverse sampling localities, showing a specimen/haplotype ratio of 1:1, although expressive levels of haplotype diversity were also detected for other sampling localities from the western side of the BOP (Tab 1). Shared haplotypes and low levels of genetic diversity represent the populations from the eastern side of the BOP, although CAE population depicts low genetic diversity, but only exclusive haplotypes.

Population structure and differentiation

Bayesian analysis of population structure (BAPS) recovered two clusters that best represent the genetic similarities among *J. rochae* haplotypes (log-marginal likelihood = -1262.1571; posterior probability of cluster assignment = 0.9987). Accordingly, populations from the eastern side of the BOP grouped into a single cluster (eastern group), except CAE, that jointed into the second group (western group), together with all populations from the western side of the BOP (Fig. 1b). AMOVA indicated that the most expressive source of genetic variation comes from between groups comparisons (eastern vs western), which accounts for 44% of the variation (Tab. 2). We did not detected isolation by distance among populations within both western and eastern haplogroups, as well as for the whole data set ($P > 0.05$), but high and significant ($P < 0.01$) levels of genetic differentiation was reported for the whole data set ($\Phi_{ST} = 0.5361$), and western haplogroup ($\Phi_{ST} = 0.3557$). Populations from the eastern cluster, however, were genetically undifferentiated ($\Phi_{ST} = 0.2283$; $P > 0.05$). A star-shape pattern was recovered by haplotype network, depicting few substructures encompassing lineages from AFO, SER, and PAR populations (Fig. 1c). In addition, an hypothetical radiation from AGU population was suggested by the haplotype network (Fig. 1c).

Demographic changes

Neutrality tests resulted in significative values favoring the hypothesis of demographic expansion for the western haplogroup defined in BAPS, as well as for the whole data set (Tab. 1). Comparatively, non-significant values from neutrality tests were obtained for most sampling localities when it was analyzed separately, although punctual exceptions expressing genetic signatures of demographic expansion were detected within the eastern haplogroup (LIM), but most pronounced within the western haplogroup (Tab. 1).

Divergence dating

The strict clock model was rejected for the molecular data set, as evidenced by the maximum likelihood test implemented in MEGA X ($P < 0.01$). Accordingly, the uncorrelated relaxed clock was favored over the strict clock model with an assignment probability higher than 99% for both path sampling, and stepping-stone sampling strategies. The maximum clade credibility tree recovered by BEAST indicated an expressive level of genetic admixture among mitochondrial haplotypes (Fig. 3), evidenced by a low number of nodes with statistical support. However, an early split divergence including the haplotype J400 (restricted to AGU population) was estimated to be occurred around 3.05 Mya (95% HPD = 1.59-4.75), suggesting an early Plio-Pleistocene differentiation with subsequent radiation and diversification events occurring along the Pleistocene.

Migration models

Migrate-n recovered model D as the most likely hypothesis to explain the gene flow of *J. rochae* across the sampling extent (Tab. 3). Model D proposes an unidirectional pattern of gene flow, in which the western haplogroup receives immigrants from the eastern cluster (Fig. 2d). According to Θ and M parameters of model D (Tab. S2), the western haplogroup receives a mean number of 17.5 immigrants from the eastern haplogroup per generation. Although Migrate-n reported model D as the most suitable migration scheme, we cannot disregard model F as a possible alternative to explain the gene flow of *J. rochae* (Tab. 3). Model F suggests that AGU population acts like a migrant source, while gene flow occurs bidirectionally through the BOP (Fig. 2f). For model F, the group of populations from the western side of the BOP receives 67 times more immigrants

per generation from AGU than the populations from the eastern side of the BOP (Tab. S2). In addition, model F depicts an asymmetric gene flow between populations through the BOP, in which, the mean number of immigrants per generation from eastern to the western side is eight times greater than that for the reverse route.

Ecological niche modelling

Overall, the ENMs reached satisfactory values for all evaluation metrics (AUC_{TEST} = 0.9107; AUC_{DIFF} = 0.0091; TSS = 0.70565; OR0 = 0.0192; OR10 = 0.0662), and the levels of autocorrelation between bioclimatic variables were kept low (Fig. S1) thus, we assume their predictions as reliable proxies for niche suitability of *J. rochae*. In terms of spatial shifts, the ENM projections suggest that the climatic conditions that make up the ecological niche of *J. rochae* remained relatively stable around the BOP since the LIG (Fig. 4a-c, f). Nevertheless, a general weak displacement of the climatic niche suitability of *J. rochae* thought the late-Quaternary could be detected, moving diagonally, from northeastern to southwestern from LIG to LGM (Fig. 4d), and in the reverse course from LGM to present (Fig. 4e). At local scale, however, spatial shifts in habitat suitability of *J. rochae* were detected from the LGM to the present, moving from the eastern side of the BOP towards the continent (Fig. 4e).

Discussion

Genetic diversity

In this study, we use the scorpion *J. rochae* as a biological model to understand how climatic and geomorphological features present in Caatinga landscapes could be related to the spatial distribution of genetic diversity, and lineage diversification in low-dispersal animals at regional scale. We found an expressive number of mitochondrial haplotypes (n = 44), which, in turn, is a product of the additive effect of the high haplotype diversity within each sampling site (Tab. 1). The spatial distribution of such genetic diversity is not random. Instead, sampling localities distributed on the western side of the BOP depicted high levels of both nucleotide and haplotype diversity, as well as an expressive proportion of geographically restricted haplotypes (Tab. 1). Such localities may have experienced

few climatic changes over time when compared to those distributed near to the Pernambuco Atlantic Forests refugium (Carnaval & Moritz, 2008; Werneck et al., 2011). Thus, the spatial pattern of genetic diversity in populations of *J. rochae* reported by us, is in accordance with the expectation that genetic diversity can be preserved by historical habitat stability (Carnaval et al., 2009; Faye et al., 2016; Paz et al., 2019). In addition, the shifts in SDTF stability around the BOP can also be a potential drive of phylogeographic endemism (sensu Carnaval et al., 2014), once almost all haplotypes from the western side of the BOP are spatially restricted to their sampling localities, while shared haplotypes were reported for localities from the eastern side of the BOP (Tab. 1).

Population structure and differentiation

The geographical distribution of the two haplogroups recovered by BAPS, suggests that the BOP offers, in some degree, a resistance to the gene flow among populations of *J. rochae*, leading to a substantial genetic differentiation among these haplogroups, as evidenced by AMOVA results (Tab. 2). Such isolation makes populations in the eastern side of the BOP more susceptible to the effects of historical vegetation shifts occurred on the eastern side of this massif along the Quaternary (Werneck et al., 2011).

In fact, recent diversification events have been observed among populations from the eastern side of the BOP (Fig. 3), suggesting that Quaternary climate change may have an effect on the lineage diversification in these populations, which is not seen in the counterparts from the westerns side of the BOP. Moreover, the role of environmental features as physical barriers for structuring communities and/or populations in Caatinga environments has received increased attention (e.g. Werneck, Leite, Geurgas, & Rodrigues, 2015; Oliveira et al., 2015, 2018; Lanna et al., 2019). These studies, however, are centered on the main hypothesis that the São Francisco river is one of the most prominent barriers influencing the patterns of diversity and endemism in Caatinga environments, giving few insights about the potential role of topographical constraints in limiting the gene flow among populations.

In the present case, the clusters obtained in BAPS did not perfectly match the eastern and westerns sides of the BOP, because CAE population grouped into the haplogroup that contains all populations from the western side of this geological formation, suggesting the existence of points of less resistance in the BOP, which

allow the gene flow between populations of *J. rochae*. Even so, our results indicate that BOP can represent a significant barrier to the gene flow of low-dispersal organisms, especially those adapted to the semi-arid conditions of Caatinga environments, favoring the genetic differentiation among populations of such taxa by keeping them geographically isolated.

Demographic changes

Although our initial expectation that habitat stability would be a predictor of demographic stationarity, we find an opposite pattern for *J. rochae*, in which genetic imprints of demographical expansion, and stability, were reported for the western and eastern haplogroups, respectively. In fact, populations with historical evidence of demographic expansion are likely to occur in stable environments, such as those with long-term size stability (Finn, Bogan, & Lytle, 2009). Interesting, neutrality tests suggests that some populations of *J. rochae* from climatically stable areas (AFO, AGU, and PAR) may have experienced demographical expansion events (Tab. 1). Some of them (AFO, and PAR) represented the main geographical substructures within the western haplogroup (Fig. 1c). Eventually, sings of demographical expansions, and reduction in genetic diversity are attributed to bottlenecks suffered by populations from historically unstable environments in South America (e.g. Prado, Haddad, & Zamudio, 2012; Novaes, Ribeiro, Lemos-Filho, & Lovato, 2013; Thomé & Carstens, 2016), including arachnids (e.g. Peres et al., 2015; Bartoleti et al., 2017).

It seems not to be the case for the western haplogroup of *J. rochae*, once the evidences of demographic expansion depicted by neutrality tests are accompanied by high levels of intrapopulation genetic diversity (Tab. 1). The demographic history of this haplogroup reveals a complex pattern, reinforcing the hypothesis of an initial radiation starting from AGU population (Fig. 1c), with subsequent local adaptation and demographic expansion evidenced by genetically structured and growing populations such as AFO, and PAR. Comparatively, the weakness or the absence of molecular evidences for a demographic expansion in the eastern haplogroup (Tab. 1), suggest that their populations may be persisting under suboptimal environmental conditions or spatial limitation, because they are surrounded at west by the BOP, and at east by the Atlantic Forest. This assumption is reinforced by the high migration rate (in number of migrants per generation) reported from eastern

populations to the western ones, as evidenced by the two best migration models recovered by Migrate-n (Tab. S2). Thus, besides the importance of habitat stability on the preservation of genetic diversity, such environmental propriety can also facilitate the radiation and demographic expansion of low-dispersal taxa in Caatinga environments.

Divergence dating

The historical refugia within the Caatinga domain proposed by Werneck et al. (2011) favored the permanence of ancestral lineages, and the maintenance of genetic diversity in populations of *J. rochae* through late-Quaternary. However, the diversification processes behind the origin of such genetic diversity are older, comprising a time slice that encompasses the Plio-Pleistocene period (Fig. 3). Consequently, it implies that the constraint minimum age of about 6.4 Mya for the end of BOP uplift (Morais-Neto, Hagarty, Karner, & Alkmim, 2009; Oliveira & Medeiros, 2012; Costa, Amorim, & Mattos, 2018) is much older than the processes of lineage diversification in *J. rochae* reported by us. Allopatric diversification in Rivulidae killifishes seems to be driven by the uplift of the BOP (Costa, Amorim, & Bragança, 2013; Costa et al., 2018), but there is no information about the role of the BOP on the genetic differentiation of terrestrial animals. Here, however, the chronological incompatibility provides a counter-argument to a vicariant-based explanation for the genetic differentiation among populations of *J. rochae* mediated by the BOP uplift.

Similarly, there are at least two reasons to refuse an hypothesis of genetic differentiation favored by habitat fragmentation due to climatic cycles: 1) the spatial configuration of Caatinga vegetation though Plio-Pleistocene lead to some controversies, in which, some advocate in favor of the maintenance/expansion of Caatinga in that time (e.g. Passoni, Benozzati, & Rodrigues, 2008; Werneck et al., 2015), while others propose a scenario of expansion of humid forests occurring at the expense of dry forests, such as Caatinga (Batalha-Filho, Fjeldså, Fabre, & Miyaki, 2013); 2) even if population of *J. rochae* was segregated in geographically isolated demes, as a result of possible climatic changes in the Plio-Pleistocene, the expected absence of gene flow combined with the accumulation of genetic variation over time, would certainly cause isolation by distance among demes, which was not supported by our data. In addition, the overall low number of shared haplotypes

(Tab. 1) suggests the absence of secondary contact among demes supposedly separated by habitat fragmentation at that time. Thus, an alternative hypothesis, is that genetic divergences in populations of *J. rochae* may have occurred in the presence of gene-flow, which proved to be a common process (Nosil, 2008) observed in some lizards of Cerrado (Werneck et al., 2012), and Caatinga environments (Oliveira et al., 2015; Werneck et al., 2015). Furthermore, the expressive levels of haplotype diversity, and the high number of geographically restricted lineages within the western haplogroup (Tab. 1), agree with the Ecological Gradient Hypothesis (Endler, 1973; Machado et al., 2019), suggesting that lineages may diverged in response to local selective pressures within a continuum landscape with clinal environmental proprieties. If it is the case, the genetic admixture and the absence of reciprocally monophyly between the western and eastern haplogroups (Fig. 3), as well as the lack of isolation by distance, can be explained by the presence of gene flow among populations of *J. rochae*. A similar diversification process seems to be occurred among lineages of the lizard *Phyllopezus pollicaris* (Spix, 1825) in Caatinga environments (Werneck et al., 2012). These examples denote that diversification processes in Caatinga environments are driven by multifactorial patterns that must take into account the historical synergistic effects of geological and climatic events at regional and local scale.

Migration models and ENMs

The asymmetric gene flow of populations of *J. rochae* is evidenced by the high migration rates observed from the eastern side of the BOP to the continent (Tab S1 migrate models). Such asymmetry reinforces the hypothesis that populations from the eastern side of the BOP may be persisting under suboptimal environmental conditions (e.g. spatial limitation, recurrent habitat fragmentation, scarcity of resources). In this sense, migration and population expansion are biological processes that require a period of establishment of the new linages into the new areas (Endler, 1973), thus, the sings of demographical stability in the eastern haplogroup of *J. rochae* (Tab. 1), as well as the increased migration toward the continent (Tab. S2) can be an indicative that migration stared recently in populations from the eastern side of the BOP, suffering a potential increase since the LGM (Fig. 4e). Furthermore, the results obtained in Migrate-n, indicate that the BOP is not a stringent barrier to the gene flow of *J. rochae*, although our results

showed that this massif substantially reduces the migration rate among populations. Because the scorpion *J. rochae* are well-adapted to the xeric conditions of Caatinga environments (Lira, deSouza, & Albuquerque, 2018; Foerster et al., 2019), one can supposes that indirect factors inherent to the BOP, such as the orographic rainfalls, and the establishment of humid semideciduous forests (Rodal & Nascimento, 2006; Rodal, Barbosa, & Thomas, 2008), could be the main source of resistance to the gene flow of this scorpion. However, a purely orographic contribution of the BOP in limiting the gene flow of this scorpion cannot be disregarded, once our ENMs suggest that the BOP provides suitable climatic conditions to the occurrence of this scorpion (Fig. 4f).

In addition, most part of the BOP is within an ecotonal zone between Caatinga and Atlantic Forest (Olson et al. 2001), which, in theory, could favors the permanence of *J. rochae* in xeric-vegetation patches, or promotes its dispersion via xeric corridors through the BOP. In such a context, the geological history of the landscape is a deterministic factor influencing lineage diversification, speciation rates, and community structure in scorpions (Husemann, Schmitt, Stathi, & Habel, 2012; Foord, Gelebe, & Prendini, 2015). In South American environments for example, the new habitats and climatic regimes originated from the Andean uplift, favored the interspecific diversification of scorpion genus *Brachistosternus* Pocock, 1893 (Ceccarelli et al., 2016, 2017). In addition, Foerster et al. (2019) use similarity patterns in species composition to demonstrate that scorpion assemblages in montane forest remnants of northeastern Brazil clustered in spatially structured groups mainly separated by the BOP. Thus, even with the marked chronological association between diversification processes of neotropical species, and the Quaternary climatic changes (Turchetto-Zolet, Pinheiro, Salgueiro, & Palma-Silva, 2013), the geological history and the eventual orographic contributions cannot be neglected in future phylogeographic studies addressing such taxa. In addition, the assumption that the Caatinga landscapes offer few geological barriers to gene flow among demes or populations (Werneck et al., 2012) must be interpreted with caution, because the permeability of such barriers can differ among taxa with distinct physiological tolerances and dispersion capabilities.

Undoubtedly, the development of new analytical tools coupled with the enhancing of computational power has improved our global knowledge on the biogeographic history of several taxa. Within the tropics, however, there is a marked

asymmetry in the number of studies that expose the scarcity of phylogeographic information regarding taxa from arid or semi-arid environments, compared to those from rainforest (Turchetto-Zolet et al., 2013; Pabijan et al., 2015). In conclusion, our results refuse a simplistic interpretation of intraspecific diversification processes of taxa distributed under the CD. In this sense, we provide empirical evidences that habitat stability within the CD can predict high levels of genetic diversity, at least for low-dispersal taxa, as suggested by Werneck et al. (2011). Such historical refuges can also facilitate the demographic and spatial expansion of populations over time, especially if it is preceded by complex diversification processes, that can occur even in the presence of gene flow. Finally, habitat stability seems to have been more important for the diversification of *J. rochae* at regional scale, than the potential changes in Caatinga environments mediated by climatic cycles of the Quaternary, or geological events such as the uplift of the BOP, although these factors are fundamental to preserve the genetic diversity of this scorpion. Finally, we advocate that the biogeographical history of the Caatinga and the evolution of its biota can only be understood if the urgent need for new phylogeographic approaches are met, which would mitigate the negative effects of meaningless generalizations.

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Supplementary information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supplementary tables.
Appendix S2 Supplementary figures.

Biosketch

Stênio Ítalo A. Foerster is interested in phylogeography and macroecology of neotropical arachnids adapted to arid environments, especially those with narrower ecological plasticity and low-dispersion capabilities. All authors are interested in population genetics and evolutionary biology.

Author contributions:
SIAF, AFAL and VQB conceived the study; SIAF and AFAL performed the fieldwork; BNSP and SIAF conducted the molecular procedures; SIAF analyzed the data and wrote the initial text, that was evaluated and discussed by AFAL, VQB, BNSP, JFL and RP-R. All authors are in accordance with the final version of this manuscript.

Tables

Table 1. Genetic diversity estimations and neutrality tests ouput for sampling locations of *Jaguajir rochae*, in northeastern Brazil: Afogados da Ingazeira (AFO), Água Branca (AGU), Buíque (BUI), Caetés (CAE), Caruaru (CAR), Cumaru (CUM), Juazeiro do Norte (JUA), Limoeiro (LIM), Parnamirim (PAR), Serra Talhada (SER), Triunfo (TRI). Results for the eastern (EAS) and western (WES) haplogroups recovered by BAPS are also shown. N = Number of specimens; h = number of haplotypes; grh = number of geographically restricted haplotypes; Hd = haplotype diversity; π = nucleotide diversity; Fs = Fu's Fs; D = Tajima's D; R_2 = R2 statistic; SD = standard deviation. *$P < 0.05$; **$P < 0.02$.

Sampling site	**N**	**h**	**grh**	**Hd (SD)**	**π (SD)**	**Fs**	**D**	**R_2**
AFO	7	7	7	1.0000 (0.00291)	0.0096 (0.0000350	-2.3853	-0.5895	0.1134*
AGU	7	7	6	1.0000 (0.00291)	0.0053 (0.0000122)	-3.8565**	-1.4217	0.1183*
BUI	8	6	6	0.8928 (0.01037)	0.0059 (0.0000141)	-0.9398	-0.9878	0.1392
CAE	7	2	2	0.2857 (0.04010)	0.0004 (0.0000003)	-0.0947	-1.0062	0.3499
JUA	4	3	2	0.8333 (0.03516)	0.0029 (0.0000060)	0.1335	-0.7801	0.3062
PAR	9	8	8	0.9722 (0.00256)	0.0079 (0.0000228)	-4.6211**	-1.3164	0.0808*
SER	6	6	6	1.0000 (0.00463)	0.0068 (0.0000201)	-2.2989	-0.6816	0.1430
TRI	10	4	4	0.7778 (0.00633)	0.0064 (0.0000153)	2.5516	1.0012	0.2088
CAR	7	1	0	0.0000 (0.00000)	0.0000 (0.0000000)	-	-	-
CUM	7	1	0	0.0000 (0.00000)	0.0000 (0.0000000)	-	-	-
LIM	6	2	1	0.5333 (0.02469)	0.0008 (0.0000007)	-3.1497**	0.8506	0.2667
WES	58	42	42	0.9806 (0.00006)	0.0087 (0.0000220)	-25.3085**	-2.1152*	0.0353*
EAS	20	2	2	0.1895 (0.01191)	0.0003 (0.0000002)	-3.8855**	-0.5915	0.0947
Total	78	44	-	0.9381 (0.00041)	0.0090 (0.0000229)	-25.2403**	-1.9887*	0.0365*

Table 2. Summary results of the Analysis of Molecular Variance (AMOVA) computed from the mitochondrial data set of *Jaguajir rochae*, showing the proportion of genetic variation explained between haplogroups (eastern and western), as well as for comparisons among populations within haplogroups, and at intrapopulation level. d.f. = degrees of freedom.

Comparative level	**d.f.**	**Variation (%)**	**P-value**
Among haplogroups	1	44.05	< 0.01
Among populations within haplogroups	9	19.40	< 0.01
Within populations	67	36.55	0.01

Table 3. Migrate-n model comparisons for different migration schemes among populations of *Jaguajir rochae*, based on the partial sequences of the mitochondrial gene cytochrome c oxidase I. Model choice was ranked by the lowest values of log Bayes Factor (LBF) computed for each migration model.

Model	**Bézier (lmL)**	**LBF**	**Model probability**	**Model choice**
A	-1774.68	-19.90	0.00	9
B	-1756.85	-2.07	0.04	7
C	-1760.46	-5.68	0.00	8
D	-1754.78	0.00	0.29	1
E	-1756.72	-1.94	0.04	6
F	-1754.88	-0.01	0.27	2
G	-1755.88	-1.10	0.10	4
H	-1755.32	-0.54	0.17	3
I	-1755.98	-1.20	0.09	5

Figure Legends

Figure 1. (a) Spatial distribution of sampling locations of *Jaguajir rochae* in northeastern Brazil: Afogados da Ingazeira (AFO), Água Branca (AGU), Buíque (BUI), Caetés (CAE), Caruaru (CAR), Cumaru (CUM), Juazeiro do Norte (JUA), Limoeiro (LIM), Parnamirim (PAR), Serra Talhada (SER), and Triunfo (TRI). The point matrix represents the spatial cover of the Caatinga domain, while the transition zone between Caatinga and Coastal Atlantic Forest (crossline matrix) is represented by the horizontal-line matrix; BOP = Borborema Plateau. (b) BAPS chart depicting the western (green) and eastern (red) recovered haplogroups; the colors in the vertical bars are in accordance to the map, identifying the population of which each specimen (horizontal bar) belongs. (c) Median-joining haplotype network illustrating the spatial pattern of sampled haplotypes; the size of each circle is proportional to haplotype frequencies, while colors are population identifiers, according to the map.

Figure 2. Migration models implemented in Migrate-n to test the hypothesis of a single panmitic population of *Jaguajir rochae* distributed around the Borborema Plateau (BOP), and three migration schemes between the western (W) and eastern (E) predefined groups of populations. Five additional migration models were tested (e-i), considering the population of Água Branca (I) as a migration source for the group comprising the remaining populations from the western side of the BOP (II), as well as for a second group containing populations from the eastern side of the BOP (III).

Figure 3. Bayesian dated phylogeny inferred for non-redundant haplotypes of *Jaguajir rochae*, estimated from a partial sequence of the mitochondrial gene cytochrome c oxidase I. Black circles represent nodes with posterior probability ≥ 0.95.

Figure 4. Binary maps reconstructed from ecological niche models, illustrating the potential distribution of niche suitability of *Jaguajir rochae* at three hypothetical climatic scenarios: (a) Last Interglacial (LIG), (b) Last Glacial Maxima (LGM), and current climate (c). Spatial shifts on niche suitability of *J. rochae* from LIG to LGM, and from LGM to the present are displayed by arrows in map (d), and (e), respectively (see Materials and Methods for details). (f) Niche suitability map

showing historically stable (black), and unstable (shades of gray) areas for the occurrence of *J. rochae* through late-Quaternary. The spatial delimitation of the Borborema Plateau ecoregion (dashed polygon) follows Velloso et al. (2002).

Figure 1

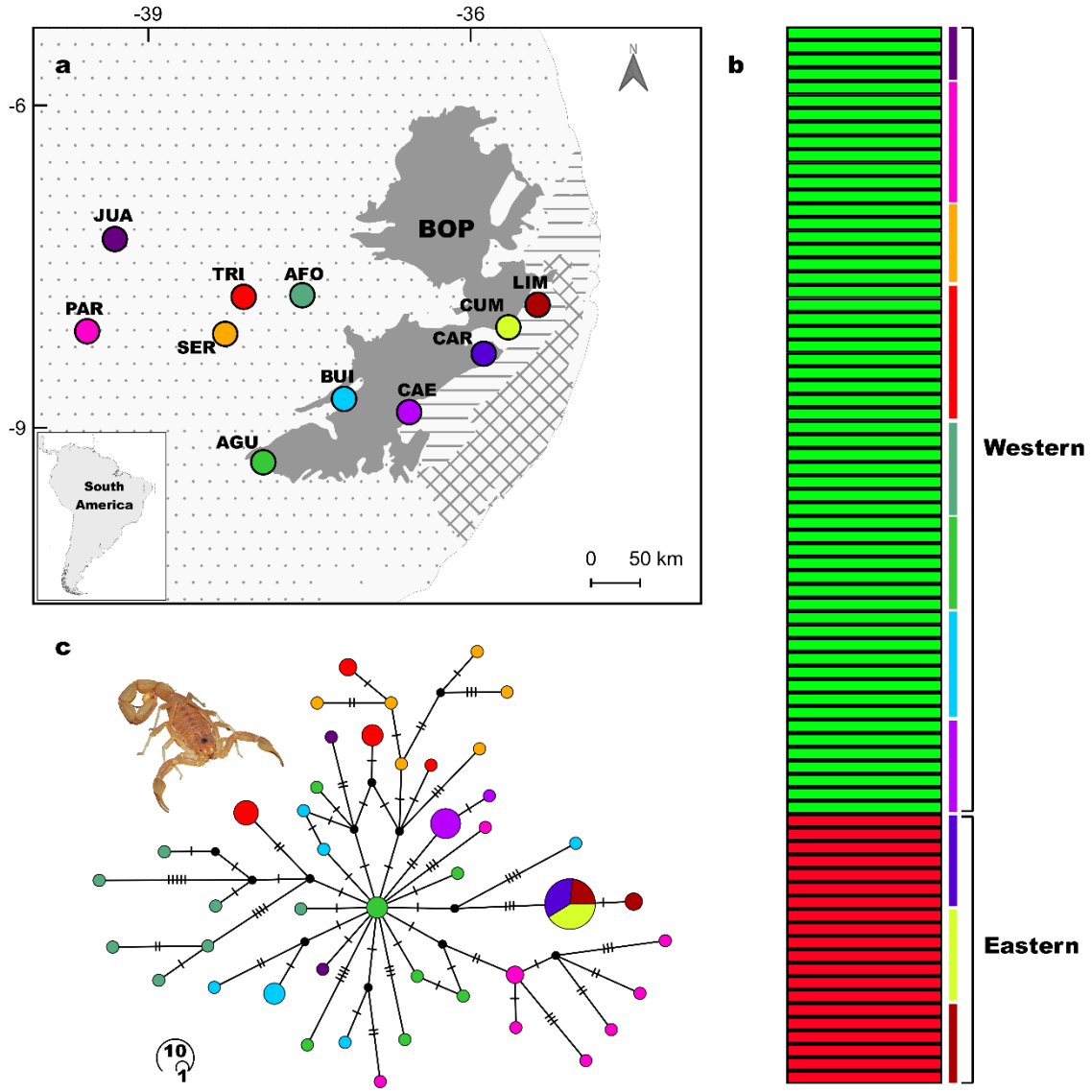
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Figure 2

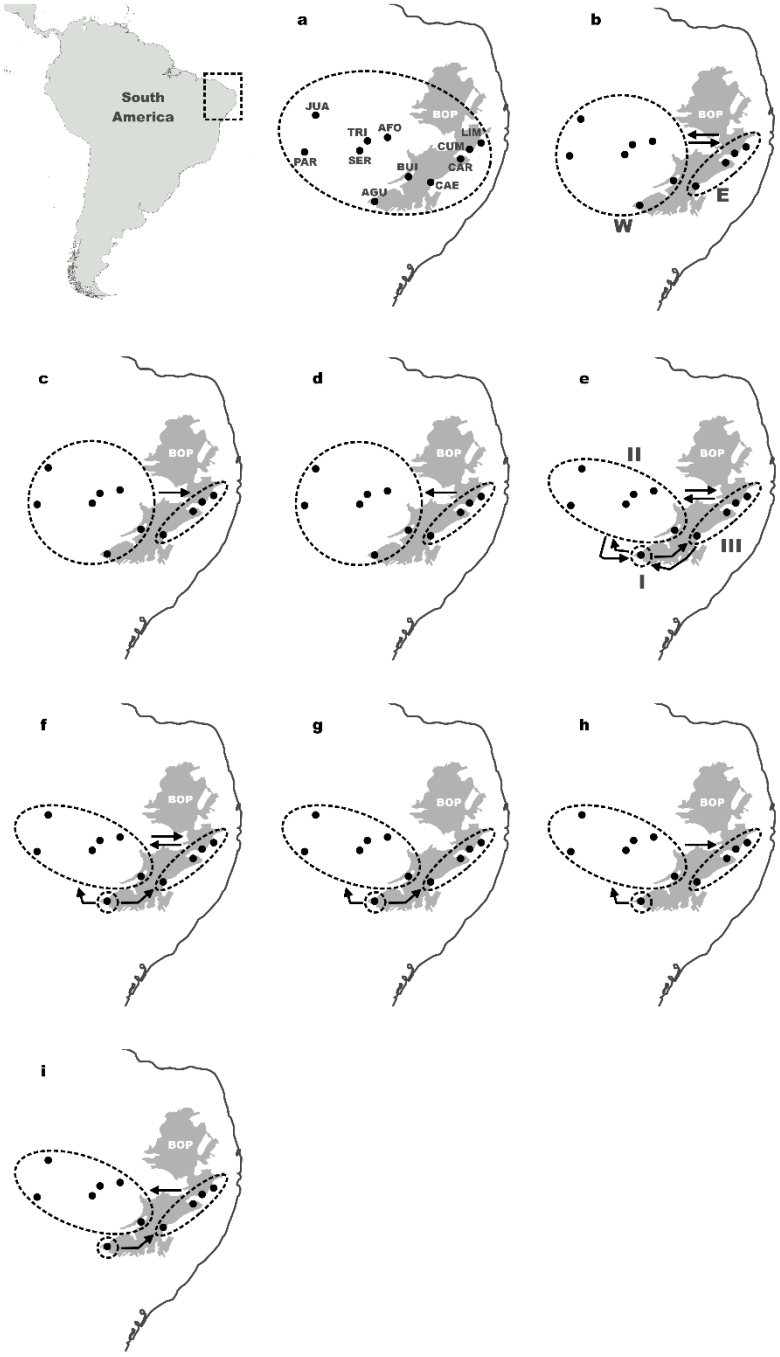
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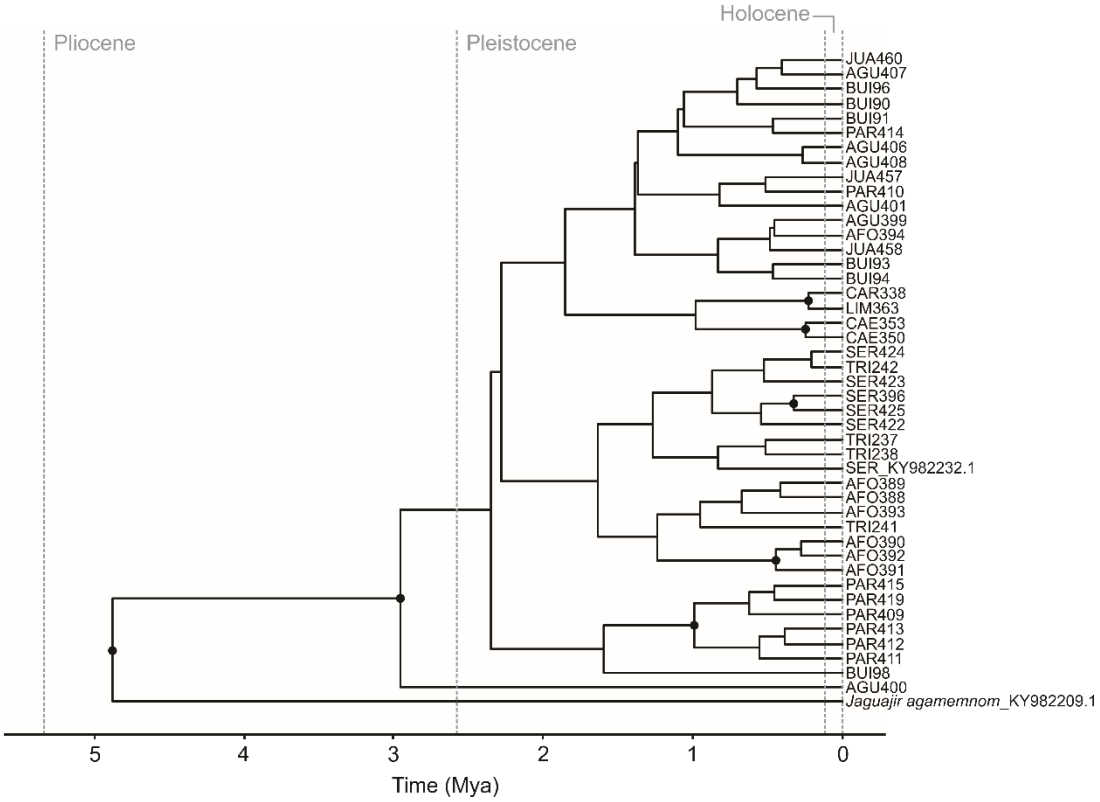
Figure 3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AGU401
AGU399
AFO394
JUA458
BUI93
BUI94
CAR338
LIM363
CAE353
CAE350
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TRI242
SER423
SER396
SER425
SER422
TRI237
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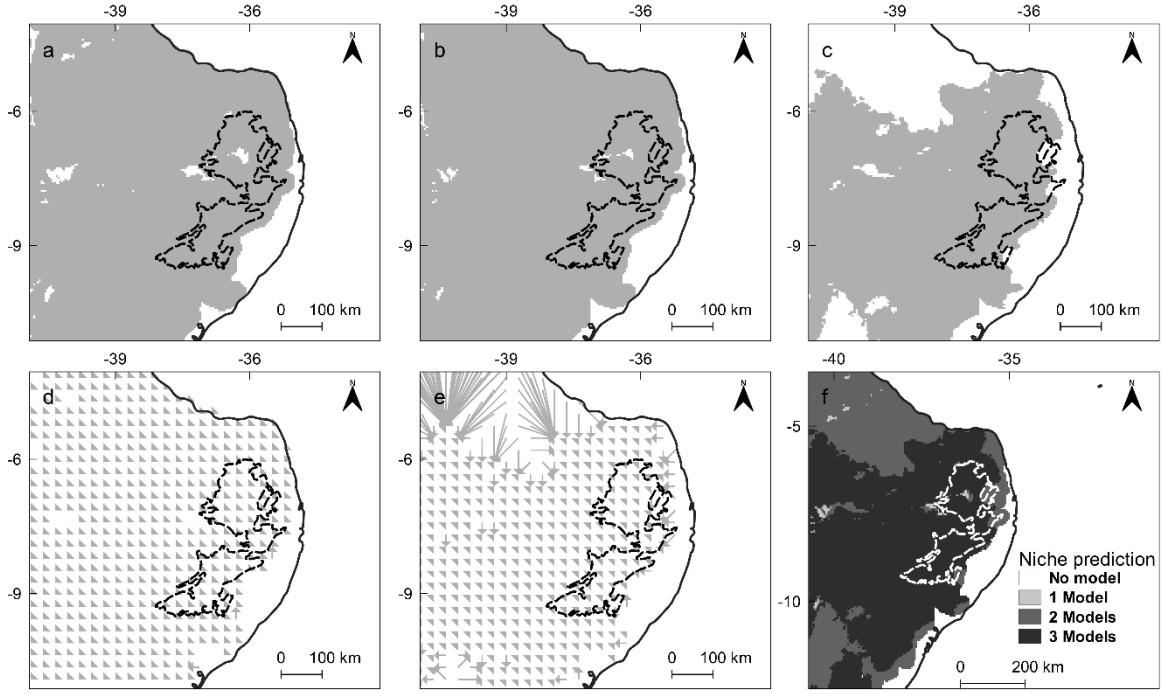
Figure 4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SUPPORTING INFORMATION

Spatial patterns of genetic diversity in the scorpion *Jaguajir rochae* (Scorpiones, Buthidae) as proxies to understand the role of historical habitat stability and geological barriers on lineage diversification processes in Caatinga environments

Stênio Ítalo A. Foerster, Bárbara Natieli S. Pereira, André Felipe de A. Lira, Juliana F. Lima, Ricardo Pinto-da-Rocha and Valdir de Queiroz Balbino

Appendix S1. Supplementary tables

Table S1. List of zoological collections (institutions) accessed to retrieve occurrence points of *Jaguajir rochae* used to construct ecological niche models.

Institution	**Location**	**Curator**
Instituto Butantan	São Paulo, Brazil	A.D. Brescovit
Museu de História Natural da Bahia	Salvador, Brazil	T.K. Brazil
Museu Nacional/Universidade Federal do Rio de Janeiro	Rio de Janeiro, Brazil	A.B. Kury
Museu Paraense Emílio Goeldi	Belém, Brazil	A.B. Bonaldo
Universidade Federal de Minas Gerais	Belo Horizonte, Brazil	A.J. Santos
Universidade Federal da Paraíba	João Pessoa, Brazil	M.B. da Silva
Universidade Federal de Pernambuco	Recife, Brazil	C.M.R. Albuquerque
Universidade Federal do Piauí	Floriano, Brazil	L.S. Carvalho

Table S2. Numerical results of model (D) and (F) estimated in Migrate-n using the mitochondrial data set of *Jaguajir rochae*. The mean values of mutation-scaled immigration rates (M) are presented, followed by the mean number of immigrants per generation given in parenthesis. The mean scaled values of effective population size (Θ) of each predefined group are also shown.

Model	**Θ_W**	**Θ_E**	**M_{E-W}**	**Θ_I**	**Θ_{II}**	**Θ_{III}**	**M_{I-II}**	**M_{I-III}**	**M_{II-III}**	**M_{III-II}**
D	0.088	0.003	198.5 (17.5)	-	-	-	-	-	-	
F	-	-	-	0.023	0.082	0.003	490.1 (40.2)	201.8 (0.60)	232.8 (0.70)	68.7 (5.63)

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Appendix S2. Supplementary figures

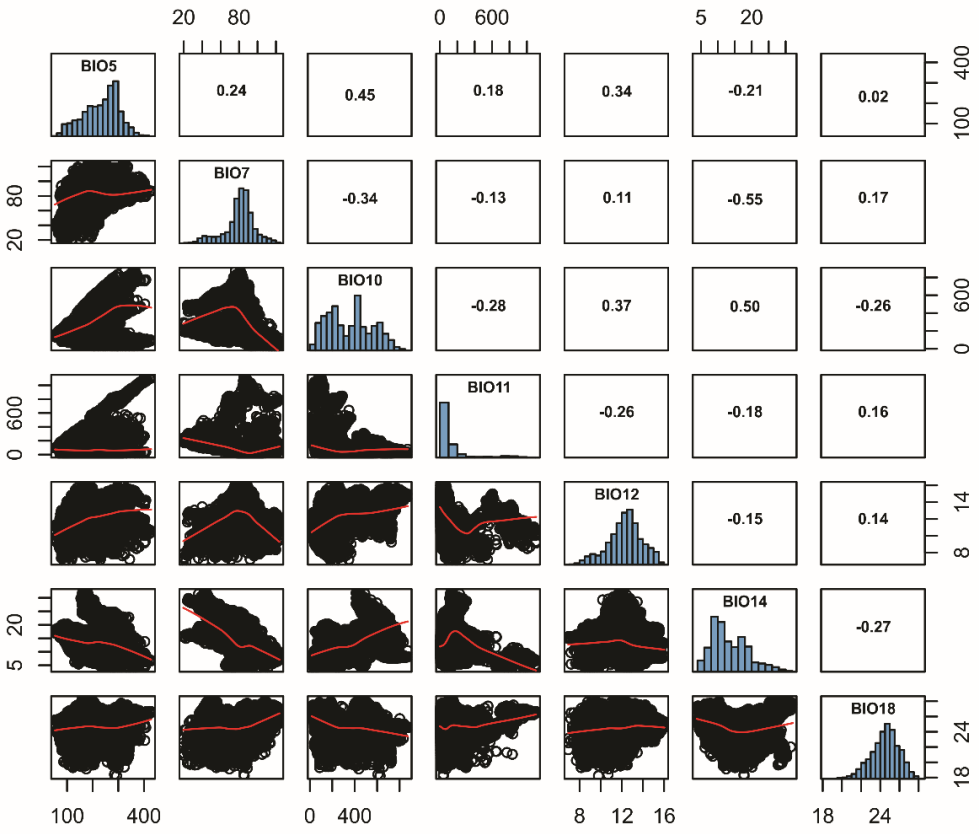

Figure S1. Pair plot depicting patterns of autocorrelation among bioclimatic variables used to construct ecological niche models for *Jaguajir rochae* (lower diagonal). Histograms at diagonal display the shape distribution of bioclimatic predictors, and Pearson correlation values among them are given at upper diagonal.

4 DISCUSSÃO GERAL

O alto poder informativo oriundo de análises filogeográficas, e a notória escassez de estudos desta natureza com invertebrados da Caatinga (Turchetto-Zolet *et al.,* 2013; Magalhães *et al.,* 2014), nos incentivaram a avaliar os padrões espaciais de diversidade genética do escorpião *Jaguajir rochae*. Nossos resultados indicam que áreas de Caatinga historicamente estáveis abrigam populações de *J. rochae* com elevados níveis de diversidade genética, mostrando que tais áreas certamente atuam como refúgios históricos para espécies com baixa capacidade de dispersão (Werneck *et al.,* 2011). Em adição, nós demonstramos empiricamente que o Planalto da Borborema restringe expressivamente o fluxo gênico entre populações de *J. rochae*, mas que sua impermeabilidade não é absoluta. Embora nossos dados não nos tenham permitido determinar os pontos de menor resistência ao fluxo gênico ao longo do Planalto da Borborema, isto pode servir como inciativa para um novo estudo, com o objetivo de testar diferentes padrões de conectividade entre populações de *J. rochae* a partir de dados genéticos, climáticos e topográficos, os quais podem por exemplo, ser implementados em modelos de conectividade baseados na teoria de circuitos (McRae *et al.,* 2008).

As análises de diferenciação genética e datação molecular indicam um padrão complexo de diversificação e divergência entre as linhagens mitocondriais de *J. rochae*, que não podem ser interpretadas unicamente por possíveis alterações de paisagem ocasionadas pelas mudanças climáticas do Quaternário. Similarmente, nossos resultados indicam que os processos de diversificação intraespecífica em *J. rochae* ocorreram após o fim do soerguimento do Planalto da Borborema, sugerindo que uma hipótese de diversificação alopátrica mediada por esta formação geológica é pouco provável. Considerando que os nossos resultados

também indicaram que o nicho climático de *J. rochae* permaneceu praticamente estável desde o último período interglacial (~ 120-140 mil anos atrás), é possível que os haplótipos tenham se diferenciado dentro de um habitat historicamente estável, mas com variações clinais, e que tais processos ocorreram na presença de fluxo gênico (Nosil, 2008). É importante destacar, no entanto, que os nossos resultados devem ser interpretados como indicativos, e que abordagens de caráter multiloci são necessárias para validar os modelos propostos por nós. Similarmente, a inclusão de informações sobre plasticidade ecológica/fisiológica e história natural (ainda indisponíveis para *J. rochae*) podem potencializar o poder preditivo e a acurácia dos modelos de distribuição de espécie (Dormann *et al.,* 2011; Mellert *et al.,* 2011), e por isso, nós incentivamos a elaboração de estudos dessa natureza não apenas com escorpiões, mas com quaisquer táxons distribuídos em ambientes de Caatinga.

Recentemente, a comunidade acadêmica tem empenhado um esforço progressivo aos estudos sobre a biodiversidade da Caatinga, favorecendo o surgimento de novas perspectivas sobre os padrões e processos responsáveis por gerar e preservar a fauna e a flora destes ambientes. Certamente, o maior legado destes avanços foi a mudança de percepção da própria comunidade acadêmica em relação à biodiversidade da Caatinga, antes vista como irrelevante perante alguns pesquisadores (Leal *et al.,* 2005). Os benéficos desta mudança de percepção podem ser traduzidos no âmbito acadêmico, pelo crescente interesse por parte dos pesquisadores, e social, uma vez que o acúmulo progressivo de informações sobre a biodiversidade da Caatinga assegura o planejamento de políticas ambientais que visam preservar os diversos serviços ecossistêmicos. Nesse sentido, nós acreditamos que o presente estudo servirá, primariamente, como fonte de estudos

para fins acadêmicos, mas com potencial para fundamentar práticas de conservação da Caatinga, visto que a estabilidade histórica do habitat deve ser incluída como critério de avaliação de áreas de conservação da biodiversidade.

5 CONCLUSÕES

Nós concluímos que, em termos históricos, a estabilidade climática da Caatinga pode predizer elevados índices de diversidade genética em *J. rochae*, e que o Planalto da Borborema constitui uma importante barreira física ao fluxo gênico entre populações desse escorpião. Em adição, há um padrão complexo de diversificação de linhagens mitocondriais de *J. rochae*, que certamente é influenciado pela estabilidade da Caatinga ao longo do tempo, ao passo em que pouco efeito é atribuído à história geomorfológica do Planalto da Borborema. Por fim, nós demonstramos que o nicho climático de *J. rochae* certamente sofreu poucas mudanças espaciais desde o último período interglacial, corroborando a hipótese de que os processos de diversificação intraespecífica ocorreram em um ambiente estável e provavelmente na presença de fluxo gênico.

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ANEXO I. NORMAS DE FORMATAÇÃO EXIGIDAS PELO PERIÓDICO *JOURNAL OF BIOGEOGRAPHY*

1. SUBMISSION

Authors should kindly note that submission implies that the content has not been published or submitted for publication elsewhere except as a brief abstract in the proceedings of a scientific meeting or symposium. All submissions must be concisely and clearly written in grammatically correct English.

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2. AIMS AND SCOPE

SCOPE:

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Manuscripts submitted to *Journal of Biogeography* should be original and innovative, concise, well written, rigorously analyzed and argued, and consequential. While many such studies will be multifaceted, comparative, and draw generalities, we also welcome exceptional case studies that illustrate particularly interesting deviations that, in their aggregate, shift preconceptions.

The *Journal of Biogeography* is edited and reviewed for the community by a team of practising biogeographers. We support open data, accessibility to publish and read, and a constructive peer-review process.

VISION:

The *Journal of Biogeography* is the discipline's first and foremost journal. It's established history publishing influential papers in biogeography, its topical breadth, and its strong reputation in the community, provide the foundation for the journal to continue to grow as the most respected journal in the field. Nonetheless, as disciplinary and publishing trends change, to remain at the forefront of biogeography, the journal must innovate such that it represents not only core biogeography but also novel advances in emerging areas. Biogeography is an integrative discipline and the journal aims to increasingly complement its strong foundations with the most exciting multidisciplinary research.

3. MANUSCRIPT CATEGORIES AND REQUIREMENTS

The Journal publishes articles under the following main headers: 1) **Research Paper**, 2) **Methods and Tools**, 3) **Data**, 4) **Synthesis**, 5) **Perspective**, 6) **Commentary** and 7) **Correspondence**. All submissions are subject to peer review.

1) Research Paper. Research papers present new biogeographic research resulting from the analysis of a question in biogeography. For a typical Research paper, in which illustrative material (Tables and Figures) occupies about 3 pages of the journal when printed at final journal sizing, the text, inclusive of abstract and reference list, should not exceed 7000 words. Manuscripts should include a biosketch (see below); tables with their legends above; list of figure legends; and embedded figures, and the main headers in the main text of Research Papers should normally be Introduction, Materials and Methods, Results, Discussion, Acknowledgements, References. Methods need to be described in a manner that allows a competent practitioner in the field to repeat the study. Authors must allow repeatability by either providing a thorough description of the methods or by providing relevant computer code.

Structured abstracts. Abstracts should be of no more than 300 words, presented as a series of factual statements under the following headings: Aim, Location, Taxon, Methods, Results and Main conclusions. The Aim should give a clear statement of the principal research question(s) or hypotheses, the Taxon indicate the main group (eg angiosperms), the Methods should give details of materials/sampling/methods of analysis, and the Main conclusions should give the main take-home message.

Biosketch/Biosketches. A short Biosketch/Biosketches entry (30-100 words for one author/150 words total for the first three authors, respectively) describing the research interests of the author(s) should be provided. For papers with four or more authors, biosketch details should be supplied for the first author only and/or a general statement of the focus of the research team (which may include a link to a group web page) plus, in all cases, a statement of author contributions, e.g. Author contributions: A.S. and K.J. conceived the ideas; K.J. and R.L.M. collected the data; R.L.M. and P.A.K. analysed the data; and A.S. and K.J. led the writing.

For an example click **here**.

2) Methods and Tools. These are structured as in Research papers, but the main focus is to present or investigate a new method, rather than to explore a biogeographical problem. Papers in this section are expected to apply new methods to the analysis of biogeographic data and discuss the potential of those methods for advancing the study of the field. For an example **click here**.

3) Data. Datasets that are likely to be of interest to the broader biogeography community are published under this category. Data papers allow scientists to publish and receive credit for work in which the nature of the collected, mobilized, or integrated data more than a specific analysis may be most impactful. The structure of a Data paper should be similar to that of a Research paper. Data papers must include a characterization of overall scope (e.g. organismal, spatial), a description of how the data were collected (protocols), a detailed characterization of all data fields and metadata, information on data records (e.g. SI or in a suitable repository), a section on technical validation, and usage notes addressing potential caveats for analysis and interpretation. Additional analyses that exemplify potential uses of the data are encouraged but not essential. Note that the Data papers category is intended for novel datasets - data used in a published or submitted research paper should be fully addressed and made available there.

4) Synthesis. Papers that have the character of a theoretical synthesis or review, even if incorporating an element of original analysis within them, should use the article type Synthesis. Guidelines are as for Research papers but submissions to the Synthesis section may be of up to 10,000 words, or exceptionally more, if the additional length is fully justified. Authors of synthesis papers are encouraged to discuss their planned paper with one of the Chief Editors, especially if the length will exceed 10,000 words. For an example click **here**.

5) Perspective. Perspectives papers are should be stimulating and reflective essays providing personal perspectives on key research fields and issues within biogeography. When published, Perspectives should be of no more than eight printed pages (main text maximum 5000 words; word count including abstract, main text and references 7000 words maximum but note that shorter articles are encouraged), and they should include a short, single-paragraph abstract. A biosketch (see below) may be included after the references providing the overall paper length limit is not exceeded. For an example click **here**.

6) Commentary. Commentary submissions should provide readily intelligible comment on the latest original research in biogeography. The prose style should be light, and the article should be written with the minimum of technical language and jargon, so as to be understandable to a general audience or an undergraduate taking an introductory course in biogeography. Contributions will be subject to rapid peer review. Commentaries should occupy a maximum of two pages of the journal, and should have a maximum of 10 references: thus the overall word count should not exceed 1600. No biosketch is included for commentaries. Should you wish to include a small figure or other illustration, this can be accommodated by a reduction in the number of words on a pro rata basis. For an example click **here**.

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vii. Main text
viii. Tables embedded in the text (each table complete with title and footnotes)
ix. Figures embedded in the text, each with a figure legend
x. Data availability statement
xi. References
xii. Biosketch
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Edited Book:
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Bacharel em Ciências Biológicas pela Universidade Federal Rural de Pernambuco (2015), e discente do Programa de Pós-Graduação em Genética da Universidade Federal de Pernambuco (2018). Atua nas seguintes temáticas: Filogeografia, Ecologia e Biogeografia, utilizando escorpiões neotropicais como organismos modelo para elucidar padrões filogeográficos e macroecológicos que podem auxiliar na identificação de refúgios e/ou centros de diversificação, bem como na compreensão dos mecanismos de formação e distribuição de comunidades biológicas em ambientes de Caatinga, Floresta Atlântica e enclaves de floresta úmida situados dentro do bioma Caatinga (Brejos de Altitude). **(Texto informado pelo autor).**

Formação acadêmica/titulação

2018 Mestrado em Programa de Pós-Graduação em Genética.
Universidade Federal de Pernambuco, UFPE, Recife, Brasil
Título: Diversidade genética e padrões filogeográficos do escorpião Jaguajir rochae (Borelli, 1910) em um gradiente de estabilidade climática da Caatinga

Orientador: Valdir de Queiroz Balbino
Bolsista do(a): Conselho Nacional de Desenvolvimento Científico e Tecnológico

2010 - 2016 Graduação em Bacharelado em Ciências Biológicas.
Universidade Federal Rural de Pernambuco, Unidade Acadêmica de Serra Talhada, UFRPE/UAST, Brasil
Título: Escorpiões do Parque Estadual Mata da Pimenteira e o escorpionismo no município de Serra Talhada, Pernambuco
Orientador: Cauê Guion de Almeida

Formação complementar

2016 - 2016 Formação Inicial e Continuada para Agente de Combate às Endemias. . (Carga horária: 40h).
Prefeitura Municipal de Afogados da Ingazeira, IPMAI, Afogados Da Ingazeira, Brasil

2016 - 2016 Curso de curta duração em Ecologia dos Crocodilianos. (Carga horária: 5h).
Universidade de Pernambuco, UPE, Recife, Brasil

2013 - 2015 Monitor Bolsista das Disciplinas Bioquímica I e II. (Carga horária: 1170h).
Universidade Federal Rural de Pernambuco, Unidade Acadêmica de Serra Talhada, UFRPE/UAST, Brasil
Bolsista do(a): Pró-Reitoria de Gestão Estudantil (UFRPE)

2013 - 2013 Curso de curta duração em Biologia, Diversidade e Taxonomia de Aranhas. (Carga horária: 8h).
Universidade Federal de Alagoas, UFAL, Maceio, Brasil

2013 - 2013 Extensão universitária em Animais Peçonhentos. (Carga horária: 15h).
Universidade do Estado do Rio de Janeiro, UERJ, Rio De Janeiro, Brasil

2013 - 2013 Curso de curta duração em Filogenia de Aranhas e Escorpiões no Brasil. (Carga horária: 8h).
Universidade Federal de Pernambuco, UFPE, Recife, Brasil

2012 - 2012 Curso de curta duração em Sequenciamento e Análise de Fragmento. (Carga horária: 4h).
Universidade Federal do Vale do São Francisco, UNIVASF, Petrolina, Brasil

2012 - 2012 Curso de curta duração em Análise da Expressão Gênica pela Técnica de PCR. (Carga horária: 4h).
Universidade Federal do Vale do São Francisco, UNIVASF, Petrolina, Brasil

2011 - 2011 Curso de curta duração em Técnicas para o Estudo em Etologia. (Carga horária: 9h).
Universidade Federal Rural de Pernambuco, Unidade Acadêmica de Serra Talhada, UFRPE/UAST, Brasil

2011 - 2011 Extensão universitária em IV Curso de Atualização em Animais Peçonhentos. (Carga horária: 20h).
Universidade Federal de Pernambuco, UFPE, Recife, Brasil

2010 - 2010 Curso de curta duração em Técnicas de Mostragem de Répteis e Mamíferos. (Carga horária: 10h).
Universidade Federal Rural de Pernambuco, Unidade Acadêmica de Serra Talhada, UFRPE/UAST, Brasil

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Validação de método de extração de DNA com Chelex 100 resin e amplificação da região COI (mtDNA) em duas espécies de escorpiões In: VIII Jornada de Pós-Graduação de Genética UFPE, 2018, Recife.
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