INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA – INPA

PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA (ECOLOGIA) – PPG-ECO

EFEITO DE FATORES HISTÓRICOS E AMBIENTAIS SOBRE A COMPOSIÇÃO E DIVERSIDADE DE ASSEMBLEIAS DE LAGARTOS NO SUDOESTE DA AMAZÔNIA BRASILEIRA

GABRIELA MARQUES PEIXOTO

Manaus, Amazonas
Julho, 2019

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Tese apresentada ao Instituto Nacional de Pesquisas da Amazônia como parte dos Requisitos para obtenção do título de Doutor em Biologia (Ecologia).

Manaus, Amazonas
Julho, 2019

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Após a exposição, o(a) discente foi argüido(a) oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

☒ APROVADO(A)　☐ REPROVADO(A)

☒ POR UNANIMIDADE　☐ POR MAIORIA

Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

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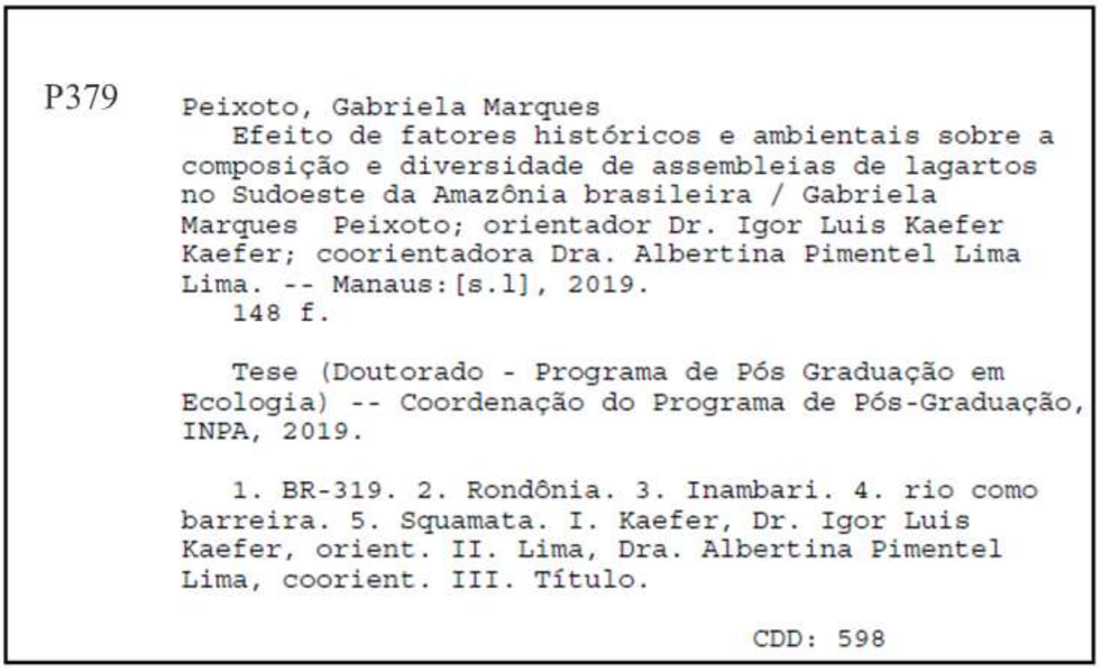

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SINOPSE

Foram investigados a composição e a influência de fatores históricos e ecológicos sobre a estruturação de assembleias de lagartos na Amazônia. Para isso, foram amostradas múltiplas unidades padronizadas distribuídas na região sudoeste da Amazônia brasileira. Os resultados mostraram que gradientes ambientais de ordem estrutural e climática atuaram sobre a composição e riqueza funcional das assembleias de lagartos da região entre os rios Purus e Madeira. Também foram demosntrado o efeito hierárquico de fatores históricos e ambientais sobre a ocorrência e distribuição das espécies na região do alto Rio Madeira.

Palavras-chave: BR-319, heterogeneidade ambiental, Inambari, rio como barreira, Rondônia, Squamata.

Dedico ao meu filho Daniel,
e aos meus pais Luiz e Tânia.

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Aos meus pais por me fornecerem um porto seguro e incentivo para nunca desistir dos meus sonhos.

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Amazônia

"Nos teus rios quero navegar
O teu ar respirar
Tua beleza contemplar
Embalando os sonhos meus
De ver-te sempre verdejante
Parte integrante
Deste país gigante
Que luta para manter-te inteira
Intacta, linda, majestosa
Amazônia, pulmão do mundo
Nossa sempre serás!"

Mazé Carvalho

Resumo

Estudos ecológicos com amostragem padronizada conduzida em ampla escala espacial podem propiciar a compreensão de padrões e processos até então desconhecidos na estruturação de assembleias megadiversas, como as Neotropicais. Nesta tese apresentamos uma análise baseada em múltiplos sítios de amostragem instalados ao longo de um transecto de aproximadamente 1000 km, no interflúvio Purus-Madeira e nas margens do Alto Rio Madeira, a fim de compreender a distribuição das assembleias de lagartos desta região. No primeiro capítulo caracterizamos a composição e abundância da assembleia de lagartos em 10 módulos de amostragem ao longo da rodovia BR-319. Contabilizamos 25 táxons pertencentes a oito famílias, distribuídas de forma heterogênea ao longo do interflúvio. Também destacamos a importância de levantamentos de fauna para futuras medidas de conservação das espécies de lagartos de regiões interfluviais frente ao crescente impacto antrópico que a Amazônia enfrenta. No segundo capítulo avaliamos como a heterogeneidade ambiental, principalmente associada às Florestas Ombrófilas Abertas e Densas da região do interflúvio Purus-Madeira, molda as assembleias de lagartos. Para isso, quantificamos as assembleias através de medidas taxonômicas e funcionais em quatorze módulos de amostragem. Observamos que fatores ambientais como o solo, vegetação e pluviosidade variam em escala biogeográfica ao longo do interflúvio e influenciam o padrão de ocorrência das espécies e riqueza funcional das assembleias. Desse modo, detectamos um padrão de substituição de espécies em larga escala moldado pela influência de filtros ambientais. No terceiro capítulo investigamos, em diferentes escalas, a influência de fatores históricos e ecológicos na estruturação das assembleias de lagartos da região do alto Rio Madeira. Para isso foram amostradas 83 parcelas ao longo das margens leste e oeste do rio. Em escala regional, o alto rio Madeira atua como uma barreira biogeográfica para 29,6% das espécies. Diferentemente, a atuação de filtros ambientais explica a estruturação das assembleias em escala local. Este estudo, pioneiro em abranger uma escala geográfica tão ampla na ecologia de lagartos amazônicos, sugere que fatores históricos e ecológicos apresentam efeitos hierárquicos na determinação da estruturação espacial das assembleias. Assim como a presente investigação, futuras pesquisas abordando diferentes escalas de acordo com métodos padronizados de amostragem prometem elucidar processos e padrões relacionados à heterogênea distribuição espacial da biodiversidade amazônica.

Historical and environmental factors on the composition and diversity of lizard assemblages in the southwest of the Brazilian Amazon

Abstract

Ecological studies with standardized sampling conducted on a large scale can provide an understanding of patterns and processes hitherto unknown in the structuring of megadiverse assemblages such as those from the Neotropics. In this thesis we present an analysis based on multiple sampling sites installed along a transect of approximately 1,000 km, in the Purus-Madeira interfluve and on the banks of the Upper Madeira River, in order to understand the distribution of the lizard assemblages of this region. In the first chapter we characterized the composition and abundance of the lizard assemblage in 10 sampling modules along the BR-319 highway. We counted 25 taxa belonging to eight families, distributed heterogeneously along the interfluve. We also we emphasize the importance of faunal surveys for future conservation measures of the species of lizards of interfluvial regions in face of the increasing anthropic impact in Amazonia. In the second chapter we evaluated how the environmental heterogeneity, mainly associated with the Open and Dense Ombrophilous Forests of the region of the Purus-Madeira interfluve forms the lizard assemblages. For this, we quantified the assemblies through taxonomic and functional measures in fourteen sampling modules. We observed that environmental factors such as soil, vegetation and rainfall vary in biogeographic scale along the interfluve and influence the pattern of occurrence of species and functional richness of the assemblages. Thus, we detected a large-scale species substitution pattern shaped by the influence of environmental filters. In the third chapter we investigated, at different scales, the influence of historical and ecological factors in the structure of lizard assemblages in the region of the upper Madeira River. For this, 83 plots were sampled along the east and west banks of the river. At the regional level, the upper Madeira River acts as a biogeographic barrier to 29.6% of the species. In contrast, the performance of environmental filters explains the structure of the assemblages at a local scale. This study, which pioneered such a wide geographic scale in the ecology of Amazonian lizards, suggests that historical and ecological factors have hierarchical effects in determining the spatial structuring of assemblages. Such as the present investigation, future research addressing different scales according to standardized sampling methods promises to elucidate processes and patterns related to the heterogeneous spatial distribution of Amazonian biodiversity.

Sumário

Lista de Tabelas

Lista de Figuras

Capítulo 1:

Capítulo 2:

Capítulo 3:

INTRODUÇÃO GERAL

O conhecimento da biodiversidade global e seus mecanismos de funcionamento tem fundamental relevância para atuações conservacionistas (Elith e Leathwick, 2009), especialmente diante da intensificação das intervenções humanas aos ecossistemas naturais e do iminente declínio na riqueza de espécies (Dixo, 2001; Cole *et al.* 2014; Esther *et al.,* 2014; Bernard *et al.,* 2014). No entanto, a biodiversidade global está distribuída de maneira irregular entre os continentes, com uma expressiva concentração de espécies na região Neotropical, a qual que se estende desde o México ao sul do continente americano (Fine *et al*., 2014; Pavan *et al.,* 2016). Tal riqueza torna estas regiões primordiais para estudos ecológicos que propiciem a compreensão dos mecanismos e processos, ainda desconhecidos pela ciência, que atuam nos padrões de formação das assembleias biológicas (Fraterrigo *et al*., 2004; Gardner *et al*., 2008).

Com posição de destaque na região Neotropical, a floresta Amazônica é considerada a maior e mais diversa floresta tropical úmida amplamente conectada do mundo, ocupando uma área equivalente a seis milhões de km^2 ao longo de nove países da América do Sul (Haseyama e Carvalho, 2011). No Brasil, o Bioma chega a ocupar mais de 40% do território nacional, desempenhando papel importante na regulação do clima, regime hidrológico, e do estoque de carbono terrestre (Nobre, 2002; Fearnside, 2006; Balmford e Whitten, 2003). Por apresentar alta complexidade estrutural, principalmente em decorrência da dinâmica geológica e climática impostas ao bioma ao longo do tempo (Hoorn *et al.,* 2010), a região é atualmente considerada um amplo mosaico de formações distintas, com alta heterogeneidade ambiental, o que torna essa riqueza estrutural um dos principais responsáveis pela magnitude de sua biodiversidade (Sombroek, 2000; Schietti *et al*., 2014).

Para compreender os padrões atuais de ocorrência das espécies amazônicas, distintas hipóteses, muitas delas não mutuamente exclusivas, têm sido propostas e submetidas a testes, tais como as mudanças geomorfológicas históricas, flutuações climáticas e a atuação de barreiras à dispersão (Wallace, 1852; Haffer, 1969; Cracraft, 1985; Bush, 1994; Racheli e Racheli, 2004; Ribas e Miyaki, 2004; Wüster *et al*., 2005; Aleixo *et al*., 2006; Antonelli *et al*., 2009; Hoorn *et al.,* 2010; Roddaz *et al*., 2010; Rossetti *et al*., 2014; Caputo e Soares, 2016). A distribuição de muitos táxons amazônicos coincide com os limites geográficos dos grandes interflúvios da Bacia, as denominadas áreas de endemismo (Cracraft e Prum, 1988; Gascon *et al*., 2000; Ron, 2000;

Silva *et al.*, 2005; Ribas *et al.*, 2012; Boubli *et al.*, 2014; Smitth *et al.*, 2014; Fouquet, *et al.*, 2015), mas tal padrão não é observado para todos os grupos (Godinho e Da Silva, 2018; Santorelli *et al.*, 2018). Desse modo, as complexas histórias evolutivas das espécies constituem um ponto primordial para a compreensão dos mecanismos pelos quais ocorrereu a diversificação e consequente acúmulo de espécies para vários grupos taxonômicos, bem como para a associação com as principais teorias biogeográficas reconhecidas acerca da evolução da paisagem amazônica (Leite e Rogers, 2013; Smith *et al.*, 2014; Antonelli *et al.*, 2010), já que diferentes organismos podem responder de formas distintas aos mesmos eventos (Ávila-Pires *et al.*, 2012, Godinho e Da Silva, 2018). De fato, estudos acerca dos processos causadores da diversificação nesta região têm sugerido o envolvimento sinergístico de forças históricas e ecológicas (Hoorn *et al.*, 2010; Losos *et al.*, 2013; Dias-Terceiro *et al.*, 2015; Quintero *et al.*, 2015; Moraes *et al.*, 2016).

Processos ecológicos decorrentes de interações entre elementos bióticos e abióticos, ao longo de paisagens contínuas ou *clines* geográficos, podem gerar especiação mesmo na ausência de alopatria (Tuomisto e Ruokolainen, 1997). Estes mecanismos se enquadram no que conhecemos como hipótese dos gradientes (Endler, 1977), pelo qual populações tendem a diferenciar-se por meio de isolamento por distância, facilitado pelas adaptações ecológicas à heterogeneidade ambiental, como o modo de dispersão e aspectos reprodutivos (Garda *et al.*, 2013). Mesmo dentro de cada área de endemismo as especiações ecológicas podem ocorrer (Ferrão *et al.*, 2017), já que estas regiões se configuram como subunidades ambientais por apresentarem componentes horizontais, verticais e qualitativos que permitem a presença de diferentes microhábitats (da-Silva *et al.*, 2005; Ximenes, 2008). Tal cenário torna regiões interfluviais sistemas promissores para a investigação da influência de filtros ecológicos na composição e estruturação espacial da biota amazônica, seja por meio de abordagens taxonômicas ou relacionadas à funcionalidade ecossistêmica dos organismos (Condit *et al.* 2002; Maldonado *et al.*, 2012; Ortiz *et al.*, 2018).

Os lagartos contituem bons bioindicadores para investigar o efeito de gradientes ecológicos/ambientais, e são comumente usados em modelos ecológicos por compreender um grupo abundante, com mobilidade restrita, e com alta partilha espacial de condições e recursos (Schoener, 1974; Werneck e Colli, 2006; Werneck *et al.*, 2009; Camargo *et al.*, 2010). Estima-se a ocorrência de aproximadamente 158 espécies de lagartos para a Amazônia brasileira (Censo da Biodiversidade/Museu Goeldi, 2019). Porém, ao longo dos anos novas espécies são descritas ou tem suas distribuições geográficas ampliadas, o que indica que a diversidade ainda deve ser subestimada (Rodrigues e Ávila-Pires, 2005; D'angiolella *et al.*, 2011; Peloso *et al.*, 2011; Murphy e Jowers, 2013; Murphy *et al.*, 2016; Oliveira *et al.*, 2016). Este cenário configura um desafio para a identificação dos principais padrões biogeográficos para os lagartos, já que muitas espécies apresentam elevado grau de diversidade críptica, necessitando abordagens integrativas envolvendo morfologia, ecologia, comportamento e diversidade molecular (Murphy e Jowers, 2013; Sturaro *et al.*, 2018).

Um dos principais padrões regionais observados para os lagartos amazônicos é a substituição de espécies com distribuição restrita às partes Ocidental-Oriental ou Leste-Oeste da Amazônia (Ávila-Pires, 1995; Ávila-Pires *et al.*, 2012). Entretanto, um padrão único de distribuição geográfica para lagartos amazônicos ainda permanece desconhecido (Souza *et al.*, 2013), e muitas lacunas precisam ser preenchidas. Localmente, o padrão de distribuição das espécies amazônicas parece estar relacionado aos aspectos da heterogeneidade dos ambientes, e diversas associações já foram descritas como determinantes na estruturação destas assembleias, como o efeito da fragmentação (Bittencourt, 2008), abertura de dossel e incidência de luz (Lobão, 2008; Moraes, 2008), densidade de árvores (Pinto, 2006; Vitt *et al.*, 2007; Bittencourt, 2008), profundidade da serrapilheira (Pinto, 2006; Vitt *et al.*, 2007; Bittencourt, 2008), porcentagem de argila no solo (Pinto, 2006), associação a áreas ripárias (Faria *et al.*, 2019), altitude e inclinação do terreno (Pinto, 2006; Lobão, 2008; Moraes, 2008), além da disponibilidade de alimentos (Lobão, 2008; Moraes, 2008). No entanto, devido às concentrações destes estudos em determinadas áreas da Amazônia Central, várias localidades ainda precisam ser inventariadas e estudadas quanto aos mecanismos de montagem das assembleias, principalmente em escalas mais amplas, já que grande parte destes estudos foi limitada a pequenas e médias escalas.

Considerando o incipiente conhecimento sobre os padrões de distribuição das espécies para muitas áreas da Amazônia e o avanço dos impactos antrópicos que o bioma vem enfrentando ao longo das décadas (Fearnside e Graça, 2006; Bernarde *et al.*, 2008; Fearnside *et al.*, 2014), esta tese, com seus três capítulos apresentados a seguir, vem ampliar o conhecimento sobre os lagartos de zonas interfluviais e compreender os mecanismos que atuam sobre as distribuições das assembleias do Interflúvio Purus-Madeira e do Alto rio Madeira. Com o emprego de um delineamento amostral de um transecto de aproximadamente 1000 km, o qual foi capaz de abranger grande parte da paisagem, e possível revelar padrões ainda inéditos relacionados à distribuição de espécies e montagem de assembleias de lagartos amazônicos.

OBJETIVOS

Objetivo geral

Investigar os potenciais efeitos de fatores ecológicos e históricos sobre as assembleias de lagartos em ambientes florestais de terra firme na Amazônia.

Objetivos específicos:

- ✓ **Capítulo 1:** Caracterizar a distribuição geográfica e a abundância das espécies de lagartos presentes ao longo da rodovia BR-319 na região do Interflúvio Purus-Madeira, gerando uma listagem de espécies inédita para a região.
- ✓ **Capítulo 2:** Compreender os efeitos de gradientes ambientais de ordem estrutural e climática sobre a composição e diversidade funcional das assembleias de lagartos da região entre os rios Purus e Madeira.
- ✓ **Capítulo 3:** Testar, através de escalas espaciais hierárquicas, o efeito de fatores históricos e ambientais sobre a ocorrência e distribuição das espécies de lagartos da região do alto Rio Madeira.

Capítulo 1

Gabriela Marques Peixoto; Pedro Henrique Leitão; Igor Luis Kaefer; Albertina Pimentel Lima. 2019. The lizards along the road BR-319 in the Purus-Madeira interfluve, Brazilian Amazonia (Squamata, Lacertilia). *Herpetology Notes* 12: 689-697.

The lizards along the road BR-319 in the Purus-Madeira interfluve, Brazilian Amazonia (Squamata, Lacertilia)

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Abstract. Here we present data on the identity and geographic distribution of lizard taxa in the Purus-Madeira interfluve, along the road BR-319 in Brazilian Amazonia. We sampled 10 modules located at least 40 kilometres from each other. Data collection was performed through active search on vegetation and leaf-litter along 250 m-long transects, and by occasional encounters. Twenty-five taxa from 16 genera and eight families were recorded. The present assessment reinforces the importance of this area to the conservation of Amazonian lizards and should be considered as basis for studies of ecology and environmental impact regarding lizard communities in this threatened region.

Keywords. Amazonas, Brazil, Inambari, Reptiles, Species richness

Introduction

Despite the relevance of the Amazon Forest to the world biodiversity, studies regarding the biodiversity of Amazonia are scattered in the literature, reflecting on incomplete knowledge about the patterns of distribution and identity of species (Magnusson et al., 2016). Since the 1990s, a huge portion of the Amazon Forest has been irreversibly deforested mainly due to farming and logging activities (Fearnside et al., 2009). For the year 2016, in comparison with 2015, it is possible to identify an advance of 29% (6,207 km²) of deforestation for the entire Brazilian Amazonia (INPE, 2016).

Squamate reptiles are, in general, vulnerable to environmental disturbances and degradation, making information about the distribution of these species essential to understand and conserve the Amazonian herpetofauna (Böhm et al., 2013). The richness of lizard species in the Brazilian Amazonia is estimated in 138 described species (Ribeiro-Júnior, 2015; Ribeiro-Júnior and Amaral, 2016). However, this number may be underestimated because most of the studies were performed on the proximity of large urban centres (Rodrigues and Ávila-Pires, 2005; Vitt et al., 2008; Turci and Bernarde, 2008; Ávila-Pires et al., 2018). Recent taxonomic assessments indicate high cryptic diversity in Amazonian species (e.g., Ávila-Pires and Hoogmoed, 2000; Peloso et al., 2011; Murphy and Jowers, 2013; Murphy et al., 2016; Ferrão et al., 2016; Oliveira et al., 2016; Melo-Sampaio et al., 2018), leading to the description of new species or changes in taxonomic status (e.g. Bergmann and Russell, 2007; Geurgas and Rodrigues, 2010; D'Angiolella et al., 2011).

The Purus-Madeira interfluve, where the road BR-319 was constructed during the decade of 1970, is a site of high biodiversity, both described and undescribed (Ferrão et al., 2017; Ortiz et al., 2018), located in an important endemism area called Inambari (Cracraft, 1985).

It is estimated that most of this biodiversity is threatened by the construction and recent paving of part of the road, which crosses the region linking the city of Manaus, in the state of Amazonas, to the city of Porto Velho, in the state of Rondônia (Fearnside and Graça, 2006). Simulations to assess the impacts of the road construction associated with human settlements predicted a resulting deforestation of up to 5.4 million hectares by 2050, reinforcing the need of mitigating measures to avoid the loss of biological diversity (Maldonado et al., 2012). In the face of such prospect of increase in the frequency of anthropic disturbances and imminent loss of biodiversity, we sampled multiple standard units over a transect of 620 km in the Interfluve Purus-Madeira aiming to: 1) inventory the lizards (Squamata, Lacertilia); and 2) characterize the geographic distribution of the taxa within this interfluvial zone.

Materials and Methods

Study site. The research was conducted along the road BR-319, which crosses the Purus-Madeira interfluve, distributed almost linearly over 620 km, from central Amazonia (municipality of Careiro da Várzea, state of Amazonas) to southwest Amazonia (municipality of Humaitá, state of Amazonas). The area has mainly a plane topography and the elevation ranges from 30 to 50 m. Approximately 90% of the area is composed of lowland ombrophilous dense forest, with occurrence of medium to large-sized trees and clean forest understory. Such formation is limited to high temperatures (25°C on average,) high rainfall (well distributed throughout the year), and the dry period varies from 0 to 60 days per year. In the southern region of our sample (near the municipality of Humaitá), the interfluve is formed by ombrophilous open forest and present more than 60 dry days per year (Maldonado et al., 2012).

We used 10 research modules installed along the BR-319 according to the RAPELD- Rapid Assessments and Long-term Ecological Research (in Portuguese, *Pesquisas Ecológicas de Longa Duração Associadas a Levantamentos Rápidos*) (Magnusson et al., 2005). These modules are part of a network of permanent standardized transects installed in the Amazon by *Programa de Pesquisas em Biodiversidade* (Biodiversity Research Program) of the Brazilian Science, Technology, Innovations and Communications Ministry (Magnusson et al., 2013). The 10 modules are located 40 to 100 kilometres from each other (Table 1) and are composed of two 5 km-long tracks (Figure 1). Each track contains 5 terrestrial transects (250 meters long) with standardized distance of one km between neighbouring transects. Each transect follows the contour line of the terrain, minimising the edaphic variation within the transects. The coordinates were obtained through GPS Garmin GPSMAP 76CSx (Datum WGS 84).

Data Collection. The lizard assemblage surveys lasted from October 2010 to September 2011. In order to maximize the taxa detection and to minimize false absences, we employed the visual transect census method using active search both in the vegetation and in the leaf-litter (Crump and Scott, 1994). In addition, we recorded occasional encounters along the transect displacement in the modules. The visual transect census consisted of inspecting the environment by looking for terrestrial, arboreal and semi-arboreal lizards throughout the 250 m of each transect. The active search in the litter consisted of rummaging the substrate (leaf litter, stems and organic matter remnants) along the transect. The sampling team consisted of one researcher and one assistant properly trained for lizard sampling. Due to the logistical restrictions faced in the region — difficulty of access to sections of the highway that are not paved and financial costs — four modules installed closer to the municipality of Manaus (M1, M2, M3, and M4) were sampled in all three campaigns, while the remaining modules were sampled just during the first campaign. Campaign I occurred between October 24 and

December 5, 2010, with a total of 100 hours/observer and 312 km covered throughout the sampling modules; Campaign II occurred from January 9 to 24, 2011 with 40 hours/observer and 128 km of modules covered; Campaign III occurred from September 12 to 27, 2011, with 40 hours/observer and 135 km of modules covered. The active search in each transect had a duration of one hour. Considering the displacement between transects, the daily effort varied, but averaged eight hours of active search per day. The sampling was concluded after 75 days of fieldwork, totalling 180 hours/observer (360 sampling hours) in the transects, with a total displacement of 1,150 km within the modules, and a total of 1,234 km traveled when considering the distance between the base camps and the sampling modules. The captured specimens were killed with peritoneal injection of 10% lidocaine chloralhydrate, and fixed in 10% formaldehyde for 24 hours, subsequently transferred to 70% ethanol and deposited at the herpetological collection of the Instituto Nacional de Pesquisas da Amazônia (INPA-H) in the municipality of Manaus, state of Amazonas, Brazil. The identification of all taxa followed the taxonomic keys available in Peters and Donoso-Barros (1970), Ávila-Pires (1995), and Vitt et al. (2008). The collection licenses were granted by ICMBio/IBAMA under permits 25685 and 29069.

Results

Twenty- five taxa (including *Plica umbra* subspecies) of eight families and 16 genera were sampled along the 10 modules (Figure 2; Appendix 1). The family Gymnophthalmidae was represented by six taxa: *Arthrosaura reticulata* (O'Shaughnessy, 1881); *Cercosaura argula* Peters, 1863; *Cercosaura ocellata* (Wagler, 1830); *Loxopholis osvaldoi* (Ávila-Pires, 1995); *Loxopholis percarinatum* (Müller, 1923); and *Tretioscincus agilis* (Ruthven, 1916). The family Dactyloidae was represented by five taxa: *Anolis fuscoauratus* D'Orbigny, 1837; *Anolis ortonii* Cope, 1868; *Anolis punctatus* Daudin, 1802; *Anolis tandai* Ávila-Pires, 1995; and *Anolis* *transversalis* Duméril, 1851. The family Teiidae was represented by four taxa: *Ameiva ameiva* (Linnaeus, 1758); *Kentropyx altamazonica* (Cope, 1876); *Kentropyx pelviceps* (Cope, 1868); and *Tupinambis cuzcoensis* Murphy, Jowers, Lehtinen, Charles, Colli, Peres, Hendry and Pyron, 2016. The family Sphaerodactylidae was represented by three taxa: *Chatogekko amazonicus* (Andersson, 1918); *Gonatodes hasemani* (Griffin, 1917); and *Gonatodes humeralis* (Guichenot, 1855). Scincidae was represented by two taxa: *Copeoglossum nigropunctatum* (Spix, 1825); and *Varzea bistriata* (Spix, 1825). Tropiduridae was represented by three taxa: *Plica umbra umbra* (Linnaeus, 1758); *Plica umbra ochrocollaris* Spix, 1825; and *Uranoscodon superciliosus* (Linnaeus,1758). The family Alopoglossidae was represented by one taxon: *Alopoglossus atriventris* Duellman, 1973. The family Phyllodactylidae also presented one taxon: *Thecadactylus solimoensis* Bergmann and Russell, 2007 (Table 2).

The locations showing the highest taxa richness were modules M1 with 15 taxa (60% of the taxa) and M2 with 13 taxa (52%), followed by M3 with with 11 taxa (44%) and M10 with 10 taxa (40%). M4 with 9 taxa (36%), M5 with 7 taxa (28%), a and modules M8 and M9 with 6 taxa each (24%) (Figure 3). The modules with the lowest number of species were M06 and M07 with five sampled taxa (20%). The module M10 was sampled only once, but some taxa were found only in this module: *Cercosaura ocellata, Gonatodes hasemani, Tretioscincus agilis,* and *Tupinambis cuzcoensis.* Two taxa (*Chatogekko amazonicus* and *Kentropyx altamazonica*) were recorded in all modules, whereas *Ameiva ameiva* was recorded in 9 out of 10 modules (Table 2).

Discussion

Variations in local species richness and composition in the Amazon Basin would rely on its configuration, which is a mosaic of distinct phytophysiognomical regions (Schietti et al., 2014). Such variations also result from the different geological ages and formations among distinct fractions of the basin, which leads to historical evolutionary differences among areas and, consequently, their biotas (Wesselingh et al., 2010; Ortiz et al., 2018). Structural complexity of the vegetation in the Madeira-Purus interfluve is strongly affected by groundwater and soil characteristics (Moulatlet et al., 2014; Schietti et al. 2014), which may also explain differences in faunal composition along the gradient (Marciente et al., 2015).

The number of taxa found in this study is consistent with other studies performed in Brazilian Amazonia which recorded a minimum local richness of 22 species and a maximum of 44 species of lizards per inventory area (Ávila-Pires et al., 2009; Magalhães-Silva et al., 2011; Prudente et al., 2013; Ribeiro-Júnior and Amaral, 2016). Studies in the Amazonian biome that showed higher species richness were carried out using complementary techniques such as pitfall traps, were conducted in environments with greater habitat heterogeneity including flooded and nonflooded forests, or considered seasonal variability (e.g. Waldez et al., 2013; Almeida et al., 2015). In relation to the richness of lizards by modules, we can associate the greater values of the modules M1–3 with the highest sampling efforts employed in these sites. However, module M4 was also sampled three times and showed fewer taxa. This suggests that the northernmost modules of the interfluve have richer lizard assemblages. Another relevant exception is module M10, which presented a richness (10 taxa) that resembles the richness found in M4 (nine taxa), although module M10 was sampled only once. This module is inserted within the open ombrophylous forest phytophysiognomy, unlike the other modules that are inserted within dense ombrophylous forest, and possibly has greater environmental heterogeneity, which may explain the presence of exclusive taxa in this module.

A study carried out along Purus-Madeira interfluve in five conservation units between November 2012 and November 2013 registered 26 species of lizards, distributed among 19 genera and eight families (Almeida et al., 2015). The broadest herpetological survey conducted in the region was the Environmental Impact Assessment (EIA) of Jirau and Santo Antônio Hydroelectric Power Plants in the state of Rondônia (upper Madeira river), with a larger number of species (n = 33) recorded (Lima et al., 2004). Among the sampled species, five were not observed in our study, despite the proximity of the areas: *Cnemidophorus* aff. *lemniscatus* Linnaeus, 1758; *Enyalioides laticeps* (Guichenot, 1855); *Enyalius leechii* (Boulenger, 1885); *Kentropyx calcarata* (Spix, 1825); and *Plica plica* (Linnaeus,1758). During the EIA of the road BR-319 (UFAM/DNIT, 2009), 23 lizard species of 15 genera and six families were recorded, and just four of them were not sampled in our study: *Alopoglossus angulatus* (Linnaeus, 1758); *Iphisa elegans* Gray, 1851; *Kentropyx calcarata*; and *Ptychoglossus brevifrontalis* Boulenger, 1912. Except for *Kentropyx calcarata*, the absence of the above-mentioned species in our survey is probably due to the active sampling method employed here (without use of pitfall and funnel traps), which is not adequate to detect species with fossorial or secretive habits (Andrade et al., 2013).

On the other hand, four species recorded in this study were not listed in the EIA conducted along the BR-319 (UFAM/DNIT, 2009): *Copeoglossum nigropunctatum*, *Leposoma osvaldoi*, *Thecadactylus solimoensis*, and *Varzea bistriata*. The sampling of the EIA was restricted to a section of the road (km 285 to km 615). In fact, the species *Thecadactylus solimoensis* and *Varzea bistriata* were previously recorded only for the lower Purus River, at Piagaçu-Purus Sustainable Development Reserve, which is located 84 km distant from the module 5 of our study (Waldez et al., 2013).

Regarding the record of *Plica umbra ochrocollaris*, it is known that *P. umbra* comprises more than one independent lineage, with distinct evolutionary units along different areas of endemism in the Amazon. This suggests that these lineages may represent distinct species, including multiple taxa within the Purus-Madeira interfluve (Carvalho et al., 2006; Oliveira et al., 2016).

Large body-sized species such as *Dracaena guianensis* (Daudin, 1802) and *Crocodilurus amazonicus* (Spix, 1825) were not observed in the present study, probably because they are associated to the environments of flooded forest (Almeida et al., 2015). Hence, the sampled environments along the road BR-319 are probably not suitable to these species, since most of the modules are normally installed in areas of plane topography and not subjected to flooding. Landscape management and conservation strategies require an understanding of species distributions. This understanding also includes predictions of species' distributions under anthropogenic impacts. These approaches are essential for the long-term maintenance of the forest and its biodiversity (Fearnside et al., 2009). Amazonian lizards are likely under threat because of human disturbance, given the pace of modification in the Amazon Basin and the lack of public policies for the effective conservation of biodiversity (Magnusson et al., 2018). The construction of roads in natural environments, such as BR 319, is an alarming scenario for biological conservation because it tends to favor the illegal colonization of the region, thus allowing the development of activities such as mining, illegal hunting, and land real estate speculation (Laurance and Balmford, 2013). These activities may affect the local fauna, especially species that respond rapidly to changes in forest cover (Ferrão et al., 2016), and contribute to the high number roadkills of wild animals (Brum et al., 2018). In this context, this study complements the most recent list on the distribution of lizards in the Brazilian Amazon (Ribeiro-Júnior and Amaral, 2016). In addition, it reinforces the importance of the Purus-Madeira interfluve for the conservation of Amazonian reptiles, a region whose biodiversity is rich, with great potential for new discoveries (De-França et al., 2011; Ferrão et al., 2016; De-Abreu et al., 2018). Finally, this list can be used as a basis for future ecological and environmental impact studies in Amazonian lizard assemblages.

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Table 1. Location of survey modules (M1–10) in the Purus-Madeira interfluve, Brazilian Amazonia.

Location in highway	**Geographic coordinates**	**Elevation**
M1: Purupuru, BR-319 km 34	-3.2112°S, -59.5120°W	35 m
M2: Manaquiri, BR-319 km 100	-3.4122°S, -60.2062°W	42 m
M3: Taboca, BR-319 km 168	-4.1739°S, -60.4343°W	43 m
M4: Taquara, BR-319 km 220	-4.2234°S, -60.5655°W	47 m
M5: Igapó-açu, BR-319 km 260	-4.3634°S, -61.1501°W	52 m
M6: Orquestra, BR-319 km 300	-4.5922°S, -61.3347°W	48 m
M7: Rio Novo, BR-319 km 350	-5.1558°S, -61.5558°W	59 m
M8: Jarí, BR-319 km 450	-5.5726°S, -62.2920°W	70 m
M9: Aracá, BR-319 km 540	-6.3347°S, -62.5611°W	77 m
M10: Puruzinho, BR-319 km 620	-7.1210°S, -63.1306°W	49 m

Table 2. Lizard taxa sampled throughout the modules (M1–M10) installed along the road BR-319 and the distance sampled by module in each of the three campaigns. The symbol "+" indicates the presence of the species and "-" indicates its absence.

Family/ Taxa	**M 1**	**M 2**	**M 3**	**M 4**	**M 5**	**M 6**	**M 7**	**M 8**	**M 9**	**M 10**
ALOPOGLOSSIDAE										
Alopoglossus atriventris (Duellman, 1973)	-	+	+	-	-	-	-	-	-	-

DACTYLOIDAE										
Anolis fuscoauratus D'Orbigny, 1837	+	+	+	+	+	-	+	+	-	+
Anolis ortonii Cope, 1868	-	-	+	-	-	-	-	-	-	-
Anolis punctatus Daudin, 1802	+	-	-	-	-	-	-	-	-	-
Anolis tandai Ávila-Pires, 1995	+	+	+	+	+	-	+	+	-	-
Anolis transversalis Duméril, 1851	-	-	+	-	-	-	-	-	-	-
GYMNOPHTHALMIDAE										
Arthrosaura reticulata (O'Shaughnessy, 1881)	+	-	-	-	-	-	-	-	-	-
Cercosaura argula (Peters, 1863)	-	+	-	-	-	-	-	-	-	-
Cercosaura ocellata (Wagler, 1830)	-	-	-	-	-	-	-	-	-	+
Loxopholis osvaldoi Ávila-Pires, 1995	+	+	-	-	-	+	-	+	-	-
Loxopholis percarinatum Müller, 1923	-	+	-	+	+	-	-	-	-	-
Tretioscincus agilis (Ruthven, 1916)	-	-	-	-	-	-	-	-	-	+
PHYLLODACTYLIDAE										
Thecadactylus solimoensis Bergmann and Russell, 2007	+	-	-	-	-	-	-	-	-	+
SCINCIDAE										
Copeoglossum nigropunctatum (Spix, 1825)	+	-	+	+	-	+	-	-	-	-
Varzea bistriata (Spix, 1825)	+	-	-	-	-	-	-	-	-	-
SPHAERODACTYLIDAE										
Chatogekko amazonicus (Andersson, 1918)	+	+	+	+	+	+	+	+	+	+
Gonatodes hasemani (Griffin, 1917)	-	-	-	-	-	-	-	-	-	+
Gonatodes humeralis (Guichenot, 1855)	+	+	-	-	-	-	-	-	+	-

TEIIDAE										
Ameiva ameiva (Linnaeus, 1758)	+	+	+	+	+	-	+	+	+	+
Kentropyx altamazonica (Cope, 1876)	+	+	+	+	+	+	+	+	-	+
Kentropyx pelviceps (Cope, 1868)	+	+	+	+	+	-	-		+	-
Tupinambis cuzcoensis Murphy et al., 2016	-	-	-	-	-	-	-	-	-	+
TROPIDURIDAE										
Plica umbra ochrocollaris (Linnaeus, 1758)	+	+	-	-	-	-	-	-	+	+
Plica umbra umbra (Linnaeus, 1758)	-	-	+	+	-	+	-	-	-	-
Uranoscodon superciliosum (Linnaeus,1758)	+	+	-	-	-	-	-	-	+	-
First campaign (km)	27	31	33	27	27	39	36	30	32	30
Second campaign (km)	38	32	33	25	-	-	-	-	-	-
Third campaign (km)	36	31	39	29	-	-	-	-	-	-
Total distance sampled (km)	**101**	**94**	**105**	**81**	**27**	**39**	**36**	**30**	**32**	**30**

Figures

Figure 1. Location of the study area with the surveyed modules (M1–M10) along the road BR-319, state of Amazonas, northern Brazil; and schematic illustration of the modules from the RAPELD sampling system, composed by two 5 km-long tracks containing 5 terrestrial transects (250 meters long each).

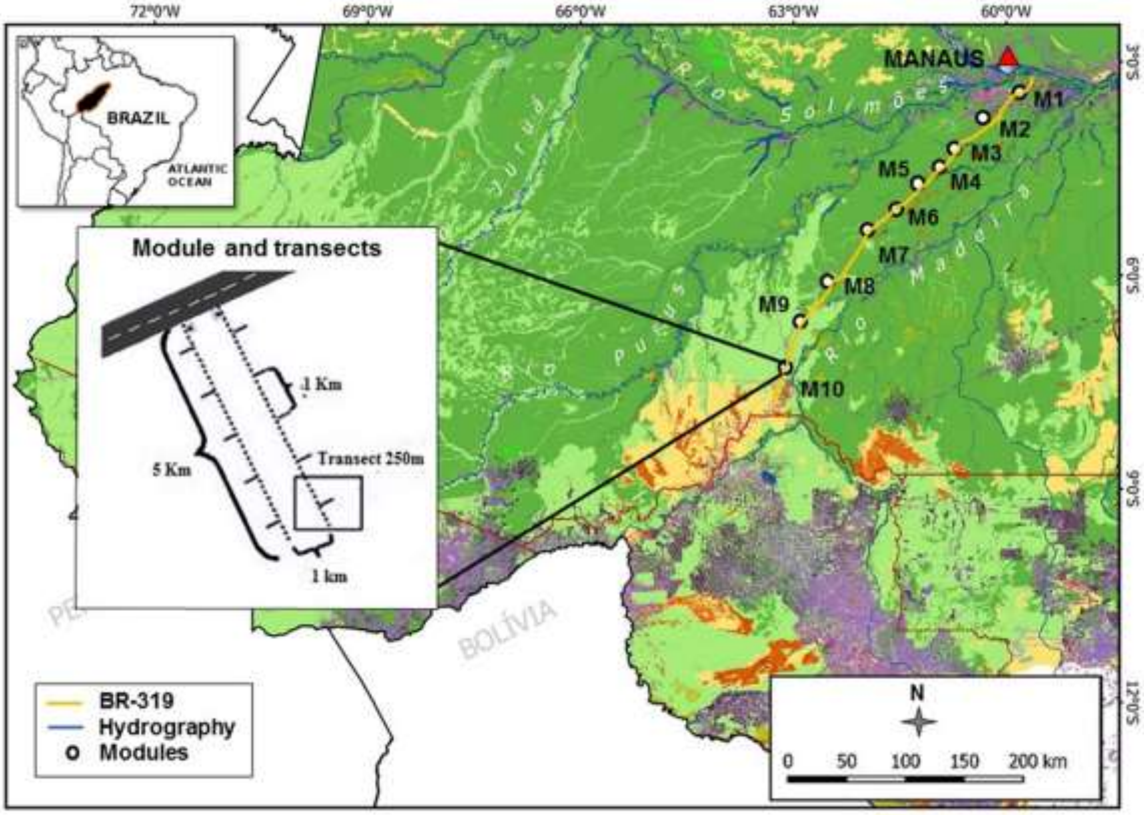

Figure 2. Lizards observed along the road BR-319 in the state of Amazonas, northern Brazil. (A) *Anolis tandai* (male, INPA-H 33522); (B) *Anolis punctatus* (male, INPA-H 33691); (C) *Anolis fuscoauratus* (female, INPA-H 33549); (D) *Plica umbra ochrocollaris* (male, INPA-H 33736); (E) *Tupinambis cuzcoensis* (male, INPA-H 33739); (F) *Kentropyx pelviceps* (male, INPA-H 33708); (G) *Arthrosaura reticulata* (INPA-H 33543); (H) *Chatogekko amazonicus* (INPA-H 33584); (I) *Plica umbra umbra* (male, INPA-H 33021); (J) *Gonatodes humeralis* (male, INPA-H 33421); (K) *Ameiva ameiva* (male, INPA-H 33473); (L) *Anolis ortonii* (INPA-H 33462); (M) *Thecadactylus solimoensis* (INPA-H 33373); (N) *Copeoglossum nigropunctatum* (INPA-H 33592; (O) *Loxopholis percarinatum* (INPA-H 30374). Photos by Pedro H. Leitão, Albertina P. Lima, and Gabriela M. Peixoto.


A
B
C
D
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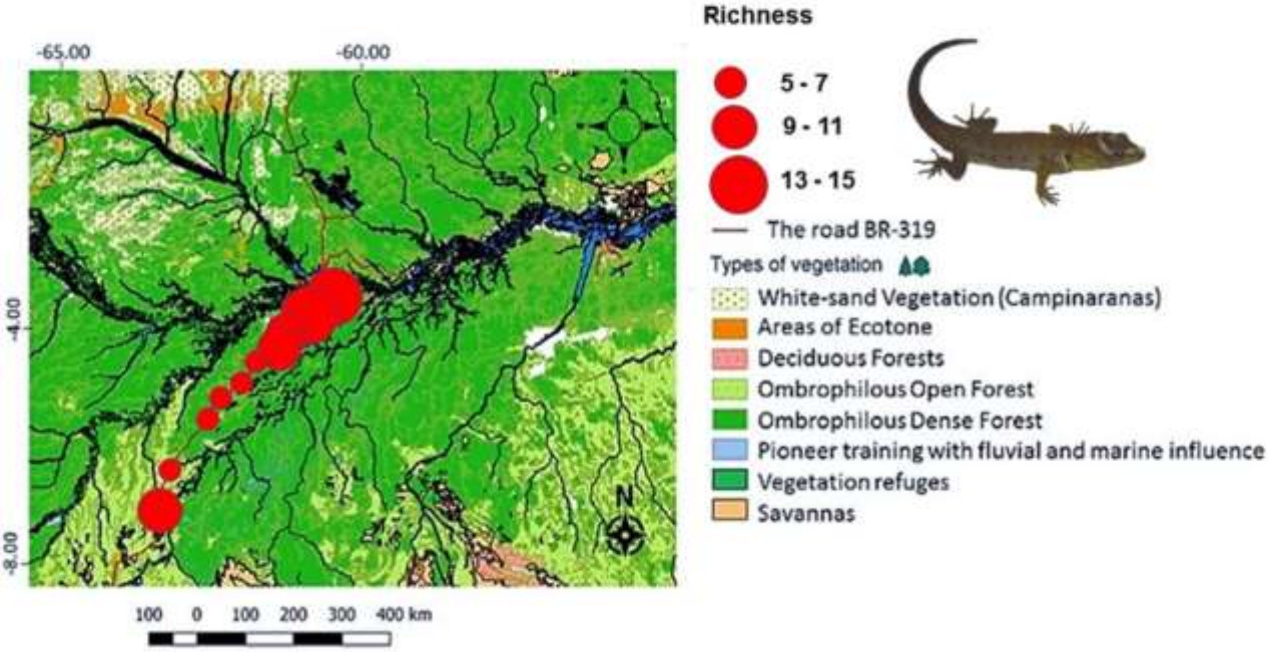
Figure 3. Richness of lizards in the surveyed modules (M1–10) along the road BR-319 in the Purus-Madeira interfluve, state of Amazonas, northern Brazil.



Appendix 1. Voucher numbers of the taxa recorded at the herpetological collection of the National Institute of Amazonian Research (INPA-H).

Alopoglossidae: *Alopoglossus atriventris* (INPA-H 33600, 33601); Dactyloidae: *Anolis fuscoauratus* (INPA-H 33480, 33482, 33494, 33516, 33530, 33531, 33536); *Anolis ortonii* (INPA-H 33424, 33471, 33583, 33702)*; Anolis punctatus* (INPA-H 33368, 33371, 33519, 33547); *Anolis tandai* (INPA-H 33496, 33683, 33684, 33695, 33696, 33722)*; Anolis tranversalis* (INPA-H 33640, 33641, 33642, 33643); Gymnophthalmidae: *Arthrosaura reticulata* (INPA-H 33514, 33570, 33651, 33671, 33672)*; Cercosaura argula* (INPA-H 33423, 33673, 33832)*; Cercosaura ocellata* (INPA-H 33389, 33430, 33438, 33470, 33534, 33543)*;*

Leposoma osvaldoi (INPA-H 25664, 30375, 30376); *Leposoma percarinatum* (INPA-H 28245, 28248, 30374); *Tretioscincus agilis* (INPA-H 28265, 33435, 33436, 33568); Phyllodactylidae*:* *Thecadactylus solimoensis* (INPA-H 33373, 33381, 33386, 33413, 33414, 33418, 33433); Scincidae: *Copeoglossum nigropunctatum* (INPA-H 33592, 33594, 33595, 33635, 33638, 33639); *Varzea bistriata* (INPA-H 33511, 33683, 33684, 33695, 33722); Sphaerodactylidae: *Chatogekko amazonicus* (INPA-H 33445, 33447, 33448, 33449, 33451, 33452, 33456, 33457, 33458, 33459, 33495, 33537, 33538, 33539)*; Gonatodes hasemani* (INPA-H 33834); *Gonatodes humeralis* (INPA-H 33403, 33404, 33443, 33576, 33612, 33613); Teiidae: *Ameiva ameiva* (INPA-H 33431, 33473, 33671); *Kentropyx altamazonica* (INPA-H 33730); *Kentropyx pelviceps* (INPA-H 33504, 33399, 33653); *Tupinambis cuscoensis* (INPA-H 33739); Tropiduridae: *Plica umbra umbra* (INPA-H 33658); *Plica umbra ochrocollaris* (INPA-H 33474, 33656, 33736); *Uranoscodon superciliosus* (INPA-H 33604, 33677, 33678).

Capítulo 2

Gabriela Marques Peixoto; Rafael de Fraga; Pedro Henrique Leitão; Igor Luis Kaefer; Albertina Pimentel Lima. Biogeographical gradients affect lizard assemblage composition and functional α-diversity in Amazonia. Manuscrito em preparação para *Biotropica*.

Biogeographical gradients affect lizard assemblage composition and functional α-diversity in Amazonia

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Abstract

Species distributions may be influenced by ecological processes and mechanisms quantified through interactions with biotic and abiotic elements. Such interactions often explain species co-occurrence via ecological filtering. Here we aimed to understand how different environmental gradients influence species richness, composition and functional diversity in heterogeneous rainforests of Amazonia, using lizard assemblage data as a model. We sampled 14 sites composed of 2 main 5 km-long trails, parallel and separated by 1 km, containing five 250 m-long plots, distributed along 880 km along the interfluvial region between the Purus and Madeira rivers, in southwestern Amazonia. We tested the general hypothesis that climatic, edaphic and vegetation-cover variables cause variation in lizard assemblages along the two ombrophylous forest types covering the region. We found that the environmental heterogeneity covered by the sampled tropical forests predicts spatial structuring of lizard assemblages. This finding is supported by distribution of taxonomic and functional diversity measures across categorical (dense and open Ombrophylous forest) and continuous habitats (biogeographical-scale environmental gradient and individual environmental variables). Our results also highlight the importance of investigating a same assemblage dataset under different dimensions of biodiversity for ecology and conservation, as well as the relevance of this region as a model for community ecology studies over wider scales.

Key words: Brazil; environmental heterogeneity; reptiles; Squamata; tropical forest.

Patterns of species distribution at wide spatial scales, such as the Amazon basin, are often determined by historical processes acting on habitat dynamics and structure (Wiens *et al*. 2011, Smith *et al*. 2014). At narrow scales (local), species distribution is primarily limited by ecological processes and mechanisms, which may be quantified through interactions with biotic and abiotic elements (Smith *et al*. 2014). Such interactions often explain species co-occurrence via ecological filtering (Mahecha & Schmidtlein 2008, Drucker *et al*. 2008, Boaratti & Silva 2015, Menger *et al*. 2017) or competition (Vitt *et al*. 2000, Vernes *et al*. 2005, Santos *et al*. 2009), and they ultimately may cause speciation even in the absence of conspicuous allopatric forces (DeFaveri *et al*. 2013). However, few studies have determined the specific contribution of different processes to the organization biological of assemblages. This is mainly due to the lack of spatially explicit data quantifying species occurrence and abundance. Although many taxa appear to be widely distributed along tropical regions, recent studies have shown that their regional distribution may be regionally limited by ecological and historical factors (Dias-Terceiro *et al*. 2015, Moraes *et al*. 2016, Alves-Martins *et al*. 2019).

Large Amazonian rivers may play important roles on species diversification, because they interrupt or reduce gene flow (Cracraft 1985, Haffer 1997, Ron 2000). The isolation of organisms on one of the riversides makes interfluvial zones promising areas for endemism, and consequently, opposite riversides represent distinct biogeographic units (Borges & Da Silva 2012, Juen & DeMarco-Jr 2012, Ribas *et al.* 2012). In addition, evolutionary processes and ecological dynamics acting in isolation between riversides have produced distinct habitats within each side, which may affect organism distribution and density, even in species (or complexes) for which the river does not limit distribution at wide scales (Ortiz *et al*. 2018). Therefore, interfluvial regions are ideal systems for investigating processes causing non-random species distribution, even in the absence of conspicuous geographical barriers to dispersal and gene flow.

Adaptation to local environmental conditions may be driven by a trade-off between availability of vital resources for species, and the ability of species to exploit resources, especially those related to foraging, breeding and thermoregulation (Silva & Araújo 2008). Specifically for Amazonian lizards, high environmental heterogeneity may strongly influence species distribution, because it determines variation in habitat quality along continuous landscapes (Vitt & Carvalho, 1992). Gradients of canopy openness and light incidence (Moraes 2008, Lobão 2008), tree density (Pinto 2006, Bittencourt 2008), leaf-litter depth (Pinto 2006, Bittencourt 2008), prey availability (Lobão 2008, Moraes 2008), clay content in the soil (Pinto 2006), terrain altitude and slope (Pinto 2006, Moraes 2008, Lobão 2008), and distance from waterbodies (Faria et al. 2019) determine the availability of foraging, resting, refuging and thermoregulating sites for distinct species subsets, and therefore structure assemblages through environmental filtering. The relationship between environmental gradients and local lizard assemblage composition may be strong enough that habitat fragmentation changes assemblage composition (Bittencourt 2008).

On the other hand, for ectotherms such as lizards, the thermal quality of habitats is essential for the maintenance of metabolic functions that support physiological functions such as growth and embryonic development (Vitt *et al*. 1997). Therefore, habitat occupancy levels are largely determined by fluctuation in temperature throughout a day or year (Karr & Freemak 1983). In addition, precipitation influences the life history of lizards (Bock *et al.* 2009), in determining food supply (Yom-Tov & Geffen 2006, James & Shine 1988, Brandt & Navas 2011). In fact, the use of climatic variables tends to gain importance in predicting species distribution or investigating ecosystem functionality, especially within the context of global climate change (Guisan *et al.* 2003, Costa *et al*. 2008, Rutschmann *et al*. 2016).

Ecosystem functionality is directly associated with local assemblage compositions, and environmental changes reducing functional diversity or increasing levels of functional redundancy imply a reduction in overall ecosystem functions (Naeem 1998). Therefore, functional diversity measures are widely informative regarding assemblage structure and habitat functionality, and consequently useful for decision-making in conservation. The practice of grouping species through functional similarities is not new to community ecology (Polis & Strong 1996). However, the development of the theme has generated methods of measuring functional diversity through mathematical indexes that generate continuous metrics instead of categorical species groups (Petchey & Gaston 2002, 2006). A drawback in quantifying functional diversity based on functional groups is that new categorical levels must be created as traits are added to the model, and one species may belong to more than one group simultaneously. In contrast, one can use numerous functional traits measured as different types of variables (e.g. continuous, binary) to quantify continuous functional diversity, despite choosing how many and which traits are relevant to the study system is often an arbitrary exercise (Petchey & Gaston 2006). Measuring continuous functional diversity may be based on species pairwise dissimilarities in morphological (Resetarits & Chalcraft 2007), physiological, behavioral, and dietary data (Chalcraft & Resetarits 2003, Straub *et al*. 2010). Although poorly exploited, this approach has revealed important insights into the structure of reptile assemblages (Powney *et al.* 2010, Rodrigues 2014, Berriozabal-Islas *et al.* 2017, Fraga *et al.* 2018), and the role of environmental heterogeneity on limiting functional diversity (Fraga *et al.* 2018).

In the present study we aimed to understand how different environmental gradients influence species richness, composition and functional diversity in heterogeneous rainforests of Amazonia, using lizard assemblage data as a model. We sampled 5 km^2 plot systems distributed along 880 km along the interfluvial region between the Purus and Madeira rivers, in southwestern Amazonia. We test the general hypothesis that climatic (temperature and precipitation), edaphic (clay, sand and silt content in the soil) and vegetation-cover (number of trees and basal area) variables cause variation in lizard assemblages along two major phytophysiognomies (open and closed ombrophylous forests) covering the region. We expect that the area covered by the sampling sites contain enough environmental heterogeneity so that sets of species and functional traits co-occurring are not randomly distributed across the landscape.

METHODS

STUDY AREA AND SAMPLING DESIGN. — Sampling sites are located along 880 km in the interfluve between the Purus and Madeira rivers, within the *Inambari* endemism zone (Ribas *et al*. 2012). The study area covers rainforests crossed by the BR-319 federal highway, which connects Careiro da Várzea to Humaitá, in the state of Amazonas, and rainforests on the west bank of the upper Madeira River, southwestern Amazonian Brazil (Rondônia state). The topography of the region is relatively flat and low (30–60 m above sea level). According to a classification proposed by the Brazilian Institute of Geography and Statistics (IBGE 1997), approximately 64.28% (n = 10) of the sampling sites were installed in areas covered by Dense Ombrophylous Forest (DOF), and 35.71% (n = 5) sampling sites are within patches of Open Ombrophylous Forest (OOF).

There are 15 sampling sites (here after modules) in the study area, but we did not include one of them (M8) in the analyzes. We were not able to fully survey this module during the rainy season, because some of the trails were flooded. The modules were installed according to the RAPELD (Brazilian acronym for rapid survey plus long-term ecological research) method (Magnusson *et al.* 2005, 2013). Each module is composed of two main 5 km-long trails, parallel and separated by 1 km. We sampled 10 modules along the BR-319, and four modules on the west bank of the upper Madeira River (Fig. 1). Each module contains ten 250 m-long plots, 10 m wide in each trail. The plots follow the altitudinal curves to minimize environmental heterogeneity within plots. In this study we used modules as sampling units, because environmental data were not available for all plots.

We collected data in August 2010 in the modules on the upper Madeira River, and October to December 2010 in the modules along the BR-319. We found lizards using active visual search (Campbell & Christman 1982) for 60 minutes per plot (average) with two simultaneous observers, 10 m apart. Additionally, we improved sampling cryptic species (e.g. Gymnophthalmidae, Alopoglossidae) by sweeping the leaf litter in a 1 m-wide lane from the central line of the plot.

For species that are difficult to identify in the field, we collected a maximum of three specimens. We killed them using a lidocaine-based anesthetic, fixed them in 10% formaldehyde, and stored them in 70% ethanol. We deposited voucher specimens in the collection of Amphibians and Reptiles of the Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (INPA-H). Collecting specimens was authorized by a permanent license (RAN-ICMBio/IBAMA nº 13777-2/2008) granted to the expedition coordinator Albertina P. Lima.

LIZARD ASSEMBLAGES. —We quantified lizard assemblages using four distinct measures of alpha (species and functional richness) and beta diversity (assemblage composition and dispersion of functional traits). We represented species richness by absolute numbers of taxa per module (including *Plica umbra* subspecies). We estimated assemblage composition by pairwise Bray-Curtis dissimilarities in taxa abundances. The dissimilarity matrix was summarized by a Principal Coordinate Analysis (PCoA).

To quantify lizard assemblages based on functional traits, we used a functional richness index (FRic) and a functional dispersion index (FDis), both implemented in the FD R-package (Laliberté *et al.* 2014). We selected functional traits that potentially represent interactions among lizards, biotic and abiotic habitat elements. We used morphometric traits because they determine diet composition (e.g. prey type and size) and the use of habitats (Vitt 1991, Vitt *et al.* 1997). We used a digital caliper to measure snout-ventral length, head width, head height, anterior limb length, and posterior limb length. We measured 5–15 individuals per taxa and used average values to estimate functional richness and dispersion. We used foraging mode (active, sedentary ambush, active ambush), because this trait reflects levels of exposure to predators, feed frequency, and consequently defensive behavior and growth rates (Vitt 1991). We used substrate type (terrestrial, arboreal) because this trait represents direct interactions between species and the available habitats (Vitt *et al.* 2001). We obtained data on foraging mode and substrate in the literature (Ávila-Pires 1995, Vitt *et al.* 2008).

We calculated Gower distances in the functional traits between paired taxa and used a cluster analysis to visualize the dissimilarities among taxa in a dendrogram (Pavoine *et al.* 2009, 2011). We estimated functional richness (FRic) and dispersion (FDis) using the dbFD function of the FD package (Laliberté *et al.* 2014), based on the sums of the branch lengths of the functional tree (dendrogram) per module. The function returns four different indexes of functional alpha and beta diversity, of which we used FRic as a measure of functional alpha diversity, and FDis as a measure of functional beta diversity. Both measures have been described as not biased by number of traits or outliers (Laliberté *et al.* 2014).

ENVIRONMENTAL GRADIENTS. — To estimate the effects of environmental heterogeneity on species richness, assemblage composition, functional richness and dispersion, we used variables that quantify vegetation-cover and soil structure. These variables potentially affect lizard taxonomic and functional diversity measures by determining the availability of foraging, resting, sheltering and thermoregulating sites (Hadden & Westbrooke 1996). Number of trees and clay, sand and silt content in the soil were measured following standard protocols of the Biodiversity Research Program (PPBio), and the methods can be found at http://ppbio.inpa.gov.br/knb/style/skins/ppbio. The basal area of the trees was measured by Schietti *et al.* (2016).

We also tested the influence of climate on each metric of lizard assemblage. We obtained climatic variables from the WorldClim database (Hijmans *et al*. 2005). The data used in this study comprised interpolated surfaces from mean values of 50 years period (1,950-2,000). To characterize climatic heterogeneity across the study area, we selected all bioclimatic variables available in WorldClim, and we extracted values per centroid geographic coordinates of each module using the DIVA-GIS software (Hijmans *et al.* 2012).

All bioclimatic variables were correlated (Pearson $r > 0.6$ in all cases). The mean annual rainfall had greatest amplitude (1,930 to 2,624 mm), so we used it as a proxy for the heterogeneity in precipitation along the study area (Table S1). Due to the multicollinearity among the measured climatic variables, it was not possible to use them as independent variables in multiple-parameter regression models. We chose to summarize all the environmental heterogeneity measured using Principal Component Analysis (PCA). The first axis of the PCA captured 91.3% of the original variance in the environmental data (precipitation, basal area of the trees and clay content in the soil) and we used it as a biogeographic gradient in the inferential analyzes.

To test differences in lizard assemblages between the main forest types sampled (DOF and OOF) we used models of ANOVA, which were constructed with each of the assemblage metrics (species richness, assemblage composition, FRic and FDis) as dependent variables, and forest type as an independent categorical variable. Additionally, we used simple linear regression models to test the influence of the biogeographic gradient summarizing environmental heterogeneity on each of assemblage metrics, separately. To check the consistency of the results, we also used simple linear regression models constructed with assemblage measures as dependent variables, and each of the raw environmental gradients as independent variables. All the models were validated by normally distributed residuals (Shapiro-Wilk P > 0.05 in all cases), not spatially autocorrelated (Moran's I *P* > 0.05 in all cases). All analyzes were performed in the R computer environment (R Core Team 2019).

RESULTS

We found 27 taxa of 17 genera distributed in nine families (Table S2). The Gymnophthalmidae family was the most taxa in the sample, represented by seven taxa. Among the most frequently sampled species are *Norops fuscoauratus* (85% of the modules, *n* = 12), *Chatogekko amazonicus* (78%, *n* = 11), and *Ameiva ameiva* (71%, *n* = 10). Taxa richness varied from 4 to 13 (mean = 8.5) among modules.

The first PCoA axis captured 54% of the original dissimilarities among assemblage composition. We found significant differences in the scores produced by the first PCoA axis between forest types (ANOVA $F_{1,12} = 22.44$, $P = 0.0004$). This finding is graphically showed in Fig. 2.

The biogeographic gradient summarizing correlated environmental variables explained 86% of the variation in assemblage composition ($F_{1,12} = 74.9$, $P < 0.001$, Fig. 3A). This finding suggests that the environmental heterogeneity measured selects different species subsets throughout the study area, which has caused continuous species turnover. The extreme limits of the species turnover gradient are represented by the two sampled forest types (Fig. 3A). Although environmental heterogeneity caused species turnover, species richness was randomly distributed along the biogeographic gradient ($P < 0.37$, Fig. 3B).

The simple linear regression models using each individual environmental variable revealed that assemblage composition is primarily characterized by species turnover along the gradient of basal area ($R^2 = 0.84$, $F_{1,12} = 64.12$, $P < 0.001$, residual error = 0.12), precipitation ($R^2 = 0.84$, $F_{1,12} = 63.02$, $P < 0.001$, residual error = 0.12), and soil clay content ($R^2 = 0.68$, $F_{1,12} = 25.70$, $P < 0.001$, residual error = 0.17). Although the environmental heterogeneity of the study area is characterized by two distinct groups of modules that are consistent with the forest types sampled, relationships between assemblage composition and environmental variables can be demonstrated as continuous gradients of species turnover (Fig. 4). None of the measured environmental variables returned significant effects on the richness ($P > 0.16$ in all cases).

The patterns of species turnover caused by precipitation and basal area are demonstrated by absence or low abundance of species at certain regions of the gradients (Fig. 5). For instance, nine species were restricted to modules with relatively small basal area (Fig. 5A). This result was expected for heliothermic species (e.g. *Hoplocercus spinosus*), which are tolerant to the higher ultraviolet radiation in open forests. However, some of the species for which distribution was restricted to these modules are not heliothermic (e.g. *Iphisa elegans*, *Dactyloa punctata*), which suggests that environmental filtering associated to basal area does not necessarily act on thermoregulation mode. The same species were restricted to modules with relatively low levels of precipitation (Fig. 5B). This finding suggests lizard assemblages structured by interactions between basal area and precipitation, although a larger proportion of species has been widely distributed along the measured precipitation gradient.

The clustering by Gower dissimilarities in functional traits among paired species revealed two main groups composed of arboreal and terrestrial species (Fig. 6). The group of terrestrial species was subdivided by foraging mode. We found differences in FRic values between forest types (ANOVA $F_{1,12} = 7.19$, $P = 0.02$). Modules in Dense Ombrophilous Forest had less trait richness. Additionally, FRIc values were not randomly distributed along modules (Fig. 7A), but negatively related ($R^2 = -0.35$, $F_{1,12} = 6.48$, $P = 0.02$, residual error = 9.61) to the biogeographic gradient summarizing environmental heterogeneity. However, these findings were not associated with significant turnover (FDis) in functional diversity (Fig. 7B) between forest types ($P = 0.21$) or along the biogeographic gradient ($P = 0.17$).

The simple-linear regression models returned FRic (Fig. 8A) values negatively affected by basal area ($R^2 = -0.39$, $F_{1,10} = 7.81$, $P = 0.01$, residual error = 8.81) and precipitation ($R^2 = -0.43$, $F_{1,12} = 9.63$, $P < 0.001$, residual error = 8.93), but not by soil clay content ($P = 0.15$). The functional turnover rates were relatively low throughout the sampled modules, which caused random variation in FDis values (Fig. 8B) along the gradients of soil clay content ($P = 0.29$), basal area ($P = 0.12$) and precipitation ($P = 0.40$).

DISCUSSION

We found that the environmental heterogeneity covered by the Purus-Madeira interfluve predicts spatial structuring of lizard assemblages. This finding is supported by non-random distribution of taxonomic and functional diversity measures across categorical (dense and open Ombrophylous forest) and continuous habitats (biogeographic gradient and individual environmental variables). Interestingly, assemblages defined in the taxonomic dimension were only structured by dissimilarities among paired modules (beta diversity), whereas assemblages defined in the functional dimension were only structured by the absolute-trait richness per module (alpha diversity). These findings suggest that the regional lizard diversity is defined by environmental filtering causing species turnover along the landscape, and selection of functional trait subsets that are nested within the global trait diversity. Although large Amazonian rivers are commonly reported as vicariant barriers promoting biodiversity in Amazonia (Haffer 1997, Simões *et al.* 2008, Antonelli *et al*. 2010, Ribas *et al.* 2012, Smith *et al.* 2014, Boubli *et al.* 2015), we showed the relevance of environmental gradients as predictors of multi-taxa organism distribution, even in the absence of conspicuous vicariance. Our results also support the importance of investigating a same assemblage dataset under different dimensions of biodiversity for ecology and conservation (see Fraga *et al.* 2018).

Although most of the species sampled in this study are widely distributed across Amazonia or even different ecosystems in South America (Ávila-Pires 1995, Vitt *et al*. 2008, Ribeiro-Júnior 2016), they were regionally restricted to optimal habitat types or fractions of environmental gradients. Lizard species turnover along environmental gradients has been demonstrated in different regions of the Amazon, specially related to distance from water courses (Pinto 2006, Moraes *et al.* 2016, Faria *et al.* 2019). However, the ecological models tested in such studies were usually set up to quantify environmental heterogeneity by multiple independent variables. Such an approach assumes certain levels of covariance among multiple environmental variables, which may be useful to control for the effects of covariates on the estimated assemblage composition. Here we demonstrated that patterns of lizard spatial structure may also be captured by reducing multivariate environmental heterogeneity in a single independent variable (biogeographic gradient represented by the first axis of a PCA). Despite the slight loss of information due to the forced dimensionality reduction, our findings suggest that species-habitat associations based on multiple environmental variables may be detected even by models that do not assume covariance.

By testing simple linear regression models, we found species turnover along a gradient of soil clay content. This is assumed as an indirect effect, because soil texture affects invertebrate prey density and water retention (Woinarski *et al.* 1999, Menger *et al.* 2017). In the Amazon, soils with higher clay content have been associated with shallower groundwater (Schietti *et al.*2014), which may contribute to the pattern of co-occurrence of the species locally. Additionally, we found species turnover along basal area gradients and precipitation. The vegetation structure for the lizards is directly responsible for the supply of microhabitats and availability of food, besides acting for the regulation of the air temperature, and affecting the direct solar incidence in the forests (Silva & Araújo 2008), able to influence demographic patterns in assemblages. These thermo-regulatory requirements are important for the physiological processes in tropical lizards, because they maintain several biological aspects of the species (Huey & Slatkin, 1976, Bergallo & Rocha, 1993, Ortega & Pérez-Mellado 2016, Pontes *et al*. 2018). Precipitation, however, is almost never approached in the studies of the spatial structure of assemblages of Amazonian lizards (Vitt 1991, Pinto 1999), but it is also an important factor for the climatic conditions of the environment, necessary for thermoregulation of the species, apart from contributing to the food niche, by influencing the increase of essential invertebrates for the diet of several species (Woinarski *et al.* 1999, Rutschmann *et al*. 2016).

We found significant effects of the biogeographic gradient measured on the functional trait richness. This finding was supported by negative relationships between FRic with basal area and precipitation, although they were not associated with trait turnover along the study area. These findings suggest that dense and very rainy forests contain functionally homogeneous lizard assemblages. Relatively low trait richness suggesting regional filtering of redundant functional traits. In contrast, relatively open and less rainy forests had higher trait richness, is usually associated with minor effects of competition, through competitive exclusion, since the available habitats allow the establishment of functionally redundant species (Petchey *et al*. 2007, Straub e*t al*. 2010). The influence of such processes changes across environmental gradients, where the environmental filtering will exert more influence in more stressful environmental. Future studies should focus on the explicit effects of an interaction between environmental conditions and competition on the regional distribution of functional traits.

Functional traits reflect environmental requirements and tolerances and are responsible for directly influencing the success of foraging, escape ability, predation, and reproductive aspects of the species (Dobson & Michener, 1995, Chown *et al*. 2004). Comparative studies among body, behavioral and habitat characteristics have been reported for a long time in the literature (Vitt *et al.* 1997, Caldwell & Vitt 1999). In our study, rainfall gradients and basal area were efficient environmental filters to predict changes in the species' functional richness.

Open Ombrophylous forest environments have lower forest densities and rainfall averages, and tend to select larger numbers of heliothermic, terrestrial species with larger hind limbs capable of improving race performance in more exposed habitats (Silva & Araújo 2008). Differently, more densely forested environments, with high annual precipitation, or subject to periodic flooding, result in forests with denser and stratified canopy, and provide more stable microenvironment for the arboreal or non-heliothermic species (Magnuson & Silva 1993). Body size and shape are also characteristics that determine the permanence of the species in the different habitats (Rickefs & Travis 1980): thinner and longer bodies (e.g., *Anolis* lizards) are associated with the finer branches, whereas for trees with larger trunks the bodies are more robust and flattened (e.g., *Plica* lizards) (Vitt *et al.* 2008).

Habitat disturbance is one important anthropogenic factor that influence ecosystems resulting in changes in environmental structure and biotic composition (Hobbs *et al.* 2009), mainly in tropical forests that harbor an exceptionally high diversity. The Amazon has been suffering from these anthropic impacts, whether through fragmentation, deforestation or changes in land use and land cover (Val & Marcovitch 2019), which tends to the imminent loss of species. Although habitat conservation is an important factor, knowledge of species distribution and coexistence is essential for conservation mitigation measures (Roll *et al.* 2017, Magnuson *et al*. 2016). For the Amazonian lizards the high phenotypic conservatism, intraspecific polymorphism, and low detection probabilities, hinders the true limits of occurrence of the species (Fouquet *et al.* 2015, Ribeiro-Júnior & Amaral 2016). For the Purus-Madeira Interfluve different structural aspects of the environment define the heterogeneity of habitats (Ximenes, 2008). This scenario consists of an opportunity to understand the patterns of distribution of lizards and the relation of these patterns to the life history traits of each species, since for environmental characteristics it has a strong influence in limiting the distribution in this group (Costa *et al.* 2008), especially when we associate diverse measures of diversity, capable of measuring the maintenance of ecosystem processes that operate in long periods (Devictor *et al.* 2010, Fraga *et al.* 2018).

In summary, our study was pioneer in evaluate the wide-scale environmental effects on Amazonian lizard assemblages and identify that the structural complexity along a biogeographic gradient have a significant impact on the composition and richness of functional characteristics of lizards. Environmental filters related to edaphic, vegetation and rainfall gradients along the region of the Purus-Madeira influence the species turnover, and determine the differences found between assemblages in the open and dense ombrophilous forests. Finally, this study reinforces the relevance of the studied area for species conservation and management. Future studies on this scale might elucidate patterns of coexistence and distribution of species of Amazonian organisms and their associations to the environment along continuous forests.

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Tables

Table S1 Environmental variables used as proxy for the wide-scale biogeographic gradient. Minimum and maximum values for each site along the Purus-Madeira interfluve.

Sampling Modules	**Soil clay contente (µm)**	**Tree basal área (m^2/há)**	**Annual Precipitation (mm)**
M-1	11.5 – 29.3	19.9 – 25.32	2156
M-2	13.25 – 21.25	25.41 – 33.12	2170
M-3	18.45 – 31.5	22.0 – 31.97	2272
M-4	12.31 – 30.23	28.6– 36.84	2410
M-5	10.5 – 14.5	27.95 – 38.9	2609
M-6	39.06 – 47.74	29.71 – 34.86	2624
M-7	13.5 – 28.7	30.93 – 35.83	2589
M-9	19 – 26	30.88 – 32.77	2556
M-10	11.75 – 14	27.8 – 32.53	2437
M-11	12.5 – 22.75	24.65 – 30.63	2270
M-12	62.2 – 70.4	10.34 – 17.46	2067.25
M-13	59.2 – 72.3	12.44 – 26.72	2004
M-14	49.2 – 54	13.5 – 20.47	1970
M-15	50.55 –68.89	13.8 – 27.1	1930

Table S2 List of lizard taxa found along the *Purus-Madeira Interfluve. OOF= Open Ombrophilous Forest, and DOF= Dense Ombrophilous Forest.*

Family/Taxa	**DOF**	**OOF**
ALOPOGLOSSIDAE		
Alopoglossus angulatus (Linnaeus, 1758)	-	+
Alopoglossus atriventris (Duellman, 1973)	+	-
DACTYLOIDAE		
Norops fuscoauratus D'Orbigny, 1837	+	+
Norops ortonii Cope, 1868	+	+
Dactyloa punctatus Daudin, 1802	+	+
Norops tandai Ávila-Pires, 1995	+	-
Dactyloa transversalis Duméril, 1851	+	+
GYMNOPHTHALMIDAE		
Arthrosaura reticulata (O'Shaughnessy, 1881)	+	-
Cercosaura argula (Peters, 1863)	+	+
Cercosaura ocellata (Wagler, 1830)	-	+
Iphisa elegans (Gray, 1851)	-	+
Loxopholis osvaldoi Ávila-Pires, 1995	+	-
Loxopholis percarinatum Müller, 1923	+	-
Tretioscincus agilis (Ruthven, 1916)	-	+
HOPLOCERCIDAE		
Hoplocercus spinosus (Fitzinger, 1843)	-	+

PHYLLODACTYLIDAE		
Thecadactylus solimoensis Bergmann and Russell, 2007	-	+
SCINCIDAE		
Copeoglossum nigropunctatum (Spix, 1825)	+	+
Varzea bistriata (Spix, 1825)	+	-
SPHAERODACTYLIDAE		
Chatogekko amazonicus (Andersson, 1918)	+	+
Gonatodes hasemani (Griffin, 1917)	-	+
Gonatodes humeralis (Guichenot, 1855)	+	+
TEIIDAE		
Ameiva ameiva (Linnaeus, 1758)	+	+
Kentropyx altamazonica (Cope, 1876)	+	+
Kentropyx pelviceps (Cope, 1868)	+	+
TROPIDURIDAE		
Plica umbra ochrocollaris (Linnaeus, 1758)	+	+
Plica umbra umbra (Linnaeus, 1758)	+	-
Uranoscodon superciliosus (Linnaeus,1758)	+	+

Figure legends

FIGURE 1. Sampling RAPELD modules along the BR-319 federal highway (M1–M11) and the upper Madeira River (M12–M15). The module M8 (in red) was not sampled because it was flooded during the rainy season. Different colors show patches of natural or anthropogenic landscapes, as detailed in the inset legend.

FIGURE 2. Lizard assemblage composition based on abundance data from 14 sampling modules installed in the Purus-Madeira interfluve, southwestern Amazonian Brazil. Assemblage composition was summarized by the first two axes of a Principal Coordinates Analysis (PCoA) applied on a Bray-Curtis pairwise dissimilarities matrix. Note the segregation in assemblage composition between Open Ombrophilous Forest (light blue circles), and Dense Ombrophilous Forest (dark blue circles).

FIGURE 3. Relationship between the biogeographic gradient summarizing environmental variables as a PCA axis and lizard assemblage composition (A) and taxa richness (B) sampled in 14 modules along the Purus-Madeira intefluve, southwestern Amazonian Brazil. Light blue circles = Open Ombrophilous Forest; dark blue circles = Dense Ombrophilous Forest.

FIGURE 4. Relationship between environmental variables and lizard assemblage composition summarized by the first axis of a PCoA applied on Bray-Curtis dissimilarities among paired sampling modules along the Purus-Madeira interfluve, Amazonia. Light blue circles = Open Ombrophilous Forest; dark blue circles = Dense Ombrophilous Forest.

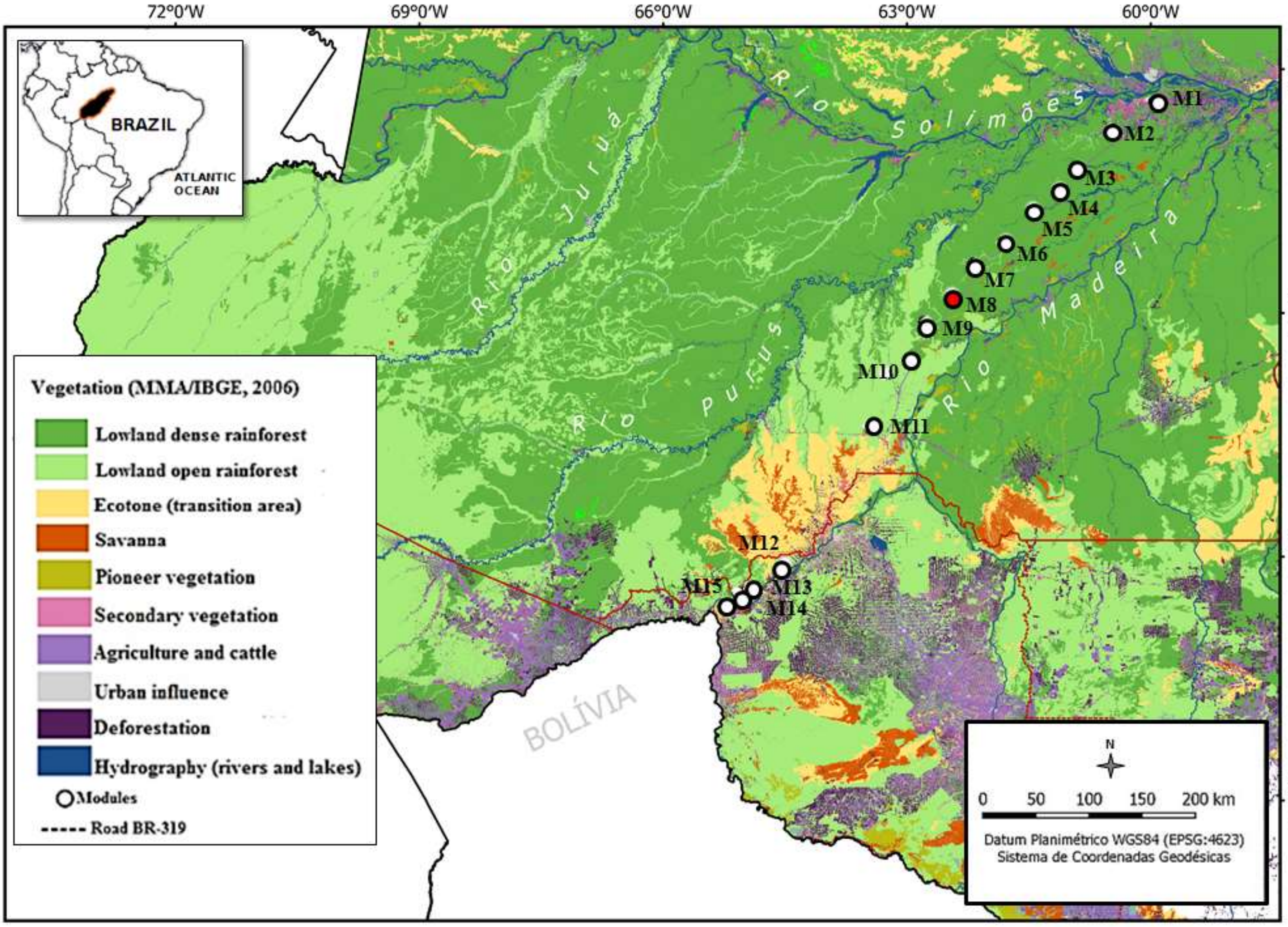
FIGURE 5. Ordination of 5 km^2 sampling modules along gradients of tree basal area (A) and annual precipitation (B) in southwertern Amazonia. The height of the rectangles denotes abundance of lizard individuals per taxon.

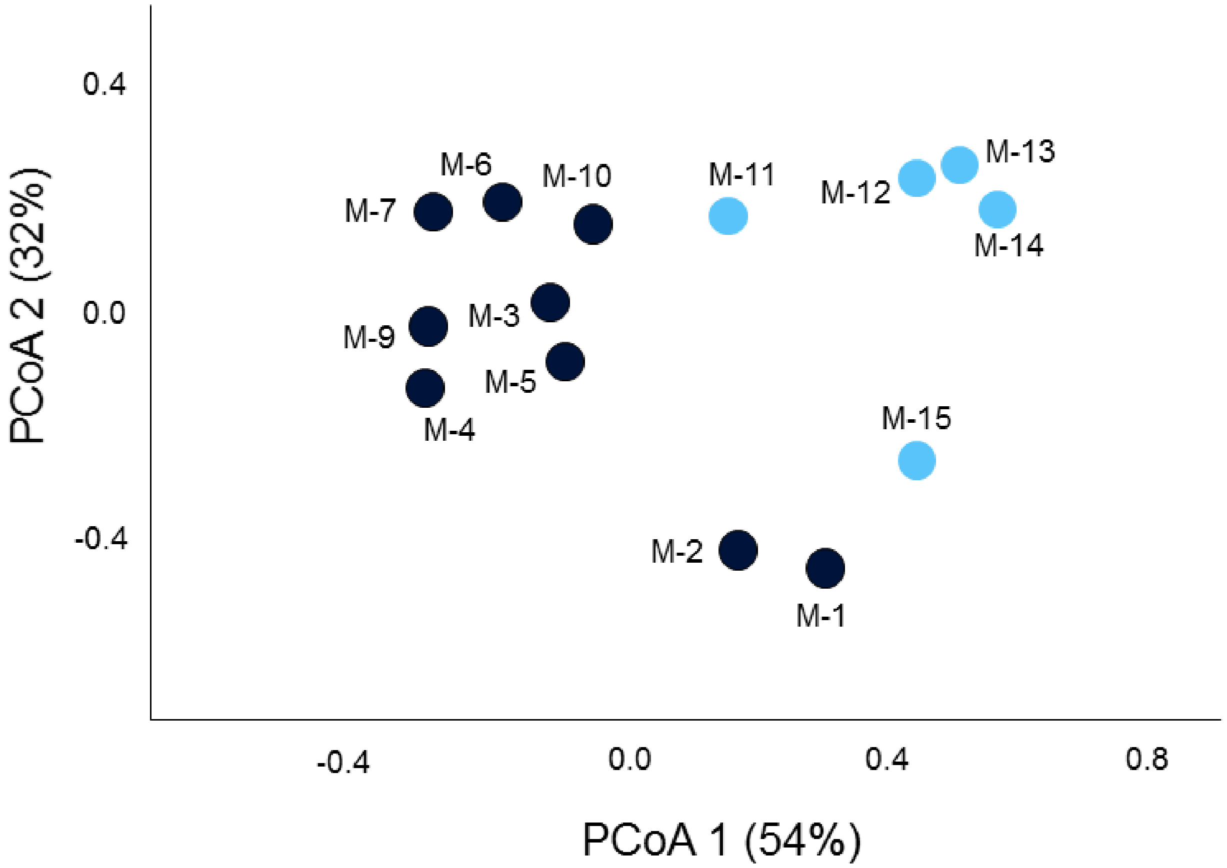
FIGURE 6. Clustering of Gower dissimilarities in functional traits of lizards sampled in 14 modules along the Purus-Madeira interfluve, southwestern Amazonia. The blue circle represents the first division of terrestrial and arboreal species. The circle in red shows a second division for the terrestrial species between the species of active foragers and ambush.

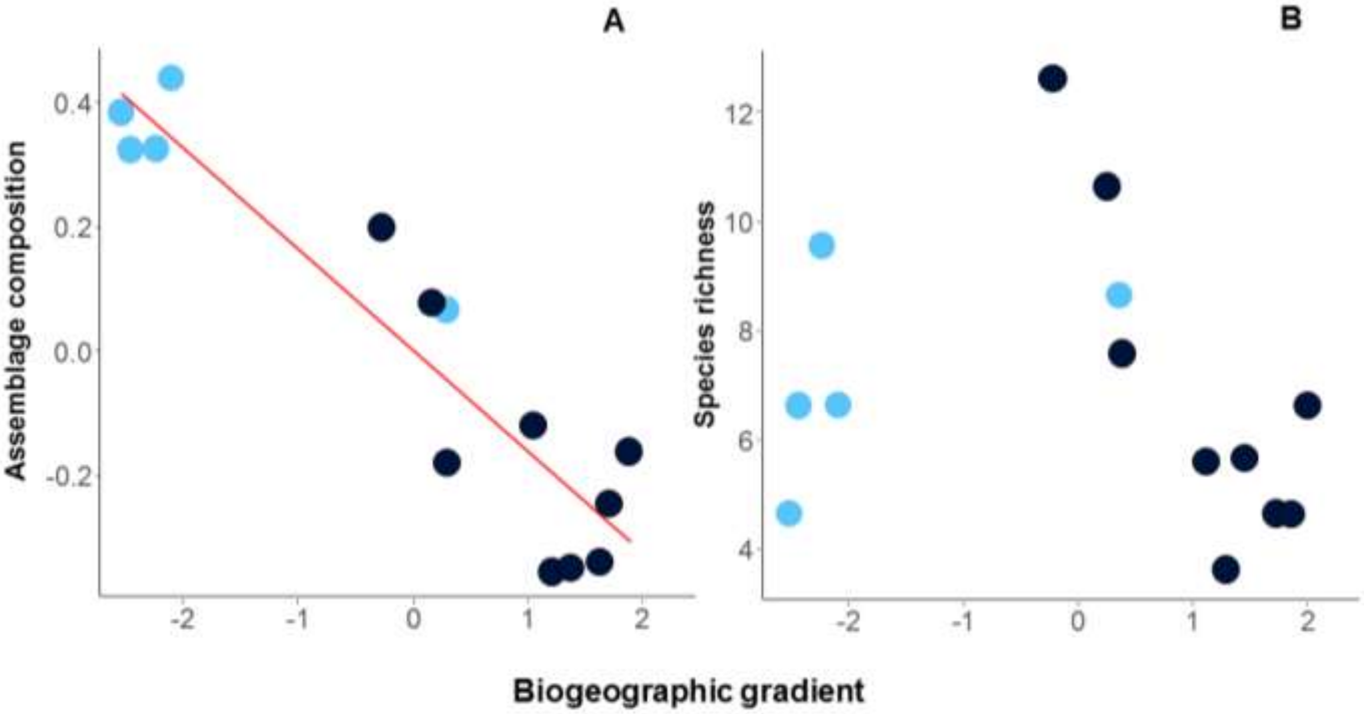
FIGURE 7. Relationships between lizard (A) functional richness (FRic) and (B) functional dispersion (FDis) with a biogeographic gradient summarizing climatic and vegetation cover variables in a PCA axis. Light blue circles = Open Ombrophilous Forest; dark blue circles = Dense Ombrophilous Forest.

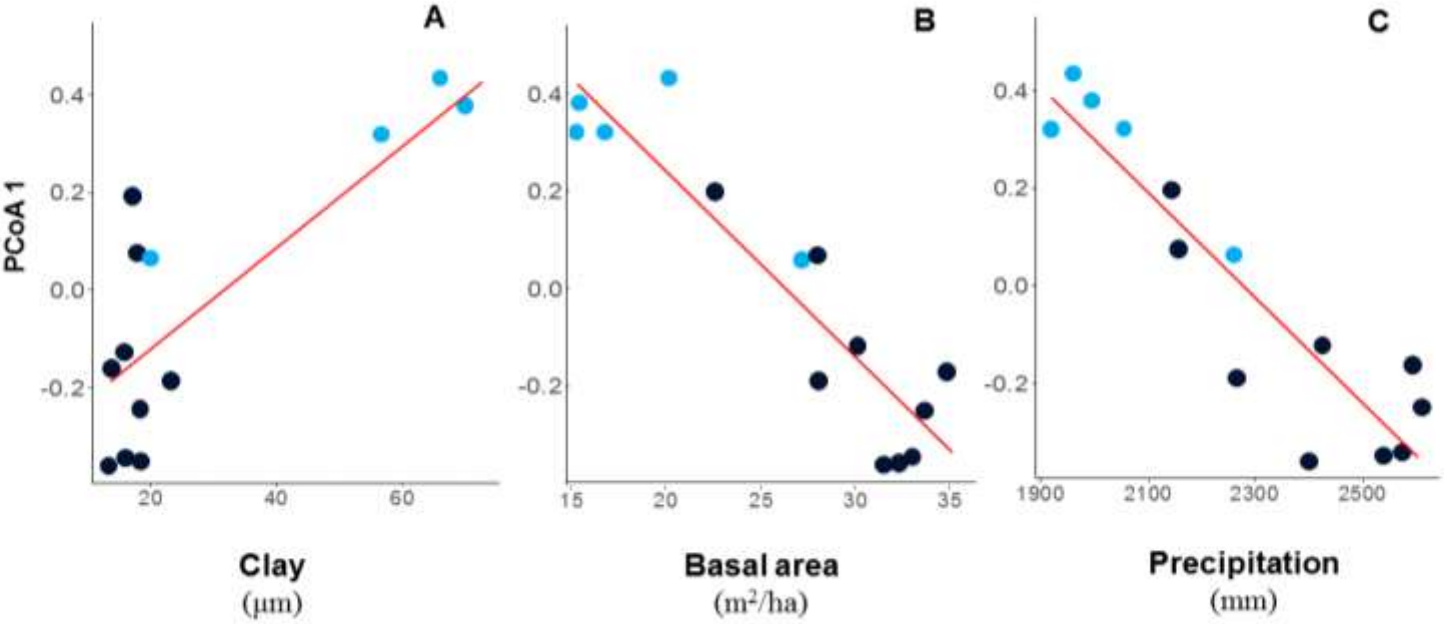
FIGURE 8. Relationships between lizard functional richness (FRic) and functional dispersion (FDis) and environmental gradients measured in 14 sampling modules along the Purus-Madeira interfluve, southwestern Amazonia. Light blue circles = Open Ombrophilous Forest, dark blue circles = Dense Ombrophilous Forest.

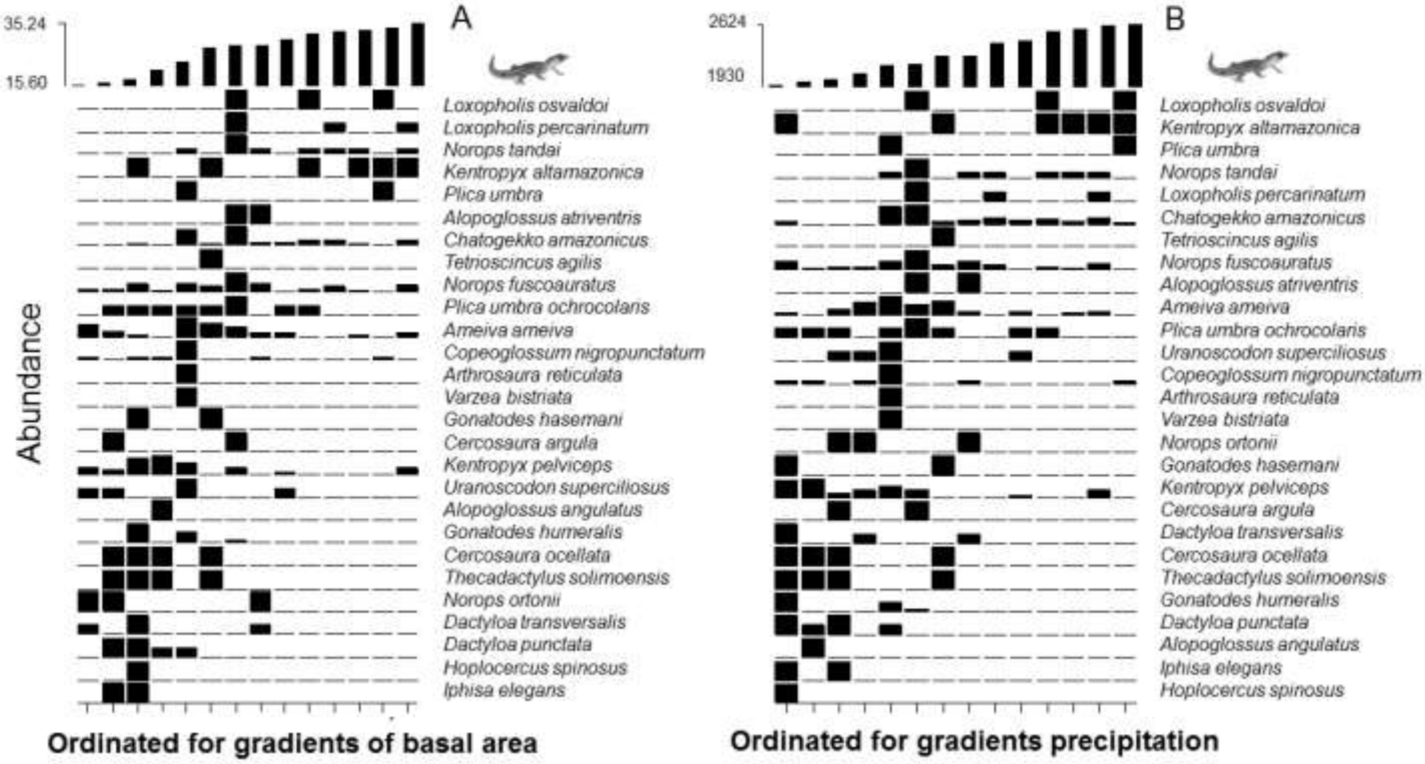
Figures

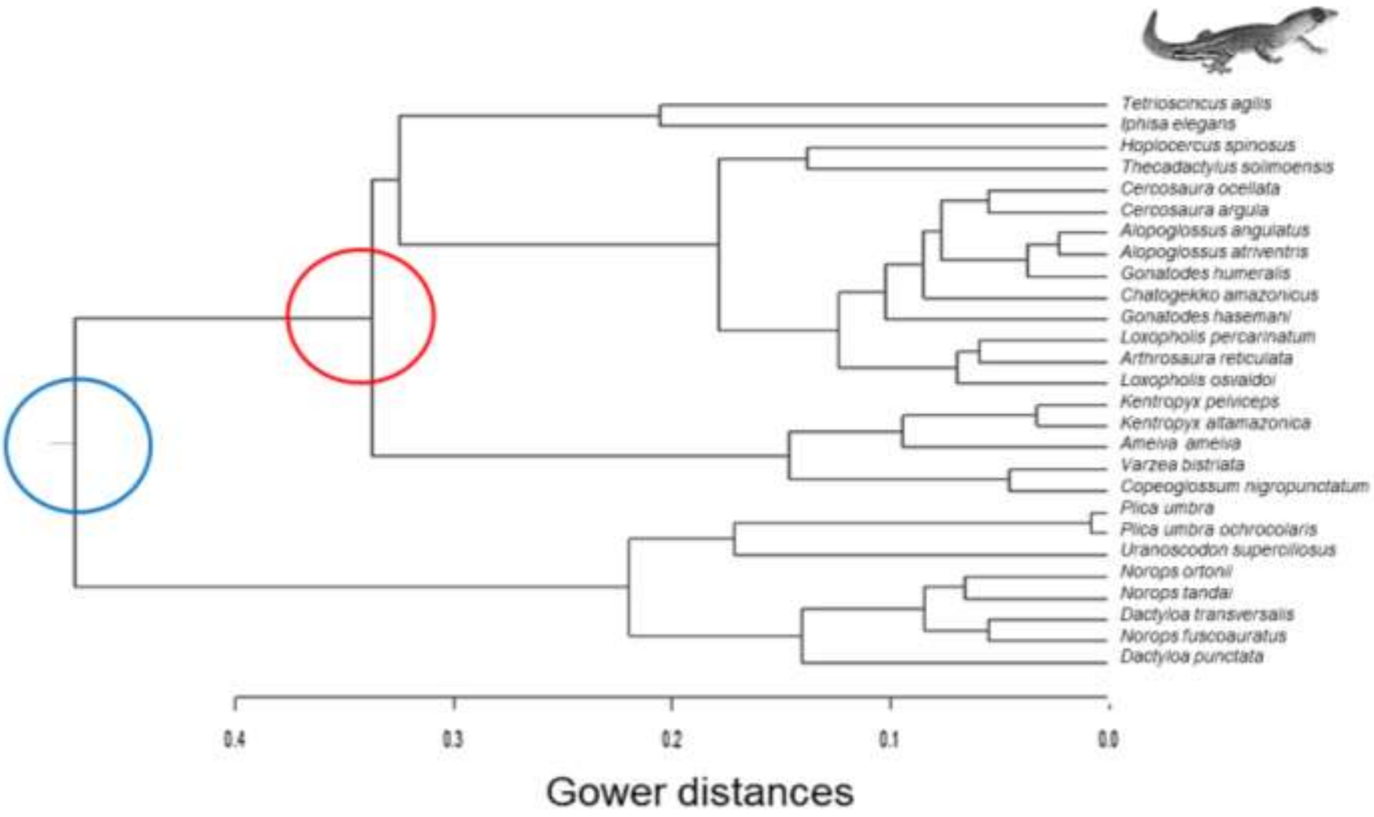

72°0′W
69°0′W
66°0′W
63°0′W
60°0′W
3°0′S
6°0′S
9°0′S
12°0′S
BRAZIL
ATLANTIC OCEAN
Rio Solimões
Rio Juruá
Rio Purus
Rio Madeira
BOLÍVIA
M1
M2
M3
M4
M5
M6
M7
M8
M9
M10
M11
M12
M13
M14
M15
Vegetation (MMA/IBGE, 2006)
Lowland dense rainforest
Lowland open rainforest
Ecotone (transition area)
Savanna
Pioneer vegetation
Secondary vegetation
Agriculture and cattle
Urban influence
Deforestation
Hydrography (rivers and lakes)
Modules
Road BR-319
N
0
50
100
150
200 km
Datum Planimétrico WGS84 (EPSG:4623)
Sistema de Coordenadas Geodésicas


0.4
0.0
-0.4
PCoA 2 (32%)
-0.4
0.0
0.4
0.8
PCoA 1 (54%)
M-6
M-10
M-11
M-12
M-13
M-7
M-14
M-3
M-9
M-5
M-4
M-15
M-2
M-1


A
B
Assemblage composition
0.4
0.2
0.0
-0.2
Species richness
12
10
8
6
4
-2
-1
0
1
2
Biogeographic gradient


A
B
C
PCoA 1
0.4
0.2
0.0
-0.2
20
40
60
15
20
25
30
35
1900
2100
2300
2500
Clay
(µm)
Basal area
(m²/ha)
Precipitation
(mm)


35.24
15.60
A
Abundance
Loxopholis osvaldoi
Loxopholis percarinatum
Norops tandai
Kentropyx altamazonica
Plica umbra
Alopoglossus atriventris
Chatogekko amazonicus
Tetrioscincus agilis
Norops fuscoauratus
Plica umbra ochrocolaris
Ameiva ameiva
Copeoglossum nigropunctatum
Arthrosaura reticulata
Varzea bistriata
Gonatodes hasemani
Cercosaura argula
Kentropyx pelviceps
Uranoscodon superciliosus
Alopoglossus angulatus
Gonatodes humeralis
Cercosaura ocellata
Thecadactylus solimoensis
Norops ortonii
Dactyloa transversalis
Dactyloa punctata
Hoplocercus spinosus
Iphisa elegans
Ordinated for gradients of basal area
2624
1930
B
Loxopholis osvaldoi
Kentropyx altamazonica
Plica umbra
Norops tandai
Loxopholis percarinatum
Chatogekko amazonicus
Tetrioscincus agilis
Norops fuscoauratus
Alopoglossus atriventris
Ameiva ameiva
Plica umbra ochrocolaris
Uranoscodon superciliosus
Copeoglossum nigropunctatum
Arthrosaura reticulata
Varzea bistriata
Norops ortonii
Gonatodes hasemani
Kentropyx pelviceps
Cercosaura argula
Dactyloa transversalis
Cercosaura ocellata
Thecadactylus solimoensis
Gonatodes humeralis
Dactyloa punctata
Alopoglossus angulatus
Iphisa elegans
Hoplocercus spinosus
Ordinated for gradients precipitation


Tetrioscincus agilis
Iphisa elegans
Hoplocercus spinosus
Thecadactylus solimoensis
Cercosaura ocellata
Cercosaura argula
Alopoglossus angulatus
Alopoglossus atriventris
Gonatodes humeralis
Chatogekko amazonicus
Gonatodes hasemani
Loxopholis percarinatum
Arthrosaura reticulata
Loxopholis osvaldoi
Kentropyx pelviceps
Kentropyx altamazonica
Ameiva ameiva
Varzea bistriata
Copeoglossum nigropunctatum
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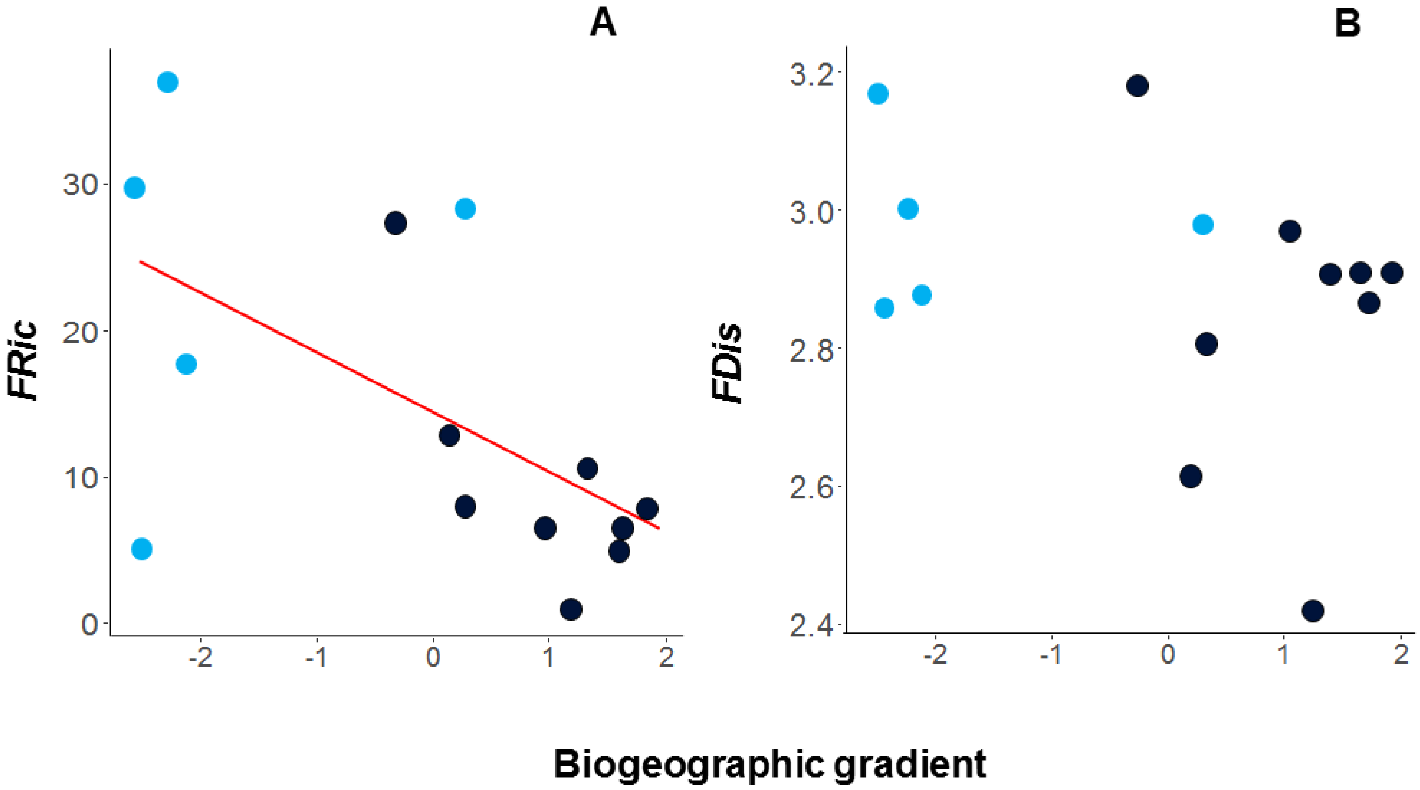
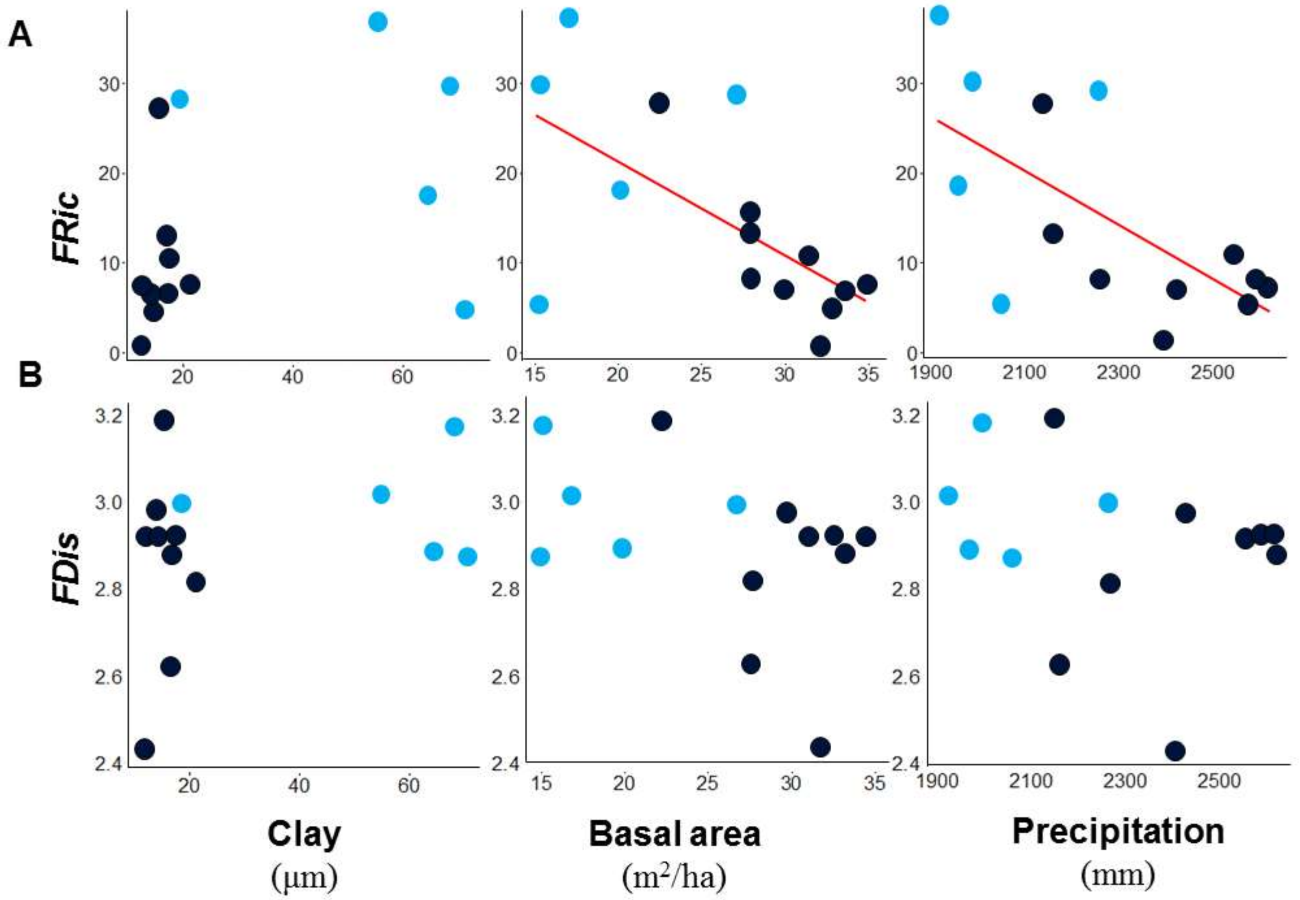
Plica umbra ochrocolaris
Uranoscodon superciliosus
Norops ortonii
Norops tandai
Dactyloa transversalis
Norops fuscoauratus
Dactyloa punctata
0.4
0.3
0.2
0.1
0.0
Gower distances


A
B
FRic
FDis
30
20
10
0
3.2
3.0
2.8
2.6
2.4
-2
-1
0
1
2
Biogeographic gradient


A
B
FRic
FDis
0
10
20
30
2.4
2.6
2.8
3.0
3.2
20
40
60
15
20
25
30
35
1900
2100
2300
2500
Clay
(μm)
Basal area
(m²/ha)
Precipitation
(mm)

Capítulo 3

Gabriela Marques Peixoto; Rafael de Fraga; Maria C. Araújo; Igor Luis Kaefer; Albertina Pimentel Lima. Hierarchical effects of historical and environmental factors on lizard assemblages in the upper Madeira river, Amazonian Brazil. Manuscrito submetido para a *PloS One*.

Hierarchical effects of historical and environmental factors on lizard assemblages in the upper Madeira river, Amazonian Brazil

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Abstract

Investigating the role of historical and ecological factors structuring assemblages is relevant to understand mechanisms and processes affecting biodiversity across heterogeneous habitats. Considering that community assembly often involves scale-dependent processes, different spatial scales may reveal distinct factors structuring assemblages. In this study we use lizard abundance data from 83 plots to investigate assemblage spatial structure at two distinct scales in southwestern Amazonian Brazil. At a regional scale, we test the general hypothesis that the Madeira River acts as a barrier to dispersal of some lizard species, which results in distinct assemblages between river banks. At a local scale, we test the hypothesis that assemblages are not evenly distributed across heterogeneous habitats but respond to a continuum of inadequate-to-optimal portions of environmental gradients. Our results show that regional lizard assemblages are structured by the upper Madeira River acting as barrier to 29.62% of the species sampled. This finding suggests species have been historically isolated at one of the river banks, although the strength of the barrier may depend on the regional shape of the river. At a local scale, different sets of environmental gradients affected assemblage composition between river banks or even within a river bank. These findings indicate that environmental filtering is a major cause of lizard assemblage spatial structure in the upper Madeira River, but predictor variables cannot be generalized over the study area. Based on a single study system we demonstrate that lizard assemblages along the forests near the banks of the upper Madeira River are not randomly structured but respond to multiple factors acting at different and hierarchical spatial scales.

Introduction

Investigating historical and ecological factors structuring assemblages may reveal patterns of biodiversity distribution across time and space [1,2]. However, defining mechanisms and processes that potentially affect assemblage structure is often highly dependent on the spatial scale applied [3-5]. Such dependence results from the fact that assemblage composition (e.g. taxonomic diversity) is influenced by complex hierarchical interactions among processes that operate at multiple spatio-temporal scales [6]. In highly heterogeneous habitats such as the Amazonian tropical rainforests the relative contribution of historical and ecological processes to assemblage structuring is poorly understood for many taxa, mainly because multi-scale ecological approaches depend on standardized sampling systems, which have been specifically designed for such purpose [e.g. 7-12]. Regarding lizards, poor knowledge on assemblage structure also results from lack of refined data on individual species distribution [13], despite few unpublished studies have shown assemblage spatial structure defined by environmental heterogeneity [e.g. 14-16].

At broad spatial scales (e.g. Amazon Basin), it has been suggested that many organisms are restrictedly distributed by their inability to cross large rivers. From the classic studies of Alfred R. Wallace on primate distribution across the Amazon Basin [e.g. 17], it has been known that the Amazon River and some of its main tributaries (e.g. Madeira, Negro) may be important biogeographic barriers to dispersal. Testing the Wallace´s hypothesis has revealed the riverine barrier as a major factor explaining limited distribution of plants [18], birds [19-22], frogs [23,12], primates [24,25] and spiny rats [26]. Additionally, studies have shown that gene flow reduced or blocked by a riverine barrier may cause genotypic and phenotypic divergence in

Amazonia [27-29]. Specifically for lizards, riverine barriers may cause intraspecific genetic divergence [27], although they do not necessarily produce different morphotypes [30]. Interspecifically, species distribution regionally limited to a single river bank may cause distinct assemblage compositions between banks [12,31].

At local scales, environmental gradients may affect species occurrence and abundance due to the filter effect of the spatial variation in habitat suitability [32,33]. In general, it is expected that habitat-specialist species find inadequate-to-optimum continuums of environmental conditions for survival and reproduction [34]. Environmental filtering has been found in Amazonia for plants [35,36], frogs [37,38], birds [39,40], snakes [41,42] and lizards [43,15]. For the latter, local assemblages may differ due to variation in individual abundance or species turnover along gradients of distance from water courses [44,31], elevation [45], climate seasonality [46], and number of trees [47,43]. Additionally, lizard assemblages may be indirectly structured by species turnover along gradients of canopy openness affecting the availability of thermoregulation sites [48,49], understory-plant density affecting the availability of foraging sites for perching species [50], and clay content in the soil affecting plant composition and food availability [43].

Integrating multiple spatial scales is relevant to estimating simultaneous effects of historical and ecological factors on assemblage structure, especially in heterogeneous habitats such as rainforests in Amazonia [51]. However, designing a sampling system which is efficient to quantify assemblages and habitats at multiple scales may be challenging. The RAPELD [1] method (Brazilian acronym for rapid sampling plus long-term ecological research) has been shown to be efficient for this purpose in the region of the upper Madeira River [13], due to (i) the adequate distribution of plot sets (5 km^2 each) so that hypotheses based on the effects of historical factors on regional assemblages may be tested (e.g. riverine barriers), and (ii) the plots following altitudinal contours reduce within-plot environmental variation, which allows them to be assumed as environmental units to test hypotheses based on environmental filtering [1]. The rationale behind testing such hypotheses in southwestern Amazonia is that the Madeira River has been recognized as a barrier to dispersal of Squamata reptiles, which causes species turnover along a longitudinal gradient [52], and the region covers two endemism zones (Rondônia e Inambari) that are distinct regarding geological history and environmental heterogeneity [53].

In this study we use plot-based lizard abundance data from the upper Madeira River (southwestern Amazonian Brazil) to investigate patterns of assemblage structure at two distinct spatial scales. At a regional scale, we test the hypothesis that lizard assemblages differ between the river banks. We expect differences in species composition and abundance as a consequence of the Madeira River historically limiting lizard dispersal. At local scale, we test the hypothesis that environmental heterogeneity causes species turnover, because species are absent or occur at low densities in suboptimal portions of environmental gradients. Specifically, we quantify the filtering effects on lizard abundance driven by gradients of number of trees, soil nutrient composition, shrub density, elevation, clay and sand content in the soil, and distance from the river bank. We expect that analyzing assemblages from two distinct perspectives will provide us with deep insights into factors that cause and maintain biodiversity at megadiverse regions such as the upper Madeira River.

Materials and methods

Study area

The study area is located near the banks of the upper Madeira River (centroid coordinates 08°48004.0″ S; 63°56059.8″ W), from the outskirts of Porto Velho (Rondônia state) to about 600 km upriver, in the southwestern portion of Brazilian Amazonia. We also surveyed plots near the Jaci Paraná River, a tributary on the east bank of the upper Madeira River (Fig 1).

Fig 1. Location of the upper Madeira River, state of Rondônia, Brazil. Five km^2 sampling modules (circles) near the banks. Gray circles show modules in the Inambari endemism zone, blue circles are modules in the Rondônia endemism zone [according to 20]. The acronyms summarize sampling modules' local names: TO = Teotônio, IB = Ilha dos Búfalos, IP = Ilha das Pedras, JL = East Jirau, JR = West Jirau, JP = Jaci-Paraná, MO = Morrinhos. In detail on the left side, the standard configuration of each module, with 14 plots (squares), 250 m-long each, distributed along a gradient of distance from the river bank (0–5,000 m).

In this study we quantified environmental heterogeneity as continuous gradients that may be broadly classified for descriptive purposes in three main habitat types. They mainly differ in canopy height, soil texture, and understory-plant density and species composition [following 54]. In the upland (terra-firme) forests habitats are never flooded by overflowing large rivers, the canopy is 30 m high, and the understory-plant density and clay content in the soil often depends on elevation [55]. The várzea forests are seasonally flooded by overflowing sediment-rich rivers, which produces nutrient-rich soils that are water-saturated for long periods. The canopy is 20 m high, and the understory is rich in bromeliads. The campinaranas are patches of palm tree-rich forests growing on a white-sand soil, which is highly drained and nutrient-poor [54].

The climate of the study area is tropical humid, with annual average temperature at 25.5 °C and average precipitation at 2,287 mm [56]. Precipitation is distributed throughout the year in well-marked dry (May to September) and rainy (October to April) seasons. During the dry season, small streams can dry completely [56].

Sampling design

We collected lizard abundance data in seven 5 km^2 RAPELD sampling sites (hereinafter modules), that were installed perpendicularly to the river bank. RAPELD [1] is a modification of the Gentry´s sampling method based on 1-ha plots [57], with the main difference being that the RAPELD plot central lines follow the altitudinal curves to reduce environmental variation within plots (PPBio - http://ppbio.inpa.gov.br). We sampled three modules on the east bank of the Madeira River (East-Jirau, Jaci-Paraná and Morrinhos), and four modules on the west bank (West-Jirau, Ilha das Pedras, Ilha dos Búfalos and Teotônio). The average distance between neighboring modules was 120 km. Each RAPELD module was composed of two 5-km long parallel trails, separated by 1 km. We surveyed seven 250 m plots (20 m wide) on each trail, totaling 98 plots (14 plots in each of the seven modules). The plots were distributed along a gradient of distance from the river bank, at 0, 500, 1000, 2000, 3000, 4000 and 5000 m.

We were not able to find lizards in 15 plots, and the excess of zeros in the dataset prevented us to reliably estimate pairwise distances among plots to summarize assemblage composition (see Data analysis). Therefore, we excluded zero-valued plots and our analyzes are based on 83 plots.

Sampling effort

We sampled each plot in four different periods (24 February to 26 April 2010, July 30 to August 19 2010, November 5 to 26 2010, and January 13 to February 4 2011) to cover large portions of the regional variation in temperature and precipitation along a year. We used species' maximum abundance values per plot in the analyzes.

We found lizards using active visual search, with two simultaneous observers positioned 10 m apart. In addition, we supplemented the sampling effort by sweeping the leaf litter and removing debris in a 2 m strip following the center line of the plot. This approach was particularly useful to increase the efficiency of sampling fossorial and leaf-litter species (e.g. Alopoglossidae, Gymnophthalmidae). The searching time in each plot varied between 40 and 60 minutes.

Environmental variables

We measured eight environmental gradients in each plot, attempting to quantify spatial heterogeneity in habitat quality. We quantified vegetation structure by measuring (i) number of trees and (ii) shrub density. Those gradients potentially affect squamates abundance by influencing availability of foraging, resting and thermoregulation sites [58-60]. We also measured edaphic gradients related to soil texture, fertility, and flat-level deviation, which are (iii) clay content, (iv) sand content, (v) nutrient composition (Soil pH, Calcium, Magnesium, Potassium, Zinc and exchangeable Aluminum), (vi) elevation, and (vii) terrain declivity. Those variables potentially affect lizard abundance by causing variation in the overall primary production [61] and availability of invertebrate prey [62]. Additionally, we measured (viii) distance from the river bank, because it has been found as a major factor structuring plant [36] and animal [31,38,39,41] assemblages in Amazonia. The methods used to measure each gradient are described in detail in Appendix 1.

Data analysis

To quantify assemblage composition, we applied the Bray-Curtis index to estimate pairwise distances in species abundance among plots. We reduced dimensionalities using Principal Coordinate Analysis (PCoA) and represented assemblage composition by the first one or two axes produced (see below).

At regional scale (riverine barrier effects) we modeled the PCoA using all data (83 plots). The two first axes captured 30% (PCoA 1 = 16%. PCoA 2 = 14%) of the original variance in species abundance, and we used them to represent assemblage composition. To assess assemblage structuring, we used Multivariate Analysis of Variance MANOVA to test differences in assemblage composition (PCoA axes 1 and 2) between the river banks. We implemented a MANOVA using the vegan [63] R-package [64].

Analyzes at regional scale revealed two distinct lizard assemblages between the river banks (see Results). In addition, preliminary analyzes at local scale revealed that in two modules (Ilha das Pedras and East Jirau) environmental gradients may affect assemblage composition in opposite directions compared to the other modules (S2 and S3 Fig). These findings suggested that the banks of the Madeira River and some of the sampling modules within a river bank are distinct environmental units, which contain distinct spatial structures of lizard assemblage composition. Therefore, to assess assemblage structure at local scale we modeled four distinct PCoA ordinations, using data from (i) the west bank, except for the module Ilha das Pedras (37 plots), which captured 86% of the original variance (PCoA 1 = 0.50, PCoA 2 = 0.36); (ii) the east bank, except for the module East Jirau (23 plots), which captured 45% of the original variance (PCoA 1 = 0.30, PCoA 2 = 0.15); (iii) the module Ilha das Pedras (12 plots), which captured 45% of the original variance (PCoA 1 = 0.32, PCoA 2 = 0.13); and (iv) the module East Jirau (11 plots), which captured 85% of the original variance (PCoA 1 = 0.49, PCoA 2 = 0.36).

The environmental gradients measured are expressed in different units and therefore in different orders of magnitude, so we transformed them using the “scale” function of the vegan R-package. This function subtracts mean values from each variable and scales centralized variables by dividing them by their standard deviation [63]. We used Mixed Linear Models to test the effects of scaled environmental gradients on assemblage composition based on data from multiple sampling modules. By using this method, we were able to include sampling modules as random effects to minimize potential abrupt differences in environmental gradients and lizard assemblages among the modules analyzed in a same model [65]. We set up two different groups of mixed models, according to the assemblage compositions summarized by PCoA for the west and east banks of the Madeira River. Each group was composed of as many models as necessary to test all possible combinations of environmental gradients, except for those that were highly correlated. For instance, clay and sand content in the soil were not used in a same model because they were highly correlated on both river banks ($r \geq 0.93$). In addition, elevation was correlated with terrain declivity on both river banks ($r \geq 0.78$) and soil-nutrient composition on the east bank ($r = 0.66$).

For the two modules that were analyzed separately (Ilha das Pedras and East Jirau), it was not necessary to control random effects of sampling sites, so we tested the effects of environmental gradients on the assemblage composition using multiple linear regression models. We tested models with assemblage composition (PCoA 1) as dependent variable, and all possible combinations of uncorrelated environmental gradients as independent variables.

To select the most parsimonious mixed-effects and multiple-regression models we ranked all the models by the Akaike´s Information Criterion corrected for few parameters [66]. We refined the model selection by penalizing nested models assuming ΔAICc < 2 as a cut-off point. All selected models were validated by normal distribution of residuals (Shapiro-Wilk $W > 0.95$, $P > 0.05$ in all cases).

For visually checking the distribution of lizard abundance values per species along river banks and environmental gradients (only those that significantly affected assemblage composition) we plotted ordinated sampling plots. These graphs will be used in this study for assessing how spread the distributions of abundance values are over the river banks and the environmental heterogeneity measured.

RESULTS

We found 27 lizard species, which are classified in 18 genera and 10 families. The most frequently found species were *Norops fuscoarautus* (Dactyloidae), *Gonatodes humeralis* (Sphaerodactylidae), and *Ameiva ameiva* (Teiidae), which occurred in both banks of the Madeira River, in 55, 49 and 30% of the plots respectively. Contrarily, *Alopoglossus angulatus* (Alopoglossidae) and *Enyalius leechii* (Leiosauridae) were found in one single plot (Table 1).

Table 1. List of lizard species sampled in the upper Madeira River, Brazil. N = total abundance per species, East and West = Madeira river banks filled with presence (1) and absence (0) data.

Family/Species	N	East	West
Dactyloidae			
Norops fuscoauratus (D'Orbigny, 1847)	103	1	1
Norops tandai (Wagler, 1830)	2	0	1
Norops ortonii (Cope, 1869)	2	1	1
Dactyloa punctata (Daudin, 1802)	27	1	1
Dactyloa transversalis (Dumeril, 1851)	9	0	1
Alopoglossidae			
Alopoglossus angulatus (Linnaeus, 1758)	2	0	1
Gymnophthalmidae			
Arthrosaura reticulata (O'Shaughnessy, 1881)	5	1	0
Cercosaura argula (Peters, 1863)	5	1	1
Cercosaura eigenmanni (Griffin, 1917)	11	1	1
Cercosaura bassleri (Ruibal, 1952)	8	0	1
Iphisa elegans (Gray, 1851)	8	1	1
Loxopholis percarinatum (Muller, 1923)	10	1	1
Hoplocercidae			

Enyalioides laticeps (Guichenot, 1855)	3	1	1
Hoplocercus spinosus (Fitzinger, 1843)	2	1	1
Leiosauridae			
Enyalius leechii (Boulenger,1885)	2	1	0
Scincidae			
Copeoglossum nigropunctatum (Spix, 1825)	14	1	1
Phyllodactylidae			
Thecadactylus rapicauda (Houttuyn, 1782)	21	1	1
Sphaerodactylidae			
Chatogekko amazonicus (Andersson, 1918)	12	1	1
Gonatodes hasemani (Griffin, 1917)	29	1	1
Gonatodes humeralis (Guichenot, 1855)	432	1	1
Teiidae			
Kentropyx altamazonica (Cope, 1876)	14	1	1
Kentropyx calcarata (Spix, 182)	37	1	0
Kentropyx pelviceps (Cope, 1868)	29	0	1
Ameiva ameiva (Linnaeus, 1758)	48	1	1
Tropiduridae			
Plica plica (Linnaeus, 1758)	7	1	1
Plica umbra ochrocollaris (Spix, 1825)	21	1	1
Uranoscodon superciliosus (Linnaeus, 758)	5	1	1
Total	**868**		

Regional assemblage structuring - Madeira River as a biogeographic barrier

We found 19 species on both banks of the Madeira River, which is equivalent to 70.37% of the total diversity sampled. This finding suggests that most of the species sampled are widely distributed throughout the study area. However, for several of the species found on both sides of the river (e.g. *Loxopholis percarinatum*, *Kentropyx altamazonica*, *Cercosaura eigenmanni*, *Plica plica*, *Uranoscodon superciliosus*, *Copeoglossum nigropunctatum*), plot-related frequency and abundance were not even between the river banks (Fig 2). Additionally, five species (18.52%) were restricted to the west bank – *Alopoglossus angulatus*, *Norops tandai*, *Dactyloa transversalis*, *Cercosaura bassleri* and *Kentropyx pelviceps*, and three species (11.11%) were restricted to the east bank –*Arthrosaura reticulata*, *Kentropyx calcarata e*

Enyalius leechii. These findings suggest two distinct assemblage compositions delimited by the Madeira River, which is strongly supported by differences in the PCoA scores (based on 83 plots) between the river banks (MANOVA Pillai Trace = 0.315, $F_{1–81}$ = 18.40, P <0.001).

Fig 2. Plots ordinated according to their position on the upper Madeira River (west and east). The heights of the black rectangles are relative to species abundance values.

Local assemblage structuring – the role of environmental gradients

On the west bank of the Madeira River (except for the module Ilha das Pedras) three mixed-effects models were selected by ΔAICc < 2 (Table 2). All the selected models consistently returned number of trees as a major gradient affecting assemblage composition (P < 0.001 in all cases). Despite some species occupied large portions of the gradient of number of trees (e.g. *Ameiva ameiva*, *Norops fuscoauratus*), species absence or low abundance in specific intervals between 144 and 613 trees caused species turnover (Fig 3). According to the models selected, assemblage composition was not affected by elevation (P = 0.76), and soil-content of sand (P = 0.84) or clay (P = 0.91).

Table 2. **Summary of the results returned by Linear Mixed-Effects Models.** The models were set up using data from the west (Teotônio, Ilha dos Búfalos and West Jirau) and east (Morrinhos and Jaci-Paraná) banks of the upper Madeira River. The models were selected by AICc Δ < 2. Shapiro-Wilk tests were applied on the residuals from each model to test normality. Bolded p-values show cases in which the null hypothesis was rejected.

Margin	Fixed effects	AICc	Weight	*df*	*t*	*p*	Variance	Shapiro-Wilk
West	Number of Trees and Elevation	12.89	0.314	Intercept:2.18	-6.92	<**0.001**	54%	P=0.109
				Trees:3.01	18.8	<**0.001**		
				Elevation:1.43	-0.31	0.76		
	Sand and Number of Trees	12.88	0.309	Intercept:3.39	-14.69	**0.001**	69%	P=0.066
				Sand:1.86	-0.19	0.84		
				Trees:3.29	18.8	<**0.001**		
	Clay and Number of Trees	12.88	0.305	Intercept:1.00	-9.07	<**0.001**	76%	P=0.153
				Clay:9.76	0.10	0.91		
				Trees:3.27	18.88	<**0.001**		
East	Elevation and Margin distance	2.0	0.412	Intercept:2.30	6.37	<**0.001**	71%	P=0.782
				Elevation:2.30	-6.27	<**0.001**		
				Margim:2.30	1.72	0.09		
	Number of Trees and Elevation	2.0	0.400	Intercept:2.30	5.92	<**0.001**	72%	P=0.413
				Trees:2.10	18.8	0.10		
				Elevation:2.30	-0.31	<**0.001**		

Fig. 3. Plots ordinated according to their position relative the number of trees in the west bank of the upper Madeira River, state of Rondônia, Brazil. The heights of the black rectangles are relative to species abundance values.

Margins	**Variables**	**AICc**	**Weight**	**Std. error**	***t***	**P**	***F***	**r2**
West	Number of Trees and Elevation	15.7	0.31	Intercept:8.76	0.00	1.00	2.746	0.37
				Trees:9.19	0.90	0.39		
				Elevation:9.19	-2.06	0.06		
	Sand and Elevation	15.8	0.29	Intercept:8.81	0.00	1.00	2.66	0.37
				Sand:9.21	0.85	0.42		
				Elevation:9.21	-2.18	**0.05**		
	Clay and Elevation	16.2	0.25	Intercept: 1.21	0.1	1.10	2.45	0.35
				Clay:6.12	-0.64	0.53		
				Elevation:1.88	-1.98	0.07		
East	Clay and Distance from the margin	6.5	0.655	Intercept: 5.69	0.00	1.00	15.42	0.81
				Clay: -1.05	-1.69	0.13		
				Margim:2.89	4.63	<**0.001**		
	Sand and Distance from the margin	7.9	0.367	Intercept: 2.30	5.92	<**0.001**	13.07	0.78
				Sand:8.81	1.28	0. 24		
				Margim:2.85	4.15	<**0.001**		

For the Ilha das Pedras module three multiple-regression models were selected (Table 3), all of them containing elevation as an independent variable. This gradient significantly affected assemblage composition according to a model constructed with soil sand content as an additional independent variable ($P = 0.05$) (Fig 4). However, the effects of elevation on the assemblage composition were marginally significant in models containing number of trees ($P = 0.06$) and soil clay content ($P = 0.07$) as independent variables.

Table 3. **Summary of the results returned by Linear Mixed-Effects Models.** The models were set up using data from the Ilha das Pedras (west river bank) and East Jirau (east river bank) modules for test the effects of environmental gradients on lizard assemblage composition. The models were selected by AICc $\Delta < 2$. Shapiro-Wilk tests were applied on the residuals from each model to test normality. Bolded p-values show cases in which the null hypothesis was rejected.

Fig. 4. Partials from a multiple linear model for the Ilha das Pedras module. Model for the effects of the elevation and sand contents in the soil on lizard assemblage composition. Assemblage composition was summarized by the first axis of an Analysis of Principal Coordinates based on abundance data of the upper Madeira River, state of Rondônia, Brazil. The shades of blue show values of sand content in the soil.

On the east river bank (except for the East Jirau module) two models were selected as most parsimonious. Both models consistently showed strong effects of elevation on assemblage composition ($P < 0.001$ in both cases). This finding suggests species turnover along an elevational gradient of 69.12–100.59 m (Fig 5). According to the same models, distance from the river bank ($P = 0.09$) and number of trees ($P = 0.1$) did not affect assemblage composition.

Fig 5. Plots ordinated according to their position relative to a gradient of elevation in the east bank of the upper Madeira River, state of Rondônia, Brazil. The heights of the black rectangles are relative to species abundance values.

Two multiple-regression models were selected for the East Jirau module. Both models consistently returned distance from the river bank (Fig 6) as a relevant gradient affecting assemblage composition ($P < 0.001$ in both cases). Soil-content of sand ($P = 0.24$) and clay ($P = 0.13$) did not affect assemblage composition.

Fig 6. Partials from a multiple linear model to test the effects of distance from the river bank, sand and clay contents in the soil on lizard assemblage composition. Assemblage composition was summarized by the first axis of an Analysis of Principal Coordinates based on abundance data from the East Jirau sampling module, located on the east bank of the upper Madeira River, state of Rondônia, Brazil. The shades of blue show values of sand and clay contents in the soil.

Discussion

At regional scale, we found that lizard assemblages are spatially structured by differences in species composition between river banks. This finding is consistent with large Amazonian rivers acting as dispersal barriers for several organisms, which have caused different species subsets composed of plants [18], birds [19,21], primates [24] and diurnal frogs

[12]. At local scale, we showed that lizard assemblages are spatially structured by species turnover along environmental gradients. However, a set of environmental gradients cannot be assumed as generalized predictors among sampling sites. Our overall results are broadly consistent with frog assemblages sampled in the same plots [12], which suggests multi-taxa ecological patterns. We relied on a single dataset to provide understanding about assemblage structure based on interacting historical and ecological processes. Therefore, we highlight the relevance of investigating multi-scale assemblage structuring for ecology and conservation decision making.

In the upper Madeira River, assemblage divergence between river banks has been attributed to historical processes regionally reducing species dispersal [12]. Approximately 50% of the species composing a frog assemblage (13 species) were absent in one of the river banks. The smaller proportion of regionally isolated lizard species (29.63%) is reasonably explained by the lower dispersal capacity of small and site-attached frogs compared with most lizards. Nonetheless, we investigated aseemblages in which about 30% of the sampled species were isolated by the river, and another 30% of the species occurred at low relative frequency or abundance at one of the river banks. This was a sufficiently adequate scenario to assume the river as a historical factor segregating assemblages between the river banks. We highlight that most of regionally isolated species in our sample are widely distributed throughout Amazonia outside our study area [13]. Such inconsistency may be explained by the strength of the river as a dispersal barrier varying along the river course, or even being nullified in response to meandering shapes [67- 69,30]. Additionally, the barriers may be seasonal, because bridges for stepping-stone dispersal may be revealed during the dry season, which allows gene flow between river banks [70]. Therefore, our results for assemblage structure at regional scale should not be extrapolated to unsampled stretches of the Madeira River or other Amazonian rivers, because lizards probably have found multiple dispersal routes through evolutionary time [27].

The isolation of species on one of the river banks may be related to the geomorphological heterogeneity of the Madeira River across our study area. The Madeira river flows over an incisive fluvial valley, with predominantly crystalline and a geologically ancient basement (ca. 16 Ma). The morphodynamical development was mainly influenced by the geomorphological and climatic changes resulting from the Andean Orogeny in the Cenozoic [71], which have produced a relatively stable course along recent geological times [72]. Such stability in the shape of the river course has prevented meandering across most of the study area, which could facilitate for species to cross the river [73]. Exceptionally, the modules located further upstream (East and West Jirau) have rocky outcrops that are exposed in the middle of the river course during the dry season, which can act as bridges for stepping-stone dispersal (field observation). Although lizard species used alternative dispersal routes to widespread their distribution throughout Amazonia, our study showed that they were regionally prevented from colonizing or maintaining populations on both banks of the upper Madeira River.

At local scale, lizard assemblages were spatially structured by environmental filtering causing non-random assemblage composition. Environmental conditions selected species that were able to survive and maintain viable conditions in given sampling plots [74]. Despite we sampled species that are generalist in relation to the environmental gradients measured (e.g. *Ameiva ameiva*, *Norops fuscoauratus*), species for which distributions were restricted to narrow regions of gradients (e.g. *Cercosaura argula*, *Norops ortonii*, *Uranoscodon superciliosus*) caused species turnover across sampling plots. Species turnover mediated by environmental filtering is a major factor structuring local assemblages in Amazonia [e.g. 41,36,39], and in the upper Madeira River it has efficiently explained assemblage structure in bats [75], frogs [12] and snakes [76]. However, we cannot generalize a single environmental dataset as a predictor for assemblage composition in all plots. Environmental predictors for assemblage composition differed between the river banks or even within a river bank. This finding suggests that the scale at which lizard assemblages respond to environmental heterogeneity may be more refined than the classification of the Madeira river banks as distinct endemism zones [77,20].

Number of trees was a major factor causing species turnover in the west bank of the Madeira River. This gradient ranged from 144 to 613 trees, which shows that the vegetation structure is quite heterogeneous throughout our study area. Heterogeneity in vegetation structure affects species occurrence and abundance due to variation in the availability of foraging, nesting, resting, and thermoregulating sites [58,60]. Additionally, tree cover may directly affect food availability, protection against predators, light intensity, temperature, humidity and wind speed [59,60]. The evidence for assemblage structuring along a gradient of number of trees is of concern from a conservation point of view, because our study area has been intensely deforested by the agribusiness and large hydroelectric plants [78]. It is widely expected that species dependent on high levels of tree cover (e.g. *Norops tandai*, *Norops ortonii*, *Dactyloa transversalis*) will either be locally extinct or migrate to more suitable habitats. Future studies should focus on investigating species turnover at time scales.

We found species turnover along an elevational gradient, although this finding was most evident on the east bank of the Madeira River. On the east bank the plots were installed on the depression of the Ji-Paraná river, which generated elevation values below 30 m. Low elevation is often related to outcropping of groundwater and high drainage density [79,71], which favors the occurrence of habitat-specific species for high humidity. For instance, *Arthrosaura reticulata* and *Uranoscodon superciliosus* typically occupy humid low areas [80,81], and in this study those species were found only on the east bank of the Madeira River. Additionally, elevation indirectly influences assemblage composition because it affects water availability and soil fertility [82-84], and therefore the overall structure of available habitats [85]. Extreme variation in elevation may cause behavioral and morphological differentiation in Andean lizards [86]. In this study we showed that even subtle variation in elevation (24 to 128 m) may be sufficient for species to be locally filtered. A similar finding was observed using frog assemblage data from the Guiana Shield [11,37].

The gradient of distance from the river caused species turnover in the East Jirau module. Although habitats may be classified in riparian and non-riparian zones [87], gradients of distance from water courses carry multiple continuous interacting variables of microclimate, nutrient availability, vegetation cover and edaphic structure. Habitats continuously changing along gradients of distance from streams (< 12 m wide) have caused species turnover structuring plant [36], frog [38], bird [39] and snake [41] assemblages. In this study, we showed a similar pattern using lizard abundance data, with the main difference being that the gradient we measured refers to the distance from the bank of one of the major tributaries of the Amazon River. However, no significant effect of distance from the river on assemblage composition was returned using data from the other modules. This finding suggests that assemblages diverging between riparian and non-riparian zones should not be generalized in relation to large rivers, or assemblage segregation should occur at distances that are greater than 5 km away from the river bank.

Some of the results found may be associated to environmental variables that were not explicitly measured in this study. For example, *Hoplocercus spinosus* (Hoplocercidae) occurred on both banks of the Madeira River but occurrence was restricted to plots with rocky outcrops. Such condition was only found in the westernmost sampling modules of the study area (East and West Jirau), where the species finds optimal availability of thermoregulation and refuge sites [88]. This finding reflects relationships between species and habitats that are dependent of biological traits affecting survival [89,90] and dispersal capacity [91,92], such as body size, diet [93], specificity level in habitat use [81], reproductive [49] and foraging mode [76]. Therefore, although patterns of assemblage structure are usually described based on dissimilarities among plots regarding subsets of cooccurring species, they may be determined by ecological requirements of individual species.

We showed that lizard assemblages in the upper Madeira River are structured by scale-dependent hierarchical factors. Historical processes related to the Andes uplift [94] have isolated regional assemblages between the river banks, and have also generated distinct habitat patches, which in turn generate distinct local lizard assemblages. It is generally well established that interacting historical and environmental factors explain hierarchical structures of assemblages [5]. However, empirical application is not common because it relies on efficient sampling designs to capture multiple scales. In the megadiverse Amazonian rainforests this has been achieved by a few studies [73,12,31]. Considering the fine levels in which such studies assessed processes affecting biodiversity, efficient methods for multi-scale sampling should be prioritized by ecology and conservation biology.

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Supporting information captions

S1 Text. Protocols for measuring the environmental gradients. Gradients used as independent variables in the ecological models to test lizard assemblage structuring in the upper Madeira River, Amazonian Brazil.

S2 Fig 1. Partials from Mixed Linear Models for the west bank of the Madeira River. Test the effects of environmental gradients on lizard assemblages composition (PCoA axis 1). The models were selected by ΔAICc < 2. (A) Ilha das Pedras (B) Ilha dos Búfalos (C) Jirau-West (D) Teotônio.

S3 Fig 2. Partials from Mixed Linear Models for the East bank of the Madeira River. Test the effects of environmental gradients on lizard assemblages composition (PCoA axis 1). The models were selected by ΔAICc < 2. (A) Jaci- Paraná (B) Jirau-East (C) Morrinhos.

Figures

Figure 1.

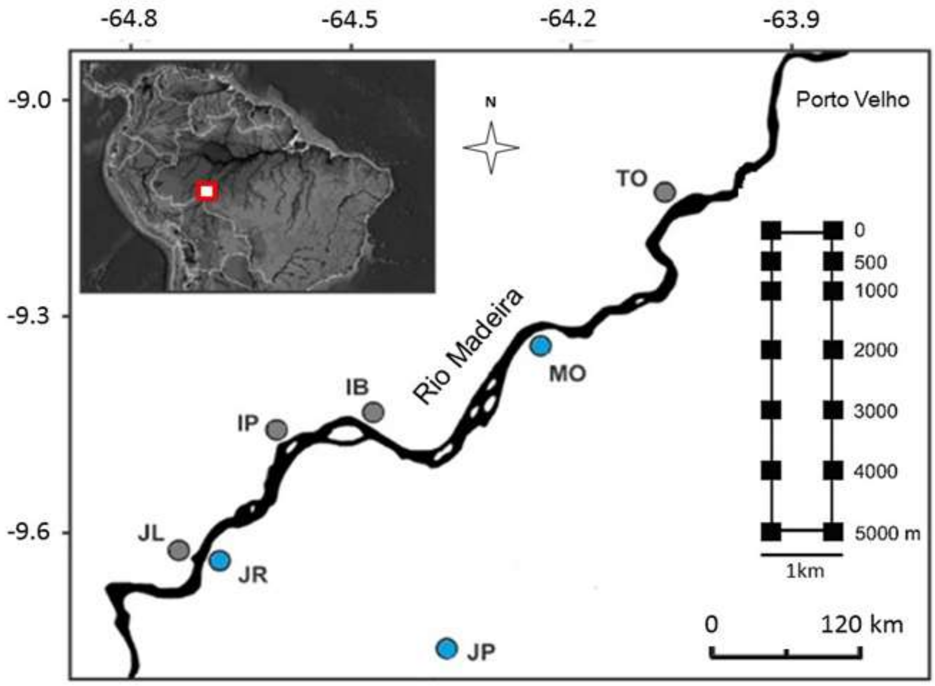


Figure 2.

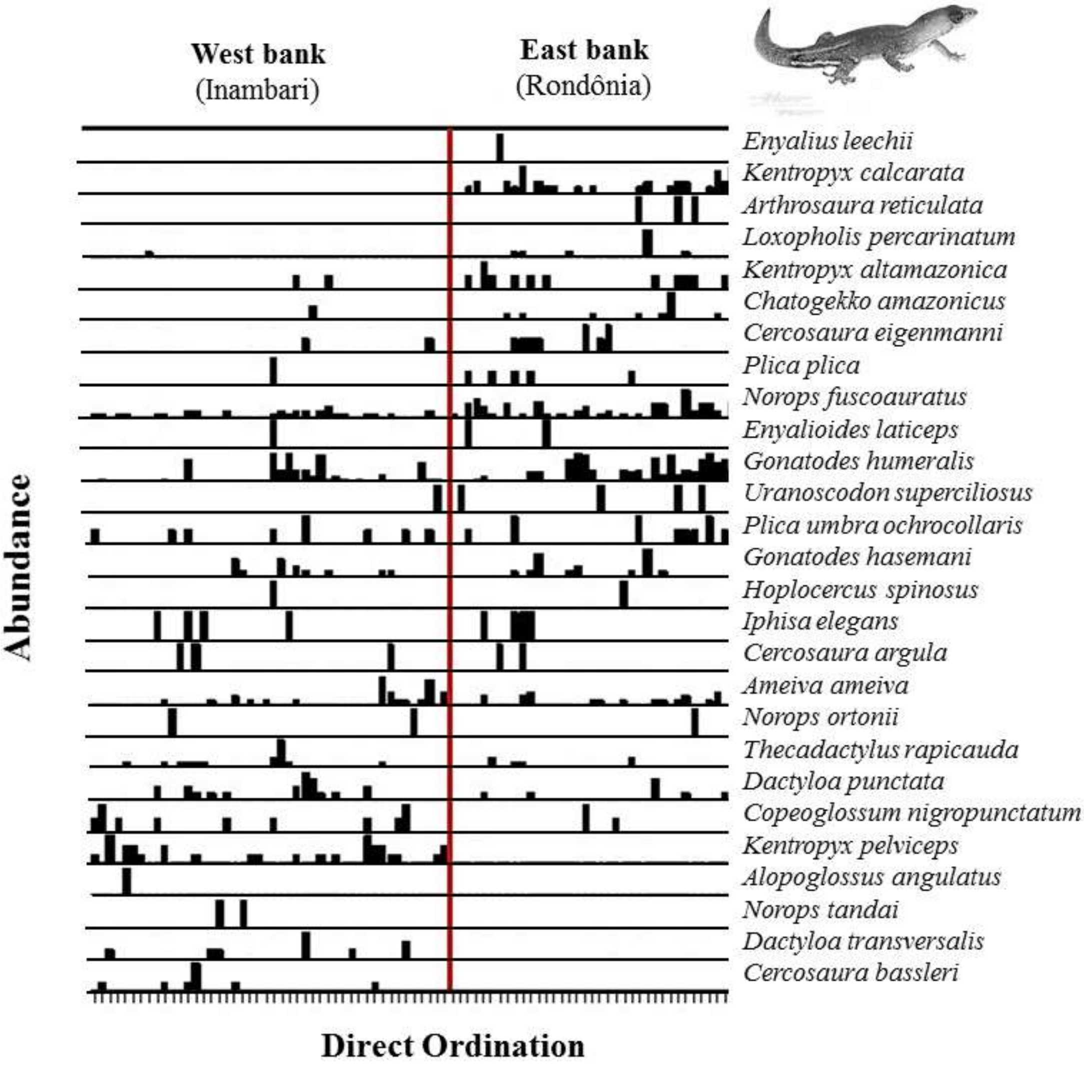

West bank
(Inambari)
East bank
(Rondônia)
Abundance
Enyalius leechii
Kentropyx calcarata
Arthrosaura reticulata
Loxopholis percarinatum
Kentropyx altamazonica
Chatogekko amazonicus
Cercosaura eigenmanni
Plica plica
Norops fuscoauratus
Enyalioides laticeps
Gonatodes humeralis
Uranoscodon superciliosus
Plica umbra ochrocollaris
Gonatodes hasemani
Hoplocercus spinosus
Iphisa elegans
Cercosaura argula
Ameiva ameiva
Norops ortonii
Thecadactylus rapicauda
Dactyloa punctata
Copeoglossum nigropunctatum
Kentropyx pelviceps
Alopoglossus angulatus
Norops tandai
Dactyloa transversalis
Cercosaura bassleri
Direct Ordination

Figure 3.

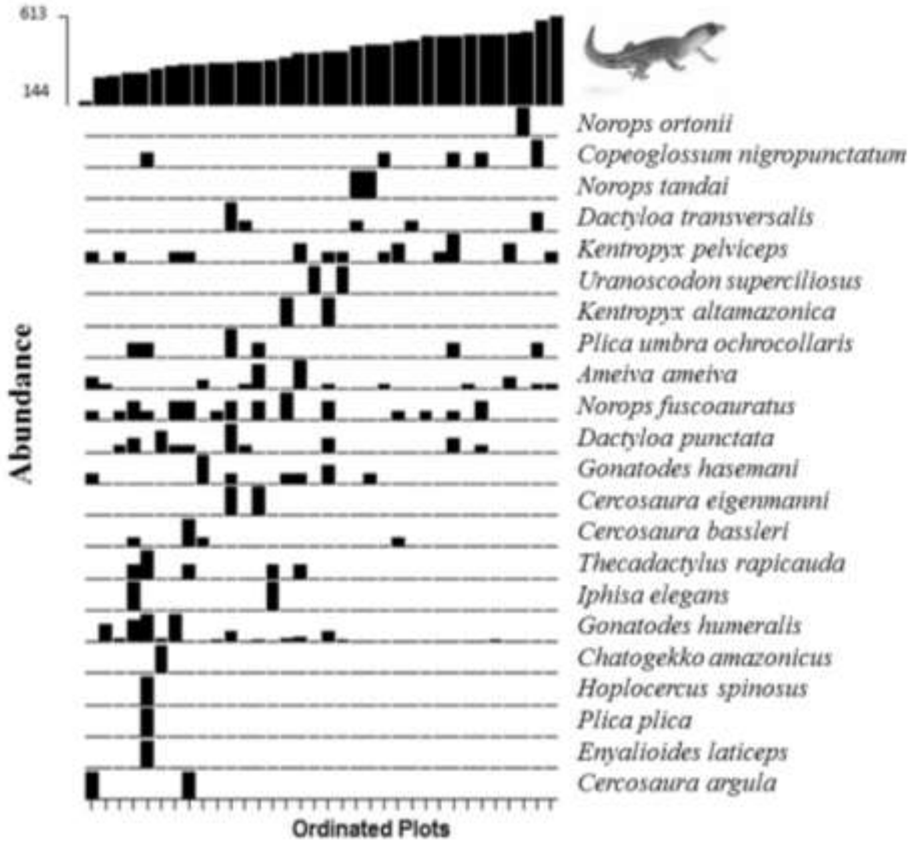

613
144
Abundance
Norops ortonii
Copeoglossum nigropunctatum
Norops tandai
Dactyloa transversalis
Kentropyx pelviceps
Uranoscodon superciliosus
Kentropyx altamazonica
Plica umbra ochrocollaris
Ameiva ameiva
Norops fuscoauratus
Dactyloa punctata
Gonatodes hasemani
Cercosaura eigenmanni
Cercosaura bassleri
Thecadactylus rapicauda
Iphisa elegans
Gonatodes humeralis
Chatogekko amazonicus
Hoplocercus spinosus
Plica plica
Enyalioides laticeps
Cercosaura argula
Ordinated Plots

Figure 4.

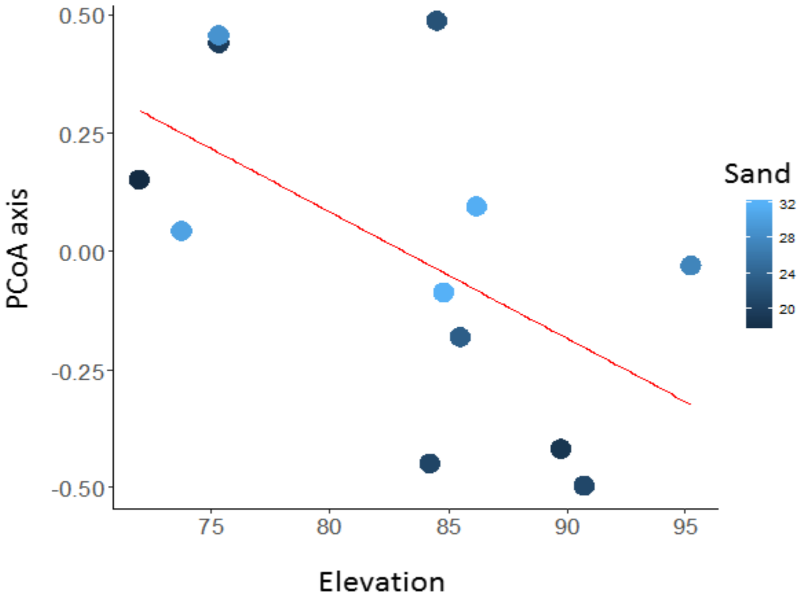

0.50
0.25
0.00
-0.25
-0.50
PCoA axis
75
80
85
90
95
Elevation
Sand
32
28
24
20

Figure 5.

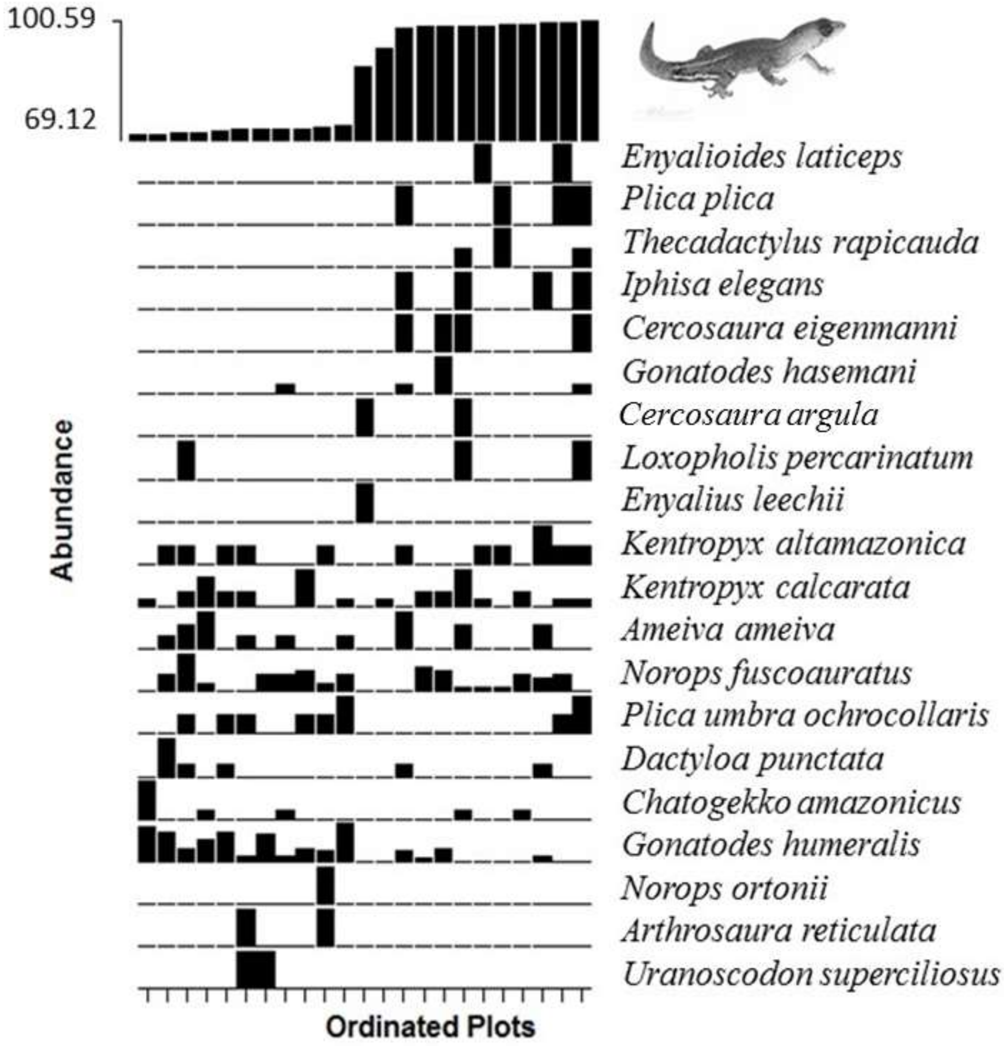
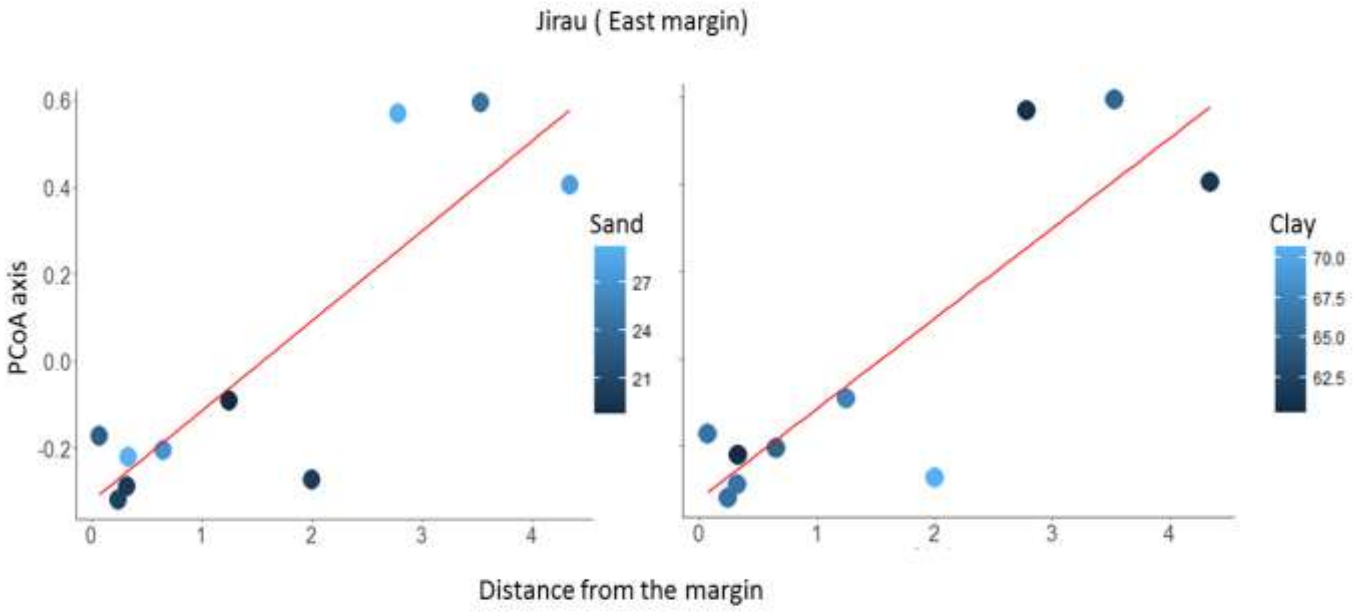

100.59
69.12
Abundance
Enyalioides laticeps
Plica plica
Thecadactylus rapicauda
Iphisa elegans
Cercosaura eigenmanni
Gonatodes hasemani
Cercosaura argula
Loxopholis percarinatum
Enyalius leechii
Kentropyx altamazonica
Kentropyx calcarata
Ameiva ameiva
Norops fuscoauratus
Plica umbra ochrocollaris
Dactyloa punctata
Chatogekko amazonicus
Gonatodes humeralis
Norops ortonii
Arthrosaura reticulata
Uranoscodon superciliosus
Ordinated Plots

Figure 6.



Jirau (East margin)
PCoA axis
0.6
0.4
0.2
0.0
-0.2
Sand
27
24
21
Clay
70.0
67.5
65.0
62.5
0
1
2
3
4
Distance from the margin

S 1. Protocols

NUMBER OF TREES. –The density sampling method used transects that varied in size depending on the size of the plant class being surveyed, as follows: (Transect 1) plants with a diameter at breast height (DBH) ≥ 1 cm were sampled in 1m-wide band to the left side of the centerline, for the entire length of the sample plot; (Transect 2) plants with DBH ≥ 10 cm were sampled in a 20m wide band, with 10 m on either side of the plot center line. On the left, this band included Transects 1 and 3; (Transect 3) plants with DBH ≥ 30 cm were sampled in a range of 40 m wide, 20 m being on each side of the center line of the plot. On the left, this range overlapped with Transects 1 and 2, where all plants with DBH greater than or equal to 1 or 10 cm were measured. On the right side, this band includes Transect 2. More details of the plant data collection component are available at: http://ppbio.inpa.gov.br/sites/default/files/Estrutura_vegetacao.pdf. For statistical analyzes the total density of plants (sum values from Transects 1, 2 and 3 combined) per plot was used.

SOIL NUTRIENT COMPOSITION. –Soil pH was obtained from the effective H+ ion concentration, determined with a combined electrode directly immersed in a soil solution diluted with distilled water at a 1:2.5ml ratio. Calcium, Magnesium and exchangeable Aluminum were extracted with KCl 1M. Exchangeable Al+3 was titrated with NaOH 0.025M using bromothymol blue as an indicator. Ca+2 and Mg+2 levels were determined by atomic absorption spectrophotometry (AAS). Potassium and soil micronutrients (iron, zinc and manganese) was extracted with Mehlich I2 extraction solution (double-acid solution), consisting of a mixture of HCl 0.05M + H2SO4 0.0125M. The mL extract ratio was 1:10. K, Fe, Zn and Mn were determined by AAS. Available phosphorus was determined with a colorimetric spectrophotometer, using 3% ammonium molybdate and ascorbic acid. Using these values, formula was applied to the sum of bases, following the methods of Quesada et al. (2010), which allowed soil fertility in each plot to be inferred. For statistical analyzes the value for the sum of bases in each plot was used.

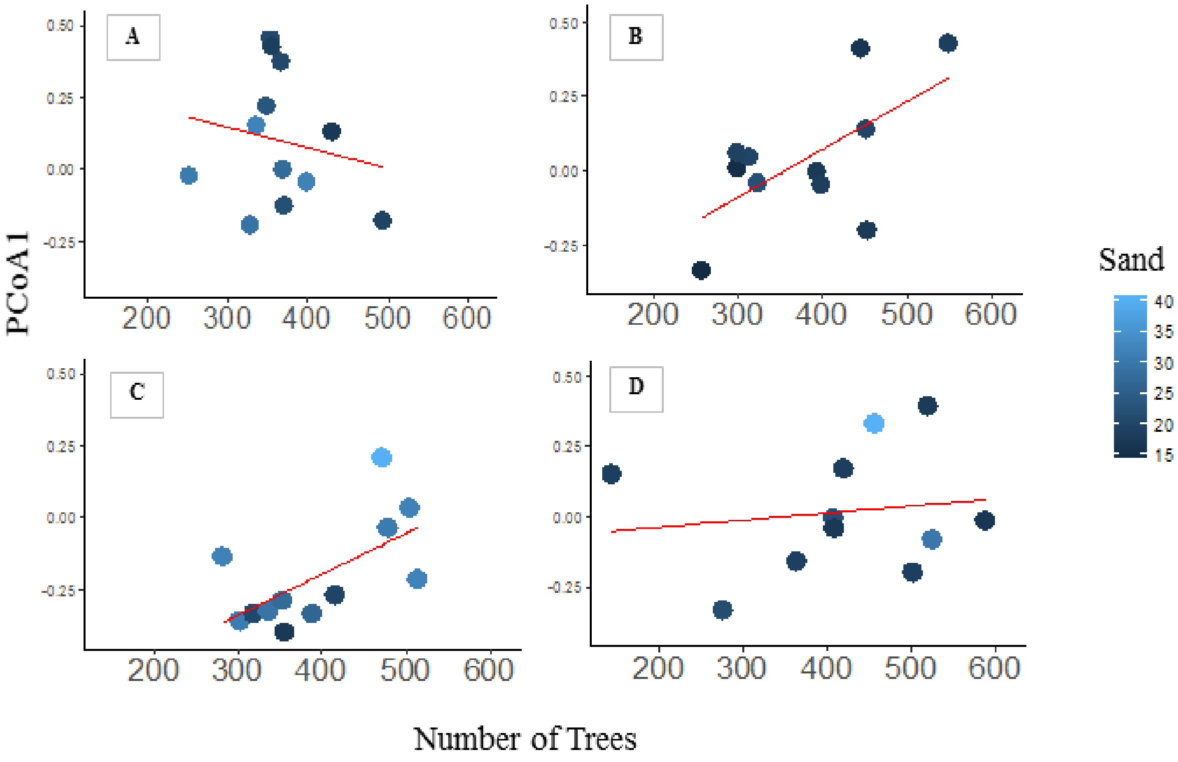
SOIL SAND AND CLAY CONTENT. –Soil samples were collected at six points on each plot (0, 50, 100, 150, 200 e 250 m along the plot length), at depths of 0 and 5 cm, once surface leaves had been removed. Samples were collected with a 5.5 cm diameter manual auger, stored in plastic bags and subsequently dried at room temperature and cleaned with tweezers, removing all pieces of leaf, root and charcoal. The material was processed and screened with a 2mm mesh sieve, then separated from other soil impurities to yield Fine Air-Dried Earth – FADE. Particle size analysis was made with composite samples (mixing sub-samples from soil obtained at 0, 50,100, 150, 200 and 250 m) at INPA's Soil and Plant Science Laboratory. Particle size was estimated from an aliquot of 10 grams of soil by adding the chemical dispersant sodium pyrophosphate to separate soil particles. Organic matter was oxidized by heating with hydrogen peroxide. The proportion of clay was determined by dry weight of 20 ml of soil suspension. The coarse fraction (fine and coarse sand) were separated by sieving, dried in an oven (105 ° C for 24 hours) and weighed to obtain the respective percentages, following the PPBio methodology (http://ppbio.inpa.gov.br/knb/metacat). The average percentage of clay in the soil of each plot was used to represent particle size and this was then used in statistical analyzes.

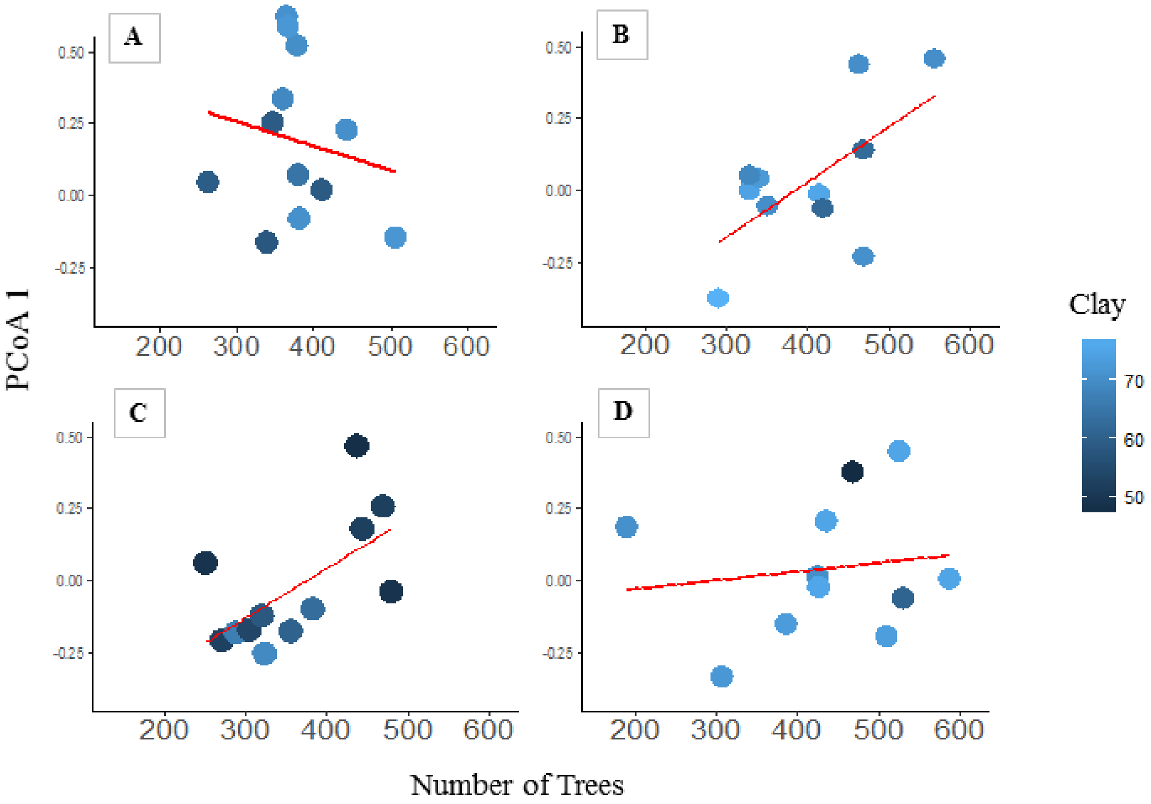
ELEVATION‒A professional surveyor measured the elevation above sea level at the starting point of the plot. This was done because, to minimize variation in vegetation, soil type and drainage, each plot follows the local contour line and, consequently, variation in elevation is minimal along its length. The value of the elevation of each plot was used for statistical analysis.

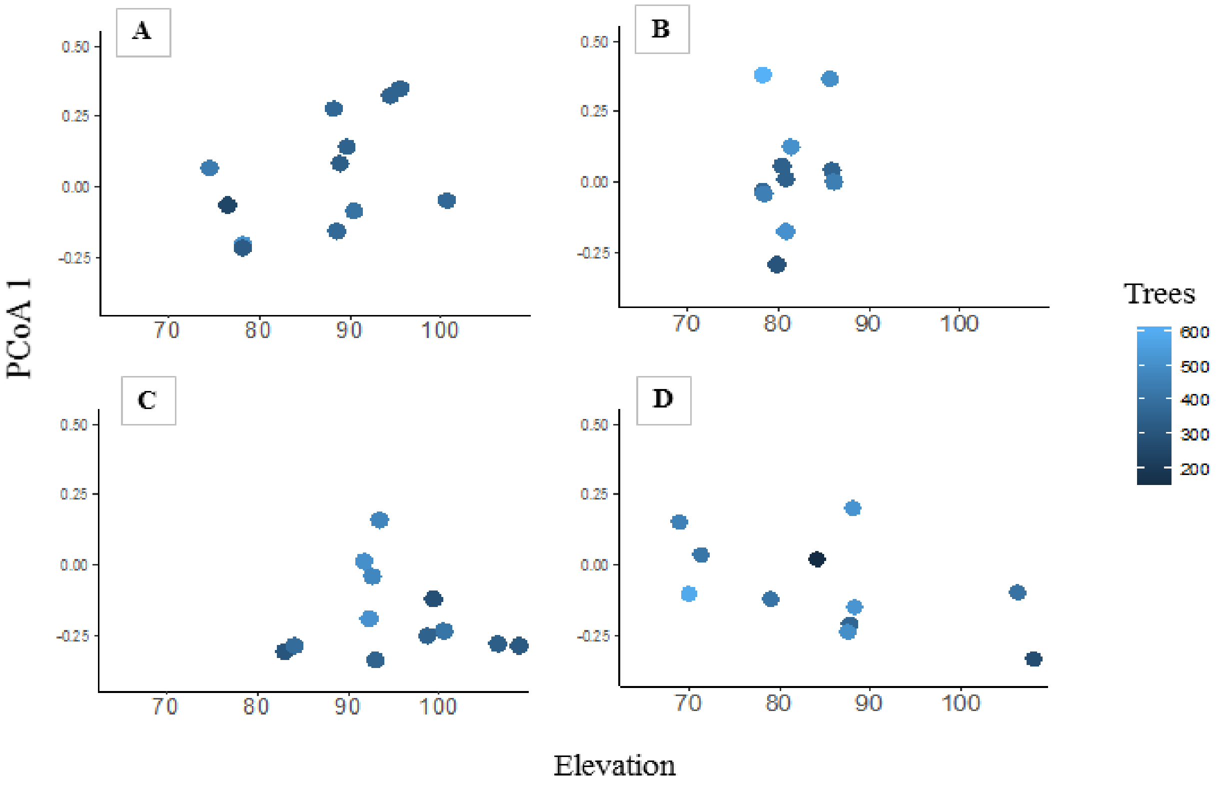
Literature Cited

Quesada CA, Lloyd J, Schwarz M, Patiño S, Baker RT, Czimczik C et al. Variations in chemical and physical properties of Amazon forest soils in relation to their genesis. Biogeosciences. 2010; 7: 1515–1541. doi: 10.5194/bg-7-1515-2010.

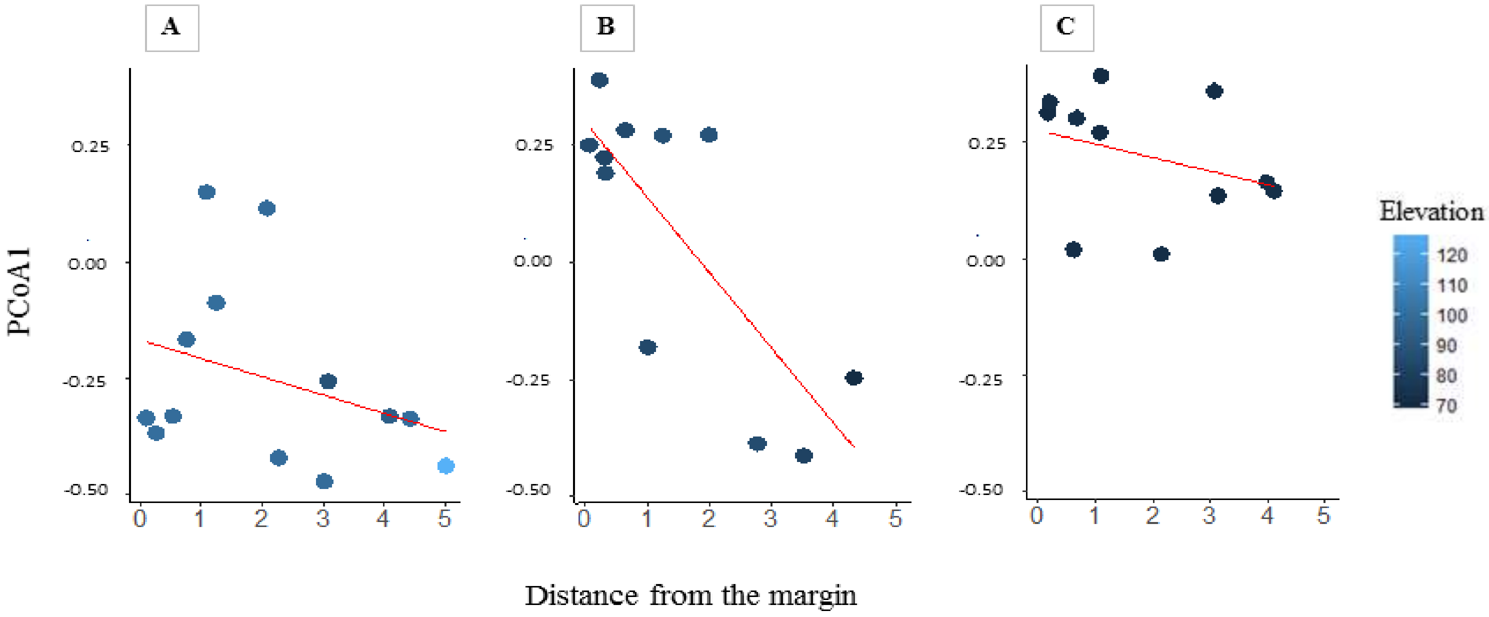
S2 Fig 1.

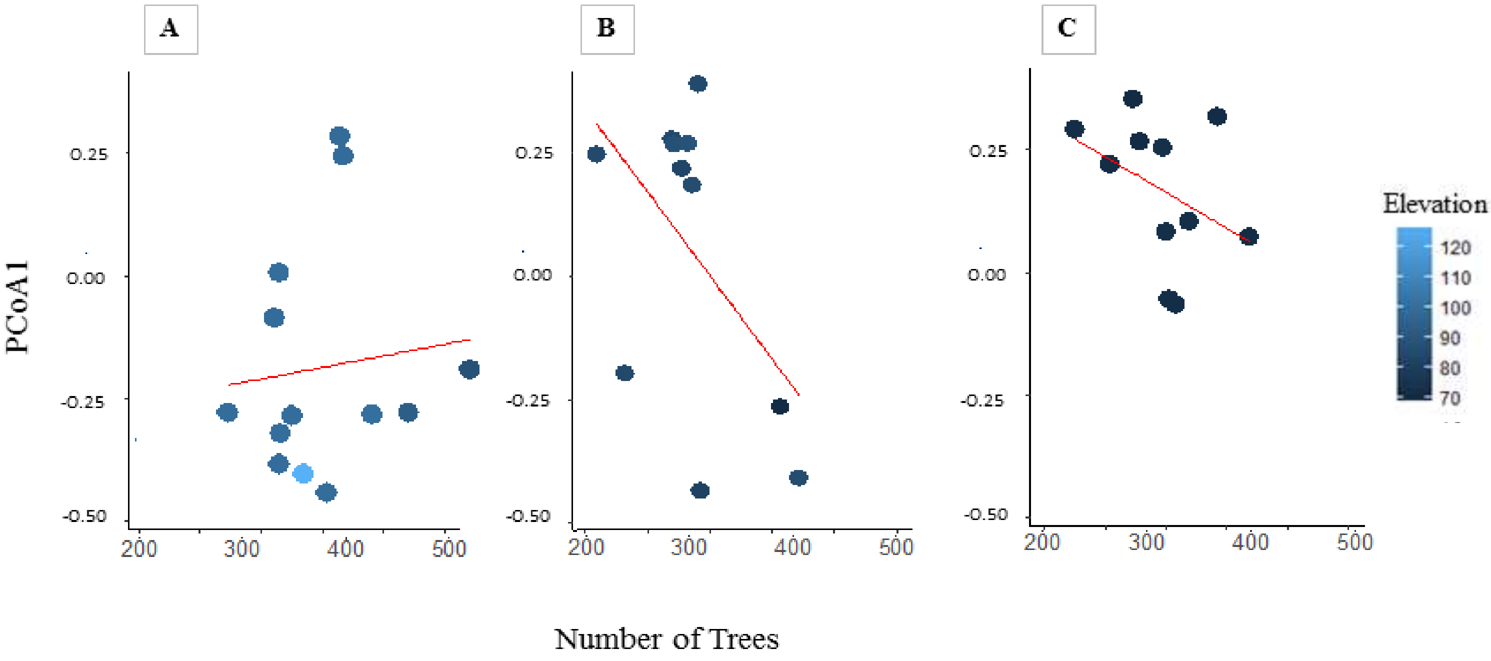



A
B
C
D
0.50
0.25
0.00
-0.25
200
300
400
500
600
PCoA 1
Number of Trees
Clay
70
60
50


A
B
C
D
0.50
0.25
0.00
-0.25
70
80
90
100
PCoA 1
Elevation
Trees
600
500
400
300
200

S3 Fig 2.


A
B
C
PCoA1
0.25
0.00
-0.25
-0.50
0
1
2
3
4
5
Distance from the margin
Elevation
120
110
100
90
80
70


A
B
C
PCoA1
0.25
0.00
-0.25
-0.50
200
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400
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Number of Trees
Elevation
120
110
100
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Síntese

A maior parte da biodiversidade mundial está concentrada na região Neotropical, especialmente na região amazônica. No entanto, diversas áreas ainda necessitam ser inventariadas. Sabe-se que dentro do espectro geográfico de ocorrência das espécies, diferentes habitats não são igualmente utilizados. Variáveis estruturais do ambiente, por sua vez, são reconhecidas por interferir na distribuição dos organismos determinando um ótimo ambiental ao longo de um gradiente de distribuição. Essas variáveis são frequentemente representadas por fatores físicos do ambiente que podem ter envolvimento na promoção de processos de especiação ecológica, mesmo com ausência de barreiras visíveis. Para lagartos amazônicos, já havia sido observada a influência de gradientes ambientais em escala local, sendo estes ligados a aspectos florestais, edáficos, de proximidade a corpos d'água, ou mesmo declividade ou altitude do terreno.

Dentre os estudos envolvendo lagartos, este foi o primeiro a abranger uma escala tão ampla de uma área intefluvial para a Amazônia brasileira com o objetivo de testar o efeito de fatores estruturais e climáticos do ambiente, além da influência de fatores históricos sobre as assembleias de lagartos em ambientes de florestas de terra firme. Todas as amostragens padronizadas, para os três capítulos, não teriam sido realizadas sem a instalação de módulos de acordo com o método RAPELD de amostragem de biodiversidade. Cada módulo foi composto por duas trilhas principais de 5 km de extensão, paralelas e separadas por 1 km, com distintas parcelas de 250 m localizadas ao longo das trilhas principais. Nossas coletas ocorreram por meio de busca ativa visual limitada por tempo e varredura na liteira.

No primeiro capítulo foi realizado o mapeamento da distribuição e abundância dos lagartos presentes nos 10 módulos, localizados ao longo da rodovia BR-319, que corta o Interflúvio Purus-Madeira, e liga as cidades de Manaus (Amazonas) a Porto Velho (Rondônia). Como resultado foram encontrados 25 táxons distribuídos em oito famílias, e observado um padrão bastante heterogêneo de ocorrência e abundância ao longo da área de estudo. Assim, estes resultados ampliam o conhecimento das distribuições de lagartos para esta área de endemismo e proporciona dados que podem ser utilizados como base em estudos ecológicos e de monitoramento dessa paisagem megadiversa e crescentemente ameaçada por mudanças de origem antrópica.

No segundo capítulo o objetivo foi testar se fatores climáticos e aspectos estruturais do ambiente estariam a moldar a riqueza, composição e diversidade funcional de assembleias de lagartos em larga-escala na Amazônia. Para isto, foram avaliados 10 módulos instalados ao longo da BR-319, e quatro módulos instalados ao longo da margem oeste do Alto Rio Madeira. Como resultado foram quantificados 26 táxons em 17 gêneros distribuídos em nove famílias, sendo a família Gymnophthalmidae a mais diversa, representada por sete espécies. As assembleias de lagartos foram distintas entre os diferentes tipos de floresta ombrófila: densa e aberta. Além disso o gradiente biogeográfico, representado pelas variáveis ambientais em conjunto, explicou uma alta proporção (86%) da variação na composição de espécies para a região. Entretanto, a riqueza de espécies não foi explicada pelo gradiente biogeográfico, o que sugere que a heterogeneidade ambiental seleciona espécies ao longo da área de estudo, tornando as assembleias distintas ao longo da paisagem amostrada. Quando foram observadas as variáveis ambientais de forma individual, foi verificado que tanto a proporção de argila no solo, quanto a área basal florestal e pluviosidade foram capazes de explicar a variação na composição. Porém, a área basal e a pluviosidade foram capazes de melhor prever, de forma contínua, a mudança na composição das assembleias de lagartos. Em relação à diversidade funcional, diferenças entre os tipos de florestas ombrófilas explicou a riqueza de traços funcionais (FRiq), porém a dissimilaridade dos traços funcionais (FDis) não foi significativamente afetada por esta mudança florestal. O gradiente biogeográfico foi capaz de explicar 35% da variação na riqueza funcional, mas não foi relacionado com a dispersão dos traços funcionais. A riqueza funcional apresentou relação com o gradiente de área basal e com pluviosidade local. As taxas de substituição de traços funcionais foram relativamente baixas ao longo do interflúvio, não sendo explicadas por nenhum dos gradientes ambientais. Assim, um complexo de fatores estruturais e climáticos atuam de forma conjunta sobre o estabelecimento dos lagartos na região do interflúvio Purus-Madeira, influenciando tanto a composição quanto a diversidade funcional das assembleias.

No terceiro e último capítulo foram abordados, de forma integrada, o efeito do alto rio Madeira, em escala regional, como possível barreira biogeográfica para as assembleias de lagartos presentes ao longo das margens leste e oeste do rio, e em escala local, a possível influência de variáveis ambientais. A coleta de dados foi realizada em 83 parcelas de 250 metros, as quais foram amostradas em quatro ocasiões distintas. As variáveis ambientais aferidas para testar o efeito de gradientes foram: número de árvores, densidade de arbustos, proporçao de argila e areia, nutrientes do solo, e elevaçao do terreno. Os resultados para as 27 espécies demonstraram que, em escala regional, o alto rio Madeira atua como uma barreira biogeográfica para 29,6% das espécies de lagartos, com cinco espécies (18.5%) restritas ao lado oeste, e três espécies (11.11%) restritas ao lado leste da região de estudo. Em relação aos gradientes ambientais, para a margem leste o gradiente de elevação melhor explicou a composição de espécies, e para a margem oeste a estrutura da vegetação foi a variável mais explicativa. Assim, foi demonstrado que tanto fatores históricos regionais quanto fatores ambientais locais moldam as assembleias de lagartos do alto Rio Madeira.

De modo geral este estudo, pioneiro em investigar assembleias de lagartos em diferentes escalas espaciais e sob diferentes métricas de diversidade, abre novas perspectivas na biogeografia e na ecologia de comunidades tropicais. E que futuros estudos envolvendo delineamentos amostrais em larga-escala e amostragem de diferentes grupos de organismos deverão colaborar no entendimento dos principais promotores da distribuição heterogênea da megadiversidade amazônica.

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