NAT CONSERVACAO. 2014; **12(1):**42-46

Natureza & Conservação
Brazilian Journal of Nature Conservation
Supported by O Boticário Foundation for Nature Protection

Research Letters

Spatial and environmental patterns of Amazonian anurans: Differences between assemblages with aquatic and terrestrial reproduction, and implications for conservation management

Victor Lemes Landeiro[a,*], *Fabiano Waldez*[b], *Marcelo Menin*[c]

[a] *Departamento de Botânica e Ecologia, Universidade Federal do Mato Grosso – UFMT, Cuiabá, MT, Brazil*
[b] *Instituto Federal de Educação, Ciência e Tecnologia do Amazonas – IFAM, Tabatinga, AM, Brazil*
[c] *Departamento de Biologia, Instituto de Ciências Biológicas, Universidade Federal do Amazonas – UFAM, Manaus, AM, Brazil*

ARTICLE INFO

Article history:
Received June 2013
Accepted August 2013

Keywords:
Metacommunities
Moran eigenvector mapping
Neotropics; frogs
Variation partitioning

ABSTRACT

We evaluated whether species with aquatic reproduction would be more dependent on environmental conditions than species with terrestrial reproduction, which we predicted to be more affected by factors that induce spatial patterns unrelated to known environmental predictors. An analysis of all the species combined indicated a stronger spatial pattern than that induced by the environmental factors. However, the observed pattern was highly dependent on the reproductive mode. The distributions of species with aquatic reproduction were more related to the environmental variables, while species with terrestrial reproduction showed strong spatial patterns. Species that are strongly influenced by environmental controls may be more sensitive to specific threats (such as conversion of riparian areas), whereas species that do not have restrictive reproductive requirements, but present strong associations with forests, could be better indicators of the general environmental degradation associated with climate change or selective timber harvesting.

Introduction

Many factors, including climate changes, habitat loss, habitat fragmentation, diseases, and pollution, pose threats to amphibian species throughout the neotropics (Loyola *et al.* 2008). Anuran distributions respond to many biotic and abiotic factors, such as the availability of breeding habitats, litter cover, vegetation structure, and the structural diversity of habitats (Indermaur *et al.* 2010; Ernst & Rödel 2006). In tropical rainforests, topography, soil texture, leaf litter depth, and vegetation are the major factors affecting anuran species distribution (Giaretta *et al.* 1999; Vonesh 2001). However, anuran species with different developmental modes might respond to habitat disturbance in different ways (Loyola *et*

---

[*] *Corresponding author at:* Departamento de Ecologia e Botânica, Instituto de Biologia, Universidade Federal de Mato Grosso, Av. Fernando Correia, Cuiabá ± MT, Brazil.

E-mail address: vllandeiro@gmail.com (V.L. Landeiro).

1679-0073/$ - see front matter.
DOI: 10.4322/natcon.2014.008

al. 2008). In Amazon forests, topography and soil features affect the abundance of terrestrial-breeding species (Menin *et al.* 2007), whereas the distance from streams is the main factor influencing the abundance and occurrence of aquatic-breeding species (Menin *et al.* 2011).

In general, as in studies with most other taxa, analyses of anuran species distribution have evaluated only environmental constraints. However, studies on a few species have evaluated spatial factors related to dispersal ability (Jones *et al.* 2006). The neutral theory of biogeography and biodiversity posits that the patterns of abundance and distribution of species can be understood through models that consider individuals as though they were equivalent in birth, death, and dispersal rates, as well as in their competitive abilities. Therefore, species' spatial distribution patterns, such as the distance decay of similarity in ecological communities, would be the result of stochasticity in dispersal limitation rather than properties of the species niche (Rosindell *et al.* 2011). Several recent studies on metacommunity dynamics have investigated the role of spatial processes in light of the predictions of the neutral theory (Siqueira *et al.* 2012), but few have focused particularly on conservation biology.

In the present study, we evaluated the environmental and spatial factors controlling anuran assemblages in an Amazon forest at a mesoscale. In addition to estimating the relative role of these factors in controlling overall assemblages, we separated the species with aquatic reproduction from those with terrestrial reproduction in order to evaluate whether they would respond to the same factors. Because anurans are very sensitive to environmental changes, we hypothesized that environmental control would be more constraining than spatial control, and that species with different types of reproduction would differ in their relationships to environmental and spatial variables. More specifically, we predicted that species with terrestrial reproduction would respond more strongly to spatial constraints, because their distribution is more restricted by limitations on dispersal than by dependence on the availability of water bodies, and that species with aquatic reproduction would respond more to niche factors associated with water availability.

Material and methods

Datasets

This study was undertaken using anuran datasets sampled at 72 plots at the Ducke Reserve of the National Institute for Research in the Amazon (INPA), located 26 km northwest of the city of Manaus, state of Amazonas, Brazil (Fig. 1). All data used in this study are freely available at the Biodiversity Research Program (PPBio) website (http://ppbio.inpa.gov.br) where more-detailed information on sampling methods and measurements can be found (see also the supplementary material online). We included the following environmental variables in our analysis: slope across the plots, percentage clay content of the soil, number of trees in the plot, litter depth, distance to the nearest stream, and soil pH (Table S1, supplementary material online, gives summary statistics for these variables).

Data analysis

Spatial variables were generated through principal coordinates of neighbor matrices (PCNM; Borcard & Legendre 2002). The PCNM eigenvectors (usually called PCNMs or spatial

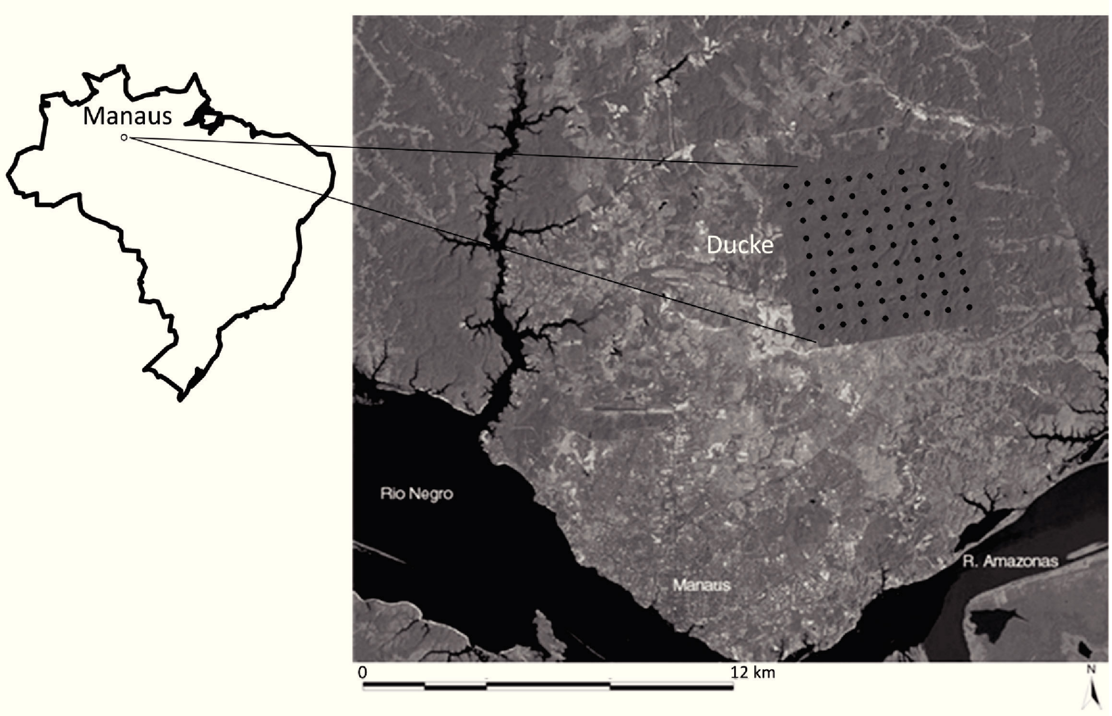

Fig. 1 – Location of Ducke Reserve, adjacent to the city of Manaus in the Brazilian Amazon. Points indicate 1 km-equidistant sample plots.

filters) represent distinct spatial patterns that are mutually orthogonal, and were used as our spatial predictor variables. PCNMs with high eigenvalues (i.e. low-order PCNMs) represent broad-scale patterns of relationships among sampling sites, whereas those associated with low eigenvalues (i.e. high-order PCNMs) represent fine-scale patterns.

The environmental data, except pH, were transformed to log (x + 1), and standardized to zero mean and unit variance before analysis. To evaluate the effects of environmental and spatial variables on the distribution of anuran species, we used partial redundancy analysis (Peres-Neto & Legendre 2010) adopting the three anuran-abundance datasets as response variables. The biotic datasets were transformed using the Hellinger transformation (Peres-Neto & Legendre 2010). We used a forward selection procedure (Blanchet *et al.* 2008) based on 10,000 permutations in order to retain only the most important environmental and spatial variables affecting the distribution of anuran assemblages. The total variation in the anuran assemblages was divided into four fractions based on adjusted fractions of variation (adj.R^2): variation explained exclusively by environmental variables [a], variation explained by environmental and spatial variables [b], variation explained exclusively by spatial variables [c], and unexplained variance [d]. All analyses were run using R (R Core Team, 2013, http://www.R-project.org).

Results

The anuran dataset contained 29 species, of which 20 have aquatic reproduction and nine have terrestrial reproduction. Seven species with aquatic reproduction that are uncommon in the sampling area occurred only sporadically (i.e. in fewer than four plots), and we omitted them from the analyses. Therefore, only 13 species with aquatic reproduction were analyzed (Table S2, supplementary material online).

The environmental and spatial variables explained around 39% of the variation of the anuran assemblages (Fig. 2). Both the environmental [a] and spatial [c] fractions were significant ($p < 0.001$). The spatial component was larger than the environmental component (23.8% and 10%, respectively), and the shared component was 5.3%. The environmental variables related to anuran assemblage distribution were: distance to the nearest stream, soil pH, number of trees in the plot, and soil clay content. We retained nine spatial variables for the partial RDA model.

Both sets of predictors explained around 34% of the variation in the assemblage of anurans with aquatic reproduction (Fig. 2). Both the environmental [a] and spatial [c] fractions were significant ($p < 0.001$). Environmental variables (distance to the nearest stream and number of trees) alone explained most of the variation (26.6%) in the assemblages of anurans with aquatic reproduction. The only three spatial variables retained accounted for merely 4.9% of the variation. The shared variation was equal to 2.9%.

For the assemblage of anurans with terrestrial reproduction, the spatial and environmental variables explained around 40% of the variation (Fig. 2). Both the environmental [a] and spatial [c] fractions were significant ($p < 0.001$). Contrarily to the anurans with aquatic reproduction, the spatial variables (eight spatial variables retained) better explained the variation in the assemblages of anurans with terrestrial reproduction, and these variables accounted for 30.3% of the variation. The two environmental variables retained (soil clay content and pH) accounted for only 5.4% of the variation; the shared fraction was 3.6%.

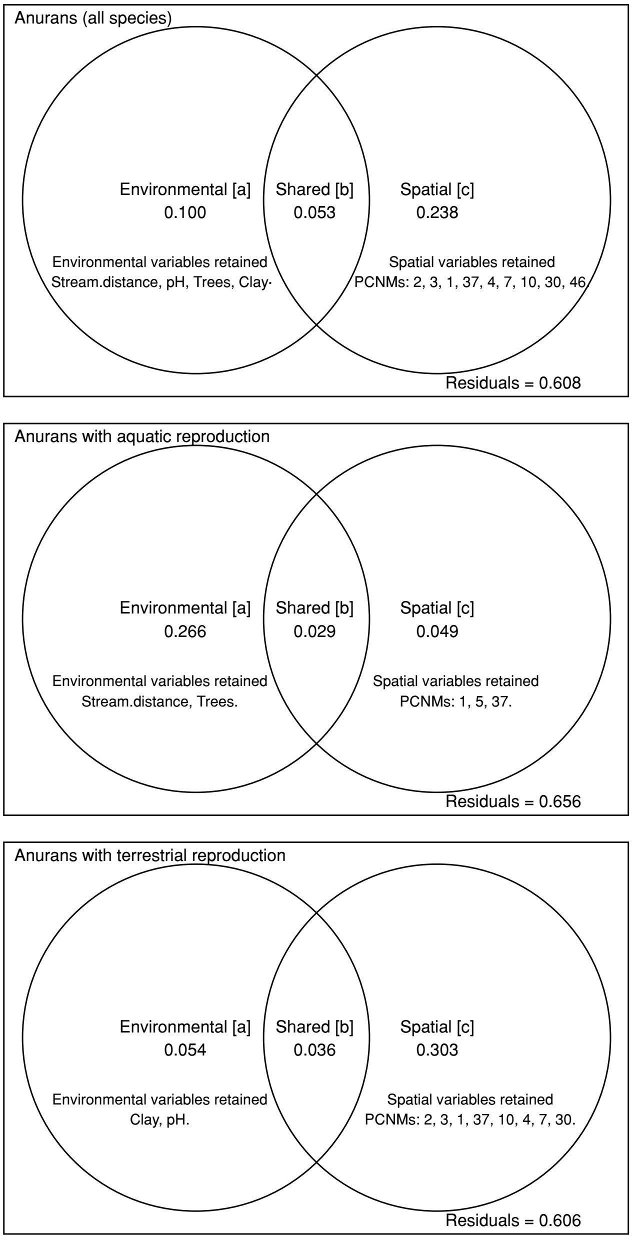

Fig. 2 – Variation partitioning results for anuran assemblages considering all species, those with aquatic reproduction and those with terrestrial reproduction. Results based on a partial redundancy analysis. Values shown are adjusted R^2.

Discussion

Our models explained at least 35% of the between-plot variation in these anuran assemblages. For all species pooled, the spatial patterns were stronger than the effects of the environmental variables included in the analyses. However, the pattern was highly dependent on the reproductive mode of the species. Species with aquatic reproduction responded more to variation in environmental factors (i.e. probable niche control), whereas species with terrestrial reproduction showed spatial patterns that were not associated with the environmental variables included in the analyses. In addition, the environmental variables associated with each group differed; soil pH and clay content were associated with species with terrestrial reproduction, while stream distance and number of trees in the plot were associated with species with aquatic reproduction.

Spatial patterns may arise from two main sources. Some spatially structured environmental variables that are important for anurans may not have been measured, and consequently were not included in the models (Landeiro & Magnusson 2011). This implies that the variation in species distribution due to such environmental variable will be attributed exclusively to spatial variables. Another possibility is that species are really not dependent on environmental constraints, and the observed spatial patterns might be attributed to dispersal limitation or other endogenous processes, such as differential reproduction. We measured environmental variables that are commonly found to affect the species distribution of several Amazonian animal groups (Landeiro *et al.* 2012). Therefore, we believe that the spatial pattern observed in species with terrestrial reproduction is more closely related to intrinsic dispersal processes than to the lack of important environmental variables. Menin *et al.* (2007) also suggested that dispersal limitation is a potential explanation for distribution patterns of anurans with terrestrial reproduction; however, they did not evaluate the anuran assemblage in relation to spatial predictors. Further studies on genetic data are crucial to confidently attribute differentiation to dispersal limitation, although metacommunity studies generally attribute spatial patterns to dispersal processes (Siqueira *et al.* 2012).

Assuming the neutral scenario for terrestrial anurans, in which species are equivalent competitors and the environmental characteristics are unimportant, it would be expected that geographic distance is important in predicting the similarity in species composition among sites (Diniz-Filho *et al.* 2012). Therefore, a search for environmental or biological surrogates/indicators would be unproductive, and geographic distance among sites would be a paramount predictor for this particular neutral assemblage. When species-sorting mechanisms shape local assemblages (Van der Gucht *et al.* 2007), environmental variables explain compositional similarity and could be reliable proxies for species' turnover (Ferrier *et al.* 2007). Therefore, the conservation of anuran species can depend strongly on life-history traits, such as the type of reproduction (Loyola *et al.* 2008). The inclusion of anuran developmental modes in analyses performed to select priority areas for the conservation of this order could improve comprehensiveness of the selection process. Compared to the usual assessments that do not consider these life-history traits, analyses that include reproductive requirements would improve the conservation of species that breed in aquatic habitats. Otherwise, the procedures used to select priority areas tend to favor species with terrestrial development (Loyola *et al.* 2008).

Since the severity and frequency of droughts affecting the Amazon region will likely increase (Lewis *et al.* 2011), together with other potential environmental changes caused by global warming, the effects on anurans might be severe for species that are dependent on aquatic habitats to reproduce (Di Minin & Griffiths 2011), and for those that rely on moist soils for terrestrial reproduction. Most terrestrial-breeding frogs occur in humid areas (Duellman 1988). Our results demonstrated that species with aquatic reproduction respond strongly to environmental conditions, mainly the distance to the nearest water source, indicating that changes in the availability of such sources will affect their occupation of the landscape. In addition, little of the beta diversity observed in terrestrially breeding frog assemblages is associated with habitat variation (Menin *et al.* 2007).

Zimmerman & Bierregaard (1986) suggested that frogs are not good indicator species for fragmentation studies, because the presence of suitable water bodies for reproduction generally determines their distributions. However, this generalization does not apply to the terrestrial-breeding species (Menin *et al.* 2007). The effects of climate change are likely to differ in aquatic-breeding and terrestrial-breeding frogs. Whereas the distribution of aquatic-breeding frogs across the landscape is possibly influenced by changes in the distribution of water bodies, aquatic-breeding species are not expected to become locally extinct until almost all water bodies are lost, and they could potentially be maintained by artificial water sources. This may explain why aquatic-breeding species are common in the driest areas of Amazonia (Duellman 1988). In contrast, few or no terrestrial-breeding species occur in these areas, suggesting that their limited dispersal abilities, together with their requirement for humid climates, might result in their complete disappearance from the landscape. Considerations about the vulnerability of different species will have to take into account differences in the requirements of the guilds and the scale of the changes.

These findings are relevant to the development of conservation strategies and biological monitoring programs under a metacommunity framework (Siqueira *et al.* 2012), because species that respond strongly to environmental controls may be more sensitive to specific threats, such as the conversion of riparian areas. Conversely, species that do not have restrictive needs for reproduction, but that present strong associations with humid forests could be better indicators of general environmental degradation associated with climate change or activities such as selective timber harvesting. Therefore, researchers, biomonitoring agencies, and biodiversity managers using different taxonomic groups with different species traits should account for these differences and remain aware of the implications of their results.

Acknowledgments

Tadeu Siqueira, William Magnusson, Pedro Peres-Neto, Marie Fortin, Thiago Rangel, and Rafael Loyola provided helpful comments on early versions. J. Lopes, M. Lima, and

E. Farias helped in fieldwork. C. Castilho provided the data on vegetation; E. Barros, J. Mertens, and T. Pimentel provided the soil data. The CNPq/PNOPG (grants 550651/01-2, and 471453/03-0) provided financial support to Albertina Lima, who supervised the data collection.

Supplementary material

Supplementary material associated with this article can be found, in the online version, at www.naturezaeconservacao.com.br.

REFERENCES

Blanchet FG, Legendre P & Borcard D, 2008. Forward selection of explanatory variables. *Ecology*, 89:2623-2632.

Borcard D & Legendre P, 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling*, 153:51-68.

Di Minin E & Griffiths RA, 2011. Viability analysis of a threatened amphibian population: modelling the past, present and future. *Ecography*, 34:162-169.

Diniz-Filho JAF *et al.*, 2012. Spatial autocorrelation analysis allows disentangling the balance between neutral and niche processes in metacommunities. *Oikos*, 121:201-210.

Duellman WE, 1988. Patterns of species diversity in anuran amphibians in the American tropics. *Annals of the Missouri Botanical Garden*, 75:79-104.

Ernst R & Rödel M, 2006. Community assembly and structure of tropical leaf-litter anurans. *Ecotropica*, 12:113-129.

Ferrier S *et al.*, 2007. Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Diversity and Distributions*, 13:252-264.

Giaretta AA *et al.*, 1999. Diversity and abundance of litter frogs in a montane forest of southeastern brazil: seasonal and altitudinal changes. *Biotropica*, 31:669-674.

Indermaur L *et al.*, 2010. Differential response to abiotic conditions and predation risk rather than competition avoidance determine breeding site selection by anurans. *Ecography*, 33:887-895.

Jones MM *et al.*, 2006. Effects of mesoscale environmental heterogeneity and dispersal limitation on floristic variation in rain forest ferns. *Journal of Ecology*, 94:181-195.

Landeiro VL *et al.*, 2012. How far can we go in simplifying biomonitoring assessments? An integrated analysis of taxonomic surrogacy, taxonomic sufficiency and numerical resolution in a megadiverse region. *Ecological Indicators*, 23:366-373.

Landeiro VL & Magnusson WE, 2011. The geometry of spatial analyses: implications for conservation biologists. *Natureza & Conservação*, 9:7-20.

Lewis SL *et al.*, 2011. The 2010 Amazon drought. *Science*, 331(6017):554.

Loyola RD *et al.*, 2008. Hung out to dry: choice of priority ecoregions for conserving threatened neotropical anurans depends on life-history traits. *PloS ONE*, 3(5):e2120.

Menin M *et al.,* 2007. Topographic and edaphic effects on the distribution of terrestrially reproducing anurans in central Amazonia: mesoscale spatial patterns. *Journal of Tropical Ecology*, 23:539-547.

Menin M, Waldez F & Lima AP, 2011. Effects of environmental and spatial factors on the distribution of anuran species with aquatic reproduction in central Amazonia. *Herpetological Journal*, 21:255-261.

Peres-Neto PR & Legendre P, 2010. Estimating and controlling for spatial structure in the study of ecological communities. *Global Ecology and Biogeography*, 19:174-184.

Rosindell J, Hubbell SP & Etienne RS, 2011. The unified neutral theory of biodiversity and biogeography at age ten. *Trends in Ecology and Evolution*, 26:340-348.

Siqueira T *et al.*, 2012. A metacommunity framework for enhancing the effectiveness of biological monitoring strategies. *PLoS ONE*, 7:e43626.

Van der Gucht K *et al.*, 2007. The power of species sorting: local factors drive bacterial community composition over a wide range of spatial scales. *Proceedings of the National Academy of Sciences of the United States of America*, 104:20404-20409.

Vonesh JR, 2001. Patterns of richness and abundance in a tropical African leaf-litter herpetofauna. *Biotropica*, 33:502-510.

Zimmerman BL & Bierregaard RO, 1986. Relevance of the equilibrium theory of island biogeography and species-area relations to conservation with a case from Amazonia. *Journal of Biogeography*, 13:133-143.