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

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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*

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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

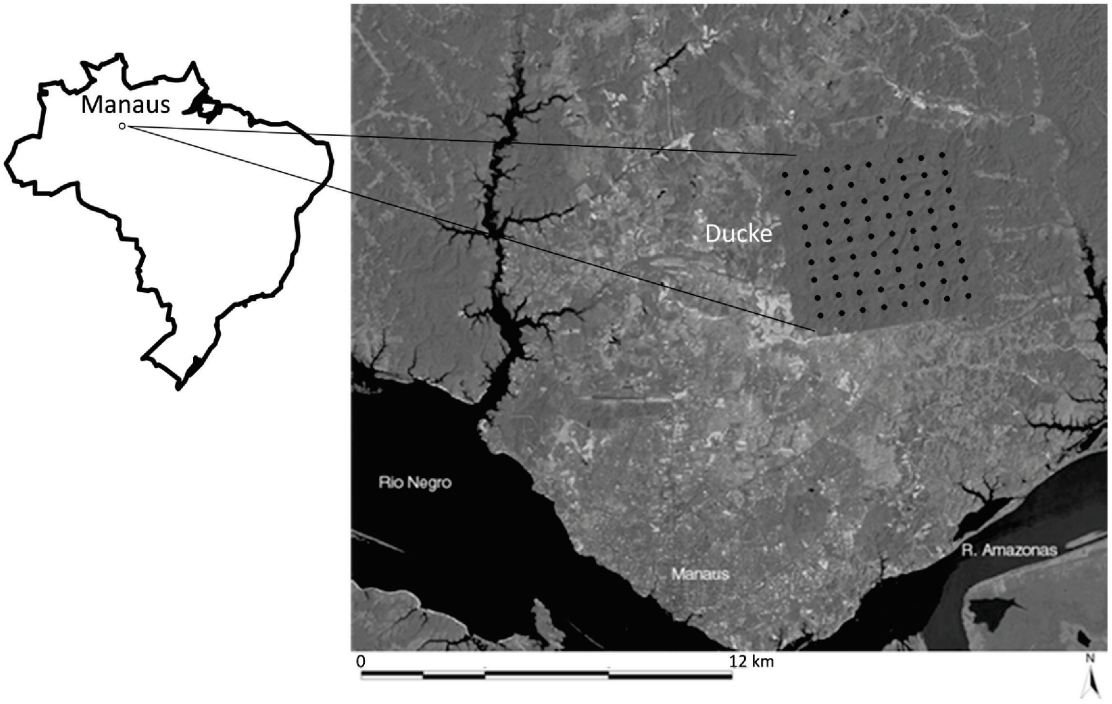

Fig. 1 – Location of Ducke Reserve, adjacent to the city of Manaus in the Brazilian Amazon. Points indicate 1 km-equidistant sample plots.