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USO DA ZONA RIPÁRIA COMO FATOR DETERMINANTE DA ESTRUTURA DE UMA ASSEMBLEIA DE LAGARTOS EM ÁREA DE TERRA-FIRME NA AMAZÔNIA CENTRAL

AYRA SOUZA FARIA DE OLIVEIRA

Manaus – Amazonas
Julho de 2017

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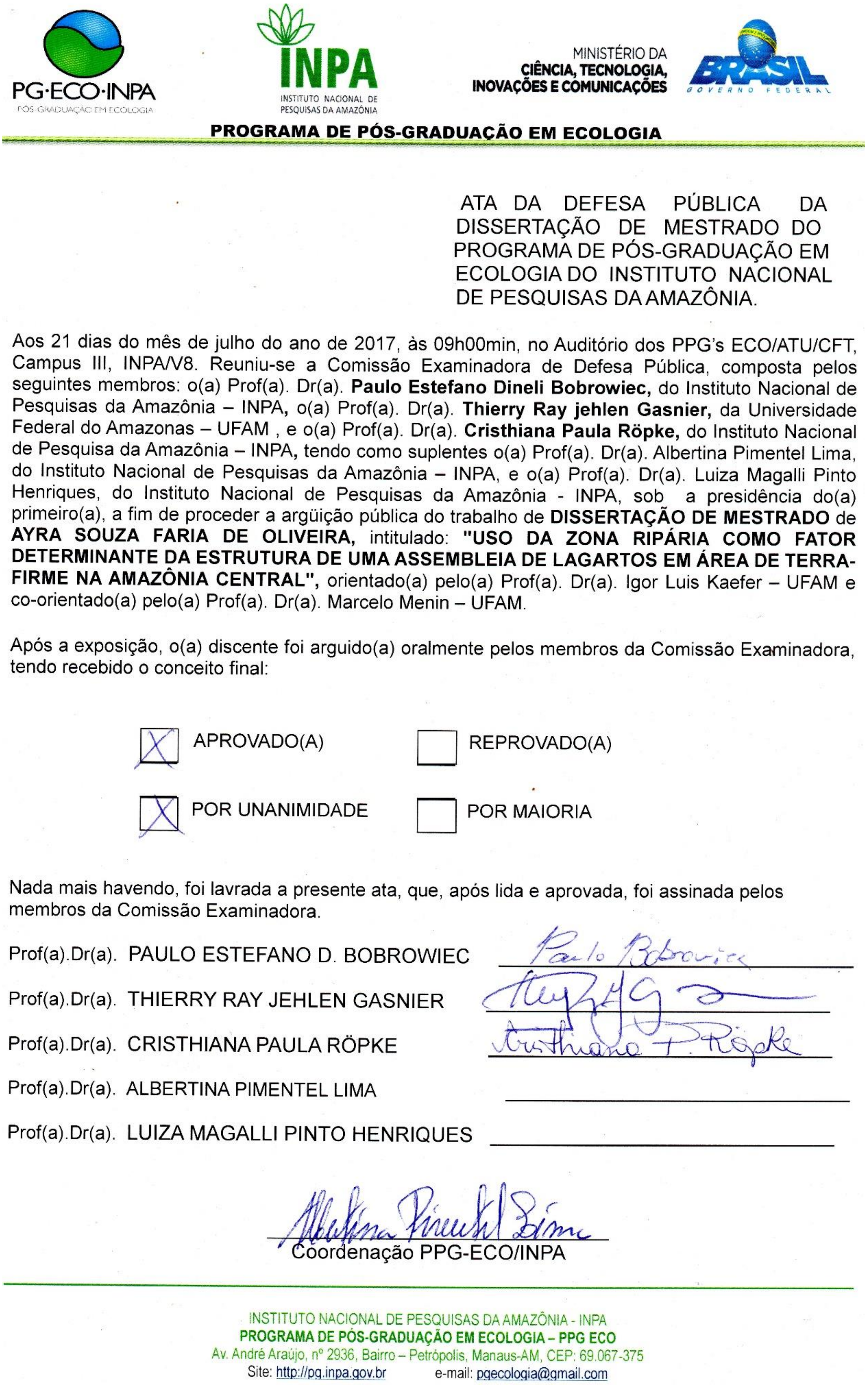

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Após a exposição, o(a) discente foi arguido(a) oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

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

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Sinopse:
Estudou-se a estrutura de uma assembleia de lagartos de uma área de terra-firme ao norte do município de Manaus, Amazonas. A assembleia foi caracterizada quanto à riqueza, abundância e composição. A composição de espécies da assembleia foi relacionada às variáveis ambientais potencialmente relevantes para o grupo. Também foi avaliada a extensão da zona ripária efetivamente utilizada pelas espécies.

Palavras-chave: Ecologia de comunidades, Squamata, conservação, gradientes ambientais.

Aos meus pais,
por tantas lições de dedicação, empenho e sacrifício.

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Resumo

Os fatores determinantes na estruturação de uma assembleia atuam em diferentes escalas, sendo a heterogeneidade predominante em escala local. Na região Amazônica, essa heterogeneidade pode ser representada pelos diferentes tipos florestais existentes, que proporcionam maior diversidade de abrigo e alimento para as espécies. Mudanças recentes na legislação ambiental brasileira puseram em risco a manutenção da heterogeneidade dos habitats por favorecer a supressão vegetal de diversas áreas, como as zonas ripárias. Diversos grupos animais estão estreitamente relacionados à presença de corpos d'água e aos gradientes ambientais proporcionados por eles. Para compreender a relação ecológica das espécies com o meio, organismos modelo como os lagartos são amplamente utilizados por serem sensíveis às alterações ambientais e em função do sucesso em ocupar diversos tipos de habitat. Neste estudo, uma assembleia de lagartos foi caracterizada quanto à distribuição e associação com variáveis ambientais biologicamente relevantes para o grupo. Foram registradas 20 espécies distribuídas em 10 famílias. Na escala adotada, os modelos de regressão múltipla não indicaram efeito significativo das variáveis ambientais. No entanto, a zona ripária exerceu forte influência sobre a composição de espécies e seu uso foi estimado em cerca de 211 m por meio de regressão segmentada. Diversas espécies tiveram sua ocorrência limitada à zona ripária. Nossos resultados demonstram que a legislação ambiental vigente no país não é suficiente para abranger a variação observada entre os lagartos amazônicos.

Palavras-chave: Ecologia de comunidades, Squamata, conservação, gradientes ambientais.

Riparian zone as a main determinant in the structure of a lizard assemblage in an upland Amazonian forest

Abstract

The factors determining assemblage structure act at different scales, with heterogeneity dominant at the local scale. In Amazonia, such heterogeneity is represented by the different forest types of the region, which provide a great diversity of shelter and food for animal species. Recent changes in Brazilian environmental legislation have put at risk the maintenance of habitat heterogeneity by favoring the suppression of several types of vegetation, notably those in riparian zones. Several Amazonian animal groups have close ecological ties to the presence of water bodies and the environmental gradients provided by them. To understand ecological relationships between species and their environment, model organisms such as lizards are widely used because they are sensitive to environmental changes and because of their success in occupying different habitat types. In this study, an assemblage of lizard species was characterized in terms of distribution and association using biological variables relevant to the group. Twenty species distributed in 10 families were studied. At the scale used in this study, multiple regression models did not indicate a significant effect of environmental variables. However, the riparian zone exerted a strong influence on the species composition and piecewise regression estimated its use to be some 211 m. Several species occurred only in the riparian zone. Our results demonstrate that the current environmental legislation in the country is not adequate to cover the observed variation in habitat use by Amazonian lizards.

Keywords: Community ecology, Squamata, conservation, environmental gradients.

Sumário

INTRODUÇÃO

Uma assembleia pode ser descrita como a associação entre espécies filogeneticamente relacionadas que ocupam um local em um determinado tempo (Fauth 1996). No entanto a composição de espécies para alguns grupos pode mudar de forma sucessiva em determinada escala de tempo (Clements 1905). Considera-se que uma assembleia está estruturada quando o padrão de organização dos indivíduos é maior do que o esperado ao acaso (Gotelli 2000, 2001). Diversas hipóteses surgiram para tentar explicar os fatores que norteiam a estruturação das assembleias. Mudanças graduais no ambiente físico que atuam como filtros determinam quais espécies serão capazes de ocupar o ambiente e afetam a composição, alterando a abundância de espécies e o nível de interação entre elas (Whittaker 1975, Futuyma & Gould 1979, Fauth 1996). As espécies podem também competir por recursos alimentares, o que pode resultar em deslocamento de nicho, sobrepondo minimamente seu uso, ou eliminando os competidores mais próximos (Hutchinson 1959, Pianka 1974). De modo geral, as hipóteses propostas consideram a partição de recursos temporais, espaciais e alimentares e podem variar principalmente em relação às escalas.

As escalas em que um estudo se desenvolve são determinantes para o estabelecimento de quaisquer relações biológicas entre as espécies e o meio (Magnusson *et al*. 2013). Estudos conduzidos em grandes escalas demonstram que tanto a composição como a substituição de espécies ao longo de um gradiente são ocasionadas por alterações ambientais bruscas, como as relacionadas à altitude, precipitação e temperatura (Duellman 1999). Em escala regional, predominam os processos biogeográficos e históricos de estruturação das assembleias, tais como dispersão, especiação e extinção (Cornell & Lawton 1992). Em escala local, a abundância e distribuição das espécies são determinadas pela disponibilidade de alimento e pela heterogeneidade ambiental (Whitford 1997, Bestelmeyer 2005, Valone & Sauter 2005).

A heterogeneidade ambiental é apontada como uma das principais questões em estudos ecológicos (Pianka 1966, MacArthur & Wilson 1967, Lack 1969, Keller 2009). Ela pode facilitar a partilha dos recursos por oferecer mais refúgios e variedade de micro-habitats, incrementando o número de espécies (Hutchinson 1957, Pianka 1974, Schall & Pianka 1978, Sebens 1991). De modo geral, a heterogeneidade é mensurada através da estrutura física resultante da composição e distribuição de espécies vegetais no ambiente (Lawton 1983, MacArthur & MacArthur 1961, Davidowitz & Rosenzweig 1998). Essa estratificação vegetal é apontada como importante fator de disponibilidade e manutenção de nichos, sendo mais evidente em habitats florestais (Scott *et al*. 2006, Marciente *et al*. 2015, Jacoboski *et al*. 2016).

As formações florestais amazônicas são caracterizadas por sua heterogeneidade ambiental, mesmo em pequenas escalas. A variação de micro-habitats proporciona maior variedade de abrigo e alimentos, permitindo a ocupação por um maior número de espécies animais (Garda *et al*. 2012). Estudos que associam o uso do habitat a alterações abióticas, na mesma escala em que ambos ocorrem, representam um importante passo na compreensão de assembleias ecológicas e como a distribuição das espécies é influenciada por fatores ambientais diversos. Embora não representem o total da variação, as categorias utilizadas para classificar o tipo de ambiente, como florestas densas, campinaranas e campinas, exemplificam parte da riqueza de habitats disponíveis à ocupação por espécies animais.

Entre os países considerados ‘megadiversos’, o Brasil ocupa posição privilegiada, com a maior diversidade biológica continental, ampla variedade de ambientes aquáticos, dois dos dezenove *hotspots* mundiais e seis biomas, entre eles a Amazônia, considerada a maior floresta tropical do mundo (Ganem *et al*. 2011). Esta diversidade é constantemente ameaçada pelo avanço rápido de atividades antrópicas, o que acentua a necessidade de conhecer a composição e distribuição das espécies no ambiente. A perda de áreas de grande importância ecológica nos traz uma maior preocupação em relação aos organismos estreitamente relacionados a esses locais, principalmente quando há lacunas no conhecimento acerca das necessidades biológicas dos mesmos.

Mudanças recentes na legislação ambiental provocaram a remoção da proteção de extensas áreas naturais, além de terem incentivado a exploração massiva de recursos e o desmatamento (Ab’Sáber 2010, Novaes & Souza 2013). Diversos estudos apontam os efeitos negativos das alterações na legislação brasileira em diversos aspectos, já que muitos serviços ecossistêmicos podem ser perdidos como resultado da supressão de áreas verdes e da biodiversidade. Uma das perdas mais significativas é a das matas ciliares e zonas ripárias, de papel fundamental em vários serviços ambientais (Tundisi & Tundisi 2010). Estudos sugerem que as zonas ripárias apresentam maior riqueza e distinção na composição de espécies em relação às áreas adjacentes (Pusey *et al*. 1995, Sabo *et al*. 2005, Fraga *et al*. 2011, Rojas-Ahumada *et al*. 2012), ou apresentam maior preferência das espécies quanto à seleção de habitat (Fraga *et al*. 2013). Além disso, são consideradas importantes para a manutenção da biodiversidade local (Bub *et al*. 2004, Lehmkuhl *et al*. 2007, Bueno *et al*. 2012).

Embora seja evidente a estruturação das assembleias em função dessas zonas (Seavy *et al*. 2009, Fraga *et al*. 2011, Rojas-Ahumada *et al*. 2012), poucos estudos investigam a extensão da zona ripária efetivamente utilizada e a importância dessas áreas para as espécies. Estudos com plantas (Drucker *et al*. 2008), serpentes (Fraga *et al*. 2011) e aves (Bueno *et al*. 2012) apontam que o uso deste ambiente vai muito além da classificação arbitrária atribuída a essas áreas em planejamentos para conservação. A redução das zonas ripárias pode levar a perdas irreversíveis da biodiversidade através da eliminação de espécies estreitamente relacionadas a essas áreas (Casatti 2010, Novaes & Souza 2013). Diversos grupos animais são apontados como suscetíveis aos efeitos da redução de matas ciliares (Casatti 2010, Develey & Pongiluppi 2010, Galetti *et al*. 2010, Imperatriz-Fonseca & Nunes-Silva 2010, Marques *et al*. 2010, Magalhães *et al*. 2011, Ledo & Colli 2016), entre eles, pelo menos três espécies de lagartos (Ribeiro-Júnior & Amaral 2016).

Os lagartos são amplamente utilizados como modelos em estudos ecológicos, evolutivos e filogeográficos (Pianka 1973, 1974, Huey *et al*. 1983, Vitt *et al*. 2003, Camargo *et al*. 2010, Pyron *et al*. 2013). Isso se dá em função da baixa diversidade local e relativa abundância deste grupo em relação a outros (Avila-Pires 1995, Vitt *et al*. 2008), além do sucesso em ocupar os mais diversos tipos de habitat (Vitt *et al*. 2003, Ribeiro-Júnior & Amaral 2016). O efeito de variáveis ambientais diversas sobre os lagartos tem sido mostrado como um importante fator na estruturação das assembleias (D’Cruze & Kumar 2011, Cosentino *et al*. 2013; Leavitt & Fitzgerald 2013). Algumas espécies são fortemente associadas aos seus habitats (Pinto 2008; Buckley & Jetz 2010, Silva *et al*. 2014, Ribeiro-Júnior & Amaral 2016), o que as torna potencialmente mais sensíveis a alterações ambientais.

OBJETIVOS

Objetivo geral

Determinar a estrutura da assembleia de lagartos de uma área de terra-firme da Amazônia Central quanto à riqueza, abundância e composição de espécies, bem como os fatores ambientais relacionados a estas métricas.

Objetivos específicos

1. Descrever a composição de espécies da assembleia local de lagartos.
2. Estabelecer associações entre a composição da assembleia e variáveis ambientais potencialmente relevantes para o grupo.
3. Determinar a extensão da zona ripária efetivamente utilizada pelos lagartos.

CAPÍTULO 1

FARIA, A. S., MENIN, M. & KAEFER, I. L. 2017. Riparian zone as a main determinant in the structure of a lizard assemblage in an upland Amazonian forest. [Journal of Tropical Ecology, submetido].

Riparian zone as a main determinant in the structure of a lizard assemblage in an upland Amazonian forest

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Abstract

The use of lizards as model organisms in ecological studies is based on their success in occupying a great diversity of habitats. The distributions of some species are closely-tied to the environment, responding to habitat heterogeneity and degradation. Changes in the Brazilian Forest Code concerning land use make these organisms susceptible to habitat loss, especially those species most restricted to riparian zones. We studied the distribution of a lizard assemblage in an upland Amazonian forest along gradients related to soil, topography, vegetation, light incidence and distance from streams. Lizards were sampled in 41 standardized plots near Manaus, Brazil. We recorded 20 species from 10 families. We used non-metric multidimensional scaling (NMDS) to reduce the dimensionality of quantitative and qualitative compositions of species. Multiple multivariate regression models indicated that the environmental gradients studied did not significantly influence assemblage species distribution. By means of piecewise regression, the use of riparian zone was estimated at ~190 m from quantitative species composition and ~211 m for qualitative composition. Several species occurred only in riparian zone. The estimates of the effective biological size of riparian zone shows that the current environmental legislation is insufficient to protect the total diversity recorded for this species assemblage.

Keywords: Amazon, Brazil, community ecology, environmental gradients, Forest Code, Squamata

INTRODUCTION

Lizards are widely used as models in ecological, evolutionary and phylogeographic studies (Pianka 1974, Vitt et al. 2003, Camargo et al. 2010). This is due to the low local diversity and relative abundance of this group in relation to other terrestrial vertebrate groups (Avila-Pires 1995, Vitt et al. 2008), as well as their success in occupying a great variety of habitat types (Vitt *et al*. 2003). In addition to behavioral (Mugabo *et al*. 2011), morphological (Abdala *et al*. 2014) and physiological (Lee 1980) aspects, several environmental variables are involved in the structuring of lizard assemblages (Cosentino *et al*. 2013, Leavitt & Fitzgerald 2013). Some species are strongly associated with particular habitats (Buckley & Jetz 2010, Silva *et al*. 2014), which makes them potentially sensitive to environmental variations.

Species respond differently to environment variations. In forest environments, variables such as vegetation distribution, litter depth and canopy openness are important for habitat selection by lizards and in maintaining their species diversity (Vitt *et al*. 2007, D'Cruze & Kumar 2011), since they are ectothermic animals that depend on external environment for thermal regulation, and because many species occupy specific microhabitats. Across a great variety of biological groups, including lizards, one of the most significant threats to species diversity is habitat loss (Ribeiro-Júnior & Rodrigues 2016), since important environmental features can disappear, mainly because of resources over-exploitation.

Studies have suggested that riparian zones have greater richness and distinctness of species composition in comparison to adjacent areas (Rojas-Ahumada *et al*. 2012). Substitution in species composition tend to be favored by the presence of riparian zones (Sabo *et al*. 2005). Riparian zones can increase spatial heterogeneity, by modifying forest species composition. This is an important factor in determining assemblage structure (Pianka 1966, Keller 2009). They also concentrate certain species because of habitat selection (Fraga *et al*.

2013), and are considered important for maintaining regional biodiversity (Bub *et al*. 2004, Lehmkuhl *et al*. 2007, Bueno *et al*. 2012). Increased spatial heterogeneity may facilitate resource-partitioning, increase the availability of refuges and microhabitats, and influence species richness and composition (Hutchinson 1957, Schall & Pianka 1978, Sebens 1991).

Recent changes in Brazilian environmental legislation have led to removal of protection from many natural areas, as well as encouraging extensive exploitation of resources and deforestation (Ab'Sáber 2010, Novaes & Souza 2013). One of the most significant losses has been in riparian forests and riparian zones, despite their key role in providing a variety of environmental services (Tundisi & Tundisi 2010). In several localities, the anthropic action in such habitats has caused alterations in the course of rivers, loss of riparian forests and has contributed to appearance of invasive species (Barrett & Guyer 2008, Bateman *et al*. 2008).

While it is clear that vertebrate assemblages in such areas are strongly structured (Seavy *et al*. 2009), few studies have investigated the extent to which the riparian zone is used and the importance of these areas for assemblages. Therefore, in this study we sought to understand the responses of a series of species to the environmental gradients present in such an environment. The objective was to characterize the lizard assemblage in terms of species abundance, richness and composition in an area of upland Amazonian forest containing a stream network. Thus, we sought to clarify lizard species distribution patterns in forest environment, relate these to variation in environmental gradients biologically relevant to the species under study, and so to understand the association of the species assemblage with the riparian environment through the evaluation of habitat use.

METHODS

Study area

We conducted the study at the Federal University of Amazonas Experimental Farm (FEX-UFAM), Manaus, Amazonas. FEX-UFAM (2° 38'57.6"S, 60° 3'11"W) is located in an upland (*terra-firme*) forest at km 921 on highway BR-174 (Fig. 1) and occupies an area of 3,000 ha of tropical rainforest with a mainly closed canopy and low-lying understory. FEX-UFAM has extensive flooded areas due the presence of large lotic streams, and an irregular topography (altitude ranges from 42 to 130 m: Rojas-Ahumada *et al*. 2012).

FEX-UFAM boundaries are connected to protected areas managed by Brazilian federal government bodies, and so form an area of continuous forest with areas of the Brazilian Institute for the Environment and Renewable Natural Resources (IBAMA) and the National Institute of Amazonian Research (INPA) (Rojas-Ahumada *et al*. 2012). The average temperature in the region varies between 24.6º C and 26.9º C, with daily relative humidity varying between 75 percent in dry-season and 92 percent in rainy-season (Araújo *et al*. 2002). The rainy-season commonly occurs from December to May, and the dry-season runs from July to November (Marques-Filho *et al*. 1981).

Sampling design and Data collection

FEX-UFAM includes a sampling grid of the Biodiversity Research Program (PPBio), installed in 2007 following RAPELD system (Rapid Assessment Program; PELD - Long-Term Ecological Research] (Magnusson *et al*. 2005). At FEX-UFAM, this is composed of 59 km of trails, arranged in four east-west oriented trails each of 8 km, and nine north-south oriented tracks each 3 km long, totaling an area of 24 km². The grid consists of 41 plots, each of 250 m, 31 evenly distributed plots, at least 1 km apart. Another 10 plots arranged along the banks of waterbodies were installed later, separated from the other plots by at least 500 m (Rojas-Ahumada *et al*. 2012).

We carried out three field visits between September to November 2015 and September to November 2016, visiting all plots of the sampling grid. We collected data only in dry-season, when higher temperatures meant the lizards to be more active. We visited the plots during the day, between 09:00 and 15:00, on days with temperatures above 26ºC and in the absence of rainfall. We used active visual search method (Crump & Scott 1994) and Time Limited Visual Search (TLVS) (Martins & Oliveira 1998). Occasional lizard records outside the plots and around the grid were not included in the analyzes.

In order to detect, respectively, terrestrial and arboreal lizards, we searched horizontally (up to five meters on each side) and vertically (up to five meters high) along the strip of each plot for one hour. This method is based on locating moving or resting animals by a detailed survey of all microenvironments. We conducted TLVS for an hour, moving litter and fallen logs in search of earth-living and fossorial animals. We performed the active visual search following the sequence of space-markers along the plots, from 0 to 250 m, while the TLVS was performed in the reverse direction. During each campaign, we surveyed each plot for two hours, with two observers, totaling a sampling effort of 246h/person. We identified all individuals found to species level using specialized literature (Vitt *et al*. 2008). Taxonomic nomenclature adopted follows Ribeiro-Júnior & Amaral (2016).

Environmental variables

We quantified the following environmental variables: distance to nearest stream, litter depth, extent of canopy openness, vegetation density, slope, percentage of clay in soil and altitude. The measurement of the distance of the plot to the nearest stream was obtained from a previous study (Rojas-Ahumada *et al*. 2012). This measure comprises the distance from the beginning of the plot to the nearest stream. We measured litter depth during the third field study visit. We derived an average for each plot, using measures derived from six equidistant points. We obtained measurements of land slope, clay percentage and altitude with a combination of data gathering during field visits and data collected from previous studies and available at the Biodiversity Research Program Data Repository (PPBio) at http://ppbio.inpa.gov.br. All sampling methods followed the protocols established by PPBio (see Appendice).

In addition, we used vegetation density and canopy opening data collected with LiDAR (Light Detection And Ranging) in previous studies (J. Schietti, personal communication). LiDAR allows the mapping of habitat types through the collection of three-dimensional vegetation structure information that helps characterize the environment (Miura & Jones 2010). We measured vegetation density through the sum of leaf area density (LAD) returns for each plot. We estimated the canopy openness from the skyshots percentage, which is the number of emitted pulses that do not return a reflection to the apparatus (Parker *et al.* 2004).

Data analysis

We calculated the dissimilarity in the composition of the lizard assemblage between the plots using a Jaccard Distance (based on presence-absence) for qualitative data, and a Bray-Curtis distance (based on abundance) for quantitative data. We considered the abundance of each species as the total number of observations in each plot in the three sampling visits. We summarized the composite patterns with non-metric multidimensional scaling (NMDS) as a way to reduce dimensionality of data to a single axis of multivariate ordering and to allow visualization of compositional patterns within the assemblage.

To determine the effects of measured environmental variables on the lizard assemblage composition, we performed a multiple regression, for which the dependent variable was the first NMDS axis of quantitative and qualitative composition. We performed previous analyzes to guarantee the independence of the predictor variables (Spearman correlation coefficients, $r < 0.60$), and so excluded the environmental variables altitude and clay percentage from the model because they had high levels of correlation with each other and with the variable distance to stream ($r > 0.8$).

To determine the width of the riparian zone effectively used by lizards, we used piecewise regression to evaluate the effect of distance from waterbodies on the quantitative and qualitative composition of the lizard species assemblage (NMDS axes). In piecewise regression, two straight lines represent variation on the NMDS axis. The point of intersection between the lines represents a discontinuity in relation to the assemblage characteristics with the increase in the distance from streams. This discontinuity point is considered to represent the distance at which organisms perceive an environmental differentiation, thus delimiting the effective extension of the riparian zone for the analyzed group. We performed the segmented regression with the SiZer statistical package, version 0.1-4. All analyzes for this study were conducted in the R computing environment (R Core Team 2014).

RESULTS

The lizard assemblage

We recorded 20 species of lizards from 10 families (Table 1). The species *Hemidactylus mabouia* and *Iguana iguana* were not observed in the plots and are considered here only as part of the description of the local assemblage composition. Therefore, in the ecological analyses we considered 429 records from 18 species.

The most abundant species were *Kentropyx calcarata*, *Chatogekko amazonicus, Gonatodes humeralis, Ameiva ameiva* and *Uranoscodon superciliosus* ($n \geq 25$). Together, these represented 72.2 percent of all observations. The species *Alopoglossus angulatus, Plica plica*, *Thecadactylus rapicauda*, *Anolis chrysolepis* and *Tupinambis teguixin* were the least abundant ($n \leq 6$) and together accounted for 4.2 percent of all observations.

The number of species recorded in each plot varied between one and nine (4.7 ± 1.9). The number of observations in each plot varied between two and 24 (10.5 ± 5.6). The total abundance of each species varied between two and 114 (23.8 ± 30.3). *Kentropyx calcarata* and *Chatogekko amazonicus* were the most abundant species, with 114 and 80 records, respectively. They were also the commonest species, being present in 83 percent and 56 percent of the study plots, respectively.

Effects of environmental variables on lizard assemblage

Quantitative composition of the lizard species assemblage per plot was reduced to an NMDS ordering axis based on an abundance matrix set according to the Bray-Curtis index ($R^2 = 39.2\%$). Lizard assemblage qualitative composition was reduced to an NMDS ordering axis based on the presence-absence matrix set according to the Jaccard Index ($R^2 = 41\%$).

Multiple regression models used to test the effect of environmental variables (distance to nearest stream, leaf litter depth, canopy openness, vegetation density, slope) on assemblage composition (NMDS axes) were not significant (Table 2; quantitative NMDS $R^2 = 0.02$, $P = 0.33$; qualitative NMDS $R^2 = 0.10$, $P = 0.11$). However, there was a marginally significant effect of litter depth on qualitative composition ($P = 0.05$).

Use of riparian habitats

The quantitative composition represented by the NMDS axis showed a change in composition with increasing distance from the nearest stream (Fig. 2). The piecewise regression indicated a significant effect of distance on the quantitative assemblage composition from ~190 m (95% CI = 3.1–857.8) of the nearest stream ($R^2 = 0.13$, df = 38, $P = 0.02$). The exclusion of the rare species ($n < 6$) did not significantly alter the result of stream distance on the quantitative composition (Change point ~188 m; $R^2 = 0.41$; df = 38; $P < 0.01$).

The qualitative composition represented by the NMDS axis also showed changes with increasing distance from streams (Fig. 3). The piecewise regression indicated a significant effect of distance on qualitative assemblage composition from ~211 m of the nearest stream (95% CI = 3.5–771.2) ($R^2 = 0.38$; df = 38; $P < 0.01$). The exclusion of the rare species ($n < 6$) had little effect on the influence of distance to stream on the qualitative composition (Change point ~200 m, $R^2 = 0.39$, df = 38, $P < 0.01$). Considering the model that explains the greatest percentage of differentiation in the assemblage composition, the riparian zone, as recognized by lizard assemblage, extends some 211 m from streams. Using this metric, 27 of the 41 plots sampled lie within the riparian zone, and 14 are outside the riparian zone (Fig. 4).

The species *A. angulatus* (n = 6), *L. percarinatum* (n = 9), *Neusticurus bicarinatus* (n = 8), *A. chrysolepis* (n = 2) and *T. teguixin* (n = 2) were recorded only in plots within the riparian zone. Only one individual of *T. rapicauda* (out of 4) and *U. superciliosus* (out of 25) was recorded in plots outside the calculated riparian zone. The species *T. agilis* (n = 8) was recorded twice in plots outside the riparian zone. The species *P. plica* (n = 4) was recorded only in upland forest. All other species were recorded in plots in both habitat types.

DISCUSSION

The lizard assemblage

Twenty species of lizards were recorded in 10 families. Other studies carried out in the Amazon region have found a similar richness to that recorded in our study area, differing little in the composition and abundance of the species involved (Zimmerman & Rodrigues 1990, Vitt *et al*. 2008, França & Venâncio 2010, Ilha & Dixo 2010, Oliveira *et al*. 2014).

The species *Gonatodes humeralis*, *Chatogekko amazonicus*, *Kentropyx calcarata*, *Anolis fuscoauratus* and *Copeoglossum nigropunctatum* were recorded by Pinto *et al*. (2008) as the five most abundant in an area close to the current study site. This list varies from the results found in FEX-UFAM in terms of individual abundance (Table 1). This suggests the existence of fluctuations in the distribution of species, with abundances combining in different ways at each locality, resulting in local-specific species compositions (Brown 1984).

The species *Alopoglossus angulatus*, *Plica plica*, *Thecadactylus rapicauda*, *Anolis chrysolepis* and *Tupinambis teguixin* had low rates of occurrence at FEX-UFAM. *Thecadactylus rapicauda* is a primarily nocturnal species and may have been under-sampled by the methods adopted. *Plica plica* and *A. chrysolepis* are extremely cryptic and could have been under-sampled, or have been genuinely rare. *Tupinambis teguixin* was recorded only twice in plots, on the margin of streams. However, *T. teguixin* was also occasionally observed outside the study plots in open areas, or hidden between fallen trunks.

Effects of environmental variables on lizard assemblage

The environmental variables (distance to nearest stream, leaf-litter depth, canopy openness, vegetation density and slope) did not contribute significantly to the model (Table 2). Leaf-litter depth marginally affected the qualitative composition of the assemblage, and the effect was weak. The marginal effect of leaf-litter litter depth can be explained by the increased habitat complexity provided by this variable. Several studies point to the importance of leaf-litter in increasing species composition and the abundance of terrestrial lizards (Watling 2005, Whitfield 2007, Folt & Reider 2013). In our study, the selected predictor variables explained less than 3 percent of the variation in the quantitative data and some 10 percent of the qualitative data.

Studies in other areas of Amazon forest suggest that assemblages may be affected differently at the local scale, and this relationship can be highly idiosyncratic (Pinto *et al*. 2008). In addition, species substitution across different environmental gradients appears, at the local scale, to be lower in forest environments (Silva & Sites 1995) than in open regions (Vitt *et al*. 2007). While the Amazonian region has 138 known species of lizard, most of which are widely distributed, most studies of Amazonian lizards detect between 20 and 30 species (Ribeiro-Júnior & Amaral 2016). This suggests that both substitution patterns and the influence of environmental variables can be detected more easily at scales broader than that employed in the present study.

Use of riparian habitats

Riparian zones play an important role in the structuring of assemblages, affecting both richness (Bub *et al*. 2004, Rojas-Ahumada *et al*. 2012) and species composition (Lehmkuhl *et al*. 2007, Fraga *et al*. 2011). Results of the piecewise regression analysis indicated that the riparian zone in the studied region influenced species composition and abundance of lizards, and that the species assemblage responded to an environmental gradient that lay between ~190 and 211 m from streams. A similar effect has been observed for other groups: for herbaceous plants, a more heterogeneous composition was observed in the areas up to ~100 m away from Amazonian streams (Drucker *et al*. 2008). Furthermore, similar to the present study, Drucker *et al*. (2008) recorded greater abundance of species in the riparian zone compared to more distant areas. For a bat assemblage, a change in species composition was shown to occur 114 m from such streams (L.G.A. Pereira, personal communication), while bird assemblages at nearby Reserva Ducke have a threshold of 140 m (Bueno *et al*. 2012). In a study carried out with the snake assemblage at Ducke, composition was shown to change around 100 m from streams, with species responding differently to the gradient, either increasing or decreasing in abundance at this threshold (Fraga *et al*. 2011). Our study corroborates the findings of Bueno *et al*. (2012), thus the lizard assemblage showing a higher number of species restricted to the riparian zone than to the non-riparian environment.

The species *A. angulatus*, *L. percarinatum*, *N. bicarinatus*, *A. chrysolepis* and *T. teguixin* were all recorded only from the riparian zone. *Alopoglossus angulatus* and *L. percarinatum* are terrestrial species normally associated with streams or marshy areas (Avila-Pires 1995). At FEX-UFAM, these two species were most commonly recorded outside the study plots, on stream banks or on moist leaf-litter and roots. *Neusticurus bicarinatus* is semiaquatic and was recorded only from very shady sites on the banks of streams, or in the water itself. Although the all within-plot records for *A. chrysolepis and T. teguixin* come from riparian plots, these species were seen at other times, far from any stream, when moving between study plots.

Two species, *T. rapicauda* and *U. superciliosus* each had only one record in non-riparian areas. *Thecadactylus rapicauda* is nocturnal, so its low numbers in the FEX-UFAM samples may well be due to the methods adopted. It was, however, observed active at night, in the areas near the camp, which was situated some 80 m from a stream. *Uranoscodon superciliosus*, in contrast, was the fifth most abundant species at FEX-UFAM. The vast majority of individuals were recorded less than 15 m from a stream, and only one individual (a juvenile) was seen outside the riparian zone. *Plica plica* was recorded only in plots with a distance from streams greater than 600 m. Despite the low frequency of this species in the study area, we can assume that it is restricted to non-riparian areas, due to its known preferences to use larger forest trees as substrate. Such trees are found in flatter areas far from streams (Castilho *et al*. 2006).

The effect of riparian zones on plant species is shown to be an important modifying factor of species composition and abundance. The composition of species in areas closer to the stream banks is distinct from the others, with a continuous gradient of change that forms an ecotone between lowland and upland areas (Drucker *et al*. 2008). These changes might modify food availability, or even provide different sort of resources, which possibly alters species abundance (Curtis *et al*. 2015). The higher abundance of lizards species in riparian zones might be explained by the increase of prey abundance in these areas during the dry seasons (Ryan & Poe 2014).

Implications for conservation

The key role of the riparian zone in increasing local biodiversity is shown by the response of assemblages to the changes in distance gradient to nearest stream. Studies at several sites and across a variety of groups have shown that, although species richness is not significantly higher in riparian zones, the assemblage composition there tends to be markedly different, and regional species richness increases significantly when diversity data from riparian and non-riparian environments are combined (Sabo *et al*. 2005). This indicates that riparian zones have a key role for the more habitat restricted species, especially those with low mobility. Comparisons of riparian and non-riparian areas found a different composition pattern for anuran assemblages (Rojas-Ahumada *et al*. 2012, Ribeiro-Jr *et al*. 2012). Like these studies, we recorded remarkable differences in the composition of the lizard assemblages in the current study area, with several species restricted to the riparian zone.

Combined, all these evidences contradict the conservation policy adopted by Brazil Forest Code vis-à-vis riparian forests.

Environmental laws for the preservation of the riparian zone have been adopted in a number of Latin American countries. Paraguay, Chile, Panama and Venezuela have minimal areas of preservation around waterbodies that vary from 100 to 400 m, while in several US states removal of native vegetation near waterbodies is expressly prohibited and permission for plant suppression occurs only in exceptional cases (Nusdeo 2012). In contrast, Brazilian environmental legislation has produced policies that are much more concessionary and less conservation-oriented. Recent changes to the Brazilian Forest Code allow the maintenance of 30 m of riparian forest for waterbodies in an urban area or from 10 m wide for rural waterways, reaching 500 m for streams with a width exceeding 600 m (Law 12.651 of May 25, 2012).

The riparian zone studied at the FEX-UFAM is formed by the low-lying areas bordering streams in upland forest, but it is just one of the many categories of wetlands in Amazonia (Junk *et al*. 1989, Piedade *et al*. 2012). According to the Forest Code of 1965 (Law 4.771 of September 15, 1965), such areas were included in the category of Permanent Preservation Area (APP), and were based on the highest flood levels attained by the adjacent waterway. One of the most controversial changes of the new Code refers to a reduction in the extent of the APP in such places, due to a change of definition of the river or stream channel, which now only considers its regular volume and extent. As the variation in the flood pulses of Amazonian rivers can reach 10 m high, this redefinition represents the loss of more than 400,000 km² of riparian forest (Piedade *et al*. 2012). In addition, the application of a single rule to the many categories comprising Brazilian wetlands does not consider the particular characteristics of each type of environment (Junk *et al*. 2011).

Establishing a fixed metric for mandatory preservation does not seem reasonable, since each species uses space in different ways. As observed in our study area, the riparian zone recognized by the lizard assembly extends much further than the extent of forest preservation that the Brazilian Forestry Code requires for small watercourses. At our study site, the widest forest streams have an average width of 4.6 m (Rojas-Ahumada *et al*. 2012). This means that only 10 m of riparian forest on either side of such streams would be protected by law, while more than 200 m on either side could be eliminated, representing about 95 percent of the riparian zone as recognized by the assemblage in the current study.

Considering that most watercourses are narrower than this, current changes pose a threat to species conservation, and many studies indicate negative consequences for the biota should habitat degradation increase (Casatti 2010, Imperatriz-Fonseca & Nunes-Silva 2010, Ribeiro-Jr. *et al*. 2012, Novaes & Souza 2013, Ledo & Colli 2016). Mammalian diversity can be severely affected by habitat reduction, resulting in decreased ecological services as a result of the loss of pollinators and seed dispersers, as well as an increase in the likelihood of disease transmission in urban centers (Galetti *et al*. 2010). The environmental heterogeneity provided by riparian zones is essential for maintaining bird assemblages, especially those restricted to riverside areas (Denveley & Pongiluppi 2010). Similarly, many species of reptiles with restricted distributions may become extinct if riparian zones are reduced by the extent to which the law permits (Marques *et al*. 2010).

The ineffectiveness of the legislation in force in Brazil has already been identified as a threat to lizard conservation elsewhere in the country. In the Brazilian Cerrado, the number of lizard species of a degraded area, with riparian forest preserved according to legislation, was less than 20 percent of that found in the protected areas, with a greater extension of riverside forest (Ledo & Colli 2016). Our results support those of Ledo & Colli (2016), providing evidence that the variation in lizard assemblages composition in the Amazon is not adequately considered under the legal tenets of the current Brazilian Forest Code, and which, indeed, excludes the great majority of riparian forest from protection.

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APPENDICE

Sampling protocols for the environmental variables that compose the regression models of lizard assemblage structure in an upland forest near Manaus, Amazonas.

DISTANCE FROM STREAMS. The distance from the plot to the nearest stream was measured from the beginning of each plot to the bank of the nearest stream with the help of a tape measure (Rojas-Ahumada *et al*. 2012).

LEAF-LITTER DEPTH. The leaf-litter depth was measured with a graduated rule in six equidistant points (0, 50, 100, 150, 200, 250 m) along the transects. For each plot, we used the mean depth obtained in the six points.

CANOPY OPENESS AND VEGETATION DENSITY. Both metrics were extracted from data collected with portable ground LiDAR. A frame is attached, sustained one meter above the ground. The frame is load horizontally by an operator, which transports the sensor in vertical position facing upwards, in constant speed. The metrics used were the proportion of skyshots and leaf area density (LAD) (Parker *et al*. 2004). The metrics were extracted by D.M. Rosas (personal communication) according to Stark *et al*. (2012).

SLOPE. Measurements of slope for 31 grid plots were obtained from PPBio Data Repository, available at https://ppbio.inpa.gov.br/manuais. The authors took ten additional measurements in plots installed by Rojas-Ahumada *et al*. (2012), totaling 41 plots. Measurements were taken at six equidistant points (0, 50, 100, 150, 200, 250 m) along the transect with a clinometer and two beacons. Two observers positioned perpendicular to the transect at a distance of 2 m from central point. For each plot, we used the mean slope obtained at the six points.

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TABLES

TABLE 1: List of lizard species by family recorded at Fazenda Experimental da Universidade Federal do Amazonas in Manaus, Brazil, with the number of observations per species. Species with a (*) symbol were recorded only outside the grid.

Family/Species	**Observations**
Alopoglossidae	
Alopoglossus angulatus	6
Dactyloidae	
Anolis chrysolepis	2
Anolis fuscoauratus	17
Anolis punctatus	12
Gekkonidae	
*Hemidactylus mabouia**	-
Gymnophthalmidae	
Arthrosaura reticulata	10
Leposoma percarinatum	9
Neusticurus bicarinatus	8
Tretioscincus agilis	8
Iguanidae	
*Iguana iguana**	-
Mabuyidae	
Copeoglossum nigropunctatum	21
Phyllodactylidae	
Thecadactylus rapicauda	4
Sphaerodactylidae	

Chatogekko amazonicus	80
Gonatodes humeralis	54
Teiidae	
Ameiva ameiva	37
Kentropyx calcarata	114
Tupinambis teguixin	2
Tropiduridae	
Plica plica	4
Plica umbra	16
Uranoscodon superciliosus	25
Total	429

TABLE 2: Results from multivariate regressions. Models' adjusted R-squared and p-values are given in parenthesis. P-values for each variable given for respective model. The nonmetric multidimensional scaling derived from Bray-Curtis distances of site-standardized data represents quantitative assemblage composition, and the nonmetric multidimensional scaling derived from Jaccard's index for presence-absence data represents qualitative composition.

Environmental variables	**Quantitative composition (R^2 = 0.02; P = 0.33)**	**Qualitative composition (R^2 = 0.10; P = 0.11)**
Distance from streams	0.20	0.20
Leaf-fitter depth	0.24	0.05
Canopy openness	0.93	0.72
Vegetation density	0.77	0.72
Slope	0.27	0.80

LEGENDS TO FIGURES

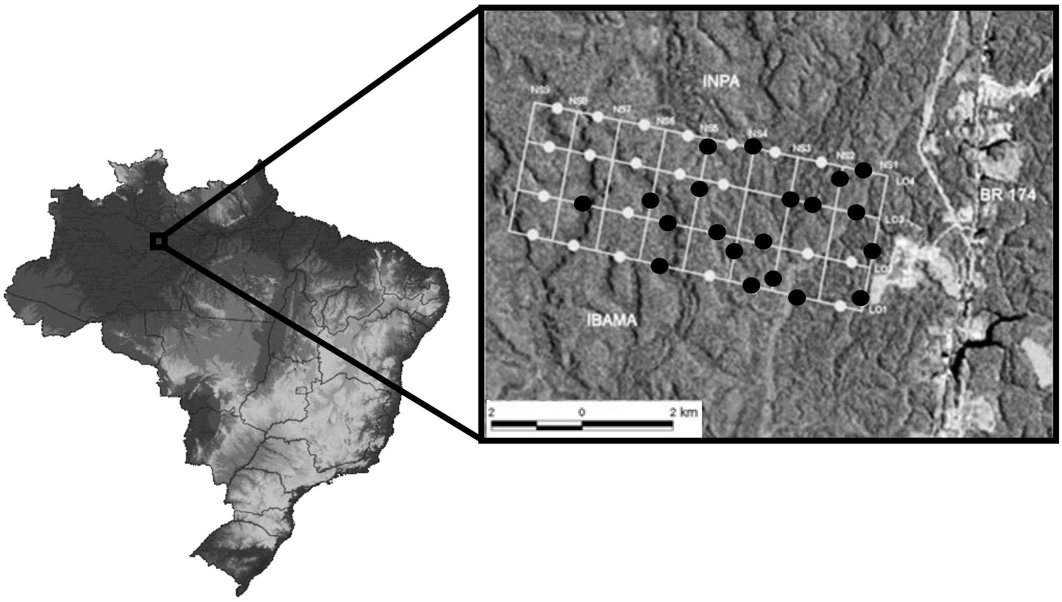
FIGURE 1: Location of the RAPELD grid in Fazenda Experimental da Universidade Federal do Amazonas, Manaus, Amazonas state, Brazil (see Methods for supporting information). Black dots indicate locations of riparian plots and white dots show positions of upland (evenly spaced) plots. Modified from: ppbio.inpa.gov.br.

FIGURE 2: Effect of distance from streams on quantitative composition of a lizard species assemblage in an upland rainforest near Manaus, Brazil. The NMDS axis represents the nonmetric multidimensional scaling derived from Bray-Curtis distances of site-standardized data. Lines represent piecewise regressions ($R^2 = 0.13$; $P = 0.02$) with breakpoint at ~190 m from nearest stream.

FIGURE 3: Effect of distance from streams on quantitative composition of a lizard species assemblage in an upland rainforest near Manaus, Brazil. The NMDS axis represents the nonmetric multidimensional scaling derived from Jaccard's Index for presence-absence data. Lines represent piecewise regressions ($R^2 = 0.38$; $P < 0.01$) with breakpoint at ~211 m from nearest stream.

FIGURE 4: Occurrence of lizard species related to distance from streams in Fazenda Experimental da Universidade Federal do Amazonas, Manaus, Brazil. Plots are ordered from left to right by distance from nearest stream, which varied from 1.74 m to 1093.4 m. Rectangles represent presence of species listed in right corner. Vertical line represents the estimated distance (obtained by piecewise regression) at which stream cease to influence in qualitative composition (~211 m).

FIGURES



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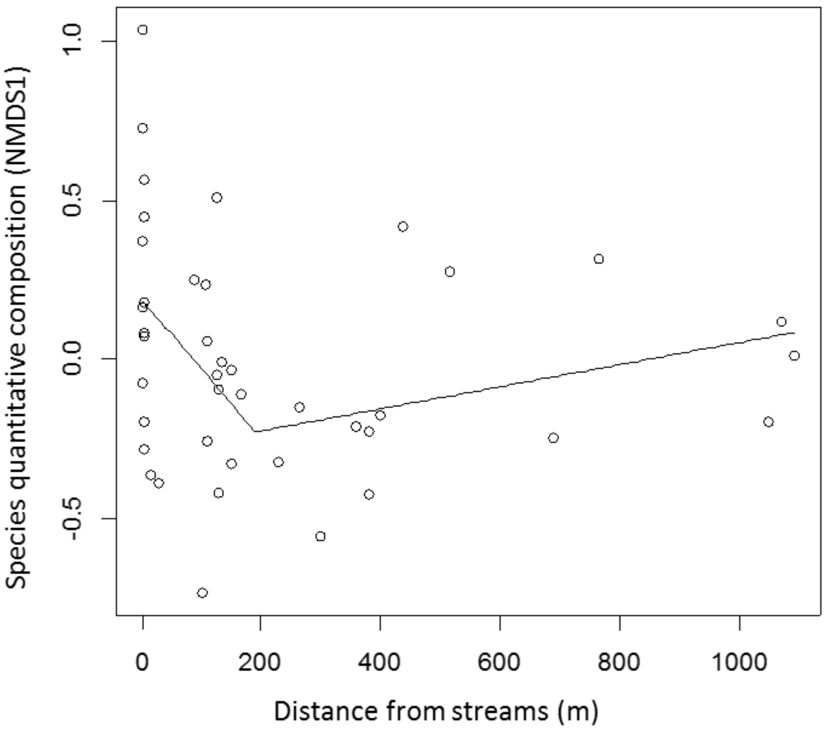

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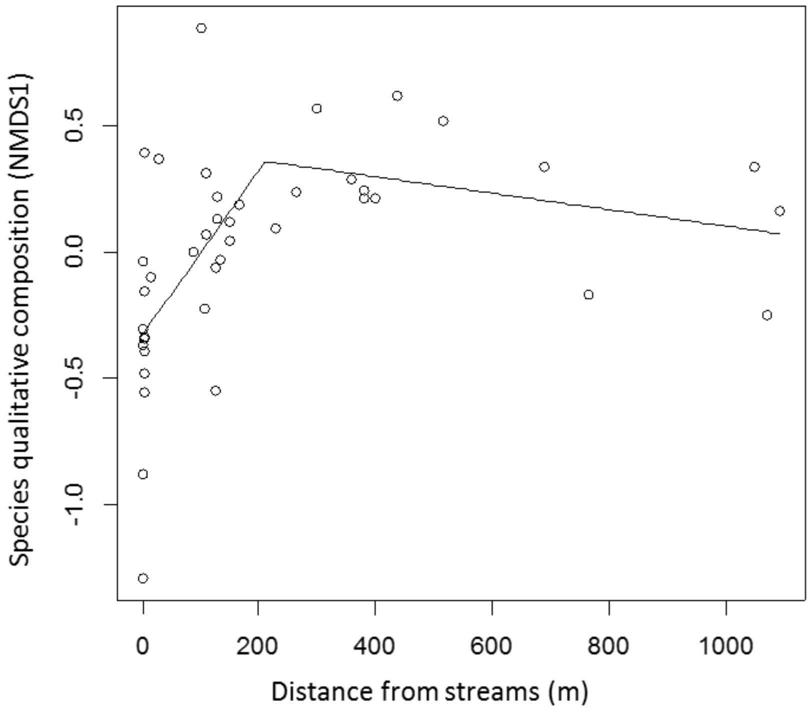

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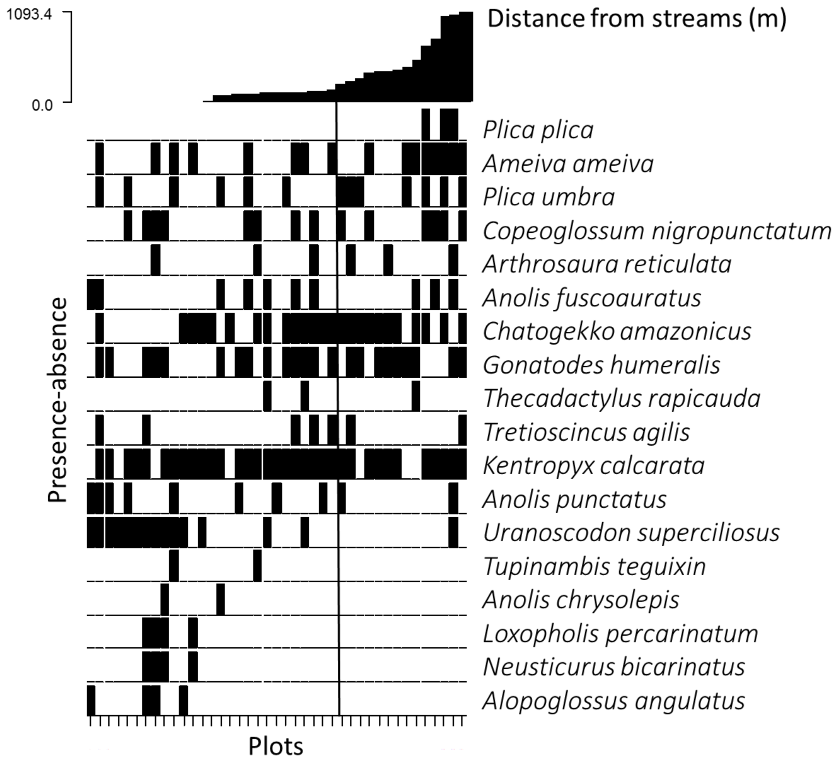

FIGURE 4: Occurrence of lizard species related to distance from streams in Fazenda Experimental da Universidade Federal do Amazonas, Manaus, Brazil. Plots are ordered from left to right by distance from nearest stream, which varied from 1.74 m to 1093.4 m. Rectangles represent presence of species listed in right corner. Vertical line represents the estimated distance (obtained by piecewise regression) at which stream cease to influence in qualitative composition (~211 m).

CONCLUSÕES

A assembleia de lagartos da área estudada foi semelhante à de outras localidades próximas quanto à composição e riqueza. O número de espécies encontradas esteve dentro do previsto, considerando outros estudos realizados na Amazônia. Da mesma forma, a composição não divergiu das áreas amostradas nas proximidades. As variáveis ambientais distância do igarapé, profundidade de liteira, abertura do dossel, densidade de vegetação e inclinação do terreno não explicaram o padrão encontrado na composição da assembleia.

Nossos resultados nos permitem sugerir que a distância até o igarapé tem o papel mais significativo na composição e na abundância de indivíduos, sendo reconhecida a zona ripária entre ~190 e ~211 m, considerando uma floresta contínua. A estimativa de uso da zona ripária demonstra que a legislação ambiental vigente no Brasil não é suficiente para abranger a totalidade de variação observada para esta assembleia de lagartos amazônicos, assim como sugerido na literatura para outros grupos de organismos.

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