

Riparian zone as a main determinant of the structure of lizard assemblages in upland Amazonian forests

AYRA SOUZA FARIA,^{1*}  MARCELO MENIN² AND IGOR LUIS KAEFER²

¹*Instituto Nacional de Pesquisas da Amazônia – Programa de Pós-graduação em Ecologia/INPA, V8, Av. André Araújo, 2936, Petrópolis, Manaus, Amazonas, CEP: 69067-375 (Email: ayrasfaria@outlook.com); and* ²*Departamento de Biologia, Universidade Federal do Amazonas – Senador Arthur Virgílio Filho – Setor Sul, Manaus, Amazonas, Brazil*

Abstract The use of lizards as model organisms in ecological studies is based on their success in occupying a great diversity of habitats, and some species are closely tied to the environment, which is disadvantaged by the legislation of several countries concerning land use. Our aim was to relate lizard species distribution patterns in rainforest environments to variation in environmental gradients, and provide ecologically based metrics for establishing buffer zones around streams. Lizards were sampled three times in 41 standardised transects near Manaus, Brazil, only in dry season, with Time Limited Visual Search associated with raking through leaf litter. We recorded 20 species from 10 families and used non-metric multidimensional scaling to reduce the dimensionality of quantitative and qualitative compositions of species. Multiple linear regression models indicated that the environmental gradients distance to nearest stream, extent of canopy openness, vegetation density and slope did not significantly influence assemblage species distribution, with an indication of effect of litter depth. By means of piecewise linear regression, the use of riparian zone was estimated at ~190 m from quantitative species composition and ~211 m from qualitative species composition. Five species occurred only in the riparian zone. Our results suggest that conservation of the entire riparian lizard assemblage in Amazonian rainforest is likely to require protection of at least a 211 m buffer on either side of streams. Abstract in Portuguese is available with online material.

Key words: Amazon, Brazil, environmental gradients, Forest Code.

INTRODUCTION

Lizards are widely used as ecological models due to their success in occupying a great variety of habitat types (Vitt *et al.* 2003). In addition to behavioural (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 (Ledo & Colli 2016).

In forest environments, gradients such as vegetation composition, 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). Across a great variety of biological groups, including lizards, one of the most significant threats to species diversity is habitat loss (Ribeiro-Júnior & Amaral 2016).

Studies have suggested that riparian zones have greater richness and distinctness of species composition than adjacent areas (Drucker *et al.* 2008; Bueno *et al.* 2012; Rojas-Ahumada *et al.* 2012). Turnover in species composition is favoured by the presence of riparian zones (Sabo *et al.* 2005). These areas can increase spatial heterogeneity, by modifying plant species composition in the landscape. This is an important factor in determining assemblage structure (Pianka 1966; Keller *et al.* 2009). Riparian zones 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; Pianka 1974; Schall & Pianka 1978; Sebens 1991). Here, we consider riparian zone as the area extending from the two borders of a stream to where the influence of the stream disappears (Zhang & Peng 2003).

Many governments around the world set fixed buffer zones for streams, and this leads to the question of how these values are derived and whether they are based on

*Corresponding author.

Accepted for publication February 2019.

ecologically reasonable values. In several localities, human actions have caused alterations in the course of rivers and loss of riparian forests, damaging the native biodiversity (Barrett & Guyer 2008; Bateman *et al.* 2008). 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 zones and their associated forests, despite their key role in providing a variety of environmental services (Tundisi & Tundisi 2010).

While it is clear that vertebrate assemblages in riparian zones are strongly structured (Seavy *et al.* 2009), few studies have investigated the extent to which the riparian zone is used or the importance of these areas for lizard assemblages (e.g. Sabo & Power 2002; Semlitsch & Bodie 2003). Therefore, our objectives were to: (i) relate lizard species distribution patterns in rainforest environments to variation in environmental gradients and (ii) provide ecologically based metrics for establishing buffer zones around streams.

METHODS

Study area

We conducted the study at the Federal University of Amazonas Experimental Farm (FEX-UFAM),

Manaus, Amazonas. FEX-UFAM ($2^{\circ} 38'57.6''S$, $60^{\circ} 3'11''W$) is located in an upland (*terra-firme*) forest at km 921 on highway BR-174 (Fig. 1) and occupies an area of 3000 ha of tropical rainforest with a mainly closed canopy and low-lying understorey. FEX-UFAM has extensive episodically flooded areas due to the presence of large streams, and an irregular topography (altitude ranges from 42 to 130 m: Rojas-Ahumada *et al.* 2012).

Federal University of Amazonas Experimental Farm is connected to protected areas managed by Brazilian federal government bodies (Brazilian Institute for the Environment and Renewable Natural Resources (IBAMA) and the National Institute of Amazonian Research (INPA)), and so is part of a much larger area of continuous forest (Rojas-Ahumada *et al.* 2012). The annual mean temperature in the region varies between 24.6 and 26.9°C, and the daily relative humidity varies between 75% in dry season and 92% in rainy season (Araújo *et al.* 2002). The rainy season usually occurs from December to May, and the dry season from June to November (Marques-Filho *et al.* 1981).

Sampling design and Data collection

Federal University of Amazonas Experimental Farm includes a sampling plot system of the Biodiversity Research Program (PPBio), installed in 2007 following the RAPELD system (Rapid Assessment Program; PELD – Long-Term Ecological Research;

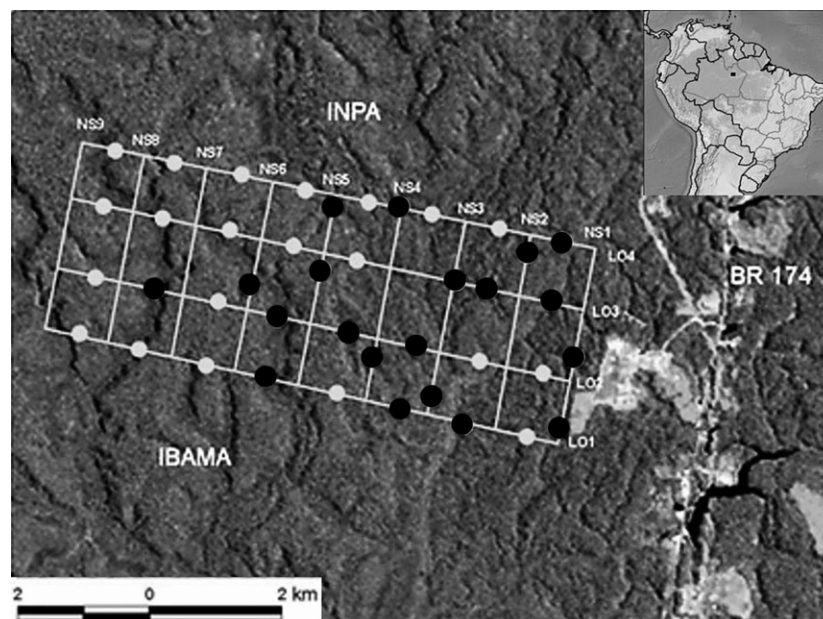


Fig. 1. Location of the RAPELD grid in Fazenda Experimental da Universidade Federal do Amazonas, Manaus, Amazonas State, Brazil (see Methods for supporting information). Black dots indicate locations of riparian transects, and white dots show positions of upland (uniformly distributed) transects. Modified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

Magnusson *et al.* 2005; Magnusson *et al.*, 2013). At FEX-UFAM, the plot system is composed of four east–west oriented trails each of 8 km long, and nine north–south oriented trails each 3 km long, covering an area of 24 km². The plot system contains 41 250-m-long plots in form of transects that follow the terrain contour (Fig. 1). Of these, 31 are uniformly distributed transects, with neighbouring transects separated by 1 km. Another 10 riparian transects that follow the banks of waterbodies are separated from other transects by at least 500 m (Rojas-Ahumada *et al.* 2012).

We sampled all transects three times between September and November 2015, or between September and November 2016, in a random order. We collected data only in dry season, when the area is not flooded and lizards were likely to be more active due to higher temperatures. We visited the transects during the day, between 09:00 and 15:00, on days with temperatures of at least 26°C and in the absence of rainfall. We used Time Limited Visual Search (TLVS) associated with raking through leaf litter (Crump & Scott 1994; Martins & Oliveira 1998). Occasional lizard records outside the transects and around the grid were not included in the analyses, and were considered only as part of the description of the local assemblage composition.

In order to detect terrestrial and arboreal lizards, the TLVS was conducted by searching horizontally (up to 5 m on each side) and vertically (up to 5 m high) along the centre line of the transects. Raking through leaf litter consisted of moving litter and fallen logs in search of fossorial animals. We conducted TLVS following the sequence of space markers along the transects, with 10 m distant from one another, from 0 to 250 m, for 1 h. Raking through leaf litter was performed in the reverse direction, also for 1 h. During each survey, we surveyed each transect for 2 h, with two observers, totalling a sampling effort of 246 person-hours. Taxonomic nomenclature adopted follows Ribeiro-Júnior and Amaral (2016).

Environmental variables

In all transects, 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 transect to the nearest stream was obtained from a previous study and ranged from 1.74 to 1093.4 m (Rojas-Ahumada *et al.* 2012). In the third survey, we measured the litter depth with a ruler in six points distributed uniformly along each transect. We used the mean leaf-litter depth value for each transect. We obtained measurements of land slope, clay percentage and

altitude data during field visits and from previous studies, available at the Biodiversity Research Program Data Repository (PPBio) at <http://ppbio.inpa.gov.br>. All sampling methods followed the protocols established by PPBio.

In addition, we used vegetation-density and canopy-opening data collected with LiDAR (Light Detection And Ranging) in previous studies (J. Schiatti, unpubl. data, 2017). We estimated vegetation density as the sum of leaf area density (LAD) returns for each transect, which is the returns of pulses in a given volume of forest (MacArthur & Horn 1969). We estimated the canopy openness from the percentage of sky shots, 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 among the transects 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 total number of observations in each transect in the three sampling visits as an index of the abundance of each species. We summarised the composite patterns with non-metric multidimensional scaling (nMDS) to reduce dimensionality of data to a single axis of multivariate ordering and to allow visualisation of compositional patterns within the assemblage.

To determine the relationship of the lizard assemblage composition to the environmental variables, we used multiple regressions, for which the dependent variable was the first nMDS axis of quantitative or qualitative composition. We tested the independence of the predictor variables (Spearman's correlation coefficients, $r < 0.60$) and 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 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). Piecewise regression uses maximum likelihood to fit multiple linear models to each x value, and then, two straight lines represent variation in the nMDS axis in relation to the predictor variable. The breakpoint represents an x value where the linear function inclination changes. This breakpoint is considered to represent the distance at which organisms perceive an environmental differentiation, thus delimiting the effective extension of the riparian zone for the analysed group. We performed the

segmented regression with the SiZer statistical package, version 0.1-4. SiZer uses a non-parametric method to approximate the response function and its derivatives. After that, it examines how those functions change across the range of the predictor variable (Sonderegger *et al.* 2009). All analyses for this study were conducted in the R computing environment (R Core Team, 2014).

RESULTS

Correlations of lizard assemblage and environmental variables

We recorded 20 species of lizards from 10 families (Table 1). After the exclusion of two species recorded in occasional encounters, in the ecological analyses we considered 18 species from 10 families, totalling 429 records. The five species greater or equal to 25 records made up 72.2% of the observations. The five least frequently encountered species accounted for only 4.2% of all observations.

The number of species recorded in each transect varied from one to nine (mean \pm SD = 4.7 ± 1.9). The number of observations in each transect varied from two to 24 (mean \pm SD = 10.5 ± 5.6). *Kentropyx calcarata* and *Chatogekko amazonicus* were the most frequently encountered species, occurring in 83% and 56% of transects. Two species, *Thecadactylus rapicauda* and *Uranoscodon superciliosus*, were recorded only once in non-riparian areas. The vast majority of *U. superciliosus* was 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 transects with a distance from streams greater than 600 m.

The nMDS axes captured 39.2% and 41% of the variance for quantitative and qualitative compositions, respectively. 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 indication of an 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

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 sampling grid

Family/Species	Observations
Alopoglossidae	
<i>Alopoglossus angulatus</i>	6
Dactyloidae	
<i>Anolis chrysolepis</i>	2
<i>Anolis fuscoauratus</i>	17
<i>Anolis punctatus</i>	12
Gekkonidae	
<i>Hemidactylus mabouia*</i>	–
Gymnophthalmidae	
<i>Arthrosaura reticulata</i>	10
<i>Leposoma percarinatum</i>	9
<i>Neusticurus bicarinatus</i>	8
<i>Tretioscincus agilis</i>	8
Iguanidae	
<i>Iguana iguana*</i>	–
Mabuyidae	
<i>Copeoglossum nigropunctatum</i>	21
Phyllodactylidae	
<i>Thecadactylus rapicauda</i>	4
Sphaerodactylidae	
<i>Chatogekko amazonicus</i>	80
<i>Gonatodes humeralis</i>	54
Teiidae	
<i>Ameiva ameiva</i>	37
<i>Kentropyx calcarata</i>	114
<i>Tupinambis teguixin</i>	2
Tropiduridae	
<i>Plica plica</i>	4
<i>Plica umbra</i>	16
<i>Uranoscodon superciliosus</i>	25
Total	429

of distance on the quantitative assemblage composition from ~190 m (95% CI = 3.1–857.8 m) 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 m; $R^2 = 0.38$; $df = 38$; $P < 0.01$). 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 recognised by lizard assemblage, extends some 211 m from streams. Using this metric, 27 of

Table 2. Results from multiple linear regressions. Models' adjusted R -squared (model adjustment) and P -values (significance) are given in parentheses. P -values for each variable are given for the respective multiple regression model. The non-metric multidimensional scaling derived from Bray–Curtis distances of site-standardised data represents quantitative assemblage composition, and the non-metric 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

the 41 transects sampled lie within the riparian zone, and 14 are outside the riparian zone (Fig. 4).

Five species were restricted to the riparian zone, all with fewer than 10 records. Only one individual of *T. rapicauda* out of 4 and one *U. superciliosus* out of 25 were recorded in transects outside the calculated

riparian zone. *Tretioscincus agilis* was recorded twice in transects outside the riparian zone. *Plica plica* was recorded only in upland forest. All other species were recorded in transects in both habitat types, indicating low species turnover (Fig. 4).

DISCUSSION

We recorded 18 species from 10 families, totalling 429 observations. Multiple regression models were not significant. Considering the models from piecewise regressions, the riparian zone extends some 211 m from streams.

The lizard assemblage and effects of environmental variables

Studies of Amazonian lizard fauna tend to show similar richness and composition to our study area (Zimmerman & Rodrigues 1990; Vitt *et al.* 2008; França & Venâncio 2010; Ilha & Dixo 2010; Oliveira *et al.* 2014). 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).

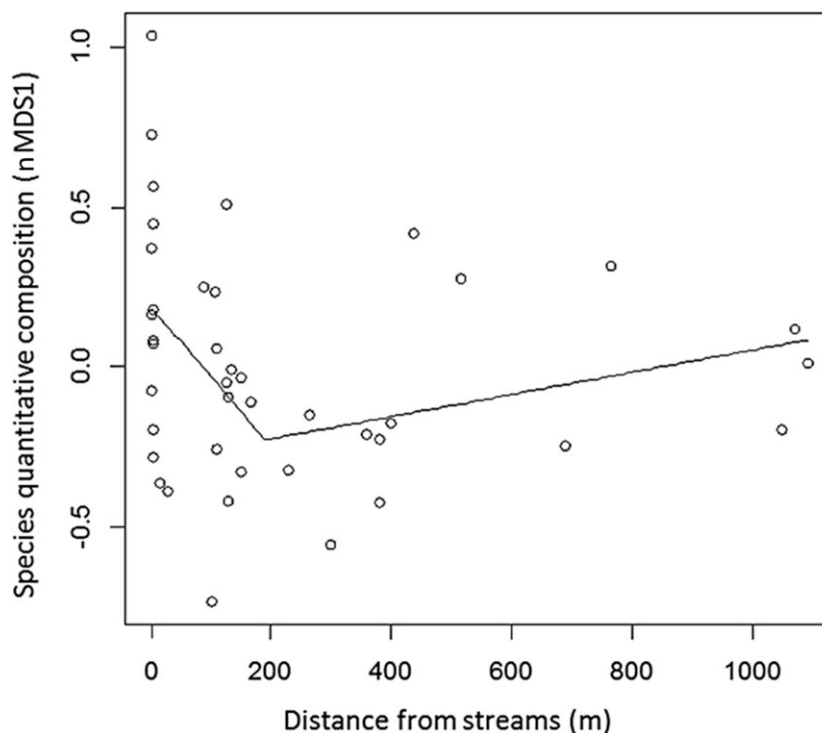


Fig. 2. Effect of distance from streams on quantitative composition of a lizard species assemblage in an upland rainforest near Manaus, Brazil. The nMDS axis represents the non-metric multidimensional scaling ordination derived from Bray–Curtis distances of site-standardised data. Lines represent piecewise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

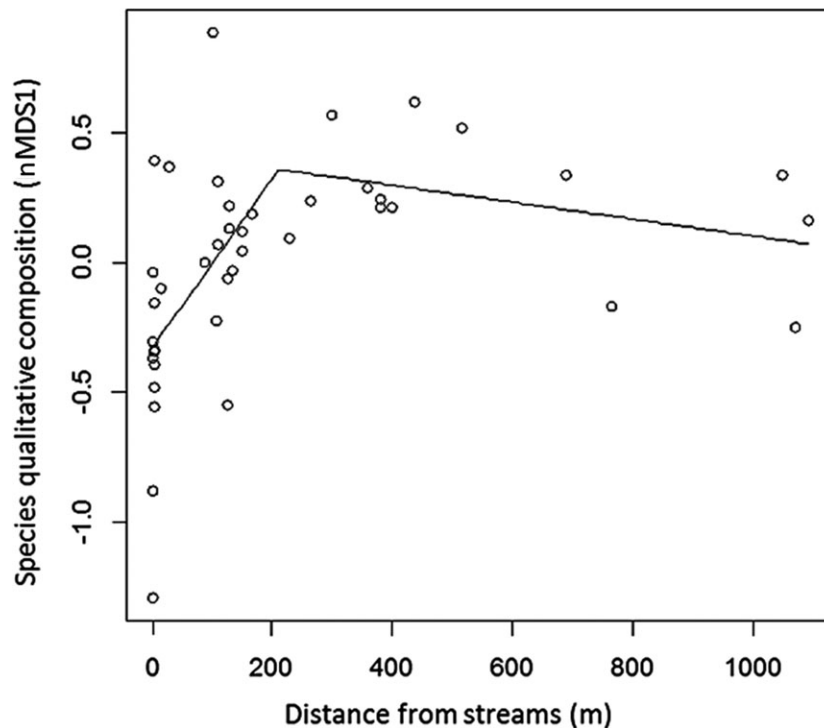


Fig. 3. Effect of distance from streams on quantitative composition of a lizard species assemblage in an upland rainforest near Manaus, Brazil. The nMDS axis represents the non-metric multidimensional scaling ordination derived from the Jaccard Index for presence-absence data. Lines represent piecewise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

Species turnover appears to be lower in forest environments (Silva & Sites 1995) than in open regions (Vitt *et al.* 2007) at the local scale. 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-Junior & Amaral 2016). This suggests that both turnover patterns and the influence of environmental variables can be detected more easily at scales broader than that employed in the present study.

Leaf-litter depth is likely to affect the lizard assemblages we studied because it increases habitat complexity. Several studies point to the importance of leaf litter in affecting lizard assemblages (Watling 2005; Whitfield *et al.* 2007; Folt & Reider 2013). This might be due to the increase in food resources, given that leaf-litter arthropods constitute a large portion of the food items consumed by lizards (Vitt *et al.* 2007).

Use of riparian habitats

Riparian zones play an important role in structuring species assemblages, affecting both richness (Bub *et al.* 2004; Rojas-Ahumada *et al.* 2012) and species composition (Lehmkuhl *et al.* 2007; Fraga *et al.*

2011). Even though we found high uncertainty about the extent of the riparian zone, both qualitative and quantitative approaches resulted in similar estimates. 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 ecotone that extended to about 200 m from streams. A change in species composition was shown to occur from 100 to 140 m for other groups as Amazonian herbaceous plants (100 m; Drucker *et al.* 2008), snakes (100 m; Fraga *et al.* 2011), bats (114 m; Pereira *et al.* 2019) and birds (140 m; Bueno *et al.* 2012). As Bueno *et al.* (2012) and Drucker *et al.* (2008), the lizard assemblage we studied showed greater abundance of species in the riparian zone. In addition, as Bueno *et al.* (2012), we found more species restricted to the riparian than to the non-riparian environment.

The composition of plant species in areas closer to the stream banks is distinct from areas further away, 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 sorts of resources, which possibly alters species abundance (Curtis *et al.* 2015). The higher abundance of lizard species in

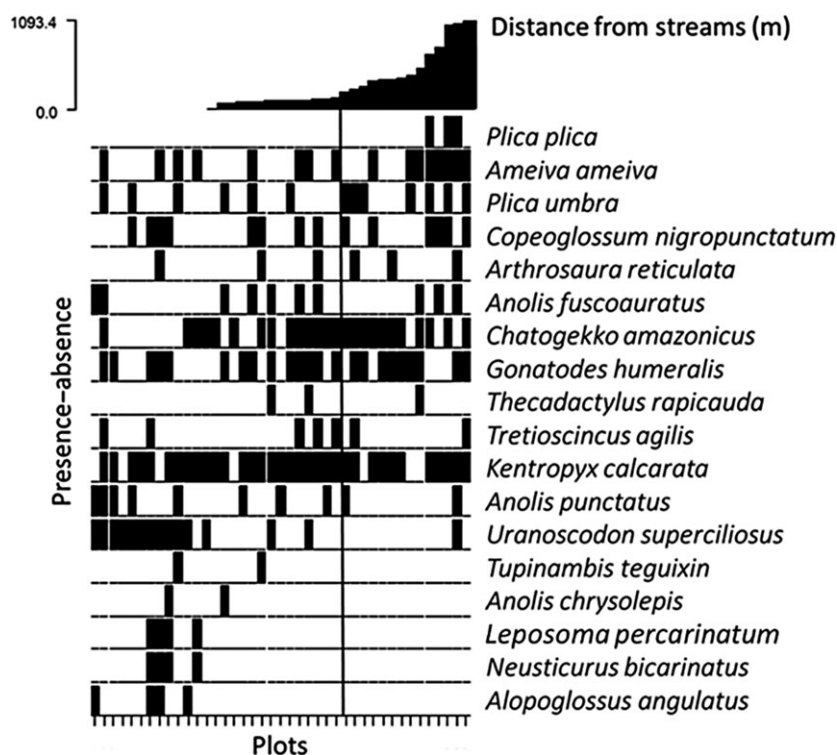


Fig. 4. Occurrence of lizard species related to distance from streams in Fazenda Experimental da Universidade Federal do Amazonas, Manaus, Brazil. Transects are ordered from left to right by distance from nearest stream, which varied from 1.74 to 1093.4 m. Bars represent presence of species listed to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

riparian zones might be explained by the higher prey abundance in these areas during the dry seasons (Ryan & Poe 2014).

Implications for conservation

Establishing a fixed metric for mandatory preservation does not seem reasonable, since each species uses space in different ways. At our study site, the widest forest streams have an average width of 4.6 m (Rojas-Ahumada *et al.* 2012). According to Brazilian laws, 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 per cent of the riparian zone as recognised by the assemblage in the current study.

Environmental laws for the preservation of the riparian zone have been adopted in a number of Latin American countries, with minimal riparian zone around 100–400 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 less

conservation-oriented. Recent changes to the Brazilian Forest Code allow the maintenance of 30 m of riparian forest for waterbodies in urban areas or 10 m wide for small rural waterways, reaching 500 m for streams with a width exceeding 600 m (Law 12.651 of May 25, 2012).

The ineffectiveness of the legislation in force in megadiverse countries, such as Brazil, has already been identified as a threat to species conservation (Casatti 2010; Imperatriz-Fonseca & Nunes-Silva 2010; Marques *et al.* 2010; Ribeiro-Jr *et al.* 2012; Novaes & Souza 2013; Ledo & Colli 2016). The habitat reduction can cause decrease in ecological services, as result of the loss of pollinators and seed dispersers, as well as an increase in the likelihood of disease transmission in urban centres (Develey & Pongiluppi 2010; Galetti *et al.* 2010).

The riparian zone in the present study is just one of the many categories of wetlands in Amazonia (Junk *et al.* 1989; Piedade *et al.* 2012). Studies at several sites and across a variety of groups have shown that 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; Ribeiro-Jr *et al.* 2012; Rojas-Ahumada *et al.* 2012).

Our results suggest that variation in the composition of Amazonian lizard assemblages is not adequately considered under the legal tenets of the current Brazilian Forest Code. The statistical methods used in the present study have proved to be effective in establishing ecologically based buffer zones. Fixed metrics, which are adopted by several countries, do not reflect the effective use of forest riparian habitats and should be reconsidered according to the ecological needs of the species.

ACKNOWLEDGEMENTS

We thank Nigel Andrew and two anonymous reviewers for valuable suggestions on an earlier version of this manuscript; Fundação de Amparo à Pesquisa do Estado do Amazonas (FAPEAM) for the scholarship to ASF; Programa de Pesquisa em Biodiversidade (PPBio), Centro de Estudos Integrados da Biodiversidade Amazônica (CENBAM) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq 461573/2014-8 – Ecologia Molecular e Comportamental de Répteis da Amazônia Central) for financial support; and Juliana Schietti and Diogo Rosas for the metrics extracted via LiDAR. We also thank our field assistants and the friends Gabriel, José Neto, José Raulino and Amanda Picelli who helped in field surveys.

REFERENCES

- Abdala V., Tulli M. J., Russell A. P. *et al.* (2014) Anatomy of the crur and pes of neotropical iguanian lizards in relation to habitat use and digitally based grasping capabilities. *Anat. Rec.* **297**, 397–409.
- Ab'Sáber A. N. (2010) Evolving from a forest code to a biodiversity code. *Biota. Neotrop.* **10**, 331–5.
- Araújo A. C., Nobre A. D., Kruijt B. *et al.* (2002) Comparative measurements of carbon dioxide fluxes from two nearby towers in a central Amazonian rainforest: The Manaus LBA site. *J. Geophys. Res.* **107**, 1–20.
- Barrett K. & Guyer C. (2008) Differential responses of amphibians and reptiles in riparian and stream habitats to land use disturbances in western Georgia, U.S.A. *Biol. Conserv.* **141**, 2290–300.
- Bateman H. L., Chung-Maccoubrey A. & Snell H. L. (2008) Impacts of non-native plant removal on lizards in riparian habitats in the southwestern United States. *Restorat. Ecol.* **16**, 180–90.
- Bub B. R., Flaspohler D. J. & Huckins C. J. F. (2004) Riparian and upland breeding-bird assemblages along headwater streams in Michigan's Upper Peninsula. *J. Wildl. Manag.* **68**, 383–92.
- Buckley L. B. & Jetz W. (2010) Lizard community structure along environmental gradients. *J. Animal Ecol.* **79**, 358–65.
- Bueno A. S., Bruno R. S., Pimentel T. P. *et al.* (2012) The width of riparian habitats for understory birds in an Amazonian forest. *Ecol. Appl.* **22**, 722–34.
- Casatti L. (2010) Changes in the Brazilian Forest Code: Potential impacts on the ichthyofauna. *Biota. Neotrop.* **10**, 31–4.
- Cosentino B. J., Schooley R. L., Bestelmeyer B. T. *et al.* (2013) Response of lizard community structure to desert grassland restoration mediated by a keystone rodent. *Biodivers. Conserv.* **22**, 921–35.
- Crump M. L., Scott N. J. Jr (1994) Visual encounter surveys. In: *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians* (eds W. R. Heyer, M. A. Donnelly, R. W. McDiarmid *et al.*) pp. 84–92. Smithsonian Institution Press, Washington.
- Curtis R. J., Brereton T. M., Dennis R. L. H. *et al.* (2015) Butterfly abundance is determined by food availability and is mediated by species traits. *J. Appl. Ecol.* **52**, 1676–84.
- D'Cruze N. & Kumar S. (2011) Effects of anthropogenic activities on lizard communities in northern Madagascar. *Anim. Conserv.* **14**, 542–52.
- Develey P. F. & Pongiluppi T. (2010) Potential impacts of the changes proposed in the Brazilian Forest Code on birds. *Biota. Neotrop.* **10**, 43–5.
- Drucker D. P., Costa F. R. C. & Magnusson W. E. (2008) How wide is the riparian zone of small streams in tropical forests? A test with terrestrial herbs. *J. Trop. Ecol.* **24**, 65–74.
- Folt B. & Reider K. E. (2013) Leaf-litter herpetofaunal richness, abundance, and community assembly in monodominant plantations and primary forest of northeastern Costa Rica. *Biodiv. Conserv.* **22**, 2057–70.
- Fraga R., Lima A. P. & Magnusson W. E. (2011) Mesoscale spatial ecology of a tropic snake assemblage: The width of riparian corridors in central Amazonia. *Herpetol. J.* **21**, 51–7.
- Fraga R., Magnusson W. E., Abrahão C. R. *et al.* (2013) Habitat selection by *Bothrops atrox* (Serpentes: Viperidae) in Central Amazonia, Brazil. *Copeia* **2013**, 684–90.
- França F. G. R. & Venâncio N. M. (2010) Reptiles and amphibians of a poorly known region in southwest Amazonia. *Biotemas* **23**, 71–84.
- Galetti M., Pardini R., Duarte J. M. B. *et al.* (2010) Forest legislative changes and their impacts on mammal ecology and diversity in Brazil. *Biota. Neotrop.* **10**, 47–52.
- Hutchinson G. E. (1957) Concluding remarks. *Cold Spring Harb. Symp. Quantitat. Biol.* **22**, 415–27.
- Ilha P. & Dixo M. (2010) Anurans and lizards, Rio Preto da Eva, Amazonas, Brazil. *Check List* **6**, 17–21.
- Imperatriz-Fonseca V. L. & Nunes-Silva P. (2010) Bees, ecosystem services and the Brazilian Forest Code. *Biota. Neotrop.* **10**, 59–62.
- Junk W. J., Bayley P. B. & Sparks R. E. (1989) The flood pulse concept in river-floodplain systems. In: *Proceedings of the International Large River Symposium (LARS)* (ed D. P. Dodge) pp. 110–27. Special Publication of the Canadian Journal of Fisheries and Aquatic Sciences, Ontario.
- Keller A., Rödel M. O., Linsenmair K. E. *et al.* (2009) The importance of environmental heterogeneity for species diversity and assemblage structure in Bornean stream frogs. *J. Animal Ecol.* **78**, 305–14.
- Leavitt D. J. & Fitzgerald L. A. (2013) Disassembly of a dune-dwelling lizard community due to landscape fragmentation. *Ecosphere* **4**, 1–15.
- Ledo R. M. D. & Colli G. R. (2016) Silent death: The new Brazilian forest code does not protect lizard assemblages in cerrado riparian forests. *South Am. J. Herpetol.* **11**, 98–109.

- Lee J. C. (1980) Comparative thermal ecology of two lizards. *Oecologia* **44**, 171–6.
- Lehmkuhl J. F., Burger E. D., Drew E. K. *et al.* (2007) Breeding birds in riparian and upland dry forests of the cascade range. *J. Wildl. Manag.* **71**, 2632–43.
- MacArthur R. H. & Horn J. W. (1969) Foliage profiles by vertical measurements. *Ecology* **50**, 802–4.
- Magnusson W. E., Braga-Neto R., Pezzini F. *et al.* (2013) *Biodiversity and Integrated Environmental Monitoring*. Áttema Editorial, Manaus.
- Magnusson W. E., Lima A. P. L., Luizão R. C. *et al.* (2005) RAPELD: A modification of the Gentry method for biodiversity surveys in long-term ecological research sites. *Biota. Neotrop.* **5**, 1–6.
- Marques O. A. V., Nogueira C., Martins M. *et al.* (2010) Potential impacts of changes in the Brazilian Forest Code on reptiles. *Biota. Neotrop.* **10**, 39–41.
- Marques-Filho A. O., Ribeiro M. N. G., Santos H. M. *et al.* (1981) Estudos climatológicos da Reserva Florestal Ducke, Manaus, AM. IV – Precipitação. *Acta Amaz.* **11**, 759–68.
- Martins M. & Oliveira M. E. (1998) Natural history of snakes in forests in the Manaus region, Central Amazonia, Brazil. *Herpetol. Nat. Hist.* **6**, 78–150.
- Mugabo M., Marquis O., Perret S. *et al.* (2011) Direct and socially-mediated effects of food availability late in life on life-history variation in a short-lived lizard. *Oecologia* **166**, 949–60.
- Novaes R. L. M. & Souza R. F. (2013) Legalizing environmental exploitation in Brazil: The retreat of public policies for biodiversity protection. *Trop. Conserv. Sci.* **6**, 477–83.
- Nusdeo A. M. O. (2012) A legislação ambiental brasileira numa perspectiva comparada. In: *Código Florestal e a Ciência: O que nossos Legisladores ainda Precisam Saber* (eds G. Souza, K. Jucá & M. Wathely) pp. 85–9. Comitê Brasil em Defesa das Florestas e do Desenvolvimento Sustentável, Brasília.
- Oliveira D. P., Souza S. M., Frazão F. *et al.* (2014) Lizards from central Jatapú River, Amazonas, Brazil. *Check List* **10**, 46–53.
- Parker G. G., Harding D. J. & Berger M. L. (2004) A portable LIDAR system for rapid determination of forest canopy structure. *J. Appl. Ecol.* **41**, 755–67.
- Pereira L. G. A., Capavade U. D. Jr, Tavares V. C. *et al.* (2019) From a bat's perspective, protected riparian areas should be wider than defined by Brazilian laws. *J. Environ. Manag.* **232**, 37–44.
- Pianka E. R. (1966) Latitudinal gradients in species diversity: A review of concepts. *Am. Nat.* **100**, 33–46.
- Pianka E. R. (1974) Niche overlap and diffuse competition. *Proc. Natl. Acad. Sci. USA* **71**, 2141–5.
- Piedade M. T. F., Wolfgang J., Souza P. T. Jr *et al.* (2012) As áreas úmidas no âmbito do Código Florestal Brasileiro. In: *Código Florestal e a Ciência: O que Nossos Legisladores Ainda Precisam Saber* (eds G. Souza, K. Jucá & M. Wathely) pp. 9–17. Comitê Brasil em Defesa das Florestas e do Desenvolvimento Sustentável, Brasília.
- Pinto M. G. M., Magnusson W. E., Lima A. P. (2008) Lagartos. In: *Reserva Ducke: A Biodiversidade Através de uma Grade* (eds M. L. Oliveira, F. B. Baccaro, R. Braga-Neto *et al.*) pp. 91–108. Áttema Design Editorial, Manaus.
- R Core Team (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. URL: <https://www.r-project.org/>
- Ribeiro J. W. Jr, Lima A. P. & Magnusson W. E. (2012) The effect of riparian zones on species diversity of frogs in Amazonian forests. *Copeia* **3**, 375–81.
- Ribeiro-Junior M. & Amaral S. (2016) Diversity, distribution, and conservation of lizards (Reptilia: Squamata) in the Brazilian Amazonia. *Neotrop. Biodiv.* **2**, 195–421.
- Rojas-Ahumada D. P., Landeiro V. L. & Menin M. (2012) Role of environmental and spatial processes in structuring anuran communities across a tropical rain forest. *Austral. Ecol.* **37**, 865–73.
- Ryan M. J. & Poe S. (2014) Seasonal shifts in relative density of the lizard *Anolis polylepsis* (Squamata, Dactyloidae) in forest and riparian habitats. *J. Herpetol.* **48**, 495–9.
- Sabo J. L. & Power M. E. (2002) River-watershed exchange: Effects of riverine subsidies on riparian lizards and their terrestrial prey. *Ecology* **83**, 1860–9.
- Sabo J. L., Sponseller R., Dixon M. *et al.* (2005) Riparian zones increase regional species richness by harboring different, not more, species. *Ecology* **86**, 56–62.
- Schall J. J. & Pianka E. R. (1978) Geographical trends in numbers of species. *Science* **201**, 679–86.
- Seavy N. E., Viers J. H. & Wood J. K. (2009) Riparian bird response to vegetation structure: A multiscale analysis using LiDAR measurements of canopy height. *Ecol. Appl.* **19**, 1848–57.
- Sebens K. P. (1991) Habitat structure and community dynamics in marine benthic systems. In: *Habitat Structure: The Physical Arrangement of Objects in Space* (eds S. Bell, E. D. McCoy & H. R. Mushinsky) pp. 211–34. Chapman and Hall publishers, Great Britain.
- Semlitsch R. D. & Bodie J. R. (2003) Biological Criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. *Conserv. Biol.* **17**, 1219–28.
- Silva N. J. Jr & Sites J. W. Jr (1995) Patterns of diversity of Neotropical squamate reptile species with emphasis on the Brazilian Amazon and the conservation potential of indigenous reserves. *Conserv. Biol.* **9**, 873–901.
- Silva D. J., Santos-Filho M. & Canale G. R. (2014) The importance of remnant native vegetation of Amazonian submontane forest for the conservation of lizards. *Braz. J. Biol.* **74**, 523–8.
- Sonderegger D. L., Wang H., Clements W. H. & Noon B. R. (2009) Using SiZer to detect thresholds in ecological data. *Front. Ecol. Environ.* **7**, 190–5.
- Tundisi J. G. & Tundisi T. M. (2010) Potential impacts of changes in the Forest Law in relation to water resources. *Biota. Neotrop.* **10**, 67–75.
- Vitt L. J., Pianka E. R., Cooper W. E. Jr *et al.* (2003) History and the global ecology of squamate reptiles. *Am. Nat.* **162**, 44–60.
- Vitt L. J., Colli G. R., Caldwell J. P. *et al.* (2007) Detecting variation in microhabitat use in low diversity lizard assemblages across small-scale habitat gradients. *J. Herpetol.* **41**, 653–62.
- Vitt L. J., Magnusson W. E., Avila-Pires T. C. S. *et al.* (2008) *Guide to the Lizards of Reserva Adolpho Ducke, Central Amazonia* p. 176. Áttema Editorial, Manaus.
- Watling J. I. (2005) Edaphically-biased distributions of amphibians and reptiles in a lowland tropical rainforest. *Stud. Neotrop. Fauna Environ.* **40**, 15–21.
- Whitfield S. M., Bell K. E., Philippi T. *et al.* (2007) Amphibian and reptile declines over 35 years at La Selva, Costa Rica. *Proc. Nat. Acad. Sci.* **104**, 8352–6.
- Zhang J. C. & Peng B. Z. (2003) Study on riparian zone and the restoration and rebuilding of its degraded ecosystem. *Acta Ecol. Sinica.* **23**, 56–63.
- Zimmerman B. L. & Rodrigues M. T. (1990) Frogs, snakes, and lizards of the INPA-WWF reserves near Manaus, Brazil. In: *Four Neotropical Rainforests* (ed A. H. Gentry) pp. 426–54. Yale University Press, Connecticut.