UNIVERSIDADE FEDERAL DE PERNAMBUCO

CENTRO DE CIÊNCIAS BIOLÓGICAS

PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA ANIMAL

ANDRÉ FELIPE DE ARAUJO LIRA

INFLUÊNCIA DO GRADIENTE BIOCLIMÁTICO ENTRE A FLORESTA ATLÂNTICA E CAATINGA SOBRE A DIVERSIDADE-BETA E PADRÃO ESPAÇO-TEMPORAL DE ESCORPIÕES (ARACHNIDA: SCORPIONES) NO ESTADO DE PERNAMBUCO

Recife

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Tese apresentada ao Programa de Pós-Graduação em Biologia Animal da Universidade Federal de Pernambuco, como requisito parcial para a obtenção do título de doutor em Biologia Animal.

Orientadora: Profa. Dra. Cleide Maria Ribeiro de Albuquerque

Recife

2018

Dados Internacionais de Catalogação na Publicação (CIP) de acordo com ISBD

Lira, André Felipe de Araújo

Influência do gradiente bioclimático entre a Floresta Atlântica e Caatinga sobre a diversidade-beta e padrão espaço-temporal de escorpiões (Arachnida: Scorpiones) no Estado de Pernambuco/ André Felipe de Araújo Lira- 2018.

120 folhas: il., fig., tab.
Orientadora: Cleide Maria Ribeiro de Albuquerque
Tese (doutorado) ï Universidade Federal de Pernambuco. Centro de Biociências. Programa de Pós-Graduação em Biologia Animal. Recife, 2018.
Inclui referências

1. Escorpião 2. Mata Atlântica 3. Pernambuco I. Albuquerque, Cleide Maria Ribeiro de (orient.) II. Título

595.46 CDD (22.ed.) UFPE/CB-2018-395

Elaborado por Elaine C. Barroso CRB4/1728

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Aprovada em: 25/07/2018

COMISSÃO EXAMINADORA

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Prof. Dr. José Roberto Botelho de Souza/Universidade Federal de Pernambuco

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Dr. Gilberto Nicacio Batista/Universidade Federal de Pernambuco

____

Dr. Bruno Karol Cordeiro Filgueiras/Universidade Federal de Pernambuco

____

Dr. Tiago Jordão Porto/Secretaria do Meio Ambiente e Recursos Hídricos-Bahia

AGRADECIMENTOS

Agradeço imensamente aos meus avós maternos, Otaviano Pereira e Maria Luiza, pelo incentivo e imenso amor dedicados a mim. Principalmente ao meu avô Otaviano Pereira por ter me iniciado na '*arte das ciências naturais*'. Se não fosse por ele com certeza eu teria ido por outro caminho e não o da biologia.

Aos meus pais, Elizabeth Alves e Antônio Francisco. A minha mãe Elizabeth Alves, por sempre apoiar as minhas escolhas e ficar no meu lado. A meu pai Antônio Francisco, por ter compartilhado comigo o seu aprendizado sobre a vida durante os poucos momentos que ficamos juntos.

A minha esposa/amiga/companheira Cinara Sales, por ser a ótima pessoa que é e por ter passado por todo o perrengue junto comigo (da graduação até o doutorado), muitas vezes não me deixando desistir ouvindo as minhas reclamações sobre as 'coisas da universidade'. Muito obrigado por ter entrado (e ficado!) na minha vida!

Ao restante da minha família por acreditar em mim, principalmente ao 'meu outro pai' Roberto Santos e a 'minha outra mãe' Iria Maria, por me socorrer e me apoiar em todos os momentos (e não foram poucos!) em que recorri a eles.

Ao meu time de campo (e amigos!): Laís Pordeus, Adriano Medeiros, Filipe Barbosa, Victor Araújo, Gabriela Cavalcanti, Welton Dionísio, Jonatas Araujo, Meykson Alexandre, Fabrícia Maria, Hugo Neves, Adriana Santos, Stênio Foerster e Arthur Costa. Obrigado a todos vocês! Por termos compartilhados as coisas boas e ruins (que quase não existiram...) do trabalho de campo (que não é nada fácil!), pelas poucas besteiras faladas antes, durante e depois das viagens e principalmente pelo fundamental auxílio na execução do meu projeto de doutorado!!!

A minha orientadora (e amiga!) profª Drª Cleide Albuquerque, por ter aceitado orientar um menino que pediu estágio a ela entre o 2º e 3º períodos da graduação (faz pouco tempo...) e desde então nunca mais deixou de aperriar ela! Poxa, quase 10 anos juntos de uma parceria formada com muito trabalho (e muitas brigas!!). Obrigado, professora! Espero ter correspondido a grande parte das expectativas depositadas em mim.

Ao pessoal do LIT, a turma do Labtei, Juliana Corrêa, Fábio Costa, Renato Portela, aos amigos Marcos Santana, Rodrigo Carmo e Eder Barbier pelas boas conversas (acadêmicas ou não) e aos (pouquíssimos) momentos de brincadeira no lab!

Ao Dr. Antônio Félix do Instituto Agronômico de Pernambuco (IPA) por ter disponibilizado o seu tempo e me ajudado bastante para a realização das coletas feitas nas bases do IPA. Agradeço a Juarez Pordeus, Meykson da Silva, Edson Júnior, Stênio Foerster por terem cedido gentilmente as suas residências como base de campo durante as coletas em Paudalho, Cumaru, Petrolina e Serra Talhada respectivamente. Agradeço as usinas Colônia e Cruangi, aos proprietários das RPPNs Karawã-ta, Pedra do Cachorro, Nossa Senhora do Oiteiro de Maracaípe, Fazenda Santa Rita, a Roberto Siqueira, responsável pelo Refúgio Ecológico Charles Darwin, a Eurico Lustosa da base de pesquisas da UFRPE em Parnamirim, pela autorização e por todo o suporte durante as coletas em suas dependências.

Aos doutores Felipe Rego, Edson Júnior e Thiago Gonçalves por toda a ajuda nas análises estatísticas da minha tese. Não sei o que faria sem o auxílio de vocês, muito obrigado!

Aos meus amigos e parceiros acadêmicos Adriano Medeiros, Felipe Rego, Everton Tizo-Pedroso, Renato Salomão, Raul Badillo-Montaño e Stênio Foerster pelas ótimas discussões. Espero que continuemos a publicar vários papers daqui para frente! Agradeço especialmente a Adriano Medeiros por sempre me salvar nos assuntos '*mapísticos*'.

A FACEPE e CAPES pelos apoios financeiros imprescindíveis para a execução das expedições de campo. Aos professores do departamento de Zoologia, em especial Dr. André Esteves, Dr. Ulisses Pinheiro, Dr. Enrico Bernard, Dr. Wendel Pontes, Dr. Gilberto Gonçalves e Dr. José Roberto pelo incentivo e 'conversas de corredor' durante a minha formação acadêmica.

A todos os meus alunos de graduação (e agora amigos!), Gabriela Cavalcanti, Victória Souza, Hugo Leonardo, Thayna Rhayane, Kamila Cavalcanti, Giuliani Melo e Hugo Rodrigo, que mesmo sabendo da minha inexperiência em orientar, me aceitaram como orientador. Aprendi um bocado com vocês!

Aos membros da banca os doutores José Roberto, Artur Maia, Gilberto Nicacio, Bruno Filgueiras e Tiago Porto, pelos ótimos comentários durante a defesa que logicamente melhoraram na apresentação da versão final da tese.

A Zion, por ser meu fiel companheiro nas madrugadas nas quais escrevia a tese e por sempre tentar tirar o estresse, as vezes oferecendo a bolinha, outras vezes querendo dormir no meu colo.

E a todos aqueles que não foram citados, mas que contribuíram de qualquer forma durante a minha caminhada acadêmica.

As asas de um coração sonhador ninguém irá roubar.

Hiroaki Matsuzawa, 1986

RESUMO

Ao longo de gradientes bioclimáticos, elevadas taxas de substituição de espécies (β-diversidade) decorrentes da alta heterogeneidade ambiental podem contribuir para a compreensão dos padrões da diversidade biológica em larga escala, os quais são pouco conhecidos para artrópodes neotropicais. No presente trabalho, analisou-se as interações entre o gradiente bioclimático (Floresta Atlântica-Caatinga), a diversidade e a distribuição espaço-temporal de escorpiões no estado de Pernambuco. Em adição foi investigado a distribuição potencial futura no cenário de aquecimento global. Foram realizadas coletas entre os meses de novembro/2014 e março/2016 em 20 municípios (Floresta Atlântica = 8 e Caatinga = 12), durante as estações seca e chuvosa. Em cada local, 12 transectos de 30 m foram amostrados através de busca ativa noturna com auxílio de lanternas UV. Durante as coletas foram anotados dados referentes ao microhabitat e estágio do desenvolvimento dos indivíduos. As diversidades beta e gama foram maiores em direção as áreas de temperatura mais elevadas no gradiente. A variação da composição das espécies foi explicada por variáveis climáticas e espaciais. Contudo, nenhuma dessas variáveis influenciou a riqueza. A sazonalidade e o estágio de desenvolvimento foram determinantes para distribuição espacial e a atividade de forrageio das espécies. Os modelos futuros para a distribuição das espécies, mostraram que o aquecimento global pode impactar significativamente a distribuição potencial dos escorpiões, sendo as espécies de Floresta Atlântica mais afetadas do que as de Caatinga.

Palavras- chave: Riqueza de espécies. Condições ambientais. Padrões de distribuição.

ABSTRACT

Along bioclimatic gradients, high species substitution rates (β-diversity) due to high environmental heterogeneity may contribute to the understanding of large-scale biological diversity patterns, which are little known for Neotropical arthropods. In the present work the interactions along the Atlantic forest-Caatinga bioclimatic gradient, the diversity and the spatial-temporal distribution of scorpions in the state of Pernambuco were analyzed. In addition, potential future distribution in the global warming scenario was investigated. Data were collected from November/2014 to March/2016 in 20 municipalities (Atlantic Forest = 8 and Caatinga = 12) during the dry and rainy seasons. In each site 12 transects of 30 m were sampled at night by active search using UV lights. During data collection microhabitat features was recorded regarding the stage of development of individuals. Beta and gamma diversities were higher toward areas with the higher temperature in the gradient. The variation in species composition was explained by climatic and spatial variables. However, none of these variables influenced species richness. Seasonality and stage of development were determinant for spatial distribution and foraging activity of the species. Future models for species distribution showed that global warming can significantly impact the potential distribution of scorpions, with species from Atlantic forest being more affected than those found in Caatinga.

Keywords: Species richness. Environmental conditions. Patterns of distribution.

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1.1 GRADIENTE BIOCLIMÁTICO ENTRE A FLORESTA ATLÂNTICA E CAATINGA EM PERNAMBUCO

O estado de Pernambuco constitui-se como uma das 27 unidades federativas do Brasil, estando localizado no centro leste da região Nordeste, fazendo fronteira ao norte com os estados da Paraíba, Ceará e Piauí, ao sul com Alagoas e Bahia e a leste com o Oceano Atlântico (PERNAMBUCO, 2018) (Figura 1). O estado apresenta uma população estimada de 9.473.266 pessoas, distribuidas numa área de 98.311 km² (IBGE, 2018).

Em Pernambuco a temperatura anual varia de 24º a 45º C, com os índices pluviométricos mais elevados na zona costeira (média de 2.000 mm) e reduções acentuadas em direção ao interior (cerca de 400 mm/ano) (HIJMANS et al., 2005) produzindo um gradiente climático com aumento de temperatura e redução de pluviometria na direção leste-oeste do estado. De acordo com a classificação de Koppen, Pernambuco apresenta majoritariamente três tipos de climas, sendo eles: Am – clima de monção (4.9% do estado), As – clima tropical com estação seca de verão (32.7%) e BSh – clima semiárido quente (61.4%) (Figura 1) (ALVARES et al., 2014).

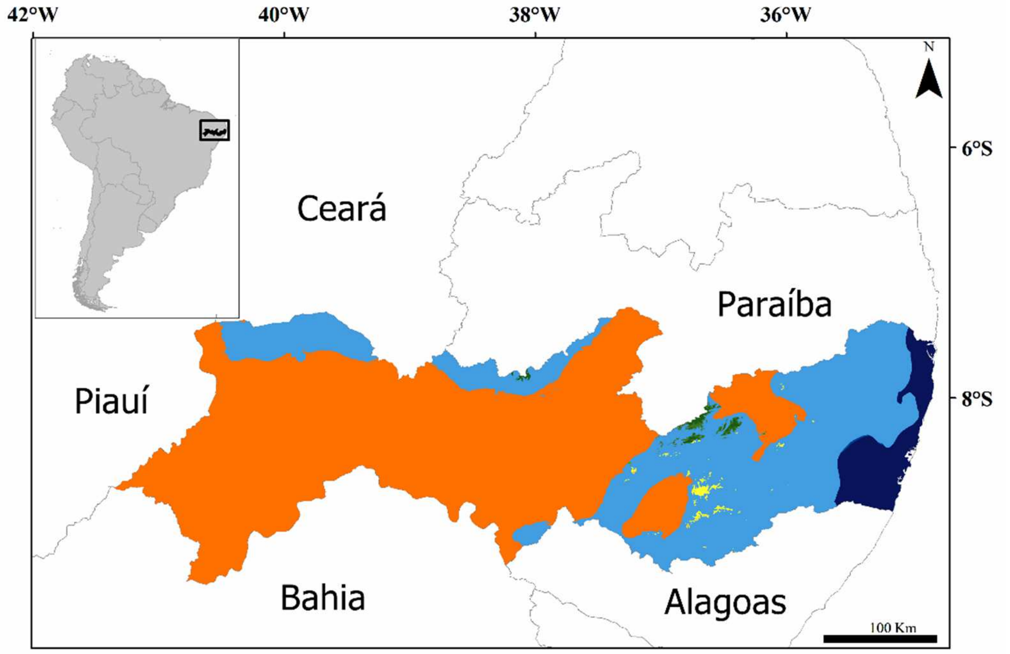


Figura 1. Classificação climátic do estado de Pernambuco de acordo com Koppen. Azul escuro = tropical monçônico, azul claro = tropical com chuvas no inverno e laranja = semiárido quente.

O gradiente formado pelas variações climáticas ao longo estado de Pernambuco é fortemente influenciado pelo planalto da Borborema que afeta a concentração de umidade, formação de solos profundo e a vegetação. Estendendo-se entre os estados de Alagoas e Rio Grande do Norte, essa formação rochosa corta o interior do estado de Pernambuco de norte a sul (Figura 2) (CORRÊA et al., 2010). O planalto da Borborema apresenta forma de elipse alongada, de forma dômica, possuindo altitude média de 500m com picos que podem atingir até 1.200 m, tendo sua origem ainda bastante discutida (OLIVEIRA; MEDEIROS, 2012). Essa formação parece atuar como uma barreira topográfica para o fluxo atmosférico, fazendo com os ventos de leste, ao encontrarem a barreira da Serra da Borborema, ascendam favorecendo a precipitação orográfica no lado leste da montanha e, dessa forma, os ventos de leste chegam secos ao outro lado (REBOITA et al., 2010; REBOITA et al., 2012). Em adição, a forma dômica do planalto da Borborema faz com o que o mesmo funcione como um domo dispersor de água do tipo drenagem radial. O planalto influencia diretamente na rede hídrica dos rios do Nordeste impedindo que a água escoe durante a estação seca (JATOBÁ; SILVA, 2015). Outra hipótese para o clima semi-árido encontrado em Pernambuco provem de informações modernas obtidas por sensoriamento remoto, especialmente as imagens de satélite, as quais levaram Jatobá (2017) a sugerir que esse tipo de clima é resultante da projeção do ar seco proveniente do deserto do Kalahari (África).

Devido a esta particularidade geográfica que causa variações climáticas e vegetacionais ao longo do estado, Pernambuco pode ser dividido em três mesorregiões: a zona da mata, o agreste e o sertão (PERNAMBUCO, 2018) , cujas características são descritas abaixo.

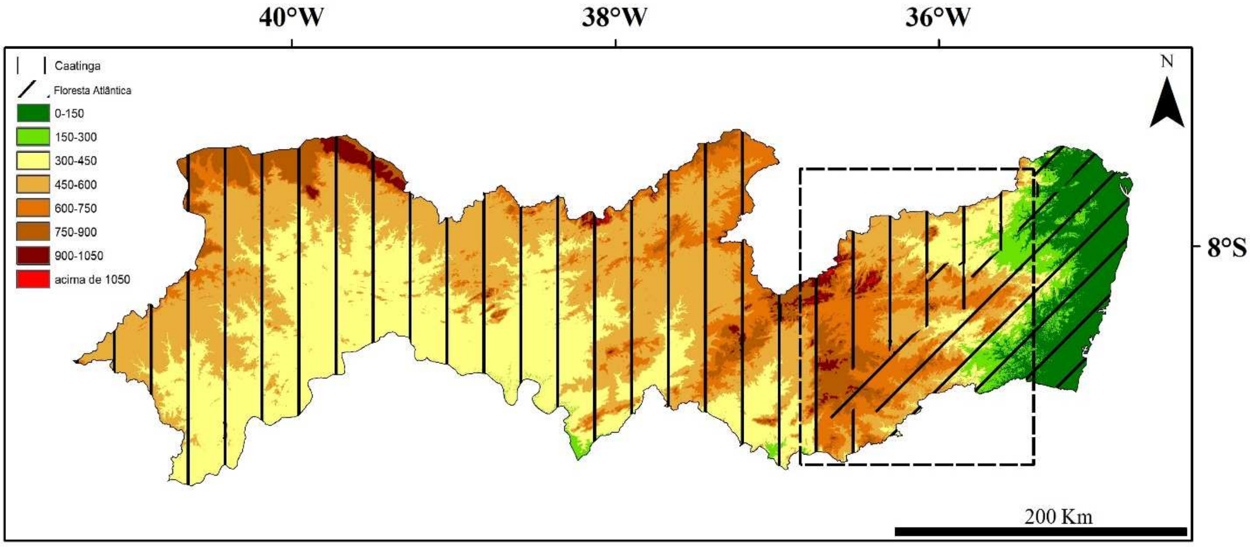


Figura 2. Relação do planalto da Borborema (quadrado pontilhado) e os biomas Floresta Atlântica (linhas diagonais) e Caatinga (linhas verticais) do estado de Pernambuco.

A Zona da Mata ocupa uma área de 8.432,40 km² do território do estado estando localizada no litoral com um clima caracterizado como quente e úmido com chuvas de outono-inverno e tropical monçônico, podendo ser classificados como As’ e Am’ respectivamente segundo a classificação de Köppen. As temperaturas médias anuais estão em torno de 24 ºC e precipitações pluviométricas abundantes, variando entre 800 mm a mais de 2.000 mm anuais, sobretudo na porção sul dessa região (PERNAMBUCO, 2006). Originalmente, a vegetação dessa mesorregião era composta por Floresta Atlântica, sendo atualmente, formada por fragmentos florestais menores do que 100 hectares usualmente inseridos em matrizes de monocultura (ex. cana-de-açúcar) (RIBEIRO et al., 2009; TABARELLI et al., 2010) amplamente dominados por espécies de árvores pertencentes as famílias Lauraceae, Sapotaceae, Moraceae e Fabaceae (GRILLO et al. 2005).

O Agreste estende-se por uma área de 24.400 km² inserida entre a Zona da Mata e o Sertão correspondendo assim a uma zona de transição entre o clima seco do interior e o clima úmido da costa. O clima do Agreste é caracterizado como seco e quente (As’ – de acordo com a classificação Köppen), com as chuvas ocorrendo entre abril - junho, e apresentando o período menos chuvoso entre setembro-janeiro (ITEP, 2006). Embora ainda possam ser encontrados trechos onde ocorre a Floresta Atlântica, a vegetação predominante do Agreste é a Caatinga hipoxerófila, caracterizada por uma vegetação com a presença de espécies decíduas em grande número armadas de espinhos, e abundância de cactos e bromélias (ANDRADE-LIMA, 2007).

A maior mesorregião pernambucana, o Sertão, corresponde a dois terços da área do estado. Apresenta o clima quente e seco (BSh), com baixos índices pluviométricos anuais (400-1200 mm). A precipitação dessa mesorregião é irregular podendo apresentar longos períodos de estiagem. A Caatinga hiperxerófila é a vegetação típica encontrada no Sertão, composta basicamente por uma vegetação mais esparsa composta pelos extratos arbustivo-arbóreos de pequeno porte (ANDRADE-LIMA, 2007; SILVA, 2009). A Caatinga, considerada como parte do bioma das florestas tropicais sazonalmente secas (PENNINGTON et al., 2009), constitui-se como a única formação vegetacional com toda a sua extensão dentro do território brasileiro (ANDRADE-LIMA, 1981; SILVA et al., 2018), e tem sido ameaçada pela perturbação crônica, particularmente devido a exploração de lenha e conversão da vegetação para agricultura e criação de animais (LEAL et al., 2005; BRASIL, 2014; RIBEIRO et al., 2016; RIBEIRO-NETO et al., 2016). Em adição a pressão antrópica, a Caatinga representa um dos mais vulneráveis ecossistemas brasileiros exposto a desertificação causada pelo aquecimento global (OYAMA et al., 2003; LIMA et al., 2011). Algumas previsões indicam que em conjunto esses dois fatores, pressão antrópica e aquecimento global, irão aumentar a frequencia e intensidade das estiagens na Caatinga (SALAZAR et al., 2007), estimando que cerca de 75-95% da região apresenta um alto potencial para desertificação (SÁ; ANGELOTTI, 2009; VIEIRA et al., 2015).

As variações de clima e vegetação ao longo do gradiente bioclimático podem ter consequências importantes na biodiversidade de espécies que dependem das interações bióticas e abióticas com o ambiente (KLANDERUD et al., 2015). Gradientes bioclimáticos envolvem diversas variáveis incluindo diferenças em altitude, temperatura e precipitação que interagem e produzem variações contínuas gerando ambientes diferenciados originando variações no padrão de diversidade e riqueza dos organismos (HAWKINS et al., 2003; VASCONCELOS et al., 2010).

Apesar disso, as consequências da heterogeneidade ambiental ao longo de gradientes climáticos regionais permanecem incertas para a maioria dos organismos. Esse conhecimento permite inferir a relação espécie-ambiente, e serve de base para projetar o potencial de distribuição futura das espécies em função das mudanças climáticas (DEL

TORO et al., 2015; GIBB et al., 2015). Constituindo-se como uma importante ferramenta para a identificação de áreas adequadas para a conservação da biodiversidade (HANNAH et al., 2002; MAWDSLEY et al., 2009).

1.2 DIVERSIDADE BETA E PADRÃO ESPAÇO-TEMPORAL EM GRADIENTES BIOCLIMÁTICOS

Como mencionado anteriormente, gradientes bioclimáticos constituem um fator determinante na distribuição das espécies, afetando de diversas maneiras a diversidade de organismos, dependendo da tolerância a heterogeneidade ambiental e capacidade de dispersão dos indivíduos (HAWKINS et al., 2003; VASCONCELOS et al., 2010). Apesar das respostas ecológicas dos organismos as mudanças globais serem diversas (KERR; DOBROWSKI, 2013), muitos estudos indicam que gradientes de variações climáticas podem modificar as comunidades de organismos que habitam diferentes regiões (PARMESAN, 2006; BELLARD et al., 2012; DEL TORO, 2013), podendo assim afetar espécies importantes para processos e serviços ecossistêmicos (DEL TORO et al., 2012). Assim, nos diferentes ambientes, a diversidade biológica de uma comunidade pode ser descrita por três componentes: diversidade alfa (dα), representando o número de espécies em determinado hábitat; diversidade beta (dβ) representando a variação de espécies entre os hábitats e, por fim, a diversidade gama (dγ), que constitui o número total de espécies observadas em todos os habitats (WHITTAKER, 1960; MAGURRAN, 2004).

Considerando que dβ descreve a variação de espécies entre habitats, ela interge diretamente com gradientes da dα, sendo ambas influenciadas pelos aspectos ambientais locais e regionais (SOININEN et al., 2018). Desse modo, a dinâmica natural dos padrões da diversidade tem sido representada de modo mais eficiente pela dβ do que somente pelas medidas da dα (SOININEN et al., 2018). A dβ também tem sido considerada como uma métrica essencial para informar padrões na biodiversidade regional, contribuindo para os planejamentos conservacionistas (SOCOLAR et al., 2016). Sendo assim, a informação sobre a variação espacial da dβ considerada como um pré-requisito para testar teorias ecológicas gerais (BASELGA, 2010), guiando decisões práticas para os gestores (SOCOLAR et al., 2016).

A identificação dos fatores que determinam a dβ e como estes influenciam a estrutura das comunidades em diferentes escalas espaciais, tem recebido uma atenção crescente por parte dos pesquisadores (CARVALHO et al., 2011). Vários estudos têm relacionado fatores geográficos, ambientais ou combinações de ambos como determinantes da dβ (TUOMISTO et al., 2003; LEGENDRE et al., 2005; SOININEN et al., 2007; QIAN et al., 2009; JIMÉNEZ-VALVERDE et al., 2009; CARVALHO et al., 2011). A importância desses fatores, no entanto, depende do grupo e nível taxonômico estudado, bem como, da escala espacial e região geográfica analisadas (RODRIGUEZ-ARTIGAS et al., 2016). Além desses aspectos, três mecanismos envolvendo a diversidade de espécies em um local e que podem atuar simultaneamente também interferem na dβ (SOININEN et al., 2007). O primeiro mecanismo se refere a similaridade das espécies que diminui com a distância geográfica. Isso ocorre em virtude da dissimilaridade ambiental que aumenta com essa distância, provocando uma maior substituição de espécies entre diferentes ambientes. Nesse mecanismo supõem-se que as espécies estejam distribuídas de acordo com os seus requisitos específicos e com a sua tolerância as condições ambientais (NEKOLA; WHITE, 1999). O segundo mecanismo sugere que o declínio na similaridade pode ser devido a propriedades estruturais da paisagem que limitam o alcance da dispersão. Esta proposta prevê uma paisagem não homogênea e a presença de barreiras à dispersão que afetam o deslocamento (GARCILLÁN; EZCURRA, 2003). Por fim, no terceiro mecanismo a diminuição na similaridade é ocasionada pelo aumento da distância entre as comunidades, devido a um limite de dispersão da própria espécie dentro de um espaço homogêneo (HUBBELL, 2001).

Neste contexto, estudos que monitoram a biodiversidade ao longo de gradientes ambientais podem ser usados como experimentos naturais para documentar como a riqueza de espécies e a estrutura das comunidades mudam em resposta a fatores bióticos e abióticos (LEPETZ et al., 2009; FRENNE et al., 2013). Gradientes latitudinais de riqueza de espécies tem sido bem documentados para uma grande gama de táxons através de diversas regiões (HILLEBRAND, 2004), contudo dados sobre gradientes longitudinais são escassos e geralmente restritos a organismos aquáticos (GRUBAUGH et al., 1996; DELONG; BRUSVEN, 1998; BAPTISTA et al., 2001; FRAMENAU et al., 2002; ANBALAGAN; DINAKARAN, 2006; DANOVARO et al., 2008).

1.3 ESCORPIÕES: DIVERSIDADE E POTENCIAL COMO BIOINDICADORES AMBIENTAIS

Em relação aos ecossistemas terrestres a maioria das espécies correspondem a artropódes, esses animais podem ser considerados como bons modelos para estudos ecológicos devido a sua sensibilidade a variações de temperatura e pluviometria (PRICE et al., 2011; SCHOWALTER, 2016). Assim, estes animais são particularmente indicadores eficientes de mudanças ambientais (PRATHER et al., 2013; NOWROUZI et al., 2016). Contudo, a compreensão acerca da distribuição das espécies em gradientes bioclimáticos continua limitada, apesar do estabelecimento de uma espécie depender de sua capacidade de tolerar as condições climáticas predominantes. O estabelecimento destes animais em uma área pode significar o fornecimento de importantes serviços ecossistêmicos, incluindo o fluxo de energia e nutrientes (ROSENBERG et al., 1986; BROWN, 1997). Nesse contexto, acreditamos que o conhecimento da riqueza e composição de espécies de artrópodes pode auxiliar no entendimento do impacto do gradiente climático encontrado entre a zona da mata e o sertão Pernambucano sobre os mecanismos de adaptação destes invertebrados. Estas informações podem também auxiliar na avaliação dos impactos decorrentes de atividades antrópicas, mudanças associadas ao aquecimento global e fornecer subsídios conservacionistas como a indicação de áreas prioritárias para a criação de unidades de conservação e adoção de técnicas de manejo assertivas (STEWART et al., 2007).

Os escorpiões constituem um dos grupos de artrópodes terrestres mais antigos do planeta, sendo seus primeiros registros datados para o Siluriano (KJELLESWIG-WAREING, 1986; JERAM, 1998; DUNLOP, 2010). Devido ao longo período evolutivo e baixa modificação no *bauplan* básico, estes animais são considerados fósseis vivos (POLIS, 1990). Correspondendo a quinta maior ordem de Arachnida em riqueza, os escorpiões atualmente são representados por cerca de 2.380 espécies (BRAZIL; PORTO, 2011; REIN, 2018), com estimativa total da diversidade em torno de 7.000 espécies (CODDINGTON; COLWELL, 2001). De modo geral, este grupo de aracnídeos apresenta uma grande plasticidade ecológica, estando distribuídos em praticamente todo o globo em uma grande gama de ecossistemas terrestres, como florestas tropicais, montanhas, desertos e cavernas (POLIS, 1990), com até mesmo algumas espécies ocorrendo em áreas urbanizadas (DEHESA-DÁVILA, 1989; CRUCITTI et al., 1998; MCINTYRE, 1999; PUCCA et al., 2014). As regiões áridas e semi-áridas representam as áreas com maior riqueza deste grupo apresentando em média 5-6 espécies (POLIS, 1990; POLIS, 1993; PORTO et al., 2014), contudo estudos recentes apontam as florestas neotropicais como possíveis áreas de elevada diversidade (LOURENÇO, 1994; BRITO; BORGES, 2015). Apesar da sua ampla distribuição os escorpiões não podem ser considerados como ecologicamente generalistas, pois a grande maioria das espécies apresentam exigências específicas com relação ao hábitat e microhabitat (POLIS, 1990; LOURENÇO; EICKSTEDT, 2009).

As assembleias dos escorpiões têm se apresentado estruturadas de acordo com a temperatura, precipitação, tipo de substrato (ex. dureza do solo, quantidade de liteira) e pela fitofisionomia (WARBURG; BEN-HORIN, 1981; POLIS, 1990; PRENDINI, 2001; PRENDINI, 2005; DRUCE et al., 2007; FOORD et al., 2015), podendo os escorpiões responder a variações destes parâmetros numa escala menor do que 100 m (RAZ et al., 2009). Por exemplo, uma forte correlação da composição de espécies com a variação climática foi descrita por Foord et al. (2015) ao investigar o efeito do gradiente altitudinal numa montanha no sul africana. Espécies dos gêneros *Hottentotta* Birulla, 1908 e *Parabuthus* Pocock, 1890 foram ausentes em áreas onde a precipitação foi acima de 600 mm. Resultados similares foram descritos por Prendini (2005) ao investigar a assembleia de escorpiões ao longo de um gradiente longitudinal na região sul do continente africano, encontrando que espécies de *Afroisometrus* Kovarik, 1997, *Lychas* C. L. Koch, 1845, *Cheloctonus* Pocock, 1892, *Pseudolychas* Kraepelin, 1911 e *Opistacanthus* Peters, 1861 foram restritas a áreas como alta pluviometria como as florestas montanas.

Numa escala local, mesmo dentro do habitat, os escorpiões não são distribuídos aleatoriamente dentro do ambiente. Diferentes substratos exercem diferentes pressões seletivas nos escorpiões, resultando em espécies microhabitat-especialistas (POLIS, 1990; PRENDINI, 2001). Em estudo realizado num encrave de floresta úmida (brejo de altitude) na região nordeste do Brasil não foi detectado sobreposição de nicho entre as três espécies de escorpião (*Tityus brazilae* Lourenço & Eickstedt, 1984, *T. neglectus* Mello-Leitão, 1932 e *T. pusillus* Pocock, 1893) que co-ocorrem na área com cada uma delas coletadas exclusivamente em microhabitats específicos (LIRA; DESOUZA, 2014). De modo semelhante, ao analisar o uso do microhabitat em espécies colombianas de um fragmento de floresta seca, Álvarez et al. (2013) descreveram que *Opistacanthus elatus* (Gervais, 1844) e *Tityus tayrona* Lourenço, 1991 utilizam preferencialmente objetos caídos (troncos e pedras) enquanto que *Tityus ashtenes* Pocock, 1893 e *Ananteris columbiana* Lourenço, 1991 foram frequentemente encontrados na vegetação e liteira, respectivamente. Essa especificidade pode até ser encontrada em espécies que coexistem no mesmo substrato. Lira et al. (2013) investigando o uso do microhabitat em um fragmento de Floresta Atlântica, encontraram uma estratificação vertical em duas espécies de liteira, com o *Tityus pusillus* colonizando as camadas superiores enquanto que *Ananteris mauryi* Lourenço, 1982 utiliza as camadas inferiores da liteira.

Devido as exigências ambientais sejam elas regionais (variação climática) ou locais (especificidade por microhabitat), os escorpiões são responsivos a alterações no habitat. Smith (1995) ao estudar o efeito da fragmentação de habitat na Austrália, encontrou que fragmentos maiores suportam elevadas abundância e riqueza de escorpiões do que os fragmentos menores. Resultados semelhantes com uma maior riqueza de escorpiões encontrada em fragmentos maiores foram descritos para uma paisagem hiper-fragmentada de Floresta Atlântica brasileira (LIRA et al., 2016). Estes autores sugeriram que fragmentos maiores possuem uma maior quantidade de microhabitats disponíveis em relação a fragmentos menores, suportando assim uma maior diversidade destes aracnídeos. Em um trabalho conduzido em diferentes locais na África do Sul, Druce et al. (2007) corroboram com a ideia de que a complexidade ambiental é determinante para a riqueza de escorpiões. Neste trabalho, os autores encontraram mais espécies nas áreas que apresentaram uma maior complexidade ambiental do que as áreas mais simples.

Portanto, a sensibilidade de muitas espécies de escorpião a variações ambientais em diferentes escalas (regional ou local) tornam estes animais bons candidatos a bioindicadores ambientais. Indicadores ambientais são uma importante ferramenta descritiva por indicarem mudanças diretas no ambiente e oferecerem uma alternativa barata para a mensuração de tais alterações (PEARCE; VENIER, 2006). Polis (1990) afirma que os escorpiões cumprem uma série de critérios que os enquadram como bioindicadores como, por exemplo, ser facilmente amostrados, classificados, armazenados. Em adição, Gerlach et al. (2013) ressaltam que estes aracnídeos apresentam um alto potencial como bioindicadores, podendo até mesmo ser utilizados como espécies bandeira, devido ao seu carisma. Contudo, os autores ressaltam que a baixa diversidade e abundância em muitas áreas pode atuar como um fator limitante para o potencial uso como bioindicadores.

Dentro deste contexto, os escorpiões têm sido utilizados como modelos para estudos ecológicos que tratam de mudanças ambientais. Nime et al. (2014) compararam a riqueza e abundancia destes aracnídeos entre áreas com vegetação primárias e secundárias com 15 anos de recuperação a um incêndio natural na ecorregião do Chaco argentino. Neste trabalho, apenas a abundancia foi diferente entre as áreas, sendo a riqueza constante. Em contraste, comparando áreas de vegetação primária e secundária com 65 anos de regeneração natural, não foram encontraram diferenças entre a riqueza e abundância para espécies em um fragmento de Floresta Atlântica brasileira (LIRA et al., 2017). Os autores sugerem que o tempo decorrido de regeneração já foi o suficiente para a recuperação da área secundária, tornando possível a manutenção de assembleias similares de escorpião para ambos os ambientes. Em trabalho recente, foi avaliado a resposta de duas espécies de escorpiões na Floresta Atlântica nordestina, *A. mauryi* e *T. pusillus* ao efeito de borda (DIONISIO-DA-SILVA et al., 2018). Foram detectadas respostas distintas ao efeito de borda, com *A. mauryi* não sendo afetado enquanto que *T. pusillus* sofreu uma redução na sua abundância em direção a borda no gradiente analisado. De modo semelhante ao comparar as respostas destas duas espécies a fragmentação de habitat, *A. mauryi* não foi responsivo a nenhuma das variáveis mensuradas, em contraste *T. pusillus* foi positivamente correlacionado com o peso seco da liteira (LIRA et al., 2015). Embora os autores não tenham tratado explicitamente os escorpiões como bioindicadores em seus trabalhos, estes aracnídeos apresentam um elevado potencial para esta função, seja como indicadores de restauração de habitat (NIME et al., 2014; LIRA et al., 2017), qualidade de habitat (LIRA et al., 2015; LIRA et al., 2016) ou efeito de borda (DIONISIO-DA-SILVA et al., 2018).

1.4 OBJETIVOS

1.4.1 Objetivo geral

Avaliar o impacto do gradiente bioclimático existente entre a Floresta Atlântica e Caatinga sobre a diversidade-beta e distribuição espacial das espécies de escorpiões no estado de Pernambuco

1.4.2 Objetivos específicos

1 - Elaborar uma lista de espécies de escorpiões para Zona da Mata e Caatinga de Pernambuco.

2 - Avaliar os efeitos relativos das variáveis bioclimáticas e estacionais sobre os padrões de riqueza taxonômica, funcional (microhabitat + comportamento) e abundância de escorpiões ao longo do gradiente Floresta Atlântica-Caatinga.

3 - Identificar refúgios para a manutenção das espécies no habitat, fornecendo subsídios que auxiliem delimitar áreas prioritárias para a conservação da biodiversidade, principalmente na Caatinga.

4 - Avaliar a existência de possível espécie preditora da intensidade da desertificação do ambiente.

2 RESULTADOS

O presente trabalho será apresentado no formato de três capítulos independentes correspondendo a manuscritos redigidos em inglês.

O primeiro manuscrito intitulado "*Scorpion assemblages across a bioclimatic dry-wet gradient in Brazil*" contempla o primeiro objetivo e parte do segundo (riqueza taxonômica). Esse manuscrito foi submetido ao periódico *Austral Ecology* (Fator de impacto 1.7, Qualis B1 na área de Biodiversidade) e encontra-se em fase de correções das sugestões emitidas pelos revisores.

O segundo manuscrito cujo título é "*Environmental variation and seasonal changes as determinants of the spatial distribution of scorpion (Arachnida: Scorpiones) in Neotropical forests*" foi publicado no *Canadian Journal of Zoology* (Fator de impacto 1.3, Qualis A2 na área de Biodiversidade) e contempla parte do segundo objetivo (riqueza funcional, uso de microhabitat e comportamento).

No terceiro e último capítulo corresponde ao manuscrito "*Modelling patterns and distribution of scorpions in future climate change scenarios of the Atlantic Forest and Caatinga, Brazil*", contemplando os objetivos três e quatro do projeto de tese. Esse manuscrito será submetido a *Zoology* (Fator de impacto 1.9, Qualis A2 na área de Biodiversidade).

Esse capítulo segue as normas para publicação da *Austral Ecology*

2.1 PATTERN OF SCORPION DIVERSITY ACROSS A BIOCLIMATIC DRY-WET GRADIENT IN NEOTROPICAL FORESTS

André Felipe de Araujo Lira[1]*, Renato Portela Salomão[2] and Cleide Maria Ribeiro de Albuquerque[3]

[1]Programa de Pós-Graduação em Biologia Animal, Departamento de Zoologia, Universidade Federal de Pernambuco – UFPE, Rua Prof. Moraes Rego S/N, Cidade Universitária, Recife, Pernambuco, CEP 50670-420, Brazil.

[2]Red de Ecoetología, Instituto de Ecología A. C., Carretera Antigua a Coatepec 351, El Haya, Xalapa, Veracruz, CP 91070, Mexico.

[3]Departamento de Zoologia, Universidade Federal de Pernambuco – UFPE, Rua Prof. Moraes Rego S/N, Cidade Universitária, Recife, Pernambuco, CEP 50670-420, Brazil.

*Corresponding author: André F. A. Lira (E-mail: andref.lira@gmail.com)

Acknowledgements

We are grateful to Instituto Agronômico de Pernambuco (IPA), Universidade Federal Rural de Pernambuco (UFRPE), Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) and to landowners of Reservas Particulares do Patrimônio Natural (RPPN) and others sites for permission to use the areas for sampling. We are also grateful to Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for granting a PhD scholarship to A.F.A. Lira and to Laboratório de Invertebrados Terrestres staff for technical assistance during fieldwork. We also grateful to Fundação de Amparo a Ciência e Tecnologia de Pernambuco (FACEPE) for a financial support (APQ-0437-2.04/15) and to Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) (Fellowship #307759/2015-6 for research productivity) for a financial support for C.M.R. Albuquerque.

Pattern of scorpion diversity across a bioclimatic dry-wet gradient in Neotropical forests

Abstract

Understanding large-scale patterns of biological diversity is one of the most important issues in ecology. Scorpions may serve as a proxy to understand how arthropod species respond to bioclimatic changes by adjusting their spatially structured distribution and assemblages. We analysed patterns of scorpion diversity, and investigated how species richness, abundance, and composition respond to climatic variations found along a longitudinal gradient between wet (Atlantic Forest) and dry (Caatinga hypo and hyperxerophilic) forests in Brazil. A total of 20 sites were sampled four times along a 712 km longitudinal wet-dry bioclimatic gradient in north-eastern Brazil. We recorded 2,653 scorpions from 12 species, belonging to five genera and two families. Environmental variables associated with precipitation, temperature, and geographical distance had a strong effect on scorpion distribution, resulting in a distinct faunal composition at both extremes of the gradient. A turnover of species composition was found, with beta diversity increasing towards the dry direction of the longitudinal gradient, similar to results found for gamma diversity. These observations coincide with increases in temperature, moisture reduction, and environmental harshness. Our study, therefore, indicates that species sensitivity to climatic variation determines scorpion distribution in Neotropical forests.

Keywords: Arachnida, beta diversity, macroecology, metacommunity, species composition

INTRODUCTION

Bioclimatic gradients reflect changes in temperature and precipitation that are under permanent threat owing to global climate change (Bellard *et al.* 2010; Del Toro *et al.* 2013). Variations in habitat structure and resource availability caused by such changes play an important role in determining the pattern of species diversity along bioclimatic gradients, since community processes are largely influenced by the capacities of species to adapt to environmental filtering and biogeographical processes (Kerr & Dobrowski 2013; Lamarre *et al.* 2016).

Along a bioclimatic gradient, a spatial change in species composition can be the result of differences in species richness between sites and the differential replacement of species through species loss and gain (Whittaker 1960; Baselga 2010; Baselga 2012). Both species richness and composition are important for understanding how species diversity is distributed through space, reflecting the biogeographic history of a taxon, as well as ecological processes, found throughout the course of its diversification (Vasconcelos *et al.* 2010). Furthermore, variation in both species richness and composition provides crucial information for identifying areas that should be given priority for conservation (McKnight *et al.* 2007).

Arthropods, which constitute the great majority of species in most terrestrial ecosystems, provide important ecosystem services, including those involving energy and nutrient cycles (Rosenberg 1986; Brown 1997). Most arthropods are highly sensitive to changes in temperature and precipitation. As such, they are particularly powerful indicators of bioclimatic and environmental changes (Prather *et al.* 2013; Nowrouzi *et al.* 2016). Even so, our understanding of the distribution of arthropod species along environmental and bioclimatic gradients is still limited to a few groups (e.g. flies and ground-dwelling arthropods) (Andrew & Hughes 2005; Martín-Vega & Baz 2013; Andersen *et al*. 2015).

Amongst arthropods, those with relatively limited dispersion and long life cycles offer a good tool for studies on patterns and processes related to biological gradient diversity (Prendini 2001; Bryson *et al*. 2013a, b; Foord *et al*. 2015). Scorpions are one of the arthropod groups that have all these features. Little is known about the effects of bioclimatic gradients on scorpion assemblages, particularly in tropical forests. Scorpion communities are the richest in arid and semi-arid regions (Warburg & Ben-Horin 1981; Polis 1990), although Lourenço and Ythier (2010) suggest that their richness in wet tropical forests is as great, or even greater, than that in arid regions. In the Neotropics, variation in temperature and precipitation can result in climatic gradients, as observed along the transition between wet and dry forests in north-eastern Brazil. These variations in temperature and precipitation influence vegetation types responsible for providing prey and shelter for scorpion assemblages. However, ecological studies of scorpions in Neotropical forests are scarce and quite new, especially with regard to Brazil (e.g. Carmo *et al*. 2013; Lira *et al*. 2013; Lira & DeSouza 2014; Lira *et al*. 2015; Lira *et al*. 2018a), a country with continental dimensions and a high diversity of habitats.

Given this context, the goal of this study was to investigate how scorpion diversity, richness, and composition respond to bioclimatic changes across a 712 km longitudinal gradient, which includes different temperatures and rainfall patterns. We tested the hypothesis that scorpion assemblages are affected by bioclimatic variables. We expected that species richness would increase with increasingly dry conditions along the longitudinal gradient, and expected that the species turnover throughout the bioclimatic gradient would increase with geographic distance.

METHODS

Characterisation of the longitudinal area

The longitudinal area evaluated corresponds to the state of Pernambuco (08º 04' S; 37° 15' W), with an area of 98,311 km², located in the eastern centre of north-eastern Brazil (Fig. 1). Annual temperatures along the longitudinal gradient range from 24 °C to 45 °C, with precipitation ranging from 400 mm to over 2,000 mm per year from the coastal zone to the interior of the continent. Elevation varies from sea level on the coast, to mountains over 1,000 m a.s.l within the interior. The study area includes two important Brazilian ecosystems, the Atlantic Forest and the Caatinga (Fig. 2). Both ecosystems, especially the Atlantic Forest, have been highly affected by anthropogenic activities, and their original areas have been reduced to small forest fragments isolated in a matrix of plantations, cattle ranches, and urban areas (Ribeiro *et al*. 2009; Ribeiro *et al*. 2015).

Currently, the Atlantic Forest of north-eastern Brazil is composed of evergreen and semi-deciduous forest remnants (Veloso *et al.* 1991), which are largely dominated by Lauraceae, Sapotaceae, Moraceae, and Fabaceae tree species (Grillo *et al*. 2005). The soil type is mainly composed of argisol, latosol, luvisol, planosol, and neosol (IBGE 2010). Forest fragments are usually embedded in a matrix of sugarcane monoculture (Tabarelli *et al*. 2010). Nevertheless, the ecosystem is a global biodiversity hotspot (in the top five with regards to levels of endemism) (Tabarelli *et al*. 2010). The northernmost portion of the Atlantic rainforest correspond to the Pernambuco Endemism Centre, which is particularly notable for its high species richness (Brasil 2014a).

Caatinga is a seasonal tropical dry forest (Pennington *et al*. 2009) that occupies an area of approximately 800,000 km², equivalent to 11% of the Brazilian territory (MMA &

IBAMA 2011). Vegetation is usually dominated by Fabaceae, Euphorbiaceae, Bignoniaceae, Apocynaceae, and Cactaceae (Leal *et al.* 2018). The soil type is mainly composed of luvisol, neosol, latosol, cambisol, and plintosol (IBGE 2010). In Pernambuco state, Caatinga is divided into two subareas. One is referred to as the hypoxerophytic Caatinga (Fig. 2), and this subarea is characterised by a denser vegetation, deeper soil, with annual rainfall ranging between 800 – 1,000 mm, most of which falls between February and July. The second subarea, referred to as the hyperxerophytic Caatinga (Fig. 2) has a shallow soil layer, sparse vegetation, with annual rainfall ranging between 500 – 800 mm, most of which falls between January and April, with prolonged periods of drought (PERH/PE 1998; Andrade-Lima 2007). This ecosystem has undergone chronic disturbance, particularly because of the unsustainable exploitation of native wood, and conversion of the vegetation to pastures and plantations (Leal *et al.* 2005; Brasil 2014b; Ribeiro *et al.* 2016; Ribeiro-Neto *et al.* 2016). In addition to these anthropogenic pressures, the north-eastern region of the Caatinga in Brazil is under increased risk of desertification caused by rising global temperatures (Vieira *et al.* 2015). Among Brazilian ecosystems, the Caatinga is one of the most vulnerable to this rapidly growing threat (Oyama *et al.* 2003; Lima *et al.* 2011).

Scorpion sampling

Fieldwork was carried out across a longitudinal gradient of 712 km, comprising two ecosystems (Atlantic Forest and Caatinga). Scorpions were collected in eight locations in the Atlantic Forest and 12 locations in Caatinga (six locations in hypoxerophytic and six in hyperxerophytic Caatinga), in the state of Pernambuco (Fig. 1; Table 1). Each location was sampled four times between November 2014 and March 2016. In each location, sampling was performed along six 30 m linear transects, which were set 20 m apart from each other, resulting in a total of 24 transects per area (representing 7,200 m²/location). Scorpion surveys were performed for a period of one hour along each transect between 19:00 and 22:00 h, by a pair of collectors equipped with UV lanterns. Specimens that were up to 5 m perpendicular from the transect line were captured manually, using forceps. Each collected scorpion was stored in vials with 70% ethanol. All specimens were identified according to Lourenço (2002), Esposito *et al.* (2017), and Lira *et al.* (2017), and voucher specimens are deposited at the Arachnological Collection at the Universidade Federal de Pernambuco, Brazil.

Data analysis

To evaluate and compare the effect of bioclimatic variables on scorpion assemblages, rasters of 19 bioclimatic variables (Appendix S1), obtained from WorldClim software version 7.0 (Hijmans *et al.* 2005) were exported at a resolution of 10 km². Information from these variables were extracted for the pixels (1 km²) from the cartographic base map of bioclimatic conditions of Pernambuco state, using ArcGIS software version 10.0 (ESRI 2012). The set of bioclimatic variables was transformed by mean/unit variance standardisation, and the degree of collinearity between these variables was determined through the variance inflation factor (VIF) (Eisenlohr 2014). Values of VIF < 10 indicate an absence of data multicollinearity in linear model analysis (Zuur *et al.* 2010). Hence, 15 of the 19 bioclimatic variables were excluded from the analyses, and the following variables were considered in this study: annual mean temperature (BIO1), isothermatility (BIO3), temperature seasonality (BIO4), and annual precipitation (BIO12). Calculations of autocorrelations between the environmental variables were conducted in R software version 3.2.0 (R Core Team 2015).

Sampling efficiency of scorpion species richness in the Atlantic Forest, and the hypoxerophytic and hyperxerophytic Caatinga, were evaluated using estimators of species richness Chao 1 and Chao 2, based on the number of samples (i.e. locations). Estimators were performed using Estimates software version 9.1.0 (Colwell 2013). Scorpion diversity in the Atlantic Forest and the hypoxerophytic and hyperxerophytic Caatinga were analysed using true components of diversity, including alpha (Dα), beta (Dβ), and gamma (Dγ) diversities (Jost 2006). We used Hill numbers based on species richness (^{0}D) and the Shannon index (^{1}D) to evaluate the components of diversity (Hill 1973; Jost 2006). These metrics were used because they represent the number of species in a community, and are sensitive both to rare species (^{0}D), and to abundant species (^{1}D) (Jost 2007; Hernández *et al.* 2014). In addition, Hill numbers have been successfully applied to analyse communities with relatively low species richness (from 14 to 16 species, see Hernández *et al.* 2014; Peguero *et al.* 2017; Loboda *et al.* 2018), similar to the species richness observed in the scorpions assemblages found in the current study. ^{0}Dα indicates the mean number of species of the Atlantic Forest and Caatinga sites, while ^{1}Dα represents the number of abundant species of the Atlantic Forest and Caatinga sites. Beta diversity indicates the number of distinct assemblages within the landscape, both based on species richness (^{0}Dβ) and relative abundance of the species (^{1}Dβ). ^{0}Dγ indicates the total number of species in the study, and ^{1}Dγ indicates the number of abundant species within the landscape. We used the transect data (per location) to calculate the components of diversity. To compare scorpion diversities among habitats, linear models (LMs) and generalized linear models (GLMs) with Poisson error distribution were used. For such analyses, we confirmed the normality of the residuals using normal q-q pots.

Homogeneity of variances was confirmed using plots of the standardised residuals vs. fitted values. The presence of outliers was evaluated using Cook's distance, but none were found (Cook's distance < 1). Data were analysed in R software version 3.2.0 (R Core Team 2015).

To determine the effects of the bioclimatic variables and geographical distance on scorpion species, richness, and components of diversity (alpha and beta), generalised linear mixed models were applied, using the NLME R package. Location type (i.e. Atlantic Forest, hypoxerophytic and hyperxerophytic Caatinga) was included as a random effect. We confirmed that the data met the assumptions of normality of the residuals, and homogeneity of variances, as well as evaluating the presence of outliers. Data were analysed in R software version 3.2.0 (R Core Team 2015).

To describe and interpret the major gradients between scorpion assemblages, we used non-metric multidimensional scaling (NMDS). The level of compositional similarity between sampling sites was evaluated using the Simpson index. This index provides a 'narrow sense' measure of beta diversity by focusing on compositional differences between sites, independent of species-richness gradients (Koleff *et al.* 2003). The statistical significance of NMDS was tested by analysis of similarity (ANOSIM). Both analyses were performed using R software version 3.2.0 (R Core Team 2015).

The effect of the geographical distance of sites on the scorpion assemblage similarity was determined by the Mantel test. We used a pairwise geographical distance matrix between all plots (Euclidean, in km) to correlate with the taxonomical composition (pairwise distances). The significance of each Mantel test was calculated after 999 permutations in R software version 3.2.0 (R Core Team 2015). Relationships between the scorpion compositions and the bioclimatic variables were calculated using partial redundancy analysis (pRDA), with the geographical distance (longitude and latitude, in decimal degrees) included as covariates to evaluate the variation in terms of spatial-autocorrelation (gradient effects), because our dataset was not randomly distributed in Pernambuco (Fig. 1). In this analysis, linear combinations of the species abundance and the bioclimatic variables were fitted, and the significance of each variable was calculated using the Monte Carlo test with 9,999 permutations (McCune & Grace 2002; Leps & Smilauer 2003; Legendre & Legendre 2012). Linear responses of changes in the species composition was confirmed by a detrended correspondence analysis (DCA) prior to the pRDA (lengths of gradients < 3) (Leps & Smilauer 2003). The species abundances were log-transformed [log(y + 1)] prior to the analyses, to minimize the variance, as were the environmental factors [log(x)], to linearise the relationship between these datasets (Gotelli & Ellison 2004). Linear regression models are sensitive to deviations in data normality and multicollinearity of the independent variables (Zar 1999; Kutner et al. 2005). DCA, pRDA, and permutations were conducted with CANOCO software version 4.5 (ter Braak & Smilauer 2002).

RESULTS

A total of 2,653 scorpions were collected, belonging to two families, five genera, and 12 species. At Atlantic Forest sites, 1,174 individuals of six species were collected, whereas 1,479 scorpions of 10 species were found at the Caatinga sites (Table 2). *Tityus pusillus* Pocock 1893 and *Ananteris mauryi* Lourenço 1982 were the most abundant and widespread scorpion species in the Atlantic Forest, and these two species were collected in all sites in this ecosystem, and comprised 82.11% and 14.39% of the samples, respectively. All other species together represented only 3.5% of the total scorpion abundance in the Atlantic Forest, and were found in one to four of the six sites (Table 2). In Caatinga, the most common species were *Bothriurus rochai* Mello-Leitão 1932, which comprised 31.03% of the scorpions collected, followed by *Jaguajir rochae* (Borelli 1910) (27.92%), *T. pusillus* (13.31%), and *Physoctonus debilis* (C. L. Koch 1840) (9.53%). *Jaguajir rochae* was the most representative species, and was found in all Caatinga sites, followed by *B. rochai*, *Tityus stigmurus,* and *P. debilis*, which occurred in eight, six, and five sites, respectively (Table 2).

Both ecosystems had a high species coverage (Atlantic Forest: Chao 1 = 100% of the expected species, Chao 2 = 93.16%; hypoxerophytic Caatinga: Chao 1 = 100%, Chao 2 = 97.44%; hyperxerophytic Caatinga: Chao 1 = 100%, Chao 2 = 90.60%). Scorpion diversities were different between habitats (Table 3). Based on the species richness ($q = 0$), the three habitats had statistically the same ^0D diversity (Table 3). Nonetheless, the diversity numbers according to the Shannon index ($q = 1$) indicated a gradual increase in scorpion diversity along the longitudinal gradient. A lower ^1D diversity was observed in the Atlantic Forest, an intermediate diversity was observed in the hypoxerophytic Caatinga, and the highest diversity was observed in the hyperxerophytic Caatinga (Table 3).

Alpha diversity based on the Shannon index ($^1D\alpha$) was positively affected by temperature seasonality (Table 4). Scorpion species richness ($^0D\alpha$) and beta diversity based on species richness ($^0D\beta$) were negatively affected by annual mean temperature (Table 4). Beta diversity based on the Shannon index ($^1D\beta$) was not affected by any geographical distance and environmental variable (Table 4). Mantel tests indicated that species composition was spatially structured in part by the geographical distance between the samples (Mantel: Global Pearson's r = 0.360; global p-value = 0.001) (Fig. 3). The two-dimensional NMDS ordination revealed a geographic/environmental gradient in scorpion species composition among survey sites (Fig. 4). These differences in species composition between the Atlantic Forest and Caatinga were statistically significant, according to ANOSIM (R-global = 0.864, p = 0.001). Only annual precipitation was correlated with the scorpion assemblage along the gradient analysed, according to pRDA (F = 3.06, p = 0.011), and explained 10.00% of the species composition variability. The environmental variables explained 18.30% of the variability in the species composition, of which 67.60% was expressed by Axis 1, and 17.70% by Axis 2 of pRDA (Fig. 5). The degree of collinearity between the explanatory variables of pRDA was low (VIF = 3.35-10), indicating that there were no problems related to data multicollinearity in the analysis.

DISCUSSION

Our study indicates that much of the observed variation in scorpion species composition and diversity, but not species richness, can be explained by the longitudinal bioclimatic gradient (precipitation and temperature) along the wet–dry forest continuum in north-eastern Brazil. Although there have been no previous studies on the influence of bioclimatic variables on the composition and diversity of Neotropical scorpion assemblages, studies on other arthropods such as spiders (Rodriguez-Artigas *et al.* 2016) and insects (Lamarre *et al.* 2016; Antonini *et al.* 2017; McCreadie *et al.* 2017) indicate effects of environmental variables on assemblage structure similar to those found in this study.

Scorpion species composition along the longitudinal gradient was partially affected by precipitation and geographical distance. Climatic factors are widely recognized as important for the large-scale distribution of species (Hawkins *et al*. 2003). For example, much of the variation in Amazonian ant species assemblages along a 2,000 km gradient was better explained by precipitation than by geographical distances (Vasconcelos *et al.* 2010). Precipitation is an important factor for the distribution of scorpion species (Warburg & Ben-Horin 1981; Polis 1990; Prendini 2005; Foord *et al*. 2015). Foord *et al.* (2015), analysed the influence of a climatic gradient from arid northern slopes to mesic southern slopes in a mountain range in South Africa, and found strong differences in the composition of scorpion species correlating with climatic variation. Endemic South African taxa such as *Hottentotta trilineatus* (Peters 1861), *Parabuthus granulatus* (Ehrenberg 1831), and *Opistophthalmus wahlbergii* (Thorell 1876) were restricted to arid (northern) slopes, and *Hottentotta* Birula 1908 and *Parabuthus* Pocock 1890 scorpions were generally absent in areas receiving more than 600 mm of rainfall (Prendini 2005).

The present study shows that *A. mauryi* and *T. brazilae* Lourenço and Eickstedt, 1984 depend on high levels of humidity, such as those found in rainforest environments, while *J. rochae*, *B. rochai*, *J. agamemnon* (Koch 1839), and *P. debilis* are associated with less humid open areas. In general, species in the genera *Ananteris*, *Tityobuthus* Pocock, 1893, and *Hadrurochactas* Pocock, 1893, are exclusively restricted to forests (Lourenço 2015). The majority of humicolous species are limited to moist conditions, although these environments should not be wet enough to cause flooding (Lourenço 2010; Lourenço 2015; Lira *et al*. 2018b). For example, all *Ananteris* spp. found in our study were restricted to leaf litter, preferentially inhabiting the bottom layers in both ecosystems (Lira *et al.* 2018), whereas *T. brazilae* is considered a forest-dependent species, and is usually found inside tree barks (Bertani *et al*. 2008; Lira *et al*. 2018; Porto *et al*. 2018). In contrast, many species, such as those in the genus *Jaguajir* would be able to survive in the extreme environments of the Brazilian savannah (the Cerrado) and the Caatinga (Lourenço &

Pinto-da-Rocha 1997). Species in this genus are typically large-bodied scorpions (50 - 110 mm) (Esposito *et al*. 2017), a feature that can provide an adaptive advantage for survival in arid environments such Caatinga. Like many others small arthropods (Entling *et al*. 2010; Horne *et al*. 2015) in dry areas, small scorpions are often at risk of desiccation due to their high surface area to volume ratio. However, the mechanisms regulating water loss are diverse, and include cuticular permeability, metabolic rate, regulation of the spiracular opening, and the reduction of excretory water loss (Gibbs *et al*., 1997), with different responses between species (Terblanche & Chown, 2009; Chown *et al*., 2011).

Temperature was also important for the beta diversity (number of distinctive assemblages) of scorpion species along the longitudinal gradient. For example, *A. mauryi,* a leaf litter-dwelling scorpion, was found in the Atlantic Forest and hypoxerophytic Caatinga (arboreal Caatinga), while the two largest scorpions, *J. rochae* and *J. agamemnom,* were found exclusively in Caatinga vegetation. Such distributional range suggests an interspecific differential heat stress tolerance, as observed for other arthropods that rely on the spatial variance of environmental conditions to thermoregulate (Caillon *et al*., 2014). The environmental temperature affects a variety of biological processes in terrestrial ectotherms (Braña & Ji 2000; Mondal & Rai 2001). Therefore, efficient thermoregulation may be necessary for scorpions to reduce rates of water loss when exposed to the higher temperatures in their habitats (Webber *et al*. 2015), as those observed in the hyperxerophilic environment studied in this work. Evapotranspiration has been indicated as the most important physical factor of the environment affecting the distribution of cryptozoic animals, such as scorpions, that live in soil and leaf litter (Lourenço 2015). This is because conservation of water is the main physiological problem for small animals with a very large surface area in proportion to their mass (Lourenço 2015). For example, *A. mauryi* a small leaf litter-dwelling is highly dependent of forested habitat (Lira *et al.* 2018b; Porto *et al.* 2018), in our study was found in all Atlantic forest sites and in two hypoxerofitic Caatinga (Arboreal Caatinga), while the two larger scorpions *J. rochae* and *J. agamemnom* were found exclusively in Caatinga vegetation.

The absence of correlation found in our analysis between species richness and the bioclimatic and geographical distance corroborates findings of previous studies in which species richness of scorpions was related to habitat structure (e.g., availability of microhabitats) (Smith 1995; Druce *et al.* 2007; Lira *et al.* 2016; Lira *et al.* 2018b). Habitats with greater microhabitat availability are associated with a high species richness once scorpion assemblage are composed of niche specialists, due to aggressive behaviour between scorpion heterospecifics (Polis 1990; Lira *et al.* 2013; Lira & DeSouza 2014). In a recent study on the effect of habitat fragmentation on the diversity of scorpions in the Brazilian Atlantic Forest, Lira *et al.* (2016) suggested that species richness is positively related to increased area and habitat structure of forest remnants. Similar results were described by Smith (1995), who reported a positive correlation between scorpion species richness and the size of forest fragments in Western Australia, suggesting that larger remnants support higher species richness because of greater availability of microhabitats. Druce *et al.* (2007) compared scorpion species richness in five different sites in South Africa, and also found a higher number of species in the more complex habitat (mixed bushveld) compared to the less complex habitat (brown sand bushveld). As such, the greater number of species found in the present study in the Caatinga than in the Atlantic Forest can be related to the fact that the Caatinga comprises a more complex landscape, ranging from forested areas (hypoxerophytic Caatinga) to areas with open vegetation (hyperxerophytic Caatinga), whereas the landscape of the Atlantic Forest is less varied.

Increased values of ^1D gamma, alpha, and beta diversity towards the drier areas of the longitudinal gradient in the present study highlight the fact that the Caatinga is the ecosystems with a higher scorpion diversity compared to the Atlantic Forest, in accordance with previous studies (Porto *et al.* 2010; Lira *et al.* 2018b). Furthermore, the hypoxerophytic Caatinga acts as an ecotonal zone, and includes species from the Atlantic Forest (e.g. *A. mauryi*) and the hyperxerophytic Caatinga (e.g. *J. rochae*), and has a higher number of distinct scorpion assemblages. Such community assembly is likely to follow the model proposed by Soliveres *et al.* (2012). In this model, abiotic factors predominate in the selection of species, allowing the establishment of natural communities according to their environmental requirements. The Caatinga experiences more severe environmental conditions, such lower rainfall and long periods of drought (Leal *et al.* 2005; Salimon & Anderson 2017), than the Atlantic Forest, where the seasonal changes are not so pronounced. In addition, although the Caatinga had a greater number of scorpion species in relation to the Atlantic Forest, its functional richness was lower (Lira *et al.* 2018), suggesting a greater conservation of the functional traits. Thus, our results may support the stress-gradient hypothesis (Brooker *et al.* 2008) that postulates that competition for resources (e.g. food and microhabitats) is lower under more severe environmental conditions (e.g. the hyperxerophytic Caatinga), whereas competition is more intense in places where resources are more abundant (e.g. the Atlantic Forest). Finally, in intermediate conditions, such as those found in the hypoxerophytic Caatinga, facilitation may predominate in the community assembly process. Establishment of new species could be achieved due to the presence of other species that facilitate their establishment, indicating that the community assembly of these arachnids may be influenced by niche-based processes.

In summary, we found that scorpion species composition and diversity, but not species richness, along a longitudinal gradient depends on bioclimatic variables (precipitation and temperature), and partially on geographical distance. Future climate change scenarios indicate that the studied region will be affected by a rainfall deficit and increased aridity in the next century (Franchito *et al.* 2014; Marengo & Bernasconi 2015; Marengo *et al.* 2016). Thus, under future climate change conditions, we expect that biotic changes will be exacerbated, due to rising temperatures, and we expect to see increased 'savanisation' of rainforests and desertification of dry areas (Salazar *et al.* 2007; Sansevero 2013; Vieira *et al.* 2015). In the Atlantic Forest, scorpion species depend on forested habitat, and avoid modified habitats, such as agricultural and pasture lands (Porto *et al.* 2018). As such, the relatively low scorpion diversity observed in the Atlantic Forest, concomitant with the highly fragmented landscape of this ecosystem (Tabarelli *et al.* 2010; Lira *et al.* 2018b), may threaten the few species that are distributed in this environment. In addition, despite the higher scorpion richness found in the Caatinga, several studies have documented that 94% of the region has a moderate to high risk of desertification, due to intense and unsustainable land use practices (Sá & Angelotti 2009; Vieira *et al.* 2015), which directly affect the native fauna. Based on the results presented in this study, we believe that scorpions can be used as environmental indicators, making this taxon a valuable tool to predict changes in Neotropical forest environments. Thus, future studies should focus on determining the effects of disturbances (including climatic changes and anthropogenic effects) on scorpion species that live in these environments.

TABLES

Table 1. Study sites along the longitudinal wet-dry bioclimatic gradient in Pernambuco state, Brazil.

Study area		Environment type	Annual temperature	Annual precipitation	Coordinates	Code
Municipality	Site					
Igarassu	Refúgio Ecológico Charles Darwin	Atlantic Forest	25.9	1734	08°00'058"S; 034°52'23"W	1
Ipojuca	RPPN Nossa Senhora do Oiteiro	Atlantic Forest	24.8	2051	08°31'48"S; 035°01'05"W	2
Tamandaré	REBIO Saltinho	Atlantic Forest	23.7	1935	08°43'43"S; 035°10'39"W	3
Moreno	Private area	Atlantic Forest	24.5	1287	08°06'38"S; 035°06'56"W	4
Paudalho	Private area	Atlantic Forest	24.8	1222	07°53'49"S; 035°10'48"W	5
Timbaúba	RPPN Engenho Água Azul	Atlantic Forest	23.5	1163	07°36'36"S; 035°22'46"W	6
Água Preta	RPPN Fazenda Santa Rita	Atlantic Forest	23.3	1827	08°41'31"S; 035°29'49"W	7
Gravatá	RPPN Karawa-Tã	Hipoxerophytic Caatinga	22.6	774	08°11'11"S; 035°33'51"W	8
Cumaru	Private area	Hipoxerophytic Caatinga	23.4	784	08°00'21"S; 035°41'49"W	9
Jaqueira	RPPN Frei Caneca	Atlantic Forest	20.7	1096	08°43'039"S; 035°50'21"W	10

Caruaru	Instituto Agronômico de Pernambuco	Hipoxerophytic Caatinga	21.7	571	08°14'24"S; 035°55'09"W	11
São Caitano	RPPN Pedra do Cachorro	Hipoxerophytic Caatinga	20.8	614	08°14'11"S; 036°11'31"W	12
São Bento do Una	Instituto Agronômico de Pernambuco	Hipoxerophytic Caatinga	22	657	08°31'45"S; 036°27'23"W	13
Arcoverde	Instituto Agronômico de Pernambuco	Hipoxerophytic Caatinga	22	657	08°31'46"S; 036°27'24"W	14
Buíque	Private area	Hiperxerophytic Caatinga	21.5	759	08°35'08"S; 037°14'29"W	15
Águas Belas	Private area	Hiperxerophytic Caatinga	20.6	915	08°56'52"S; 037°25'22"W	16
Sertânia	Instituto Agronômico de Pernambuco	Hiperxerophytic Caatinga	24.7	634	08°04'14"S; 037°15'57" W	17
Serra Talhada	Parque Estadual Mata da Pimenteira	Hiperxerophytic Caatinga	23.4	742	07°53'48"S; 038°18'13"W	18
Parnamirim	Estação de Agricultura Irrigada de Parnamirim – UFRPE	Hiperxerophytic Caatinga	24.8	422	09°19'40"S; 040°32'55"W	19
Petrolina	Campus UNIVASF	Hiperxerophytic Caatinga	24.8	422	08°56'52"S; 037°25'22"W	20

Table 2. Abundance and richness of scorpion fauna in eight Brazilian Atlantic Forest and 12 Caatinga sites in Pernambuco state, Brazil.

Scorpion diversity	Sampled sites																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Family Bothriuridae																				
Bothriurus asper	-	21	-	-	-	-	-	-	2	-	-	18	-	-	27	16	-	-	-	-
Bothriurus rochai	-	-	-	-	-	-	-	23	-	-	151	-	35	98	-	-	25	35	61	31
Family Buthidae																				
Ananteris franckei	-	-	-	-	-	-	-	-	-	-	-	67	-	-	-	-	-	-	-	-
Ananteris mauryi	2	20	13	22	4	51	44	18	-	13	14	-	-	-	-	-	-	-	-	-
Ananteris otavianoi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	87	-	-	-	-	-
Tityus brazilae	-	-	-	-	1	2	4	-	-	5	-	-	-	-	-	-	-	-	-	-
Tityus neglectus	-	-	2	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-
Tityus pusillus	112	119	151	245	86	95	2	52	-	154	-	-	30	-	115	-	-	-	-	-
Tityus stigmurus	-	3	-	-	-	-	-	-	-	-	2	7	2	-	3	1	-	-	-	-
Jaguajir rochae	-	-	-	-	-	-	-	130	67	-	21	9	4	22	2	10	23	35	45	45
Jaguajir agamemnom	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Physoctonus debilis	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	11	39	48	2	37

Table 3. Diversity numbers based on species richness (^0D) and the Shannon index (^1D) for Atlantic forest and Caatinga vegetations in Pernambuco state, Brazil.

Vegetation type	Diversity numbers					
	$^0D\gamma$	$^0D\alpha$	$^0D\beta$	$^1D\gamma$	$^1D\alpha$	$^1D\beta$
Atlantic Forest	6	3	2	1.81	1.54	1.17
Hypoxerophytic Caatinga	8	3.66	2.18	4.51	2.72	1.98
Hyperxerophytic Caatinga	8	3.66	2.18	5.78	2.82	2.04

Table 4. Results of the statistical models analysing the influence of bioclimatic variables and geographical distance on scorpion alpha and beta diversities in the Atlantic Forest and Caatinga. Variables with significant effects are shown in bold, with their r^2 values. "+" = positive relation; "–" = negative relation.

Climatic variables	$^0D\alpha$	$^1D\alpha$	$^0D\beta$	$^1D\beta$
Annual mean temperature	**$F_{1,12}$ = 9.637; p = 0.009; r^2 = 0.366 (–)**	$F_{1,12}$ = 0.094; p = 0.764	**$F_{1,12}$ = 7.397; p = 0.018; r^2 = 0.244 (–)**	$F_{1,12}$ = 2.710; p = 0.125
Isothermality	$F_{1,12}$ < 0.001; p = 0.981	$F_{1,12}$ = 1.339; p = 0.269	$F_{1,12}$ = 0.010; p = 0.919	$F_{1,12}$ < 0.001; p = 0.992
Temperature seasonality	$F_{1,12}$ = 0.109; p = 0.746	**$F_{1,12}$ = 7.142; p = 0.020, r^2 = 0.263 (+)**	$F_{1,12}$ = 2.468; p = 0.142	$F_{1,12}$ = 0.239; p = 0.633
Annual precipitation	$F_{1,12}$ = 0.112; p = 0.746	$F_{1,12}$ = 0.239; p = 0.633	$F_{1,12}$ = 2.320; p = 0.153	$F_{1,12}$ = 0.215; p = 0.650
Longitud	$F_{1,12}$ = 0.532; p = 0.479	$F_{1,12}$ = 0.239; p = 0.633	$F_{1,12}$ = 0.256; p = 0.621	$F_{1,12}$ = 0.174; p = 0.683

FIGURES

Fig. 1 Map of Pernambuco state in Brazil (A). Study sites along a longitudinal wet-dry bioclimatic gradient (B). Some of scorpion species found: *Physoctonus debilis* (D), *Jaguajir rochae* (E) and *Tityus brazilae* (F). Circle = Atlantic Forest; triangle = hypoxerophytic Caatinga, and squares = hyperxerophytic Caatinga.

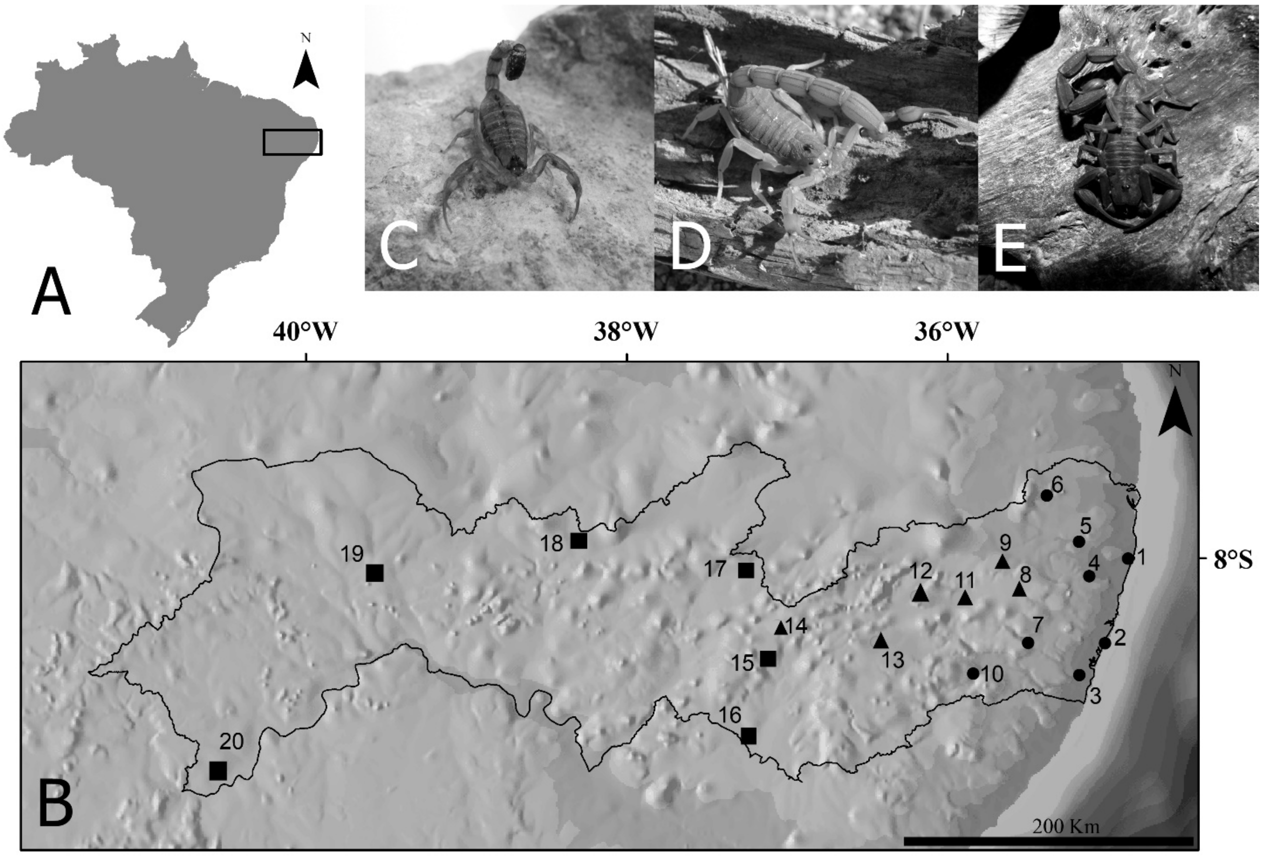


Fig. 2 Vegetation occupied by scorpion species along a longitudinal gradient in Pernambuco state, Brazil. A) Atlantic Forest; B) hypoxerophytic Caatinga; and C) hyperxerophytic Caatinga.

Fig. 3 Similarity of scorpion assemblages from Atlantic forest-Caatinga gradient as a function of distance between sampling sites.

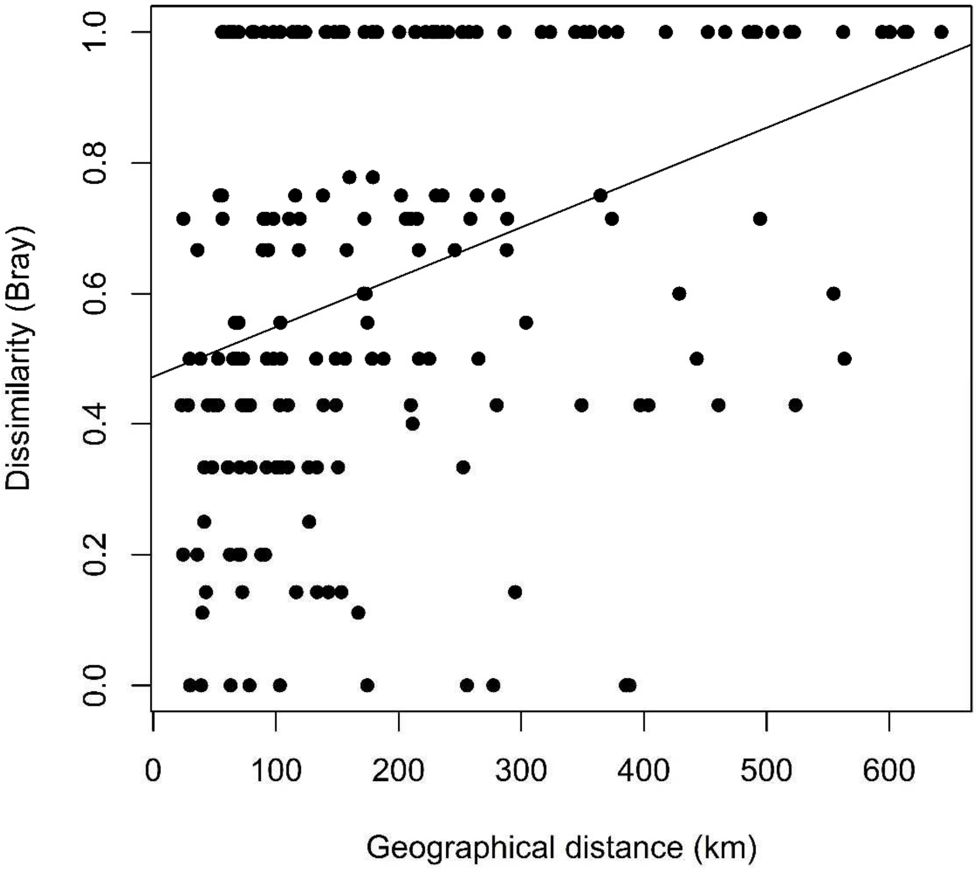


Fig. 4 NMDS ordination of the sampling sites (Atlantic Forest (black circles), hypoxerophytic Caatinga (black triangles), and hyperxerophytic Caatinga (black squares) according to their similarity in scorpion species composition (Simpson index for presence or absence data).

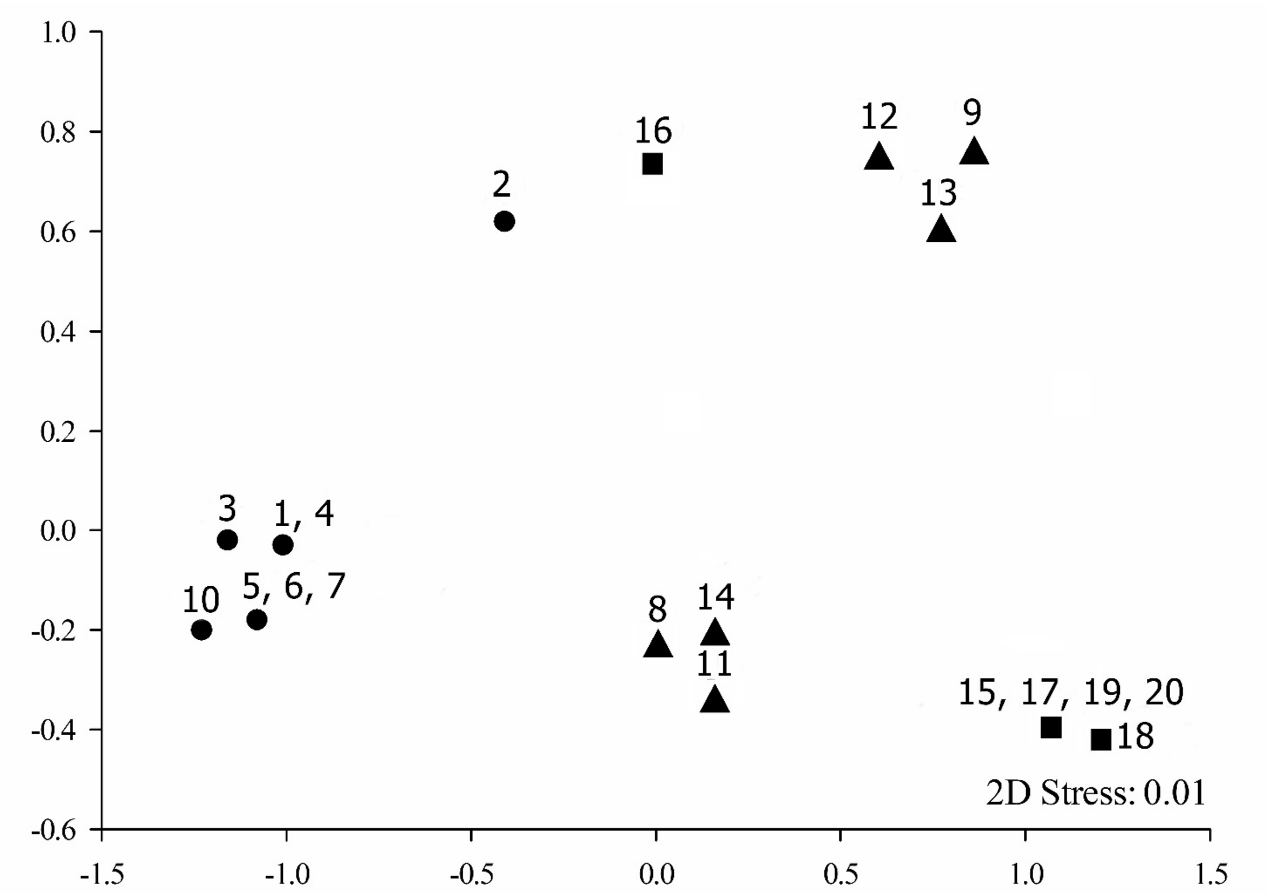
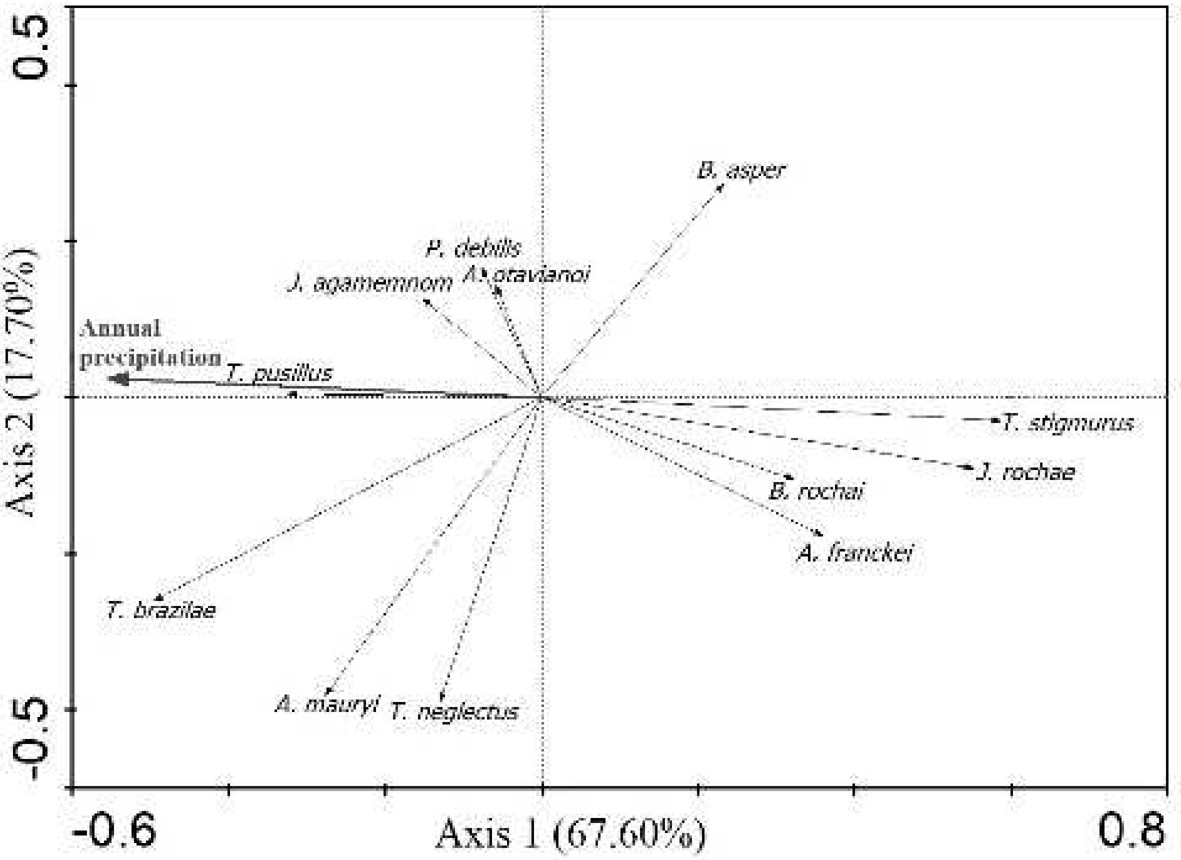


Fig. 5 pRDA ordination diagram of the species composition of the scorpion assemblage in relation to the annual precipitation in Pernambuco state, Brazil.



Appendix S1. Bioclimatic variables in eight Brazilian Atlantic Forest and 12 Caatinga sites in Pernambuco state, Brazil.

Bioclimatic variables	Sampled sites																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
BIO1	25.9	24.8	23.7	24.5	24.8	23.5	23.3	22.6	23.4	20.7	21.7	20.8	22.0	22.0	21.5	20.6	24.7	23.4	24.8	24.8
BIO2	6.4	5.9	6.0	6.8	8.6	9.4	7.5	8.3	9.0	8.3	9.1	9.2	9.3	9.3	9.3	9.3	11.8	10.0	13.1	13.1
BIO3	6.9	6.7	6.7	6.8	7.2	7.1	7.0	7.0	7.0	7.0	7.1	6.9	6.7	6.7	6.7	6.7	7.5	6.8	7.5	7.5
BIO4	10	9.74	9.72	10.89	11.59	13.11	10.92	12.15	12.89	13.01	13.20	14.96	16.75	16.75	16.87	16.15	12.51	15.89	14.49	14.49
BIO5	30.3	28.9	28.0	29.3	30.8	30.4	28.7	28.7	30.0	27.0	28.5	27.9	29.3	29.3	28.7	27.7	32.6	30.8	33.1	33.1
BIO6	21.1	20.2	19.0	19.4	19.0	17.2	18.1	16.9	17.2	15.2	15.7	14.7	15.6	15.6	15.0	14.1	16.9	16.2	15.7	15.7
BIO7	9.2	8.8	9.0	9.9	11.8	13.2	10.6	11.8	12.8	11.8	12.8	13.2	13.8	13.8	13.7	13.6	15.8	14.6	17.4	17.4
BIO8	24.8	23.9	22.8	23.4	23.6	22.0	22.3	21.4	22.2	19.2	21.2	21.2	22.3	22.3	21.7	20.9	25.1	24.4	26.1	26.1
BIO9	26.4	25.1	24.0	24.9	25.3	24.1	23.8	23.1	24.0	21.5	22.4	21.1	22.5	22.5	22.0	21.1	23.5	22.7	23.0	23.0
BIO10	26.9	25.8	24.7	25.6	26.0	24.9	24.4	23.8	24.6	22.0	23.1	22.3	23.6	23.6	23.1	22.1	26.2	25.0	26.1	26.1
BIO11	24.4	23.4	22.3	22.9	23.1	21.5	21.7	20.8	21.4	18.7	19.7	18.6	19.4	19.4	18.9	18.1	22.9	21.0	22.6	22.6
BIO12	1734	2051	1935	1287	1222	1163	1827	774	784	1096	571	614	657	657	759	915	634	742	422	422
BIO13	288	320	299	201	205	190	312	119	131	187	84	97	107	107	121	137	155	180	108	108
BIO14	32	47	43	28	21	26	38	15	12	25	9	11	16	16	17	19	4	5	2	2
BIO15	67	56	58	58	62	58	60	60	65	59	60	59	57	57	54	54	89	89	93	93
BIO16	822	901	875	578	572	505	844	332	359	501	240	264	287	287	325	379	359	438	231	231
BIO17	115	169	158	104	89	92	147	61	51	89	39	44	52	52	62	71	18	25	8	8
BIO18	345	428	390	272	269	251	355	189	181	206	149	183	209	209	172	187	195	170	191	191
BIO19	686	802	556	504	481	449	743	280	300	451	204	193	180	180	200	278	25	60	12	12

Esse capítulo segue as normas para publicação da Zoology

2.2 MODELING PATTERNS AND DISTRIBUTION OF SCORPIONS IN FUTURE CLIMATE CHANGE SCENARIOS IN THE BRAZILIAN NORTHEASTERN REGION

André Felipe de Araujo Lira[1]*, Raúl Badillo-Montaño[2], Andrés Lira-Noriega[2] and Cleide Maria Ribeiro de Albuquerque[1]

[1]Programa de Pós-Graduação em Biologia Animal, Departamento de Zoologia, Universidade Federal de Pernambuco – UFPE, Rua Prof. Moraes Rego S/N, Cidade Universitária, Recife, Pernambuco CEP 50670-420, Brazil.

[2]Red de Estudios Moleculares Avanzados, Instituto de Ecología A.C. Carretera Antigua a Coatepec 351, El Haya, Xalapa, Veracruz, CP 91070, México.

*Corresponding autor: andref.lira@gmail.com

Highlights

- Climate change may promote a break in the distribuition patterns of species
- Species habitat specialists responded differently to future models taking into account the climate change

Abstract

Current predictions about species’ responses to climate change strongly rely on projecting altered environmental conditions on their distributions, which level of vulnerability varies due to differences in species' sensitivity and adaptive capacity. In this context, we investigated the effect of climate change on the potential distribution of eight species of scorpions in northeastern Brazil. Firstly, species were classified as habitat specialists or generalists according to IndVal. After this, present and future species distribution models were performed through the smaller volume ellipsoids. According to IndVal, four species were classified as closed forest specialist (*Ananteris mauryi*, *Tityus brazilae*, *Tityus pusillus* and *Tityus neglectus*), four as open forest specialists (*Jaguajir agamemnom*, *Jaguajir rochae*, *Physoctonus debilis* and *Bothriurus rochai*) and two as generalists (*Tityus stigmurus* and *Bothriurus asper*). The potential future distribution was inddependent on the type of habitat with both closed and open forest-specialists presenting a reduction. Generalist species also showed an contraction in their potential future distribution area. Climate change is predicted to lead to changes in community composition through variation in the rates that species' ranges shift; our results suggest communities could change further owing to constituent species shifting along different trajectories.

Key words: desertification; bioindicators; distribution shifts; arthropods; global warming

Introduction

Climate changes have been unequivocally documented with projected impacts on all global ecosystems (IPCC, 2013). Animals and plants may respond to changing climates by shifting their distributions, adapting to new environments or acclimating through phenotypic plasticity (Walther et al., 2002; Hoffmann and Sgrò, 2011; Munday et al., 2013; Mulhouse et al., 2017). However, the magnitude of such responses depend on the individual's physiological tolerance and dispersion capacity in modified landscapes (Hawkins et al., 2003; Kearney and Porter, 2009; Vasconcelos et al., 2010).

Together with habitat loss, climate change represents a major threat to the integrity of ecosystems, and organisms, particularly those inhabiting most vulnerable ecosystems, such as arid, semi-arid, subhumid regions and biodiversity hotspot areas (Maestre et al., 2012; Vicente-Serrano et al., 2012; Bellard et al., 2014). In a warmer climate, due to enhanced evapotranspiration and reduced precipitation, drought-prone regions may undergo lengthier and more severe droughts (Dai, 2013). Thus, semi-arid and arid regions are more prone to drying as a result of global warming, leading to an intensification of the rainfall cycle, with wet regions becoming wetter and dry regions becoming drier (Chou et al., 2009; Held and Soden, 2006; Seager et al., 2010). For example, Rodrigues et al. (2015) modeling the species distribution for tree specialists in a future pessimist scenarios of climate change in the Caatinga (seasonally dry tropical forests - STDF), suggest that areas currently occupied by rainforest and savannas could become more suitable for occurrence of the SDTF specialist trees. These authors suggest that regions occupied by SDTF could not support the future level of unsustainable (e.g., aridity).

Different ecosystems may respond in potentially similar way to climate change; wet regions such as rainforests are also subject to potentially large losses of forest biomass in modeling scenarios of increased drying and warming (Cox et al., 2000; Cox et al., 2004; Betts et al., 2004; Lyra et al., 2016). Among these rainforests, the Atlantic Forest, one of five biodiversity hotspots of the world, with highly heterogeneous relief conditions that led to outstanding levels of endemism and species richness, presents a high level of threat caused by global warming (Ribeiro et al., 2011; Béllard et al., 2014). In this ecoregion, climate change is likely to acts acts in synergy with land use (e. g. fragmentation and deforestation), which may result in a warmer and drier climate in a process called as '*savannization*' with closed rainforest being converted to areas of open vegetation (Scarano and Ceotto, 2015).

Shifts in the distribution of numerous species have been attributed to global climate changes over the last decades (e.g. Thomas and Lennon, 1999; Parmesan and Yohe 2003; Konvicka et al., 2009), along with the prediction of 18-35% species extinction by 2050 worldwide (Thomas and Lennon, 1999). Ectothermic organisms are especially prone to be affected by global warming as a result of their particular ecological requirements such as thermal tolerance (Gibbons et al., 2000; Paaijmans et al., 2013). Among these, many invertebrate are especially sensitive to climatic conditions, and parameters such as temperature, rainfall, relative humidity and soil moisture have all proved useful for predicting important events in their populations such as population decreases (e.g. Klapwijk et al., 2012; Chen et al., 2014; Macfadyen et al., 2018). The impact of global warming on invertebrates, specially arthropods, are still poorly understood (Kiritani, 2006; Johnson and Jones, 2016), with a small margin of this groups being evaluated (e.g. Saupe et al., 2011; Moo-Llanes et al., 2013; Estrada-Peña et al., 2016; Ferreira et al., 2016; Gálvez et al., 2017). This lack of research investment is surprising given the fact that arthropods are the most diverse and abundant extant metazoans (Stork, 1988; Giller, 1996). Noticeably in tropical environments, they contribute to several important ecosystem services, such as the maintenance of soil structure, regulation of water resources, nutrient cycling, and decomposition of litter (reviewed in Laurance et al., 2002). For the large majority of arthropods, the range of distribution in response to climate change is yet to be completelly assessed, with large uncertainties in their spatial variation in a future scenarios projection (Moritz and Agudo, 2013).

Arthropod species with low mobility have been considered highly susceptible to environmental pertubation, while highly mobile species show the highest survival rate (Murphy et al. 1990; Stockman et al. 2006; Bowden et al. 2014). In addition, habitat specialist are also considered more suscetible to changes in their habitat than generalist (Dapporto and Dennis 2013; Trivellini et al. 2016). Among arthropods, scorpions tipically possess a small dispersion rate and very specific habitat requirements (Polis, 1990; Lira et al., 2018). For example, scorpions possess associations with many physical and biological factors (e.g. Nime et al. 2014; Lira et al. 2016; Dionisio-da-Silva et al. 2018; Lira et al. 2018), including precipitation, soil type, temperature, light levels, microhabitat availability, vegetation type and distribution (Prendini 2001; Druce et al. 2007; Foord et al. 2015; Lira et al. 2016; Lira et al. 2018). Thus, possibly make these animals strong candidates to be adversely affected by global warming and ecossystem changes.

The impact of human-mediated global warming on wildlife and future potential distribution of species can be measured using species distribution modeling (SDM) tools (Iverson et al., 1999; Dormann et al.; 2007; Lee et al., 2012). SDM tools became an increasingly popular methodology to study species' potential distributions in recent years and, as a result, several applications have been developed to facilitate generation of such models and distributions (e.g. Peterson et al. 2011; Garcia et al. 2014; Pecl et al. 2017; Guevara et al. 2018). Thus, in the present study we aimed to identify patterns and relationships between scorpion distributions in differents ecosystems in a Brazil (rainforests, savannas and tropical dry forests), modelling how these patterns may change in future climatic conditions at local and regional scales. To do so, we first determine species habitat specialization across a regional gradient spanning three biomes – Atlantic forest, Caatinga and Cerrado – and then we assess whether species predictably shift their habitat distribution in response to future climatic changes. We expect a decline in habitat specialist-species in their future potential distribution, while a non-change for habitat-generalists.

Methodology

Study region

The Brazilian northeastern region from 38°31' W long and 12°58' lat comprises four ecosystems: Atlantic forest a long the coast; following by Caatinga and Cerrado inland, with small portion in north dominated by Amazon forest. This region possess an area of 1,554,292 km², corresponding to 18% of the country total area. Annual mean temperatures along the region range from 20 °C to 28 °C, with precipitation ranging from over 2000 mm to 300 mm per year from the coastal zone to the interior of the continent (Hijmans et al., 2005). Elevation varies from sea level on the coast to mountains over 1,000 m within the interior. This ecosystem is composed by evergreen and semi-deciduous fragments usually embedded in a matrix of sugarcane monoculture (Veloso et al., 1991; Tabarelli et al., 2010), largely dominated by Lauraceae, Sapotaceae, Moraceae, and Fabaceae tree species (Grillo et al., 2005). Nevertheless, the Atlantic forest is a global biodiversity hotspot (Myers et al., 2000). The second, the Caatinga, is a mosaic of a seasonal tropical dry forests and thorn scrub vegetation (Pennington et al., 2009) that occupies an area of about 72.24% of Northeastern region. This ecosystem shows a unsustainable exploitation of native wood and conversion of the vegetation to pastures and plantations (Leal et al., 2005; Brasil, 2014; Ribeiro et al., 2016; Ribeiro-Neto et al., 2016). In addition to acute and chronic anthropogenic pressures, the northeastern region of the Caatinga is under increased risk of desertification caused by global temperature rises. Among Brazilian ecosystems, the Caatinga is one of the most vulnerable to this rapidly growing threat (Oyama et al., 2003; Lima et al., 2011). Other ecosystems, such as the Cerrado (*Brazilian Savannah*) and the Amazon rainforest also compreend a small portion of the Northeastern region (Castro and Martins, 1999; Castro et al., 2007; Muniz, 2008). These two ecosystems have been also highly affected by anthropogenic activities, with their original areas reduced to small forest fragments isolated in a matrix of plantations, cattle ranches or urban areas (Skole and Tucker, 1993; Brannstrom and Filippi, 2008).

Species habitat specialization

We used species ocurrence data obtained from Global Biodiversity Information Facility (www.gbif.org), Brazilian diversity database (www.splink.org.br), scientific collections (Universidade Federal de Pernambuco-UFPE, Universidade Federal da Paraíba-UFPB, Universidade Federal da Bahia-UFBA) and scientific literature on each of the species. All occurrences were inspected carefully to detect and correct problems associated with taxonomic misidentification, duplication, and geographically discordant localities (Chapman, 2005).

Scorpions were classified as specialists or generalists, using IndVal index based on the ocurrence scorpions in each forest type: closed forested area - Atlantic forest or Amazon forest and open forested area – Caatinga or Cerrado. The IndVal was used because it provides a good measure of species specialization once it determines the association between the target species and each site group in the partition (De Cáceres et al., 2010). IndVal was compared with randomized values obtained by 999 Monte Carlo permutations to test the null hypothesis in that there is no relationship between the species and the habitat (De Cáceres and Legendre, 2009). Species that had a significant association with some forest type were classified specialists when the IndVal analysis results in a non-significant association of a species with any ecosystem or both categories, the species was considered a generalist. IndVal analysis were performed using the "multipatt" function in the indicspecies package (De Cáceres, 2013) using R v. 3.4.3 (R Core Team, 2017).

Ecological niche models

Previous to modeling species potential distribution we used a distance filter of 20 km using the "Clean_dup" function of the ntbox package (Osorio-Oliveira et al., 2016) in R (R Core Team, 2017) to reduce problems of spatial autocorrelation and overfitting of the model (Boria et al., 2014). In order to assess whether scorpion species would shift their habitat distribution in response to future climatic changes together with the occurrence points we used 19 current and future bioclimatic layers from the WorldClim database at a 2.5 minutes spatial resolution (Hijmans et al., 2005) These layers contain worldwide annual mean temperature, mean diurnal range, isothermality, maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation, precipitation seasonality, precipitation of the driest quarter (Hijmans et al., 2005). We identified the total amount of range contraction and expansion for each species by calculating the difference between their current modeled and future distribution.

For the future modeling, we used the same variables to forecast future potential distribution, and projected for the year 2050 by the climate models CCSM4, CNRM-CM5,HadGEM2-ES, INMCM4, IPSL-CM5A-LR, MIROC-ESM-CHEM (downloaded at www.worldclim.org), we selected these scenarios since according to Faleiro et al. (2018), these scenarios of climate change have at least 25% of dissimilarity, which allows the heterogeneity of the different climate projections for 2050 to be covered. We also used the Representative Concentration Pathways (RCP) 4.5 and 8.5, which specifies a probable increase in the global average surface temperature towards the end 21st century from 2.6 to 4.8 °C (IPCC, 2014). In this way, the models will represent the impact of climate change on scorpion species in a wide range of future climate projections (Faleiro et al., 2018). Because bioclimatic variables are strongly correlated with each other, we used principal components analysis (PCA) transformation of the 19 layers to reduce dimensionality and collinearity among them, and we used the same component loadings from the PCA in the present to transform the future climate model prediction. PCA analysis was carried out using the "PCAprojection" function in ntbox packages (Osorio-Olvera et al., 2016) in R (R Core Team, 2017).

Present and future SDMs wereas performed through the Minimum Volume Ellipsoids (MVEs) (Osorio-Olvera et al., 2016). This method calculates a suitability envelope for the species based on Mahalanobis distances from the species' observed occurrences, where the envelope represents the physiological limits of tolerance and itsthe centroid represents the set of optimal conditions for the species of the fundamental niche species from the values of the environmental variables in the observation points species, and considers that the centroids are the optimal conditions for the development of the species. Suitability values at the centroid equal where the suitability of the environment will be equal to 1 and least environments suitability sites approximatemore distant from the centroid will have suitability values equal to 0 (Farber and Kamon, 2003; Osorio-Olvera et al., 2016). For calibrating the MVESDMs we used the three first principal components axes of the environmental, which data because these explained ≥85% of the overall variance. We calibrated the MVEs with an allowed omission error thresholds of E = 5% and implemented this method with the function "ellipsoidfit" in ntbox package (Osorio-Olvera et al., 2016) in R (R Core Team, 2017).

All models obtained were evaluated using a one-tailed cumulative binomial test to calculate the probability of obtaining that sensitivity level by chance alone. We performed this test with independent points to the calibration model, which were between 9 and 54 points (Lira-Noriega and Peterson, 2014). The binary prediction of *Physoctonus debilis* and *Jaguajir agamemnom* (species with 13 and 21 occurrences, respectively) were evaluated using a jack-knifing approach (Pearson et al., 2007), which requires that a model be executed for each subset of n - 1 occurrences and the performance of the model to be tested on the deleted coordinate; these probabilities were calculated using pValueCompute (Pearson et al., 2007). The final models were considered to represent in the geography the main areas where scorpion's species could find the most suitable climate conditions now and in the near future. For these models, we obtained a consensus forecast with the median projected range shift for each species across all 6 models projections (Araújo et al., 2005). Finally, based on the climatic suitability values obtained from the SDMs, we established a threshold of 10% to generate binary maps, a value of zero was assigned when the potential distribution of the species was low and one when it was above the suitability threshold. To asses the impact of the climate change, we calculated the percentage of change between current and future total area, the calculus of these metrics is the difference between the total sum of the predicted area in the binary maps for the future and the current period divided by the area predicted in the current period. Subsequently, a geographical overlap of the binary maps was made to show where the ten scorpion species could coincide, thus defining areas with greater current and future potential richness.

Results

Species habitat specialization

In total 542 species occurrences belonging ten species were used in our analyses which present frequency of occurrence are shown in Table 1. According to IndVal value, eight species were classified as habitat specialists (four for the closed forested area and four for the open forested area) and and two species were considered as habitat generalist (Table 1). The strength of species–habitat association measured by the IndVal value ranging 39 to 99% for closed forested species and 32 to 91% for open forested species (Table 1) According our criteria, two species were considered as generalist, *Tityus stigmurus* was associated with Atlantic forest and Caatinga (IndVal = 0.60; p = 0.0004) and Bothriurus asper exhibited no association with any forest type (p> 0.05).

Ecological species distribution model

We used 395 spatial occurrences of ten scorpion species. Most data were from *Bothriurus asper*, *Tityus stigmurus* and *Jaguajir rochae*, and species with low data were *Ananteris mauryi, Physoctonus debilis* and *Jaguajir agamemnom* (Table S1). Our evaluations of the potential distribution models were significantly better than random expectations ($P < 0.001$).

Regarding changes in geographic distributions of Northeastern Brazilian scorpion species, we observed that future distribution predictions varying according to habitat specialization. Overall, species classified as open forest specialists (Table 1) exhibited a retraction in their future potential distribution of 49±20.29% with *P. debilis* and *J. agamemnom* being more affected presents a retraction in area towards to eastern portion in their future potential distribution with 57.33% and 72.25% more regarding to the current model respectively (Table 2; Fig 1). These two especies exhibits a shift in their distribution with only two small areas being more suitable (Fig. 1). Others two open forest specialists, *B. rochai* and *J. rochae* also exhibits a contraction in their future potencial distribution towards to eastern portion of Brazilian northeastern region (Table 1, Fig. 1).

Closed forest forest specialists were strong negatively affected with reduction of 64.39±4.69%, with *T. brazilae*, *A. mauryi*, *T. pusillus* and *T. neglectus* decreases in 67.58%, 67.26%, 65.21% and 57.54% their potential distribution by 2050, respectively (Table 2), exhibiting a shift in their future suitables areas (Fig. 1). Two major future suitables areas closed forest specialists correspond more eastern portion and a south portion to coastal zone of Atlantic forest (Fig. 1). Scorpion classified as habitat generalist also showed an decreases in their potential distribution of 54.58% and 45.84% for *B. asper* and *T. stigmurus*, respectively (Table 2). The future potential decrease of occurrence areas, *T. stigmurus* showed a pattern with the suitable scattered areas corresponding to eastern portion of Caatinga and Atlantic forest (Fig. 1). Similarly, *B. asper*, the most suitable future potential areas were modified to the east direction (Fig. 1).

Potential areas with higher diversity (6 or more species) showed an contraction in their extension in the future model when compared to the present (Fig. 2). Suitable areas were from coastal to the eastern portion of the northeastern region, corresponding to ecotonal zone where Caatinga that is near the Atlantic forest (Fig. 2).

Discussion

Our approach addresses the impact of climate change on the future potential distribution of scorpion species in closed (Atlantic and Amazon Forest) and open (Caatinga and Cerrado) forests in northeastern region, Brazil. Future potential species distribution was found to be a function of scorpion habitat specialization with species from open environment a less reduction in their range distribution, contrasting with species from cloesd environments from the Atlantic forest which are predicted to undergo a descrease in their distribution areas. Our data are in agreement with previous studies showing a negative effect of climate change, reducing suitable areas for many Atlantic forest organisms, such as, birds, amphibians and trees (Haddad et al., 2008; Colombo and Joly, 2010; Souza et al., 2011; Lemes et al., 2013). The Atlantic Forest is classified as one of the three biodiversity hotspots most vulnerable to climate change (Béllard et al., 2014) due to the imminent threats of climate change and land use that this biome has been suffering since the beginning of European colonization (Tabarelli et al., 2010; Souza et al., 2011; Béllard et al., 2014). Future scenarios pointed out that the northeastern portion of Atlantic Forest should hold high annual mean temperatures, and biome boundaries should undergo dramatic changes in precipitation patterns towards treeless areas (Lemes et al., 2013; Anadón et al., 2014). Forested areas will be displaced to the coastal zone (Anadón et al., 2014) and suffering a structural reorganization and woody plants homogenization (Zwiener et al. 2017). In addition, the availability of new climatically favorable areas under climate change outside of the current limits of the Atlantic Forest will not translate into new areas for colonization when it comes to forest dwellers (Souza et al., 2011). Forested areas are important in diverse ways for the studied scorpion species. *Ananteris mauryi* is a small species (20-25 mm) considered as humicolous because it depends on places with high humidity, such as the lower layers of the litter to establish their populations (Lourenço, 1982; Lira et al., 2013). In addition, *T. pusillus* is a scorpion that despite being found in Caatinga vegetation is sensitive to environmental changes, such as those caused by habitat fragmentation (Lira et al., 2015; Dionisio-da-Silva et al., 2018). In a similar way, *T. brazilae* a corticulous scorpion exhibits an intimate relation with bark of trees that this species uses as refuge (Bertani et al., 2008; Lira et al., 2018). Therefore, future changes in current scenario are potentially negative for these animals with a lower dispersion capacity and specific habitats requirements such as Atlantic Forest.

Similar to the closed forest specialists, all of open forest specialist scorpions showed decreases in their potential distributional areas in the northeastern region. Future predictions, indicate that due to climate change there will be an increase in the arid and semi-arid regions of the world (Huang et al., 2016), such as the Caatinga (e.g. Salazar et al., 2007; Anadón et al., 2014). Despite the expansion in the area dominated by the Caatinga vegetation, the global warming will also lead to increase in aridity in the region, (Nascimento, 2015; Torres et al., 2018). In this scenario, it is predicted a deserfitication of about 94% of the Caatinga area (Vieira et al., 2015; Costa et al., 2016; Salvatierra et al., 2017). Despite, *Jaguajir* and *Physoctonus* species are considered as typicall elements of open vegetation areas (e.g. Cerrado and Caatinga) (Lourenço and Pinto da Rocha, 1997; Esposito et al., 2017) and *Bothiurus* species exhibit a great ecological plasticity occurring from humid forests (e.g. Atlantic forest) to grasslands (e.g. Pampas) (Lourenço, 2002), the most suitable areas for these species showed to be located in eastern portions, next to coastal zone and to higher elevations. Such observation suggest that scorpions might migrate towards a coastal zone and higher elevations to compensate for a warmer climate. These shifts of habitat from low to higher altitudes have been recorded in many organisms and it is often strongly linked to recent global temperature increase (Parmesan and Yohe, 2003; Chen et al., 2011; Gottfried et al., 2012; Lenoir and Svenning, 2014; Pauchard et al., 2016).

Althought the two scorpions species classified as generalists in our analyses exhibit a retraction in their future potential distribution, they present a differential response to the the future scenario of climate change. *Bothriurus asper* is a fossorial scorpion widely distributed over the northeastern Brazil and can be found from opened savana to forested areas (Santos-da-Silva et al., 2017; Lira et al., 2018). In their future potential distribuition *B. asper* acts similarly to open forest specialists with most of their suitable areas being found in a eastern sites. In contrast, *T. stigmurus* acts like as closed forest specialists, with their potential areas modified towards the coastal zone. This species is widespread in northeastern Brazil, can be found in natural environments (Caatinga and Atlantic forest) but is mainly found in urban environment and can be considered a sinantropic species (Souza et al., 2009; Brazil, 2009). This future scenario is potentially dangerous, since this species is the main causative agent of human scorpionism in northeastern Brazil, including death (Albuquerque et al., 2013; Pucca et al. 2014). The high population density in costal cities potentially favor an increase in the incidence of scorpion acidents.

Our study shows a potential for major range retraction of potential areas with higher scorpion richness (6 or more) in a RCP scenarios. However, although the climate is adequate to maintain a large number of species, in particular for scorpions, the habitat structure (availability of microhabitats) plays a key role in maintaining species in a given area (Smith, 1995; Druce et al., 2007; Lira et al., 2018). Although, in the present study deforestation was not assessed and the analyses assumed that the entire suitable area for a species corresponds to its geographic distribution. However, in northeastern all the biomes have been suffering an intense devastation over the years. For example, more than 80% of the Atlantic Forest has been lost and most remnant forest is within small and isolated fragments (Ribeiro et al., 2009). Similarly, the Caatinga currently suffers from a chronic disturbance, resulting in the impoverishment of biodiversity (Rito et al., 2017; Arnan et al. 2018). Even if we assume no further deforestation, our results for species' distribution sizes would be grossly overestimated because large portions of the predicted distributions will not have suitable habitats for the species. By overestimating the distribution size, we reduced the chance that a species would reach the threshold distribution size for threat. Therefore we present the general patterns for species habitat-specialists and generalists in a Neotropical region. Although the response has been similarly among specialist habitats, depending on the type of environment in which they inhabit (rainforest or seasonally dry forest). We corroborate with our initial hypothesis that climate change will act negatively on future potential distribution in habitat-specialists, and this effect will be greater on closed forest species. Open forest scorpions in spite of the potential distribution reduction will be reallocated to regions of high altitudes and more close to coastal zone, a probable means to escape the desertification of the Caatinga. Studies about the possible impacts of climate change on Neotropical biodiversity are scarce (Vale et al., 2009; Souza et al., 2011) and, despite its limitations, distribution modeling represents one of the best available predicting tools, especially in tropical countries where empirical data from long term monitoring programs are scarce. Other studies are needed, with different taxa, to draw a more complete picture of the possible impacts of climate change on the distribution and threat status of Neotropical species.

Acknowledgments

We are grateful to Coordenaçãoo de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for granting a PhD scholarship to A.F.A. Lira and to Consejo Nacional de Ciencias y Tecnología (CONACYT) for the PhD scholarship to R. Badillo-Montaño. We also grateful to Fundação de Amparo a Ciência e Tecnologia de Pernambuco (FACEPE) for a financial support (APQ-0437-2.04/15) and to Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for a financial support (Fellowship #307759/2015-6 for research productivity) for C.M.R. Albuquerque. We also thanks to the curators Dra. Tânia K. Brazil (MZUFBA-UFBA) and Dr. Márcio B. daSilva (CA-UFPB) for kindly giving in data from their collections

Table 1. Vegetation of occurrence and habitat classification for scorpion species from Brazilian northeastern region.

Species	Vegetation of occurrence	IndVal value	*p* value	Habitat classification
Ananteris mauryi	Atlantic forest and Caatinga	0.992	0.0002	Closed forest specialist
Bothriurus asper	Atlantic forest, Caatinga and Cerrado	-	> 0.05	Generalist
Bothriurus rochai	Caatinga and Cerrado	0.474	0.0012	Open forest specialist
Jaguajir rochae	Caatinga and Cerrado	0.916	0.0002	Open forest specialist
Jaguajir agamemnon	Caatinga and Cerrado	0.608	0.0004	Open forest specialist
Physoctonus debilis	Caatinga and Cerrado	0.320	0.0082	Open forest specialist
Tityus brazilae	Atlantic forest	0.612	0.0004	Closed forest specialist
Tityus pusillus	Atlantic forest and Caatinga	0.964	0.0002	Closed forest specialist
Tityus neglectus	Atlantic forest and Caatinga	0.391	0.0098	Closed forest specialist
Tityus stigmurus	Atlantic forest, Caatinga and Cerrado	0.608	0.0004	Generalist

Table 2. Current (and future potential area distribution (in km²) predicted for Northeast scorpions of Brazil and exchange rate for each species. This area were calculated with de predictions of EDM converted to binary.

Species	Habitat specialization	Current area (1961-2000)	Future area (2045-2069)	Change area (%)
Ananteris mauryi	Closed forest	75,595.67	24,510.52	-67.58
Bothriurus asper	Generalist	1,263,577	573,880.4	-54.58
Bothriurus rochai	Open forest	448,893.7	335,590.6	-25.24
Jaguajir agamemnom	Open forest	438,618.6	121,723.9	-72.25
Jaguajir rochae	Open forest	631,595	371,505.9	-41.18
Physoctonus debilis	Open forest	157,038.5	67,015.91	-57.33
Tityus brazilae	Closed forest	173,941.8	5,6952.73	-67.26
Tityus neglectus	Closed forest	196,458.1	83,415	-57.54
Tityus pusillus	Closed forest	114,434.8	39,806.66	-65.21
Tityus stigmurus	Generalist	542,992.9	294,073.6	-45.84

Figure 1. Consensus map of potential geographic distribution for closed forest specialist (A-D), habitat generalist (E and J) and open forest specialist (F-I) in northeast of Brazil between current (1961-2000) and future (2045-2069) scenarios for six climate models and two RCPs. Potential presence is represented in blue, absence in yellow, biome delimitation in black line.

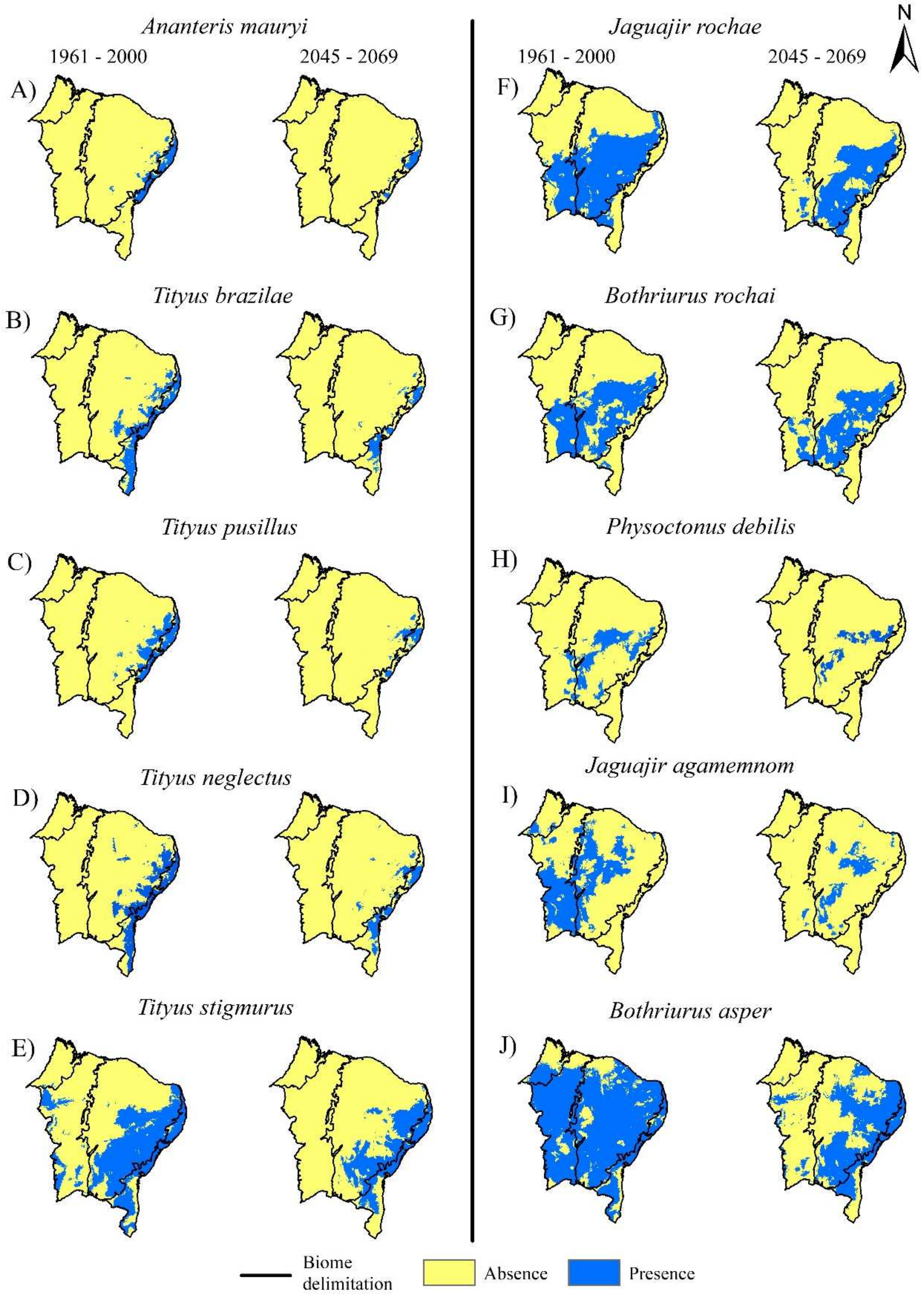
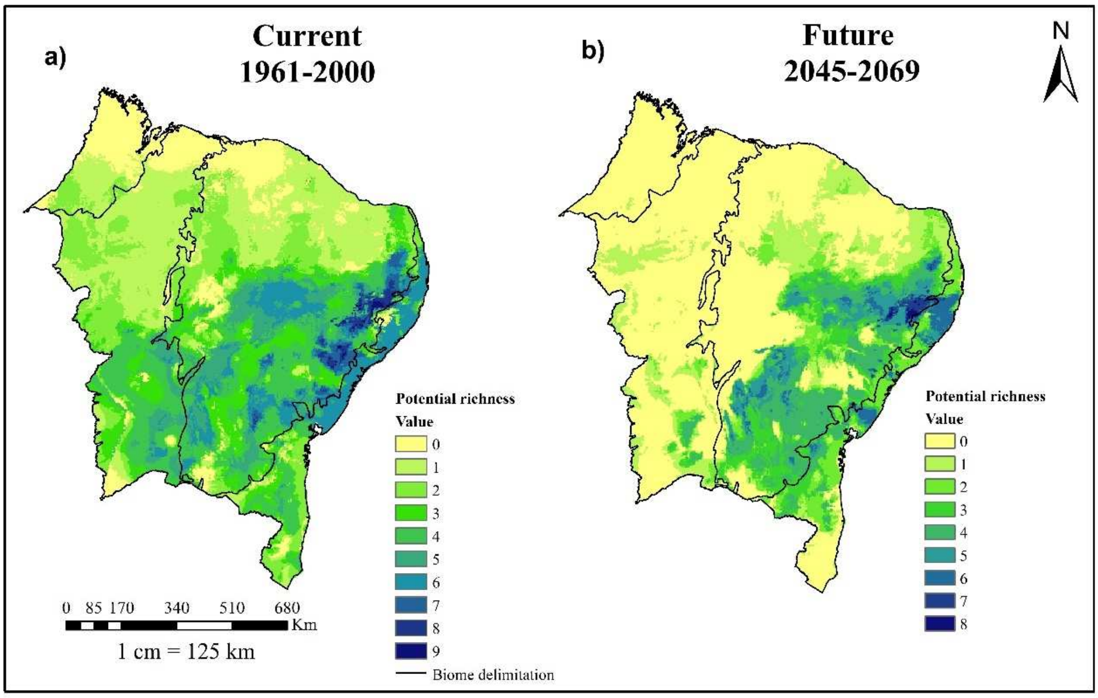


Figure 2. Consensus map of current (1961-2000) and future (2045-2069) potential scorpion species richness in the northeast of Brazil derived from six scenarios climate models and two RCPs. This metric were calculated with de predictions of EDM converted to binary.



3 CONCLUSÕES

A escorpiofauna do estado de Pernambuco constitui-se até o presente como uma das mais ricas dentre as unidades federativas brasileiras, totalizando 12 espécies registradas, seis das quais exclusivas à ecoregião da Caatinga, quatro à Floresta Atlântica e quatro compartilhadas pelas duas. Apesar da elevada riqueza taxonômica, a Caatinga apresentou uma baixa riqueza funcional quando comparada à Floresta Atlântica, sendo caracterizada particularmente por espécies fossoriais e epigéicas. A composição da assembleia de escorpiões foi responsiva ao gradiente bioclimático encontrado entre a Floresta Atlântica e a Caatinga, ocorrendo um aumento na diversidade beta em direção ao sentido de temperatura mais elevada do gradiente. Também foram detectados efeitos estacionais sobre a abundância e uso de microhabitat, principalmente nas espécies de Floresta Atlântica, cujas atividades de forrageio aumentam na estação seca. Ao contrário, na Caatinga, esse padrão variou de acordo com a espécie. Atráves de modelagens foi possível detectar áreas prioritárias para conservação em um cenário de mudanças climáticas. Os escorpiões de vegetação fechada apresentaram uma diminuição nas suas areas potenciais em conjunto com alterações em suas distribuições. Similarmente, as espécies de vegetação aberta apresentaram um decréscimo em áreas potenciais de ocupação, priorizando áreas próximas a costa, indicando a importância destes locais para a manutenção da escorpiofauna. Não foram encontradas espécies com potencial para predizer a intensidade de desertificação do ambiente.

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APÊNDICE A – ARTIGO PUBLICADO NA CANADIAN JOURNAL OF ZOOLOGY

Environmental variation and seasonal changes as determinants of the spatial distribution of scorpion (Arachnida: Scorpiones) in Neotropical forests

A.F.A. Lira[1]*, A.M. DeSouza[2], C.M.R. Albuquerque[3]

[1]Programa de Pós-Graduação em Biologia Animal, Departamento de Zoologia, Universidade Federal de Pernambuco, Recife, PE, CEP 50670- 420, Brazil.

[2]Programa de Pós-Graduação em Ciências Biológicas, Departamento de Sistemática e Ecologia, Centro de Ciências Exatas e da Natureza, Universidade Federal da Paraíba, João Pessoa, PB, CEP 58051-090, Brazil.

[3]Departamento de Zoologia, Universidade Federal de Pernambuco, UFPE, Rua Prof. Moraes Rego S/N, Cidade Universitária, Recife, Pernambuco, CEP 50670-420, Recife, PE, Brazil.

*Author for correspondence: andref.lira@gmail.com

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A.F.A. Lira, A.M. DeSouza, C.M.R. Albuquerque

Abstract

Habitat selection and seasonal changes are key drivers of the population dynamics of many species. We analyzed how the environmental structure influences species establishment in an area by comparing microhabitat preference and functional richness of scorpions (Arachnida: Scorpiones) in wet (Atlantic forest) and semiarid (Caatinga) areas. Variations in superficial foraging activity and microhabitat colonization during dry and rainy seasons were evaluated as an indication of the climatic impact on population dynamics. We collected twelve scorpion species using ultraviolet light lamps. We found that differential patterns in spatial distribution were independent of forest type, and we provide evidence for partial niche partitioning among scorpion species based on age class and climatic conditions. Foraging activity was also seasonally influenced. Functional richness was higher in wet forests than in dry forests, whereas taxonomical richness exhibited an opposite pattern. We conclude that spatio-temporal resource partitioning and refuge sharing are important drivers of the population dynamics and spatial distribution of scorpion species in Neotropical forests.

Keywords: Assemblage structure, Atlantic forest, Caatinga, coexistence, habitat distribution, scorpion, Scorpiones

Introduction

High levels of invertebrate diversity and abundance are commonly observed in tropical rainforests, largely dependent on the spatial distribution of species, and they reflect the importance of suitable habitat selection that facilitates survival of species which is a key factor for understanding the population dynamics of an organism (Gagnon et al. 2011; Schowalter 2012; Delarue et al. 2015). However, the complexity associated with habitat selection makes understanding this process quite difficult. Habitat use depends on the relationship between a given species and its ecological attributes, such as abiotic tolerance, dispersal capacity, and biotic interactions, which vary in time and space (Wisz et al. 2013). Moreover, such attributes are closely associated with different life history traits that determine population dynamics, such as survival, fecundity, and age (Clutton-Brock and Sheldon 2010).

Habitat selection is crucial for survival mainly due to intra- and interspecific interactions in generalist predators with low dispersion rates such as scorpions (Polis 1990; Uetz 1991; Chen and Wise 1999; Lira et al. 2013; Nime et al. 2016). Structurally diverse sites provide a broad range of microhabitats that support a large amount of prey and reduce encounters with potential predators (Schmitz and Suttle 2001; Gunther et al. 2014; Lira et al. 2015). However, such sites may also provide shelter, supporting structures, and perches for predators, thereby benefiting predators (Klecka and Boukal 2014). The complexity involved in habitat selection results in non-random distribution of many organisms, including scorpions, with assemblages being dominated by niche specialists (Polis 1990). Therefore, species can be grouped according to the habitats where they live and move around (Prendini 2001; Stockamnn and Ythier 2010). This functional differentiation between species reflects the different competitive potentials and factors that influence community structure (Polis 1990). In addition, a few species often dominate scorpion assemblages (constituting upward of 80% of all individuals) (Dias et al. 2006; Araújo et al. 2010; Lira and Albuquerque 2014; Izzat-Husna et al. 2014), suggesting that species with particular traits may be favored under selective pressures. Ecological plasticity of dominant species allows them to exploit a larger amount of resources and thus expand their microhabitat use. Therefore, the presence of other species in the same habitat will most likely result in competition for resources, especially for food and shelter (Brown and O'Connel 2000; McReynolds 2008; Pizarro-Araya et al. 2011; Lira et al. 2013; Lira and DeSouza 2014). Scorpion species have also been reported to expand or contract their foraging activity depending on the season (Polis 1990; Dias et al. 2006; Araujo et al. 2010; Lira et al. 2013). In some tropical arid and semiarid areas, activity levels typically decrease during periods of extreme summer heat (e.g. Polis 1990; Araujo et al. 2010). Moreover, in wet areas, activity levels usually decline during periods of intensive rainfall (e.g. Dias 2006; Cala-Riquelme and Colombo 2010).

Research on scorpion microhabitat selection in the Neotropics is often limited to one species or assemblage in a single locality (Álvarez et al. 2013; Lira and DeSouza 2014; Ramirez-Arce 2015; Nime et al. 2016). However, studies on microhabitat preference based on the diversity of scorpions in areas with different environments would improve our understanding of how the functional composition of the community is related to ecosystem functioning. Lira et al. (2013) have already demonstrated that the spatial distribution pattern exhibited by the litter-dwelling scorpions *Tityus pusillus* Pocock 1893 and *Ananteris mauryi* Lourenço 1982 differ according to species, age class (adult and juvenile), and season (wet and dry) in a Brazilian coastal Atlantic forest. These findings provide additional evidence of partial niche partitioning between coexisting scorpion species based on age class, sex, and climatic conditions, indicating that niche differentiation is a key mechanism of species coexistence. In addition, Nime et al. (2016) evaluated microhabitat use of *Brachistosternus ferrugineus* (Thorell 1876) in an area of Arid Chaco and found that spatial distribution and frequency of behaviors were highly dependent on developmental stage and sex. However, these studies provide only limited explanations of how spatial distribution patterns of species are affected by habitat structure.

In the present study, we surveyed spatio-temporal distribution of scorpion assemblages in 20 sites from two structurally different Neotropical forests, consisting of an Atlantic forest (wet forest) and a Caatinga (dry forest), with the objective of addressing the following questions: I) How important are habitat structure (closed or open forest) and seasonality (dry or rainy seasons) in determining microhabitat colonization in wet and dry forests? II) Is microhabitat use influenced by scorpion age class or sex? III) Does microhabitat availability (e.g., vegetation, rocks, burrows, leaf litter) influence spatial use by dominant scorpion species? IV) What role does habitat structure play in determining the functional richness (i.e., substrate specialization) of scorpions? V) How does climatic seasonality affect scorpion foraging activity in wet and dry forests due to changes in microhabitat structure? We predicted that: I) Scorpion species exhibit microhabitat specificity and are affected by the rainfall regime; therefore, we believe that seasonality (dry or rainy seasons) rather than structural differences between dry and wet forests is the key factor determining species distribution; II) Juvenile, male and female scorpions colonize different microhabitats to minimize inter- and intraspecific competition; III) Dominant species most likely occupy a greater number of microhabitats; IV) Functional richness should be greater in more structurally complex habitats such as rainforests with a greater vegetation density (providing more shelter) than in habitats with lower structural complexity such as open forest presenting a lower resource source; V) Foraging activity of scorpions inhabiting rainforests will be reduced during the rainy season and will be reduced in dry forests during periods of low precipitation.

Materials and methods

Study area

Fieldwork was carried out in 8 sites in an Atlantic forest (wet forest) and 12 sites in a Caatinga (dry forest) in the state of Pernambuco (08º 04' S; 37° 15' W), northeastern Brazil (Figs. 1, 2). The Northeastern Atlantic forest is composed of evergreen or semi-deciduous forest remnants (Veloso et al. 1991) largely dominated by Lauraceae, Sapotaceae, Moraceae, and Fabaceae tree species (Grillo et al. 2005), whereas Caatinga is a mosaic of xerophytic, deciduous, semiarid thorn scrub and forest (Leal et al. 2005). Average rainfall over the study period in the Atlantic forest was 39.08 and 248 mm in dry (September-February) and rainy seasons (March-August), respectively, and in Caatinga, it was 24.79 and 37.15 mm in dry (March-August) and rainy seasons (September-February), respectively (APAC 2017).

Scorpion sampling

We sampled scorpions on two nights (19:00-22:00 h) in each season (dry and wet seasons) from November 2014 to March 2016. In each site (divided into 2 sub-areas separated by

300 m), six linear transects (30 m in length and set 20 m apart) were established and each transect was sampled for one hour by a pair of collectors equipped with UV lanterns. Scorpions up to 5 m perpendicular to the transect line were captured. In total, 24 transects (12/season) per area (with a total sample effort of 7,200 m²/site) were prepared. Each collected animal was stored in a container with 70% ethanol. The specimens were recorded and preliminarily identified by sex, age class (adults or juveniles) and species during the search period, with later confirmation of species identification performed according to Lourenço (2002). Voucher specimens were deposited in the Arachnological Collection of the Universidade Federal de Pernambuco, Brazil.

Microhabitat use

The following environmental structures were used as potential microhabitat for scorpions in both forest types: burrows, termite mound, trees (> 20 cm diameter at breast height), rocks (on the ground, usually > 10 cm in diameter), the ground (soil), logs (fallen dead trees at various stages of decomposition), bromeliads (all Bromeliaceae > 30 cm diameter found at the ground level), vegetation (up to 15 cm in height), and leaf litter. The leaf litter was subdivided into layers, as described by Lira et al. (2013). The epi-leaf litter was considered to be the top 2–3-cm layer, which primarily consisted of intact leaves and fallen branches. The layer below the epi-leaf litter, or the sub-leaf litter, was approximately 3–4 cm thick and consisted mostly small pieces of leaves and branches in different states of decomposition. We determined the functional richness of scorpions based on substrate affinities demonstrated by each scorpion species. Terminologies used were based on those described by Prendini (2001), Stockmann, and Ythier (2010). For example, for animals found on tree bark, we used functional classification “corticolous”, bromeliad as “dendricolous”, superior leaf litter layers or ground as “epigean”, under stones as “lapidicolous”, bottom leaf litter layers (moist layer) as “humicolous” and ground or burrows (species that shows adaptations for digging into the substrate) as “fossorials”.

Data analysis

Nonmetric multidimensional scaling (NMDS) was used to assess patterns of microhabitat preference among species. Ordination was determined with an abundance matrix and the Bray–Curtis index using "vegan" package (v. 2.4-3) (Oksanen et al. 2013) of R (v 3.3.3) (R Core Team 2013). Effects of age class, sex and season on habitat colonization were evaluated via a G-test on a contingency table of pooled data (Sokal and Rohlf 1981) using Statistica software (v. 10) (StatSoft 2011). Dominance and abundance were estimated for each scorpion species in both Atlantic forest and Caatinga biomes. Dominance was calculated as $D\% = (i/t) \times 100$, where i is the abundance of species A and t is the total abundance. In this study, species were classified as eudominant ($D > 10\%$), dominant ($5\% < D \leq 10\%$), subdominant ($2\% < D \leq 5\%$), recessive ($1\% < D \leq 2\%$), or rare ($D < 1\%$) (Palissa et al. 1979). A *t*-test was used to verify whether scorpion species abundance differed between seasons in both forest types using Statistica software (v. 10) (StatSoft 2011). We used a Wilcoxon signed-rank test to evaluate the relationship between dominance and the amount of colonized microhabitat. Dominances were scored as follows: 1) rare, 2) recessive, 3) subdominant, 4) dominant, and 5) eudominant. Statistical analysis was performed using R version 3.0.1 (R Core Team 2013). Differences in functional richness between the Atlantic forest and Caatinga biomes were assessed via an analysis of similarity (ANOSIM) using a matrix of Bray–Curtis and 999 randomizations in R software (v. 3.3.3, vegan package 2.4-3) (R Core Team 2013, Oksanen et al. 2013).

Results

Effects of seasonality on microhabitat use in wet and dry forests

We identified a total of 2,681 individual scorpions in both the Atlantic forest and Caatinga. These individuals belonged to two families, five genera, and 12 species. In total 1,499 animals of 10 species were collected from the dry forest (Caatinga), whereas 1,182 individuals of 6 species were found in the wet forest (Atlantic forest) (Table 1).

Tityus pusillus and *A. mauryi* were the most common scorpion species in the wet forest, comprising 82.23 and 14.29% of the samples, respectively, with all other species varying between 0.25–1.77% of the samples (Table 1). The most common species in the dry forest was bothriurid *Bothriurus rochai* Mello-Leitão 1932, which composed 30.62% of the samples, followed by buthids *Jaguajir rochae* (Borelli 1910) (28.88%), *T. pusillus* (13.14%), and *Physoctonus debilis* (C. L. Koch 1840) (9.40%). All other species varied between 1.26–5.80% (Table 1).

Scorpions in the wet forest exhibited a higher degree of microhabitat specialization (Table 2), resulting in microhabitat grouping of scorpion species by NMDS (Fig. 3), which showed a low-stress value (< 0.01) indicating the reliability of the analysis. This finding was further confirmed by significant differences in species preference indices ($G_{(6,11)}$ = 336.94, $p < 0.01$). In contrast, scorpions in the dry forest were predominantly found in forest floor (leaf litter layers, burrows, and under stones), and thus indicated a relatively low habitat specialization ($G_{(10,10)}$ = 1595.07, $p > 0.05$) (Fig. 4).

Microhabitat use by scorpion species in the wet forest was not influenced by seasonality (dry and rainy seasons), with the exception of *T. pusillus*. In *T. pusillus*, 82.32% of individuals were found on the forest floor, and 15.46% in vegetation and trees during the dry season; during the rainy season, 70.24% of individuals were found on the forest floor and 28.30% in vegetation and trees.

In the dry forest, seasonality was a key factor driving microhabitat colonization by *Ananteris otavianoi* Lira, Pordeus and Albuquerque 2017, *B. rochai*, *J. rochae*, and *T. pusillus*. During the dry season, most *A. otavianoi* individuals were found in the sub-leaf (70.58%) and epi-leaf (23.52%) litter layers. In contrast, during the wet season, individuals occupied approximately the same extent in both layers (sub-leaf litter: 50%; epi-leaf litter: 42.85%). Both, *B. rochai* and *J. rochae* exhibited a similar pattern, preferring the forest floor (89.27% and 77.09%, respectively) and burrows (3.44% and 7.05%, respectively) during the dry season. However, during the rainy season, fewer animals were collected from the ground (*B. rochai*: 64.36%; *J. rochae*: 60.18%) whereas the number collected from burrows increased markedly (*B. rochai*: 12.76%; *J. rochae*: 13.59%) for both species. *Tityus pusillus* abundance on the forest floor (80.45%) increased during the dry season, but this species was commonly found both on the forest floor (53.63%) and in the vegetation (30.90%) during the rainy season.

Effects of age class and sex on microhabitat use in wet and dry forests

In the wet forest, the influence of seasonality on microhabitat use was recorded only for *T. pusillus*. In this species, both age class (dry season: $G_{(2,8)} = 70.88$, $p < 0.01$; rainy season: $G_{(2,7)} = 56.13$, $p < 0.01$) and sex (dry season: $G_{(2,8)} = 18.41$, $p < 0.01$; rainy season: $G_{(2,6)} = 12.30$; $p < 0.05$) changed microhabitat use according to the seasonality.

Specifically, during the dry season, adult individuals were mainly found in the epi-leaf litter layer (70.82%), whereas juveniles were found in the epi-leaf litter (36.11%), vegetation (35.18%), and sub-leaf litter (22.22%) layers. During the wet season, adults were generally found in the epi-leaf litter layer (58%), whereas juveniles preferred the vegetation (45.31%). Although both sexes primarily use the leaf litter as microhabitat (dry season: males = 71.53%; females = 88.48%; rainy season: males = 65.62%; females = 79.03%), males secondarily use the vegetation layer more than females (dry season: males = 14.59%; females = 4.41%; rainy season: males = 21.87%; females = 10.75%).

We found that microhabitat use by age class was also influenced by seasonality in the dry forest in *B. rochai* (dry season: $G_{(2,7)} = 41.37$, $p < 0.01$; rainy season: $G_{(2,9)} = 25.85$, $p < 0.01$), *J. rochae rochae* (dry season: $G_{(2,7)} = 23.49$, $p < 0.01$; rainy season: $G_{(2,8)} = 21.35$, $p < 0.01$), and *T. pusillus* (dry season: $G_{(2,5)} = 12.40$, $p < 0.05$; rainy season: $G_{(2,5)} = 16.28$, $p < 0.01$). During the dry season, *B. rochai* adults were principally found on the ground (92.85%), whereas juveniles occupied ground (78.46%), vegetation (35.18%), and under stones (15.38%) microhabitats. However, during the rainy season, adults were found on the ground (64.59%) and burrow (14.90%) microhabitats, whereas juveniles were most common on the ground (65.38%) and sub-leaf litter layer (26.92%). Adult *J. rochae* were predominately found on the ground (dry: 69.10%; rainy: 59.54%) and in burrows (dry: 12.19%; rainy: 19.84%) during both seasons. Most *J. rochae* juveniles were found on the ground (86.54%) during the dry season and on the ground (61.33%), among rocks (13.33%), and in the vegetation (9.33%) during the rainy season. We also detected sex differences on microhabitat use in these species, but only during the rainy season (*B. rochai*: $G_{(2,8)} = 12$, $p < 0.01$; *J. rochae*: $G_{(2,7)} = 12.39$, $p = 0.05$) when males used vegetation (*B. rochai* = 14.81%; *J. rochae* = 9.30%) more than females which were mostly found in burrows (*B. rochai* = 17.30%; *J. rochae* = 22.72%).

Adult *T. pusillus* adults were found mainly in the epi-leaf litter (44%) and on the ground (24%) during the dry season, and in the epi-leaf litter (27.27%), on the ground (35.27%), and in the vegetation (22.72%) during the rainy season. However, juvenile *T. pusillus* were found in the epi-leaf litter (25%), the sub-leaf litter (25%), and in vegetation (41.66%) during the dry season, but they were most common in vegetation (63.63%) during the rainy season. We also found sex differences on microhabitat use ($G_{(2.5)} = 21.00$, $p < 0.01$) in the rainy season when more males used the ground (46.51%) more than females (24.44%).

Microhabitat use and scorpion dominance in wet and dry forests

The two eudominant species (*T. pusillus* and *A. mauryi*) in the wet forest presented greater ecological plasticity and colonized significantly more microhabitats ($Z = 2.20$, $p < 0.01$) (nine and six different microhabitats, respectively). Other scorpion species colonized a maximum of five microhabitats, whereas the rarest species inhabited up to four microhabitats (Table 1). In the dry forest, most of the species preferred microhabitats on the forest floor such as the ground (*A. mauryi, Bothriurus asper* Pocock 1893*, B. rochai, J. rochae*, and *Tityus stigmurus* (Thorell 1876)) and leaf litter layers (*A. otavianoi, Ananteris franckei* Lourenço 1982, and *T. pusillus*), with the exception of *P. debilis* individuals, which were mainly found on trees (Table 3), as revealed by NMDS (stress < 0.09) microhabitat grouping (Fig. 4). The most abundant species exhibited greater ecological plasticity and colonized significantly more microhabitats. For instance, *B. rochai* (eudominant), *B. asper* (subdominant), and *J. rochae* (eudominant) were found in eight of the ten possible microhabitats, respectively. On the other hand, *T. stigmurus* (recessive) and *P. debilis* (dominant) individuals were found in four and three microhabitats, respectively (Table 1).

Functional richness in wet and dry forests

The functional classification of scorpion species is presented in Table 4. We detected a significantly higher functional richness of scorpion species in the wet forest than in the dry forest (n = 6 and 5, respectively). The difference in functional richness between the forest types was statistically significant (ANOSIM, $R = 0.2626$, $p < 0.001$).

Seasonality effects on foraging activity in wet and dry forests

Overall, scorpion foraging activity in the wet forest was significantly higher during the dry season (t = -2.5062, df = 14, $p < 0.05$), with 66.24% of these arachnids being sampled in this season. Only two species, *B. asper* and *T. stigmurus* increased their foraging activity in the rainy season (Fig. 5). In contrast, there were no differences in scorpion abundance between the dry and rainy seasons in the dry forest (t = -0.3818, df = 22, p = 0.7062), except *Ananteris* spp. and *P. debilis*, whose foraging activity increased in the wet and dry seasons, respectively (Fig. 6). In addition, the percentages of males, females and juveniles was also variable according to the seasonality and forest type, these data are presented in Table 5.

Discussion

Our study investigated the spatio-temporal distribution of scorpion communities in two structurally different Neotropical (wet and dry) forests. Spatial distribution of these arachnids was found to be a function of environment type, with species assemblages in wet forests consisting primarily of niche specialists, whereas in the dry forest, assemblages consisted mainly of ground-dwelling species. Food resources, predation risk, and microhabitat availability largely defined these spatio-temporal distribution patterns (Polis and McCormick 1987; McReynolds 2008). These factors were more prominent in the wet forest. Lira and DeSouza (2014) also reported that different species of buthids colonized different microhabitats in a montane Atlantic rainforest in Brazil, and attributed their results to differential substrate use by different species as a means of reducing the frequency of contact and thus the subsequent potential conflict between scorpion species.

The majority of the species inhabiting the dry forest occurred on the forest floor and used burrows, litter, and rocks as shelter. Such behavior is typical of scorpion assemblages in arid and semiarid areas, which are typically composed of ground-dwelling species that remain in shelters or burrows during the day (Polis 1990; Polis and Yamashita 1991). Similar to several species of spiders (Fernández-Montraveta and Cuadrado 2008; Canning et al. 2014), scorpions inhabiting arid areas may use burrows for to protect against predators, prey capture, and control thermal stress. The degree to which scorpions were found in the underground shelters, mainly burrows, in the Caatinga where the temperature can reach up to 40 °C during the dry season, suggested that these habitat features are vital to scorpion species inhabiting arid habitats (Adams et al. 2016). High temperatures cause greater rates of water loss in drier environments than in wet environments. Water loss may also be a problem for scorpions in wet environments. However, small invertebrates have a very large surface area relative to their mass, and consequently lose water easier than larger animals (Lourenço 2015); this could be one of the reasons why we observed a greater abundance of small-sized scorpion species (e.g. *A. mauryi* [13.6-24.1 mm in length], *T. pusillus* [24.1-34.9 mm], and *B. asper* [19.7-30.4 mm]) in the leaf litter layers in the wet forest, whereas mid- to large-sized (e.g. *T. neglectus* [58.7-72 mm] and *T. stigmurus* [44.7-61.1 mm]) were more commonly found in bromeliads and under rocks.

Body size due to age class was also a key factor in scorpion spatial distribution in these environments, similar to that described in previous studies (Polis and McCormick 1987; McReynolds 2008; Lira et al. 2013). Body size has been recognized as an important factor in interactions among scorpion species, with larger-sized species often acting as predators of juveniles or smaller-sized species (Polis and McCormick 1987; Moreno-González and Hazzi 2014; Lira et al. 2017*a*; Lira et al. 2017*b*). For example, adult *T. pusillus* individuals were recorded cannibalizing juveniles of their own species and preying on adult *A. mauryi* in an Atlantic forest (Lira et al. 2017*a*), as well as preying on adult *A. otavianoi* in a Caatinga (Lira et al. 2017*b*). In a desert, large-sized *Smeringurus mesaensis* (Stahnke 1957) adults have been observed preying on their own juveniles and those of *Hadrurus arizonensis* Ewing 1928, and even smaller-sized adults of *Paruroctonus luteolus* (Gertsch and Soleglad 1966) and *Vaejovis confusus* Stahnke 1940 (Polis and McCormick 1987). Larger individuals of these species often prey on the smallest ones, and therefore the different microhabitat use exhibited by *T. pusillus* depending on age class observed in our study could represent a way of reducing the overlap between juveniles and adults and potential for cannibalistic predation as proposed by Warburg (2000) for other scorpion species.

Our results supported the prediction that dominant species would occupy the majority of available microhabitats. The eudominant species in the wet forest, *A. mauryi,* and *T. pusillus* were found in most litter microhabitats, as previously noted by Lira et al. (2013), and the eudominant species in the dry forest, *B. rochai,* and *J. rochae*, also occupied the greater proportion of available ground microhabitats. Similarly, in the Coachella Valley desert in California, the numerically dominant scorpion (ca 95% of total) *S. mesaensis* was found in all available microhabitats and restricted other species to microhabitats where the abundance of adult *S. mesaensis* was low (Polis and McCormick 1987). The authors of that study suggested that intraguild predation rather than exploitative competition was the major factor determining the distribution structure of scorpions in the Coachella Valley.

In our study, however, not all species distributions were influenced by rainfall. Only the distribution of the eudominant species *T. pusillus* was affected by the precipitation regimes in the wet forest, and only distribution of the eudominant species *B. rochai*, *J. rochae*, and *T. pusillus*, and the dominant *Ananteris otavianoi* were affected by rainfall in the dry forest. During the wet seasons in both forest types, *T. pusillus* increased its use of vegetation layer relative to leaf litter as its preferential microhabitat which is a behavior that may be related to reducing the risk of predation because climbing vegetation has been previously shown to be a form of predation avoidance behavior by the scorpion (Brown and O'Connor 2000; Sanchéz-Piñero and Urbano-Tenório 2016). Spatial distribution of scorpions was also influenced by seasonality in both forest types, similar to what has been described in previous studies (Lira et al. 2013; Nime et al. 2016). Precipitation rates modify the landscape by changing the environmental structure of a given area. In a wet forest, such as the Brazilian Atlantic forest, rainfall can promote the growth of new plants, as well as the flooding of leaf litter, whereas in a dry forest, such as the Caatinga, the rainy season is correlated with renewed plant growth, accelerated decomposition of the leaf litter that accumulated during the dry season, and increased movement of insects restricted to moister sites during the dry season (Wolda 1988; Whitford 1996). In the dry forest, *B. rochai* and *J. rochae* were found twice as often assuming a 'doorkeeping' posture in burrows. The beginning of the rainy season in arid and semi-arid ecosystems provides favorable environmental conditions for the development of many prey organisms such as insects (Júnior and Schlindwein 2005; Moura et al. 2006; Vasconcelos et al. 2010; Medeiros et al. 2012) and allows scorpions to reduce their time spent in foraging and hunting closer to shelters. These changes in environmental structure may result in modification of microhabitats available to scorpions. For example, individual *Thestylus aurantiurus* Yamaguti and Pinto-da-Rocha 2003 in the Parque Estadual da Serra da Cantareira of southeastern Brazil prefer higher elevations during the rainy season, most likely due to the frequency of flooding of shelters in lower areas (Yamaguti and Pinto-da-Rocha 2006).

In addition to spatial distribution, scorpion foraging activity was also influenced by seasonality. However, the effects of rainfall regime differed between the two forest types.

Foraging activity increased in the wet forest, which corroborates the findings of previous studies in rainforests (Dias et al. 2006; Yamaguti and Pinto da Rocha 2006; Cala-Riquelme and Colombo 2010; Lira et al. 2013; Ott and Ott 2014). Increase in foraging activity may be associated with the onset of the reproductive season, as proposed for *Bothriurus signatus* Pocock 1893, *Microtityus jaumeii* Armas 1974, and *T. aurantiurus* Yamaguti and Pinto da Rocha 2006; Cala-Riquelme and Colombo 2010; Ott and Ott 2014). In contrast to scorpions in the wet forest, the foraging activity of most scorpions in the dry forest was unchanged during both the dry and rainy seasons. However, the foraging rates of *Ananteris* spp. and *P. debilis* increased during the rainy dry seasons, respectively. Therefore, our results contrast with previous studies in semi-arid regions, which reported increasing foraging activity during the rainy season (Araujo et al. 2010; Carmo et al. 2013; Schwerdt et al. 2016). Araujo et al. (2010) suggested that the reproductive season of *Bothriurus* spp. occurs during the rainy season based on the observed increase in male foraging. Similarly, in our study, the higher abundances of *Ananteris* spp. and *P. debilis* were largely due to increases in the number of males. In addition, differential reproductive periods suggested that these species have evolved behavioral mechanisms to avoid predation by larger species (e.g. *J. rochae* and *B. rochai*).

Although more species (n=10) were found in the dry forest than in the wet forest (n=6), functional richness was lower in the dry forest (n=5) than in the wet forest (n=6). Species assemblages can be modified by the severity of the environment. The stress-gradient hypothesis (Brooker et al. 2008) postulates that positive interactions predominate under more severe environmental conditions (such as in the Caatinga) (Leal et al. 2005; Salimon and Anderson 2017), whereas competition is more intense in places where resources are more abundant (such as the Atlantic forest). The differences in habitat structure complexity between the two forests in the present study may be partly due to the history of these sites. The dry forest is an ancient Caatinga, dating to the formation time of the Andes, and therefore the floral community at this site is old and stable (Roig-Juñent et al. 2006). In contrast, the wet forest has undergone numerous cycles of expansion and contraction started relatively recently (i.e., the Pleistocene) (Tabarelli and Santos 2004). Thus, the higher taxonomical and lower functional richness found in the dry forest may be due to organisms inhabiting this older and more stable area where had more time to accumulate richness (taxonomical richness) through speciation and longer periods to adapt to the prevailing environmental conditions (functional richness).

In summary, our study showed that scorpion spatial distribution was highly influenced by age class, sex, and seasonality, regardless of forest type (wet or dry). The species assemblages of these arachnids were structured to avoid cannibalism and intraguild predation. Rainfall regime also differentially influenced the activity of scorpion species depending on the forest type. Finally, the differences we observed in the functional richness of species between wet and dry forests may be explained by the broader historical context of species and ecosystem development.

Acknowledgments

We are grateful to Instituto Agronômico de Pernambuco (IPA), Universidade Federal Rural de Pernambuco (UFRPE), Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) and to owners of Reservas Particulares do Patrimônio Natural (RPPN) and others sites for permission to use the areas for sampling. We are also grateful to Coordenaçãoo de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for granting a PhD scholarship to A.F.A. Lira and A.M. DeSouza and to Laboratório de Invertebrados Terrestres staff for technical assistance during field work. We also grateful to Fundação de Amparo a Ciência e Tecnologia de Pernambuco (FACEPE) for a financial support (APQ-0437-2.04/15) and to Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for a financial support (Fellowship #307759/2015-6 for research productivity) for C.M.R. Albuquerque. We also thank two reviewers and to editor for valuable suggestions on an earlier draft of this manuscript.

TABLES

Table 1. Dominance classification, relative frequency, abundance, and the number of microhabitats used by scorpion species in the wet (Atlantic forest) and dry (Caatinga) forests.

Caatinga	Dominance	Relative frequency (%)	Abundance	Number of microhabitats colonized
Family Bothriuridae				
Bothriurus rochai	Eudominant	30.62	459	8
Bothriurus asper	Subdominant	4.2	63	8
Family Buthidae				
Ananteris otavianoi	Dominant	5.80	87	4
Ananteris mauryi	Subdominant	2.13	32	3
Ananteris franckei	Subdominant	4.47	67	4
Physoctonus debilis	Dominant	9.41	141	3
Tityus pusillus	Eudominant	13.14	197	5
Tityus stigmurus	Recessive	1.27	19	4
Jaguajir rochae	Eudominant	28.90	433	8
Jaguajir agamemnon	Rare	0.06	1	1
Total		100	1,499	
Atlantic forest				
Family Bothriuridae				
Bothriurus asper	Recessive	1.77	21	5

Family Buthidae				
Ananteris mauryi	Eudominant	14.29	169	6
Tityus pusillus	Eudominant	82.23	972	9
Tityus stigmurus	Rare	0.25	3	2
Tityus brazilae	Recessive	1.01	12	4
Tityus neglectus	Rare	0.50	6	4
Total		100	1,182	

Table 2. Percentages of microhabitat use by scorpions inhabiting a wet forest in Brazil.

	Microhabitats									
Scorpion species	Bromeliad	Burrow	Termite mound	Epi-leaf litter	Sub-leaf litter	Stone	Ground	Tree	Fallen log	Vegetation
Bothriuridae										
Bothriurus asper	0	0	0	38.23	5.88	0	38.23	11.78	0	5.88
Family Buthidae										
Ananteris mauryi	0	0	0	28.4	58	0	11.2	0.6	1.2	0.6
Tityus pusillus	0	0.1	0.3	58.8	16.15	0.5	2.05	5.37	1.33	15.4
Tityus brazilae	0	0	0	8.33	16.67	0	0	66.67	8.33	0
Tityus stigmurus	0	0	0	66.67	0	33.33	0	0	0	0
Tityus neglectus	33.33	0	0	0	0	16.67	16.67	33.33	0	0

Table 3. Percentages of microhabitat use by scorpions inhabiting a dry forest in Brazil.

Scorpions species	Microhabitats								
	Burrow	Termite mound	Epi-leaf litter	Sub-leaf litter	Stone	Ground	Tree	Fallen log	Vegetation
Family Bothriuridae									
Bothriurus asper	3.17	0	15.87	22.22	6.34	39.7	1.6	4.76	6.34
Bothriurus rochai	7.18	0.22	0.45	3.26	3.48	78.23	1.08	0	6.1
Family Buthidae									
Ananteris mauryi	0	0	3.12	15.63	0	81.26	0	0	0
Ananteris franckei	0	0	28.35	56.71	3	11.94	0	0	0
Ananteris otavianoi	0	0	39.08	54.02	1.15	5.75	0	0	0
Tityus pusillus	0	0	31.47	14.72	0	25.9	4.56	0	23.35
Tityus stigmurus	0	0	10.52	0	26.32	57.9	5.26	0	0
Physoctonus debilis	0	0	0	0	0	4.96	93.61	0	1.43
Jaguajir rochae	10.16	0	1.15	1.39	8.77	69.05	3.25	0.46	5.77
Jaguajir Agamemnon	0	0	0	0	0	100	0	0	0

Table 4. Functional classification of scorpions collected in wet and dry forest ecosystems in Brazil.

Scorpion species	Functional classification	Forest type
Family Bothriuridae		
Bothriurus asper	Fossorial	Atlantic Forest and Caatinga
Bothriurus rochai	Fossorial	Caatinga
Family Buthidae		
Ananteris mauryi	Humicolous	Atlantic Forest and Caatinga
Ananteris franckei	Humicolous	Caatinga
Ananteris otavianoi	Humicolous	Caatinga
Physoctonus debilis	Corticolous	Caatinga
Tityus pusillus	Epigean	Atlantic Forest and Caatinga
Tityus stigmurus	Lapidicolous	Atlantic Forest and Caatinga
Tityus brazilae	Corticolous	Atlantic Forest
Tityus neglectus	Dendricolous	Atlantic Forest
Jaguajir rochae	Epigean	Caatinga

Table 5. Percentages of males (M), females (F), and juveniles (F) of scorpion species in the wet (Atlantic forest) and dry (Caatinga) forests.

Species	Atlantic forest						Caatinga					
	Dry season			Rainy season			Dry season			Rainy season		
	M	F	J	M	F	J	M	F	J	M	F	J
Family Bothriuridae												
Bothriurus asper	37.5	62.5	0	38.5	62.5	0	28.6	61.9	9.5	35.7	61.9	2.4
Bothriurus rochai	-	-	-	-	-	-	33.8	42.3	23.9	28.9	57.2	13.9
Family Buthidae												
Ananteris mauryi	35.1	52.3	12.6	32.8	63.8	3.4	44.4	55.6	0	56.5	43.5	0
Ananteris franckei	-	-	-	-	-	-	33.3	66.7	0	38.5	50	11.5
Ananteris otavianoi	-	-	-	-	-	-	41.2	58.8	0	38.6	57.1	4.3
Jaguajir agamemnom	-	-	-	-	-	-	100	0	0	0	0	0
Jaguajir rochae	-	-	-	-	-	-	20.7	33.5	45.8	20.9	42.7	36.4
Physoctonus debilis	-	-	-	-	-	-	43	48.4	8.6	23	77	0
Tityus brazilae	22.2	55.6	22.2	0	60	40	-	-	-	-	-	-
Tityus neglectus	66.7	33.3	0	0	0	100	-	-	-	-	-	-
Tityus pusillus	21	62.5	16.5	20	59.6	20.4	28.7	57.5	13.8	27.3	52.7	20
Tityus stigmurus	0	100	0	50	50	0	42.9	42.9	14.2	16.7	25	58.3

Figures

Figure 1. Study area showing the spatial position of the 20 sampling sites. Diagonal lines = Brazilian Atlantic forest (wet forest); vertical lines = Caatinga (dry forest).

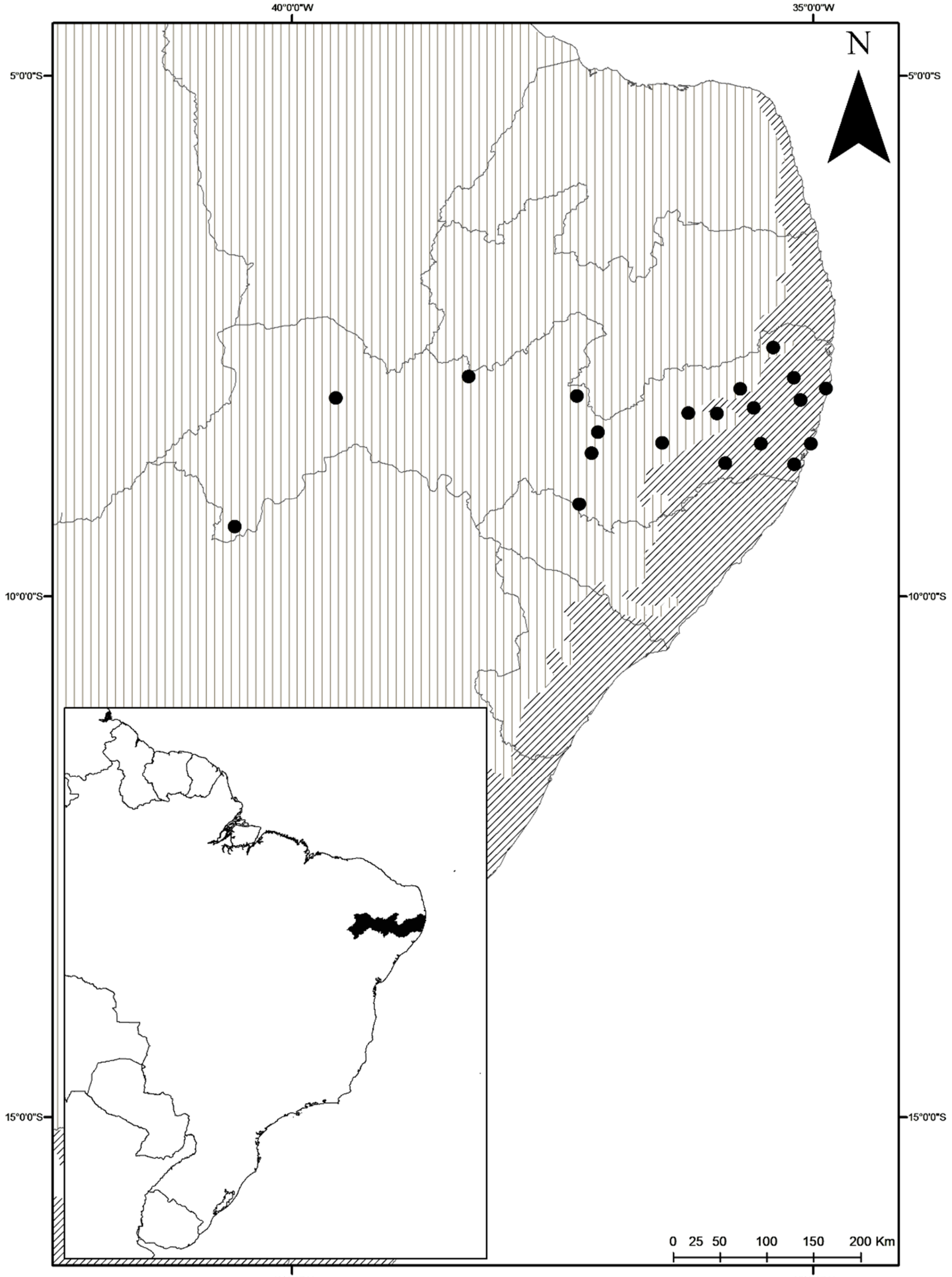

Figure 2. Habitat occupied by scorpions. (A) wet forest; (B) dry forest.

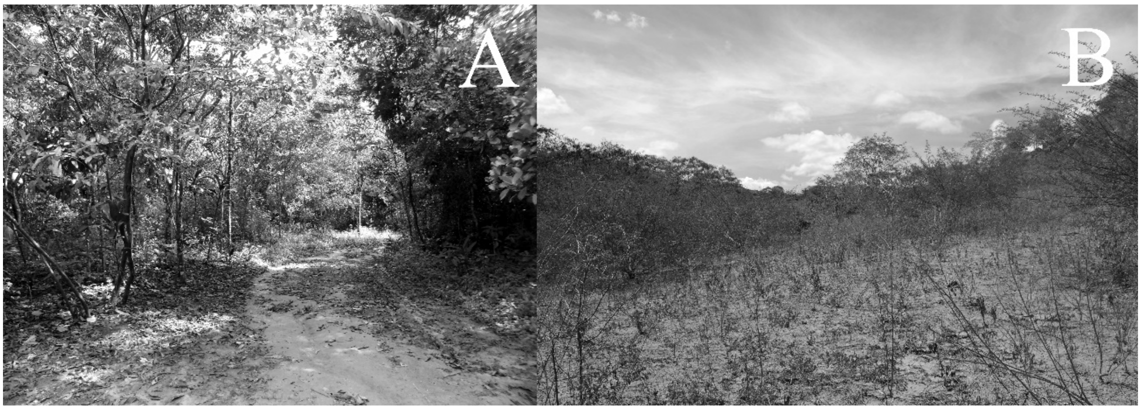

Figure 3. Nonmetric multidimensional scaling (NMDS) ordination using a Bray–Curtis similarity matrix of scorpion abundance and microhabitat use in a wet forest.

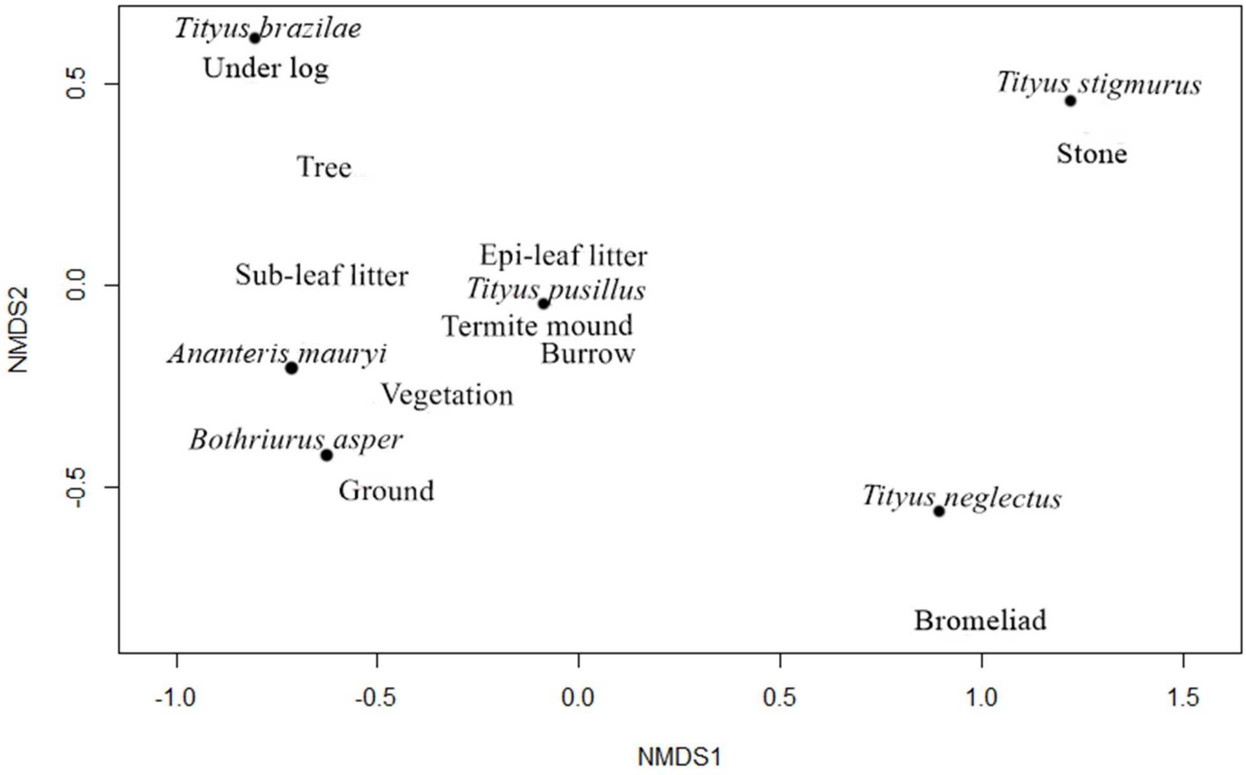

Figure 4. Nonmetric multidimensional scaling (NMDS) ordination using a Bray–Curtis similarity matrix of scorpion abundance and microhabitat use in a dry forest.

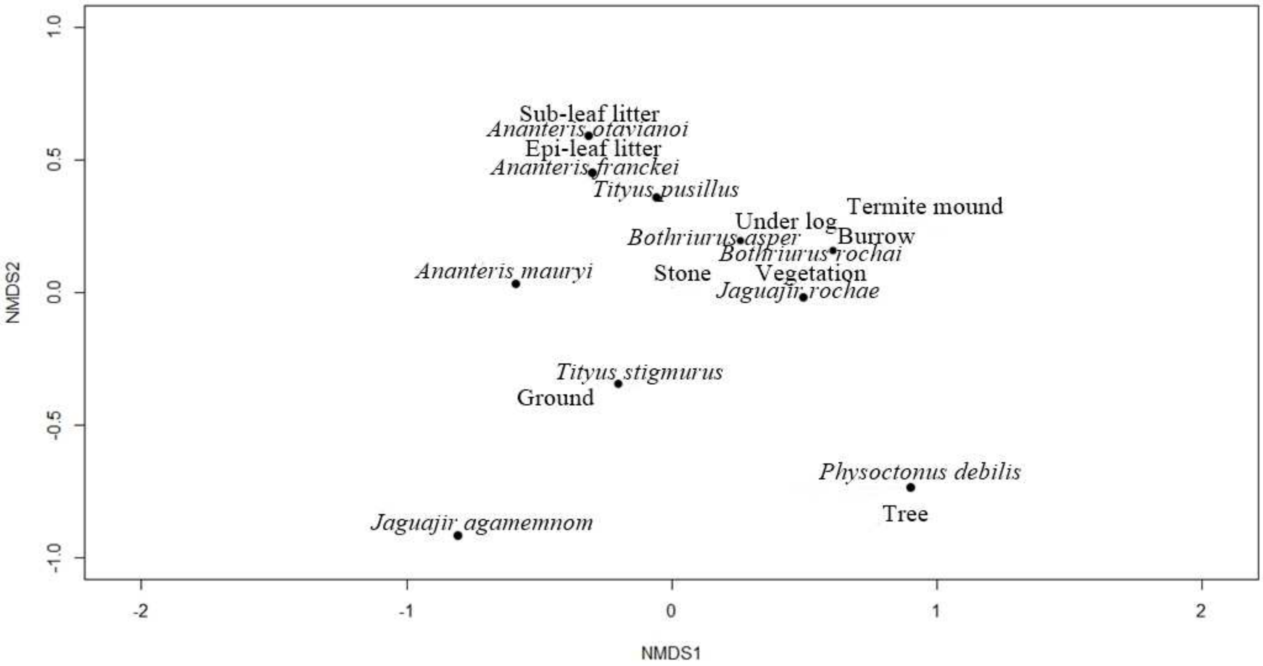

Figure 5. Scorpion species abundances (%) during the dry and rainy seasons in a wet forest in northeast Brazil.

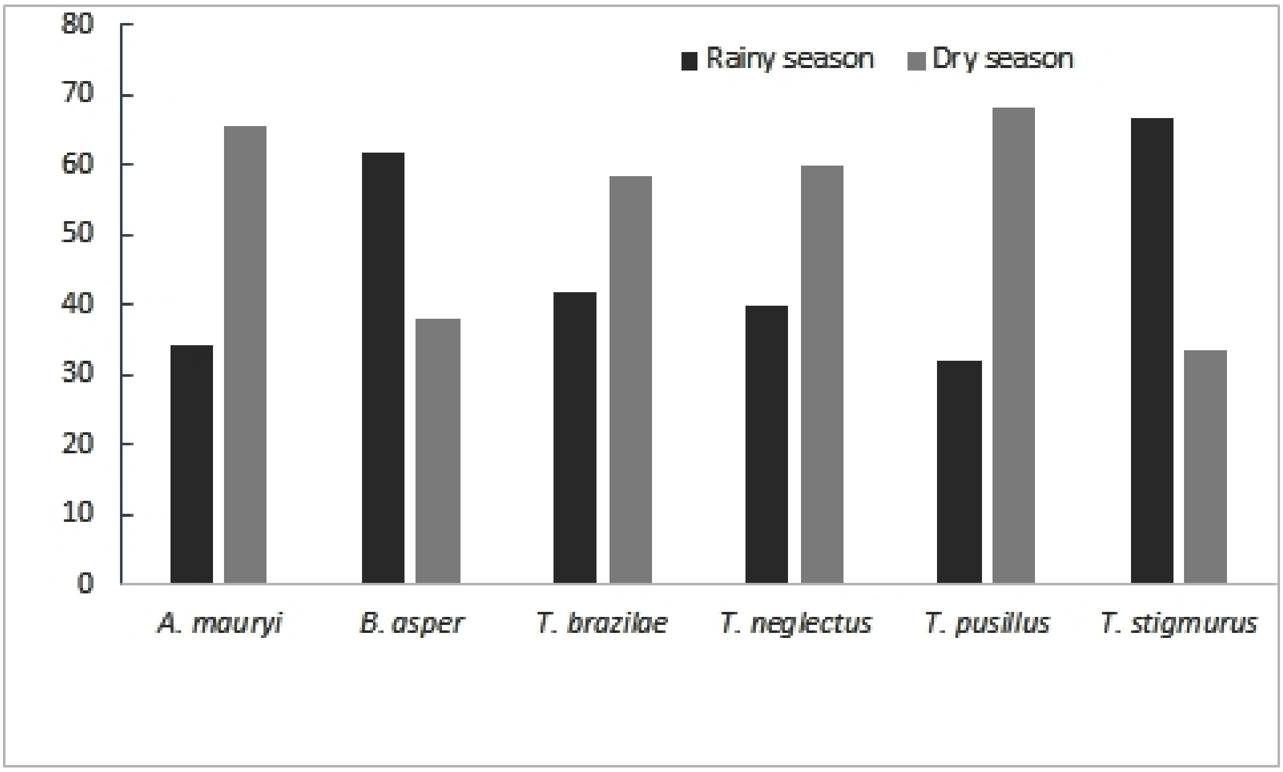

Figure 6. Scorpion species abundances (%) during the dry and rainy seasons in a dry forest in northeast Brazil.