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Functional traits explain amphibian distribution in the Brazilian Atlantic Forest

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43

44 **Abstract**

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

51 **Location:** Atlantic Forest, Brazil.

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

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

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

71

72 **KEYWORDS**

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

75

76 INTRODUCTION

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

94 Because ectothermic species are largely limited by climatic zones (Pfrender et
95 al., 1998), both dispersal limitation and climate variation can be critical determinants of
96 species ranges (Baselga et al., 2012). Further, the distribution of a species is often
97 related to species characteristics, such as body size and local abundance (Brown &
98 Maurer, 1989; Gaston, 1990; Lawton, 1993). For example, small ectothermic species
99 can dehydrate faster than large species (MacLean, 1985), and many are prey to
100 vertebrates and invertebrates (Toledo et al., 2007; Wells, 2007). Thus, ectotherms rely
101 upon their morphological and physiological adaptations to succeed in surviving and
102 dispersing. In this sense, understanding functional traits (Jimenez-Valverde et al., 2015)
103 may be key to understanding the potential distribution of the ectotherms (Díaz et al.,
104 2007; Gómez-Rodrigues et al., 2015).

105 Geographical distributions of amphibians are strongly affected by the terrestrial
106 and aquatic preferences of juveniles and adults, and their ability to disperse across the
107 landscape (Patrick et al., 2008). Microclimate characteristics of forests and open areas
108 can provide physiological and ecological constraints for many species because they
109 influence forage, reproduction and survival (Huey, 1991). Such constraints strongly
110 affect the causes and consequences of dispersal abilities as well as the nature of species
111 interactions (McGill et al., 2006), including reproductive modes and antipredator
112 mechanisms (Monkkonen & Reunanen, 1999; Fahrig, 2001; Ferreira et al., 2019).
113 Given that short-term impacts of habitat loss increase with dispersal ability of

114 amphibians (Homan et al., 2004), there is a critical need to investigate the spatial
115 mismatches between the distribution of species and environmental changes under
116 functional-traits approaches (Cushman, 2006; Berg et al., 2010). Forest isolation is a
117 critical factor in biological community structure and fundamentally important in a
118 habitat fragmentation context (Dixo et al., 2009). Understanding beta diversity patterns
119 and evaluating their different compositions (i.e. turnover or nested) along a latitudinal
120 and longitudinal gradient can be an important tool for understanding the dispersal
121 processes of these species (Baselga, 2008, 2010).

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

133

134 **MATERIALS AND METHODS**

135 **Study region**

136 The Brazilian Atlantic Forest has a latitudinal range extending into both tropical and
137 subtropical regions (Myers et al., 2000). The longitudinal range extends from the coast
138 to 1000 km inland, and the altitudinal range extends from 0 to 2000 m a.s.l. (Cavarzere
139 & Silveira, 2012). Originally, this biome covered around 150 million ha with a wide
140 range of climatic belts and vegetation formations (Tabarelli et al., 2005; Ribeiro et al.,
141 2009). Currently only about 12% of the original biome remains (Ribeiro et al., 2009).
142 This biome occurs across 14 states from the south to the northeast of Brazil (Fig. 1). To
143 test the hypothesis that functional traits explain the current pattern of amphibian species
144 composition (see Appendix 1, Fig 1.1) and understand the pattern of beta diversity in
145 each study sites, we analysed differences in species compositions (richness and
146 endemism) and mapped out potential dispersal routes. We delimited the study sites in
147 relation to: i) geomorphological barriers (see Dominguez et al., 1987; Bittencourt et al.,
148 2007); ii) abiotic barriers (Worldclim database; see below); iii) forest composition
149 barriers (see Olson et al., 2001); iv) names based in political divisions; and v) size of
150 area.

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

171

172 **Species distribution data**

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

183 We used ArcGIS 10.1 software (ESRI, 2011) to build presence/absence matrices
 184 from the species distribution data by superimposing a grid system with cells of 0.1
 185 latitude/longitude degrees, creating a network with 10,359 grid cells. We used the
 186 “Spatial Join” ArcGIS toolbox to transform species' spatial occurrences in matrices,
 187 matching rows from the join features to the target features based on their relative spatial
 188 locations. Then, we combined vector files based on expert knowledge of the species'

189 ranges and forest remnant polygons into an overall coverage for species distribution
190 modelling. We only considered spatial occurrences by those species where the
191 distribution data intersected at least a grid cell. We used forest remnant data to meet the
192 habitat patch requirements based on visual interpretation at a scale of 1:50,000,
193 delimiting more than 260,000 forest remnants with a minimum mapping area of 0.3
194 km². Therefore, we considered a species present in a cell if its spatial range intersected
195 more than 0.3 km². We also used the “Count Overlapping Polygons” ArcGIS toolbox to