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LOURIVAL BAÍA DE VASCONCELOS NETO

A HETEROGENEIDADE AMBIENTAL DAS SAVANAS AMAZÔNICAS DETERMINA A DISTRIBUIÇÃO LOCAL DE LAGARTOS *Cnemidophorus cryptus* (SQUAMATA: TEIIDAE)

SANTARÉM, PARÁ
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Orientador: Dr. Alfredo P. dos Santos Júnior.

Co-orientador: Dr. Rafael de Fraga.

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Assim, aos dois dias do mês de dezembro do ano de dois mil e vinte, às dez horas e trinta minutos, foi apresentado on-line a apresentação de seminário público da dissertação de mestrado do aluno LOURIVAL BAIA DE VASCONCELOS NETO. Deu-se início a abertura dos trabalhos, onde o Professor Dr. ALFREDO PEDROSO DOS SANTOS JR, após esclarecer as normativas de tramitação da defesa e seminário público, de imediato solicitou o candidato que iniciasse a apresentação da dissertação, intitulada "A HETEROGENEIDADE AMBIENTAL DAS SAVANAS AMAZÔNICAS DETERMINA A DISTRIBUIÇÃO LOCAL DE LAGARTOS *Cnemidophorus cryptus* (SQUAMATA: TEIIDAE)". Concluída a exposição, o orientador comunicou ao discente que a versão final da dissertação deverá ser entregue ao programa, no prazo de 30 dias; contendo as modificações sugeridas pela banca examinadora e constante nos formulários de avaliação da banca.

A banca examinadora foi composta pelos examinadores professores doutores listados abaixo. Os pareceres assinados seguem em sequência.

Alfredo Santos

ALFREDO PEDROSO DOS SANTOS JR
Orientador

Rafael de Fraga

RAFAEL DE FRAGA
Co-orientador

Lourival Baia de Vasconcelos Neto

LOURIVAL BAIA DE VASCONCELOS NETO
Discente

A Raul Lazzaretti, o "Raulzito", meu amado
filho e melhor amigo.

Aos guerreiros da Brigada de Incêndio de Alter
do Chão e demais ativistas ambientais que
lutam para manter a floresta amazônica de pé
em meio a esse cenário catastrófico.

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À minha família pelo apoio, confiança e compreensão nos momentos alegres e nos mais difíceis durante esses anos de academia. Especialmente agradeço meus pais, Toca e Marly, minhas irmãs, Ana e Lívia, e minha esposa e filhão, Larissa e Raul, que suportaram minhas alterações de humor ao longo dessa jornada e sempre me deram forças para seguir firme em busca desse objetivo.

Essa dissertação é fruto do trabalho coletivo de algumas pessoas às quais quero dedicar aqui um agradecimento especial. A Alfredo por ter aceitado me orientar e por confiar nesse projeto, me deixando muitas vezes livre para tomar decisões importantes sobre o andamento, sempre dando dicas e conselhos importantes. A Rafael, o grande “Rato”, que teve papel imprescindível para a execução desse trabalho. Obrigado, meu velho, por topar me orientar e proporcionar bons momentos de produção e aprendizagem ao som de Frank Zappa. Ao meu manuelo Pedro, que também foi fundamental durante essa jornada em diversos momentos, desde os longos e árduos dias de sol na savana, até os exaustivos momentos na “Zog-zog house” onde a gente tentava botar no papel todo o emaranhado de ideias de forma coesa. Esse trabalho é nosso, galera! E posso garantir que sem vocês ele não seria possível.

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À coordenação e toda a equipe do Parque Estadual Monte Alegre, em nome da amiga Patrícia, que autorizou a realização da pesquisa e deu todo apoio durante a coleta de dados.

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À Coordenação de Aperfeiçoamento de Pessoal de Ensino Superior (CAPES) por fornecer apoio para a pós-graduação no Brasil.

Existe uma coisa que uma longa existência me ensinou: toda a nossa ciência, comparada à realidade, é primitiva e inocente; e, portanto, é o que temos de mais valioso.

Albert Einstein

RESUMO

A distribuição espacial dos organismos pode ser direta e indiretamente afetada por vários gradientes ambientais. A heterogeneidade ambiental geralmente causa variação na qualidade do habitat local e nos níveis de competição, o que pode levar à filtragem ambiental e alterar a densidade populacional em uma determinada faixa geográfica da distribuição de uma espécie. Neste estudo, testamos a hipótese generalizada de que savanas na Amazônia podem conter heterogeneidade ambiental suficiente para que as estimativas de densidade de lagartos não sejam homogêneas no espaço. Em uma Unidade de Conservação foram amostradas 26 parcelas, cada uma cobrindo 1500 m^2 (250 m de comprimento, 6 m de largura), para testar a influência da temperatura do ar, altitude, número de cupinzeiros, cobertura de arbustos, cobertura do dossel, densidade do concorrente e interações entre alguns desses gradientes na densidade de *Cnemidophorus cryptus* (Squamata, Teiidae). Foram encontrados efeitos positivos do número de cupinzeiros e cobertura de arbustos nas densidades de *C. cryptus*. Esses achados sugerem que a alta disponibilidade de locais de refúgio contra temperaturas elevadas (até 40 ºC) experimentadas pelas savanas favorece altas densidades de lagartos. Além disso, foram encontrados efeitos negativos da altitude e temperatura nas densidades estimadas, o que sugere filtragem ambiental em locais termicamente inadequados. No entanto, um gráfico de interação mostrou que os efeitos da altitude na densidade de *C. cryptus* são significativos apenas sob temperaturas mais amenas. No geral, nossas descobertas sugerem que *C. cryptus* não ocupa homogeneamente os habitats disponíveis, mas a filtragem ambiental pode surgir da falta de abrigo e termorregulação ineficiente em relação à perda de calor corporal em altitudes relativamente baixas (<104 m) e ganho de calor em temperaturas relativamente altas (> 104 m). Discutimos nossas descobertas do ponto de vista ecológico e de conservação da biodiversidade.

Palavras-chave: Ecologia de populações. Filtragem ambiental. Gradientes ecológicos. Squamata. Teiidae.

ABSTRACT

The spatial distribution of organisms may be directly and indirectly affected by multiple environmental gradients. Environmental heterogeneity often causes variation in local habitat quality and levels of competition, which may lead to environmental filtering changing population density over a species geographic range. In this study we test the generalized hypothesis that savannas in Amazonia may contain enough environmental heterogeneity that lizard density estimates are not homogeneous across space. In a protected area we sampled 26 plots, each of which covering 1500 m^2 (250m long, 6 m wide), to test the influence of air temperature, altitude, number of termite mounds, shrub cover, canopy openness, competitor density, and interactions between some of these gradients on *Cnemidophorus cryptus* (Squamata, Teiidae) density. We found positive effects of number of termite mounds and shrub cover on *C. cryptus* densities. These findings suggest that high availability of refuge sites from the high temperatures (up to 40 ºC) experienced by midday savannas favor high densities. Additionally, we found negative effects of altitude and temperature on the estimated densities, which suggests environmental filtering at thermally unsuitable sites. However, an interaction plot showed that altitude effects on *C. cryptus* density are only significant under mild temperatures. Overall, our findings suggest that *C. cryptus* does not homogeneously occupy available habitats, but environmental filtering may emerge from lack of shelter and inefficient thermoregulation toward body heat loss at relatively low altitudes (< 104 m), and heat gain at relatively high temperatures (> 104 m). We discuss our findings from ecological and biodiversity conservation perspectives.

Keywords: Ecological gradients. Environmental filtering. Population ecology. Squamata. Teiidae.

SUMÁRIO

INTRODUÇÃO GERAL

Como o ambiente pode influenciar a densidade de lagartos em savanas na Amazônia?[1]

Qual o problema da pesquisa?

Lagartos podem viver em diversos tipos de ambientes, como savanas, florestas alagáveis e não alagáveis, desertos e áreas urbanizadas. As espécies desse grupo mostram uma grande variedade de formas, cores e tamanhos corpóreos ao longo de sua ampla distribuição que ocupa quase todo o globo terrestre, com exceção dos polos. A ausência nos polos da Terra é explicada por limitações fisiológicas impostas pelo frio extremo, uma vez que esses animais precisam de fontes externas de calor para desempenhar suas atividades primordiais como comer, fugir de predadores e reproduzir. Embora algumas espécies sejam altamente tolerantes a amplitudes térmicas (intervalo entre temperatura mínima e máxima) relativamente grandes, outras são muito mais sensíveis a variações termais, podendo deixar de ocupar locais termalmente inadequados. A qualidade termal de hábitats geralmente não é homogênea ao longo de paisagens naturais, mas dependente da cobertura vegetal e da altitude, as quais variam muito. Portanto, podemos esperar que a densidade de lagartos (número de indivíduos por unidade de área) também não seja homogênea, mas varie ao longo de mosaicos de hábitats mais ou menos adequados (Figura 1).

Savanas diferem consideravelmente de florestas por serem ambientes abertos, muito ensolarados e quentes. Em imagens de satélite savanas são facilmente distinguíveis de florestas, mas a variação ambiental dentro de savanas geralmente não é óbvia. Saber o quanto a temperatura e a cobertura vegetal mudam ao longo de savanas geralmente depende de medir essas

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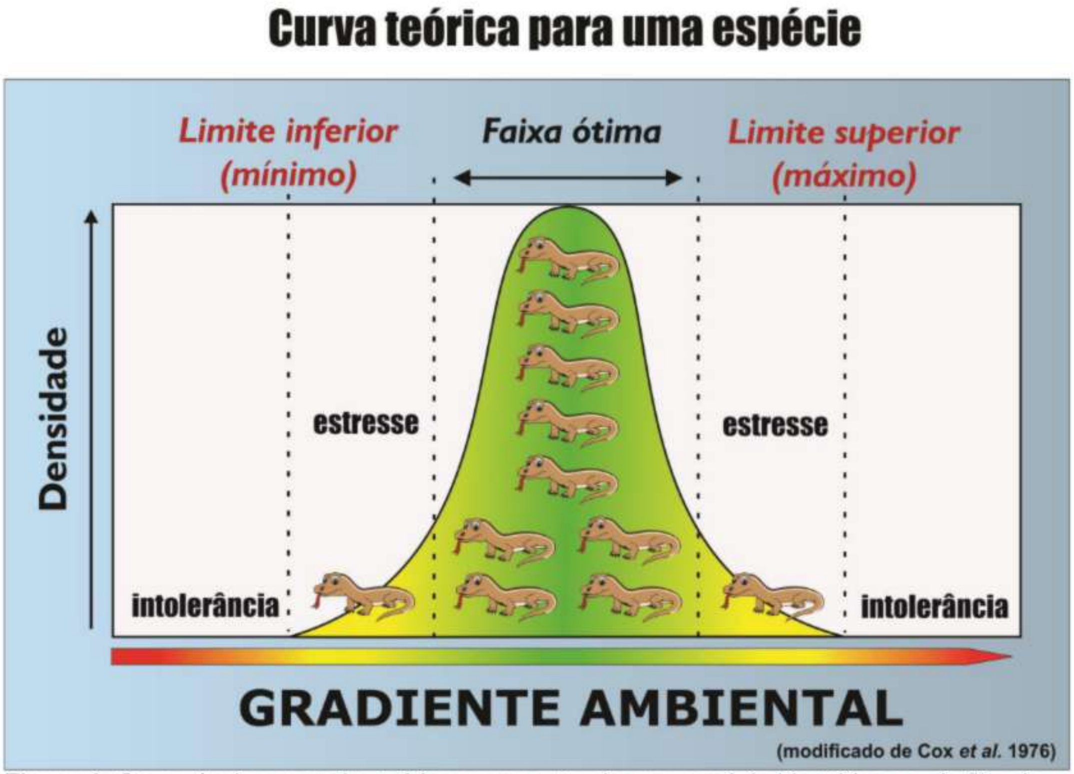
[1] Texto de comunicação científica formatado conforme as normas do “Canal Ciência - Portal de Divulgação Científica e Tecnológica”, do Instituto Brasileiro de Informação em Ciência e Tecnologia (Ibict).



(modificado de Cox *et al.* 1976)

Figura 1: Curva de desempenho teórico representando uma espécie hipotética sendo filtrada ao longo de um gradiente ambiental. Na faixa ótima onde a espécie atinge seu desempenho máximo, a densidade é maior, já nos limites da distribuição essa métrica é reduzida até chegar a zero nas faixas intoleráveis.

variáveis localmente em campo. Essa abordagem pode revelar muita variação espacial na abundância de árvores, arbustos, capins e solo exposto, e, portanto, é muito mais eficiente que imagens de satélite para quantificar a variação ambiental dentro de savanas. Isso é relevante, porque as espécies residentes de savanas precisam ser bem adaptadas ao estresse hídrico e termal, e por isso savanas contêm biodiversidade única, diferente das florestas adjacentes. Biodiversidade única é um ótimo critério para definir savanas como ecossistemas de alta relevância para conservação.

Entre os mais variados tipos de animais e plantas que ocorrem nas savanas amazônicas, os lagartos são um dos grupos mais abundantes e disseminados. Algumas manchas de savana podem abrigar até 15 espécies distribuídas nos mais variados habitats. Os lagartos do gênero *Cnemidophorus* (conhecidos popularmente como calangos listrados, Figura 2a) são uns dos mais abundantes e facilmente detectáveis devido à necessidade de forragearem ativamente em busca de alimentos e sítios para termorregulação, como cupinzeiros e arbustos, por exemplo. Como as savanas são ecossistemas que normalmente possuem temperaturas mais elevadas, a presença desses locais para perda de calor corporal pode ser determinante para os lagartos na seleção de hábitat.

Como a pesquisa foi realizada?

Sob a orientação dos herpetólogos Rafael de Fraga (Doutor em Ecologia) e Alfredo Santos-Jr (Doutor em Zoologia), o biólogo Lourival Vasconcelos Neto, acadêmico do Programa de Pós-Graduação em Biodiversidade e responsável pela pesquisa, estudou uma população de *Cnemidophorus cryptus* (Figura 2a) em savanas Amazônicas, com o objetivo de testar a hipótese de que as densidades de lagartos são limitadas por alterações locais na qualidade de hábitats. Essa hipótese é baseada na ideia de que as variações locais nas características desses ambientes de savana promovem mosaicos com diferentes qualidades e, por isso, os lagartos tendem a ser filtrados (estar em baixa densidade ou mesmo ausentes) em locais com condições adversas. O estudo foi conduzido no Parque Estadual de Monte Alegre (PEMA, Figura 2b), uma Unidade de Conservação estadual com área de 3.678 ha, situada no município de Monte Alegre – PA, ao norte do Rio Amazonas, sendo uma das poucas reservas destinadas à conservação de

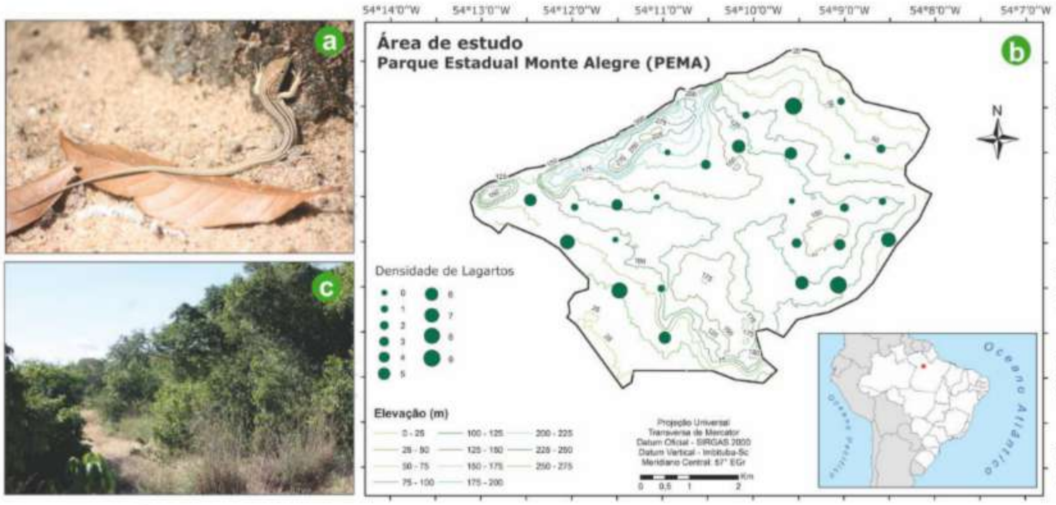


Figura 2: Informações gerais sobre o estudo no Parque Estadual Monte Alegre: a = exemplar de *Cnemidophorus cryptus*; b = mapa da área de estudo com os locais de coleta de dados representados pelos círculos verdes e a densidade de lagartos pelo tamanho do círculo; C = tipo vegetacional predominante nas savanas amazônicas.

áreas de savana na Amazônia (Figura 2c).

A pesquisa consistiu em coletar dados sobre a densidade de indivíduos (número de lagartos em parcelas de 250 x 6 m), seguindo o protocolo RAPELD (ver sugestões de leitura) para definir o eixo central de parcelas de amostragem seguindo as curvas de nível naturais do terreno. Os locais selecionados para a coleta (Figura 2b) de dados abrangeram hábitats com variação nas configurações do estrato vegetal, altitude, temperatura e disponibilidade de sítios para termorregulação e alimentação. O objetivo é investigar se essas variáveis ambientais podem influenciar na densidade local de *C. cryptus*.

Qual a importância da pesquisa?

Como principal resultado, os pesquisadores evidenciaram que a distribuição espacial dos lagartos na área estudada não é aleatória, e que a heterogeneidade ambiental das savanas amazônicas é determinante para a estruturação espacial da população de *C. cryptus*. De acordo com as análises estatísticas realizadas, a proporção de arbustos, altitude, temperatura e número de cupinzeiros são atributos do habitat responsáveis por promover modificação espacial na densidade local de lagartos. Em locais com mais arbustos e cupinzeiros, a densidade de lagartos é maior, porque ambas as variáveis definem a disponibilidade de refúgios contra as altas temperaturas nas horas mais quentes do dia, e a disponibilidade de refúgios contra predadores. Em locais com temperaturas elevadas a densidade é menor, porque calor excessivo limita os processos fisiológicos e metabólicos de ectotérmicos como lagartos. A altitude também foi uma variável importante, embora tenha influenciado a densidade de lagartos indiretamente, porque gradientes altitudinais promovem variação espacial em diversas características do ambiente, como variação na cobertura vegetal, por exemplo, podendo configurar alterações na qualidade termal de hábitats disponíveis em diferentes cotas altimétricas. Além disso, a pesquisa evidenciou, também, que as variáveis podem interagir e influenciar a distribuição dos indivíduos. Especificamente, foi observado que sob condições de alta temperatura os efeitos da altitude sobre a densidade dessa espécie de lagarto são relativamente fracos. Ao contrário, em locais que mostraram temperaturas mais amenas, os efeitos negativos da altitude na densidade de lagartos foram fortes.

Esse resultado geral é relevante para a ecologia e conservação de populações naturais, pois fornece informações sobre mecanismos e processos que determinam a distribuição local dos indivíduos. Por exemplo, é possível argumentar que a escolha de uma área para conservação dessa espécie deve abranger locais heterogêneos, uma vez que a estrutura espacial da população depende da interação entre variáveis ambientais para garantir a disponibilidade locais adequados para a termorregulação. Apesar de que diversas pesquisas nas florestas Amazônicas evidenciaram respostas significativas de diferentes espécies de animais e plantas à variação ambiental, poucos estudos tiveram como foco os organismos que ocorrem nas áreas de savana. De modo geral, savanas têm sido negligenciadas pelas ciências naturais, a despeito do fato de serem ecossistemas regionalmente raros, e biologicamente complementares às florestas adjacentes.

Autores

Lourival Baía de Vasconcelos Neto[1,2,*]; Pedro Henrique Salomão Ganança[1,2]; Alfredo Pedroso dos Santos Júnior[1,2] e Rafael de Fraga[2,3]

Filiações

[1] Programa de Pós-Graduação em Biodiversidade, Universidade Federal do Oeste do Pará, Santarém, Brasil;

[2] Laboratório de Ecologia e Comportamento Animal, Universidade Federal do Oeste do Pará, Santarém, Brasil

[3] Programa de Pós-Graduação em Recursos Naturais da Amazônia, Universidade Federal do Oeste do Pará, Santarém, Brasil.

[*] Autor para correspondência: vasconcelosnetobio@hotmail.com

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CAPÍTULO I

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ENVIRONMENTAL HETEROGENEITY OF AMAZONIAN SAVANNAS DETERMINING THE LOCAL DISTRIBUTION OF A RACERUNNER LIZARD

Lourival B. V. Neto[1,*], Alfredo P. Santos-Jr[1], Pedro H. S. Ganança[1], Rafael de Fraga[2]

[1]*Programa de Pós-Graduação em Biodiversidade, Universidade Federal do Oeste do Pará, Santarém, Brazil*

[2]*Programa de Pós-Graduação em Recursos Naturais da Amazônia, Universidade Federal do Oeste do Pará, Santarém, Brazil*

*corresponding author: vasconcelosnetobio@hotmail.com

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Environmental heterogeneity of Amazonian savannas determining the local distribution of a racerunner lizard

Abstract

The spatial distribution of organisms can be affected directly and indirectly by multiple environmental gradients. Environmental heterogeneity often causes variation in local habitat quality and levels of competition, which may lead to environmental filtering changing population density over a species geographic range. In this study we test the generalized hypothesis that savannas in Amazonia may contain enough environmental heterogeneity that lizard density estimates are not homogeneous across space. We sampled 26 plots located in an area dedicated to the conservation of savannas in the Amazon, each of which covering 1500 m^2 (250m long, 6 m wide), to test the influence of air temperature, altitude, number of termite mounds, shrub cover, canopy openness, competitor density, and interactions between some of these gradients on racerunner lizard (*Cnemidophorus cryptus*) density. We found positive effects of number of termite mounds and shrub cover on *C. cryptus* densities. These findings suggest that high availability of refuge sites from the high temperatures (up to 40 ºC) experienced by midday savannas favor high densities. Additionally, we found negative effects of altitude and temperature on the estimated densities, which suggests environmental filtering at thermally unsuitable sites. Through an interaction graph we show that the effects of altitude on the density of racerunner lizards are significant only under mild temperatures. In general, our results suggest that *C. cryptus* does not occupy the habitats available homogeneously, but environmental filtration may arise from the need for shelter for efficient thermoregulation towards the loss of body heat. We discuss our findings from ecological and biodiversity conservation perspectives.

Keywords: ecological gradients, environmental filtering, population ecology, Squamata, Teiidae

Introduction

Environmental heterogeneity may play a key role in shaping the spatial distribution of organisms, because occurrence and density are often limited by environmental filtering (Kinnup and Magnusson, 2005; Cornwell, Schwilk and Ackerly, 2006). Although species distribution at macroscales may be best predicted by historical factors (Ribas et al. 2011; Dias-Terceiro et al., 2015), at local scales it is expected that spatial variation in resource availability generates habitat-quality mosaics across species ranges (Vitt et al., 2007; Garda et al., 2013). At suboptimal conditions (e.g. low availability of nutrients and thermoregulation sites, high competition and exposure to predators), low levels of birth/death ratio and immigration tend to negatively affect population density estimates, because individuals are unable to survive and reproduce under certain habitat conditions (Franklin et al., 2000). Therefore, species may be locally filtered from sites through physiological intolerance, high exposure to intolerable temperatures and predators, competition, or a combination of multiple factors (Cornwell, Schwilk and Ackerly, 2006; Laliberté, Zemunik and Turner, 2014). Environmental filtering has been widely demonstrated as affecting biodiversity in Amazonia, both at population (Fraga et al., 2013; Fraga et al., 2017), and animal (Menin et al., 2007; Menger et al., 2017; Faria, Menin and Kaefer, 2019) and plant (Costa, Magnusson and Luizão, 2005; Kinnup and Magnusson, 2005) assemblage levels.

Although biotic and abiotic factors are widely expected to limit species distribution locally, most studies in Amazonia have been focused on forest ecosystems (e.g. Costa, Magnusson and Luizão, 2005; Kinnup and Magnusson, 2005; Fraga et al., 2013; Faria, Menin and Kaefer, 2019). However, the Amazon ecosystems contain 267.164 km^2 of savannas (4.8% of total territory) which have been poorly sampled (Carvalho and Mustin, 2017). Although Amazonian savannas appear homogeneous in satellite images, they may show levels of environmental heterogeneity at finer scales (e.g. field-measured environmental gradients, Magnusson et al. 2008). For instance, while savannas may be regionally characterized by predominantly grassy, herbaceous and shrubby vegetation cover, wide local variation in the density of trees, shrubs and exposed soil may be spatially expected (Eiten, 1983; Sarmiento, 1984; Magnusson et al., 2008). Such variation causes heterogeneous distribution of refuge, foraging and thermoregulation sites within savannas, which is expected to influence the local fauna (Chamaillé-Jammes, Valeix and Fritz, 2007). Therefore, environmental filtering structuring populations and assemblages should be expected not only by comparing extreme portions of environmental gradients (e.g. savanna *vs.* forest), but also within local patches of habitat types (Vitt et al., 2007; Garda et al., 2013; Nogueira et al., 2019).

In this study we investigate the influence of environmental heterogeneity within Amazonian savannas on the spatial structure of racerunner lizards *Cnemidophorus cryptus* Cole & Dessauer, 1993 (Teiidae, Squamata). Racerunner lizards are often considered as models for quantitative studies (e.g. based on density), because it is relatively easy to detect in the field, which generates reliable data (Mesquita and Colli, 2003; Menezes and Rocha, 2013). This species is widely distributed along the Amazonia, although its distribution is regionally limited to open habitats such as savanna patches, forest edges and human occupations (Harvey, Ugueto and Gutberlet Jr, 2012; Ribeiro-Jr and Amaral, 2016).

As ectotherms, body temperature mediated by habitat temperature determines the efficiency of processes necessary for survival and reproduction of racerunner lizards (Diele-Viegas et al., 2018). This is particularly critical in savannas, because these habitats often experience excessively high temperatures, which leads lizards to occupy thermoregulation sites that contain a variety of fine-scale features that can ameliorate temperature extremes (Scheffers et al., 2014), leading the lizards toward body heat loss. Holes in the ground, termite mounds, fallen logs, shrubs, grass and other vegetated habitats are among the shelters available for lizards to thermoregulate. Additionally, the high openness of savannas generates relatively high exposure to predators and seasonal fires (compared to forests), which makes shelter availability a relevant factor determining lizard-occupied habitat proportions (Faria, Lima and Magnusson, 2004; Souza et al., 2020). However, in the Amazonian savannas, the vegetation cover changes considerably throughout the landscape (Magnusson et al., 2008), accordingly, thermally suitable habitats are not equally available throughout the ecosystem. Topographic variations usually carry a great deal of information about changes in soil and vegetation characteristics across the landscape (Luizão et al., 2004; Kinnup and Magnusson, 2005).

In addition, considering that thermoregulating and foraging sites (e.g. shrubs, termite mounds) are spatially patch distribuited in open ecosystems (Eiten, 1983; Magnusson et al., 2008), interespecific competition resource can also be expected as a predictor for the species density (Mesquita, Costa and Colli, 2006). Therefore, it is plausible to assume environmental gradients that quantify thermal habitat quality, availability of thermoregulation and refuge sites, and levels of competition may predict estimates of *C. cryptus* density.

In this study we test the general hypothesis that the local distribution of *C. cryptus* is not homogeneous across space but determined by multiple environmental and competition-level gradients. Specifically, we test the effects of number of termite mounds, shrub cover, competitor density, altitude, temperature, and interactions between some of these gradients on *C. cryptus* density. We expect low densities or absence of the species in certain regions of the measured gradients (e. g. places with inadequate temperature and the lack of resources), which would be interpreted as environmental filtering at suboptimal habitats. We argue that testing non-random habitat occupation determined by environmental filtering across habitats is particularly relevant for ecology and conservation in Amazonian savannas, because they are locally rare, ecologically poorly known, and often contain complementary biodiversity to adjacent forests.

Material and methods

Study area

We sampled lizards at the Parque Estadual Monte Alegre (PEMA), a state reserve located in Monte Alegre, Pará, Brazil (headquarters at 2°03'24.9" S, 54°10'46.1" W). PEMA covers 3,678 ha (Figure 1), which main objective is to protect natural ecosystems of great ecological relevance and scenic beauty (MMA 2009). The vegetation cover of the study area is open, dominated by herbs and grasses, and showing wide local variation in tree and shrub densities (Eiten, 1983; Sarmiento, 1984; Magnusson et al., 2008). In the central region of PEMA there is a portion of secondary forest that differs substantially from the adjacent savannas, mainly because it is covered by trees up to 30 m high. We did not sample this region, because our target species (*C. cryptus*) is absent from forests. The altitude of the study area (including not-sampled forests) ranges from 10 to 250 m above sea level (MMA, 2009). The average annual temperature is 27.2 °C, and the average annual rainfall is 1700 mm, which are unevenly

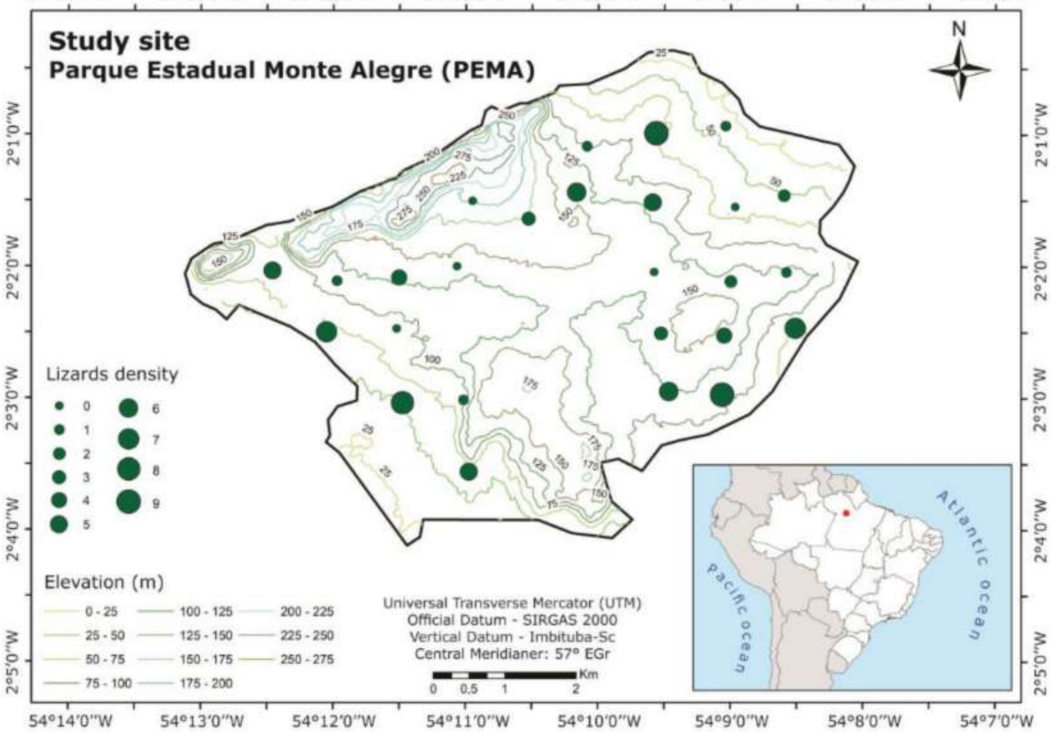

Figura 1: Study Area at Parque Estadual de Monte Alegre (PEMA), Pará, Brazil. The green circles show sampling plots, each of which 250 m long and 6 m wide, where we collected density (number of individuals) data of the racerunner lizard *Cnemidophorus cryptus*. The size of the green circles is relative to the maximum number of lizards detected in three surveys per plot. The lines mark altitudinal quotas. No plot has been installed in the central PEMA because this region is covered by forest, where *C. cryptus* is absent.

distributed throughout the year, but characterized by a rainy season between December and July, and a dry season between August and November (Moraes et al., 2005).

Sampling design and data collection

We sampled 26 plots, each of which 250 m long and 6 m wide, systematically distributed to cover 16.43 km^2 of savannas, at least 700 m apart. We followed the RAPELD sampling protocols (Portuguese acronym composed of RAP - rapid sampling plus PELD - Long Term Ecological Surveys; Magnusson et al. 2005, 2013). This method has been modified (from Gentry, 1982) to define the main axis of the plots following the natural contour lines of the terrain. This modification has been described as efficient to minimize environmental heterogeneity within the sampling units. The RAPELD method has been shown to be effective for investigating the spatial distribution of many organism groups (Magnusson et al., 2013), including Squamata reptiles (Fraga, Lima and Magnusson, 2011; Fraga et al., 2013; Faria et al., 2019).

We counted *C. cryptus* individuals in each plot using visual active search employed over 19 days of field work, from February to May 2019. Since plot size and configuration are standardized, we used numbers of individuals as a proxy for population density. We sampled all plots during the day, between 10:00 AM and 5:00 PM, on days with temperatures above 30 °C and no rain. We defined these specifications based on the climatic influence on the detection of Teiidae lizards, which are mostly diurnal and active in the warmer times of the day (Diele-Viegas et al., 2018). We limited the sampling sections by time (60 minutes per plot) and space (plot area, 1500 m^2) with two simultaneous observers. To optimize detectability, we kicked grass bushes and shrubs to encourage lizard movement. When the lizards were counted by an observer, he informed the other about the sighted lizard and made sure to chase the lizard out of the parcel's limits and avoid overestimation. This technique has been shown to be quite efficient for estimating lizard population densities in Amazonian savannas (Magnusson et al., 1996; Faria, Lima and Magnusson, 2004; Souza et al., 2020). We also reduced possible detectability effects on population density estimates by performing three temporal replications in each plot at different times of the day and using the maximum lizard density as a dependent variable in linear models. Because *C. cryptus* is easily detected visually, using the maximum of three counts made on alternate days and times is the simplest way for reducing possible sampling biases caused by detectability.

Environmental gradients

We measured six gradients potentially predictive of the *C. cryptus* spatial distribution, which we thought to be determinants of availability of refuge and thermoregulation sites, and competition levels (Table 1). We measured air temperature because it directly affects the performance of physiological and metabolic processes determining fitness for foraging, fleeing from predators, and searching for thermoregulation sites (Diele-Viegas et al., 2018). We measured the temperature during lizard sampling using a thermohygrometer positioned 10 cm above the ground under the shade. We measured altitude as a proxy for variation in vegetation cover, microclimate, and soil water stress (Luizão et al., 2004, Costa, Magnusson and Luizão, 2005; Kinupp and Magnusson 2005). We use a GPS to collect data on the elevation quota in each plot. We measured number of termite mounds because they provide resting, foraging and thermoregulating sites for *C. cryptus* (Magnusson, Franke and Kasper, 1986; Faria, Lima and Magnusson, 2004). We used total values of sighted termite mounds within plots. We measured shrub cover proportions because shrubs provide refuge from visual predators and excessively high temperatures (Magnusson, Franke and Kasper, 1986; Faria, Lima and Magnusson, 2004). We observed presence or absence of shrubs every two meters along the plot to estimate the proportion of the plot area covered by shrub vegetation. We measured the percentage of canopy cover because this gradient broadly defines the amount of solar energy reaching *C. cryptus* habitats. We used a digital camera positioned 1.5 m above the ground, with the lens positioned upwards. We captured an image of the canopy at 25 m, totaling 11 photos per plot. We processed the photos in an image editor software to verify black (closed canopy) and white (open canopy) ratios. We used average values per plot. We measured density of competing species because Teiidae lizards eventually compete for food and thermoregulation sites in Amazonian savannas (Mesquita, Costa and Colli, 2006), which ultimately could lead to local competitive exclusion (Hoffer, Bersier and Borcard, 2004). We used active visual search to account for densities of ecologically similar sympatric Teiidae lizards (*Ameiva ameiva* and *Kentropyx striata*). These competitors are selected because previous studies in the study area indicate that the species in have considerable niche overlap, favoring competition for resources (Mesquita, Costa and Colli, 2006). We quantified competitor density by summing estimated densities of both potentially competitor species. Further details on all the measured environmental and competition gradients can be found in the supplementary material (Appendix 1).

Table 1. Summary of ecological gradients used as independent variables in predictive models of *Cnemidophorus cryptus* density in Amazonian savannas. Data were collected in 26 plots (250 x 6 m each), following the natural contour lines. SD = standard deviation.

Gradient	Range	Mean	SD
Air temperature (°C)	31.1–39.9	34.27	2.22
Altitude (m)	39–195	104.4	39.15
Termite mounds (N)	0–18	2.65	4.27
Shrub cover (%)	0–30.6	13.94	7.61
Canopy cover (%)	0.35–45.69	16.33	13.28
Competitor density (N)	0–9	3.46	2.06

Data analysis

We preliminarily selected a subset of gradients as independent variables, estimating Pearson multicollinearity levels. We did not use percentage of canopy cover in the inferential model because it was 80% correlated with shrub cover. The other variables did not violate the assumptions of the statical test used and, therefore, were included in inferential analysis.

To test the influence of the gradients measured on the *C. cryptus* density estimates we generated a full multiple linear model given by $lizard\ density = a + b_1\ (temperature) + b_2\ (altitude) + b_3\ (number\ of\ termite\ mounds) + b_4\ (shrub\ cover) + b_5\ (competitor\ density) + b_6\ (altitude * temperature) + b_7\ (altitude * shrub\ cover)$. We included interactions in the full model because the effects of altitude on ectotherms are often indirect, since they reflect variation in environmental factors relevant to the ecology of active thermoregulators. For example, variation in soil structure, vegetation and consequently microclimate over altitudinal gradients is widely expected (Luizão et al., 2004). We used the ggplot2 R-package (Wickham, 2019) to plot the interaction between some of the measured gradients.

We applied a stepwise regression on the full model to select the most parsimonious subset of gradients. Less informative predictor variables were sequentially removed, and a final model was selected by the lowest Akaike Information Criterion (AIC) value. We validated the most parsimonious model by testing normality of the residual distribution using a Shapiro-Wilk test. We also evaluated the effects of spatial autocorrelation on the residuals from the most parsimonious model using a global Moran´s I test, which was applied in the ape R-package (Paradis et al., 2019), and a local Geary´s C test, which was applied in the pgirmess R-package (Giraudoux et al., 2018). We defined number of distance classes in the

Geary´s C model based on the best possible solution in terms of homogeneity in the numbers of comparisons within each distance class.

Results

We found 182 individuals of *C. cryptus*. The maximum density per plot was nine individuals (average 3.46). The occurrence frequency relative to sample size was 88.46%, and we did not find lizards in only five plots (11.54%). The most parsimonious multiple linear model was identified with temperature, altitude, number of termite mounds, and shrub cover as independent variables (AIC = 49.38). The difference in AIC between the global model and the most parsimonious model was 3.71. Detailed stepwise regression results are shown in Table 2

Table 2. Summary of a stepwise regression applied to select the most parsimonious combination of environmental gradients as predictors of *Cnemidophorus cryptus* density in Amazonian savannas. - denotes removal of a variable or interaction between variables, * denotes interaction between variables. The bold value of AIC shows the most parsimonious model.

step	Model	AIC
1	Full	53.09
2	- altitude * shrub cover	51.14
3	- competitor density	**49.38**

The most parsimonious multiple linear model explained 50% of the spatial variation in lizard density ($F_{5–20}$ = 4.12, P = 0.009). According to this model, the variation in lizard density at a local scale is not random, but negatively related to altitude (t = -3.275, P = 0.003) and temperature (t = -2.982, P = 0.007), and positively related to the number of termite mounds (t – 2.428 P – 0.02) and shrub cover (t – 2.650, P – 0.01) (Figure 2). Additionally, we found significant effects (P – 0.004) of an interaction between elevation and temperature on *C. cryptus* density. Such interaction is characterized by the fact that under high temperature conditions the effects of elevation on the *C. cryptus* density are relatively weak. However, in sites where the temperature is milder, the negative effects of altitude on lizard density are strong (Figure 3). Summarized results indicate that the density of *C. cryptus* is highly dependent on the variation in the availability of refuge, foraging and thermoregulation sites.

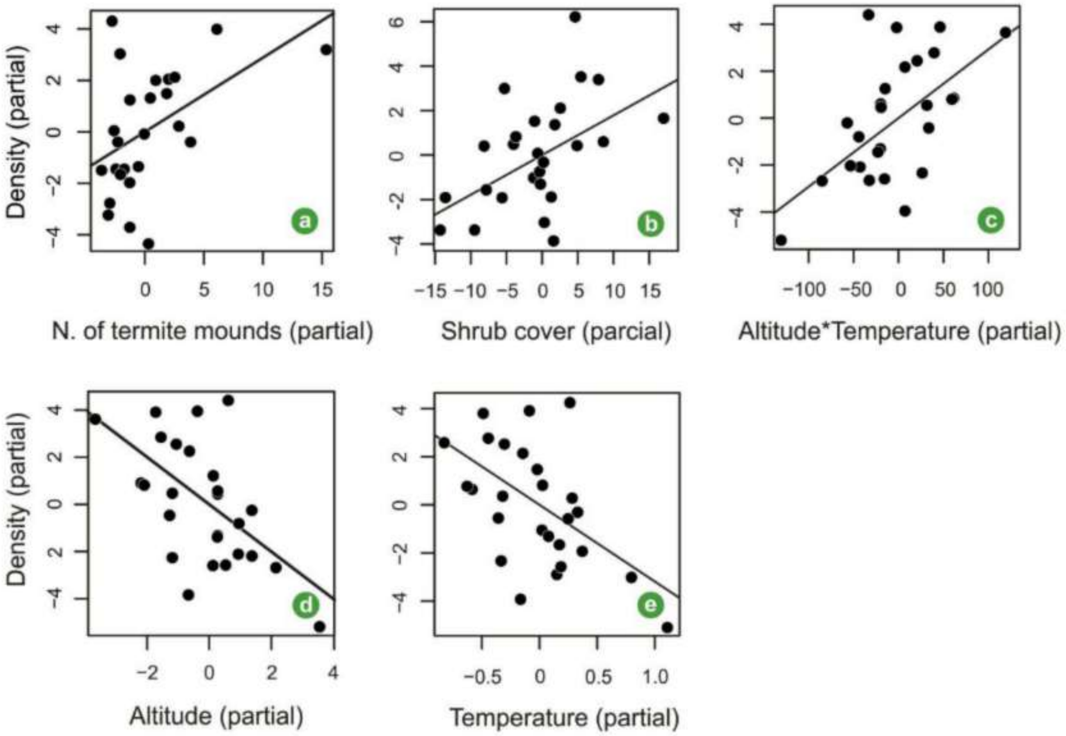

Figure 2: Relationships (partials derived from a multiple linear regression) between environmental gradients and *Cnemidophorus cryptus* density. Data were collected in 26 plots distributes along Amazonian savannas, each of which 250 m long and 6 m wide.

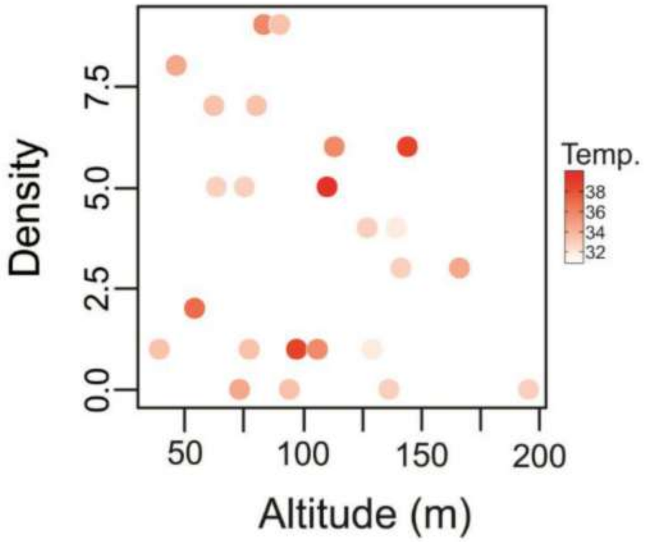

Figura 3: Effects of an interaction between altitude and temperature on *Cnemidophorus cryptus* density. Data comes from 26 sampling plots, each of which 250 m long and 6 m wide. Transparency levels in shades of red denote variation in temperature.

We validated the most parsimonious model by residuals not differing from a heoretical normal distribution (Shapiro-Wilk W = 0.97, P = 0.80), and not spatially autocorrelated. Independence of geographical distance was shown by a global Moran´s I test (P = 0.49), and a local Geary´s C test (P > 0.24 in all distance classes). Results from the Geary´s C test are summarized in Table 3.

Although we have found that some abiotic gradients predict the estimated *C. cryptus* density, we did not find any evidence that competitor density affects lizard density. Competitor density was removed by the stepwise regression from the most parsimonious linear model and showed no effect on *C. cryptus* even when we used it as an independent variable in the full model (P – 0.67).

Table 3. Summarized results of a Geary´s C test applied to evaluate spatial autocorrelation in the residuals from the most parsimonious multiple linear regression used to test effects of environmental gradients on *Cnemidophorus cryptus* density across Amazonian savannas. The Geary´s C model was set up with six geographic distance classes. N = number of pairwise comparisons per distance class; P = significance value.

Dist. (km)	Coef	P	N
0.700	1.134	0.810	90
2.079	0.940	0.300	150
3.457	1.017	0.541	146
4.836	0.948	0.343	148
6.215	0.859	0.248	86
7.593	1.031	0.538	30

Discussion

Our results showed that *C. cryptus* does not randomly occupy the sampled savannas, but densities depend on multiple interacting environmental gradients. This finding is consistent with environmental filtering assumptions that predict spatially explicit mosaics of varying habitat quality (Franklin et al. 2000, Cornwell, Schwilk and Ackerly, 2006). Specifically, we show that for a lizard species occupying open and very hot environments, the habitat selection is mediated by habitat quality defined mainly by the availability of thermoregulation sites. This is directly related to adaptation in the life history of *C. cryptus* and the environmental characteristics of the ecosystem in which the species evolved. In other savanna environments in the Amazon, the density of lizard species also varies locally depending on the spatial variation of vegetation cover (Souza et al., 2020), showing that the availability of places for thermoregulation can be decisive for the habitat selection of the species that live in these ecosystems that have naturally high temperatures.

In general, our findings converge to the clear evidence that temperature is a key factor determining the local distribution of *C. cryptus*. Temperature is widely expected to affect the performance of physiological and metabolic processes of ectotherms (Huey and Slatkin, 1976; Cano and Nicieza, 2006; Diele-Viegas et al., 2018). In our study system it was possible to show that a variation of 8 ºC (31.9–39.9 ºC) in environment temperature may be sufficient to promote local changes in the density of the lizards. However, through the set of variables selected in the best fit model, we have specifically shown that the availability of thermoregulation sites towards body heat loss limits local lizard density. This finding is supported by direct negative effects of temperature on lizard density, and also by the positive effects of shrub density and number of termite mounds. Shrubs are important thermal refuges for terrestrial lizards occupying sunny habitats such as savannas (Magnusson, Franke and Kasper, 1986; Faria, Lima and Magnusson, 2004, Souza et al., 2020), and low shrub density means that the travel distance between shrubs is relatively high, which may cause increase in predation pressure (Wilson and Cooper, 2006). Additionally, we found positive effects of number of termite mounds on *C. cryptus* density, and termites have been described as important dietary components of the species (Vitt, Zani and Caldwell, 1997; Mesquita, Costa and Colli, 2006). Termite mounts as thermal refuges are particularly relevant during the dry season when the sampled savannas experience frequent fire events (Sanaiotti and Magnusson 1995; Barbosa and Fearnside, 2005, Sousa et al., 2020). In fact, mortality by fire tends to be considerably reduced in Teiidae lizards by the availability of refuges such as termite mounds and holes in the ground (Caughley, 1985; Faria, Lima and Magnusson, 2004).

Our findings suggest that the spatial distribution of *C. cryptus* is highly dependent on the thermal quality of habitats, mainly because lizard density is limited by the availability of adequate sites to lose body heat. Thermal quality may be directly measured by the local variation in temperature, but also by the availability of thermoregulation sites, which may be quantified by vegetation cover varying along local-scale altitudinal gradients. Thermoregulation sites provided by vegetation cover often depend on soil texture and water stress, which in turn may depend on altitude (Costa, Magnusson and Luizão, 2005; Kinupp and Magnusson, 2005). Therefore, our results suggest that an interaction between temperature and altitude should be interpreted as a proxy for multivariate environmental heterogeneity predicting *C. cryptus* density. Specifically, we observed that under high temperature conditions the effects of altitude on the lizard density are relatively weak. Contrarily, in plots that have shown mild temperatures, the negative effects of altitude on lizard density were stronger. The indirect effects of altitude on the spatial structure of the sampled lizards were potentially mediated by changes in the thermal quality of the available habitats along the measured altitudinal gradient, which was partially supported in our study system by a negative correlation (Pearson r = -0, 27) between altitude and shrub cover. Therefore, our results indicate that the local density of *C. cryptus* is mediated by the availability of habitats for thermoregulation, which in turn is given by means of environmental variables that interact and promote the availability of sites for loss or gain of body heat.

Although environmental filtering determined the spatial structure of a savanna lizard, interspecific competition was not an efficient predictor of the estimated density. This finding is relevant because it suggests that biotic interspecific interactions play a minor role in determining the local spatial structure of the species studied. This is consistent with lizard species from southeastern US (Buckley and Jetz, 2010) and suggests that relationships among environmental gradients and lizard density are more likely mediated by the sensitivity of physiological processes to environmental conditions than by the carrying capacity of habitats. We argue that although levels of overlap in habitat use may be expected among the sampled lizards (Mesquita, Costa and Colli, 2006), interspecific competition has been considerably reduced by high resource availability (e.g. places for thermoregulation) favoring sympatry (Colli et al., 2003, Hibbitts et al., 2005; Rocha and Anjos, 2007). Competitive exclusion is also expected to be indefinitely delayed as potentially competing species show differences in dispersal capacity and habitat use. For instance, although *Ameiva ameiva* and *Kentropyx striata* may eventually compete with *C. cryptus* for foraging sites, competition for thermoregulation sites is unlikely, since *A. ameiva* tends to disperse to adjacent habitats under adverse conditions (e.g. fire, very high temperatures), and *K. striata* tends to climb the vegetation rather than fleeing into termite mounds (Faria, Lima and Magnusson, 2004, Ribeiro-Jr and Amaral, 2016). This is important because the habitat quality determined by the availability of thermoregulation sites (e.g. termite mounds) was the main factor structuring the *C. cryptus* population. Additionally, *A. ameiva* and *K. striata* also occur in forests, which suggests that they show higher levels of ecological plasticity compared to *C. cryptus* (Ribeiro-Jr and Amaral, 2016). Ecological plasticity often emerges from low levels of specialized habitat use, which should generate low levels of local competition (Agrawal, 2001). Therefore, although savannas are often considered as extreme portions of temperature and water stress gradients in Amazonia (Hutyra et al., 2005), a combination of high resource availability and interspecific variation in thermoregulatory behavioral strategies leads competitive interactions to be negligibly relevant for the *C. cryptus* local distribution.

Although *C. cryptus* is widely distributed in different savannas and forest edges in Amazonia (Ribeiro-Jr, 2015), our study showed that the environmental heterogeneity locally limits the species distribution. This finding suggests that species distribution models and predictions of climate change responses at macroscales such as the Amazon Basin (e.g. Pontes-da-Silva et al., 2018) or the Planet (e.g. Sinervo et al., 2010) may not be adequate to capture the fine scale at which lizards recognize distinct habitats (Gillingham et al., 2012). For instance, the plant stratification provided by shrub cover, and the availability of termite mounts may considerably reduce habitat temperature, and therefore they act as local layers of thermal buffer. These layers hardly would be detected by traditional assessments of climate effects on biodiversity, which are typically derived from macroscale environmental heterogeneity (Scheffers et al., 2014). Therefore, our local-scale ecological model highlights the importance of field validation for species distribution models based on algorithms applied to pixels derived from satellite images (Shoo, Williams and Hero, 2006; Ashcroft, Chisholm and French, 2009; Suggitt et al., 2011; Gillingham et al., 2012; Scheffers et al., 2014). Field validation should be used as a tool to optimize the accuracy of climate impact assessments on biodiversity, which is highly useful for defining management and conservation strategies. This is particularly relevant for our study area, because it is a reserve specifically designed to protect patches of Amazonian savannas. These ecosystems are regionally rare (covering less than 5% of the Amazonian territory) and are relatively fragile since they are characterized by very poor sandy soils, very high noon temperatures, and seasonal fires (Sanaiotti and Magnusson, 1995; Prance, 1996; Borghetti et al., 2019). Therefore, the biodiversity of Amazonian savannas should be considered as unique, and biotically complementary to regional ecosystem mosaics.

We showed that the spatial distribution of *C. cryptus* is not random but depends on environmental gradients associated with the thermal quality of habitats, which can only be detected at fine scales. This overall result is relevant for ecology because it provides insights into mechanisms and processes that determine the local distribution of species, and also for conservation, since lizard occurrence is not homogeneous across available habitats. We highlight that lizard ecology may vary among savannas within distinct regions in Amazonia, for example in diet or habitat use (Vitt, Zani and Caldwel, 1997; Mesquita and Colli, 2003). Therefore, the environmental gradients we found as predictors of *C. cryptus* density would not necessarily be efficient predictors in other savannas that we have not sampled. However, only by using a standardized sample design (e.g. RAPELD) it would be possible to estimate levels of variation in species-habitat relationships among savannas across different regions.

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Amphibia-Reptilia

Environmental heterogeneity of Amazonian savannas determining the local distribution of a racerunner lizard

Lourival B. V. Neto[1,*], Alfredo P. Santos-Jr[1], Pedro H. S. Ganança[1], Rafael de Fraga[2]

[1]*Programa de Pós-Graduação em Biodiversidade, Universidade Federal do Oeste do Pará, Santarém, Brazil*

[2]*Programa de Pós-Graduação em Recursos Naturais da Amazônia, Universidade Federal do Oeste do Pará, Santarém, Brazil*

*corresponding author: vasconcelosnetobio@hotmail.com

Supplementary Material

S supplementary text S1: Details of data collection on environmental variables.

Temperature was measured at the plot site during lizard sampling by a thermohygrometer positioned under the shade at the beginning of the plot. The indicated temperature was recorded at the beginning and end of each transect and the average obtained between the initial and final temperatures was considered as the local temperature value. As we performed three surveys in each plot there were three temperature values, however, for the analyses we considered only the temperature recorded during the transect with the largest number of *C. cryptus,* as was done with the density data.

The **competitor density** was accounted for the same as the density of *C. cryptus.*

The **number of termites mounds** was obtained by counting termites mounds larger than 20 cm within the limits of each plot. Smaller termites mounds have not been accounted for because they do not provide efficient lizard thermoregulation sites.

Altitude was measured on each plot with the aid of a Garmin GPSMAP 64SC ® GPS. As the plots were made to minimize relief variations in relation to the central axis of the plot, the altitude values are relatively homogeneous over the entire length, allowing the use of this variable as a predictor of density in our models.

Shrub cover was estimated by a measuring tape stretched along the right lateral line of each plot, and every 2 m a thin metal wand was positioned vertically touching the tape measure. At each touch the data was characterized by 1 for when the wand touched a bush, and 0 for when it did not touch. Binary data collected over the entire plot (125 points) was used to calculate the proportion of each plot covered by shrubs.

Canopy cover was measured with the aid of a digital camera, stabilized on a tripod 1.5 m from the floor, with the lens positioned upwards. Each 25m one canopy photo was captured, totaling 11 photos per plot. To estimate the ratio of canopy obstruction using the Photoshop CS6® softwere, we first stripped the colors from the photos to black and gray. Later these grayscale images were converted to high contrast black and white through the threshold function. From this command all pixels lighter than the threshold were converted to white (component without vegetation), while all darker pixels were converted to black (component with vegetation). To quantify the proportion of the obstructed canopy, we calculate the ratio of black pixel to total pixel in the image. The value of the tree cover variable in each plot was the average proportion obstructed by vegetation in each image.

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