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Functional traits explain amphibian distribution

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Abstract

Aim: Species distributions are one of the most important ways to understand how communities interact through macroecological relationships. The functional abilities of a species, such as its plasticity in various environments, can determine its distribution and beta diversity patterns. In this study, we evaluate how functional traits influence the distribution of amphibians, and hypothesize which functional traits explain the current pattern of amphibian species composition in the Atlantic Forest.

Location: Atlantic Forest, Brazil.

Methods: Using potential distributions of Brazilian Atlantic Forest of amphibian species, we analysed the relative importance of abiotic factors and species functional traits in explaining species richness, endemism (with permutation multivariate analysis), and beta diversity components (i.e. total, turnover and nestedness dissimilarities).

Results: Environmental variables explained 59.5% of species richness, whereas functional traits explained 15.8% of species distribution for Anuran and 88.8% for Gymnophiona. Body size had the strongest correlation with the species distribution. Results of nestedness dissimilarities showed that species with medium to large body size, and species that are adapted to living in open areas tended to disperse from west to east direction. Current forest changes directly affected beta diversity patterns (i.e. most species adapted to novel environments increased their ranges). Beta diversity partitioning between humid and dry forests showed decreased nestedness and increased turnover by increasing altitude in the southeastern region of the Atlantic Forest.

Main conclusions: Our study shows that functional traits directly influence the ability of the species to disperse. With the alterations of the natural environment, species more apt to these alterations have dispersed or increased their distribution, which consequently changes community structure. As result, there is nested species distribution patterns and homogenization of amphibian species composition throughout the Brazilian Atlantic Forest.

KEYWORDS

Anura, beta diversity partitioning, conservation, functional abilities, Gymnophiona, spatial distribution

INTRODUCTION

Distribution patterns, dispersion processes, and permanence of species are some of the most studied topics by ecologists and biogeographers. The distribution of organisms is the basis of ecological studies and can be determined by biotic and abiotic factors (Hutchinson, 1957; Soberón, 2007). For example, current patterns of species distributions are linked to historical and contemporary dispersal, which is influenced by species characteristics (Ricklefs, 1987; Oberdorff et al., 1997; Svenning & Skov, 2007; Carnaval & Moritz, 2008; Carnaval et al., 2009; Baselga et al., 2012; Silva et al., 2014). On the other hand, habitat characteristics influence the spatial and temporal distributions of species (Hawkins, 2001; Ferreira et al., 2016; Figueiredo et al., 2019). Historical events can promote favourable environments for organisms, generating specializations, endemic species, high species richness and high phylogenetic and functional diversity (Pfrender et al., 1998; Batalha-Filho et al., 2013; Campos et al., 2017). Environmental variations generate habitat diversity, with different species assemblages determined by species dispersion capacity reflecting in the beta diversity patterns (Arnan et al., 2015). In the context, historical dispersal can be understood using environmental data of the localities at which species have been recorded and the geographical boundaries that restrict them (Gaston, 1991).

Because ectothermic species are largely limited by climatic zones (Pfrender et al., 1998), both dispersal limitation and climate variation can be critical determinants of species ranges (Baselga et al., 2012). Further, the distribution of a species is often related to species characteristics, such as body size and local abundance (Brown & Maurer, 1989; Gaston, 1990; Lawton, 1993). For example, small ectothermic species can dehydrate faster than large species (MacLean, 1985), and many are prey to vertebrates and invertebrates (Toledo et al., 2007; Wells, 2007). Thus, ectotherms rely upon their morphological and physiological adaptations to succeed in surviving and dispersing. In this sense, understanding functional traits (Jimenez-ValVerde et al., 2015) may be key to understanding the potential distribution of the ectotherms (Díaz et al., 2007; Gómez-Rodrigues et al., 2015).

Geographical distributions of amphibians are strongly affected by the terrestrial and aquatic preferences of juveniles and adults, and their ability to disperse across the landscape (Patrick et al., 2008). Microclimate characteristics of forests and open areas can provide physiological and ecological constraints for many species because they influence forage, reproduction and survival (Huey, 1991). Such constraints strongly affect the causes and consequences of dispersal abilities as well as the nature of species interactions (McGill et al., 2006), including reproductive modes and antipredator mechanisms (Monkkonen & Reunanen, 1999; Fahrig, 2001; Ferreira et al., 2019). Given that short-term impacts of habitat loss increase with dispersal ability of amphibians (Homan et al., 2004), there is a critical need to investigate the spatial mismatches between the distribution of species and environmental changes under functional-traits approaches (Cushman, 2006; Berg et al., 2010). Forest isolation is a critical factor in biological community structure and fundamentally important in a habitat fragmentation context (Dixo et al., 2009). Understanding beta diversity patterns and evaluating their different compositions (i.e. turnover or nested) along a latitudinal and longitudinal gradient can be an important tool for understanding the dispersal processes of these species (Baselga, 2008, 2010).

Knowing that amphibians are dispersal limited due to their morphological, physiological and ecological characteristics (Richter-Boix et al., 2007), we evaluated the beta diversity of amphibians in the Atlantic Forest, while assessing their potential dispersal based on functional traits. In this context, species typical in open areas can benefit from the alteration of forests due to the increase of their habitat area; and smaller species should be more associated with areas with milder temperatures (e.g. areas of high altitude) due to lower water loss rate to the environment. In this study, we tested the hypothesis that functional traits explain the current pattern of amphibian species composition in the Atlantic Forest. Depending on the functional trait (e.g. body size and ecological specializations) the species may have more ability to disperse and increase its distribution.

MATERIALS AND METHODS

Study region

The Brazilian Atlantic Forest has a latitudinal range extending into both tropical and subtropical regions (Myers et al., 2000). The longitudinal range extends from the coast to 1000 km inland, and the altitudinal range extends from 0 to 2000 m a.s.l. (Cavarzere & Silveira, 2012). Originally, this biome covered around 150 million ha with a wide range of climatic belts and vegetation formations (Tabarelli et al., 2005; Ribeiro et al., 2009). Currently only about 12% of the original biome remains (Ribeiro et al., 2009). This biome occurs across 14 states from the south to the northeast of Brazil (Fig. 1). To test the hypothesis that functional traits explain the current pattern of amphibian species composition (see Appendix 1, Fig 1.1) and understand the pattern of beta diversity in each study sites, we analysed differences in species compositions (richness and endemism) and mapped out potential dispersal routes. We delimitated the study sites in relation to: i) geomorphological barriers (see Dominguez et al., 1987; Bittencourt et al., 2007); ii) abiotic barriers (Worldclim database; see below); iii) forest composition barriers (see Olson et al., 2001); iv) names based in political divisions; and v) size of area.

Given that each state has different environmental laws (e.g. IAP-Instituto Ambiental do Paraná- Paraná state, COTEC - ComissãoTécnico-Científica do Instituto Florestal, São Paulo state, INEMA - Instituto do Meio Ambiente e Recursos Hídricos, Bahia state), we used spatial data that allow different conservation strategies at local scales (i.e. environmental state policies). Two states have all of their territory included in determining the composition of species, RJ (Rio de Janeiro) and ES (Espírito Santo), due to their smaller sizes, similar forest composition and abiotic features. Four states have all of their territory separated into eastern and western sections, because they are large and have different forest composition (eastern rain forest, western seasonal forest): EPR (eastern Paraná),WPR (western Paraná), ESC (eastern Santa Catarina),WSC (western Santa Catarina), ERS (eastern Rio Grande do Sul),WRS (western Rio Grande do Sul); and the "SMGM" refers to four connected states in seasonal forests (includes western of São Paulo-S, north Mato Grosso do Sul-M, south Goiás -G and extreme south Minas Gerais - M);MS refers to the south-western Mato Grosso do Sul . The Pernambuco, Sergipe, Ceará, Paraíba and Rio Grande do Norte states were included in region N (Northeast), due to their smaller territories inside this biome, and similar forest composition and abiotic features. We also separated two states in regions north and south, due to their large territory, and different forest composition and abiotic features – SBA (south Bahia), NBA (north Bahia), SMG (south Minas Gerais) and NMG (north Minas Gerais). In total, we assessed 16 study sites (see Fig. 2).

Species distribution data

We included species occurrence records available through the Global Biodiversity Information Facility (GBIF: http://www.gbif.org), and added range maps of each species from the IUCN Red List of Threatened Species (IUCN, 2017: http://www.iucnredlist.org/technical-documents/spatial-data). In addition, we conducted acoustic and visual nocturnal/diurnal amphibian survey (Crump & Scott Jr., 1994; Zimmerman, 1994) in 11 Protected Areas (PAs), from the southern to the northeastern Brazil (see Appendix 1, Fig. 1.2). We followed Frost (2019) for the amphibian nomenclature with exception of the species synonymized as *Allobates olfersioides* which we consider to be distinct species (*A. olfersioides*, *A. alagoanus* and *A. capixaba* see Forti et al., 2017).

We used ArcGIS 10.1 software (ESRI, 2011) to build presence/absence matrices from the species distribution data by superimposing a grid system with cells of 0.1 latitude/longitude degrees, creating a network with 10,359 grid cells. We used the "Spatial Join" ArcGIS toolbox to transform species' spatial occurrences in matrices, matching rows from the join features to the target features based on their relative spatial locations. Then, we combined vector files based on expert knowledge of the species' ranges and forest remnant polygons into an overall coverage for species distribution modelling. We only considered spatial occurrences by those species where the distribution data intersected at least a grid cell. We used forest remnant data to meet the habitat patch requirements based on visual interpretation at a scale of 1:50,000, delimiting more than 260,000 forest remnants with a minimum mapping area of 0.3 km^2. Therefore, we considered a species present in a cell if its spatial range intersected more than 0.3 km^2. We also used the "Count Overlapping Polygons" ArcGIS toolbox to