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Functional and Phylogenetic Diversity of Amphibians in the Brazilian Atlantic Forest: Implications for a Systematic Conservation Planning

Felipe Siqueira Campos

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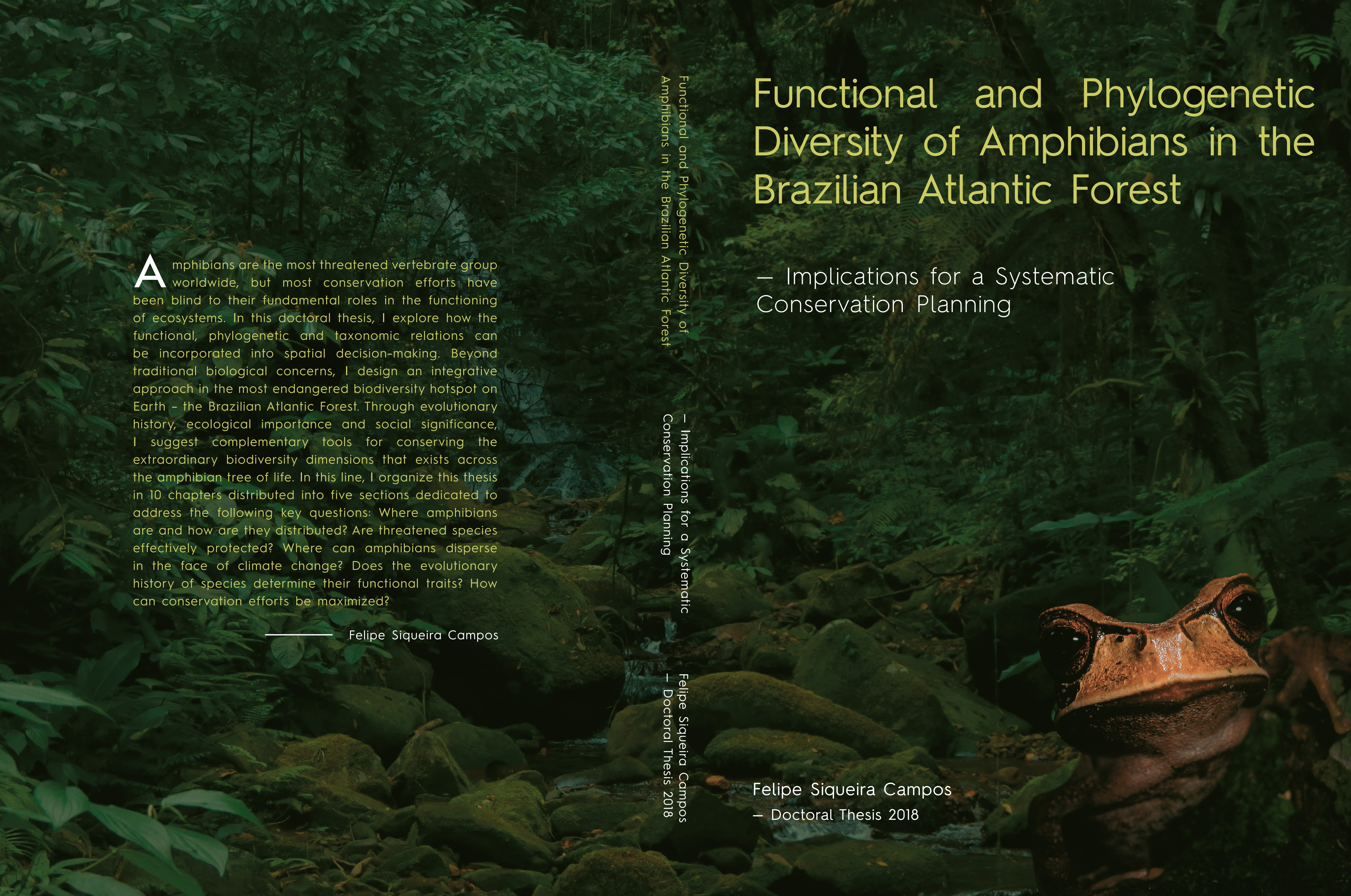

Amphibians are the most threatened vertebrate group worldwide, but most conservation efforts have been blind to their fundamental roles in the functioning of ecosystems. In this doctoral thesis, I explore how the functional, phylogenetic and taxonomic relations can be incorporated into spatial decision-making. Beyond traditional biological concerns, I design an integrative approach in the most endangered biodiversity hotspot on Earth – the Brazilian Atlantic Forest. Through evolutionary history, ecological importance and social significance, I suggest complementary tools for conserving the extraordinary biodiversity dimensions that exists across the amphibian tree of life. In this line, I organize this thesis in 10 chapters distributed into five sections dedicated to address the following key questions: Where amphibians are and how are they distributed? Are threatened species effectively protected? Where can amphibians disperse in the face of climate change? Does the evolutionary history of species determine their functional traits? How can conservation efforts be maximized?

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— Implications for a Systematic
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Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals
Programa de Doctorat en Biodiversitat

Functional and Phylogenetic Diversity of Amphibians in the Brazilian Atlantic Forest

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Implications for a Systematic Conservation Planning

Memoria presentada por **Felipe Siqueira Campos**
para obtener el grado de **Doctor** por la
Universitat de Barcelona

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Dr. Gustavo A. Llorente

El codirector de tesis:
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"Expedição científica é feita na mais rigorosa rotina... se eu ficar até duas da manhã no brejo, no dia seguinte acordo mais tarde. Se num dia estiver chovendo, não saio, fico na rede. Uma vez por semana paro de trabalhar. É preciso descansar, tomar uma cerveja..."

Paulo Emílio Vanzolini,
Brazilian Scientist, Herpetologist, PhD in Zoology at
Harvard, Emeritus Professor at USP, Bohemian,
and Samba Composer with more than 150
scientific papers (1924–2013)

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Abstract

ABSTRACT

Biodiversity patterns are results of ecological and evolutionary processes. Understanding the forces shaping biodiversity patterns help to predict the responses of ecosystems to environmental change. Considering the role of amphibian species in the functioning of ecosystems, we explored how their functional, phylogenetic and taxonomic relations can be incorporated into spatial decision-making in the Brazilian Atlantic Forest. We used these considerations for developing an integrative strategy based on species dispersal patterns, threats and conservation status, susceptibility to climate change, functional trait evolution and cost-effective conservation. In this line, we organized this thesis in 10 chapters distributed into five sections. We used different dimensions of the amphibians' ecological niches regarding morphology, life history, and behaviour. Our findings highlighted that functional trait-based approaches can be efficient strategies for conserving species in endangered ecosystems. Atlantic Forest reserves are failing to protect threatened species, and anticipated climate change can also be threatening the currently protected species. Therefore, we introduced new priorities for landscape assessments using ecological connectivity under current and future conditions. In the near future, most species can become threatened and tend to disperse towards areas with milder temperatures at high altitudes/latitudes, reducing their geographical ranges. By framing evolutionary ecology into conservation science, we revealed that phylogenetic metrics can be relevant tools for functional landscape planning. Using evolutionary history of functional traits, we also determined the species adaptation across different taxonomic lineages. In addition, under a complementarity-based analysis, we showed a practical suggestion to represent taxonomic indicator groups and estimates of land values. We designed an innovative assessment strategy, showing that prioritization models focused on different dimensions of biodiversity can incorporate cost-benefit relationships through payment for ecosystem services schemes. From theory to practice, our study suggests an eco-evolutionary framework regarding the usefulness of amphibian conservation from regional to global scales.

Keywords: spatial distribution, threatened species, climate change, evolutionary ecology, biodiversity conservation.

Spanish Abstract

SPANISH ABSTRACT (RESUMEN)

Los patrones de biodiversidad son resultado de procesos ecológicos y evolutivos. Comprender las fuerzas que determinan estos patrones ayuda a predecir la respuesta de los ecosistemas al cambio ambiental. Considerando el papel de las especies de anfibios en el funcionamiento de los ecosistemas, exploramos cómo sus relaciones funcionales, filogenéticas y taxonómicas pueden ser incorporadas en la toma de decisiones espaciales en el Bosque Atlántico brasileño. Utilizamos estas consideraciones para desarrollar una estrategia basada en patrones de dispersión de especies, amenazas y estado de conservación, susceptibilidad al cambio climático, evolución de rasgos funcionales y conservación rentable. En esta línea, organizamos esta tesis en 10 capítulos distribuidos en cinco secciones. Según diferentes dimensiones ecológicas basadas en morfología, ciclo de vida y comportamiento de anfibios, mostramos que el uso de los rasgos funcionales puede ser eficiente para la conservación de especies en ecosistemas en peligro de extinción. Las reservas del Bosque Atlántico no son suficientes para sus especies amenazadas, y las especies actualmente protegidas sufren efectos del cambio climático. Por lo tanto, proponemos prioridades de conservación usando conectividad ecológica para condiciones actuales y futuras. En un futuro próximo, la mayoría de las especies pueden verse amenazadas y tienden a dispersarse hacia áreas con temperaturas más suaves, a altitudes y latitudes elevadas, reduciendo sus rangos geográficos. Empleando la ecología evolutiva en la conservación, revelamos que métricas filogenéticas pueden ser herramientas relevantes para la planificación funcional del paisaje. Según la historia evolutiva de los rasgos funcionales, determinamos la adaptación de las especies en diferentes linajes taxonómicos. Además, bajo un análisis de complementariedad, representamos grupos taxonómicos indicadores y valores economicos de la tierra. Diseñamos modelos de priorización centrados en diferentes dimensiones de la biodiversidad, incorporando relaciones de coste-beneficio a través de esquemas de pago por servicios ecosistémicos. De la teoría a la práctica, nuestro estudio sugiere un marco eco-evolutivo con respecto a la utilidad de la conservación de anfibios desde escalas regionales a globales.

Palabras clave: distribución espacial, especies amenazadas, cambio climático, ecología evolutiva, conservación de la biodiversidad.

General Introduction

GENERAL INTRODUCTION

An integrative biodiversity science

The role of biodiversity in the functioning of ecosystems is under research for three decades. The term biodiversity has been exponentially used since 1988, when it was first published and widely defined as the "diversity of life on Earth" (Wilson 1988). Since then, a central question has been to determine how biodiversity patterns can influence ecosystem stability (Loreau et al., 2001; Hooper et al., 2005; Naeem et al., 2012). The key strategy to address this issue is assessing the relationships between functional and phylogenetic biodiversity components (Cadotte et al., 2009; Gravel et al., 2011). Understanding the associations between ecological similarity and phylogenetic relatedness among species helps to formulate hypothesis about evolutionary changes on functional ecology (Hof et al., 2010).

Several studies have focused on spatial prioritization to represent species richness by taxonomic diversity (TD), while ignoring other biodiversity components, such as functional diversity (FD) and phylogenetic diversity (PD) (Devictor et al., 2010). Functional diversity (FD) is a biodiversity dimension that represents the extent of the functional differences among species based on the distinction of their morphological, physiological and ecological traits (Petchey & Gaston, 2006). Many FD indices have been published and the lack of consensus about what indices quantify, how redundant they are and which ones are recommended, get an important concern on this matter. In this context, Petchey & Gaston's FD index is a high annalistic power to detect assembly rules, particularly for assemblages represented by presence/absence matrices with species richness levels higher than 30 species (Petchey & Gaston, 2006; Mouchet et al., 2010). In an extent overview on the FD measures, Mouchet et al. (2010) suggested that the use of the Petchey & Gaston's FD index associated with null models has shown to be a measure of functional diversity that best relates to community functioning and ecosystem processes. The values provided by such null models are more sensitive to preserving both site diversity and species frequency of occurrence while randomizing the pairs of species/sites, which ensure that patterns of trait assembly do not simply reflect differential occurrence of species (Ackerly et al., 2006; Swenson, 2014). Although observed and null FD metrics indicate very similar responses (Mouchet et al., 2010; Swenson, 2014), the values generated by these metrics do not necessarily represent redundant information. Observed FD is highly correlated with species richness, whereas its null model is totally independent of the species richness of an assemblage (Swenson et al., 2014), which provides expected values at different species richness levels (Mouchet et al., 2010), addressing feedbacks among biodiversity changes and ecosystem functioning.

Phylogenetic diversity (PD) provides additional values to theoretical and applied ecology by distinguishing species according to their evolutionary histories (Schweiger et al., 2008), reflecting the time and mode of divergence across the tree of life (Webb et al., 2002). Evolutionary ecology was introduced by Brooks (1985) that incorporated a "tree thinking" into ecology. It consisted in the analysis of interspecific relationships and species dispersal with a phylogenetic perspective. Faith (1992) and Clarke & Warwick (1998) further developed alternative measures of biodiversity that considered phylogenies or taxonomic hierarchies. In this context, Faith's PD index has been widely used since then to inform conservation practices (Vamosi et al., 2009). The Faith's PD index (Faith, 1992) comprises the sum of the lengths of the branches from a given phylogenetic tree of species. Measuring the Faith's PD index in species assemblages is considered as a hopeful approach to explain the role of species interactions and biogeographic histories in community structure (Webb et al., 2002).

The focus on both functional and phylogenetic diversity of a community can improve the understanding of the consequences of biodiversity loss in an age of extinction (Figure 1). The search for the environmental factors associated with the species richness, as well as the variations in space and time, has been one of the main research topics among ecological scientists (Begon et al., 2007). Ecosystem functioning and stability are often correlated with evolutionary processes, producing several implications for ecological and human wellbeing on short time scales (Alberti, 2015). Understanding how these processes drive biological communities under multiple disturbances is a core challenge in ecology, evolution and conservation science. Ecosystems worldwide are quickly losing taxonomic, phylogenetic, and functional diversity due to the human appropriation of natural resources, habitat loss and climate change (Naeem et al., 2012). However, to describe how environmental actions can protect multiple dimensions of biodiversity, comparative methods on the consequences of species extinction in relation to ecological and evolutionary traits have yet to be applied (Joseph et al., 2009).

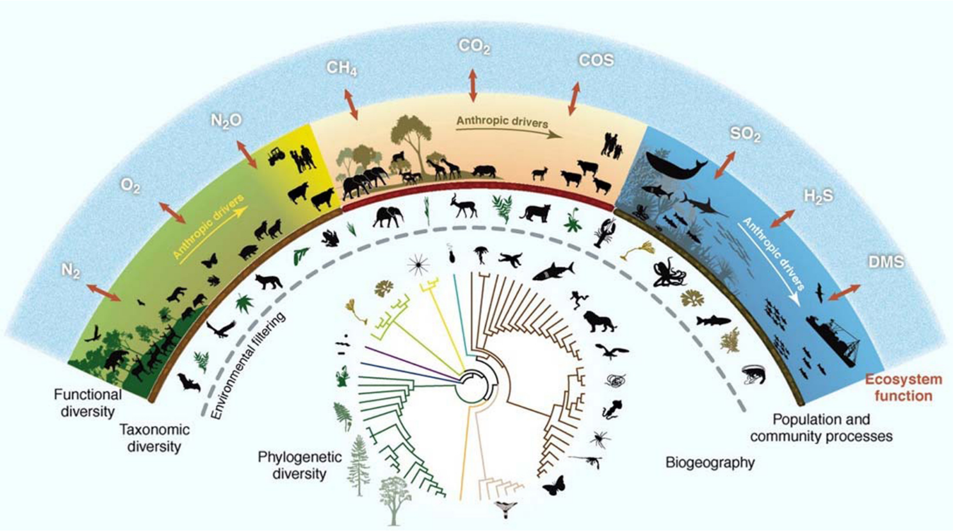

Figure 1. Biodiversity and ecosystem functioning in an age of extinction. Functional, phylogenetic and taxonomic diversity, biogeography, population and community processes, ecosystem functions and environmental filtering in a synergetic contribution to different dimensions of biodiversity that characterize the biota of the ecosystems. Modified from Naeem et al. (2012).

Conversations in conservation

The establishment of priority actions for the conservation of biodiversity has been one of the most important aspects in relation to the biological conservation (Cabeza & Moilanen, 2001). Considering the increasing loss of species and the availability of human and financial resources, several criteria should be used to establish these conservation priorities (Diniz-Filho et al., 2008). For this, the knowledge about species distribution ranges is of fundamental importance (Tognelli, 2005; Whittaker et al., 2005; Bini et al., 2006). To understand patterns of spatial and temporal distributions in biological communities it is necessary to investigate the characteristics of the environments in which they are found (Hawkins, 2001). Even in highly fragmented landscapes, we still have time to save critical habitats through systematic conservation planning (e.g., Margules & Pressey, 2000; Margules & Sarkar, 2007; Loyola et al., 2008; Sarkar & Illoldi-Rangel, 2010).

In almost all circumstances, biodiversity conservation is not the only ethically relevant use of a landscape. Other potential uses include socio-economic production, agriculture, livestock and mineral resource extraction. Human interests are fundamentally relevant when areas prioritized by conservationists for natural values are also linked to the well-being of economically deprived groups, as is the case of the most biologically important areas (Sarkar & Illoldi-Rangel, 2010). Systematic conservation planning is therefore a high-benefit strategy in which social, economic and political requirements can use scientific predictions (Margules & Pressey, 2000). However, this strategy depends both on translating science into recommendations, and on the application of these recommendations in conservation policy (Webb & Raffaelli, 2008). In this context, systematic conservation planning can be separated into six stages (Box 1).

Box 1: Stages in Systematic Conservation Planning

1. Compile data on the biodiversity of the planning region
2. Identify conservation goals for the planning region
3. Review of the existing conservation areas
4. Select additional conservation areas
5. Implement conservation actions
6. Management and monitoring

An effective systematic conservation planning requires detailed prior knowledge of the species distribution to be evaluated. Current research has yet not tackled the necessity to understand the most effective strategies for benefit-targeting conservation (Purvis & Hector, 2000; Carbayo & Marques, 2011). A key question is how much it costs and which are the targets that should be selected in conservation strategies. Every ecosystem features key functions in primary production and nutrient cycling, which give rise to ecosystem services that improve human well-being, such as the provisioning of clean water, fertile soils, timber and food (Cardinale et al., 2006; Daily & Matson, 2008). Ecosystem functions and services are shaped by their biodiversity, which allows an intuitive perspective that should be linked to human well-being (Naeem et al., 2016). This context suggests the need to develop conservation plans that optimally balance economic and ecological cost (Petersen et al., 2016). Therefore, effective conservation plans should consider the maintenance of ecosystem functioning as a justification for long-term investments (Gering et al., 2003; Brooks et al., 2006; Lee & Jetz, 2008).

Threats to biodiversity: amphibians as conservation targets

Although generally unseen, amphibians are the most abundant land vertebrates in tropical humid forests (Stebbins & Cohen, 1995). Currently, they are globally distributed in over 6,000 frogs (Anura), 700 salamanders (Caudata) and 200 caecilians (Gymnophiona) (Frost, 2018). Amphibians play a fundamental role in the functioning of ecosystems, from soil bioturbation and nutrient cycling to pest control and ecosystem engineering (Hocking & Babbitt, 2014). Their vast ecological contributions can affect aquatic and terrestrial ecosystems, as well as the flux between them (Whiles et al., 2006). Some studies suggest that the loss of amphibians from stream ecosystems can alter primary production, algal community structure and faunal food chains – from aquatic insects up to riparian predators (Whiles et al., 2006; Hocking & Babbitt, 2014; Meredith et al., 2016). Predator-prey interactions such as antipredator mechanisms also render a strong evolutionary selection in amphibian functional traits (Wells, 2007). Functional differences between primary consumers tadpoles and insectivorous adults suggest that the loss of a single amphibian species is equal to losing several different species (Whiles et al., 2006). Threats to amphibian biodiversity have been frequently cited due to their permeable skin, high rates of contaminant bioaccumulation, climate-sensitive breeding cycles, and high humidity dependence (DeGarady & Halbrook, 2006; Lebboroni et al., 2006; Hopkins, 2007).

More than 2,000 amphibian species are listed as threatened by extinction, to the extent that amphibians are the most threatened vertebrate group in the world (Stuart et al., 2004). Although many reductions and extinctions of amphibians have occurred due to the habitat loss (Stuart et al., 2004; Becker et al., 2007; Ferreira et al., 2016), some unidentified processes still threaten 48% of amphibian species around the world (Stuart et al., 2004). The intensity of these threats may be inversely related to the abundance or geographic range of the species (Schiesari et al., 2007), so that many cases associated with declining populations were recorded at long distances from the research institutes or in areas with little investment in science and technology (King, 2004). Amphibians are declining practically throughout the world, but the lack of long-term regional data hinders the identification of their possible causes, thus hampering the establishment of conservation efforts (Stuart et al., 2004; Nystrom et al., 2007) Furthermore, over the past three decades, the emergence of a pandemic lineage of chytrid fungus (*Batrachochytrium dendrobatidis*) has caused declines of amphibian species in North America, Central America, South America, Europe and Oceania (Bower et al., 2017). The level of threat to neotropical amphibians remain underestimated due to the lack of knowledge on approximately 30% of species, which are classified as "Data Deficient" – DD (Moraes et al., 2013). According to the Global Amphibian Assessment, this trend is occurring at a global level (IUCN et al., 2006; IUCN, 2017). Aside from these trends, wildlife disease is often an additional threat to species already exposed to habitat loss, pollution and climate change.

Climate change is also a widespread threat to global biodiversity (Thomas et al., 2004; Pereira et al., 2010) by continuously promoting changes in physiological and ecological processes that directly affect the distribution and persistence of species in an environment (Stenseth et al., 2002). Several studies are evaluating how climate changes affect individual performances (Huang et al., 2013; Holt & Jørgensen, 2015), demographic dynamics (Pomara et al., 2014), and species richness (Lemes & Loyola, 2013; Ferro et al., 2014). Predictive outcomes have included adaptation to novel conditions (Quintero & Wiens, 2013), shift, expansion or retraction of ranges (Ferro et al., 2014; Lemes et al., 2014), isolation to unaffected areas or climatic refuges (Puschendorf et al., 2009), and species extinctions (Thomas et al., 2004). Such effects account for the growing consensus incorporating climate change on conservation decisions (Araújo & Rahbek, 2007).

Environmental changes reducing amphibian distributions are leading some populations to decrease genetic diversity, increasing the risk of genetic drift and inbreeding (Becker et al., 2007; Dixo et al., 2009). These factors make species more vulnerable and susceptible to stochastic effects due to lower evolutionary potential (Holt et al., 2004). Other factors can be associated to declines of amphibians, such as increased ultraviolet-B radiation (Pounds et al., 2006), illegal trafficking in animals (Pistoni & Toledo, 2010), changes in environmental legislation (Toledo et al., 2010), and the introduction of invasive species (Kats & Ferrer, 2003). Environmental changes may not only alter communities at local scales, but can also alter the functional space by removing species with traits poorly adapted to the new environment, allowing colonization by better-adapted species (Mouillot et al., 2013). Therefore, the current species distribution patterns of amphibian biodiversity result from their functional and phylogenetic relationships (Pyron & Wiens, 2013), which display a strong latitudinal diversity gradient (Figure 2).

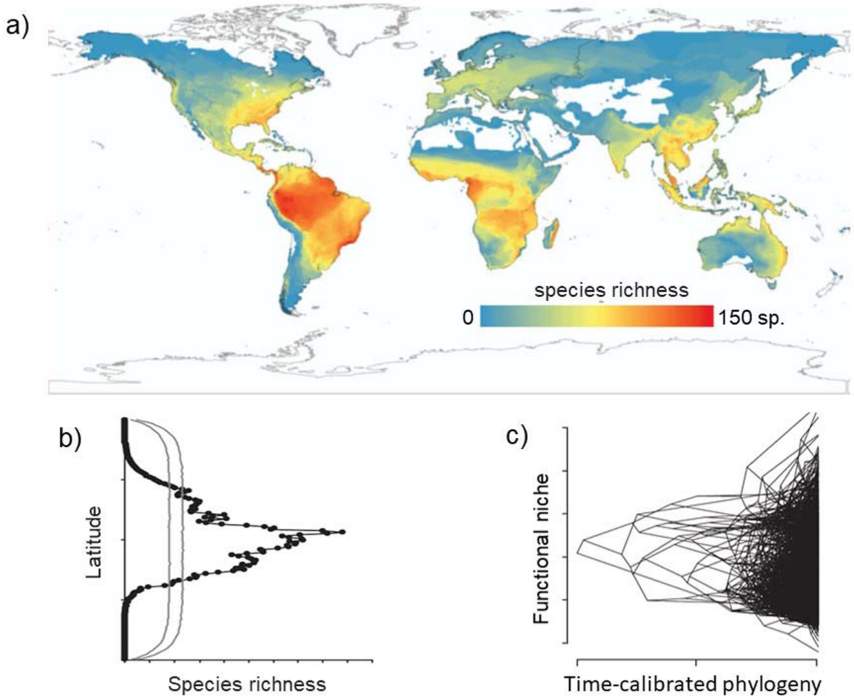

Figure 2. Global species richness patterns of 6117 amphibians (a); latitudinal species distribution under 95% confidence intervals (b); time-calibrated phylogeny of extant amphibian species compared to their functional niche (c). Modified from (Pyron & Wiens, 2013).

Amphibian research efforts in a megadiverse country

Brazil stands out globally as a continental megadiverse country, being considered one of the richest countries in biodiversity over the Earth (Mittermeier et al., 2005). The country presents a huge variety of ecosystems, which extends its potential to harbour different taxonomic groups (Lewinsohn & Prado, 2005). Brazil has three Wilderness Areas – Amazon, Caatinga and Pantanal (Mittermeier et al., 2003), and two Biodiversity Hotspots – Atlantic Forest and Cerrado (Myers et al., 2000; Mittermeier et al., 2005), which harbours approximately 14% of the world's known biota (Lewinsohn & Prado, 2005), being always in the forefront of global biodiversity issues. Brazil alone is responsible for the great majority (~ 75%) of new protected areas created since 2003 (Jenkins & Joppa, 2009), although policy-making efforts to promote sustainability research have not kept up with this (Pimm et al., 2010). This is even exacerbated by high disordered anthropic activities and landscape changing policies.

Compiling data about species distribution ranges is key to planning conservation actions (Hurlbert & Jetz, 2007), as shown by recent studies on Brazilian amphibian communities (e.g., Trindade-Filho et al., 2012; Verdade et al., 2012; Morais et al., 2013; Campos et al., 2017). The greatest diversity of amphibians in the world is recorded in Brazil, with 1.080 described species (Segalla et al., 2016), among which 37 are listed in the IUCN Red List of Threatened species, with 15 vulnerable, 9 endangered, 12 critically endangered, and one extinct (IUCN, 2017). Despite this, the knowledge generated about biogeography and taxonomy of Brazilian amphibians is still recent, because several species are often revalidated, and mainly because every year new species have been discovered (Silvano & Segalla, 2005; Toledo & Batista, 2012; Campos et al., 2014a).

Although the number of publications on amphibian conservation has increased in recent years, most conservation strategies for amphibian preservation are still directed at areas of low biodiversity and with non-threatened species (Brito, 2008). The increasing number of publications on amphibians from Brazil can be regarded as a result of the progressive increase in the number of researchers interested in Brazilian herpetology. In a comprehensive review on the Brazilian amphibian literature, Campos et al. (2014a), showed many differences in the allocation of research efforts for different research topics over the last decade. In this review, taxonomy and systematics were the main research topics covered by the authors considered (i.e., about 20% of the studies), indicating a progressive increase of articles related to the taxonomic reviews and descriptions of new species (Figure 3). This is also increasing attention to Brazilian amphibians conveyed by the number of published articles over the years 2001 and 2010, which presented 28 and 177 papers respectively (Campos et al., 2014a).

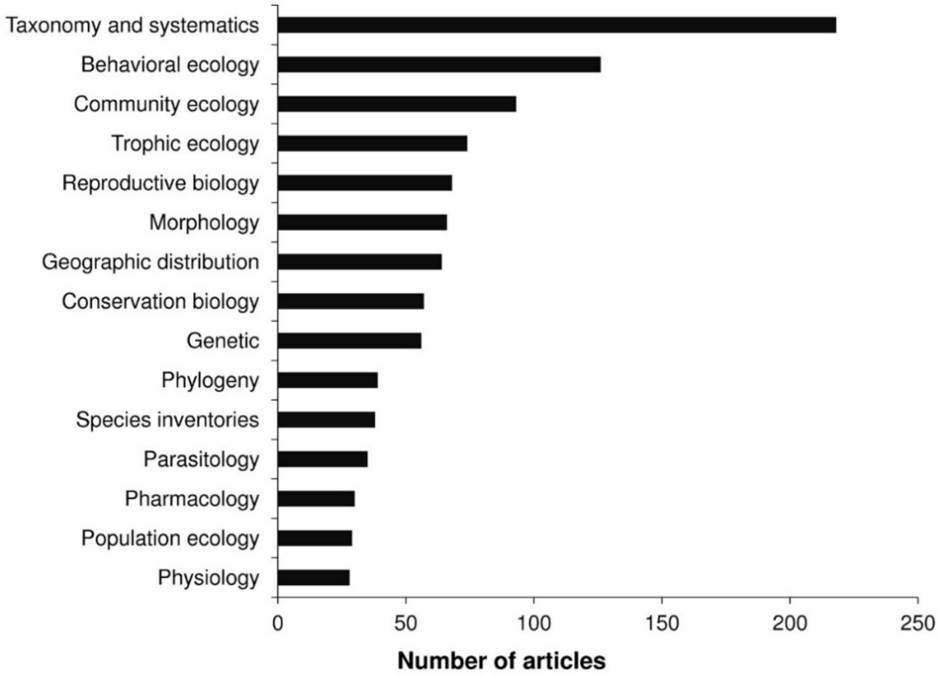

Figure 3. Total number of scientific papers published between 2001 and 2010 on amphibians from Brazil (N = 892) according to their respective research topics. Modified from Campos et al. (2014a).

About ten years after the publication of the first official list of Brazilian amphibians with 751 species (SBH, 2004), there has been a 36 % increase in listed amphibian species in the country (Campos & Solé, 2015). After some updates with descriptions of new species, new genetic allocations and other taxonomic changes, the Brazilian Herpetological Society (SBH) announced the occurrence of 1,080 amphibian species with confirmed records for the country (Segalla et al., 2016). Studies conducted on Brazilian amphibians between July 2004 and July 2014 added 275 new species, including 265 anurans, six caecilians and four salamanders (Campos & Solé, 2015). The updated number reflects a progressive increase in the number of active researchers in Brazilian herpetology, although this is still a largely unexplored field.

This high number of new amphibian species discovery is related to the growth of the local investments in research infrastructure in recent years. One measure of a nation's knowledge base is the output of Ph.D. students, which is directly associated with the growth of infrastructure investment. In this example, the science budget allocated in Brazil rose from US$575 million in 2002 to more than US$3.3 billion in 2010 (Massarani, 2013). Despite this, Brazil is one of the largest ecosystems in the world and many more species undoubtedly remain unknown to science. Therefore, more research efforts must be made to cover this topic. It is incumbent on policymakers, conservationists and scientists to continue to direct resources toward the research of amphibian diversity in Brazil, ensuring the protection of that biodiversity before it is lost.

The role of amphibian biodiversity in the Brazilian Atlantic Forest

Globally considered as one of the most threatened biodiversity hotspots on Earth (Myers et al., 2000), the Atlantic Forest biome originally covered an area around 1,500,000 km^2, of which only about 12% (~194,500 km^2) still remains in Brazil, Paraguay, and Argentina (Ribeiro et al., 2009), corresponding to approximately 100,000 km^2 of Brazilian forest remnants (Figure 4). The large fragments are distributed in hilly terrain, which hinder human occupation (Silva et al., 2007). Moreover, the different ranges of altitudinal and latitudinal gradients covered by these fragments have favored high levels of endemism and biodiversity (Ribeiro et al., 2009).

Amphibians are the most diverse group of vertebrates with high endemism in the Brazilian Atlantic Forest (Haddad et al., 2013). Despite having a rapid rate of habitat loss (Teixeira et al., 2009), which is one of the main risk factors for amphibian extinction (Stuart et al., 2004), the Atlantic Forest is considered the leader biome in amphibian diversity in Brazil, comprising ~90% endemics species and accounting for more than 50% of the total species richness of the country's amphibians (Conservation

International et al., 2000; Silvano & Segalla, 2005; Haddad et al., 2013). Their specific geographical characteristics and climatic conditions have likely contributed to the high species richness, including more than 543 recognized amphibian species and several more that still need to be described (Silva & Casteleti, 2003; Haddad et al., 2013). However, the high number of studies in the Atlantic Forest can be explained by the strong presence of amphibian researchers in the Brazilian southeastern region. This stands in contrast to what occurs in the Amazon, where information on the diversity of amphibians is fragmented and not readily available in the scientific literature (Azevedo-Ramos & Galatti, 2002).

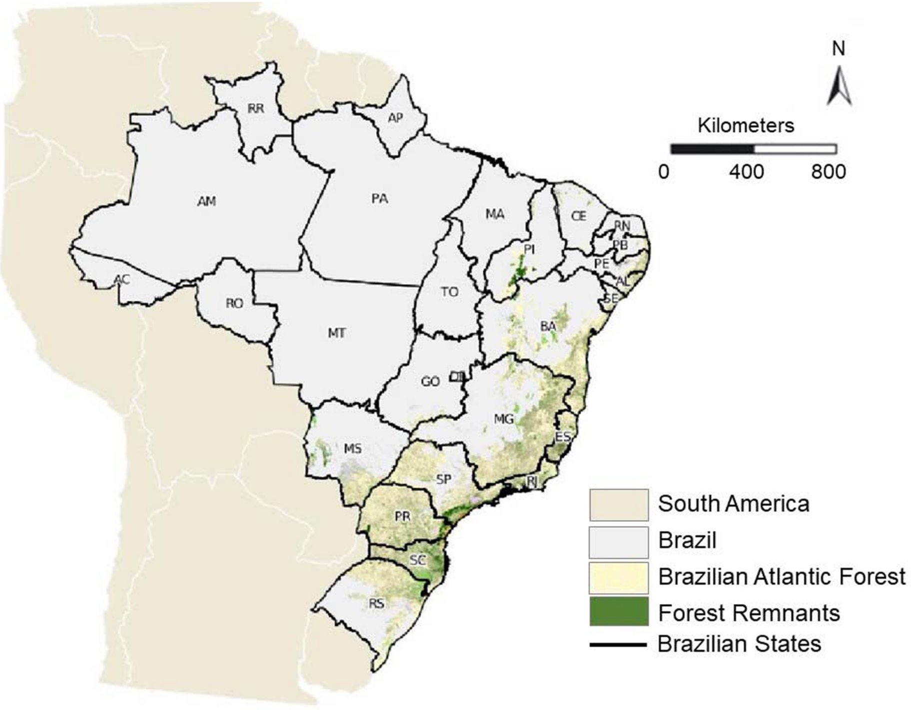

Figure 4. Distribution of the Brazilian Atlantic Forest remnants in South America. Modified from SOS Mata Atlântica & Instituto Nacional de Pesquisas Espaciais (2017).

The increased concern of researchers with the Brazilian amphibians in the last decade is reflected by published articles over the years 2001 and 2010, which presented 28 and 177 papers respectively (Campos et al., 2014a). This probably occurred due to amphibians having been widely related to environmental quality (Lebboroni et al., 2006; Sewell & Griffiths, 2009), which draws a special attention to then in conservation programs. Moreover, amphibians are important components of many types of ecosystems, playing a key role in the dynamics between predators and prey (Blaustein et al., 1994).

Amphibian taxonomic groups from small Atlantic Forest remnants also have been identified as potential biodiversity surrogates (Campos et al., 2014b). Despite the importance and usefulness of systematic research on the effectiveness of surrogates to guide conservation actions and decision-making processes, only a few studies have explicitly evaluated this aspect (e.g., Araújo et al., 2001; Manne & Williams, 2003; Bani et al., 2006; Lawler & White, 2008; Trindade-Filho & Loyola, 2011; Campos et al., 2014b). Bioindicator groups follow predictors of complementarity performance, such as variability between extents of occurrence, occupation of different ecoregions, variability of records of geographic distribution, and average body size in relation to the species pool considered in the analyses (Manne & Williams, 2003). In this context, the use of Atlantic Forest amphibians as indicator of biodiversity can be a powerful strategy to maximize the conservation value of small spatial scales (Campos et al., 2014b).

In the particular case of the Atlantic Forest, there is a need for a more efficient and systematic way to set ecological research priorities. Additional attention is also needed on the engagement of decision makers in understanding scientific studies. Such efforts can help applied ecologists to engage with the ethical and political implications of their research (Minteer & Collins, 2005). Political decision-making determines what species and how many of these will be able to survive in nature through the establishment of protected areas (Jenkins et al., 2015). The effectiveness of these selected sites in reaching conservation goals depends on how well the ecological diversity is represented in a given area (Dietz et al., 2015). However, amphibian conservation actions have been blind to biodiversity patterns in a cost-effective conservation policy (Campos et al., 2017). The selection criteria analysed must be complemented with social participation, which includes decision makers to promote and understand the socio-economic related issues. Therefore, defining spatial priorities for amphibian conservation at different levels is a key strategy for avoiding population declines and local extinction processes.

Aims, Objectives & Structure

AIMS, OBJECTIVES & STRUCTURE

Overall aim

Using amphibians as a conservation target, the aim of this thesis was to explore how the functional, phylogenetic and taxonomic relations can be incorporated into spatial decision-making in the Brazilian Atlantic Forest. To achieve this overall aim, we developed an integrative approach using species dispersal patterns (Part I), to assess threats and conservation status (Part II), which were needed to determine susceptibility to climate change (Part III), relating functional trait evolution processes (Part IV), and finishing with an innovative design based on cost-effective conservation strategies (Part V).

Specific objectives and thesis structure

We organized this thesis in 10 chapters presented as scientific papers, where each paper has its own introduction, materials and methods, results and discussion. We distributed these papers into five sections with their specific objectives dedicated to understanding the following:

Part I – Spatial distribution:

Where amphibians are and how are they distributed? In a world of big data, deep biodiversity-based knowledge leads to new questions beyond traditional research. However, the reliability of primary data remains hard to assess unless new species inventories are produced. Such spatial descriptive information is usually required as a starting point for any comprehensive biodiversity assessment, even on macroscales. Therefore, to complement the current amphibian dataset in the Atlantic Forest, we conducted fieldwork to provide distribution data and observed functional traits (**Chapter 1**). Using this updated database, we aimed to assess the relationship between amphibian dispersal abilities and environmental features, exploring how species' functional traits can influence spatial distribution, endemism rates and beta diversity patterns under different geographic conditions (**Chapter 2**).

Part II – Threatened species:

Are threatened species effectively protected? Global Red list categories or local threatened species lists are often designed to provide estimated extinction risks among species. Despite the reliability of these estimates, they should be used to inform decision-making processes and sampling effort gaps. In line with these gaps, the objective of this section was to assess the mismatches between protected areas chosen by decision-makers and threatened amphibian species. To understand the real extent of declining populations and the potential threats to these species, we provided two case studies, one focused at a macroecological scale represented by the entire Brazilian Atlantic Forest (**Chapter 3**), and the other focused on the northeastern Brazilian region (**Chapter 4**).

Part III – Climate change:

Where can amphibians disperse in the face of climate change? Considering the potential effects of global warming on amphibian distributions, the effectiveness of the Atlantic Forest remnants can be called into questions of climate change. To evaluate how changing climate might affect the protected network effectiveness, it is essential to develop ecological niche models, which help to anticipate the climate consequences at different spatial scales. Specifically, we aimed to explore the probability of the ecological connectivity of forest remnants and amphibian species distributions for current and future climate scenarios across the Central Corridor of the Atlantic Forest (**Chapter 5**). Under the hypothesis that high elevation areas can work as amphibian-climate refuges in the Atlantic Forest, we tested the effectiveness of modeling functional and phylogenetic diversity for present and future times, suggesting conservation status assessments (**Chapter 6**).

Part IV – Evolutionary ecology:

Does the evolutionary history of species determine their functional traits? Understanding the associations between ecological similarity and phylogenetic relatedness among species can be useful in formulating hypothesis about the impact of evolutionary changes on functional ecology. Given that amphibians have high adaptive plasticity and suffer strong environmental pressure, we aimed to evaluate the ancestral character states of amphibian functional traits and their evolutionary history in the Atlantic Forest, relating the functions that this taxonomic group plays within the ecosystems (**Chapter 7**). We know that ecological niches tend to be conserved when descendant species occur in similar geographical areas. However, we went beyond this to explore whether phylogenetically related species may exhibit different ecological functions. Assuming the defensive behaviour of amphibians as a deterministic functional trait, we expected a general phenotypic plasticity in response to predation risks. To address this assumption, we tested how the diversity of antipredator mechanisms can be associated with the functional traits that determine the amphibian dispersal processes (**Chapter 8**).

Part V – Biodiversity conservation:

How can conservation efforts be maximized? A conservation dilemma arises from the question of how much it costs and which are the biodiversity indicator groups that should be selected in systematic conservation planning with limited resources. Amphibians are a crucial group for the maintenance of ecosystem functioning, which renders them an excellent biodiversity surrogate in face of traditional landscape planning tools. In this line, we assessed the performance and consistence of taxonomic indicator groups for representing amphibian diversity patterns (**Chapter 9**). We developed innovative cost-effective models of conservation planning in the Brazilian Atlantic Forest, based on increasing the coverage of biodiversity with the lowest cost possible. To achieve sustainable development goals, we drafted a blueprint for linking functional, phylogenetic, and taxonomic diversity of amphibians into an economic framework of payment for ecosystem services (**Chapter 10**). This work has sought to move forward the knowledge on setting conservation priorities through evolutionary distinctiveness, ecological importance and social significance.

Supervisors' Report

SUPERVISORS' REPORT

Dr. Gustavo A. Llorente and Dr. Mirco Solé, supervisors of the doctoral thesis entitled: "Functional and Phylogenetic Diversity of Amphibians in the Brazilian Atlantic Forest: Implications for a Systematic Conservation Planning" certify that the dissertation presented here has been carried out by Felipe Siqueira Campos in its totality and grants him the right to defend his thesis in front of a scientific committee. The thesis is organized in 10 chapters presented as scientific papers (5 published and 5 under review).

As supervisors, we have participated in designing, guiding and correcting earlier drafts of the chapters and manuscripts written by the doctoral candidate. Published papers are of a sufficiently high scientific quality as assessed by the reviewers and editors in prestigious journals in the field of ecology, evolution and conservation. The scientific impact of each journal is based on 2017 data release, provided by Journal Citation Reports (JCR/Thomson Reuters) and SCImago Journal Rank (SJR/Scopus). Author contributions to each manuscript is detailed below:

- **Chapter 1:** Anurans from the mountain chain Serra do Mar: a critical area for amphibian conservation in the Atlantic Forest, Brazil.

F. S. Campos & R. Lourenço-de-Moraes (2017). Herpetology Notes, 10, 547–560. JCR: –, SJR: 0.28, Q3 (Animal Science and Zoology). FSC conceived the study and wrote the manuscript with contributions of RLM in the study design, data acquisition and scientific writing. Status: Published.

- **Chapter 2:** Explaining the dispersal of amphibians through functional traits.

R. Lourenço-de-Moraes, F. S. Campos, R. B. Ferreira, M. Solé, K. H. Beard & R. P. Bastos (2018). Diversity and Distributions. JCR: 4.39, SJR: 2.65, Q1 (Ecology, Evolution, Behavior and Systematics). RLM conceived the study and wrote the manuscript with contributions from all coauthors. FSC and RLM designed the analyses, collected the data, and created the figures. All authors discussed the results and edited the manuscript. Status: Under Review.

- **Chapter 3:** Protected areas network and conservation efforts concerning threatened amphibians in the Brazilian Atlantic Forest.

F. S. Campos, G. A. Llorente, L. Rincón, R. Lourenço-de-Moraes & M. Solé (2016). Web Ecology, 16, 9–12. JCR: 0.94, SJR: 0.35, Q3 (Ecology). FSC conceived the study and wrote the manuscript with contributions from all coauthors. FSC designed the analyses, collected the data, and created the figures. All authors discussed the results. Status: Published.

- **Chapter 4:** Threatened amphibians and their conservation status within the protected area network in northeastern Brazil.

F. S. Campos, D. Brito & M. Solé (2013). Journal of Herpetology, 47, 277–285. JCR: 0.91, SJR: 0.49, Q2 (Animal Science and Zoology). FSC conceived the study and wrote the manuscript with contributions of DB and MS. FSC designed the analyses, collected the data, and created the figures. All authors discussed the results and edited the manuscript. Status: Published.

- **Chapter 5:** Looking for network: ecological connectivity of forest amphibians under climate change.

F. S. Campos, R. Lourenço-de-Moraes, D. S. Ruas, C. V. Mira-Mendes, M. Solé, M. Franch & G. A. Llorente (2018). Journal for Nature Conservation. JCR: 1.65, SJR: 1.01, Q1 (Ecology). FSC conceived the study and wrote the manuscript with contributions from all coauthors. FSC, RLM and DSR designed the analyses and collected the data. FSC, DSR and MF created the figures. All authors discussed the results. MS and GL reviewed the manuscript. Status: Under Review.

- **Chapter 6:** Back to the future: Conserving functional and phylogenetic diversity in the amphibian-climate refuges.

R. Lourenço-de-Moraes, F. S. Campos, R. B. Ferreira, M. Solé & R. P. Bastos (2018). Biodiversity and Conservation. JCR: 2.26, SJR: 1.17, Q1 (Ecology).

RLM conceived the study and wrote the manuscript with contributions from all coauthors. FSC and RLM designed the analyses, collected the data, and created the figures. All authors discussed the results and edited the manuscript. Status: Under Review. Status: Under Review.

- **Chapter 7:** Functional trait evolution in amphibian phylogenetic relationships.

F. S. Campos, R. Lourenço-de-Moraes, A. Rudoy, G. A. Llorente & M. Solé (2018). Ecology and Evolution. JCR: 2.44, SJR: 1.58, Q1 (Ecology). FSC conceived the study and wrote the manuscript with contributions from all coauthors. FSC and RLM collected the data. FSC, RLM and AR designed the analyses. FSC created the figures. All authors discussed the results. GL and MS reviewed the manuscript. Status: Under Review.

- **Chapter 8:** Evolutionary history of antipredator mechanisms of amphibians.

R. Lourenço-de-Moraes, F. S. Campos, R. B. Ferreira, M. Solé & R. P. Bastos (2018). Animal Behaviour. JCR: 2.86, SJR: 1.66, Q1 (Animal Science and Zoology). RLM conceived the study and wrote the manuscript with contributions from all coauthors. FSC and RLM designed the analyses, collected the data, and created the figures. All authors discussed the results and edited the manuscript. Status: Under Review.

- **Chapter 9:** The efficiency of indicator groups for the conservation of amphibians in the Brazilian Atlantic Forest.

F. S. Campos, J. Trindade-Filho, D. Brito, G. A. Llorente & M. Solé (2014). Ecology and Evolution, 4, 2505–2514. JCR: 2.44, SJR: 1.58, Q1 (Ecology). FSC conceived the study and wrote the manuscript with contributions from all coauthors. FSC collected the data. FSC and JTF designed the analyses. FSC created the figures. All authors discussed the results. GL and MS reviewed the manuscript. Status: Published.

- **Chapter 10:** Cost-effective conservation of amphibian ecology and evolution.

F. S. Campos, R. Lourenço-de-Moraes, G. A. Llorente & M. Solé. (2017). Science Advances, 3, e1602929. JCR: –, SJR: –, Q1 (Multidisciplinary). Recently founded journal with expected JCR >10 (2018 JCR release). FSC conceived the study and wrote the manuscript with contributions from all coauthors. FSC and RLM designed the analyses, collected the data, and created the figures. All authors discussed the results and edited the manuscript. GL and MS reviewed the manuscript. Status: Published.

The scientific contribution of the doctoral candidate in this thesis was very relevant, as it proves to be the first author in seven of them. He has participated actively in the design, sampling and analysis of the samples as well as in the scientific writing of all the works presented.

The supervisors report that none of the coauthors participating in the articles that make up this thesis have implicitly or explicitly used the heads of these works for the elaboration of their own thesis. Except for the chapters 2, 6 and 8 of this thesis, of which the coauthor R. Lourenço-de-Moraes used them in the framework of his doctoral thesis – presented on August 8, 2016 at the Universidade Estadual de Maringá, Brazil.

Barcelona, 18 April 2018.

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Part I Spatial Distribution

Back Cover: *Proceratophrys boiei* (Wied-Neuwied, 1824)
– Photo by Felipe S. Campos

Chapter 1

Anurans from the mountain chain Serra do Mar: a critical area for amphibian conservation in the Atlantic Forest, Brazil

Herpetology Notes – Article Published
https://biotaxa.org/hn/article/view/31357

Anurans from the mountain chain Serra do Mar: a critical area for amphibian conservation in the Atlantic Forest, Brazil

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Anuros de la cadena montañosa Serra do Mar: un área crítica para la conservación de anfibios en el Bosque Atlántico, Brasil. Presentamos un inventario de anuros de la región montañosa de la Serra do Mar, Brasil, ubicado en el bioma del Bosque Atlántico. Realizamos un trabajo de campo en los remanentes más grandes y mejor conservados de todo el Bosque Atlántico brasileño, utilizando evaluaciones acústicas y visuales por monitoreo nocturno y diurno. En total, registramos 99 especies de anuros, de las cuales cerca de 70% son endémicas del Bosque Atlántico y representan un alrededor del 20% de todas las especies de anfibios descritas para este bioma. Los altos niveles de endemismo, los patrones de distribución y los estados de conservación de las especies, convierten a las montañas de Serra do Mar en una región de conservación clave para todos los anfibios que viven en el punto caliente de biodiversidad del Bosque Atlántico brasileño.

– Spanish Abstract (Resumen)

Herpetology Notes, volume 10: 547-560 (2017) (published online on 16 October 2017)

Anurans from the mountain chain Serra do Mar: a critical area for amphibian conservation in the Atlantic Forest, Brazil

Felipe Siqueira Campos[1, 2,*] and Ricardo Lourenço-de-Moraes[3]

Abstract. We present an anuran inventory of the mountain region of the Serra do Mar, Brazil, located in the Atlantic Forest biome. We conducted a fieldwork comprising the major and best well-preserved Atlantic Forest remnants from Brazil, using acoustic and visual nocturnal/diurnal assessments. In total, we recorded 99 anuran species, of which about 70% are endemic to the Atlantic Forest and represent around 20% of all amphibian species described for this biome. The high levels of endemism, the distribution patters and the conservation status of the anuran species turn the mountains of the Serra do Mar into a key conservation region for amphibians within the Atlantic Forest hotspot.

Keywords. Amphibia, Atlantic Forest, species inventory, species distribution, conservation.

Introduction

The Atlantic Forest biome represents one of the five most important biodiversity hotspots on Earth (Mittermeier et al., 2011). Originally, it covered around 1,500,000 km^2 of which only about 12% (194,524 km^2) remains in Brazil, Paraguay and Argentina (Ribeiro et al., 2009), corresponding to about 100,000 km^2 of Brazilian forest remnants (Tabarelli et al., 2005). This biome faces high rate of habitat loss (Teixeira et al., 2009), which is one of the main causes of amphibian extinctions (Stuart et al., 2004; Becker et al., 2007; Ferreira et al., 2016). Despite this, Atlantic Forest is still considered the leader biome in amphibian diversity in Brazil (Haddad et al., 2013), accounting for more than 50% of all amphibian species (Haddad et al., 2013). Their geographical characteristics with wide altitudinal range have favoured high species richness and high levels of endemism, including more than 500 recognized amphibian species and several more species that still need to be described (Silva and Casteleti, 2003; Haddad et al., 2013).

The Serra do Mar is a mountain chain that extends for more than 1,000 km (Almeida and Carneiro, 1998), stretching from the south of the Espírito Santo state to the North of the Rio Grande do Sul state (Rizzini, 1979; Olson et al., 2001). This is an area of extreme biological importance that covers 8% of the Atlantic Forest biome and accounts more than 13% of the remaining forest (Ribeiro et al., 2009). The Brazilian Ministry of the Environment has rated this region with the highest priority towards conservation within the Atlantic Forest hotspot (MMA, 2000). According to the biogeographical sub-regions proposed by Silva and Casteleti (2003), Serra do Mar covers the best well-preserved remnants, which holds 36.5% of its original vegetation (Ribeiro et al., 2009). This region has been highly fragmented, with 79% of the remaining forests smaller than 0.5 km^2. However, part of the biome still covers wide forest remnants, with fragments larger than 1,000 km^2 along the coastal mountains of São Paulo state, larger than 500 km^2 in the Paraná state, and larger than 300 km^2 in the Santa Catarina state (Ribeiro et al., 2009). On the altitudinal gradient, Serra do Mar also has continuous forests ranging from the sea level up to 2,300 m (Almeida and Carneiro, 1998).

A key factor accounting for amphibian species richness in the Atlantic Forest is the large number of habitats and microhabitats (Haddad, 1998), which favours the

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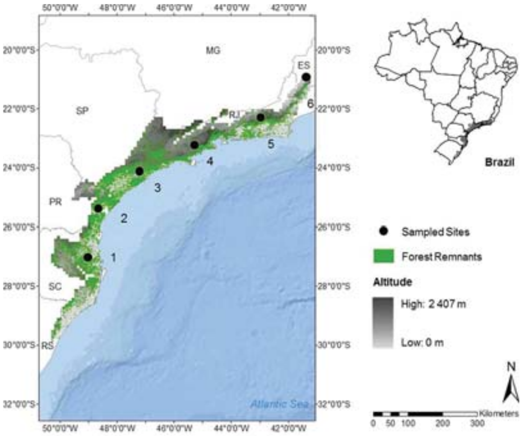

Figure 1. Map of the sampled sites in the mountain chain Serra do Mar, Brazil, representing their corresponded forest remnants and altitude at a spatial resolution of 0.1 latitude/longitude degrees. 1. Parque Ecológico Spitzkopf, SC; 2. Parque Estadual Pico do Marumbi, PR; 3. Estação Ecológica de Juréia-Itatins, SP; 4. Parque Estadual da Serra do Mar Núcleo Caraguatatuba, SP; 5. Parque Nacional da Serra dos Órgãos, RJ; 6. Reserva Biológica Augusto Ruschi, ES.

number of habitat-specialist species (Lourenço-de-Moraes et al., 2013). In addition, there is a high degree of isolation among populations, due to the rugged relief with rivers and mountains that may represent biogeographic barriers (Haddad, 1998; Marques et al., 1998).

Species inventories are crucial for answering central questions in biogeography (Lomolino, 2004), ecology (Brown et al., 1996) and evolutionary biology (Holt, 2003). Additionally, species lists are critical to indicate knowledge gaps, as well as to identify priority areas for conservation (e.g., Toledo and Batista, 2012; Verdade et al., 2012; Campos et al., 2014). In this context, we carried out fieldwork comprising the major forest remnants of the mountain chain Serra do Mar, supplementing the current amphibian dataset for this region and highlighting the importance of these forests for the species conservation status.

Material and Methods

We conducted fieldwork at six Protected Areas located in the mountain chain Serra do Mar, Brazil (Figs. 1 and 2). The general climate of this region is tropical wet with frequent rain occurring every month (Walsh, 1996). This non-seasonal tropical rain forest climate is characterized by monthly mean temperatures of at least 18 °C and high annual rainfall averages (> 2,000 mm; Walsh, 1996). Vegetation types comprise tree mosaics with different shifts in floristic composition as elevation increases and are classified as montane and sub-montane rain forest composed of moist broadleaf trees (Rizzini, 1979; Olson et al., 2001).

We sampled each Protected Area for 10 days between January and March 2015 (wet season) from 5 pm to 1 am, totalling 480 hours of sampling effort per person (i.e., two researchers). In all localities, we used acoustic and visual nocturnal/diurnal assessments at different microhabitats along a 2,000 m forest transect in each sampled site (e.g., streams, swamps, bromeliads, bamboos, burrows, rocks, vegetation, and leaf-litter). We focused the study in an altitudinal range lower than 300 m and higher than 700 m above sea level (asl). We identified the species by comparing their morphological characteristics observed in the field and reviewing their original or revalidated descriptions to support the taxonomic identifications. We followed Frost (2017) for the amphibian nomenclature.

Results and Discussion

In the six Protected Areas surveyed in the mountain chain Serra do Mar, we found 99 anuran species distributed in 13 families and 31 genera (Table 1, Figs. 3–8). About 70% of the sampled species are endemic to the Brazilian Atlantic Forest and represents around 20% of all amphibian species described for this biome. We found the highest species richness in the “Parque Estadual da Serra do Mar Núcleo Caraguatatuba” (34 species) and the lowest in the “Parque Ecológico Spitzkopf” (23 species). We found approximately twice the number of species in lowland areas (<300 m asl.) than highland areas (>700 m asl.), of which 60 species occurred exclusively below 300 m, 22 species exclusively above 700 m, and 17 species in both altitudinal ranges (Table 1). Among the different microhabitats searched, we observed 36% of the species in swamps, 18% in streams, 17% in leaf-litter, 15% in trees, 8% in bromeliads, 3% in rocks, 2% burrows, and 1% in bamboos.

In this study, we presented the first anuran species list for the Parque Ecológico Spitzkopf, in the Santa Catarina state, and the Parque Estadual da Serra do Mar Núcleo Caraguatatuba, in the São Paulo state. Our results showed four new species distribution records for the studied region, expanding the knowledge about the occurrence of anurans in the mountain chain Serra do

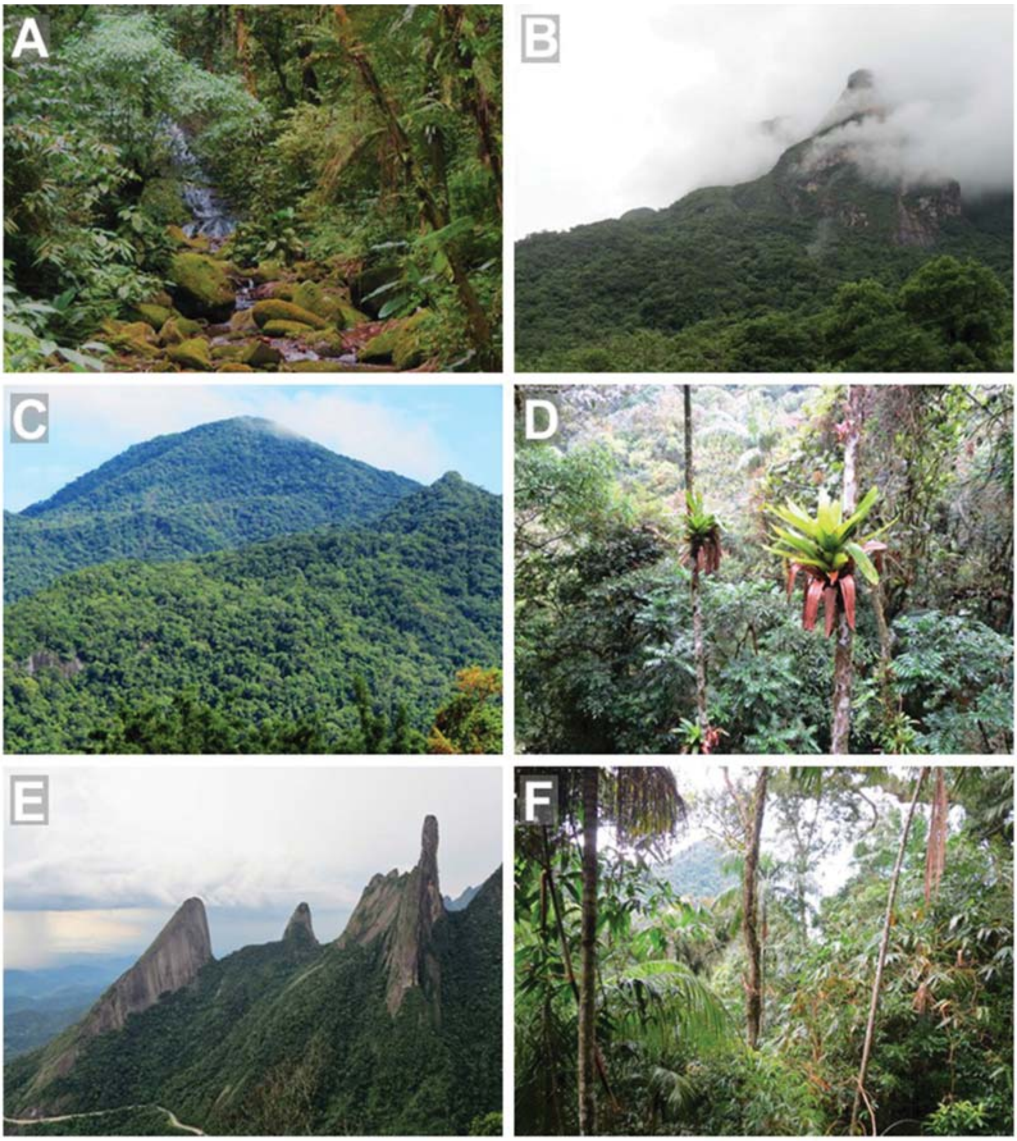

Figure 2. Some environments of the sampled sites in the mountain chain Serra do Mar, Brazil. A) Rocky stream in the Parque Ecológico Spitzkopf, SC; B) Mountain chain in the Parque Estadual Pico do Marumbi, PR; C) Forest fragment in the Estação Ecológica de Juréia-Itatins, SP; D) Forest bromeliads in the Parque Estadual da Serra do Mar Núcleo Caraguatatuba, SP; E) Mountain chain in the Parque Nacional da Serra dos Órgãos, RJ; F) Dense ombrophylous forest in the Reserva Biológica Augusto Ruschi, ES.

Mar. We reported the first state records for *Ischnocnema erythromera* in the Espírito Santo state, *Rhinella henseli* and *Adenomera nana* in the Paraná state, and *Hylodes pipilans* in the São Paulo state.

Table 1 shows the conservation status of the recorded species according to the IUCN red list categories (IUCN, 2017). We found only one species classified as Vulnerable (VU), three as Near Threatened (NT), and four as Data Deficient (DD). In this context, several studies have highlighted that the lack of information regarding amphibian species occurrence needs to be straightaway addressed by scientific researchers,

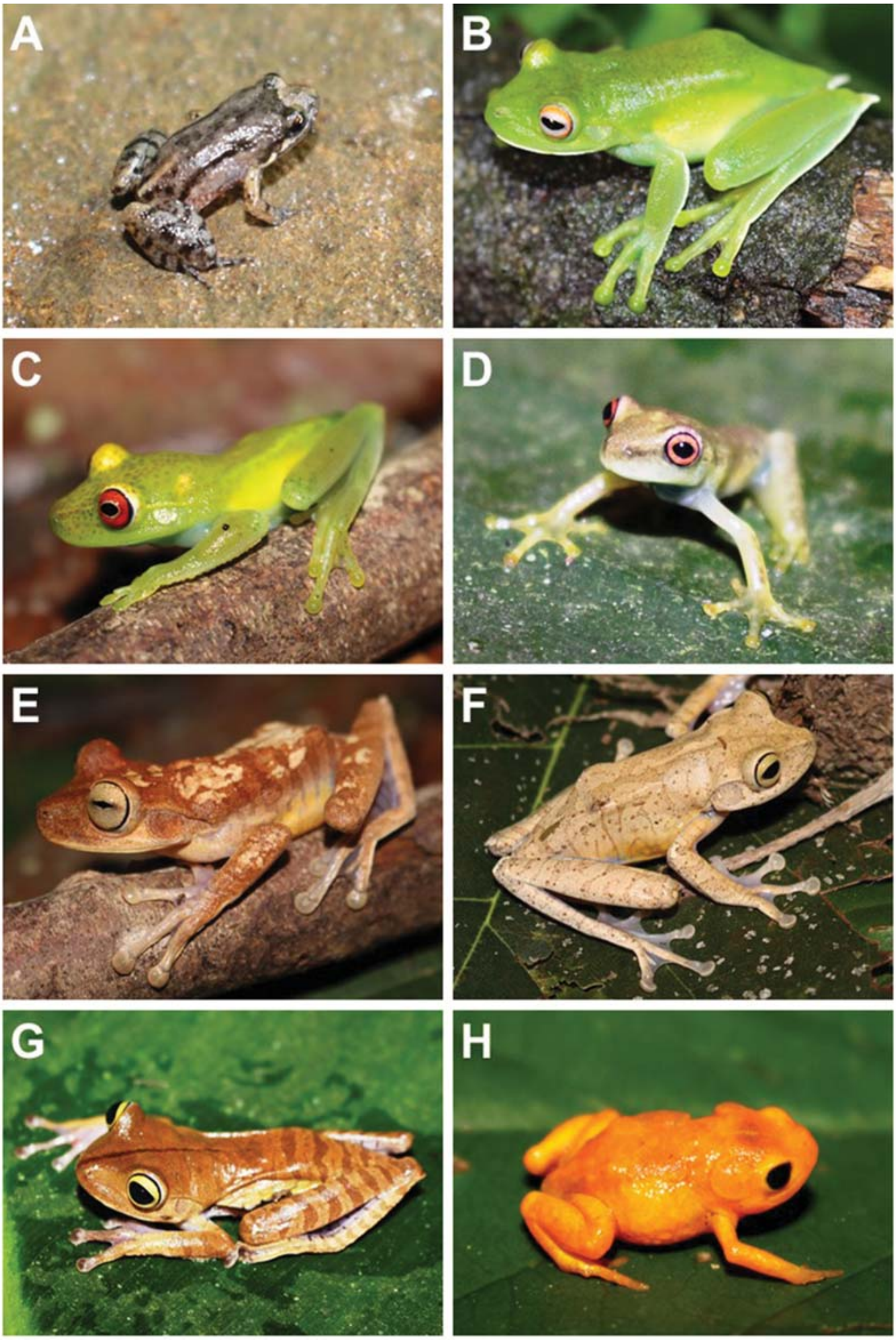

Figure 3. Some amphibian species sampled in the mountain chain Serra do Mar, Brazil. A) *Adenomera bokermanni*; B) *Aplastodiscus albosignatus*; C) *Aplastodiscus arildae*; D) *Aplastodiscus ehrhardti*; E) *Bokermannohyla caramaschii*; F) *Bokermannohyla circumdata*; G) *Bokermannohyla hylax*; H) *Brachycephalus ephippium*.

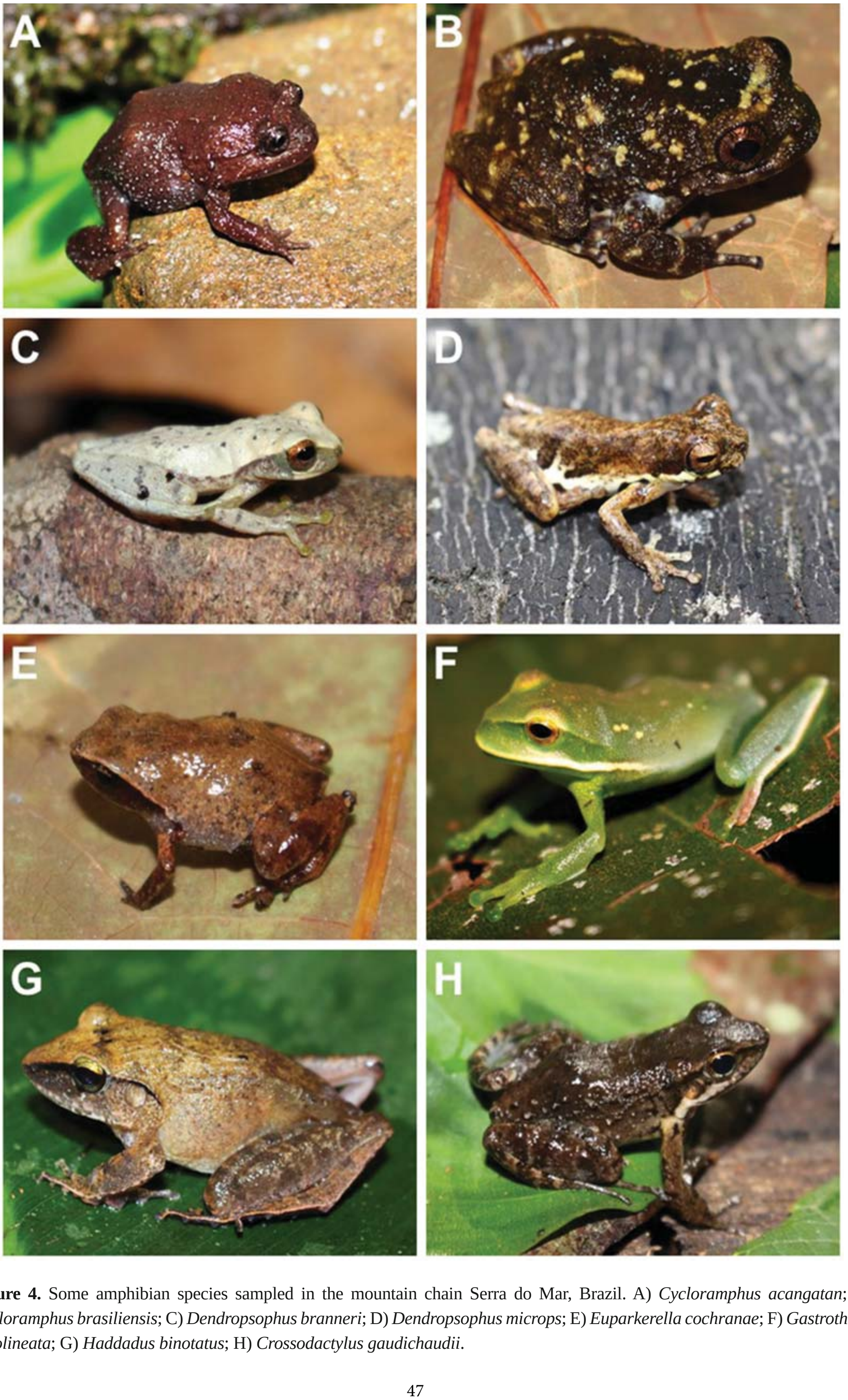

Figure 4. Some amphibian species sampled in the mountain chain Serra do Mar, Brazil. A) *Cycloramphus acangatan*; B) *Cycloramphus brasiliensis*; C) *Dendropsophus branneri*; D) *Dendropsophus microps*; E) *Euparkerella cochranae*; F) *Gastrotheca albolineata*; G) *Haddadus binotatus*; H) *Crossodactylus gaudichaudii*.

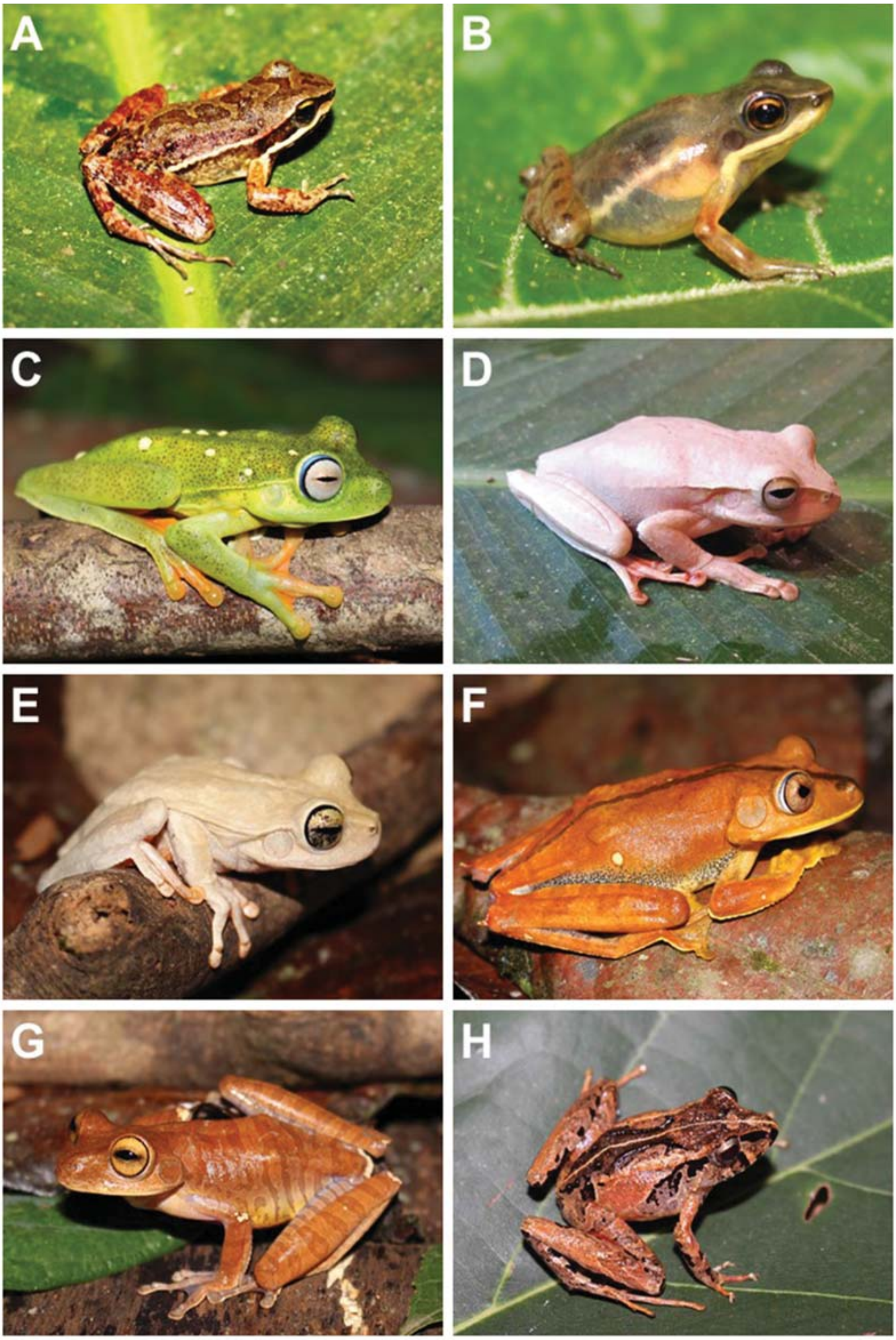

Figure 5. Some amphibian species sampled in the mountain chain Serra do Mar, Brazil. A) *Hylodes heyeri*; B) *Hylodes pipilans*; C) *Boana albomarginata*; D) *Boana bischoffi*; E) *Boana crepitans*; F) *Boana semilineata*; G) *Boana faber*; H) *Ischnocnema erythromera*.

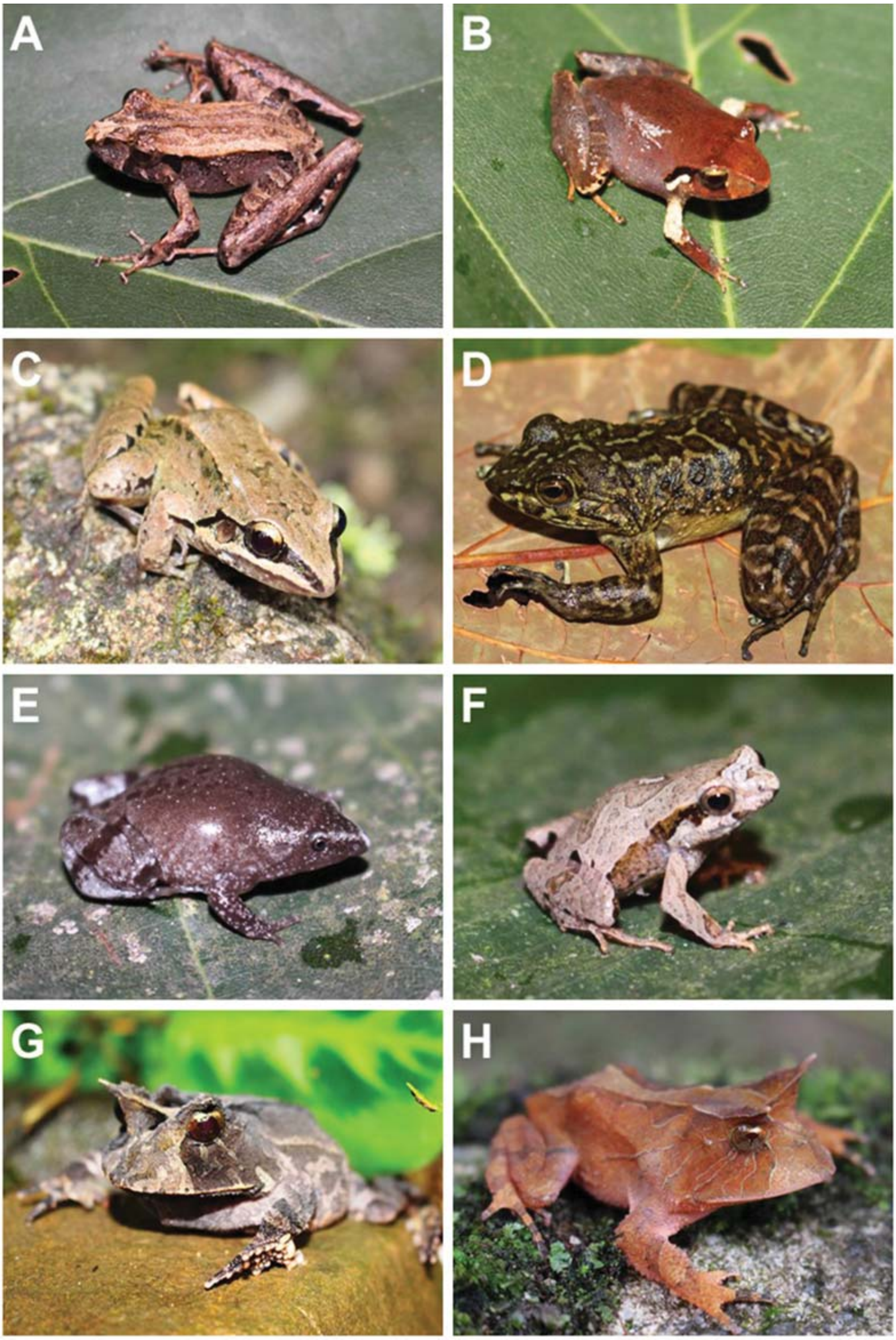

Figure 6. Some amphibian species sampled in the mountain chain Serra do Mar, Brazil. A) *Ischnocnema guentheri*; B) *Ischnocnema parva*; C) *Leptodactylus notoaktites*; D) *Megaelosia goeldii*; E) *Myersiella microps*; F) *Physalaemus nanus*; G) *Proceratophrys boiei* (gray pattern); H) *Proceratophrys boiei* (orange pattern).

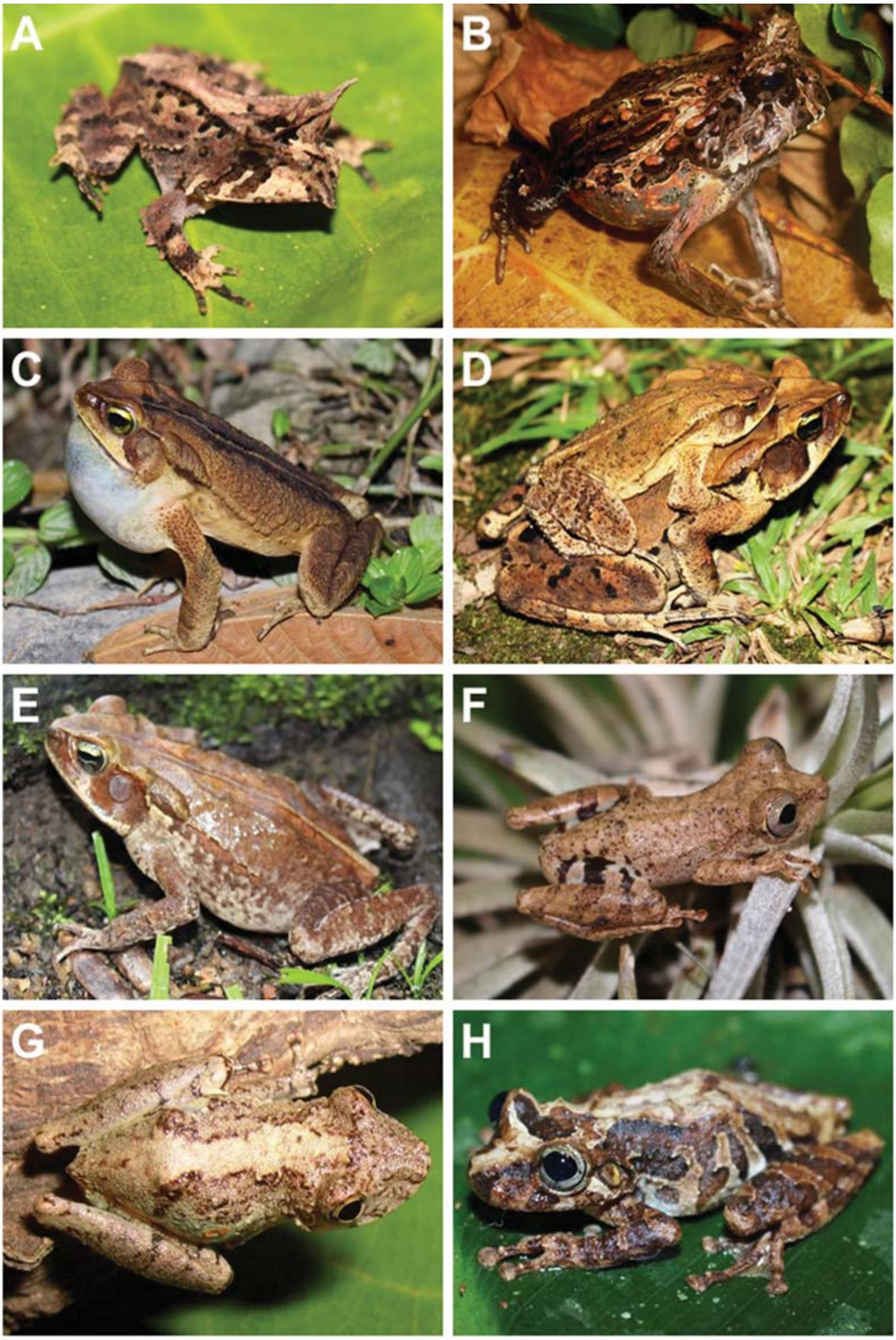

Figure 7. Some amphibian species sampled in the mountain chain Serra do Mar, Brazil. A) *Proceratophrys appendiculata*; B) *Macrogenioglottus alipioi*; C) *Rhinella abei*; D) *Rhinella henseli*; E) *Rhinella ornata*; F) *Ololygon albicans*; G) *Ololygon argyreornata*; H) *Ololygon catharinae*.

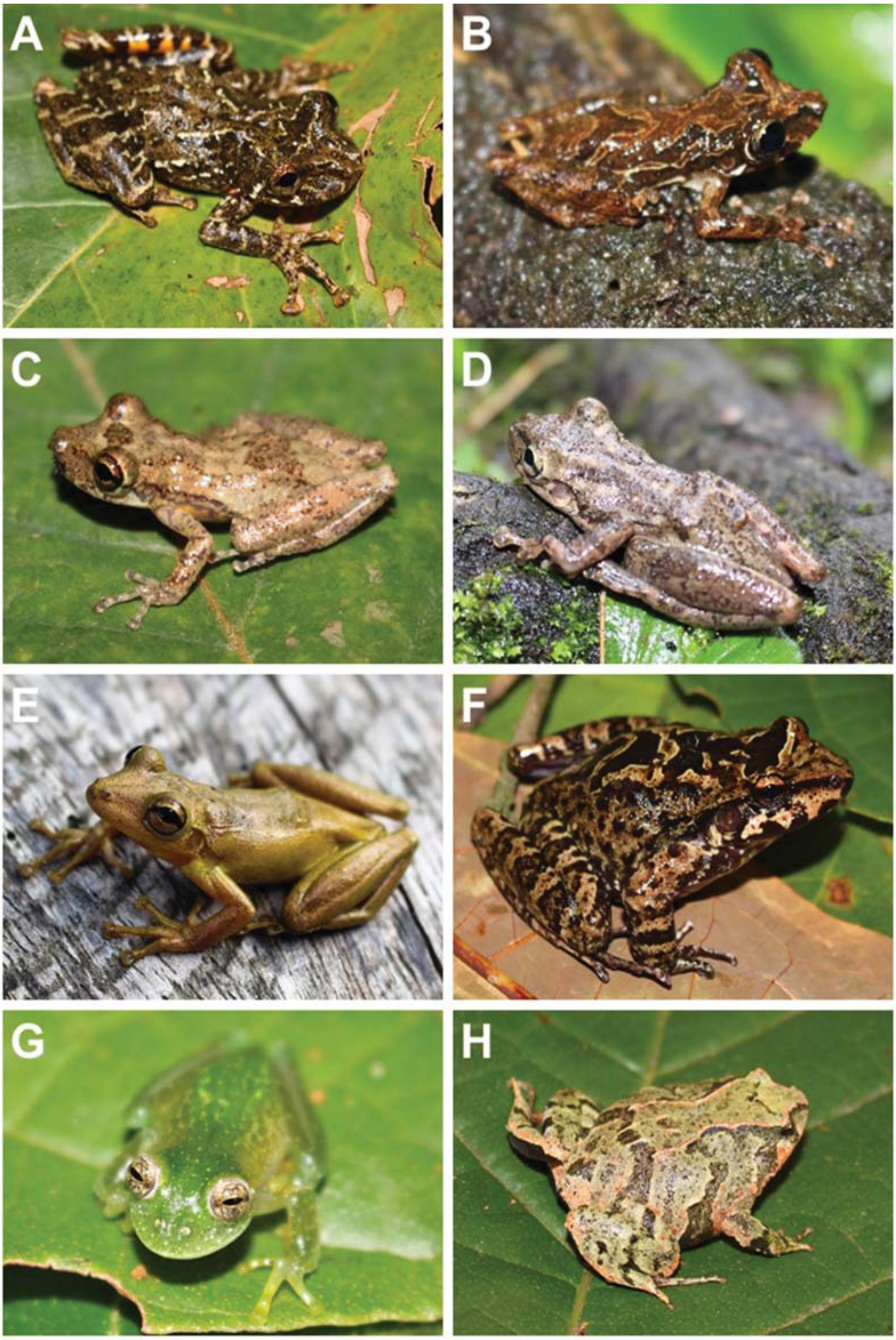

Figure 8. Some amphibian species sampled in the mountain chain Serra do Mar, Brazil. A) *Ololygon flavoguttata*; B) *Ololygon littoralis* C) *Ololygon v*-signatus D) *Scinax granulatus*; E) *Scinax hayii*; F) *Thoropa miliaris*; G) *Vitreorana uranoscopa*; H) *Zachaenus parvulus*.

Table 1. Anuran species registered in the six Protected Areas surveyed in the mountain chain Serra do Mar, Brazil, according to their Red List categories (IUCN, 2017) and altitudinal ranges recorded. 1. Parque Ecológico Spitzkopf, SC; 2. Parque Estadual Pico do Marumbi, PR; 3. Estação Ecológica de Juréia-Itatins, SP; 4. Parque Estadual da Serra do Mar Núcleo Caraguatatuba, SP; 5. Parque Nacional da Serra dos Órgãos, RJ; 6. Reserva Biológica Augusto Ruschi, ES.

Species	**Sampled sites**						**Red list Category**	**Altitude**	
	1	**2**	**3**	**4**	**5**	**6**		**<300m**	**>700m**
Family Brachycephalidae									
Brachycephalus ephippium (Spix, 1824)					■		LC		X
Ischnocnema erythromera (Heyer, 1984)					■	■	DD		X
Ischnocnema aff guentheri (Steindachner, 1864)		■	■	■	■	■	LC	X	X
Ischnocnema henselii (Peters, 1872)	■	■					LC	X	
Ischnocnema oea (Heyer, 1984)						■	NT		X
Ischnocnema parva (Girard, 1853)				■	■		LC		X
Family Bufonidae									
Dendrophryniscus brevipollicatus Jiménez de la Espada, 1870				■			LC	X	
Dendrophryniscus leucomystax Izecksohn, 1968				■			LC	X	
Rhinella abei (Baldissera-Jr, Caramaschi & Haddad, 2004)	■	■					LC	X	X
Rhinella crucifer (Wied-Neuwied, 1821*)*					■	■		X	
Rhinella granulosa (Spix, 1824)						■	LC	X	X
Rhinella henseli (Lutz, 1934)	■	■					LC	X	
Rhinella hoogmoedi Caramaschi & Pombal, 2006			■				LC	X	
Rhinella icterica (Spix, 1824)			■	■			LC	X	
Rhinella ornata (Spix, 1824)		■	■	■	■		LC	X	X
Rhinella schneideri (Werner, 1894)		■	■			■	LC	X	
Family Centrolenidae									
Vitreorana eurygnatha (Lutz, 1925)				■			LC	X	
Vitreorana uranoscopa (Müller, 1924)			■	■			LC	X	
Family Craugastoridae									
Euparkerella cochranae Izecksohn, 1988					■		LC		X
Haddadus binotatus (Spix, 1824)	■	■	■	■	■	■	LC	X	X
Family Cycloramphidae									
Cycloramphus acangatan Verdade & Rodrigues, 2003			■				VU	X	
Cycloramphus boraceiensis Heyer, 1983				■			LC	X	
Cycloramphus brasiliensis (Steindachner, 1864)					■		NT	X	
Thoropa miliaris (Spix, 1824)				■	■	■	LC	X	X
Zachaenus parvulus (Girard, 1853)					■		LC		X
Family Eleutherodactylidae									
Adelophryne glandulata Lourenço-de-Moraes, Ferreira, Fouquet & Bastos 2014						■	NE		X
Family Hemiphractidae									
Fritziana fissilis (Miranda Ribeiro, 1920)				■			LC	X	
Fritziana ohausi (Wandolleck, 1907)				■			LC	X	
Gastrotheca albolineata (Lutz & Lutz, 1939)					■		LC		X
Family Hylidae									
Aplastodiscus albofrenatus (Lutz, 1924)				■			LC	X	X
Aplastodiscus albosignatus (Lutz & Lutz, 1938)		■	■				LC	X	X
Aplastodiscus arildae (Cruz & Peixoto, 1987)					■	■	LC		X
Aplastodiscus ehrhardti (Müller, 1924)	■						LC	X	
Aplastodiscus leucopygius (Cruz & Peixoto, 1985)			■				LC	X	
Aplastodiscus perviridis Lutz, 1950		■	■				LC	X	
Aplastodiscus weygoldti (Cruz & Peixoto, 1987)						■	NT		X
Boana albomarginata (Spix, 1824)			■	■		■	LC	X	
Boana albopunctata (Spix, 1824)				■			LC	X	
Boana bischoffi (Boulenger, 1887)	■	■	■				LC	X	
Boana caingua (Carrizo, 1991)			■				LC	X	
Boana crepitans (Wied-Neuwied, 1824)						■	LC	X	X

Table 1. Continued.

Species	Sampled sites						Red list Category	Altitude	
	1	2	3	4	5	6		<300m	>700m
Boana faber (Wied-Neuwied, 1821)	■	■	■	■		■	LC	X	X
Boana prasina (Burmeister, 1856)		■	■				LC	X	
Boana raniceps (Cope, 1862)				■			LC	X	
Boana semilineata (Spix, 1824)	■					■	LC	X	
Bokermannohyla caramaschii (Napoli, 2005)						■	LC		X
Bokermannohyla circumdata (Cope, 1871)		■		■	■	■	LC	X	X
Bokermannohyla hylax (Heyer, 1985)	■						LC	X	
Dendropsophus bipunctatus (Spix, 1824)						■	LC	X	
Dendropsophus branneri (Cochran, 1948)						■	LC	X	
Dendropsophus decipiens (Lutz, 1925)			■			■	LC	X	
Dendropsophus elegans (Wied-Neuwied, 1824)						■	LC	X	
Dendropsophus giesleri (Mertens, 1950)					■		LC	X	
Dendropsophus microps (Peter, 1872)				■			LC	X	X
Dendropsophus minutus (Peters, 1872)	■	■	■	■		■	LC	X	
Dendropsophus nanus (Boulenger, 1889)	■	■	■	■		■	LC	X	
Dendropsophus werneri (Cochran, 1952)	■	■					LC	X	
Dendropsophus sanborni (Schmidt, 1944)	■	■					LC	X	
Itapotihyla langsdorffii (Duméril & Bibron, 1841)			■				LC	X	
Ololygon albicans (Bokermann, 1967)					■		LC		X
Ololygon arduous Peixoto, 2002						■	DD		X
Ololygon argyreornata (Miranda-Ribeiro, 1926)				■			LC	X	
Ololygon brieni (Fouquete & Pyburn, 1972)		■					LC	X	
Ololygon catharinae (Boulenger, 1888*)*	■	■					LC	X	X
Ololygon flavoguttata (Lutz & Lutz, 1939)					■		LC		X
Ololygon littoralis (Pombal & Gordo, 1991)			■	■			LC	X	
Ololygon perpusilla (Lutz & Lutz, 1939)				■			LC	X	
Ololygon v-signatus (Lutz, 1968)					■		LC		X
Scinax fuscovarius (Lutz, 1925)	■			■			LC	X	
Scinax granulatus (Peters, 1871)	■	■					LC	X	
Scinax hayii (Barbour, 1909)			■	■			LC	X	
Trachycephalus mesophaeus (Hensel, 1867)				■			LC	X	
Family Hylodidae									
Crossodactylus caramaschii Bastos & Pombal, 1995		■					LC	X	
Crossodactylus gaudichaudii Duméril and Bibron, 1841						■	LC		X
Hylodes asper (Müller, 1924)					■		LC	X	X
Hylodes cardosoi (Lingnau, Canedo & Pombal, 2008)		■					LC		X
Hylodes heyeri Haddad, Pombal & Bastos, 1996	■	■	■				DD	X	
Hylodes meridionalis (Mertens, 1927)	■						LC	X	
Hylodes pipilans Canedo & Pombal, 2007				■	■		DD	X	X
Megaelosia goeldii (Baumann, 1912)					■		LC		X
Family Leptodactylidae									
Adenomera bokermanni (Heyer, 1973)			■				LC	X	
Adenomera marmorata (Steindachner, 1867)			■	■			LC	X	
Adenomera nana Müller, 1922			■				LC		X
Leptodactylus fuscus (Schneider, 1799)		■					LC	X	
Leptodactylus labyrinthicus (Spix, 1824)						■	LC	X	
Leptodactylus latrans (Steffen, 1815)		■		■			LC	X	
Leptodactylus mystacinus (Burmeister, 1861)		■					LC	X	
Leptodactylus notoaktites Heyer, 1978	■	■					LC	X	X
Leptodactylus podicipinus (Cope, 1862)		■	■				LC	X	
Physalaemus cuvieri Fitzinger, 1826	■	■	■	■	■	■	LC	X	
Physalaemus nanus (Boulenger, 1888)	■						LC		X
Physalaemus signifer (Girard, 1853)				■			LC	X	

Table 1. Continued.

Species	Sampled sites						Red list Category	Altitude	
	1	2	3	4	5	6		<300m	>700m
Family Microhylidae									
Myersiella microps (Duméril & Bibron, 1841)					■		LC		X
Family Odontophrynidae									
Macrogenioglottus alipioi Carvalho, 1946				■			LC	X	
Proceratophrys appendiculata (Günther, 1873)					■		LC		X
Proceratophrys boiei (Wied-Neuwied, 1825)	■	■	■		■		LC	X	X
Family Phyllomedusidae									
Phyllomedusa burmeisteri Boulenger, 1882						■	LC	X	
Phyllomedusa distincta Lutz, 1950	■	■					LC	X	
Phyllomedusa rohdei Mertens, 1926						■	LC	X	
Total	**23**	**31**	**29**	**34**	**25**	**29**	**-**	**78**	**40**

environmental managers and policy-makers (e.g., Haddad, 2008; Trindade-Filho et al., 2012, Morais et al., 2013).

The current forest remnants from the Serra do Mar are considered as key conservation sites within the Brazilian Atlantic Forest hotspot, which reveal a high congruence of ecological and evolutionary patterns of amphibian biodiversity (Campos et al., 2017). Our findings highlighted valuable occurrence data regarding the anuran species in one of the most species-rich regions on Earth. According to Vasconcelos et al. (2014), the Serra do Mar between São Paulo and Rio de Janeiro states comprise a high richness of small-ranged species and is classified as a distinct biogeographic domain for anurans. Rödder et al. (2007) also highlighted the portion of Serra do Mar from the Espírito Santo state with extraordinary amphibian species richness. Antecedent biogeoclimatic factors as the refuges of the late Pleistocene may have an important role in this current species richness pattern (Carnaval et al., 2009). However, processes determining anuran occurrence in specific environments, such as highland areas remain poorly known, where information on the diversity of amphibians remains fragmented (Garey et al., 2014; Garey and Provete, 2016). Due to the difficulty of access, the highland areas of Serra do Mar have historically suffered little interference from anthropogenic activities compared to lowland areas (Garey and Provete, 2016), which hampered the human occupation and helped to preserve the amphibian species that occur in these regions.

The establishment of conservation efforts along the current forest remnants in the Serra do Mar can ensure the amphibian species persistence in the mountainous regions, which probably will keep lower temperatures in the future (Lourenço-de-Moraes, 2016). Therefore, we recommend that the design of amphibian conservation plans in this region must attempt to incorporate ecological connectivity assessments in the remaining fragments of both lowlands and highlands areas. This may represent an alternative mechanism to mitigate potential impacts related to the Atlantic Forest amphibians. In this context, future researches should address ways to improve or implement these conservation practices. In line with our findings, some other studies in the Atlantic Forest have also warned about the need to invest in amphibian conservation near high altitude areas (Carnaval et al., 2009; Lemes and Loyola, 2013; Dias et al., 2014; Loyola et al., 2014), which retain high humidity provided by well-preserved forest cover. Although the strength of this study heavily relies on good studies on amphibian conservation in the Serra do Mar, our results highlight the importance of maintaining forest remnants in an attempt to provide a straightforward representation of the amphibian species that occur in this region.

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Chapter 2

Explaining the dispersal of amphibians through functional traits

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Explaining the dispersal of amphibians through functional traits

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La dispersión de anfibios a través de rasgos funcionales. El análisis de dispersión de especies es uno de los temas más importantes para entender las relaciones macroecológicas. Dado que las características ecológicas pueden determinar la capacidad de dispersión de las especies, los enfoques basados en rasgos funcionales ofrecen herramientas prometedoras para abordar los desafíos en la biogeografía. En este estudio, nos enfocamos en las especies de anfibios del Bosque Atlántico para evaluar cómo los rasgos funcionales pueden estar relacionados con los procesos de dispersión. Utilizando atributos morfológicos, comportamentales y de historia de vida, evaluamos el papel funcional de los factores ambientales en la riqueza de especies, en el endemismo y en los componentes de la diversidad beta. Rasgos funcionales, tales como tamaño del cuerpo y hábitat son las principales características que explican la diversidad beta que encontramos. Nuestros hallazgos destacan que, bajo la pérdida de hábitat, las especies más adaptadas a los cambios en el uso de la tierra tienden a aumentar sus rangos de distribución, lo que lleva a la homogeneización de la composición de las especies a escalas locales. Para incorporar los rasgos funcionales a la dispersión de especies, debemos considerar que la deforestación ha limitado a la mayoría de los anfibios a fragmentos pequeños y dispersos. Teniendo esto en cuenta, el mantenimiento de procesos funcionales como justificación para la conservación de anfibios puede ser clave para reducir el riesgo de extinción y evitar la pérdida de especies.

– Spanish Abstract (Resumen)

Explaining the dispersal of amphibians through functional traits

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ABSTRACT

Species dispersal is one of the most important topics to understand macroecological relationships. Given that ecological features can determine the species' ability to disperse, functional trait-based approaches offer promising tools to address challenges in biogeography. Here, we focus on amphibian species from the Atlantic Forest to evaluate how functional traits can be related to dispersal processes. Using amphibians' ecological niches regarding morphology, life history, and behaviour, we assess the role of the environment on species richness, endemism, and beta diversity components. We find that functional traits such as body size and habitat are the main features that explain the beta diversity patterns. Our results highlight that under habitat loss, species more adapted to land-use changes tend to increase their distribution ranges, leading to the homogenization of species composition at local scales. To incorporate functional traits into species dispersal assumptions, we need to consider that deforestation has limited most amphibians to small and scattered fragments. Taking this into account, the maintenance of functional processes as a justification for amphibian conservation can be can be key to reduce extinction risk and avoid species loss.

INTRODUCTION

Current patterns of species dispersal are usually linked to historical and contemporary processes (Ricklefs, 1987; Oberdorff et al., 1997; Svenning & Skov, 2007; Carnaval & Moritiz, 2008; Carnaval et al., 2009; Baselga et al., 2012; Silva et al., 2014). These processes are often related to ecological interactions on species abundances, geographical ranges and body size traits (Brown & Maurer, 1989; Gaston, 1990; Lawton, 1993). It can be refined using environmental details on the localities at which species have been recorded across geographical boundaries that encloses them (Gaston, 1991).

Ectothermic species are largely limited by climatic zones (Pfrender et al., 1998). Therefore, climate and dispersal limitation are both critical determinants of species' geographical ranges. (Baselga et al., 2012). Small species for example, can lose water and suffer desiccation faster than large species (MacLean, 1985), reflecting adaptive processes to the environment (i.e., generalist, specialist or opportunistic species) (Bell, 2001; Legendre et al., 2005). In this sense, potential dispersal of the ectothermic species is related to their morphological and physiological characteristics (Jimenez-ValVerde et al., 2015), and this may be key to understanding these processes. Functional traits go beyond the species composition and can determine the functioning of ecosystems (Díaz et al., 2007), as well as the species dispersal processes among them (Gómez-Rodrigues et al., 2015). Amphibians are highly sensitive to environmental changes (Blaustein et al., 1994), mainly because of their physiological characteristics and dispersal limitations (Duellman & Trueb, 1994). Furthermore, many species are prey to vertebrates and invertebrates (Wells, 2007), which makes them dependent on adaptive morphological, physiological and behavioural specializations to succeed in dispersing.

Anthropogenic impacts have been responsible for the well documented declining amphibian populations in the tropics (Lips & Donnelly, 2002; Becker et al., 2007, 2010; Ferreira et al., 2016). 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 the different compositions (i.e. turnover or nested) along of a latitudinal and longitudinal gradient, can be an important tool for understanding the dispersal processes of these species (Baselga, 2008; 2010).

For amphibians, dispersal processes are strongly affected by the terrestrial preferences of juveniles and adults, and their ability to cross a landscape (Patrick et al., 2008). Spatial characteristics of forest and open areas can be physiological and ecological constraints for many species, and may strongly influence their capacity to forage, reproduce and survive (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, range sizes, habitat specificity, and antipredator mechanisms (Monkkonen & Reunanen, 1999; Fahrig, 2001). 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 dispersal of species and environmental changes under functional-traits approaches (Cushman, 2006; Berg et al., 2010).

Knowing that amphibians are limited to dispersal due to their ecological characteristics (Richter-Boix et al., 2007), we evaluated the beta diversity of amphibians in the Brazilian Atlantic Forest for the orders Anura and Gymnophiona, assessing their potential dispersal based on functional traits. For this, we tested the hypothesis that: i) some functional traits can be associated with greater dispersal adaptations to new environmental conditions (e.g. body size and ecological specializations) (Fig. 1); and ii) amphibians from the Brazilian Atlantic Forest are smaller at high altitudes and low latitudes.

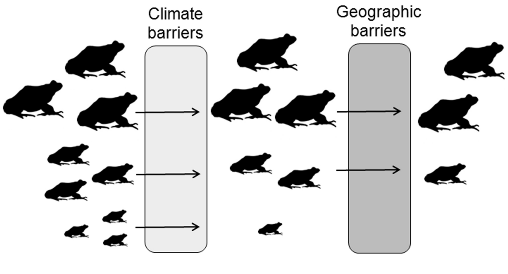

Fig. 1. Hypothetical diagram showing that large and medium species are better adapted to climate and geographical barriers, suggesting greater dispersal abilities.

We also evaluated the relation between species composition and environmental factors, identifying points of endemism, and partitioning beta diversity patterns across the Brazilian states.

MATERIALS AND METHODS

Study Area

We focused our sudy on the Atlantic Forest Biodiversity Hotspot. This biome has a latitudinal range extending into tropical and subtropical regions (Myers et al., 2000). The longitudinal range extends from the coast to 1,000 km inland, and the altitudinal range extends from 0 to 2,000 m a.s.l. (Cavarzere & Silveira, 2012). Originally, the 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 forest remains (Ribeiro et al., 2009).

The Brazilian Atlantic Forest occurs across 14 states from the south to the northeast of Brazil (Fig. S1). To understand the pattern of beta diversity in each state, we analysed differences of species compositions (richness and endemism) and mapped out potential dispersal routes. We delimitated the study sites in relation to: i) political divisions; ii) size of area; iii) geomorphological barriers (see Dominguez et al., 1987; Bittencourt et al., 2007); iv) abiotic barriers (Worldclim database; see below); and v) forest composition barriers (see Olson et al., 2001).

Given that each state has different environmental laws (e.g. IAP-Instituto

Ambiental do Paraná - Paraná state, COTEC – Comissão Técnico-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 had all territory included as separated study sites, due to their small territories and different ecosystems: RJ (Rio de Janeiro) and ES (Espírito Santo). Three states had all territory separated in east and west, due to their large territories and different forest compositions (eastern rain forest, western seasonal forest): EPR (East Paraná), WPR (West Paraná), ESC (East Santa Catarina), WSC (West Santa Catarina), ERS (East Rio Grande do Sul), WRS (West Rio Grande do Sul). Connected seasonal forests from four states were separated in a single study site: SMGM (West São Paulo – S, North Mato Grosso do Sul – M, South Goiás – G and extreme South Minas Gerais – M). The southern section of Mato Grosso do Sul state was included in a separated study site – MS, due to its particular seasonal forest. The states of Pernambuco, Sergipe, Ceará, Paraíba and Rio Grande do Norte were included in a single study site – N (Northeast), due to their small territories and similar ecosystems. Two states were separated in north and south, due to their large territories and different forest compositions – SBA (South Bahia), NBA (North Bahia), SMG (south Minas Gerais) and NMG (north Minas Gerais). In total, 16 study sites were evaluated (see Fig 2).

Species distribution data

We included species occurrences records available through the Global Biodiversity Information Facility (GBIF: http://www.gbif.org), and added range maps of each species according to the IUCN Red List database (IUCN, 2017). In addition, we conducted amphibian survey in 11 Protected Areas (PAs), stretching from the South to the Northeast of the country (see Fig. S2). We conducted fieldwork to supplement the dataset with observed functional traits using acoustic and visual nocturnal/diurnal assessments (Crump & Scott Jr., 1994; Zimmerman, 1994), through an active search around water bodies, streams and along 2,000 m forest transects for each surveyed area. We followed Frost (2018) for the amphibian nomenclature.

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.

Environmental variables

We calculated the mean of six environmental variables for each grid cell evaluated, which included one topographic (altitude), one biotic (tree cover) and four climates (annual precipitation, mean annual temperature, annual evapotranspiration, and net primary productivity).

We obtained variables from altitude, annual precipitation and mean annual temperature through the WorldClim database at 0.05 degrees of spatial resolution (http://www.worldclim.org/). We obtained annual evapotranspiration (AET) from the Geonetwork database (http://www.fao.org/geonetwork/srv/); net primary productivity (NPP) from the Numeral Terra Dynamic Simulation Group (http://www.ntsg.umt.edu/data), and tree cover from the Global Forest Change 2000–2014 database (http://earthenginepartners.appspot.com/science-2013-global-forest/). All these variables are known to represent either potential physiological limits for amphibians or barriers to dispersal (Vasconcelos et al., 2010; Silva et al., 2012). We created the maps using the ArcGis10.1 software (ESRI, 2011).

Functional traits

We characterized 531 amphibian species through six functional traits that determine different dimensions of the amphibians' ecological niches regarding morphology, life history, and behavior. We used the trait categories reported by Haddad et al. (2013), with some additional data obtained in our fieldwork. We also included ecological information from the IUCN database (IUCN, 2017) and scientific literature on the original descriptions of the species. We set out the following functional traits: i) body size (cm); ii) development mode (subtraits: direct or indirect); iii) habitat (subtraits: forested areas, open areas, and both open/forested areas); iv) activity time (subtraits: nocturnal, diurnal, and both); v) poisonous (subtraits: toxic, unpalatable or bad odour, and non-toxic); and vi) habit (subtraits: arboreal, phytotelmate, terrestrial, cryptozoic, fossorial, rheophilic, semi-aquatic, and aquatic). All these functional traits have direct or indirect roles in the ecosystem (Duellman & Trueb, 1994; Wells, 2007; Toledo et al., 2007; Haddad et al., 2013; Hocking & Babbitt, 2014).

Data Analyses

We evaluated the response of species richness and endemic species separately to the following predicted variables: altitude, annual precipitation, mean annual temperature, annual evapotranspiration, net primary productivity, and tree cover. We used the term endemic species for species that occur in only one of the 16 study sites. For these analyses, we used permutation multivariate analysis of variance (PERMANOVA), with 1,000 permutations based on a Euclidean distance matrix through the "adonis" function of the package "vegan" (Oksanen et al.,2013), in the R software (R Development Core Team, 2017).

We used simple linear models to test the association of species' body sizes on species richness. For this, we calculated mean body size for each grid cell of 0.1 degrees of spatial resolution. Thus, we evaluated the relationship between mean body size with latitude, longitude and altitude. We performed these analyses using the package 'vegan' (Oksanen et al., 2013) in the R software (R Development Core Team, 2017).

We evaluated the geographical range of each species to the predicted body size, poisonous, development mode, habit, habitat and activity time for Anura and body size, development mode, habitat and habit for Gymnophiona. For this, we also used PERMANOVA with 1,000 permutations through the R package 'vegan' (Oksanen et al., 2013. In addition, we used boxplots and percentage histograms to ilustrate the fuctional traits that better explain the species dispersal.

We analyzed the differences between the traits separately for anurans (ANOVA) and gymnophionas (Kruskal-Wallis), depending on normality using the Shapiro test (parametric and non-parametric data). We performed these analyses separately due to lack of information on Gymnophiona and their different characteristics of ecological traits and body size (Haddad et al., 2013). We calculated these analyses for each grid cell (10,359 cells), using the R packages'vegan' (Oksanen et al., 2013), 'car' (Fox & Weisberg, 2011), 'FSA' (Ogle, 2016), and 'lattice'(Sarkar, 2008), in the R software (R Development Core Team, 2017).

We assessed whether there was independence of spatial correlation of species composition across the 16 study sites (i.e. matrix of spatial data vs. matrix of species composition, and Euclidean distance matrix). For this, we used Pearson's correlation tests by the Mantel permutation (Legendre & Legendre, 1998). We used a similarity measure of Euclidean distance for the 16 study sites to rank the groups of similar species composition, based on the matrix of species composition, which was submitted to a nonparametric multidimensional scaling analysis (NMDS, Legendre & Legendre, 1998). The most likely solution was evaluated by Pearson correlation. The calculation of the variance was captured by a regression matrix from the original distances (Bray-Curtis) and the final array distances (Euclidean) (Fig. 2B).

Therefore, we draw a dendrogram by taking Euclidean distance as the measure of resemblance and average linkage procedure as the linkage rule (Fig. 2C). We performed these tests using the package 'vegan' (Oksanen et al., 2013), in the R software (R Development Core Team, 2017).

Beta diversity partitioning

First, we used two complementary metrics for beta diversity analysis by considering species presence and absence. In order to determine if the pattern among anuran communities is nested, we calculated a nestedness metric based on overlap and decreasing fill (index NODF) of Almeida-Neto et al. (2008) and Ulrich et al. (2009) across the 16 study sites (Fig. 2A). The matrix in decreasing both columns and rows, columns ranking the areas according to their species richness and ordering the species in lines, the most frequent to the rarest. Creating and ordering the study sites as larger biota and its subsets biota. To perform this analysis, original matrices were submitted to 1,000 simulations. We performed this analysis for all localities separately using the package 'vegan' (Oksanen et al., 2013) in the R software (R Development Core Team, 2017).

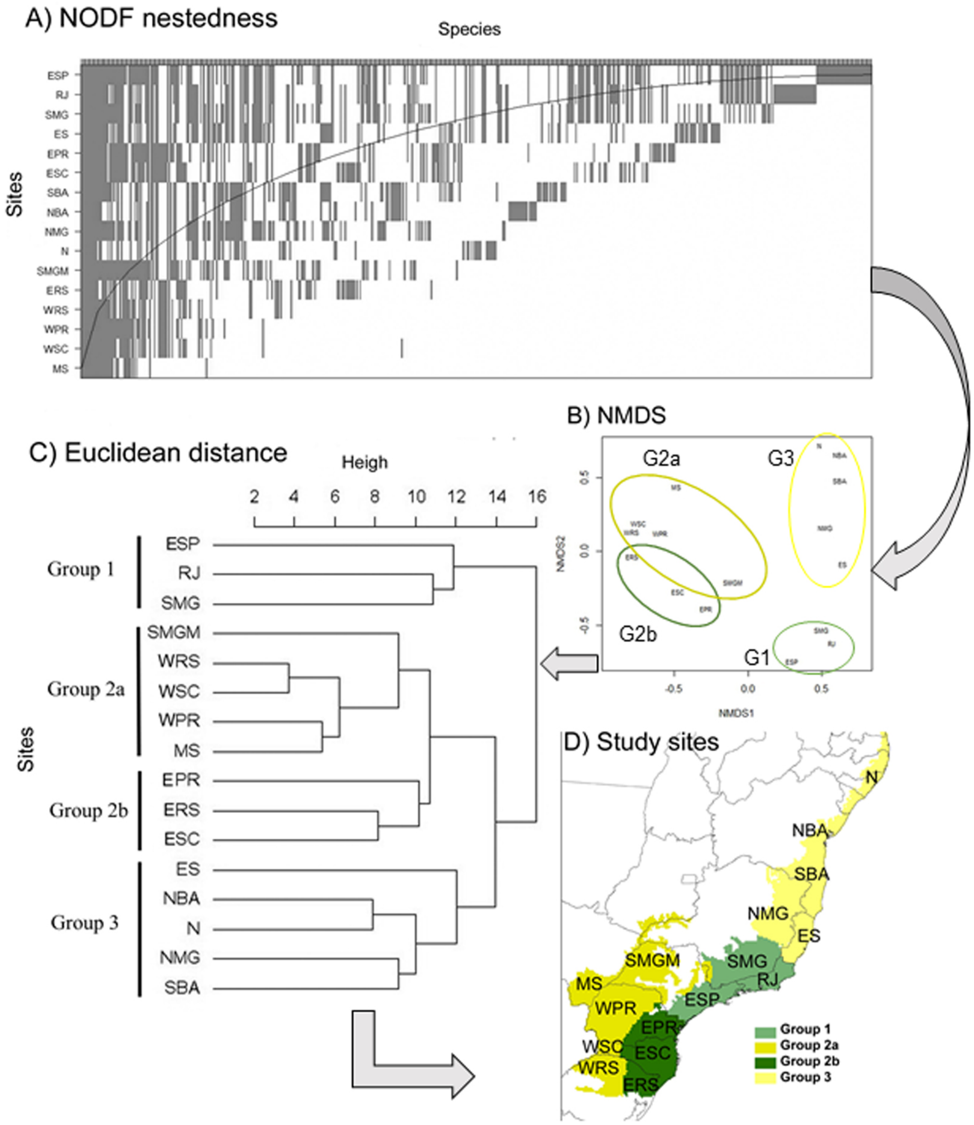

Fig 2. Steps designed to determine the amphibian beta diversity patterns in the Brazilian Atlantic Forest. A) NODF for the study sites with greater species richness and subset, B) NMDS for the species composition across the study sites, C) NMDS clusters, and D) map showing the groups similarities among the study sites. Acronyms: RJ (Rio de Janeiro); ES (Espírito Santo); EPR (East Paraná); WPR (West Paraná); ESC (East Santa Catarina); WSC (West Santa Catarina); ERS (East Rio Grande do Sul); WRS (West Rio Grande do Sul); SMGM (West São Paulo – S, North Mato Grosso do Sul – M, South Goiás – G, and extreme South Minas Gerais – M); MS (Mato Grosso do Sul); N (Northeast); SBA (South Bahia), NBA (North Bahia); SMG (South Minas Gerais); and NMG (North Minas Gerais).

Second, we conducted beta diversity partitioning and computed the distance matrices using pairwise dissimilarities βsor (i.e. measure total beta diversity), βsim (i.e. measure spatial turnover), and βnes (i.e. measure nesting) (Baselga, 2010). We computed these analyses among the 16 study sites to show the directions of the species distributions. We considered that larger nesting values means more species similar to the area of major species richness, and larger numbers of turnover means less similar species composition. We followed the sequence provided by NODF for the analysis of beta diversity partitioning. This method partitions the pairwise Sørensen dissimilarity between two communities (βsor) into two additive components, accounting for species spatial turnover (βsim) and nestedness-resultant dissimilarities (βsne). Since βsor and βsim are equal in the absence of nestedness, their difference is a net measure of the nestedness-resultant component of beta diversity, thus βsne = βsor – βsim (Baselga, 2010).

Third, to assess the topographic effects between study sites and species composition, we computed the beta diversity in four altitudinal ranges: i) all altitudes; ii) 0–300 m a.s.l.; iii) 300–700 m a.s.l.; iv) 700–2000 m a.s.l.. We performed these tests using the package 'betapart' (Baselga & Orme, 2012), in the R software (R Development Core Team, 2017).

RESULTS

We found that the environmental factors can explain 59.5% of the amphibian species richness. Our results showed that temperature was the main explanatory variable (39.3%), followed by precipitation (11.4%), and NPP (8.6%) (Table S1). For the study sites with endemic species, the environmental factors can explain 26% of the endemism, of which temperature was also the main explanatory variable (22%), followed by altitude (2%) (Table S2).

For Anuran, the functional traits explained 15.8% of the species dispersal. Habitat was responsible for about 9%, body size 3%, habit 1% and poisonous 0.8% of the variation in the dispersal patterns. Development mode and activity time traits did not show any significant relationship to the spatial distribution (Table S3).

For Gymnophiona, two main traits explained 88.8% of the species dispersal. Habitat was responsible for about 67.4% and development mode 15.7% of the variation in the dispersal patterns. The body size and habit traits did not show any relationship to spatial distribution (Table S4).

For Anura and Gymnophiona, the trait body size showed low but significant correlations with species richness (r^2=0.398; *P*<0.001), longitude (r^2=0.103; *P*<0.001), latitude (r^2=0.025; *P*<0.001), and altitude (r^2=0.006; *P*<0.001).

Considering the functional subtraits results, the greatest dispersal distances in Anura was found in species of open areas, open/forested areas, medium body size, terrestrial habit, and with toxic and non-toxic characteristics (*P*<0.01) (Fig. 3A). The subtraits in Gymnophiona had no statistic significance (*P*>0.01) (Fig. 3B), but 35% of species from this group showed wide ranges (>20,000 km^2).

The Mantel tests indicated spatial correlation of species composition and distance across the 16 study sites (r^2= 0.30; *P*= 0.019). The dendrogram used the

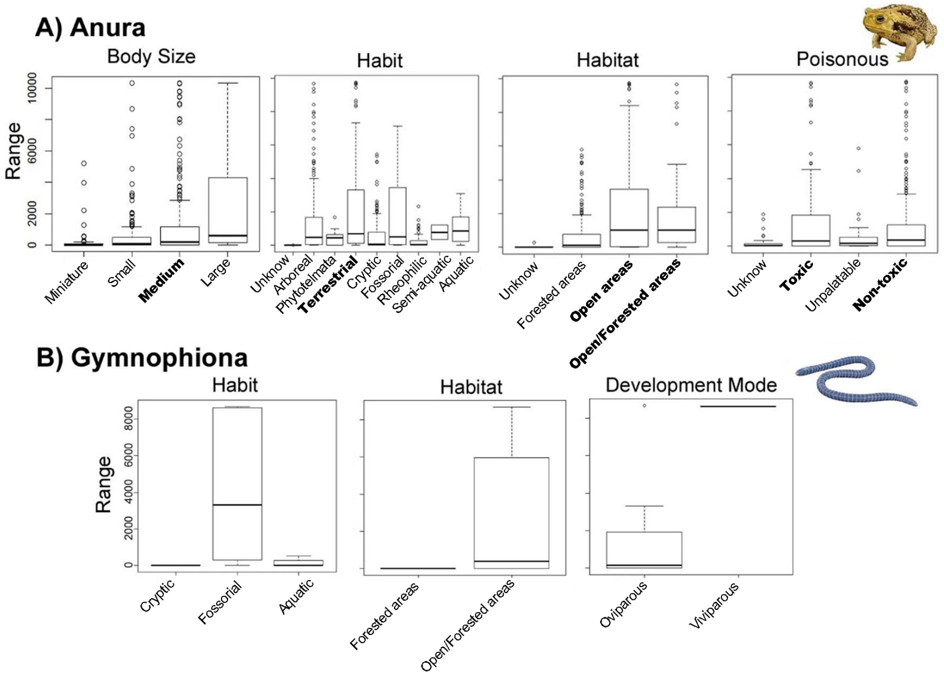

Fig. 3. Boxplots showing the fuctional traits that better explain the spatial ranges for (A) Anura and (B) Gymnophiona in the Brazilian Atlantic Forest. Statistically significant *P*-values are in blue (*P*<0.01).

scores of the NMDS axes (7 dimensions, r^2=0.99; *P*>0.001) and showed the presence of three groups of similarity faunal regions in Atlantic Forest. The major biota was ESP, RJ and SMG (group 1), characterized by humid forests (species richness: 644 spp; endemism: 76 spp). The group 2 was divided into two subgroups: one formed by MS, WPR, WSC WRS, and SMGM (subgroup 2a), characterized by dry seasonal forests (species richness: 316 spp; endemism: 2spp); and another one formed by EPR, ESC and ERS (subgroup 2b), characterized by humid forests with presence of Araucarias (species richness: 343 spp; endemism: 31 spp). The group 3 was formed by ES, NMG, SBA, NBA and N, characterized by hot humid forests with little or no seasonality (species richness: 571 spp; endemism: 72 spp) (Fig. 4).

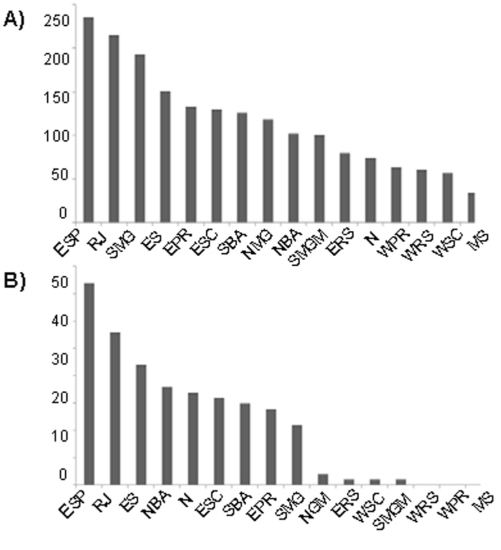

Fig. 4. A) Number of species, and B) Number of endemic species per sampling unit in the Brazilian Atlantic Forest.

Our results of the NODF indicated significant nesting values (NODF = 38.7, $P < 0.001$), showing the study sites ESP, RJ and SMG as the major biota. The beta diversity partitioning revealed that the highest values were between the groups 1 and 3 (βsor mean 0.684 ± 0.093), followed by the group 2a (βsor mean 0.675 ± 0.126). Among the group 3, the values increase by increasing the difference in species composition according to altitude, decreasing βsim and increasing βnes. The study site N showed the highest values of βnes (0.281) among the species that occur in 700–2000 m a.s.l., and the study site SBA showed the highest values of βsim (0.582) among the species that occur in 0–300 m a..s.l..

There is a similar pattern among species from the group 2a. However, the βnes decreases and βsim decreases then increases slightly at higher altitudes, wherein the MS showed the highest value of βnes (0.669) and the WRS showed the highest value of β sim (0.397), among species that occur in 300–700 m a.s.l.. Between the groups 1 and 2b, the values of βsor increases abruptly with increasing altitude (βsor mean 0.215± 0.609). The mean differences in the values of βsim (0.353±0.395) increase by increasing the differences in the species composition between altitudes. The study site ERS showed the highest value of βnes (0.281) among the species that occur in 700–2000 m a.s.l., as well as the highest value of βsim (0.480) among the species that occur in 300–700 m a.s.l. (Fig. 5; Table S5).

DISCUSSION

Our results showed that mean annual temperature has the greatest influence on amphibian richness and endemic species in the Atlantic Forest. Temperatures between 19° C and 21° C are optimal for amphibians, and promoted high species richness. Due to their physiological characteristics, amphibians are often considered dependent of humidity and mild temperatures (Wells, 2007; Crump, 2010). We also found a correlation between species richness to precipitation and temperature, corroborating with other related studies (Casemiro et al., 2007; Ortiz-Yusty et al., 2013; Vasconcelos et al., 2014). According to Rueda et al. (2010), the correlation of species richness with NPP and natural forest formations were also strongly related to rainfall, as measured by tree distributions strongly related to water-balance. Amphibian dispersal at high altitude has a higher number of endemic species due to the milder temperatures and higher humidity. However, lowland areas also have high endemism, and this may be related to historical events (Carnaval et al., 2012).

Due to high humidity and great diversity of microhabitats, many Neotropical amphibians evolved small size (Rittmeyer et al., 2012). Miniaturized species are more susceptible to humidity loss (MacLean, 1985) and many are restricted to preserved forest formations to maintain their environmental favourability (Lourenço-de-Moraes et al., 2012, 2014, Ferreira et al., 2016). Because of this limitation, miniaturized species are

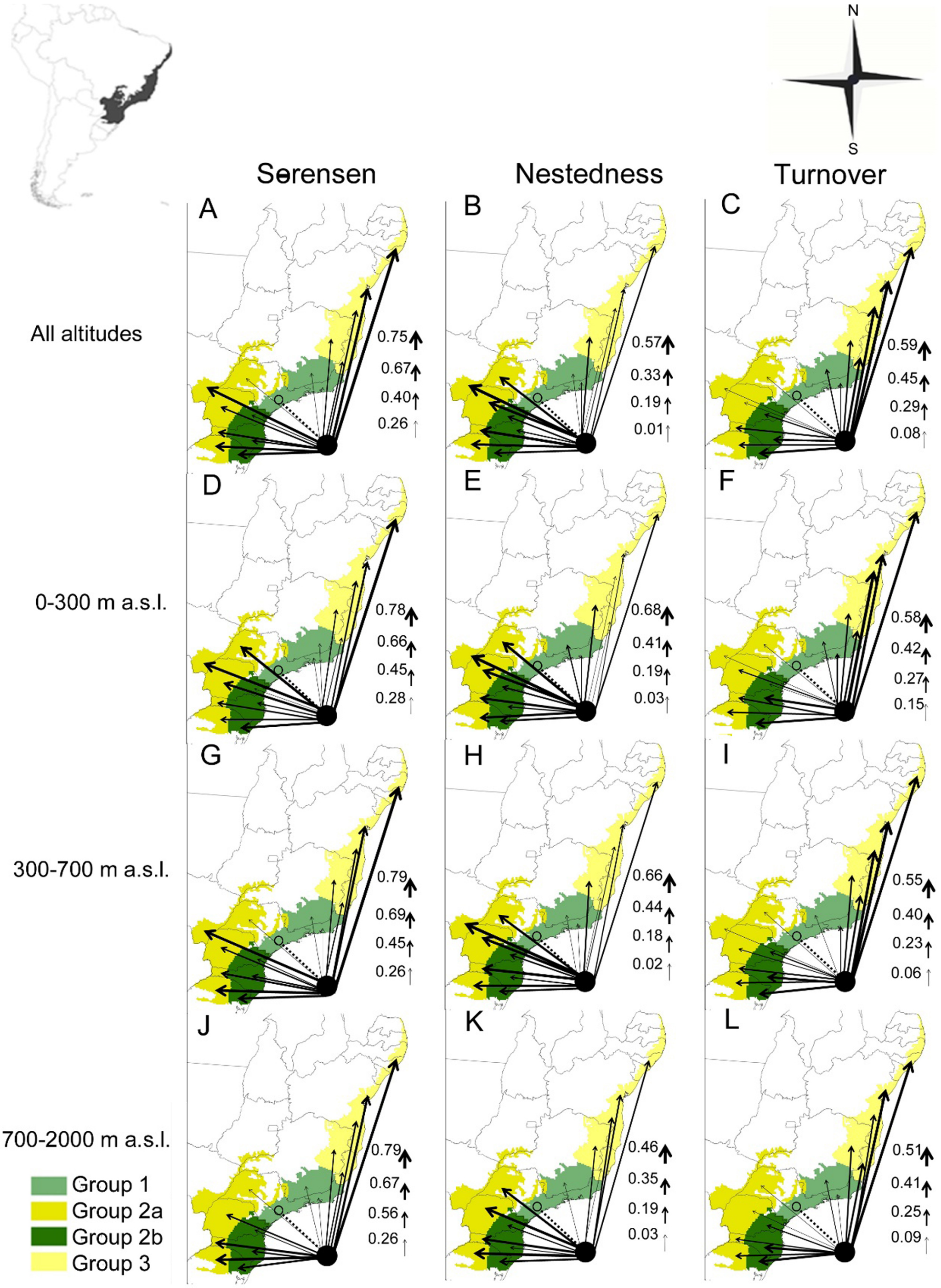

Fig. 5. Relative partitioning of beta diversity across the groups of study sites assessed in the Brazilian Atlantic Forest. Thinner arrows indicate smaller values, thicker arrows larger values. Beta diversity values are shown from the large biota ESP (circle) to the subsets.

concentrated in areas of milder temperatures, higher rainfall, and higher vegetation cover. For Atlantic Forest amphibians, areas with high latitudes, longitudes and altitudes tend to have smaller species. Therefore, we highlight relationships between species richness and body size that directly related to environmental conditions. This may lead to restricted gene flow between populations and accelerate genetic differentiation (Pabijan et al., 2012). Consequently, it may have limited these species to rainforests where such genetic differentiation is most commonly observed (Rodríguez et al., 2015), and these factors may have contributed to the large number of small species.

Our results showed that amphibians species with greatest dispersal are adapted to live in open areas and open forest areas, have medium body size and be toxic or non-toxic. In our study, species with the medium body size have better dispersal abilities (i.e. specialists in open areas or open/forest and toxic), such as *Odontophrynus americanus* (Haddad et al., 2013). Species with the same features of *O. americanus* but non-toxic, also had large geographical ranges due to other ecological factors that may assist in their range expansion. Species with a variety of antipredator mechanisms may be more likely to avoid a wider range of predators (Lourenço-de-Moraes et al., 2016), that allows successful dispersal. In addition, species from open areas with larger ranges also occur in drier biomes, such as the Cerrado and the Caatinga biomes.

Our findings revealed that the dispersal of Atlantic Forest amphibians is related to their functional traits, of which the habitats comprising open areas can favour larger species better adapted to high temperatures and low humidity rates. However, most of the species that occur in the Atlantic Forest are under 30 mm, which lose water more quickly to the environment (MacLean, 1985). Even small species, such as *Dendropsophus nanus* and *D. minutus*, have great ability to dispersal due to their ability to occur in open areas (Haddad et al., 2013). Many open area species are expanding or expanded their ranges due to forest destruction. Species of open areas are not found in forests, or they are found in low abundance. Therefore, we suggest that these species are not generalists, but specialists of open areas and opportunistic.

We revealed a homogenized pattern of species in Atlantic Forest, this can be explained by the results of beta diversity (NODF nestedness). Species of open areas tend to disperse from west to east due to deforestation. The mountains of Serra do Mar and Mantiqueira can be limiting geographical barriers for small amphibians and strictly forest habits (Haddad, 1998; Morellato & Haddad, 2000). Moreover, the geographical barrier Rio Doce divides the region ES and part of NMG (Bates et al., 1998; Costa et al., 2000) and influenced in dispersal and composition of species from the group 3. ES has southern (group 1) and northern (group 3) species of the Atlantic Forest, while NMG is more related to northern (group 3) species of the Atlantic Forest.

Few strictly forest species have large ranges in the Atlantic Forest. *Haddadus binotatus* is a wide-range species probably dispersed by the drier forests of the west region, through the Glacial period due to ocean regression (Atlantic Forest hypothesis, Leite et al., 2016). However, it is possible that this is a species complex (Dias et al., 2011). The same applies to small and miniature species with wide distribution as *Dendropsophus minutus* and *Pseudopaludicola falcipes,* which Gehara et al., (2014) and Langone et al., (2016) indicated respectively through molecular techniques that are a species complex.

Our results pointed out nesting differences between the groups 1 and 2a, showing a decrease of nesting by increasing altitude and increasing turnover for the species occurring between 700–2000 m and 0–300 m a.s.l. Between the groups 1 and 2b, there is a reduction of nesting and increased composition turnover by increasing elevation, which has slight increase in beta-diversity between species that occur in 300–700 m a.s.l.. Between the groups 1 and 3 nesting increases and then decreases gradually by increasing altitude turnover. These results indicate differences in the species composition according to its topographic location. Different species compositions are related to species that occur in lowlands (0–300m) and hilltops (700–2000m). The group 2b indicates higher endemism rate in the mountainous regions, while the group 3 in the lowland areas. Therefore, as suggest by Haddad (1998), we highlight that mountain areas from the Atlantic Forest are key geographical barriers to amphibian dispersal processes.

According to our findings, it is possible to separate the Atlantic Forest in three major regions of endemism. Our results point groups 1, 2b and 3 as the areas with the highest rates of endemic and rare species. The beta diversity values corroborate the hypothesis of endemism during the Pleistocene glacial (Carnaval et al., 2009; Carnaval et al., 2014). The two extreme regions of this biome (i.e. southern and northern-most sites) have high turnover rates. The group 3 has shared genera with the Amazon forest as *Pristimantis*, *Adelophryne* and the newly described *Allophryne* – genera that do not occur in other groups of the Atlantic Forest. These data support the hypothesis connection between the north of the Atlantic Forest and the eastern Amazon rainforest (Batalha-Filho et al., 2013; Sobral-Souza et al., 2015). However, the group 3 also includes species from the Atlantic Forest as *Boana faber*. The groups 2a and 2b also show high turnover rates at some study sites (i.e. group 2a – at WRS; and group 2b – at ESC and ERS.

The southern Atlantic Forest region has a strong influence of the Western Amazon composition and the Andean forests (Batalha Filho et al., 2013; Sobral-Souza et al., 2015). Most *Melanophryniscus*, *Scythrophrys* and *Lymnomedusa* species occur in the group 2. These genera tolerate colder areas of the Atlantic Forest. Moreover, the nesting areas of greatest values are observed in the groups 1 and 2a, which have warmer forests and more pronounced seasonality, especially in the MS and WPR sites, where the most species are specialists of open areas and opportunistics. In addition, amphibians that occurr in the SMGM site can be directly related to the Cerrado biome, where many species of open areas and forest edges are distributed.

Late Pleistocene glaciations seems to be the main driver of amphibian species composition in the Atlantic Forest, showing historical predictions of habitat suitability (Carnaval & Moritz, 2008). The species richness provided by these events can be associated to specialization processes from several functional traits, wich can be key to understand amphibian dispersal in a current panorama. Given that species dispersal is a cycle that has been evolved for thousands of years, the current human-induced environmental change are further aggravated by mass extinction processes (Barnosky et al., 2011; Dirzo et al., 2014).

Amphibian composition and dispersal are directly affected by anthropogenic actions, while habitat loss is the most important threat to species survival in highly fragmented landscapes such as the Brazilian Atlantic Forest (Dixo et al., 2009). Despite the strength of this study is its innovative approach to incorporating functional traits into species dispersal assumptions, we need to consider that deforestation has limited most amphibians to small and scattered fragments. This situation rest heavily on good research in systematic conservation planning, and demands political will based on highest-priority conservation areas.

The maintenance of functional processes as a justification for amphibian conservation actions can be an effective strategy to reduce extinction risk and avoid species loss (Campos et al., 2017). In this context, our research highlights the importance of maintaining the forest cover remnants in the Atlantic Forest, and may help to move forward the usefulness of functional-traits approaches for other biodiversity hotspots.

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APPENDIX. Supporting Information

Supplementary files:

Table S1. Association of amphibian species richness to environmental variables in the Brazilian Atlantic Forest by PERMANOVA. Statistically significant *P*-values are in bold (*P*<0.01).

Table S2. Association of endemic amphibian species to environmental variables in the Brazilian Atlantic Forest by PERMANOVA. Statistically significant *P*-values are in bold (*P*<0.01).

Table S3. Association of spatial ranges to the functioal traits for Anuran species in the Brazilian Atlantic Forest by PERMANOVA. Statistically significant *P*-values are in bold (*P*<0.01).

Table S4. Association of spatial ranges to the functional traits for Gymnophiona species in the Brazilian Atlantic Forest by PERMANOVA. Statistically significant *P*-values are in bold (*P*<0.01).

Table S5. Relative partitioning of beta diversity across the groups of study sites assessed in the Brazilian Atlantic Forest. In bold are shown the greatest diversity beta values.

Fig. S1. Map showing the Brazilian Atlantic Forest hotspot in South American. The right box shows the acronimous of the Brazilian states studied: RS: Rio Grande do Sul; SC: Santa Catarina; PR: Paraná; MS: Mato Grosso do Sul; SP: São Paulo; GO: Goiás; MG: Minas Gerais; RJ: Rio de Janeiro; ES: Espirito Santo; BA: Bahia; SE: Sergipe; AL: Alagoas; PE: Pernambuco: PA: Paraíba; RN: Rio Grande do Norte.

Fig. S2. Map showing the complementary fieldwork areas (black dots) surveyed in the Brazilian Atlantic Forest. 1. Parque Ecológico Spitzkopf, SC; 2. Parque Estadual Pico do Marumbi, PR; 3. Parque estadual de Campinhos, PR; 4. Parque municipal das Perobas, PR; 5. Parque Estadual Mata dos Godoy, PR; 6. Refúgio municipal da vida Silvestre, Horto Florestal de Jacarezinho, PR; 7. Estação Ecológica de Juréia-Itatins, SP; 8. Parque Estadual da Serra do Mar Núcleo Caraguatatuba, SP; 9. Parque Nacional da Serra dos Órgãos, RJ; 10. Reserva Biológica Augusto Ruschi, ES; 11. Reserva Biológica de Una, BA.

Table S1. Association of amphibian species richness to environmental variables in the Brazilian Atlantic Forest by PERMANOVA. Statistically significant *P*-values are in bold ($P<0.01$).

Variables	df	*F* model	R^2	*P* value
Altitude	1	4.4	0.00017	0.036
AET - Evapotranspiration	1	38.3	0.0015	0.001
NPP - Net primary production	1	2198	0.08597	0.001
Precipitation	1	2917.4	0.11411	0.001
Temperature	1	10046.3	0.39294	0.001
Tree cover	1	10.9	0.00043	0.001
Residuals	10352	–	0.40489	–
Total	10358	–	1.00	–

Table S2. Association of endemic amphibian species to environmental variables in the Brazilian Atlantic Forest by PERMANOVA. Statistically significant *P*-values are in bold ($P<0.01$).

Variables	df	*F* model	R^2	*P* value
Altitude	1	413.2	0.02948	0.001
AET - Evapotranspiration	1	19.3	0.00137	0.001
NPP - Net primary production	1	4.1	0.00029	0.049
Precipitation	1	0.3	0.00002	0.578
Temperature	1	3202.0	0.22845	0.001
Tree cover	1	25.5	0.00182	0.001
Residuals	10352	–	0.73856	–
Total	10358	–	1.00	–

Table S3. Association of spatial ranges to the functioal traits for Anuran species in the Brazilian Atlantic Forest by PERMANOVA. Statistically significant *P*-values are in bold (P<0.01).

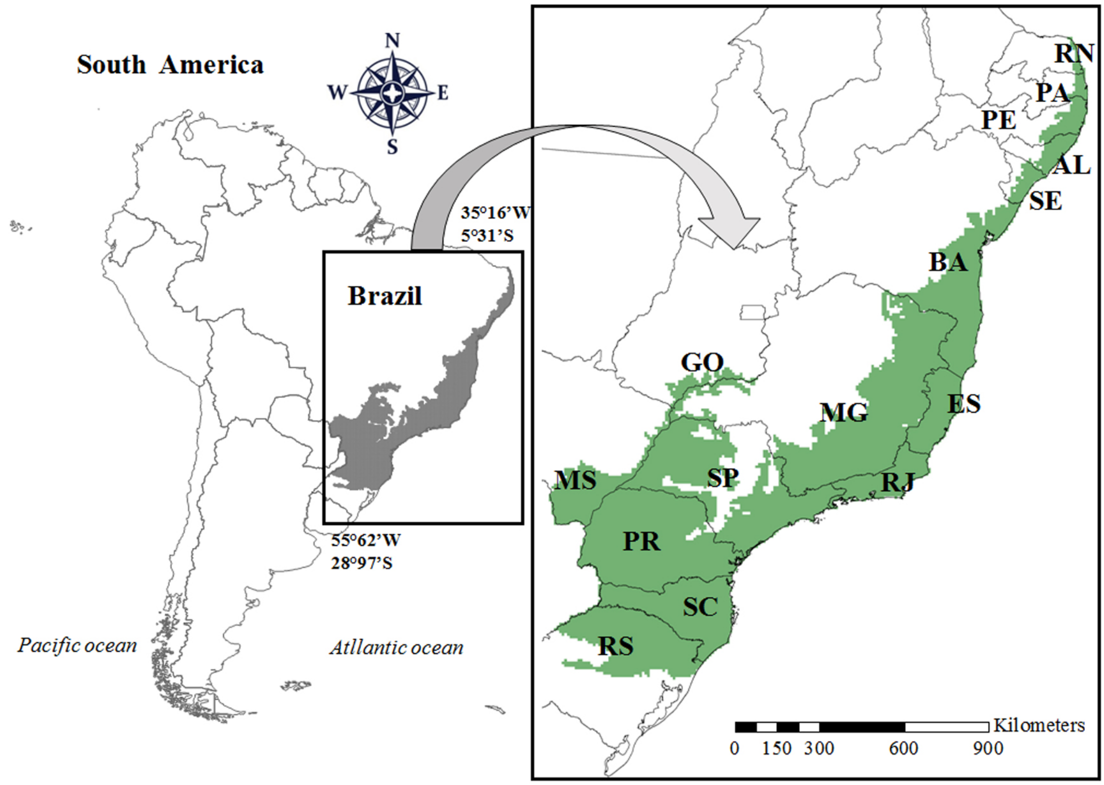
Variables	df	*F* model	R^2	*P* value
Activity	1	0.086	0.00014	0.772
Body size	1	22.14	0.03613	0.001
Poisonous	1	5.011	0.00818	0.021
Habit	1	12.056	0.01967	0.002
Habitat	1	57.575	0.09394	0.001
Development mode	1	1.013	0.00165	0.312
Residuals	515	–	0.84029	–
Total	521	–	1.00000	–

Table S4. Association of spatial ranges to the functional traits for Gymnophiona species in the Brazilian Atlantic Forest by PERMANOVA. Statistically significant *P*-values are in bold (P<0.01).

Variables	Df	*F* model	R^2	*P* value
Body size	1	1.346	0.02823	0.282717
Habit	1	2.674	0.05609	0.175824
Habitat	1	32.126	0.67401	0.001
Development mode	1	7.519	0.15775	0.027
Residuals	4	–	0.08392	–
Total	8	–	1.00000	–

Table S5. Relative partitioning of beta diversity across the groups of study sites assessed in the Brazilian Atlantic Forest. In bold are shown the greatest diversity beta values.

	Sorensen (βsor)				**Nestedness** (βnes)				**Turnover** (βsim)			
Groups	ESP											
Group1	All altitudes	300m	300-700m	700-2000m	All altitudes	300m	300-700m	700-2000m	All altitudes	300m	300-700m	700-2000m
ESP	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
RJ	0.282	0.263	0.263	0.269	0.035	0.016	0.029	0.039	0.247	0.247	0.234	0.229
SMG	0.329	**0.403**	0.268	0.314	0.075	0.195	0.069	0.060	0.254	**0.416**	0.199	0.254
Mean	0.203	0.222	0.177	0.194	0.037	0.070	0.033	0.033	0.167	0.332	0.217	0.242
DP ±	0.178	0.205	0.153	0.170	0.037	0.108	0.035	0.031	0.144	0.119	0.025	0.017
Group2a												
SMGM	0.460	0.751	0.446	0.448	0.361	0.551	0.381	0.357	0.099	0.200	0.065	0.091
WPR	0.666	0.719	0.736	0.654	0.459	0.452	0.444	0.460	0.206	0.267	0.210	0.194
WSC	0.734	0.713	0.727	0.741	0.418	0.436	0.393	0.447	0.316	0.277	0.333	0.294
MS	0.770	0.750	0.757	0.000	0.682	0.574	0.669	0.000	0.088	0.176	0.088	0.000
WRS	0.744	0.710	0.749	0.785	0.367	0.330	0.353	0.460	0.377	0.379	0.397	0.326
Mean	**0.675**	**0.729**	**0.683**	**0.657**	**0.457**	**0.469**	**0.448**	**0.431**	0.217	0.260	0.218	0.226
DP ±	0.126	0.020	0.133	0.150	0.132	0.098	0.128	0.050	0.128	0.079	0.146	0.106
Group2b												
EPR	0.491	0.248	0.457	0.499	0.197	0.248	0.237	0.194	0.293	0.154	0.220	0.305
ESC	0.612	0.148	0.592	0.595	0.158	0.148	0.181	0.168	0.454	0.429	0.410	0.427
ERS	0.747	0.250	0.736	0.733	0.247	0.250	0.256	0.281	0.500	0.478	0.480	0.452
Mean	**0.616**	0.215	**0.595**	**0.609**	0.201	0.215	0.225	0.214	**0.416**	0.353	0.370	0.395
DP ±	0.128	0.058	0.140	0.118	0.044	0.058	0.039	0.059	0.109	0.175	0.134	0.079
Group3												
ES	0.576	0.511	0.546	0.567	0.119	0.095	0.142	0.153	0.457	0.416	0.404	0.414
SBA	0.702	0.673	0.693	0.679	0.130	0.091	0.152	0.268	0.571	0.582	0.541	0.412
NBA	0.757	0.718	0.743	0.765	0.159	0.144	0.187	0.258	0.598	0.574	0.556	0.507
NMG	0.599	0.576	0.589	0.589	0.201	0.199	0.207	0.243	0.398	0.378	0.382	0.346
N	0.787	0.757	0.791	0.798	0.233	0.195	0.245	0.281	0.554	0.562	0.545	0.517
Mean	**0.684**	**0.647**	**0.672**	**0.680**	0.168	0.145	0.187	0.241	**0.516**	**0.502**	**0.486**	**0.439**
DP ±	0.094	0.102	0.103	0.103	0.048	0.052	0.042	0.051	0.085	0.098	0.085	0.072



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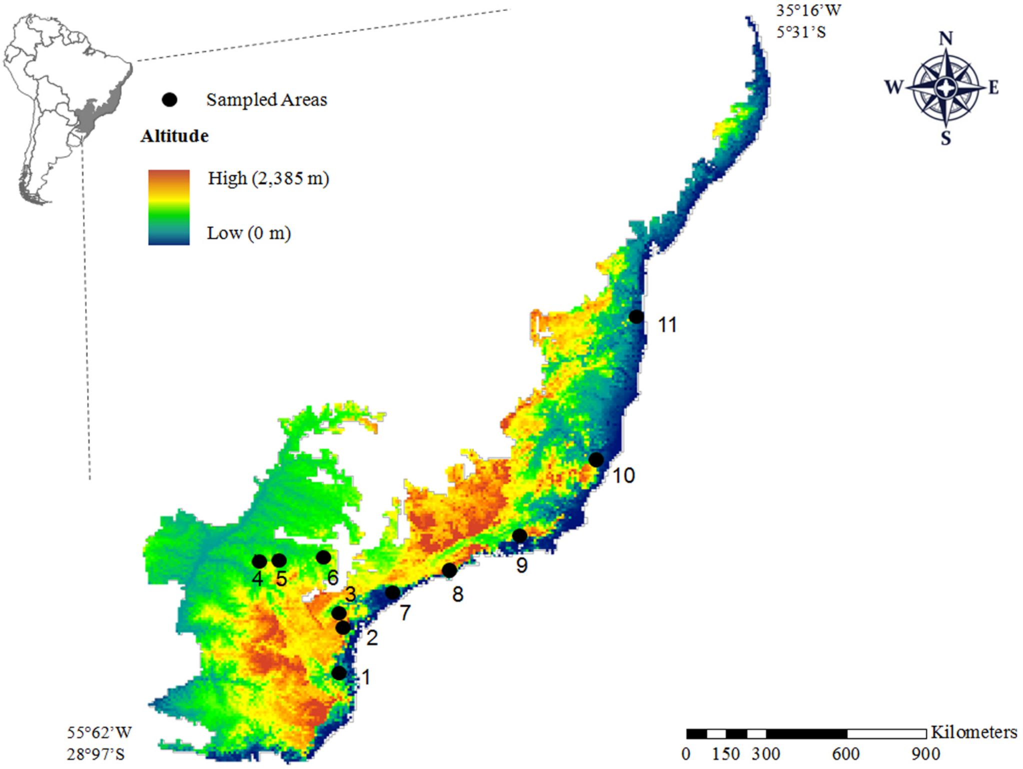

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Part II Threatened Species

Back Cover: *Hylomantis aspera* (Peters, 1873)
– Photo by Mirco Solé

Chapter 3

Protected areas network and conservation efforts concerning threatened amphibians in the Brazilian Atlantic Forest

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Protected areas network and conservation efforts concerning threatened amphibians in the Brazilian Atlantic Forest

Red de áreas protegidas y esfuerzos de conservación de anfibios amenazados en el Bosque Atlántico brasileño. El Bosque Atlántico brasileño es uno de los 35 puntos calientes de biodiversidad del planeta, con una alta tasa de pérdida de hábitat, uno de los principales factores que contribuye a la extinción de anfibios. Teniendo en cuenta que los anfibios son el grupo de vertebrados con el mayor número de especies desprotegidas, se empleó un análisis de brechas para evaluar si las áreas protegidas existentes son suficientes para conservar las especies de anfibios amenazados en esta región. Se utilizó la lista oficial de especies amenazadas de la Fauna Brasileña y los mapas de la base de datos de la Lista Roja de la Unión Internacional para la Conservación de la Naturaleza. Se encontraron 38 especies amenazadas, con 17 especies en peligro crítico, 10 en peligro y 11 vulnerables. En todo el área evaluada, solo el 9% se encuentra protegido, lo que cubre cerca de 30% del rango geográfico total de las especies evaluadas. Además, un cambio en la política ambiental de Brasil ha llevado a la degradación de varias áreas protegidas existentes. Por lo tanto, el mantenimiento de la integridad de las reservas actuales es esencial, así como una mayor inversión es necesaria para la creación de nuevas reservas, evitando la pérdida de especies y reduciendo el riesgo de extinción de las especies de anfibios amenazados en el Bosque Atlántico brasileño.

– Spanish Abstract (Resumen)

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Protected areas network and conservation efforts concerning threatened amphibians in the Brazilian Atlantic Forest

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Abstract. One of the most common conservation strategies used to preserve threatened species is the establishment of protected areas (PAs), providing a maximum representation of biodiversity with the smallest possible cost. The Brazilian Atlantic Forest is one of the 35 global biodiversity hotspots for conservation priorities, having high rate of habitat loss, which is one of the main factors driving threatened amphibians to extinction. Considering that amphibians are the vertebrate group with the largest number of species geographically excluded from global PAs, gap analysis was employed to evaluate whether or not the PAs of the Brazilian Atlantic Forest safeguard the threatened amphibian species in this region. Species status were compared through the official list of threatened species of the Brazilian Fauna and occurrence maps were obtained from the IUCN (International Union for Conservation of Nature) Red List database. Thirty-eight threatened amphibian species were found, accounting for 17 critically endangered (CR), 10 endangered (EN), and 11 vulnerable (VU). The PAs distributed in the Brazilian Atlantic Forest corresponds to only 9 % of the region's entire area. This protected network covers only 30 % of the total geographical range of the assessed species. Besides, a shift in Brazil's environmental policy has led to PAs downgrading. Therefore, the maintenance of PAs integrity is essential, as well as further investment is necessary for the creation of new reserves, avoiding species loss and reducing the extinction risk of the threatened amphibian species in the Brazilian Atlantic Forest.

1 Introduction

The establishment and maintenance of protected areas (PAs) are the most effective methods for natural environment conservation, acting as a cornerstone of conservation policies (Le Saout et al., 2013). Given that habitat loss is the most important threat to species survival, the protected sites chosen by decision-makers determine what species and how many of these are able to survive in the nature (Jenkins et al., 2015). In this sense, the most important criterion for locating and designing PAs should be to achieve maximum representation of biodiversity with the smallest possible cost (Margules and Pressey, 2000).

The Brazilian Atlantic Forest is one of the 35 global biodiversity hotspots for conservation priorities, having high rate of habitat loss (Mittermeier et al., 2011), which is the main factor driving threatened amphibians to extinction (Becker et al., 2007). Among all the vertebrates, amphibians are the group with the largest number of species geographically excluded from global PAs, which corresponds to 24 % of the

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living amphibian species (Nori et al., 2015). Some attempts to conserve threatened amphibians were proposed by previous studies which highlight parts of the Atlantic Forest as high priority areas (e.g., Loyola et al., 2008; Campos et al., 2013). In addition, some taxonomic groups of amphibians from small areas within the Atlantic Forest were identified as potential surrogates of biodiversity (Campos et al., 2014). However, the survival of threatened amphibians in fragmented landscapes is dependent on PAs, which ensure the habitat quality for these species (Urbina-Cardona, 2008; Ochoa-Ochoa et al., 2009). Therefore, this study aimed to evaluate if the PAs network of the Brazilian Atlantic Forest safeguards the populations of threatened amphibians that occur in this region.

2 Material and methods

Spatial data on the PAs were obtained from Brazil's Ministry of Environment database (http://www.mma.gov.br/areas-protegidas/cadastro-nacional-de-ucs; MMA, 2015b), including their categories and land coverage. ArcGIS 9.3® software (ESRI, 2008) was used to overlap the PAs data set on the geographical range of the threatened amphibians from the Brazilian Atlantic Forest. The distribution of each species was designed from a presence/absence matrix based on the IUCN (International Union for Conservation of Nature) Red List of Threatened Species database (IUCN, 2015).

Gap analysis (see Scott and Schipper, 2006) was performed to assess if the PAs network of Brazilian Atlantic Forest is able to support the distribution of the threatened amphibian species that occur in this region. The PAs were separated into two categories (IUCN, 2015): strict protection (IUCN categories I–II) and sustainable use (IUCN categories III–VI), identifying relative differences in the allocation of protection by each category. National, state and municipal areas were considered in the PAs network evaluated.

Finally, the conservation status of the assessed species were compared using the National Red List categories, through the official list of threatened species of the Brazilian fauna (e.g., critically endangered – CR, endangered – EN, and vulnerable – VU; MMA, 2015a).

3 Results and discussion

A total of 9309 km^2 of PAs were identified in the Brazilian Atlantic Forest, which corresponds to only 9 % of the region's entire area. In total, 38 threatened amphibian species were found, accounting for 17 critically endangered – CR, 10 endangered – EN, and 11 vulnerable – VU (see Table S1 in the Supplement). The PAs network evaluated comprises 2316.74 km^2 strict protection areas and 6992.41 km^2 sustainable use areas. This network covers only 30 % of the total geographical range of the assessed species, leaving out 70 % of the threatened amphibian species that occur in this region (Fig. 1).

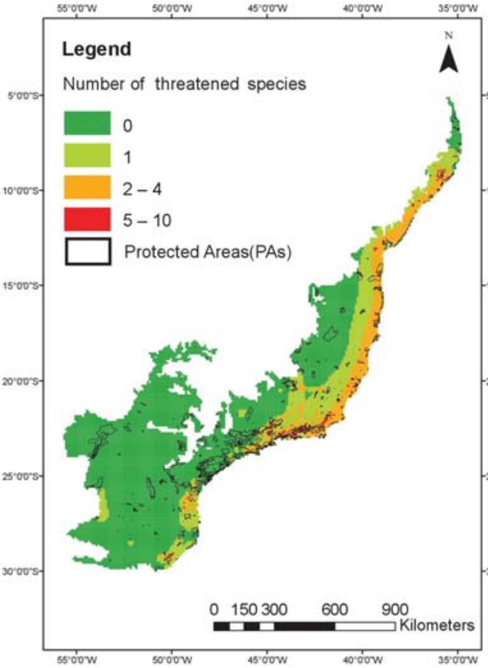

Figure 1. Map of protected areas network and geographical range of the threatened amphibian species that occur in the Brazilian Atlantic Forest.

The selection of PAs is often aimed to preserve species of different taxonomic groups, communities of high biological relevance or combinations of different abiotic conditions favourable to local ecosystems, assuming that these sites will protect a wider range of biodiversity (Lawler and White, 2008). However, many case studies have revealed the inefficiency of the PAs network in representing species diversity (Rodrigues et al., 2004). In North-eastern Brazil, Campos et al. (2013) showed that the size of the PAs along the geographical range of threatened amphibian species do not necessarily safeguard their persistence in the future, as well as observed in this study. Moreover, the number of amphibian species of the Brazilian Atlantic Forest will decline within the PAs network due to the changing climate conditions (Lemes et al., 2014). Furthermore, there is an additional risk regarding this network as it is situated within the economic core of Brazil (Ribeiro et al., 2009), with a high human population density, and the presence of mining and logging industries in the region (Lemes et al., 2014). Despite the legal restrictions on deforestation, vegetation is still extracted illegally, representing a mean rate of forest loss of around 0.15 % per year (SOS Mata Atlântica and INPE, 2015).

Most PAs in the Atlantic Forest were designed in absence of any ecological criterion and lacked consideration of species representation needs (Lemes et al., 2014). To make matters worse, a shift in Brazil's environmental policy has led to PAs downgrading, downsizing and degazettement (Bernard et al., 2014). Given this context, the results of this study are worrying and reveal that local conservation policies aimed at Brazilian Atlantic Forest PAs do not guarantee the survival of the majority of threatened amphibian populations present in this region. Despite this, the present study does not provide quantitative estimates of species extinction risk, but it does show evidence of inefficient protection for the threatened amphibian species that are covered by the current PAs network.

With the intention of proposing a cost-effective solution for local regions to implement new PAs in a stepwise fashion, Bode et al. (2008) established an economic cost of USD 68 733 for each km^2 of Brazilian Atlantic Forest. This value corresponds to only 0.2 % of the mean annual budget of the Brazilian Ministry of the Environment, which has increased in recent years (MMA, 2015b). However, this budget increase has not prevented a shift in Brazil's environmental policy, negatively affecting resources for improved PAs.

This brief overview highlights not only the crisis faced by unprotected amphibians, but it also sounds the alarm regarding the situation of species covered by the PAs network. Such context renders political will and improved environmental actions essential for the maintenance of PAs integrity, avoiding species loss and reducing the extinction risk of the threatened amphibian species in the Brazilian Atlantic Forest.

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Supplement of

Protected areas network and conservation efforts concerning threatened amphibians in the Brazilian Atlantic Forest

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Supplementary Table

Table S1. Threatened amphibian species from the Brazilian Atlantic Forest according to their National Red List categories (MMA, 2014). CR = Critically Endangered, EN = Endangered, VU = Vulnerable.

Family	Species	Category
Aromobatidae	*Allobates olfersioides*	VU
Brachycephalidae	*Brachycephalus pernix*	CR
Brachycephalidae	*Ischnocnema manezinho*	VU
Bufonidae	*Melanophryniscus admirabilis*	CR
Bufonidae	*Melanophryniscus cambaraensis*	VU
Bufonidae	*Melanophryniscus dorsalis*	VU
Bufonidae	*Melanophryniscus macrogranulosus*	EN
Bufonidae	*Melanophryniscus setiba*	CR
Craugastoridae	*Holoaden bradei*	CR
Craugastoridae	*Holoaden luederwaldti*	EN
Cycloramphidae	*Cycloramphus diringshofeni*	CR
Cycloramphidae	*Cycloramphus faustoi*	CR
Cycloramphidae	*Cycloramphus ohausi*	EN
Cycloramphidae	*Thoropa petropolitana*	EN
Cycloramphidae	*Thoropa saxatilis*	VU
Eleutherodactylidae	*Adelophryne maranguapensis*	VU
Hylidae	*Agalychnis granulosa*	VU
Hylidae	*Aparasphenodon pomba*	CR

Hylidae	*Bokermannohyla vulcaniae*	CR
Hylidae	*Hypsiboas curupi*	VU
Hylidae	*Hypsiboas cymbalum*	CR
Hylidae	*Hypsiboas semiguttatus*	EN
Hylidae	*Phyllodytes gyrinaethes*	CR
Hylidae	*Scinax alcatraz*	CR
Hylidae	*Scinax duartei*	VU
Hylidae	*Scinax faivovichi*	VU
Hylidae	*Scinax peixotoi*	CR
Hylidae	*Xenohyla truncata*	EN
Hylodidae	*Crossodactylus dantei*	EN
Hylodidae	*Crossodactylus lutzorum*	CR
Leptodactylidae	*Physalaemus caete*	EN
Leptodactylidae	*Physalaemus maximus*	VU
Leptodactylidae	*Physalaemus soaresi*	CR
Leptodactylidae	*Paratelmatobius lutzii*	CR
Microhylidae	*Chiasmocleis alagoanus*	EN
Odontophrynidae	*Proceratophrys moratoi*	EN
Odontophrynidae	*Proceratophrys palustris*	CR
Odontophrynidae	*Proceratophrys sanctaritae*	CR

Chapter 4

Threatened amphibians and their conservation status within the protected area network in northeastern Brazil

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Threatened amphibians and their conservation status within the protected area network in northeastern Brazil

Anfibios amenazados y su estado de conservación dentro de la red de áreas protegidas en el noreste de Brasil. Los anfibios son el grupo de vertebrados más amenazado del mundo. Una de las estrategias de conservación más utilizadas para preservar especies amenazadas es el establecimiento de áreas protegidas. Utilizamos un análisis de brechas para evaluar hasta qué punto la red de áreas protegidas del noreste de Brasil protege efectivamente las poblaciones de anfibios amenazados. Los datos sobre los rangos geográficos de las especies se obtuvieron de la Unión Internacional para la Conservación de la Naturaleza (UICN) y se superpusieron en la red de áreas protegidas del noreste de Brasil utilizando el programa ArcGIS 9.3. Los anfibios amenazados encontrados en el noreste brasileño estuvieron representados por poblaciones remanentes de *Adelophryne baturitensis*, *Adelophryne maranguapensis*, *Allobates olfersioides* y *Agalychnis granulosa*. Se registraron 174 áreas protegidas en la red de áreas protegidas evaluada. La red abarca 65 áreas estrictas de protección estricta (categorías I-II de la UICN) y 109 áreas de uso sostenible (categorías III-VI de la UICN). La red corresponde a más de 15 millones de hectáreas, lo que equivale a alrededor del 10% del área total de la región. Sin embargo, el tamaño de las áreas protegidas a lo largo del rango geográfico de estas especies no garantiza necesariamente su persistencia en el futuro. La principal amenaza para estas especies es la pérdida de hábitat debido a la deforestación y la expansión agrícola. Por lo tanto, la viabilidad de nuevas reservas con una diversidad de ecosistemas representativos en el noreste de Brasil puede ser la mejor solución para evitar los procesos de extinción en esta región.

– Spanish Abstract (Resumen)

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Threatened Amphibians and Their Conservation Status within the Protected Area Network in Northeastern Brazil

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ABSTRACT.—**Amphibians are the most threatened vertebrate group in the world. One of the conservation strategies most used to preserve threatened species is the establishment of protected areas. We used gap analysis to evaluate whether or not the protected area network of northeastern Brazil safeguards populations of threatened amphibians that occur in this region. Data on species geographical ranges were obtained from the International Union for the Conservation of Nature (IUCN) and were overlapped on the northeastern Brazilian protected area network using ArcGIS 9.3. The threatened amphibians found in northeastern Brazil were represented by remnant populations of *Adelophryne baturitensis*, *Adelophryne maranguapensis*, *Allobates olfersioides*, and *Agalychnis granulosa*. There are 174 protected areas in the protected area network in northeastern Brazil. The network is made up of 65 strict protection areas (IUCN categories I–II) and 109 sustainable use areas (IUCN categories III–VI). The network corresponds to more than 15 million ha, which equates to about 10% of the region's total area. However, the size of the protected areas along the geographical range of these species doesn't necessarily guarantee their persistence in the future. The main threat to these species is loss of habitat due to deforestation and agricultural expansion. Therefore, the viability of new reserves with a diversity of representative ecosystems in northeastern Brazil may be the best solution to avoid extinction processes in this region.**

More than 2,000 amphibian species are listed as threatened by extinction, such that amphibians are the most threatened vertebrate group in the world (Stuart et al., 2004). The main drivers of amphibian population declines and extinctions are habitat loss, invasive species, overexploitation, pollution, emergent infectious diseases, and climate change (Daszak et al., 2003; Kats and Ferrer, 2003; Stuart et al., 2004; Blaustein et al., 2010). The level of threat to amphibians is underestimated due to the lack of knowledge for approximately 25% of species worldwide which are categorized as "Data Deficient" (DD) (IUCN, 2011). According to the Global Amphibian Assessment (IUCN et al., 2006), the real number of threatened and extinct species of amphibians may be much larger than currently acknowledged.

The issue of protecting threatened amphibians becomes more urgent when we realize that most of the group's diversity is found in regions where scientific knowledge on amphibian biology is still scarce (Brito, 2008). Northeastern Brazil has a high amount of endemism in relation to other Brazilian regions that are considered of great biological relevance to the study and conservation of amphibians (Conservation International et al., 2000). Yet, few studies have been conducted in this area (e.g., Silvano and Pimenta, 2003; Juncá, 2006; Bastazini et al., 2007; Loebmann and Mai, 2008; Valdujo et al., 2009). According to IUCN (2011), the threatened amphibians distributed in northeastern Brazil are represented by remnant populations of *Adelophryne baturitensis*, classified as "Vulnerable" (VU), *Adelophryne maranguapensis*, classified as "Endangered" (EN), *Allobates olfersioides*, also classified as "Vulnerable" (VU), and *Agalychnis granulosa*, classified as "Least Concern" (LC) on the IUCN Red List but as "Critically Endangered" (CR) on the national red list of threatened amphibians in Brazil (Haddad, 2008). The strong decline of several amphibian species in different regions of Brazil highlights the urgent need to expand research programs and conservation efforts for these species, especially in regions such as northeastern Brazil where there are few data on diversity and species distribution (Wake, 1998; Young et al., 2001).

Amphibians are affected by different environmental factors which often operate in complex ways (Alford and Richards, 1999; Blaustein and Kiesecker, 2002; Stuart et al., 2004). Some amphibian populations declined without warning before threats could be identified (Laurance et al., 1996; Pounds et al., 1997; Lips, 1998; 1999; Wake, 1998; Pounds, 2001). The causes of decline may vary from region to region and may show synergistic interactions between more than one threat factor (Davidson and Knapp, 2007; Blaustein et al., 2010). No single factor is responsible for all amphibian declines nor is it helpful to identify particular factors as more important than others (Halliday, 2005). However, habitat alteration accounts for more declines than any other factor (e.g., Beebee and Griffiths, 2005; IUCN et al., 2006; Halliday, 2008; Becker et al., 2010).

Although there is a substantial amount of evidence showing declining populations of amphibians around the world, strategies for the study of this problem have been developed mainly by scientists from the United States, western Europe, and Australia (Houlahan et al., 2000; Young et al., 2001; Brito, 2008). Countries such as Australia and the United States already had a good knowledge about threatened species and some possible causes have been investigated and discussed (Juncá, 2001). In Brazil, few cases of the decline of amphibians have been published (e.g., Heyer et al., 1988; Weygoldt, 1989; Bertoluci and Heyer, 1995; Guix et al., 1998; Pombal and Haddad, 1999; Izecksohn and Carvalho-e-Silva, 2001; Eterovick et al., 2005). As in other Latin American countries, understanding and perhaps preventing population declines and extinctions of amphibians is hampered by a lack of information and a lack of appropriate policies to address this issue (Juncá, 2001; Silvano and Segalla, 2005). Despite this, Brazil and Mexico have published the greatest number of scientific papers on amphibians, with a conservation biology focus, in the last few years (Urbina-Cardona, 2008). Gap analysis is one neglected aspect of amphibian conservation in Brazil as well as the development of priorities to expand the protected area network (Urbina-Cardona, 2008).

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As indicated by the Amphibian Conservation Action Plan (Gascon et al., 2007), the long-term success of efforts to recover species from decline depends on society's capacity to preserve natural habitats as well as on the establishment of additional conservation area networks in order to include the distribution ranges of threatened species that are not protected by the current protected area systems. Therefore, the conservation of amphibians in fragmented landscapes is directly related to the establishment of protected areas and requires special management tools such as habitat restoration and management of forest patches, ensuring habitat quality and, hopefully, the permanence of the species (Rodrigues et al., 2004; Urbina-Cardona et al., 2006; Urbina-Cardona, 2008; Ochoa-Ochoa et al., 2009).

In this context, our objective was to evaluate if the protected area network of northeastern Brazil protects populations of threatened amphibians that occur in this region.

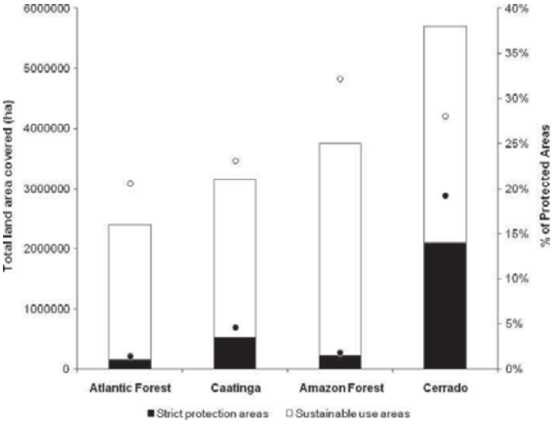

FIG. 1. Total land area covered (dots) and percentage of protected area network (bars) per biome in northeastern Brazil, according to the categories of strict protection and sustainable use.

MATERIALS AND METHODS

Northeastern Brazil extends over more than 156 million ha and includes nine states: Maranhão, Piauí, Rio Grande do Norte, Ceará, Paraíba, Pernambuco, Alagoas, Sergipe, and Bahia (Agra et al., 2008). It is a region with a rich diversity of habitats ranging from forested formations, such as the Amazon Forest in northern Maranhão and the Atlantic Forest in the coastal region, and open, arid, savannah-like habitats such as the Caatinga and the Cerrado (Ab'Saber, 1980; Andrade-Lima, 1981; Lleras, 1997).

Data on the protected area network was obtained from Brazil's Ministry of Environment database (MMA, 2011), including their categories and land coverage (see Appendix 1). All non-continental marine protected areas that are not influenced by coastal forest environments were excluded from this analysis. We obtained data on species distributions from the 2011 IUCN Red List of Threatened Species database (IUCN, 2011), which overlapped the northeastern Brazilian protected area network, using ArcGIS 9.3 (ESRI, 2008).

Gap analyses (Scott and Schipper, 2006) were used to access if the protected area network of northeastern Brazil overlaps the geographical range of the threatened amphibian species that occur in this region. The protected areas were divided into two categories (MMA, 2011): strict protection (IUCN categories I–II) and sustainable use (IUCN categories III–VI).

In addition, we compared the IUCN Red List categories and the Red Book of Threatened Brazilian Fauna categories (Machado et al., 2008) on the threatened amphibians of northeastern Brazil, identifying differences among the criteria established for each of these lists.

RESULTS

There are 174 protected areas in the network in northeastern Brazil; 65 strict protection areas (IUCN categories I–II) and 109 sustainable use areas (IUCN categories III–VI), corresponding to more than 15 million ha, which equates to about 10% of the region's total area. All of these protected areas are distributed in approximately 16% of Atlantic Forest, 21% of Caatinga, 25% of Amazon Forest, and 36% of Cerrado (see Appendix 1) according to their respective conservation categories (Fig. 1).

The threatened amphibians found in northeastern Brazil were represented by *Ad. baturitensis*, *Ad. maranguapensis*, *Al. olfersioides*, and *Ag. granulosa*. These four species have part of their geographical range overlapping protected areas (Fig. 2). Our results show that less than 10% of the protected areas that house populations of threatened amphibians are in the strict protection categories of IUCN. However, there is a mismatch on the distribution of protected areas that cover the geographical ranges of these species because 100% of occurrence areas of *Ad. maranguapensis*, 30% of *Ad. baturitensis*, 9% of *Al. olfersioides*, and 4% of *Ag. granulosa* are overlapped with sustainable use areas. Therefore, even though we may consider these species as protected, only a small fraction of their populations are within protected areas that have biodiversity protection as its main goal. The great majority of populations (i.e., approximately 90%) are under different scenarios and may be susceptible to human disturbance.

Comparing the Red Book of Threatened Brazilian Fauna with the IUCN Red List, a different relationship was identified among the criteria established for two threatened species of amphibians from northeastern Brazil (Table 1), showing that there is a mismatch between these two databases. *Agalychnis granulosa* was categorized as CR on the national red list of threatened amphibians in Brazil but was classified as LC on the IUCN Red List. The other species that showed conflicting results between these lists was *Al. olfersioides*, which wasn't classified in any category of threat for the national red list but was categorized as VU on the IUCN Red List.

DISCUSSION

A huge amount of study on threatened amphibians in northeastern Brazil is still necessary to understand the real extent of declining populations and threats to these species (Carnaval et al., 2009). In addition to monitoring threatened species populations, there is a widespread need to improve knowledge for species that are DD to ascertain whether or not they are threatened and need legislative protection (IUCN, 2011).

We provide examples for our target species that indicate where current information fails to include some extant populations and how fragmentation may indicate stricter protections. The IUCN considers the remaining populations of *Ad. baturitensis* to be endemic to Baturité Mountain (04°05′S, 38°30′W), state of Ceará, Brazil (Hoogmoed et al., 1994; Borges-Nojosa, 2008a; IUCN, 2011), where this species can be found in

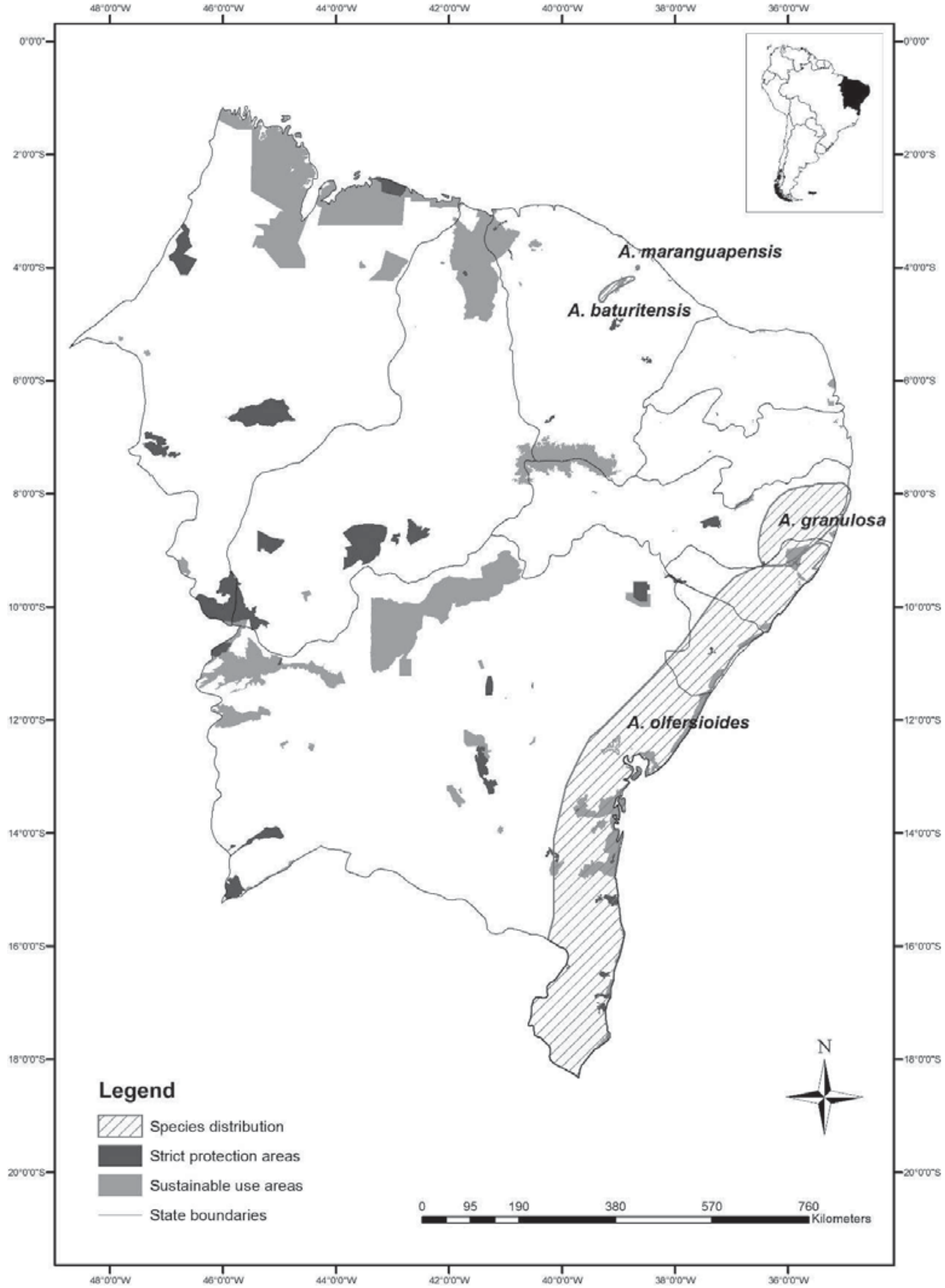

FIG. 2. Map of protected area network and geographical ranges of the threatened amphibians in northeastern Brazil.

leaf-litter, bromeliads, and stream margins of closed forests (Borges-Nojosa, 2008a). However, a new population of this species was discovered in 2010 in the Plateau of Ibiapaba (03°48′S, 40°54′W) about 220 km from its type locality (Loebmann and Haddad, 2010). Recently, Loebmann et al. (2011) reported another specimen of *Ad. baturitensis* in a mountainous region of the Atlantic Forest known as "Brejo dos Cavalos" (08°22′S, 36°02′W), state of Pernambuco, Brazil,

TABLE 1. Threatened amphibians of northeastern Brazil according to their national red list status and IUCN Red List categories.

Species	National red list status	IUCN Red List categories
Adelophryne baturitensis	Vulnerable	Vulnerable
Adelophryne maranguapensis	Endangered	Endangered
Agalychnis granulosa	Critically Endangered	Least Concern
Allobates olfersioides	—	Vulnerable

further expanding its geographical distribution. We suggest that this species must remain categorized as vulnerable according to IUCN criteria and to the national red list because of the high fragmentation of its occurrence, which seriously threatens the permanence of future generations of this species.

Adelophryne maranguapensis has a distribution restricted to the Maranguape Mountain (03°54′S, 38°32′W), state of Ceará (Borges-Nojosa, 2008b; Cassiano-Lima et al., 2011). The same information is corroborated by Frost (2011) and IUCN (2011). It is known that this location covers an enclave of the Atlantic Forest surrounded by insurmountable xeric environments (Borges-Nojosa, 2008b). This species lives in the leaf-litter of primary and secondary forests, but not in open habitats, and its occurrence is incorporated into an important protected area, the Environmental Protection Area of the Maranguape Mountain known as "APA da Serra do Maranguape" (Borges-Nojosa, 2008b). However, this species occurs in areas where there are no strict protection areas but which are affected by human activities (Borges-Nojosa, 2008b). Monocultures and other anthropogenic activities were established in this area, gradually replacing the native forest and contributing to the impoverishment of the quality of these habitats (Silvano and Borges-Nojosa, 2004; Cassiano-Lima et al., 2011). Thus, this species must remain categorized as endangered according to IUCN criteria and the national red list. Because of its restricted geographical range, we must consider that it suffers a very high risk of extinction in the wild, so the areas of occurrence of this species should be monitored.

The geographical range of *Ag. granulosa* has increased according to new reports that are emerging in the literature (e.g., Carnaval et al., 2003; Carnaval and Peixoto, 2004; Cruz, 2008). Frost (2011) records this species singly for the states of Bahia and Pernambuco at the same time when the IUCN reports its distribution in several localities between the states of Alagoas and Pernambuco (IUCN, 2011). This species is classified as LC by the IUCN Red List because it has a wide geographical distribution (Carnaval and Peixoto, 2004). Nevertheless, the Red Book of Threatened Brazilian Fauna lists this species as CR, but may change this status (Cruz, 2008; Haddad, 2008) once those new areas of occurrence have been published (Carnaval et al., 2003; Cruz, 2008). This species generally occurs in lowland Atlantic Forest with secondary forest, and at the margin of small streams, not occurring in open or severely degraded areas (Carnaval and Peixoto, 2004). We suggest that this species should be removed from the national red list because the new records reported for this species expand its known occurrence. Therefore, we should maintain the status as least concern as it is currently considered by the IUCN Red List.

Allobates olfersioides is found in several coastal areas of the Atlantic Forest from sea level to about 1,000 m above sea level (Verdade, 2010). During the last 20 yr, this species has been recorded at 33 locations in the states of Rio de Janeiro, Espírito Santo, Minas Gerais, Bahia, Sergipe, and Alagoas (e.g., Weygoldt, 1989; Izecksohn and Carvalho-e-Silva, 2001; Eterovick et al., 2005; Carnaval et al., 2006; Verdade and Rodrigues, 2007; Camurugi et al., 2010; Almeida et al., 2011). Several cases of declining populations have been reported among sites studied within the known distribution (Weygoldt, 1989; Izecksohn and Carvalho-e-Silva, 2001; Eterovick et al., 2005; Silvano and Segalla, 2005; Verdade, 2010). However, there are no clear causes to explain these observations (Heyer et al., 1988). Habitat change and fragmentation are possible factors. In Bahia, this species was considered as one of the most threatened by habitat loss in the same region where its occurrence was strongly related with the presence of bromeliads (Tinoco et al., 2008). Despite these threats, no river in the coastal region of northeastern Brazil appears to be a geographical barrier for *Al. olfersioides*, and continuous character gradients suggest uninterrupted gene flow between adjacent populations (Verdade and Rodrigues, 2007) which increases the movement of individuals among these populations. Because of its wide extent of occurrence and high encounter rate, we suggest that this species should be removed from the category of vulnerable, where it figures in the IUCN Red List, and receive the status of least concern.

Occurrence maps may overestimate the geographic range sizes of the species, distorting broadly their ecological patterns and conservation priorities (Hurlbert and White, 2005; Graham and Hijmans, 2006; McPherson and Jetz, 2007; Gaston and Fuller, 2009). The effective area of occupancy of each species evaluated within their extents of occurrence is relatively low and represents only 1% for *Ad. maranguapensis*, 5% for *Ad. baturitensis*, 31% for *Ag. granulosa*, and 33% for *Al. olfersioides* (IUCN, 2011). Based on the Post-2010 Strategic Plan of the Convention on Biological Diversity (Conservation International, 2010), we suggest that, to maintain the persistence of the ecosystem processes provided by threatened amphibians in northeastern Brazil, new protected areas should be created and should cover at least 25% of the area of occupancy of each species analyzed, which corresponds to a minimum of approximately 800 ha of Atlantic Forest ecosystems.

The most suitable and economically viable way to protect threatened amphibians in countries like Brazil with high biodiversity is by means of in situ conservation through the establishment of protected areas (Haddad, 2008), such that new reserves with a representative diversity of Atlantic Forest ecosystems in northeastern Brazil may be the best solution to avoid the local processes of extinction. According to Haddad (2008), the ex situ conservation, which is based on maintenance and reproduction of threatened species outside their natural habitats, is not a good strategy for the Brazilian amphibians. In the ecosystems already heavily fragmented by anthropogenic activities, other actions are necessary; for example, the recovery of degraded areas and the creation of forest corridors connecting patches of the isolated habitats (Eterovick et al., 2005).

In developing effective actions to reverse threats and address declines, the governmental agencies responsible for public policy and management of Brazilian biodiversity should incorporate published studies on threatened amphibians in Brazil. Support and resources from national or international non-governmental organizations will be useful in achieving this (Machado et al., 2008).

As we do not know exactly what we have in terms of species richness and little is known about the populations of the species already described, conservation is a very difficult task. Our study provides a simple approach that could be replicated in other regions and other countries, addressing detailed information about the conservation status of other threatened species.

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APPENDIX 1. Protected areas analyzed in northeastern Brazil according to MMA (2011).

Name of the protected area	Federal unit[a]	Hectares	Biome
Reserva Biológica do Gurupi[b]	MA	271,197.50	Amazon
Estação Ecológica do Castanhão[b]	CE	12,574.44	Caatinga
Parque Nacional das Nascentes do Rio Parnaíba[b]	PI, MA, BA	730,188.43	Cerrado
Parque Nacional de Ubajara[b]	CE	6,271.22	Caatinga
Parque Nacional de Sete Cidades[b]	PI	6,303.64	Caatinga
Estação Ecológica do Seridó[b]	RN	1,123.59	Caatinga
Estação Ecológica de Aiuaba[b]	CE	11,755.13	Caatinga
Reserva Biológica Guaribas[b]	PB	2,703.31	Atlantic Forest
Parque Nacional do Catimbau[b]	PE	62,294.20	Caatinga
Parque Nacional da Serra das Confusões[b]	PI	523,923.56	Cerrado/Caatinga
Reserva Biológica de Serra Negra[b]	PE	624.84	Caatinga
Reserva Biológica de Saltinho[b]	PE	562.56	Atlantic Forest
Estação Ecológica de Murici[b]	AL	6,131.54	Atlantic Forest
Reserva Biológica de Pedra Talhada[b]	AL, PE	3,742.12	Atlantic Forest
Estação Ecológica do Raso da Catarina[b]	BA	104,842.52	Caatinga
Refúgio de Vida Silvestre das Veredas do Oeste Baiano[b]	BA	128,048.97	Cerrado
Parque Nacional do Pau-Brasil[b]	BA	18,952.51	Atlantic Forest
Parque Nacional do Descobrimento[b]	BA	21,145.05	Atlantic Forest
Parque Nacional da Chapada Diamantina[b]	BA	151,941.21	Cerrado/Caatinga
Parque Nacional Grande Sertão Veredas[b]	BA	230,853.41	Cerrado
Parque Estadual da Serra do Conduru[b]	BA	9,365.53	Atlantic Forest
Parque Nacional do Monte Pascoal[b]	BA	22,331.90	Atlantic Forest
Parque Estadual das Sete Passagens[b]	BA	2,822.07	Caatinga
Parque Nacional da Serra de Itabaiana[b]	SE	7,998.98	Atlantic Forest
Parque Estadual da Pedra da Boca[b]	PB	258.33	Caatinga
Parque Estadual do Jacarapé[b]	PB	383.57	Atlantic Forest
Parque Estadual do Aratu[b]	PB	351.53	Atlantic Forest
Parque Estadual Pico do Jabre[b]	PB	851.24	Caatinga
Monumento Natural da Cachoeira do Ferro Doído[b]	BA	362.09	Caatinga
Parque Estadual de Morro do Chapéu[b]	BA	48,504.27	Caatinga
Parque Nacional dos Lençóis Maranhenses[b]	MA	156,605.73	Cerrado
Estação Ecológica de Wenceslau Guimarães[b]	BA	2,419.40	Atlantic Forest
Monumento Natural dos Cânions do Subaé[b]	BA	404.46	Atlantic Forest
Estação Ecológica da Chapada da Serra Branca[b]	PI	24,603.29	Caatinga
Parque Municipal da Lagoa do Frio[b]	SE	113.13	Caatinga
Monumento Natural Grota do Angico[b]	SE	2,142.76	Caatinga
Monumento Natural dos Monólitos de Quixadá[b]	CE	28,782.19	Caatinga
Monumento Natural das Falésias de Beberibe[b]	CE	31.31	Atlantic Forest
Parque Ecológico do Rio Cocó[b]	CE	1,046.90	Atlantic Forest
Estação Ecológica do Pecém[b]	CE	978.23	Atlantic Forest
Monumento Natural Vale dos Dinossauros[b]	PB	39.19	Caatinga
Parque Estadual do Poeta[b]	PB	6.84	Caatinga
Parque Estadual Dunas de Natal[b]	RN	1,135.08	Atlantic Forest
Parque Estadual Mapa da Pipa[b]	RN	290.73	Atlantic Forest
Parque Estadual Florêncio Luciano[b]	RN	445.60	Caatinga
Estação Ecológica de Uruçuí-Una[b]	PI	138,681.28	Cerrado
Refúgios de Vida Silvestre do Rio dos Frades[b]	BA	888.39	Atlantic Forest
Parque Estadual do Mirador[b]	MA	446,446.97	Cerrado
Parque Estadual do Itapiracó[b]	MA	355.32	Amazon
Parque Estadual do Bacanga[b]	MA	2,622.70	Amazon
Estação Ecológica do Sítio Rangedor[b]	MA	127.00	Amazon
Monumento Natural do Rio São Francisco[b]	BA, SE, AL	26,736.29	Caatinga
Reserva Biológica de Santa Isabel[b]	SE	5,547.41	Atlantic Forest
Parque Nacional de Jericoacoara[b]	CE	8,379.62	Atlantic Forest
Estação Ecológica Serra Geral do Tocantins[b]	BA	718,387.94	Cerrado
Parque Nacional de Boa Nova[b]	BA	12,065.30	Atlantic Forest
Refúgio de Vida Silvestre de Boa Nova[b]	BA	15,023.85	Atlantic Forest
Refúgio de Vida Silvestre de Una[b]	BA	23,423.33	Atlantic Forest
Reserva Biológica de Una[b]	BA	18,515.14	Atlantic Forest
Parque Nacional de Serra das Lontras[b]	BA	11,343.69	Atlantic Forest
Parque Nacional do Alto do Cariri[b]	BA	19,237.54	Atlantic Forest
Parque Estadual de Dois Irmãos[b]	PE	392.75	Atlantic Forest
Estação Ecológica de Caetés[b]	PE	167.31	Atlantic Forest
Parque Estadual Sítio Fundão[b]	CE	93.93	Caatinga
Parque Estadual das Carnaúbas[b]	CE	9,955.10	Caatinga
APA Costa dos Corais[c]	AL, PE	404,281.23	Atlantic Forest
APA do Maracanã[c]	MA	950.95	Amazon
APA do Pratagy[c]	AL	13,743.29	Atlantic Forest
APA das Nascentes do Rio Vermelho[c]	BA	176,322.22	Cerrado
ARIE Manguezais da Foz do Rio Mamanguape[c]	PB	5,769.47	Atlantic Forest
RESEX do Quilombo Flexal[c]	MA	8,740.53	Amazon
RESEX do Ciriáco[c]	MA	7,162.06	Amazon
RESEX Marinha da Lagoa do Jequiá[c]	AL	10,203.80	Atlantic Forest

APPENDIX 1. Continued.

Name of the protected area	Federal unit[a]	Hectares	Biome
Floresta Nacional de Sobral[c]	CE	593.24	Caatinga
Floresta Nacional de Cristópolis[c]	BA	12,790.53	Cerrado
APA Cabeceira do Rio das Balsas[c]	MA	60,831.10	Cerrado
APA do Rangel[c]	PI	21,269.75	Cerrado
APA da Cachoeira do Urubu[c]	PI	3,280.03	Caatinga
APA da Bica do Ipu[c]	CE	3,469.70	Caatinga
Floresta Nacional Contendas do Sincorá[c]	BA	11,215.77	Caatinga
RESEX de Canavieiras[c]	BA	100,726.35	Atlantic Forest
APA Santo Antonio[c]	BA	25,921.66	Atlantic Forest
ARIE Serra do Orobó[c]	BA	7,398.44	Caatinga
APA das Onças[c]	PB	39,016.24	Caatinga
APA do Estuário do Rio Curu[c]	CE	872.59	Atlantic Forest
APA do Lagamar do Cauípe[c]	CE	775.49	Atlantic Forest
APA do Estuário do Rio Mundaú[c]	CE	1,549.47	Atlantic Forest
APA das Dunas de Paracuru[c]	CE	3,754.28	Atlantic Forest
APA da Serra de Maranguape [c]	CE	6,453.20	Atlantic Forest
APA da Serra de Baturité[c]	CE	30,239.70	Atlantic Forest
Floresta Nacional de Palmares[c]	PI	168.20	Caatinga
APA Gruta de Brejões/Vereda do Romão Gramado[c]	BA	11,889.58	Caatinga
ARIE Nascente do Rio de Contas[c]	BA	4,764.42	Caatinga
APA Serra do Barbado[c]	BA	68,038.20	Caatinga
APA Marimbus-Iraquara[c]	BA	124,967.26	Caatinga
APA Lagoa Itaparica[c]	BA	78,142.99	Caatinga
APA Baixada Maranhense[c]	MA	1,788,463.84	Amazon
APA Upaon-Açu/Miritiba/Alto Preguiça[c]	MA	1,565,066.32	Amazon
APA do Delta do Parnaíba[c]	MA, PI	280,515.32	Cerrado/Amazon
APA Serra Branca/Raso da Catarina[c]	BA	67,515.44	Caatinga
APA de Piaçabuçu[c]	AL	8,894.12	Atlantic Forest
APA Barra do Rio Mamanguape[c]	PB	14,924.21	Atlantic Forest
APA da Lagoa de Jijoca[c]	CE	3,938.25	Atlantic Forest
RESEX Marinha do Corumbau[c]	BA	89,647.61	Atlantic Forest
APA Caraíva-Trancoso[c]	BA	25,460.39	Atlantic Forest
APA Ponta da Baleia-Abrolhos[c]	BA	345,330.75	Atlantic Forest
APA Serra da Ibiapaba[c]	PI	1,617,873.13	Cerrado/Caatinga
APA Joanes-Ipitanga[c]	BA	66,637.55	Atlantic Forest
APA Lagoas e Dunas do Abaeté[c]	BA	1,242.23	Atlantic Forest
APA Dunas e Veredas do Baixo Médio São Francisco[c]	BA	1,024,802.12	Cerrado/Caatinga
RESEX Marinha do Delta do Parnaíba[c]	MA	27,021.63	Cerrado/Amazon
Floresta Nacional do Ibura[c]	SE	144.13	Atlantic Forest
RESEX Chapada Limpa[c]	MA	11,973.04	Cerrado
RESEX Acaú-Goiana[c]	PE, PB	6,676.66	Atlantic Forest
Floresta Nacional de Negreiros[c]	PE	3,004.51	Caatinga
APA Lago do Sobradinho[c]	BA	1,235,356.62	Cerrado/Caatinga
APA da Serra do Ouro[c]	BA	50,689.81	Atlantic Forest
APA do Rio Preto[c]	BA	1,138,497.69	Cerrado
APA Bacia do Rio de Janeiro[c]	BA	300,305.61	Cerrado
APA de São Desidério[c]	BA	11,130.23	Cerrado
ARIE Cocorobó[c]	BA	7,473.38	Caatinga
APA Plataforma Continental do Litoral Norte[c]	BA	350,144.36	Atlantic Forest
APA Mangue Seco[c]	BA	2,711.53	Atlantic Forest
APA Bacia do Cobre/São Bartolomeu[c]	BA	1,170.59	Atlantic Forest
APA Rio Capivara[c]	BA	3,309.05	Atlantic Forest
APA Lago de Pedra do Cavalo[c]	BA	47,244.25	Caatinga
APA Guaibim[c]	BA	2,071.81	Atlantic Forest
APA Caminhos Ecológicos da Boa Esperança[c]	BA	230,351.28	Atlantic Forest
APA das ilhas Tinharé e Boipeba[c]	BA	31,071.40	Atlantic Forest
APA Pratigi[c]	BA	93,486.64	Atlantic Forest
APA Baía de Camamu[c]	BA	103,146.96	Atlantic Forest
APA Lagoa Encantada e Rio Almada[c]	BA	158,031.40	Atlantic Forest
APA Costa de Itacaré/Serra Grande[c]	BA	63,577.15	Atlantic Forest
APA Litoral Norte do Estado da Bahia[c]	BA	144,688.64	Atlantic Forest
APA Lagoas de Guarajuba[c]	BA	2,028.69	Atlantic Forest
APA do Litoral Norte[c]	SE	45,729.00	Atlantic Forest
APA do Litoral Sul[c]	SE	43,916.69	Atlantic Forest
APA Morro do Urubu[c]	SE	215.00	Atlantic Forest
APA da Foz do Rio Vaza-Barris[c]	SE	976.94	Atlantic Forest
APA das Dunas da Lagoinha[c]	CE	498.45	Atlantic Forest
APA do Pecém[c]	CE	122.15	Atlantic Forest
APA do Estuário do Rio Ceará[c]	CE	2,365.64	Atlantic Forest
APA do Rio Pacoti[c]	CE	2,910.44	Atlantic Forest
APA da Lagoa do Uruaú[c]	CE	2,734.14	Atlantic Forest
APA Coroa Vermelha[c]	BA	3,715.23	Atlantic Forest

APPENDIX 1. Continued.

Name of the protected area	Federal unit[a]	Hectares	Biome
APA de Murici[c]	AL	129,526.17	Atlantic Forest
APA do Catolé e Fernão Velho[c]	AL	3,712.24	Atlantic Forest
APA de Santa Rita[c]	AL	9,565.91	Atlantic Forest
APA da Marituba do Peixe[c]	AL	18,534.41	Atlantic Forest
ARIE Mata de Goiamunduba[c]	PB	112.02	Caatinga
RDS Ponta do Tubarão[c]	RN	12,901.63	Atlantic Forest
APA Piquiri-Una[c]	RN	12,010.32	Atlantic Forest
APA Bonfim-Guaraíra[c]	RN	42,973.49	Atlantic Forest
APA de Jenipabu[c]	RN	1,749.85	Atlantic Forest
APA das Reentrâncias Maranhenses[c]	MA	979,553.78	Amazon
RESEX de Cururupu[c]	MA	185,195.13	Amazon
APA Serra da Meruoca[c]	CE	29,361.27	Caatinga
RESEX do Batoque[c]	CE	601.43	Atlantic Forest
RESEX Mata Grande[c]	MA	10,571.84	Cerrado
Floresta Nacional de Açu[c]	RN	432.56	Caatinga
APA da Foz do rio Preguiças[c]	MA	275,207.64	Cerrado/Amazon
RESEX de Cassurubá[c]	BA	100,767.56	Atlantic Forest
RESEX Prainha do Canto Verde[c]	CE	29,804.99	Atlantic Forest
Floresta Nacional de Nísia Floresta[c]	RN	168.83	Atlantic Forest
APA dos Morros Garapenses[c]	MA	234,793.34	Cerrado
APA Chapada do Araripe[c]	CE, PE, PI	972,590.45	Caatinga
Floresta Nacional do Araripe-Apodi[c]	CE	38,330.94	Caatinga
RESEX Marinha da Baía do Iguape[c]	BA	10,082.44	Atlantic Forest
APA Baía de Todos os Santos[c]	BA	137,970.82	Atlantic Forest
APA de Guadalupe[c]	PE	44,306.60	Atlantic Forest
APA de Santa Cruz[c]	PE	37,885.67	Atlantic Forest
Floresta Nacional da Restinga de Cabedelo[c]	PB	113.17	Atlantic Forest
ARIE da Barra do Rio Camaratuba[c]	PB	168.33	Atlantic Forest
ARIE do Sítio Curió[c]	CE	50.78	Caatinga

[a] AL = Alagoas, BA = Bahia, CE = Ceará, MA = Maranhão, PB = Paraíba, PE = Pernambuco, PI = Piauí, RN = Rio Grande do Norte, SE = Sergipe.
[b] Strict protection areas (IUCN categories I–II).
[c] Sustainable use areas (IUCN categories III–VI).

Part III

Climate Change

Back Cover: *Gastrotheca albolineata* (Lutz and Lutz, 1939)
– Photo by Felipe S. Campos

Chapter 5

Looking for networks: ecological connectivity for amphibians under climate change

Article Submitted to Journal for Nature Conservation
Status: Under Review

Looking for networks: ecological connectivity for amphibians under climate change

Buscando redes: conectividad ecológica para anfibios bajo cambio climático. La conectividad ecológica depende de elementos clave dentro del paisaje, que pueden soportar los flujos ecológicos, la riqueza de especies y la viabilidad a largo plazo de una comunidad biológica. En este estudio, evaluamos la relación entre las variables ambientales y la distribución de especies de anfibios en los remanentes forestales a lo largo del Corredor Central del Bosque Atlántico, utilizando métricas complementarias de conectividad ecológica y cambio climático. Realizamos una clasificación de paisaje basada en teorías gráficas y de circuitos para identificar la sensibilidad de las áreas conectadas a los cambios dependientes del clima. Nuestros resultados indican una pérdida de conectividad forestal de más del 70% por el cambio climático. Destacamos que las bajas tasas de reemplazamiento en áreas de gran altitud pueden contribuir a hacer de las montañas del Bosque Atlántico un poderoso refugio climático de anfibios para 2080. Recomendamos un monitoreo a largo plazo para comprender la sostenibilidad de los anfibios en este mosaico de fragmentos de bosques, con énfasis en la región sur de Bahía. Este trabajo ha buscado avanzar en el conocimiento sobre la conectividad ecológica de restos forestales en peligro y respalda estrategias de conservación frente a los desafíos del cambio climático.

– Spanish Abstract (Resumen)

Looking for networks: ecological connectivity for amphibians under climate change

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KEYWORDS

Anura
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ABSTRACT

Ecological connectivity depends on key elements within the landscape, which can support ecological fluxes, species richness and long-term viability of a biological community. Landscape planning requires clear aims and quantitative approaches to identify which key elements can reinforce the spatial coherence of protected areas design. In this study, we evaluate the relation between environmental variables and amphibian species distribution in the forest remnants across the Central Corridor of the Atlantic Forest, using complementary metrics of ecological connectivity and climate change. We conduct a landscape-scale analysis based on graph and circuit theories for identifying the sensitivity of connected areas to climate-dependent changes. Our results indicate a forest connectivity loss of more than 70% by predicted climate change that in turn can drastically reduce amphibian dispersal in this region. However, low turnover rates in high altitude areas can support the Atlantic Forest mountains as a powerful amphibian climatic refuge by 2080. We reveal a general pattern of low-conductance areas in the landscape surface, yet with some well-connected patches suggested as potential corridors. Our findings highlight the importance of the southern Bahia region in this mosaic of forest remnants, drafting a blueprint for functional connectivity within the landscape. We introduce new priorities for landscape assessments in the Atlantic Forest within the wider concept of habitat availability, validating a useful approach for practical conservation planning.

INTRODUCTION

The implementation of Protected Areas (PAs) is among the most effective methods for long-term biodiversity conservation plans (Rodrigues et al., 2004), working as a key-strategic tool in the development of environmental policies and efforts to sustain natural ecosystem processes (Le Saout et al., 2013; Laurance, Sayer, & Cassman, 2014). The selection of PAs is often aimed to preserve species of different taxonomic groups, communities of high biological relevance or combinations of different abiotic conditions favourable to local ecosystems, assuming that these sites will protect a wider range of biodiversity (Lawler & White, 2008). Given that habitat loss is the most important threat to species survival, the protected sites chosen by decision-makers determine what species and how many of these will be able to survive in the nature (Jenkins et al., 2015).

Among all vertebrates, amphibians are the group with the largest number of species geographically excluded from global PAs, corresponding to 24% of the living amphibian species (Nori et al., 2015). Conservation strategies aimed at protecting threatened amphibians were proposed by previous studies that highlighted parts of the Brazilian Atlantic Forest as high priority areas (e.g., Loyola et al., 2008; Campos, Brito, & Solé, 2013; Lemes & Loyola, 2013; Dias, Medeiros, Nova, & Solé, 2014). In addition, some taxonomic groups of amphibians from small areas within the Atlantic Forest were identified as potential surrogates of biodiversity in Brazil (Campos, Trindade-Filho, Brito, Llorente, & Solé, 2014). However, the survival of threatened amphibians in fragmented landscapes is dependent on the integrity and persistence of PAs, which can ensure the habitat quality for these species (Urbina-Cardona, 2008; Ochoa-Ochoa, Urbina-Cardona, Vázquez, Flores-Villela, & Bezaury-Creel, 2009).

The economic growth policy in Brazil is widely based on the expansion of agricultural frontiers (Ribeiro, Metzger, Martensen, Ponzoni, & Hirota, 2009), directly affecting the availability and the distribution of forest remnants in scattered private lands, which are gradually becoming crop and pasture production areas (Tabarelli, Cardoso Da Silva, & Gascon, 2004). Forest isolation is a critical factor in biological community structure and fundamentally important in a habitat fragmentation context (Metzger, 2009). This means that the use of ecological connectivity metrics can be good indicators for measuring the isolation of PAs and their biological relations (Gurrutxaga, Rubio, & Saura, 2011). Assessing ecological connectivity among PAs is becoming a relevant subject of growing international effort in relation to nature conservation policies (Bennett & Mulongoy, 2006; Worboys, Francis, & Lockwood, 2010). The reason behind this seems to be the importance given of avoiding the functional isolation of protected areas (Carroll, Noss, Paquet, &

Schumaker, 2004), halting the biodiversity loss and mitigating the effects of climate change on the population structure of endemic species (Bennett & Mulongoy, 2006; Opdam & Wascher, 2004).

How could ecologists predict when, how and where those climate changes will happen? In an attempt to answer this question, modelling species responses to different climatic scenarios of environmental conditions has proved to be an effective tool (Carnaval & Moritz, 2008; Diniz-Filho et al., 2009; Austin & Van Niel, 2011; Araújo & Peterson, 2012). Trying to reach more consistent outcomes, researchers have implemented mechanistic approaches to forecasts by combining environmental spatial data to ecological processes (Elith, Kearney, & Phillips, 2010; Franklin, 2010; Kearney, Wintle, & Porter, 2010). These predictions can make useful contributions to decision-making regarding biodiversity conservation. However, uncertainties about the input data constrain the effectiveness of the model outcomes.

Some studies suggest that tropical species have narrow thermal tolerance and are already living close to their upper thermal limits (Deutsch et al., 2008; Tewksbury, Huey, & Deutsch, 2008; Huey et al., 2009; Dillon, Wang, & Huey, 2010; Duarte et al., 2012). If the heating forecast is confirmed (IPCC, 2014), species that are living close to their thermal limit will need to migrate in search of climatic refuges to ensure the viability of their populations. Many studies revealed that climate change can alter species' dispersal patterns (Pearson & Dawson, 2003; Raxworthy et al., 2008), as well as significant species turnover (Peterson et al., 2002), but only few studies considered the potential impact of climate change on fragmentation of populations (Duan, Kong, Huang, Varela, & Ji, 2016). In this context, ecological connectivity of forest landscapes is of paramount importance to ensure the flow of species among potential climate refuges (Pearson & Dawson, 2005). Spatial arrangements and geographic ranges of species reflect the outcomes of a balance between several ecological processes, of which dispersal is a critical driver of range dynamics (Brown, Stevens, & Kaufman, 1996; Kirkpatrick & Barton, 1997; Holt & Keitt, 2000; Gaston, 2003; Bridle & Vines, 2007). Species dispersal can affect the ecological connectivity and play an important role in determining the probability of species persistence in suitable landscapes across space and time (Martensen, Saura, & Fortin, 2017).

Ecological corridors and landscape connectivity are usually linked, with a series of short-term implications for ecosystem functioning, yet their efficiency relies on landscape patterns and species responses at different spatial scales (Ribeiro et al., 2017). Functional connectivity strategies depend not only on the existence of structural connections between habitat patches but also on habitat suitability, stepping stones, matrix permeability and the target organisms' responses to these elements (Tischendorf & Fahrig, 2000; Baum, Haynes, Dillemuth,

& Cronin, 2004). Graph and circuit theories are complementary methods that have been used to provide efficient approaches for identifying biodiversity corridors (McRae, Dickson, Keitt, & Shah, 2008; Spear, Balkenhol, Fortin, McRae, & Scribner, 2010). While circuit theory models outline high-conductance areas between patches (McRae et al., 2008), graph-based models determine the optimal least cost routes pairwise landscape distances (Urban & Keitt, 2001). However, efficient ecological corridors must facilitate dispersal movements and consider species life-history requirements (Rosenberg, Noon, & Meslow, 1997). In this context, amphibians have been cited as highly appropriate species for examining landscape effects on community structure, due to their relatively limited mobility, sensitivity to dispersal barriers and strong microhabitat associations (Austin, Lougheed, Neidrauer, Chek, & Boag, 2002; Spear, Peterson, Matocq, & Storfer, 2005; Lee-Yaw, Davidson, McRae, & Green, 2009).

Here, we explore the probability of the ecological connectivity of forest remnants and amphibian species distributions for current and future climate scenarios. For this purpose, we aim to: (1) show how the ecological connectivity can be used to represent the forest remnants that most contribute to uphold amphibian connectivity in the Central Corridor of the Atlantic Forest; (2) estimate the species turnover between current and future amphibian species distributions; (3) evaluate if the protected area network of this corridor safeguards the amphibian species that occur in this region, testing if this network can work as an effective biodiversity corridor; and (4) assess the relation between environmental variables and amphibian species distributions in the protected network evaluated. We also provide spatial predictions and enable further comparisons possibilities of both correlative and mechanistic approaches effectiveness in biodiversity corridors under climate change.

MATERIALS AND METHODS

Study Area

The Atlantic Forest represents one of the five most important biodiversity hotspots on Earth (Mittermeier, Turner, Larsen, Brooks, & Gascon, 2011). Originally, it covered around 1,500,000 km^2, of which only about 12% (i.e., 194 524 km^2) still remains in Brazil, Paraguay and Argentina (Ribeiro et al., 2009), corresponding to about 100,000 km^2 of Brazilian forest remnants (Tabarelli, Pinto, Silva, Hirota, & Bede, 2005). Despite having high rates of habitat loss (Teixeira, Soares-Filho, Freitas, & Metzger, 2009), which is one of the main factors driving amphibians to extinction (Stuart et al., 2004; Becker, Fonseca, Haddad, Batista, & Prado, 2007), the Atlantic Forest is the leader biome in amphibian diversity in Brazil (Haddad et al., 2013), accounting more than 50% of all Brazilian amphibian species (Haddad et al., 2013).

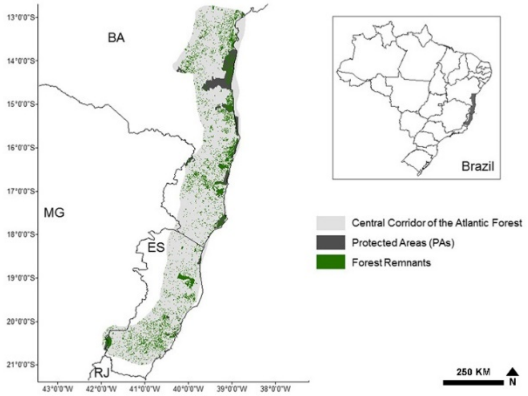

Fig. 1. Location of the Central Corridor of the Atlantic Forest, in eastern Brazil, representing their Protected Areas and Forest Remnants. BA: Bahia; MG: Minas Gerais; ES: Espírito Santo; RJ: Rio de Janeiro.

We focused our study in the Central Corridor of the Atlantic Forest (Fig. 1), which comprises about 8% of the total biome area (i.e., 7,913.42 km^2), covering 14% of forest remnants (SOS Mata Atlântica & INPE, 2015). Here, we used the term Brazilian Atlantic Forest to refer to the forest remnants map provided by SOS Mata Atlântica and INPE (2015).

Protected networks

We evaluated all the PAs covered by the Central Corridor of the Atlantic Forest, providing information on the political categories and the sizes of each PA, as well as their associated amphibian species richness and local environmental data. We measured the PAs spatial data through the Brazil's Ministry of Environment database (MMA, 2015).

We also performed a permutational multivariate analysis of variance (PERMANOVA) to assess the response of the species richness by political category of each PA against four environmental variables (i.e., altitude, temperature, precipitation, and forest cover). For this, we used 1,000 permutations based on a Euclidean distance matrix, through the "adonis" function in the "vegan" R package (Oksanen et al., 2013; R Core Team, 2015).

Species distribution data

We obtained spatial data of amphibian species from a joint research through four procedures types: 1) we selected the species that occur in the Central Corridor of the Atlantic Forest through the Atlantic Forest dataset proposed by Haddad et al. (2013); 2) we included the species occurrences records available through the Global Biodiversity Information Facility (GBIF: http://www.gbif.org); 3) we added maps of geographical ranges for each species from the IUCN Red List of Threatened Species database (IUCN, 2016); 4) we selected and filtered out the species that only occur in forested environments overlapping the spatial species data by the Atlantic Forest remnant map (SOS Mata Atlântica & INPE, 2015), excluding all urban and non-forested areas from the species distribution data. Thus, we referred only to the species distributed in the forest remnants assessed.

We used ArcGIS 10 software (ESRI, 2011) to build presence/absence matrices from the species distribution data by overlapping a grid system with cells of 0.1 latitude/longitude degrees, creating a network with 838 grid cells. In total, we assessed the spatial occurrence of 146 amphibian species in our grid system. We only considered spatial occurrences by those species where the distribution data intersected at least a grid cell. We also used the "Count Overlapping Polygons" ArcGIS toolbox to obtain the species richness at the spatial resolution assessed, removing all duplicate records from the analyses (i.e., repeated records of a species at a single locality).

Climate models and environmental data

Given that species occurrence patterns are determined at large-scales by responses of organisms to different climatic conditions (reflecting the Grinellian component of the ecological niche; see Soberón, 2007), we used Ecological Niche Models (ENMs) to predict the distribution area of amphibian species in the Central Corridor of the Atlantic Forest. For this, we used the species occurrence matrix and the layers of climatic variables, resulting in a suitability matrix, which we used to modeling and mapping the potential distribution of each species evaluated.

To develop the spatial range models, we used current and future climate data according to the CMIP5 – Coupled Models Intercomparison Project Phase 5 (http://cmip-pcmdi.llnl.gov), from one coupled atmosphere-ocean global climate models (AOGCMs). We used the MIROC5 model simulation for 2080 (mean of simulations for 2080-2100), which represents a moderated emission scenario within an optimistic context (RCP 4.5; Taylor, Stouffer, & Meehl, 2012). We based the model projections on seven climatic variables: 1) annual mean temperature, 2) temperature seasonality, 3) mean temperature of the warmest and 4) coldest quarters, 5) annual precipitation, and 6) precipitation of the driest and 7) wettest quarters. We obtained these climatic data through the EcoClimate database (http://ecoclimate.org; Lima-Ribeiro et al., 2015), and downscaled to the resolution of 0.1 latitude/longitude degrees to fit our spatial scale. We also used altitude as predictor of richness and dispersion from the dataset available at WorldClim Global Climate Data (www.worldclim.org; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005).

To develop the potential distribution map for the forest remnants associated with all the climatic variables adopted in these predictions, we used the maximum entropy method implemented in the software MaxEnt (Phillips, Anderson, & Schapire, 2006). This method is a machine learning technique that estimates the distribution in probability nearest in the uniform distribution under the restriction that the expected values for each environmental variable are consistent with the empirical values observed in the occurrence points (Phillips et al., 2006). For each ENM, we converted the continuous predictions of suitability into a binary vector of 1/0 (presence/absence), finding the threshold that maximizes sensitivity and specificity values in the receiver operating characteristic (ROC). The ROC curve is generated by plotting values of the relative frequency of true positive records predicted by a given model against the values of the relative frequency of pseudo absence records, generating the Area Under the Curve (AUC). For this purpose, one third of the occurrence records are set aside from modeling as test points (Phillips et al., 2006). Values of AUC range from 0.5 (i.e., random) for models with no predictive ability to 1.0 for models giving perfect predictions. According to the classification of Swets (1988), AUC values above 0.9 describe “very good”, 0.8 “good”, and 0.7 “useful” discrimination abilities.

We assessed the potential current and future distributions of the forest cover according to the current vegetation remnants map of the Brazilian Atlantic Forest (SOS Mata Atlântica & INPE, 2015), of which we excluded all the areas where there are currently agriculture, urban zones or settlements, only representing forest remnants without overlaps.

Species turnover

To determine the species geographic distribution patterns, we also used the maximum entropy method implemented in the software MaxEnt (Phillips et al., 2006), following the same climatic variables adopted in the modeling process for the forest remnants assessed. However, in this case we employed the modeling strategy at the community level of “predict first, assemble later” (Overton, Stephens, Leathwick, & Lehmann, 2002), where the ranges of individual species are modelled one at a time as a function of environmental predictors and then overlapped for obtaining the species richness. We calculated the species turnover between current and future amphibian species distributions according to the equation proposed by Thuiller, Lavorel, Araujo, Sykes, & Prentice (2005):

$$\mathit{Species\ Turnover} = 100*((G+L)/(S+G))$$

where “G” refers to the number of species gained, “L” the number of species lost and “S” the contemporary species richness found in the forest remnants assessed. We obtained the final maps of species richness for the current and future times, as well as the species turnover rates through the average of values projected by the MaxEnt model for each grid cell assessed (i.e., 0.1 latitude/longitude degrees of spatial resolution).

Forest connectivity assessment

We assessed the forest remnants through the probability of connectivity (PC) index (Saura & Rubio, 2010), calculated for the patches of the Central Corridor of the Atlantic Forest under two environmental scenarios (i.e., current and future), using the software Conefor 2.6 (http://www.conefor.org; Saura & Torné, 2009). The PC is a graph-based habitat availability metric that quantifies functional connectivity (Saura & Rubio, 2010). It is defined as the probability that two points randomly placed within the landscape fall into habitat areas that are reachable from each other (interconnected), given a set of “n” habitat patches and the links (direct connections) among them (Saura & Pascual-Hortal, 2007). It is given by the equation:

$$PC = (\sum_{i=0}^{n}\sum_{i=0}^{n} a_i \; x \; a_j \; x \; p_{ij}^{*})/A_{L^2} \; = \; PCnum/A_{L^2}$$

where *ai* and *aj* are the attributes of patches *i* and *j* (i.e., ID and area). A_L is the maximum landscape attribute, which corresponds to the total landscape area (i.e., area of the study region, comprising both habitat and non-habitat patches). The product probability of a path is the product of all the values of probability of direct dispersal (*Pij*) for all the links in that path. Thus, *Pij* is the maximum product probability of all the possible paths between patches *i* and *j*, including direct dispersal between the two patches.

We performed a prioritization ranking of the landscape elements (i.e., patches) by their contribution to overall habitat availability and connectivity from the percentage of the variation in PC (dPCk), achieved by the removal of each patch from the overall landscape (see Saura & Pascual-Hortal, 2007; Saura & Rubio, 2010). The dPCk is a relative measure of the increase in the PC value that resulted from the improvement in the strength of that link after the implementation of the defragmentation measures (Saura & Rubio, 2010), which is given by the equation:

$$dPC_k = 100 \text{ x } \frac{PC - PC_{remove,k}}{PC} = 100 \text{ x } \frac{dPC_k}{PC}$$

where *PCremove,k* is the index value after removal of the landscape element (i.e., after a certain habitat patch loss). This measure corresponds to the “link change” analysis mode implemented in the software Conefor 2.6 (Saura & Torné, 2009). For all the connectivity analyses, we used a mean dispersal distance for amphibians according to the review conducted by Smith & Green (2005), where an estimative average distance of 400 m for amphibians in general was proposed. Whereas some amphibians can disperse over distances greater than 400 m (Smith & Green, 2005), we also assessed scenarios with a greater potential for dispersal, using distances of 600 and 800 m. To assess the ecological connectivity results for the future scenario, we considered only the areas with an assessed likelihood greater than 50%, considering the potential distribution areas with a minimum favourable condition for the forest persistence under the climate change predictions used.

Landscape resistance models

We performed a landscape resistance approach to calculate the functional connectivity between the forest remnants expressed as least-cost paths. To compare the sensitivity of dPC models within the landscape, we used a resistance surface based on the landscape heterogeneity with isolation-by-resistance (IBR), following the model proposed by McRae (2006). We also assessed null models through isolation by Euclidean distance (IBD), and isolation by Euclidean 3D distance with elevation data (IB3D), both of which did not consider the influence of landscape heterogeneity. IBD and IB3D represent landscape-free models and consider a maximum conductance for different land uses types, while IBR is strongly based on landscape heterogeneity. We estimated the resistance values on the potential amphibian dispersal across the land use types within the landscape matrix, according to a systematic mapping of land use at a 1:250.000 scale, provided by the Brazilian Institute of Geography and Statistics (IBGE, 2014).

To determine the resistance values assigned to each land use type, we considered a conceptual framework for scoring the matrix permeability (cost surface) associated with landscape features based on empirical data and expert opinion (e.g., Ray, Lehmann, & Joly, 2002; Joly, Morand, & Cohas, 2003; Semlitsch, Conner, Hocking, Rittenhouse, & Harper, 2008; Janin et al., 2009; Popescu & Hunter, 2011). Thus, we followed a rank-based criterion to reflect the relative order of landscape conductance for amphibian ecological connectivity (e.g., Gibbs, Whiteleather, & Schueler, 2005; Grant, 2005; Patrick, Hunter, & Calhoun, 2006; Semlitsch, Conner, Hocking, Rittenhouse, & Harper, 2008; Popescu & Hunter, 2011; Decout, Manel, Miaud, & Luque, 2012). We used 27 detailed land use classes to generate our land cover input file, assuming different resistance values to each land use type (Table S1; supplementary files). We estimated null conductance values to each land use type for evaluating the extent to which the results were influenced by the magnitude of these values, where a low conductance value indicates a high resistance to dispersal. We assessed the importance of the landscape resistance models in predicting ecological connectivity between the forest remnants by means of a series of simple Mantel tests examining the correlation between the pairwise dPC values (present and future) and the pairwise landscape resistance distances (IBR, IBD and IB3D). We performed the Mantel tests using 200,000 permutations in the PASSaGE 2 software (Rosenberg & Anderson, 2011). We used the Circuitscape 2.2 software (McRae, 2006) to generate the pairwise matrices of landscape resistance and to produce the cumulative land conductance maps based on circuit theory.

RESULTS

We found 110 PAs covered by the Central Corridor of the Atlantic Forest, comprising 6,607.98 km^2 and corresponding to about 8% of the total corridor area. Considering the 146 species distributed in the forest remnants assessed, only 20% occurs within the current PAs network. According to the PERMANOVA, when we compared species richness and PA categories with all the environmental variables together, we found direct relations with precipitation, temperature, evapotranspiration and forest cover (Table 1), where precipitation was the variable most associated with the amphibian species richness in the Central Corridor of the Atlantic Forest.

The potential distribution of the forest remnants for the future scenario showed an average AUC value of 0.86, which indicated a good predictive ability by the dataset provided (Fig. 2A). The climate change models predict a reduction of 75% in the probability of occurrence of the Atlantic Forest remnants in the central region of the Corridor. The northern and southern edges of the Corridor, as well as high altitude areas showed the higher probability of forest occurrence. On the species distribution predictions, we observed a high amphibian turnover rate, given that more than 50% of the grid cells had species turnover ratios greater than 0.7 (Fig. 2B). However, these expected changes in species composition tend to be greater on the northern edge than the southern edge of the Corridor.

Considering a dispersal distance of 400 m, our analyses of connectivity showed that the Central Corridor of the Atlantic Forest does not guarantee a good connectivity among the fragments, with an average dPC value of 8.43. When we assessed the dispersal distances of 600 and 800 m, the average dPC was the same than the observed with a 400 m distance. However, our results showed higher connectivity areas in the north-eastern region of the Central Corridor of the Atlantic Forest, mainly in the southern Bahia region (Fig. 3). We found that 95% of the values pointed by the connectivity index were directed to the sustainable use areas (IUCN categories III–VI), only of which 5% are classified as integral protection areas (IUCN categories I–II) (Table S2; supplementary files).

Table 1. Results from the PERMANOVA on the species richness and PA categories by the variables altitude, temperature, precipitation and forest cover in the Central Corridor of the Brazilian Atlantic.

Environmental Variables	df	*F* model	R^2	*P* value
Altitude	1	21.27	0.06	0.98
Temperature	1	43.70	0.14	0.00*
Precipitation	1	130.71	0.42	0.00*
Forest cover	1	27.88	0.09	0.02*
Residuals	105	–	0.29	–
Total	109	–	1.00	–

*Significant values

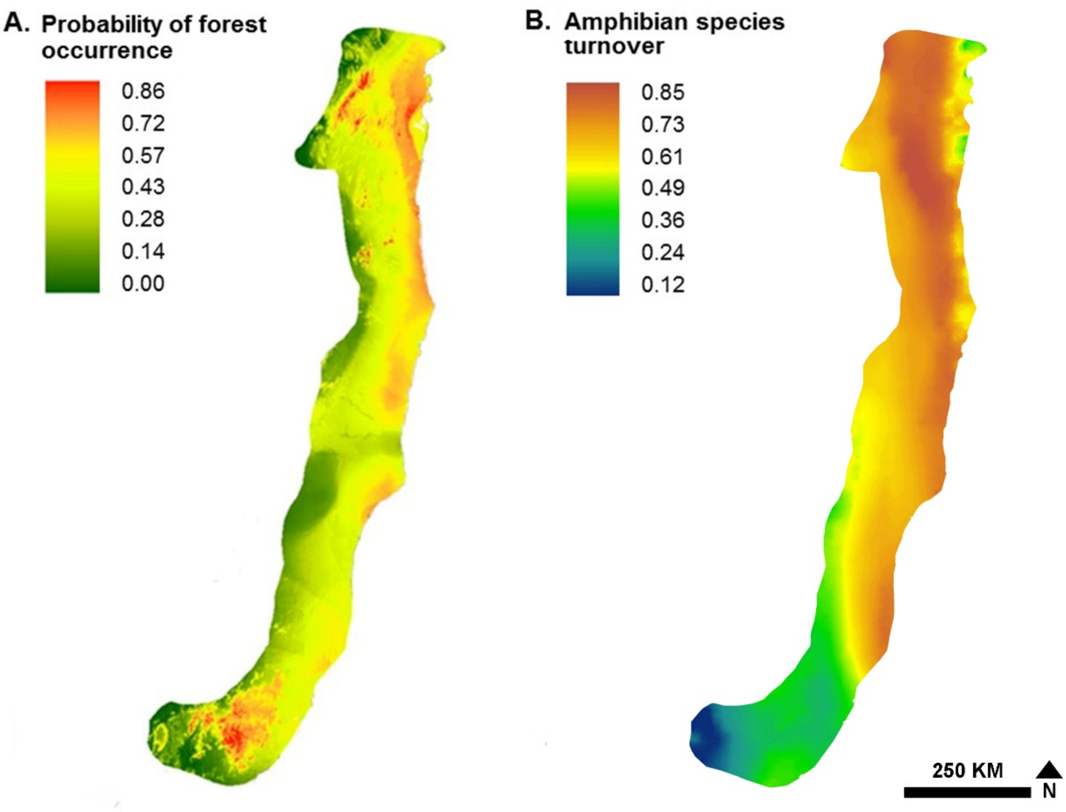

Fig. 2. Probability of forest cover according to the MaxEnt model (A), and amphibian species turnover rate (B), under climate change in the Central Corridor of the Atlantic Forest.

For the current scenario, we only found 10 PAs with high connectivity (dPC > 60.0), although 71 had very low values (dPC < 1.0). This situation can still be aggravated considering the climate model results for the future, which showed a high probability of forest remnants retraction in the evaluated region. This represents 74% of connectivity loss in a total of 4,889.90 km^2 of Atlantic Forest areas (Fig. 3). According to these future predictions, we estimated that 83 PAs would be without any ecological connectivity by the year 2080 (dPC < 0.0), while only six PAs will remain with dPC higher than 1.0. The PAs with a better expected connectivity under climate change were represented by the RPPN Renascer, RPPN Refúgio do Guigó I and II, and RPPN Boa União, in the Bahia state, and RPPN Mata da Serra, APA Serra da Vargem Alegre, and Parque Estadual do Forno Grande, in the Espírito Santo state.

Circuit theory current flow maps predicted a high likelihood of connectivity in the central portion of our study area (i.e., in southern Bahia) (Fig. 4). The landscape surface was represented by a general pattern of low-conductance areas

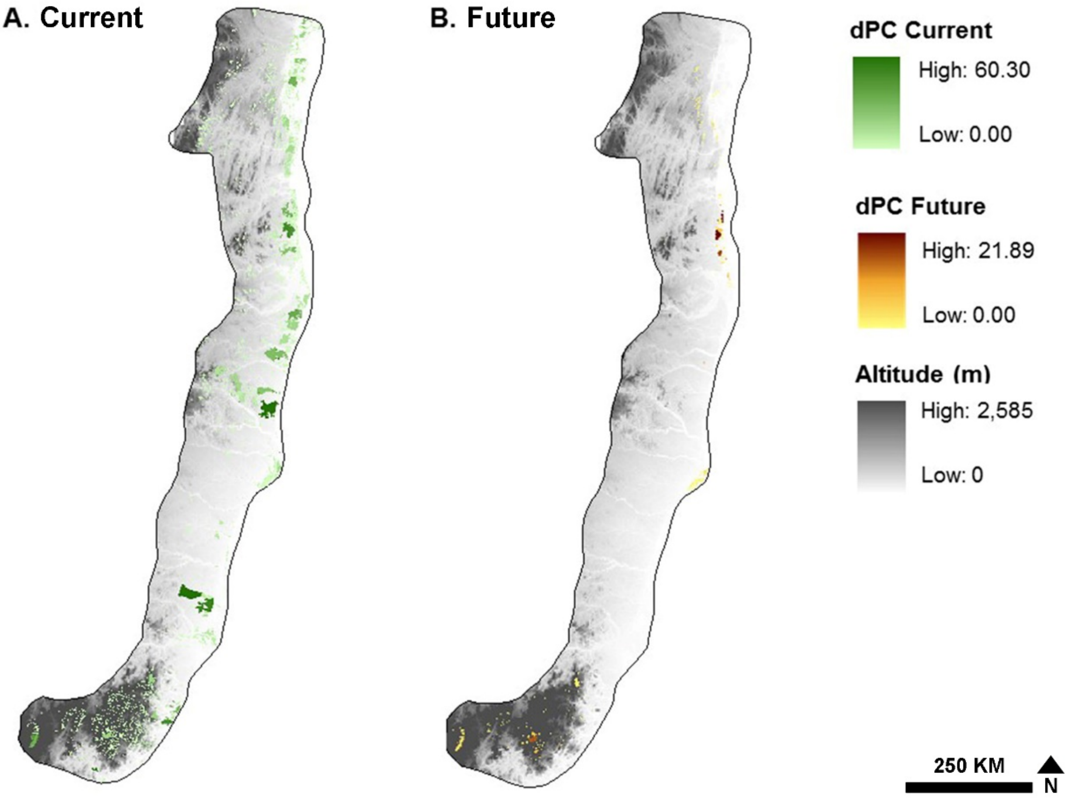

Fig. 3. Potential amphibian ecological connectivity under dPC models for current (A), and future (B) scenarios, across the forest remnants in the Central Corridor of the Atlantic Forest with altitudinal representation.

(i.e., low potential for amphibian dispersal), yet with some well-connected areas showing low resistance for species moving between patches. These well-connected areas (i.e., with high-conductance) can be potential amphibian biodiversity corridors, which would connect the National Parks Monte Pascual, Pau Brasil and Serra das Lontras, located in the southern Bahia region. Landscape resistance models that incorporated absolute dispersal barriers resulted in significant correlations when compared with those based on a landscape-free models (i.e., null resistances). Overall, Mantel tests showed significant relationships between dPC values (present and future) and resistance distances (IBD, IB3D and IBR) (Table S3; supplementary files), indicating the sensitivity of the functional connectivity models within the landscape.

DISCUSSION

Our findings showed that the proportion of forest fragments with good connectivity rate is very low along the

Central Corridor of the Atlantic Forest, which consequently may reduce the flow of species among the fragments and significantly restricts the functional role of this ecological corridor. We focused on an approach for allowing decision-makers to make the best use of the available data at a local scale, considering the extent to which such decisions might affect conservation outcomes at broad scales. According to (Maréchaux, Rodrigues, & Charpentier, 2017), the complementary use of species range maps with occurrence data is a promising route for advancing efforts to local-scale conservation decisions, supporting our species distribution data. Such approaches for improving decision-making effectiveness are even more urgent in species-rich regions, where conservation strategies should ensure the lack of biodiversity data (Maréchaux et al., 2017). In this context, we revealed that the forest fragments located in the coastal part of southern Bahia state deserve special attention in conservation plans because they hold the highest proportion of ecological connectivity along the Central Corridor of the Atlantic Forest.

Our proposal of special attention to the southern Bahia is reinforced due to their resistance surface values within a landscape matrix composed by shaded cocoa plantations (i.e., "cabrucas"), as pointed by Pardini et al. (2009). This agroforestry system has allowed the conservation of large amounts of native plant species, besides hosting typical mature forest fauna species (Pardini et al., 2009). Many species of amphibians use the bromeliads that are in the "cabrucas" system during their entire life cycle and others only as diurnal shelter (Ferreira, Lourenço-de-Moraes, Teixeira, & Beard, 2016). Given their forest-like structure, shaded cocoa plantations of the Forest remnants from the southern Bahia perform a fundamental role in maintaining connectivity between forest fragments (Sperber, Nakayama, Valverde, & Neves, 2004; Delabie et al., 2007; Faria & Baumgarten, 2007). Our results indicated this region with high probability of occurrence in a climate change scenario, which highlight the reason for future action plans aimed at conserving local biodiversity in these remnant areas.

Considering the effectiveness of habitat suitability models used in the circuit theory approach, we also indicated the southern Bahia region with the best ecological distances between forest remnants. Circuit theory relies on the habitat suitability into resistance surface values and considers multiple paths simultaneously, which makes it well adapted to modelled connectivity pathways in heterogeneous and fragmented landscapes (McRae, Dickson, Keitt, & Shah, 2008). Habitat suitability is known to play a key role in habitat use (Manly, McDonald, Thomas, McDonald, & Erickson, 2002), but the relative importance of functional connectivity for species persistence is unclear (Hodgson, Thomas, Wintle, & Moilanen, 2009; Doerr, Barrett, & Doerr, 2011). Therefore, given the landscape resistance surface and the connectivity metrics used as an aid for

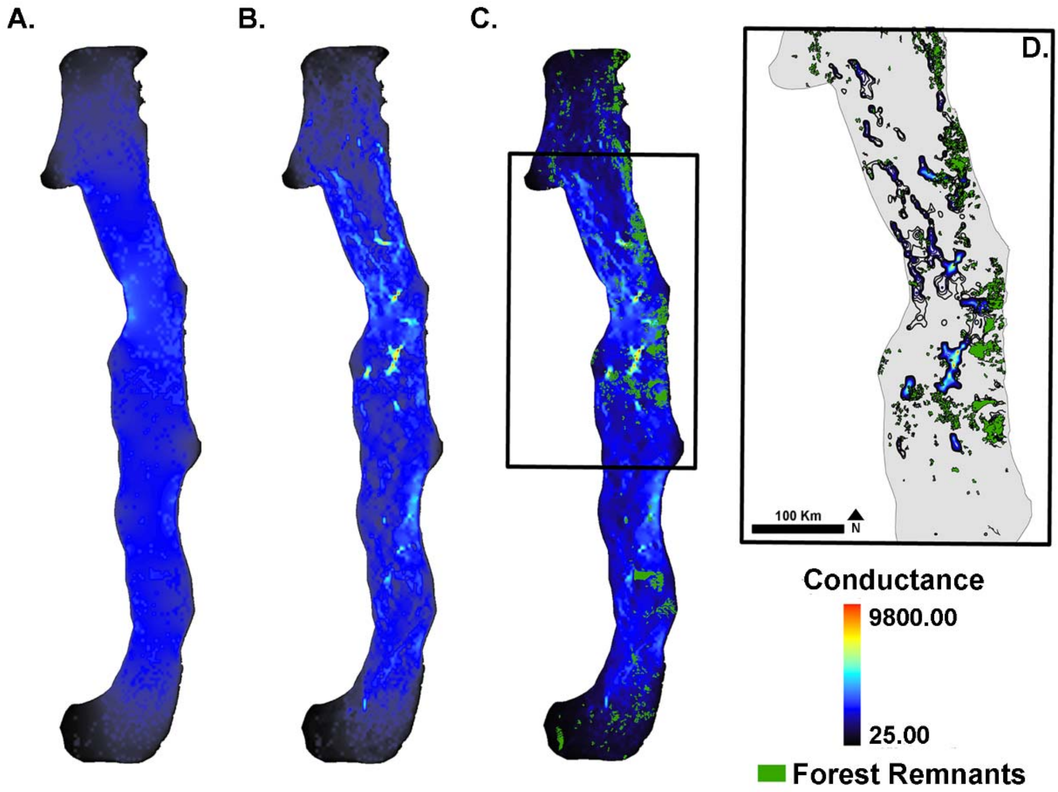

Fig. 4. Maps of landscape resistance models for amphibian ecological connectivity between forest remnants in the Central Corridor of the Atlantic Forest. Null model for isolation-by-distances – IBD/IB3D (A), landscape model for isolation-by-resistance –IBR (B); landscape model for IBR showing the distribution of forest remnants with a frame in the highest conductance areas (C); zoom in the frame with high-conductance areas showing the potential landscape connectivity between patches with low resistance surface (D).

amphibian conservation, we highlight that efficiency of the landscape planning depends on the species responses to changing environmental conditions.

The selection of critical habitats for amphibian conservation under climate change is important for making effective management decisions (Guisan et al., 2013). Areas of high species turnover rate can be specific places with largest shifts in the populations with potential distribution in this zone (Duan et al., 2016). Many studies conduct turnover assessments using turnover ratios (Erasmus, Van Jaarsveld, Chown, Kshatriya, & Wessels, 2002; Peterson et al., 2002). Our results reveal that the areas with high turnover rates are not the same areas with high occurrence probability of forest remnants under climate change. Areas with high turnover rates can be associated to areas with low species richness under the current climate (Duan et al., 2016), which in the case of the Atlantic Forest may be represented by higher altitude areas.

Moreover, low turnover rates in high altitude areas can strengthen mountainous regions as potential climatic refuges (Carnaval et al., 2009; Randin et al., 2009; Araújo, Alagador, Cabeza, Nogués-Bravo, & Thuiller, 2011).

In tropical regions, the temperature variation in a latitudinal gradient is scarcely significant (Colwell, Brehm, Cardelus, Gilman, & Longino, 2008), meaning that species affected by warming are more likely to search for refuges in mountainous areas than by latitudinal migration (Bush, 2002; Bush & Hooghiemstra, 2005). The conservation and restoration of a functional ecological connectivity requires adequate territorial planning, especially in transition areas between mountain ranges. Therefore, the establishment of conservation efforts along the areas with better connectivity values can ensure the species access to the mountainous regions, which probably will keep lower temperatures in the future. It is also expected that assumptions of land-use change will exert a strong influence over the future amphibian species distributions in the forest remnants of the whole Atlantic Forest biome (Lemes, Melo, & Loyola, 2014).

Forest remnants management is critical to ensure the persistence of species but dynamic threats as land-use change and climate change can directly reduce the effectiveness of PAs planned under a static approach (Faleiro, Machado, & Loyola, 2013). Due to developing technologies in remote sensing, there are several approaches to improve how we assess and monitor forest remnants through a variety of spatial and temporal scales (Tehrany, Kumar, & Drielsma, 2017). In this context, there is an urgent need to incorporate species' range shifts in spatial conservation plans to ensure their effectiveness in the future (Hannah, 2010). We recommend that the design of new conservation plans in the Central Corridor of the Atlantic Forest must attempt to re-establish ecological connectivity between the remaining fragments and the higher altitude areas. This may represent an alternative mechanism to mitigate potential impacts related to climate change and land-use change in the Atlantic Forest Hotspot. Corroborating our findings, some other studies in the Atlantic Forest have also warned about the need to invest in PAs near high altitude areas (Lemes & Loyola, 2013; Loyola, Lemes, Brum, Provete, & Duarte, 2014), mainly in the southern Bahia region (Carnaval, Hickerson, Haddad, Rodrigues, & Moritz, 2009), which retain high humidity provided by well-preserved forest cover.

Our predictions on the environmental variables for amphibian species richness in the Atlantic Forest are dependent on their limited dispersal abilities. Therefore, dispersal capability might severely limit the ability of species to track suitable climatic conditions geographically (Massot, Clobert, & Ferrière, 2008; Early & Sax, 2011). The use of various environmental variables has been demonstrated as an efficient strategy to reach outcomes closer to reality, being one of the keys to understanding how communities can respond to climatic factors (Araújo & New, 2007; Marmion, Parviainen, Luoto, Heikkinen, & Thuiller, 2009).

Amphibians are particularly sensitive to environmental changes and depending on the species, the dispersal ability can be associated with their evolutionary specialization processes (Pyron & Wiens, 2013), the complexity and diversity of their antipredator mechanisms (Toledo, Sazima, & Haddad, 2011), or simply to their diminutive body sizes (Early & Sax, 2011; Lourenço-de-Moraes, Ferreira, Fouquet, & Bastos, 2014). Most amphibian species that occur in the Atlantic Forest are a little under 30 mm (Haddad et al., 2013), and even small species like *Dendropsophus nanus*, and *D. minutus* have great dispersal ability due to their specialty of living in open areas. Therefore, amphibian species with high abundance in open areas or high phenotypical plasticity might expand their geographical ranges under future scenarios (Lemes et al., 2014). Some other opportunistic species adapted to warmer and drier environments can also increase their distributions under climate change. Furthermore, species with a high variety of antipredator mechanisms may be more likely to avoid a wider range of predators (Lourenço-de-Moraes et al., 2016), achieving more success in their dispersal abilities.

Our findings indicate that potential impacts of climatic changes should occur in almost the entire Central Corridor of the Atlantic Forest, which could affect the ecological connectivity of the whole biome. We suggest that the PAs with the better expected connectivity under climate change need a critical attention in future conservation plans (e.g., RPPN Renascer, RPPN Refúgio do Guigó I and II, and RPPN Boa União, in the Bahia state, and RPPN Mata da Serra, APA Serra da Vargem Alegre, and Parque Estadual do Forno Grande, in the Espírito Santo state). In this context, these mitigations can be useful to avoid potential extinction process expected for the amphibians from Central Corridor of the Atlantic Forest PAs.

Amphibian species from Atlantic Forest PAs are more threatened with extinction than in other Brazilian protected networks (Campos, Llorente, Rincón, Lourenço-de-Moraes, & Solé, 2016). This happens mainly because the Southeast Region of Brazil is the economic core of the country, with highly fragmented forest remnants (Ribeiro et al., 2009), with a high human population density, and the presence of mining and logging activities (Lemes et al., 2014). Our approach does not specifically estimate a quantitative species extinction risk, but shows evidence of a potential regional extinction within limited dispersal models. We highlight that many PAs will become less effective in future scenarios, which can dramatically affect the diversity and distribution of the amphibian species that occur in the forest remnants.

Conserving biodiversity under climate change comes out as a challenge for conservation scientists. For being a dynamic system, controlling all the climatic variables and synergies related to environmental conditions and its consequences is a huge task. If the rates of climate change overtake the response potential of biological systems to ecological connectivity and its impacts on ecosystem functioning, effects on community structure and species distributions can be irreversible. Therefore, enhanced conservation efforts of forest management will play a critical role for mitigating effects of environmental change. In some human-modified landscapes characterised by secondary forest, environmental heterogeneity can be maintained and even increased, thus contributing to the community structure (Tscharntke et al., 2012). A recent meta-analysis showed that ecological restoration success can be higher for natural regeneration than for active restoration in tropical forests (Crouzeilles et al., 2017). In this context, our research highlights the importance of maintaining the mosaic of forest remnants and the landscape heterogeneity in the Central Corridor of the Atlantic Forest, providing dynamic tools to prioritise conservation investment for ecological connectivity assessments.

This situation demands political will for improved cost-effective outcomes in the highest-priority areas, which can reduce extinction risk and avoid species loss. Considering potential biodiversity corridors in human-modified landscapes, it seems promising to investigate how agroecosystems could be incorporated on conservation actions. Nearly 40% of the landscape surface in southern Bahia is dominated by shade cocoa plantations (Faria & Baumgarten, 2007; IBGE, 2014), which hold important characteristics of primary forest, because the cacao trees are planted under thinned-out native forests (Sambuichi et al., 2012). This agroforestry system facilitates ecological processes and represents biologically rich habitats (Faria, Paciencia, Dixo, Laps, & Baumgarten, 2007), encompassing an amphibian biodiversity hotpoint within the Atlantic Forest hotspot (Dias et al., 2014). We assume that the higher likelihood of connectivity and the low resistance for species moving across the southern Bahia sheds some light on the potential role of the shade cocoa plantations for amphibian conservation in this region. Despite to be a monoculture sustained by secondary forest, the landscape heterogeneity of this forest-like structure preserves a wide variety of breeding habitats, bromeliads, and deep leaf litter, which are essential for sustaining amphibian life cycles (Teixeira et al., 2015). Pardini et al. (2009) demonstrated that shade cocoa plantations can also safeguards forest specialist amphibian species, but the responses of this species to habitat fragmentation may be delayed and not necessarily stable over time (Metzger et al., 2009). Therefore, we suggest long-term monitoring to understand population dynamics and amphibian sustainability in this mosaic of forest fragments dominated by cocoa agroecosystems.

To improve conservation management, ecologists must quantify the risks of uncertainties and trade-offs associated with different climate scenarios by testing the sensitivity of different model results (Kujala, Moilanen, Araújo, & Cabeza, 2013). Strategies should be sensible for species adaptation, impact mitigation, and should prioritize the protection and connectivity of heterogeneous landscapes (Richardson & Whittaker, 2010). Our study provides an illustration of ways to incorporate landscape paths with low resistance into potentially connected areas and denotes the fundamental role of the Central Corridor of the Atlantic Forest to amphibian dispersal. The methodological approach proposed here is not only amphibian-specific, but can also be used in conservation plans for other taxonomic groups. This work has sought to move forward the knowledge on ecological connectivity of endangered forest remnants and supports conservation actions facing climate change challenges.

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APPENDIX. Supporting Information

Supplementary files:

Table S1. Resistance values assigned to each land use type for calculating the landscape connectivity between forest remnants in the in the Central Corridor of the Atlantic Forest. IBD: null model through isolation by Euclidean distance; IB3D: null model through isolation by Euclidean 3D distance with elevation data; IBR: resistance model through isolation-by-resistance between patches based on landscape matrix permeability.

Table S2. Protected areas data assessed in the Central Corridor of the Atlantic Forest according to MMA (2015).

Table S3. Statistical significance for Mantel test between dPC values (Present and Future) and resistance distances (IBD, IB3D and IBR) for calculating the landscape connectivity between forest remnants in the in the Central Corridor of the Atlantic Forest. IBD: null model through isolation by Euclidean distance; IB3D: null model through isolation by Euclidean 3D distance with elevation data; IBR: resistance model through isolation-by-resistance between patches based on landscape heterogeneity.

Table S1. Resistance values assigned to each land use type for calculating the landscape connectivity between forest remnants in the in the Central Corridor of the Atlantic Forest. IBD: null model through isolation by Euclidean distance; IB3D: null model through isolation by Euclidean 3D distance with elevation data; IBR: resistance model through isolation-by-resistance between patches based on landscape matrix permeability.

Land use	**Resistance values**		
	IBD	**IB3D**	**IBR**
Agroforestry systems	1	1	50
Agroforestry systems with different land uses	1	1	80
Crops	1	1	90
Crops and agroforestry systems	1	1	50
Crops and ombrophylous forest	1	1	30
Crops and semi-deciduous forest	1	1	30
Crops with different land uses	1	1	80
Crops, pastures and different land uses	1	1	80
Different land uses	1	1	50
Livestock areas	1	1	60
Natural grasslands	1	1	20
Ombrophylous and semi-deciduous forest	1	1	1
Ombrophylous forest	1	1	1
Ombrophylous forest and shaded cocoa plantations	1	1	10
Ombrophylous forest and pastures	1	1	30
Pastures and agroforestry systems	1	1	50
Pastures and crops	1	1	90
Permanent crops	1	1	90
Planted forest	1	1	30
Planted pastures	1	1	60
Semi-deciduous forest and pastures	1	1	40
Semi-natural pastures	1	1	70
Temporary crops	1	1	80
Urban areas	1	1	100
Woodlands with >10% of agricultural area	1	1	30
Woodlands with 10–25% of agricultural area	1	1	40
Woodlands with 25–50% of agricultural area	1	1	50

IBD and IB3D represent landscape-free models and consider a maximum conductance for different land uses types, while IBR is strongly based on landscape heterogeneity.

Table S2. Protected areas data assessed in the Central Corridor of the Atlantic Forest, according to MMA (2015).

Protected Areas	**Political category**	**Species richness**	**Altitude (m)**	**Annual mean temperature**	**Annual mean precipitation**	**Forest Cover (%)**	**dPC Current**	**dPC Future**
Parque Natural Municipal do Manguezal de Itanguá	PI	85	16.97	9.40	511.51	84.56	0.06	0.00
Reserva Biológica do Córrego do Veado	PI	79	98.03	10.50	475.63	93.92	0.29	0.00
Monumento Natural Estadual Serra das Torres	PI	90	329.60	11.43	587.43	30.96	0.51	0.00
Floresta Nacional de Rio Preto	US	78	44.80	9.13	439.29	91.14	0.16	0.00
Floresta Nacional de Pacotuba	US	88	148.78	12.35	609.51	68.86	7.44	0.00
Área de Proteção Ambiental baía de Camamu	US	64	121.40	10.66	447.35	83.41	0.03	0.08
Reserva Particular do Patrimônio Natural Pianissoli	US	75	83.01	10.07	419.59	64.84	0.02	0.00
Reserva Particular do Patrimônio Natural Cachoeira da Fumaça	US	72	730.03	13.48	645.64	80.00	0.03	0.00
Parque Estadual de Itaúnas	PI	73	17.42	8.66	428.95	100.00	0.03	0.00
Reserva Particular do Patrimônio Natural Bom Sossego II	US	71	79.42	9.62	421.52	3.98	6.45	0.00
Reserva Particular do Patrimônio Natural Rio do Brasil IV	US	69	55.36	9.53	417.44	80.94	15.36	0.00
Parque Estadual da Fonte Grande	PI	85	16.97	9.40	511.51	100.00	0.12	0.00
Reserva Particular do Patrimônio Natural Rio Do Brasil I	US	69	55.36	9.53	417.44	80.94	15.36	0.00
Área de Proteção Ambiental da Lagoa Grande	US	81	8.09	9.28	509.40	92.84	0.00	0.00
Área de Proteção Ambiental Municipal da Lagoa Jacuném	US	83	35.17	9.29	506.14	96.77	0.01	0.00
Parque Natural Municipal Vale do Mulembá	PI	86	8.63	9.59	515.33	100.00	0.03	0.00
Área de Proteção Ambiental Municipal Manguezal Sul da Serra	US	86	8.63	9.59	515.33	100.00	0.01	0.00
Parque Estadual da Serra do Conduru	PI	63	119.73	10.12	441.12	100.00	0.49	0.01
Reserva Particular do Patrimônio Natural Bozi	US	71	46.98	9.66	409.88	71.64	0.00	0.00
Parque Natural Municipal do Aricanga Waldemar Devens	PI	88	110.68	10.20	524.48	6.47	0.01	0.00
Reserva Particular do Patrimônio Natural Vovó Dindinha	US	88	559.55	12.82	598.43	22.92	0.19	0.00
Parque Nacional Pau Brasil	PI	75	93.61	10.35	431.51	100.00	0.03	0.03
Reserva Biológica de Sooretama	PI	82	105.71	10.31	497.30	6.47	0.08	0.00
Monumento Natural do Itabira	PI	90	144.91	11.02	569.10	90.82	0.42	0.00
Reserva Particular do Patrimônio Natural Reserva Terravista I	US	69	55.36	9.53	417.44	80.94	15.36	0.00
Reserva Biológica Augusto Ruschi	PI	100	767.36	10.96	546.06	3.44	0.25	0.04
Reserva Particular do Patrimônio Natural Reserva Maria Vicentini Lopes	US	68	41.90	9.34	424.52	16.86	4.27	0.00

Reserva Particular do Patrimônio Natural Rio da Barra	US	69	55.36	9.53	417.44	4.59	0.08	0.00
Reserva Biológica do Córrego Grande	PI	75	60.04	9.52	441.36	100.00	0.06	0.00
Reserva Particular do Patrimônio Natural Renascer	US	75	79.42	9.95	424.08	80.94	15.36	6.50
Reserva Particular do Patrimônio Natural Engelhardt	US	75	83.01	10.07	419.59	83.69	60.30	0.00
Reserva Biológica de Una	PI	74	202.07	10.39	441.52	100.00	0.02	0.01
Reserva Particular do Patrimônio Natural Rio Do Brasil II	US	69	55.36	9.53	417.44	80.94	15.36	0.00
Reserva Particular do Patrimônio Natural Cahy	US	75	50.84	9.64	411.91	83.69	60.30	0.00
Floresta Nacional de Goytacazes	US	85	26.14	9.57	495.15	0.27	0.00	0.00
Reserva Particular do Patrimônio Natural Jacuba Velha	US	75	79.42	9.95	424.08	80.94	15.36	0.00
Parque Nacional do Monte Pascoal	PI	73	123.80	10.51	431.38	93.18	0.27	0.00
Reserva de Desenvolvimento Sustentável Municipal Piraque-Açú e Piraque-Mirim	US	85	26.07	9.59	510.54	100.00	0.03	0.00
Reserva Particular do Patrimônio Natural Santa Maria II	US	75	83.01	10.07	419.59	83.69	60.30	0.00
Parque Natural Municipal de Domingos Martins	PI	97	584.15	10.65	543.52	44.13	0.10	0.00
Reserva Particular do Patrimônio Natural Rio Fundo	US	96	709.27	10.85	550.98	1.84	0.68	0.00
Área de Proteção Ambiental Ponta da Baleia	US	58	6.11	8.77	397.67	0.11	0.03	0.01
Reserva Extrativista Corumbau	US	70	40.96	9.60	406.91	100.00	0.01	0.00
Reserva Particular do Patrimônio Natural Rio do Brasil V	US	69	55.36	9.53	417.44	80.94	15.36	0.00
Parque Nacional da Serra Das Lontras	PI	77	268.68	11.17	455.01	63.77	0.00	0.00
Reserva Particular do Patrimônio Natural Santa Maria I	US	75	90.85	10.46	428.54	83.69	60.30	0.00
Reserva Particular do Patrimônio Natural Toca da Onça	US	76	662.61	13.27	627.16	21.70	0.20	0.53
Área de Proteção Ambiental do Pico Do Goiapaba-Açú	US	93	287.10	10.51	534.75	95.89	0.05	0.01
Área de Proteção Ambiental Monte Urubu	US	77	17.02	9.64	524.75	100.00	0.16	0.00
Área de Proteção Ambiental de Praia Mole	US	78	13.65	9.24	506.10	0.03	18.19	0.00
Área de Proteção Ambiental Caraíva / Trancoso	US	73	44.10	9.77	417.86	100.00	0.00	0.00
Parque Natural Municipal do Monte Mochuara	PI	93	132.44	9.85	523.08	100.00	0.05	0.00
Refúgio de Vida Silvestre de Boa Nova	PI	42	694.35	13.64	521.72	43.51	0.04	0.00
Reserva Particular do Patrimônio Natural Lembrança	US	75	93.61	10.35	431.51	80.94	15.36	0.00
Reserva Extrativista de Cassurubá	US	67	11.27	8.96	407.58	100.00	0.03	0.26
Reserva Particular do Patrimônio Natural Flor Do Norte II	US	75	50.84	9.64	411.91	83.69	60.30	0.00
Reserva Particular do Patrimônio Natural Refúgio do Guigó I e II	US	69	58.16	9.57	432.29	97.79	5.04	4.85
Parque Natural Municipal Pedra dos Olhos	PI	85	16.97	9.40	511.51	8.22	5.14	0.00
Reserva Particular do Patrimônio Natural Oiutrem	US	92	657.99	11.01	558.36	25.21	0.49	0.00
Refúgio de Vida Silvestre de Una	PI	74	202.07	10.39	441.52	84.98	0.12	0.11

Reserva Particular do Patrimônio Natural Rio Capitão	US	58	93.71	9.86	438.76	100.00	7.81	0.00
Refúgio de Vida Silvestre do Rio dos Frades	PI	67	30.57	9.47	415.31	100.00	0.01	0.00
Reserva Particular do Patrimônio Natural Santa Maria III	US	74	71.29	10.00	416.28	83.69	60.30	0.00
Área de Proteção Ambiental Municipal do Morro do Vilante	US	89	76.35	9.74	518.08	72.70	0.03	0.00
Área de Proteção Ambiental Baía de Todos os Santos	US	39	8.59	10.28	437.86	24.05	0.10	0.00
Refúgio Estadual de Vida Silvestre Mata dos Muriquis	PI	54	732.58	12.51	495.56	99.99	0.02	0.00
Parque Nacional do Descobrimento	PI	74	58.95	10.40	425.21	100.00	0.01	0.00
Reserva Particular do Patrimônio Natural Rancho Chapadão II	US	97	548.72	10.65	541.04	34.40	0.43	0.00
Área de Proteção Municipal do Monte Mochuara	US	96	339.07	10.30	534.64	100.00	0.01	0.02
Reserva Particular do Patrimônio Natural Riacho das Pedras	US	74	58.95	10.40	425.21	83.69	60.30	0.00
Área de Proteção Ambiental Costa De Itacaré / Serra Grande	US	66	125.91	10.57	446.40	100.00	0.04	0.00
Parque Natural Municipal Dom Luiz Gonzaga Fernandes	PI	86	8.63	9.59	515.33	93.19	1.26	0.00
Reserva de Desenvolvimento Sustentável Municipal do Manguezal de Cariacica	US	86	8.63	9.59	515.33	89.72	0.03	0.00
Reserva de Desenvolvimento Sustentável Municipal Papagaio	US	75	17.03	9.48	521.82	98.70	1.29	0.00
Área de Proteção Ambiental Conceição da Barra	US	67	26.55	8.80	441.94	100.00	0.02	0.00
Reserva Particular do Patrimônio Natural Mata Da Serra	US	91	745.53	11.13	565.41	0.69	3.52	6.20
Reserva Particular do Patrimônio Natural Fazenda Boa Esperança	US	88	111.21	11.97	596.54	41.98	0.07	0.00
Área de Proteção Ambiental Santo Antônio	US	71	36.50	9.29	418.76	100.00	0.00	0.00
Reserva Particular do Patrimônio Natural Reserva Terravista II	US	69	55.36	9.53	417.44	80.94	15.36	0.00
Reserva Particular do Patrimônio Natural Helico	US	70	116.74	9.97	436.86	1.44	16.98	0.00
Área de Proteção Ambiental Estadual Mestre Álvaro	US	89	76.35	9.74	518.08	100.00	0.04	0.01
Reserva Particular do Patrimônio Natural Olho d’água	US	100	767.36	10.96	546.06	9.45	0.36	0.02
Área de Proteção Ambiental Serra da Vargem Alegre	US	66	898.27	13.92	666.50	76.55	26.70	2.81
Reserva Particular do Patrimônio Natural Reserva São José	US	68	108.08	10.00	437.85	1.44	16.98	0.00
Reserva Particular do Patrimônio Natural Flor do Norte I	US	75	50.84	9.64	411.91	83.69	60.30	0.00
Reserva Particular Do Patrimônio Natural Primavera I	US	74	71.29	10.00	416.28	83.69	60.30	0.00
Área de Proteção Ambiental Costa das Algas	US	75	23.00	9.14	499.84	90.08	0.08	0.00
Parque Natural Municipal dos Puris	PI	81	23.71	9.90	534.09	95.81	0.03	0.00
Reserva Extrativista de Canavieiras	US	66	38.87	9.49	431.55	100.00	0.08	0.07
Parque Nacional de Boa Nova	PI	42	694.35	13.64	521.72	100.00	0.05	0.00
Reserva Particular do Patrimônio Natural Primavera	US	74	71.29	10.00	416.28	83.68	0.52	0.00
Reserva Particular do Patrimônio Natural Bom Sossego III	US	68	41.20	9.25	417.18	21.11	0.02	0.00
Reserva Particular do Patrimônio Natural Pau A Pique	US	97	548.72	10.65	541.04	6.23	0.58	0.00

Parque Estadual Alto do Cariri	PI	61	421.12	12.34	487.15	100.00	0.03	0.00
Reserva Particular do Patrimônio Natural Córrego Floresta	US	84	457.27	12.93	598.35	59.29	0.14	0.00
Parque Natural Municipal Goiapaba-Açú	PI	93	287.10	10.51	534.75	67.20	1.30	0.15
Área de Proteção Ambiental do Maciço Central	US	85	16.97	9.40	511.51	100.00	1.26	0.00
Reserva Particular do Patrimônio Natural Triângulo	US	74	71.29	10.00	416.28	83.69	60.30	0.00
Área de Proteção Ambiental Lagoa Encantada	US	65	405.18	12.32	479.95	5.39	0.02	0.00
Estação Ecológica Estadual Wenceslau Guimarães	PI	56	381.06	13.02	482.16	48.27	0.06	0.00
Reserva Particular do Patrimônio Natural Alimercino Gomes Carvalho	US	72	730.03	13.48	645.64	21.02	0.00	0.00
Reserva Particular do Patrimônio Natural Boa União	US	68	61.95	9.60	433.05	12.20	1.96	1.89
Reserva Particular do Patrimônio Natural Rancho Chapadão	US	97	548.72	10.65	541.04	34.40	0.43	0.00
Reserva Particular do Patrimônio Natural Rio do Brasil III	US	69	55.36	9.53	417.44	80.94	15.36	0.00
Reserva Particular do Patrimônio Natural Jatobá	US	63	210.99	11.59	456.33	34.68	0.00	0.00
Reserva Particular do Patrimônio Natural Cachoeira Alta	US	68	854.33	13.71	656.59	97.49	17.49	0.00
Parque Estadual do Forno Grande	PI	91	635.15	12.07	591.47	57.86	1.95	2.15
Parque Nacional de Caparaó	PI	66	898.27	13.92	666.50	1.78	0.00	0.50
Estação Ecológica Municipal Ilha do Lameirão	PI	86	8.63	9.59	515.33	100.00	18.19	0.00
Parque Nacional do Alto Cariri	PI	54	732.58	12.51	495.56	100.00	0.00	0.00

PI = Integral protection areas (IUCN categories I–II).
US = Sustainable use areas (IUCN categories III–VI).

Table S3. Statistical significance for Mantel test between dPC values (Present and Future) and resistance distances (IBD, IB3D and IBR) for calculating the landscape connectivity between forest remnants in the in the Central Corridor of the Atlantic Forest. IBD: null model through isolation by Euclidean distance; IB3D: null model through isolation by Euclidean 3D distance with elevation data; IBR: resistance model through isolation-by-resistance between patches based on landscape heterogeneity.

Matrix	**Mantel r**	**P-value**
dPC_Present-IBD	0.01091	0.00000
dPC_Present-IB3D	0.01055	0.00000
dPC_Present-IBR	0.00962	0.00000
dPC_Future-IBD	0.00316	0.03253
dPC_Future-IB3D	0.00295	0.04637
dPC_Future-IBR	0.00310	0.03871

All tested pairs for dPC-Present and dPC-Future are significant ($p > 0.05$).

Chapter 6

Back to the future: Conserving functional and phylogenetic diversity in the amphibian-climate refuges

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Back to the future: Conserving functional and phylogenetic diversity in the amphibian-climate refuges

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Regreso al futuro: conservación de la diversidad funcional y filogenética en refugios climáticos para anfibios. Los refugios climáticos han sido utilizados por diferentes especies en respuesta a cambios climáticos históricos. Las especies ectotérmicas son buenos modelos para los estudios del cambio climático porque son sensibles al cambio de temperatura. Analizando la pérdida de especies, comparando con los valores ecosistémicos y evolutivos, podemos comprender los procesos ambientales y minimizar los impactos climáticos. En este estudio, asociamos la diversidad funcional y filogenética de los anfibios en el Bosque Atlántico brasileño, utilizando múltiples modelos para las condiciones presentes y futuras. Mediante un enfoque innovador, estimamos el estado de amenaza de las especies para el año 2080, según el criterio B1 de la UICN. Nuestros resultados mostraron una reducción drástica de la riqueza de especies, las funciones ecosistémicas y las historias evolutivas en zonas de bajas latitud y altitud. Mostramos que las especies tienden a dispersarse hacia las áreas donde las temperaturas son más suaves (es decir, en zonas montañosas), que tienden a ocurrir en los mismos puntos que se han sugerido como refugios durante el Pleistoceno, así como en nuevas áreas de refugios potenciales. Destacamos que el 60% de las especies evaluadas pueden verse amenazadas para el año 2080. Este trabajo ha permitido avanzar en el conocimiento de los refugios climáticos, los procesos ecológicos y evolutivos de los anfibios, y puede ayudar en la toma de decisiones en relación a la conservación biológica.

– Spanish Abstract (Resumen)

Back to the future: Conserving functional and phylogenetic diversity in the amphibian-climate refuges

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ABSTRACT

Climate refuges have been used by several species over historical climate changes. Ectothermic species often display good models for climate change studies because they are highly sensitive to temperature. Analysing species-loss with ecosystem and evolutionary values help to understand environmental processes and climatic consequences. Here, we associate the functional and phylogenetic diversity of amphibians in the Atlantic Forest hotspot, using multiple models for the present and future conditions. Through an innovative approach, we predict the species' threat status by 2080, following the IUCN's criterion B1. Our results show drastic reduction in species richness, ecosystem functioning and evolutionary history at low latitudes and low altitudes. We show that species tend to disperse to the areas with milder temperatures (i.e. high latitudes/altitudes), tending to occur in the same regions that have been suggested as refuges during the late Pleistocene, as well as in new potential refuges-areas. We highlight that 60% of the Atlantic Forest amphibians can become threatened under future conditions. This work advances the knowledge on climate refuges for amphibian ecology and evolution, supporting complementary tools for conservation strategies.

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INTRODUCTION

Over millions of years, the Earth has undergone several transformations that seem to appear cyclically (Raup and Sepkoski, 1982). During these changes, most species had to take refuge in areas with milder environments and better resource availability (Haffer, 1969; Mayr and O'Hara, 1986; Bush, 1994; Bush and Oliveira, 2006; Carnaval et al., 2009; Bush et al., 2011). However, these cyclical events lead to five massive extinctions (Raup and Sepkoski, 1982; Jablouski, 1994; Bambach, 2006; Barnorsky et al., 2011). The current Anthropocene Age is directing toward the sixth mass extinction of the biodiversity (Wake and Vredenburg, 2008; Barnosky et al., 2011; Dirzo et al., 2014). Anticipating climatic consequences on biogeographic patterns is key to address changes on functional and phylogenetic relations to organism-mediated ecosystem goods and services (Montoya and Raffaelli, 2010; Cardinale et al., 2011; Prather et al., 2012), as well as evolutionary processes (Thuiller et al., 2011; Pio et al., 2014). In this context, studies available about climate change should be integrated into functional phylogenetic assessments (Sobral and Ciacianruso, 2012; Campos et al., 2017). Thus, it is possible to associate ecological and evolutionary approaches into spatial decision-making for conservation. The assumption that closely phylogenetic species have the same ecosystem roles is still an uncertain issue. (Webb et al., 2002). Phylogenetic structure of communities depends on how the ecological characteristics evolved (Sobral and Cianciaruso, 2012). The ecosystem functioning and stability are often correlated with changes in evolutionary process, producing several implications for ecological and human wellbeing on short time scales (Alberti, 2015).

Climate change is one of the main threats to global biodiversity (Thomas et al., 2004; Pereira et al., 2010), continuously promoting variations in physiological and ecological processes that are directly affecting the distribution and persistence of species (Stenseth et al., 2002; MacDonald et al., 2004; Huey et al., 2009). Some studies have been addressed how climate change affect the individual performance (Huang et al., 2013; Holt and Jorgensen, 2015), demographic dynamics (Lukoscheck et al., 2013; Pomara et al., 2014), and species richness (Lemes and Loyola, 2013; Ferro et al., 2014), from a variety of environmental perspectives on the living organisms. Predictive outcomes have included adaptation to novel conditions (Quintero and Wiens, 2013), expansion or retraction of species' extent of occurrence (Ferro et al., 2014; Lemes et al., 2014), isolation to climate refuges (Puschendorf et al., 2009), and in the worst cases, species extinctions (Thomas et al., 2004). Rapid human–induced species losses and dynamic responses of ecosystems offer a new challenge to the scientific community – they forecast what would be the future patterns of environmental conditions to prevent further extinctions.

Ecological niche models (ENMs), also referred to as species distribution models (SDMs) (Rangel and Loyola, 2012), have been increasingly used to estimate species ranges for future scenarios of climate change (Peterson et al., 2011). These models can be used to evaluate the current and future hotspot of functional and phylogenetic diversities (Thuiller et al., 2011; Loyola et al., 2013; Pio et al., 2014), working as effective conservation tools (Del Toro et al., 2015). Ectothermic species are highly susceptible to climate change (Pounds et al., 2006; Sinervo et al., 2010) due to the interplay of their behavioural-physiological functions into environmental conditions (Ribeiro et al., 2012). Amphibians are very sensitive to global changes (Lourenço-de-Moraes et al., 2014) due to their metabolic features (Duellman and Trueb, 1994). At high temperatures, amphibians rapidly lose water to the atmosphere (Wells, 2007), which can induce local extinction processes (Becker et al., 2007). Therefore, using ENMs may be an effective tool in predicting the possible dispersions driven by climate change for amphibian species (Pie et al., 2013; Ribeiro et al., 2015), advancing conservation strategies.

The consequences of human activities go further than the loss of species and various studies reported losses of both evolutionary history and functional diversity at different landscapes (Purvis et al., 2000; Flynn et al., 2009; Mayfield et al., 2010). The Anthropocene age is characterized by drastic climate change (especially warmer temperature), causing a massive defaunation (Dirzo et al., 2014). Facing this scenario, many species may be underestimated as to their threat status (e.g. Ocampo-Peñuela et al., 2016). Recent studies have suggested that areas of high altitude may be important refuges for vertebrates during the Anthropocene Age (Loyola et al., 2013; Lemes et al., 2014; Campos et al., 2017). In this context, we tested the hypothesis that the high elevation areas are refuges for amphibians and may maintain their contribution to ecological and evolutionary processes. For this purpose, we analysed the present and future distribution of taxonomic, phylogenetic and functional diversity of Atlantic Forest amphibian species. We correlated these biodiversity components with altitude in both periods and analysed the expansion and retraction of species' extent of occurrence. We also projected the potential species conservation status for 2080, fitting the IUCN's criterion B1 (IUCN, 2017), which considers species' extent of occurrence.

MATERIALS AND METHODS

Study Area

We focused our analyses on the Atlantic Forest Biodiversity Hotspot (Myers et al., 2000), which originally covered around 150 million ha with heterogeneous environmental conditions provided by a wide range of climatic belts and vegetation formations (Tabarelli et al., 2005; Ribeiro et al., 2009). This biome has an altitudinal range from sea level to mountain chains Serra do Mar and Serra da Mantiqueira (Cavarzere and Silveira, 2012). This region has a longitudinal range harbouring differences in forest composition due to a diminishing gradient in rainfall from the coast to the interior. Its latitudinal range extends to tropical and subtropical environments (Ribeiro et al., 2009) (Fig. 1).

Spatial species data

We obtained spatial data of amphibian species from a joint research through six steps: 1. we built a dataset with all the species distributed in the Atlantic Forest according to Haddad et al. (2013); 2. We included the species occurrences records available through the Global Biodiversity Information Facility (GBIF; www.gbif.org); 3. We added maps of geographical ranges for each species from the IUCN Red List of Threatened Species database (IUCN, 2017); 4. We filtered out the species that only occur in forested environments overlapping the spatial species data by the Atlantic Forest remnant map (SOS Mata Atlântica and INPE, 2015), excluding all urban areas from the species distribution data; 5. We conducted a complementary fieldwork in the major Atlantic Forest remnants of Brazil (see Fig. S1), obtaining observed functional traits on the amphibian species. 6. We modelled the species distribution ranges for present and future conditions through ecological niche modeling.

Ecological niche modeling and species turnover

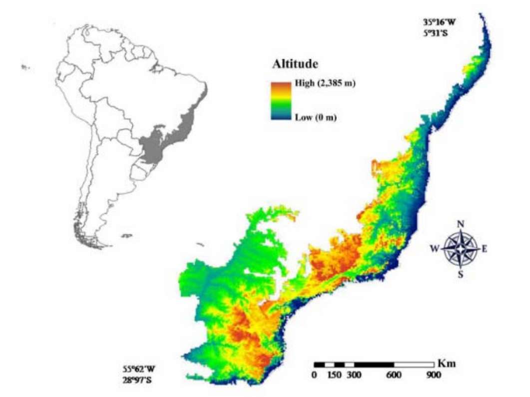

Fig. 1. Map of the Brazilian Atlantic Forest showing the altitudinal range at a spatial resolution of 0.1 degrees.

We used ArcGIS 10 software (ESRI, 2010) 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. In total, we assessed the geographical ranges of 453 amphibian species (five Gymnophionas and 448 Anurans) covered by our grid system. We only considered a grid cell occupied by those species where the centre of the grid cell intersected with the species ranges. We also used the "Count Overlapping Polygons" ArcGIS toolbox to obtain the species richness at the spatial resolution assessed, removing all duplicate records from the analyses (i.e. repeated records of a species at a single locality).

Considering that species occurrence patterns are determined at large-scales by responses of organisms to different environmental conditions (reflecting the Grinellian component of the ecological niche, sensu Soberón, 2007), we used ecological niche models (ENMs) to predict the distribution area of amphibian species in the Atlantic Forest. For this, we used the species occurrence matrix and the layers of climatic-environmental variables, resulting in a suitability matrix, which we used to modeling and mapping the potential distribution of each species evaluated.

We used the following bioclimatic variables in the modeling process: 1. annual mean temperature; 2. annual temperature range; 3. precipitation of wettest month; 4. precipitation of driest month; and 5. precipitation of warmest quarter. We obtained these variables for the present and future conditions (mean of simulations for 2080-2100), from the Coupled Models Intercomparison Project Phase 5 - CMIP5 (http://cmip-pcmdi.llnl.gov/cmip5/). We downscaled the data to a spatial resolution of 0.1 degrees through the ecoClimate database (www.ecoclimate.org) (see Lima-Ribeiro, 2015). We also used altitude as predictor of richness and dispersion from the dataset available at WorldClim Global Climate Data (www.worldclim.org). We assumed the temporal stationary of this variable to perform future predictions. For the future, we used the greenhouse gas concentration trajectory corresponded to the Representative Concentration Pathway (RCP) 4.5, which represents a moderated emission scenario within an optimistic context. We used simulations provided by four Atmosphere-Ocean General Circulation Models (AOGCMs): CCSM, CNRM, MIROC and MRI, which were also obtained from the CMIP5 Project. Original data resolution varied from 1 to 2.8 degrees (in longitude and latitude). We rescaled both present and future climate variables to fit our grid resolution.

We performed four conceptually and statistically different ENMs based on presence data (i.e. only occurrences are known, absences are unknown – pseudo-absence) using the algorithms: 1. Bioclim (BIO; Busby, 1991) based on bioclimatic envelope logic; 2. Gower Distance and Euclidean Distance (GD, EUD; Carpenter et al., 1993) based on environmental distance approach; 3. Maximum Entropy (ME; Phillips et al., 2006) and random forest (RF; Breiman, 2001) based on machine learning technique; and 4. Ecological Niche Factor Analysis (ENFA; Hirzel et al., 2002) based on multivariate analysis, and Genetic Algorithm for Rule set Production (GARP; Stockwell and Noble, 1992). Given the particularities of each model, they provided different predictions, generating uncertainties about which model is more appropriate to represent the geographical distribution of species (Diniz-Filho et al., 2009). To overcome potential uncertainties, we employed the ensemble forecasting approach, which offers a consensus of multiple models (Araújo and New, 2006). The main idea of ensemble forecasting is that different sources of errors will affect each niche model in different ways and, by obtaining a consensus result of these models, errors will tend to cancel each other out and produce a more conservative solution (Diniz-Filho et al., 2010). Given that the richness consensus model (CONS) reduces uncertainties associated to ENMs, we interpreted only the range sizes from the CONS model.

We randomly partitioned presence and absence (pseudo-absence in the case of Maxent) data of each species into 75% for calibration (or training) and 25% for evaluation (or test); repeating this process 10 times by cross-validation for all models. For each ENM, we converted the continuous predictions of suitability into a binary vector of 1/0 (presence and absence in each cell), finding the threshold that maximizes sensitivity and specificity values in the receiver operating characteristic (ROC). The ROC curve is generated by plotting the fraction of true positives vs. the fraction of false positives at various threshold settings.

We estimated the spatial distribution areas by 280 predictions (7 models x 10 randomizations x 4 AOGCMs) for each species and time-period of climatic conditions (present and 2080). This allowed us to generate a frequency of projections in the ensemble. Then, we generated the frequency of projections weighted by the total sum of squares (TSS) statistics for the present and future (the best models according to this metric have more weight in our consensus projections). The TSS range from -1 to +1, where values equal to +1 is a perfect prediction and values equal to or less than zero is a prediction no better than random (Allouche et al., 2006; Eskildsen et al., 2013). We considered the species present only in cells where at least 50% of models retained in the ensemble point out the species as present. In our analyses, we obtained the CONS for each AOGCM and time (present and 2080).

We obtained the final maps of richness for present, future and turnover through the average of values projected by CONS for each grid cell – considering the different GCMs. We ran all models using the computational platform Bioensembles (Diniz-Filho et al., 2009), and mapped results using the software SAM v.4.0 (Rangel et al., 2010). To determine the species patterns of amphibians of Atlantic Forest, we employed the modeling strategy at the community level of "predict first, assemble later" (sensu Overton et al., 2002), where the ranges of individual species are modelled one at a time as a function of environmental predictors to obtain an overlapped species richness.

We calculated species turnover between present and future species distributions in each cell according to formula 100*((G+L)/(S+G)). (Thuiller, 2005), where "G" refers to the number of species gained, "L" the number of species lost and "S" the species richness.

Functional and Phylogenetic Diversity

We used the following functional traits according to Haddad et al. (2013), and added complements from our fieldwork: 1. body size; 2. appendices (apodal and tetrapod); 3. activity (nocturnal, diurnal, and both); 4. toxicity (toxic, nontoxic, unpalatable, or bad odour); 5. habitat (forested area, open area, and both); 6.

habit (arboreal, phytotelmate, terrestrial, cryptozoic, fossorial, rheophilic, semi-aquatic, and aquatic); 7. calling site (bamboo grove, swamp or lake, bromeliad, forest floor, tree canopy, caves or burrows, rock wall, backwater river, stream, river, shrubs, grasslands and not sings); and 8. reproductive mode (1 to 39 modes; see Haddad and Prado, 2005). Amphibian functional traits are key conservation tools for the maintenance of ecosystem functioning (Hocking and Babbitt, 2014).

We followed the protocol proposed by Petchey and Gaston (2006) to calculate functional diversity (FD): 1. construction of a species-trait matrix; 2. conversion of species-trait matrix into a distance matrix; 3. clustering distance matrix into a dendrogram (UPGMA); 4. calculating functional diversity by summing dendrogram branch lengths of species community. To create the distance matrices, we used the method Gower distance proposed by Pavoine et al. (2009).

We used the phylogenetic diversity index (Faith, 1992) to quantify the phylogenetic diversity (PD), which comprises the sum of the lengths of the branches lengths of the phylogenetic tree of all species assessed and is often used in the assessment of phylogenetic diversity of co-ocurrent species (e.g. Rodrigues and Gaston, 2002; Safi et al., 2011; Trindade-Filho et al., 2012). The PD index has appropriate ways of accounting for relatedness between taxa and evolutionary history (Pio et al., 2011).

We based the phylogenetic distance through 207 species nucleotide sequences obtained from GenBank database (Benson et al., 2013). Following the protocol proposed by Pyron and Wiens (2011) in an extant amphibian phylogeny, we used 12 genes to produce a novel estimate phylogeny for the Atlantic Forest amphibians (i.e. 11,906 bp for each species), through three mitochondrial genes were included: cytochromeb (cyt-b), and the large and small sub-units of the mitochondrial ribosome genes (12S/16S); and nine nuclear genes: C-X-C chemokine receptor type 4 (CXCR4), histone 3a (H3A), sodium–calcium exchanger (NCX1), pro-opiomelanocortin (POMC), recombination-activating gene 1 (RAG1), rhodopsin (RHOD), seventh-in-absentia (SIA), solute-carrier family 8 (SLC8A3), and tyrosinase (TYR). For the length-variable regions, we performed multiple pairwise comparisons by the online version of MAFFT v.6.8 and the G-INS-i algorithm (Katoh and Toh, 2008). After, we put together alignments of all genes in the same alignment using the software SequenceMatrix 1.7.7 (Vaidya et al., 2011) to concatenate the supermatrix previously produced.

We conducted the phylogenetic relationships with Bayesian analyses in software BEAST 1.8 (Drummond and Rambaut, 2007). We generated the phylogeny based on the combined data matrix using a HKY model of sequence evolution for one partition for all genes, under a Yule speciation process as the tree prior and an uncorrelated relaxed clock.

After removal of the burn-in, we run the Yule process for 100 million generations, ensuring that the number of generations after convergence were sufficient assessed with Tracer v1.6 (Drummond and Rambaut, 2007), combining the results with the use of Logcombiner 1.8 and Treeanotator 1.8 (Drummond and Rambaut, 2007). We considered the nodes strongly supported if they received posterior probability ≥ 0.95. To edit the new phylogenetic tree, we used the package 'ape' (Paradis, 2012), in the R software (R Development Core Team, 2017).

To verify whether functional diversity (FD) and phylogenetic diversity (PD) was influenced by species richness (Devictor et al., 2010), we used independent swap null models (Gotelli and Entsminger, 2001), according to the protocol proposed by Swenson (2014). The values provided by such models are more sensitive to preserving both site diversity and species frequency of occurrence while randomizing the pairs of species/sites, which ensure that patterns of trait assembly do not simply reflect differential occurrence of species (Ackerly et al., 2006; Swenson, 2014) for present and future times. The null model is totally independent of the species richness of an assemblage (Swenson, 2014), which provides expected values at different species richness levels (Mouchet et al., 2010). Hence, we tested if the functional and phylogenetic diversity were higher, equal or lower than expected by chance for each grid cell (random or non-random pattern), assuming a random distribution in which every species could occupy any grid cell in the biome. For each pruning event (present and future), we computed 1,000 replicates of random remaining PD and FD, allowing us to obtain a P-value of predicted PD and FD as compared to the distribution of the random replicates. All analyses were performed using the packages "ade4", "picante", "FD" and "vegan" through the R software (R Development Core Team, 2017).

Species Richness, FD and PD vs. Topography and Spatial References

We used correlation matrices to compare topographic patterns and spatial references (i.e. altitude and latitude) with the values of species richness consensus (CONS), species turnover, FD and PD in each grid cell for present and future times, using simple linear regression models.

Threat status of species under climate change

From the individual range sizes (i.e. number of occupied cells) of each species in the present and future, we estimated the expected threat status of amphibian species by 2080, fitting the species' extent of occurrence under the IUCN's criterion B1 (IUCN, 2017). We considered the following threat categories: 1. Extinct (EX) = 0 km^2; 2. Critically Endangered (CR) = occurrence < 100 km^2; 3. Endangered (EN) = occurrence < 5,000 km^2; 4. Vulnerable (VU) = occurrence <

20,000 km^2; 5. Nonthreatened (NT) = occurrence > 20,000 km^2.

We also evaluated the percentage of range loss for the future. We considered the following categories: 1. species with total loss 100%; 2. species whose loss is estimated at 80% for the projected time interval; 3. species whose loss is estimated at 50% for the projected time interval; 4. species whose loss is estimated at 30% for the projected time interval; and 5. species whose loss is estimated at below 30% for the projected time interval.

RESULTS

The results from the total sum of squares (TSS) for most species presented values of 0.61 ± 0.11, indicating relatively high fit model. The overlap of individual species ranges generated by the CONS model evidenced the highest species richness values were restricted for almost all eastern-central portion of the Atlantic Forest for present and future times (see Figs. 2 to 4).

Species richness patterns showed no significant relationships with the altitude (r^2= 0.000, P = 0.182; Fig. 4c). The future predictions produced by CONS from different AOGCMs pointed out the losses of climatically suitable areas in this region by 2080, with the species richness directed to the east-central portion of the Atlantic Forest. In this case, the species richness increases toward higher altitude (r^2 = 0.132, P < 0.001). In general, CCSM and MRI showed two distinct species-rich areas, while CNRM and MIROC produced more homogeneous results, with the latter more restrictive (Fig. 2). By combining the results of AOGCMs in a full ensemble model, we found that in the future, the species richness peaks are likely to be restricted to a reduced portion from the central-eastern region of the biome in locations closer to the mountain regions of the Atlantic Forest (Fig. 3).

Species turnover rates increased after the combination from the results of AOGCMs in a full ensemble model.

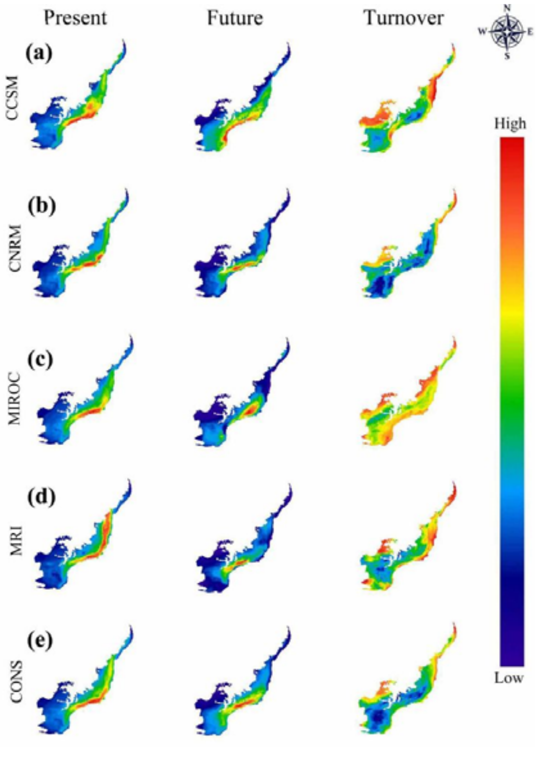

Fig. 2. Species richness and turnover rates derived from different Global Circulation Models (a) CCSM, CNRM (b), MIROC (c), MRI (d) and Richness Consensual Model-CONS (e), according to the Atlantic Forest amphibians under present and future conditions.

We demonstrated that predicted changes on the species composition tend to be greater in the western and northeastern edges of the biome. In this sense, we found higher turnover rates from high to low latitudes ($r^2 = 0.308$, $P < 0.001$) and from low to high altitudes ($r^2 = 0.307$, $P < 0.001$) (Fig. 4).

Our results showed high Functional diversity (FD) in the regions of the eastern Atlantic Forest with the highest rates in the east-central region rising to the northeast in the present time (Fig. 5a, c). In 2080, these values will decrease from 17.296 to 15.532 at its maximum value (Fig. 5b), and will have a significant higher loss in areas of lower altitudes (Fig. 5b, d). High rates of FD were mainly found in the south of Bahia to the south of São Paulo states. High values of FD were correlated with high altitudes for both present ($r^2 = 0.004$, $P < 0.001$; Fig. 5c) and future conditions ($r^2 = 0.101$, $P < 0.001$; Fig. 5d).

The highest values of Phylogenetic diversity (PD) in the present time are distributed in the east-central region, mainly in the region of Serra do Mar rising to Central Corridor and a small part of Pernambuco (in high altitude areas) (Fig. 6a, c). For 2080, PD can decline from 5.652 to 5.440 at its maximum value (Fig. 6b), decreasing in the northeastern region, and increasing in the southern region, especially in the Serra do Mar mountain chain). The regions of highest altitude will be replaced by significantly values in the future ($P < 0.001$; Fig. 6d). The built null models for the FD and PD in present and

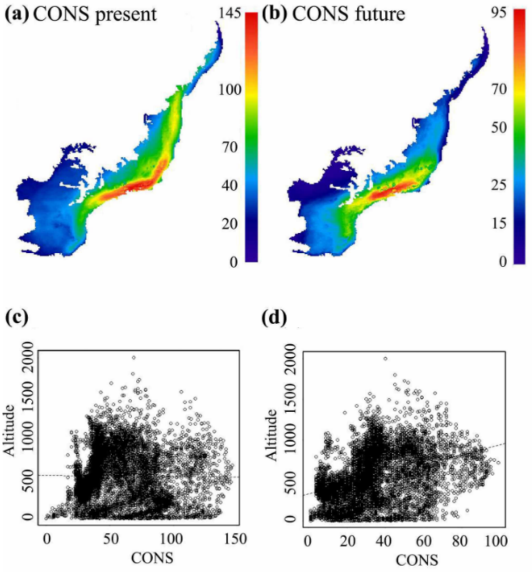

Fig. 3. Map of amphibian species richness in the Atlantic Forest derived from the consensus model for the present (a) and future (b). Correlations between species richness and altitude (meters) for the present (c) and future (d).

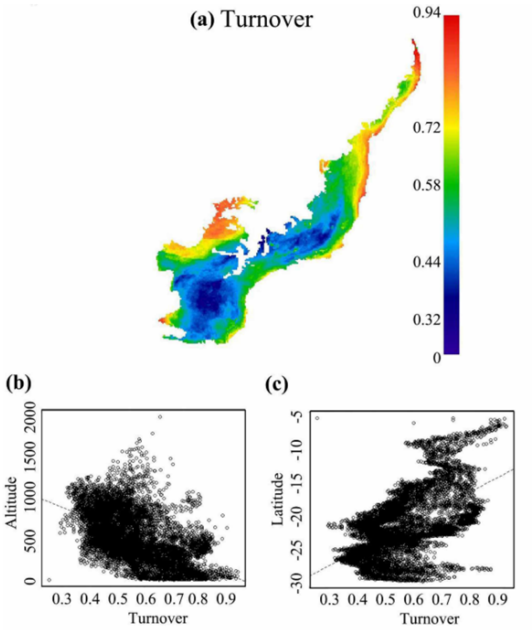

Fig. 4. Map of amphibian species turnover derived from the consensus model (a). Correlations between species turnover with altitude (meters) (b), and latitude (c) in the Atlantic Forest.

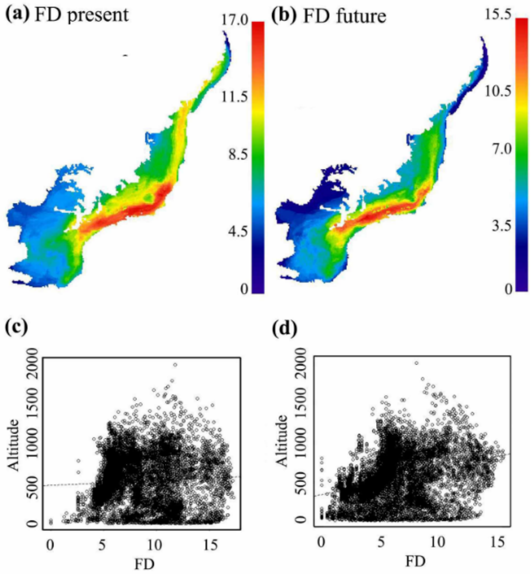

Fig. 5. Maps of Functional diversity (FD) derived from the amphibian species richness consensus model for the present (a) and future (b). Correlations between FD consensus model and altitude (meters) for the present (c) and future (d).

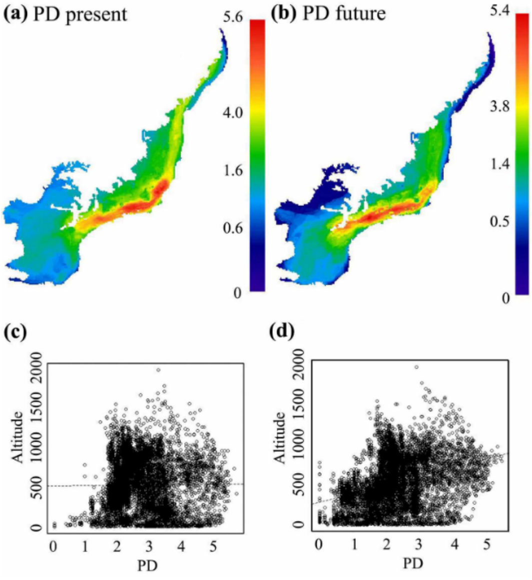

Fig. 6. Maps of Phylogenetic diversity (PD) derived from the amphibian species richness consensus model for the present (a) and future (b). Correlations between PD consensus model and altitude (meters) for the present (c) and future (d).

future times showed different values than expected by chance ($P < 0.001$), indicating a non-random pattern of functional and phylogenetic diversity. FD and PD were highly correlated (present: $r^2 = 0.91$, $P< 0.001$; future: $r^2 = 0.94$, $P < 0.001$), based on comparison of the CONS consensus model (present: FD – $r^2 = 0.87$, $P < 0.001$, PD – $r^2 = 0.89$, $P < 0.001$; future: FD – $r^2 = 0.86$, $P < 0.001$, PD – $r^2 = 0.84$, $P < 0.001$).

The predicted loss of species richness in the future may be accompanied by the loss of FD and PD (Fig. 7). The prediction of massive habitat suitability losses under climate change will negatively affect the most amphibians of the Atlantic Forest (i.e. 60% of species can be subject to some level of threat by 2080) (Fig. 8).

According to our estimations under the IUCN's criterion B1, 40% (n= 181 spp) of the species will be not threatened by 2080. However, 15% (n= 62 spp) of the species tend to lose less than 30% of their original distribution ranges, considering the projections for a moderate carbon emission scenario. Our results indicated that 21.6 % (n= 97 spp) of the species are expected to be locally extinct by 2080. The summary of the impacts of future climatic consequences on each individual species is detailed in the Supporting Information (Table S1).

DISCUSSION

Our findings showed a dramatic reduction of species' extent of occurrence (CONS, FD and PD) in the near future.

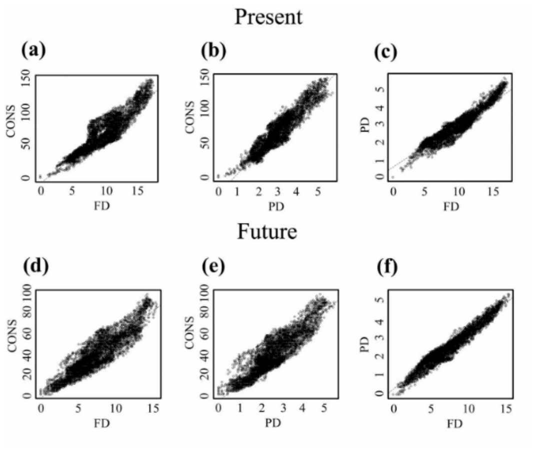

Fig. 7. Correlations between species richness consensual model (CONS), and Functional (FD) and Phylogenetic (PD) diversity of amphibians in the Brazilian Atlantic Forest. Present time: CONS vs FD (a), CONS vs PD (b) and FD vs. PD (c); Future time: CONS vs FD (d), CONS vs PD (e) and FD vs PD (f).

High amphibian species turnover rates in the high-altitude regions strengthen the mountains of Atlantic Forest as key climate refuges areas (Randin et al. 2009; Araújo et al. 2011). The persistence of the species in their original ranges will be dependent on their degree of physiological and phenotypic plasticity, antipredator mechanisms, reproductive strategies, and evolutionary adaptation to environmental change (Holt, 1990; Visser, 2008; Toledo et al. 2012; Urban et al. 2014; Ferreira et al. 2016; Lourenço-de-Moraes et al. 2016). As potential result of climate change, some species can also increase their spatial ranges, although it expected to feature low ranges in the future (i.e. less than 30% of their original distribution). For instance, opportunistic species adapted to warmer and drier environments also had a spatial range expansion (e.g. *Rhinella crucifer, Dendropsophus branneri, Leptodactylus troglodytes* and *Siphonops annulatus*). Species that live in high altitudes and high latitudes had their ranges little affected. *Brachycephalus brunneus*, a species that due to its morphology and great dependence on abiotic factors (i.e. temperature and rainfall – 1,300 m a.s.l.; Ribeiro et al., 2005), had low range changes in our model, which can enable this species to remain in the future. However, species of this genus that occur in the north portion of the Atlantic Forest – *B. pulex* (Napoli et al., 2011), also can become extinct according to the same model.

Our results showed that FD and PD have high correlation among themselves and a non-random pattern of species composition for both present and future times. This pattern suggests that environmental factors may act as a filter that does not allow the co-existence of similar species (Diamond, 1975; Weiher and Keddy, 1999). In addition, historical factors provided biogeographic barriers acting to determine the regional bank of some species assemblages (Ricklefs and Schluter, 1993).

We revealed three major areas of FD and PD in the mountain chain Serra do Mar, the Central Corridor of the Atlantic Forest and the altitude areas of Pernambuco state. Carnaval et al. (2009) pointed out three climate refuges for amphibians during the Pleistocene: 1. Southern Bahia state (located in the Central Corridor of the Atlantic Forest); 2. Pernambuco state; 3. east-north region of

São Paulo (i.e. Serra do Mar). We showed higher rates of phylogenetic and functional diversity in these areas, supporting Carnaval et al. (2009) hypothesis. Our results also suggested amphibian-climate refuges in the Espírito Santo state, the Serra da Mantiqueira region that corresponds to the South of Minas Gerais state, and the South of Serra do Mar that corresponds to the east of Paraná state. In the future (i.e. 2080), these same areas will continue as potential refuges, but changing the scenario for the higher altitudes areas (i.e. mountain chains). Our model showed that species may have suitable habitat in higher latitudes and altitudes (see Figs. 3 and 4). Species with access to mountainous regions may migrate to higher altitude areas, which have lower temperatures (Colwell et al., 2008), and in the case of the Atlantic Forest, should retain greater humidity due to better-preserved forests cover (Ribeiro et al., 2009).

Loyola et al. (2013) indicated high values of phylogenetic diversity of amphibians in the Atlantic Forest to present and future representations (i.e. 2080). Our data contradicts these values, indicating low PD values and significant correlations with low richness consensus model (CONS) for the future. However, our findings corroborate the data obtained by Thuiller et al. (2011), which showed that the loss of species richness may be accompanied by the loss of phylogenetic diversity. We also indicated that the loss of species richness for the future will follow the loss of FD and PD. We suggested that FD and PD can be directly associated to ecological and evolutionary processes provided by amphibians. Closely phylogenetic species may not coexist due to a possible competitive exclusion (Arnam et al., 2016). Phylogenetic related species may have different roles on the ecosystem funtioning (Webb et al., 2002; Gomez et al., 2010). By framing evolutionary ecology into conservation science, we revealed that phylogenetic metrics can be relevant tools for functional landscape planning for threatened amphibian species.

According to our results, 60% of the studied species will be threatened or extinct by 2080. It is highly concerning that 92% of the species of our study are not included in any threatened status under the IUCN criteria (IUCN, 2017; see Table S1). Moreover, amphibian species under protection in Atlantic Forest are more threatened by extinction than in other Brazilian biomes (Campos et al., 2016). The Atlantic Forest was severely destroyed and fragmented, resulting in 12% of its original formation (Ribeiro et al., 2009). The science of global warming has reached a consensus on environmental impacts driven by ambitious targets of urbanization, agriculture and livestock (Nordhaus et al., 2010). Given the accelerated land-use change, the results for the future may be even more alarming.

Studies in the Atlantic Forest have been warning about the need to invest in Protected Areas at high altitude areas (Lemes et al., 2013; Loyola et al., 2013),

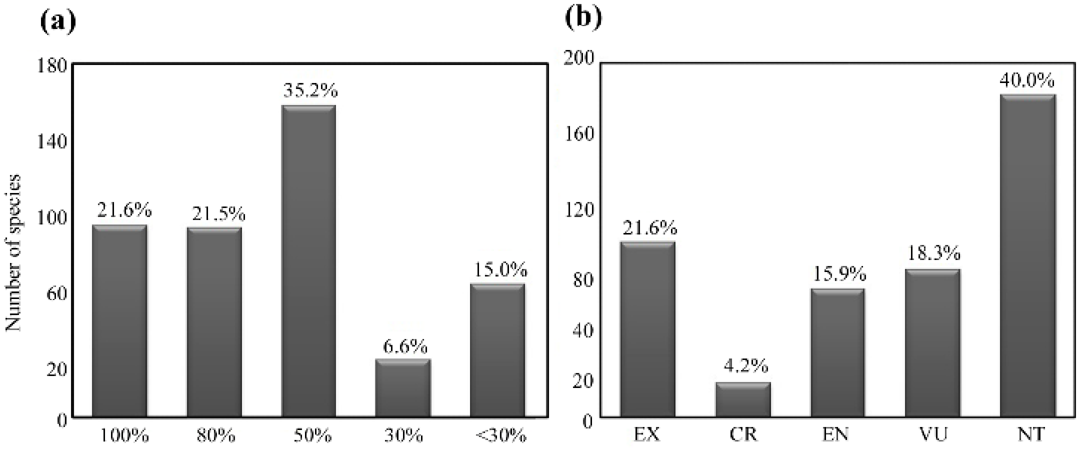

Fig. 8. Threat status of amphibian species in the face of climate-change consequences expected by 2080 in in the Atlantic Forest hotspot. In the top of the bars are the percentage of species richness. (a) percentage of loss of species range; (b) status of species: Extinct (EX) = 0 km^2; Critically Endangered (CR) < 100 km^2; Endangered (EN) < 5,000 km^2; Vulnerable (VU) < 20,000 km^2; Non-threatened (NT) > 20,000 km^2.

mainly in the areas of Serra do Mar and the southern Bahia region (Carnaval et al., 2009; Campos et al., 2017; Campos and Lourenço-de-Moraes, 2017). Therefore, considering the dramatic evolutionary and ecological loss showed in this study, we suggest four large areas as priority for conservation efforts in the Atlantic Forest: the Serra do Mar, the Serra da Mantiqueira, the Central Corridor and areas of high altitude in the Pernambuco state.

Both biotic and abiotic factors can influence the richness and composition of species in an ecosystem (Diamond, 1975). Amphibians are particularly sensitive to environmental changes, and depending on the species, the dispersion may be difficult because of its specializations as diminutive size (Crump, 2010; Early and Sax, 2011; Lourenço-de-Moraes et al., 2012, 2014). The use of various algorithms to reach a better consensus has been demonstrated as an effective strategy to reach outcomes closer to reality, and is one of the keys to understanding how communities can respond to climate change (Araújo and New, 2006; Marmion et al., 2009). Therefore, our consensus model showed useful results to plan conservation actions in relation to spatial and temporal patterns in ecology and evolution. We introduced a new conservation framework that has sought to understand the functioning of ecosystems from the amphibian-climate refuges in an age of extinction.

Given that amphibians are very sensitive to climate change due to mainly their metabolic characteristics, species dispersal across disturbed areas may be unfeasible for most species. The management of the current forest suggested as potential climate refuges is key for an effective conservation planning.

Therefore, integrating the amphibian-climate refuges in the highest-priority conservation areas is essential for spatial decision-making in the Atlantic Forest hotspot, reducing extinction risk and avoiding species loss.

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APPENDIX. Supporting Information

Supplementary files:

Table S1. List of amphibian species assessed in Atlantic Forest, present and future threat status under the IUCN criteria (2017), and climatic consequences on the species' extent of occurrence (Km^2).

Figure S1. Map of the Brazilian Atlantic Forest hotspot (in gray) in South American territory and complementary fieldwork areas (black dots). (a) Parque Ecológico Spitzkopf, SC, (b) Parque Estadual Pico do Marumbi, PR, (c) Parque estadual de Campinhos, PR, (d) Parque municipal das Perobas, PR, (e) Parque Estadual Mata dos Godoy, PR, (f) Refúgio municipal da vida Silvestre, Horto Florestal de Jacarezinho, PR, (g) Estação Ecológica de Juréia-Itatins, SP, (h) Parque Estadual da Serra do Mar Núcleo Caraguatatuba, SP, (i) Parque Nacional da Serra dos Órgãos, RJ, (j) Reserva Biológica Augusto Ruschi, ES, (k) Reserva Biológica de Una, BA. We sampled amphibians using acoustic and visual nocturnal and diurnal surveys (Crump and Scott Jr., 1994; Zimmerman, 1994). We searched at the margins of water bodies, streams, and along 2,000 m forest transects in each sampled area.

Table S1. List of amphibian species assessed in Atlantic Forest, present and future threat status under the IUCN criteria (2017), and climatic consequences on the species' extent of occurrence (Km^2).

Order/Family/Species	Current Threat Status	Future Threat Status	Present Extent of Occurrence	Future Extent of Occurrence
Gymnophiona				
Typlonectidae				
Chthonerpeton indistinctum	Not Evaluated	Vulnerable	55,125	5,200
Siphonopidae				
Luetkenotyphlus brasiliensis	Not Evaluated	Non-threatened	333,725	171,800
Siphonops annulatus	Not Evaluated	Non-threatened	868,175	788,925
Siphonops hardyi	Not Evaluated	Vulnerable	56,250	12,400
Siphonops paulensis	Not Evaluated	Non-threatened	826,475	608,775
Anura				
Alsodidae				
Limnomedusa macroglossa	Not Evaluated	Vulnerable	155,325	57,050
Aromobatidae				
Allobates alagoanus	Not Evaluated	Extinct	550	0
Allobates capixaba	Not Evaluated	Endangered	44,925	2,225
Allobates olfersioides	Vulnerable	Non-threatened	270,475	181,675
Brachycephalidae				
Brachycephalus alipioi	Not Evaluated	Critically Endangered	1,325	75
Brachycephalus brunneus	Not Evaluated	Endangered	375	2,525
Brachycephalus didactylus	Not Evaluated	Vulnerable	62,350	14,100
Brachycephalus ephipium	Not Evaluated	Non-threatened	220,025	83,000
Brachycephalus ferruginus	Not Evaluated	Extinct	1,550	0
Brachycephalus garbeanus	Not Evaluated	Critically Endangered	975	50
Brachycephalus guarani	Not Evaluated	Endangered	6,525	200
Brachycephalus hermogenesi	Not Evaluated	Vulnerable	50,500	14,100
Brachycephalus izecksohni	Not Evaluated	Extinct	425	0
Brachycephalus margaritatus	Not Evaluated	Critically Endangered	1,175	50
Brachycephalus nodoterga	Not Evaluated	Critically Endangered	2,275	25
Brachycephalus pernix	Critically Endangered	Extinct	200	0
Brachycephalus pitanga	Not Evaluated	Endangered	1,225	450
Brachycephalus pombali	Not Evaluated	Extinct	1,200	0
Brachycephalus pulex	Not Evaluated	Extinct	1,225	0
Brachycephalus toby	Not Evaluated	Critically Endangered	850	25
Brachycephalus tridactylus	Not Evaluated	Extinct	1,125	0
Brachycephalus vertebralis	Not Evaluated	Endangered	14,700	1,225

Ischnocnema abdita	Not Evaluated	Extinct	1,425	0
Ischnocnema bolbodactyla	Not Evaluated	Vulnerable	40,950	13,575
Ischnocnema concolor	Not Evaluated	Extinct	525	0
Ischnocnema erythromera	Not Evaluated	Endangered	3,575	350
Ischnocnema guenteri	Not Evaluated	Non-threatened	377,600	123,775
Ischnocnema henselli	Not Evaluated	Non-threatened	130,575	58,700
Ischnocnema hoehnei	Not Evaluated	Vulnerable	46,925	8,775
Ischnocnema holti	Not Evaluated	Extinct	925	0
Ischnocnema izecksoni	Not Evaluated	Extinct	5,550	0
Ischnocnema juipoca	Not Evaluated	Non-threatened	192,425	94,725
Ischnocnema karst	Not Evaluated	Extinct	650	0
Ischnocnema manezinho	Vulnerable	Vulnerable	21,725	9,975
Ischnocnema melonopygia	Not Evaluated	Extinct	100	0
Ischnocnema nasuta	Not Evaluated	Non-threatened	383,725	199,000
Ischnocnema nigriventris	Not Evaluated	Extinct	525	0
Ischnocnema octavioi	Not Evaluated	Vulnerable	44,550	7,150
Ischnocnema oea	Not Evaluated	Vulnerable	400	8,150
Ischnocnema parva	Not Evaluated	Non-threatened	182,875	68,825
Ischnocnema randorum	Not Evaluated	Extinct	475	0
Ischnocnema sambaqui	Not Evaluated	Endangered	2,925	2,200
Ischnocnema spanios	Not Evaluated	Endangered	17,875	1,450
Ischnocnema verrucosa	Not Evaluated	Non-threatened	99,825	30,725
Ischnocnema vizottoi	Not Evaluated	Extinct	6,275	0
Bufonidae				
Dendrophryniscus berthalutzae	Not Evaluated	Vulnerable	34,125	13,050
Dendrophryniscus brevipollicatus	Not Evaluated	Non-threatened	93,975	42,675
Dendrophryniscus carvalhoi	Not Evaluated	Extinct	4,075	0
Dendrophryniscus krause	Not Evaluated	Extinct	850	0
Dendrophryniscus leucomystax	Not Evaluated	Non-threatened	97,050	33,275
Dendrophryniscus oreites	Not Evaluated	Extinct	2,475	0
Dendrophryniscus proboscideus	Not Evaluated	Non-threatened	78,625	28,200
Frostius erythrophthalmus	Not Evaluated	Endangered	29,050	300
Frostius pernambucensis	Not Evaluated	Non-threatened	91,150	39,850
Melanophryniscus admirabilis	Critically Endangered	Extinct	700	0
Melanophryniscus alipioi	Not Evaluated	Extinct	550	0
Melanophryniscus cambaraensis	Vulnerable	Extinct	2,675	0
Melanophryniscus dorsalis	Vulnerable	Endangered	9,750	2,300
Melanophryniscus macrogranulosus	Endangered	Critically Endangered	200	50
Melanophryniscus moreirae	Not Evaluated	Extinct	4,725	0
Melanophryniscus setiba	Critically Endangered	Endangered	6,600	2,475
Melanophryniscus simplex	Not Evaluated	Endangered	775	2,325
Melanophryniscus spectabilis	Not Evaluated	Extinct	100	0

Melanophryniscus tumifrons	Not Evaluated	Vulnerable	156,975	11,725
Melanophryniscus vilavelhensis	Not Evaluated	Extinct	1,300	0
Rhinella abei	Not Evaluated	Vulnerable	48,000	19,000
Rhinella achavali	Not Evaluated	Endangered	32,950	750
Rhinella crucifer	Not Evaluated	Non-threatened	209,375	225,700
Rhinella dorbignyi	Not Evaluated	Extinct	7,225	0
Rhinella fernadezae	Not Evaluated	Vulnerable	81,475	19,400
Rhinella granulosa	Not Evaluated	Non-threatened	867,275	915,125
Rhinella henseli	Not Evaluated	Vulnerable	100,100	18,950
Rhinella hoogmoedi	Not Evaluated	Non-threatened	276,425	198,775
Rhinella icterica	Not Evaluated	Non-threatened	755,400	340,275
Rhinella jimi	Not Evaluated	Non-threatened	280,525	278,125
Rhinella ornata	Not Evaluated	Non-threatened	220,275	91,525
Rhinella pygmaea	Not Evaluated	Vulnerable	39,225	16,600
Rhinella schneideri	Not Evaluated	Non-threatened	928,875	712,825
Ceratophryidae				
Ceratophrys aurita	Not Evaluated	Non-threatened	489,350	258,425
Craugastoridae				
Eleutherodactylus bilineata	Not Evaluated	Vulnerable	46,875	9,150
Euparkerella brasiliensis	Not Evaluated	Vulnerable	44,350	10,550
Euparkerella cochranae	Not Evaluated	Vulnerable	25,125	6,950
Euparkerella robusta	Not Evaluated	Extinct	225	0
Euparkerella tridactyla	Not Evaluated	Endangered	575	125
Haddadus aramunha	Not Evaluated	Vulnerable	350	17,575
Haddadus binotatus	Not Evaluated	Non-threatened	487,650	236,600
Holoaden bradei	Critically Endangered	Endangered	4,475	275
Holoaden luederwaldti	Endangered	Vulnerable	49,075	10,525
Holoaden pholeter	Not Evaluated	Vulnerable	600	8,225
Pristimantis paulodutrai	Not Evaluated	Vulnerable	65,075	12,000
Pristimantis ramagii	Not Evaluated	Non-threatened	129,525	117,000
Pristimantis vinhai	Not Evaluated	Non-threatened	96,725	32,275
Cycloramphidae				
Cycloramphus acangatan	Not Evaluated	Endangered	16,100	2,750
Cycloramphus bandeirensis	Not Evaluated	Endangered	450	2,650
Cycloramphus bolitoglossus	Not Evaluated	Vulnerable	28,950	9,875
Cycloramphus boraceiensis	Not Evaluated	Non-threatened	64,925	22,975
Cycloramphus brasiliensis	Not Evaluated	Vulnerable	38,900	5,725
Cycloramphus carvalhoi	Not Evaluated	Critically Endangered	1,125	50
Cycloramphus catarinensis	Not Evaluated	Critically Endangered	250	50
Cycloramphus dubius	Not Evaluated	Endangered	6,700	250
Cycloramphus eleutherodactylus	Not Evaluated	Non-threatened	187,925	47,250
Cycloramphus izecksohni	Not Evaluated	Vulnerable	24,050	5,325

Cycloramphus juimirim	Not Evaluated	Extinct	575	0
Cycloramphus lithomimeticus	Not Evaluated	Extinct	11,875	0
Cycloramphus lutzorum	Not Evaluated	Vulnerable	61,625	11,975
Cycloramphus migueli	Not Evaluated	Extinct	3,025	0
Cycloramphus organensis	Not Evaluated	Endangered	2,800	325
Cycloramphus rhyakonastes	Not Evaluated	Extinct	1,400	0
Cycloramphus valae	Not Evaluated	Endangered	9,750	100
Thoropa lutzi	Not Evaluated	Non-threatened	69,525	27,800
Thoropa miliaris	Not Evaluated	Non-threatened	396,750	258,675
Thoropa saxatilis	Vulnerable	Endangered	12,375	3,075
Thoropa taophora	Not Evaluated	Vulnerable	49,225	11,700
Zachaenus carvalhoi	Not Evaluated	Vulnerable	525	7,375
Zachaenus parvulus	Not Evaluated	Vulnerable	34,300	10,300
Eleutherodactylidae				
Adelophryne mucronatus	Not Evaluated	Extinct	3,450	0
Adelophryne pachydactyla	Not Evaluated	Extinct	22,075	0
Hemiphractidae				
Flectonotus fissilis	Not Evaluated	Non-threatened	117,575	39,875
Flectonotus goeldii	Not Evaluated	Non-threatened	216,200	78,750
Flectonotus ohausi	Not Evaluated	Non-threatened	109,150	41,875
Gastrotheca albolineata	Not Evaluated	Non-threatened	79,025	26,925
Gastrotheca ernestoi	Not Evaluated	Endangered	39,800	4,775
Gastrotheca fissipes	Not Evaluated	Non-threatened	172,250	100,550
Gastrotheca fulvorufa	Not Evaluated	Endangered	47,525	3,850
Gastrotheca megacephala	Not Evaluated	Vulnerable	76,900	16,275
Gastrotheca microdiscus	Not Evaluated	Non-threatened	200,575	86,200
Gastrotheca prasina	Not Evaluated	Extinct	925	0
Gastrotheca pulchra	Not Evaluated	Extinct	425	0
Gastrotheca recava	Not Evaluated	Extinct	450	0
Hylidae				
Aparasphenodon arapapa	Not Evaluated	Non-threatened	117,950	37,775
Aparasphenodon bokermani	Not Evaluated	Endangered	525	1,100
Aparasphenodon brunoi	Not Evaluated	Non-threatened	280,450	142,575
Aplastodiscus albofrenatus	Not Evaluated	Vulnerable	51,875	13,650
Aplastodiscus albosignatus	Not Evaluated	Non-threatened	128,100	45,375
Aplastodiscus arildae	Not Evaluated	Non-threatened	221,850	86,800
Aplastodiscus callipygius	Not Evaluated	Vulnerable	42,900	11,200
Aplastodiscus cavicola	Not Evaluated	Vulnerable	73,800	16,925
Aplastodiscus cochranae	Not Evaluated	Endangered	15,250	4,175
Aplastodiscus ehrhardti	Not Evaluated	Vulnerable	35,725	14,250
Aplastodiscus eugenioi	Not Evaluated	Endangered	27,850	3,850
Aplastodiscus flumineus	Not Evaluated	Extinct	800	0
Aplastodiscus ibirapitanga	Not Evaluated	Vulnerable	46,800	5,075
Aplastodiscus leucopygius	Not Evaluated	Non-threatened	169,200	53,975

Aplastodiscus perviridis	Not Evaluated	Non-threatened	588,075	316,225
Aplastodiscus sibilatus	Not Evaluated	Extinct	18,075	0
Aplastodiscus weygoldti	Not Evaluated	Critically Endangered	2,950	75
Bokermanohyla ahenea	Not Evaluated	Extinct	375	0
Bokermanohyla astartea	Not Evaluated	Non-threatened	133,375	43,975
Bokermanohyla capra	Not Evaluated	Extinct	3,350	0
Bokermanohyla caramaschii	Not Evaluated	Non-threatened	48,850	23,075
Bokermanohyla carvalhoi	Not Evaluated	Vulnerable	29,525	8,525
Bokermanohyla circumdata	Not Evaluated	Vulnerable	108,575	15,625
Bokermanohyla diamantina	Not Evaluated	Non-threatened	450	30,475
Bokermanohyla gouveiai	Not Evaluated	Vulnerable	3,275	5,750
Bokermanohyla hylax	Not Evaluated	Non-threatened	92,325	38,175
Bokermanohyla ibitipoca	Not Evaluated	Extinct	550	0
Bokermanohyla itapoty	Not Evaluated	Extinct	2,625	0
Bokermanohyla izecksohni	Not Evaluated	Extinct	200	0
Bokermanohyla lucianae	Not Evaluated	Extinct	100	0
Bokermanohyla luctuosa	Not Evaluated	Endangered	34,550	3,600
Bokermanohyla martinsi	Not Evaluated	Endangered	15,575	1,275
Bokermanohyla nanuzae	Not Evaluated	Extinct	7,325	0
Bokermanohyla oxente	Not Evaluated	Extinct	125	0
Dendropsophus anceps	Not Evaluated	Non-threatened	242,050	116,150
Dendropsophus berthalutzae	Not Evaluated	Non-threatened	142,900	54,100
Dendropsophus bipunctatus	Not Evaluated	Non-threatened	173,975	157,125
Dendropsophus branneri	Not Evaluated	Non-threatened	333,925	377,400
Dendropsophus decipiens	Not Evaluated	Non-threatened	424,425	315,075
Dendropsophus elegans	Not Evaluated	Non-threatened	496,500	434,275
Dendropsophus giesleri	Not Evaluated	Non-threatened	94,925	39,100
Dendropsophus haddadi	Not Evaluated	Non-threatened	83,875	25,375
Dendropsophus meridianus	Not Evaluated	Vulnerable	28,150	9,650
Dendropsophus microps	Not Evaluated	Non-threatened	327,275	152,625
Dendropsophus minutus	Not Evaluated	Non-threatened	952,050	716,050
Dendropsophus nahdereri	Not Evaluated	Vulnerable	32,150	11,325
Dendropsophus nanus	Not Evaluated	Non-threatened	735,550	626,925
Dendropsophus novaisi	Not Evaluated	Vulnerable	5,100	6,025
Dendropsophus oliveirai	Not Evaluated	Non-threatened	75,800	23,050
Dendropsophus pseudomeridianus	Not Evaluated	Endangered	32,975	4,725
Dendropsophus ruschii	Not Evaluated	Endangered	3,925	2,200
Dendropsophus samborni	Not Evaluated	Non-threatened	349,475	172,650
Dendropsophus seniculus	Not Evaluated	Non-threatened	293,475	143,500
Dendropsophus soaresi	Not Evaluated	Non-threatened	47,575	22,750
Dendropsophus studarae	Not Evaluated	Extinct	200	0
Dendropsophus werneri	Not Evaluated	Non-threatened	75,475	28,875
Boana albomarginatus	Not Evaluated	Non-threatened	493,300	360,275

Boana albopunctatus	Not Evaluated	Non-threatened	766,550	465,950
Boana atlanticus	Not Evaluated	Non-threatened	89,375	30,675
Boana bichoffi	Not Evaluated	Non-threatened	249,750	79,000
Boana caingua	Not Evaluated	Non-threatened	127,325	28,050
Boana caipora	Not Evaluated	Extinct	2,275	0
Boana crepitans	Not Evaluated	Non-threatened	794,475	730,375
Boana curupi	Vulnerable	Endangered	12,550	1,450
Boana exastis	Not Evaluated	Extinct	4,925	0
Boana faber	Not Evaluated	Non-threatened	904,200	509,025
Boana freicanecae	Not Evaluated	Extinct	100	0
Boana guenteri	Not Evaluated	Vulnerable	38,375	19,500
Boana joaquini	Not Evaluated	Vulnerable	17,750	5,250
Boana latistriatus	Not Evaluated	Endangered	1,600	250
Boana leptolineatus	Not Evaluated	Vulnerable	155,775	12,825
Boana lundii	Not Evaluated	Non-threatened	308,025	159,325
Boana marginatus	Not Evaluated	Endangered	18,750	3,950
Boana pardalis	Not Evaluated	Non-threatened	263,000	129,825
Boana poaju	Not Evaluated	Extinct	750	0
Boana polytaenius	Not Evaluated	Non-threatened	176,475	64,325
Boana pombali	Not Evaluated	Non-threatened	106,025	48,125
Boana prasinus	Not Evaluated	Non-threatened	284,575	82,525
Boana pulchellus	Not Evaluated	Non-threatened	223,250	58,875
Boana punctatus	Not Evaluated	Non-threatened	654,600	631,225
Boana raniceps	Not Evaluated	Non-threatened	343,600	368,900
Boana secedens	Not Evaluated	Vulnerable	73,275	9,050
Boana semiguttatus	Endangered	Vulnerable	21,550	10,225
Boana semilineatus	Not Evaluated	Non-threatened	498,000	373,025
Boana stellae	Not Evaluated	Extinct	19,375	0
Boana stenocephalus	Not Evaluated	Extinct	700	0
Itapotihyla langsdorffii	Not Evaluated	Non-threatened	450,450	346,975
Ololygon agilis	Not Evaluated	Vulnerable	63,150	5,000
Ololygon albicans	Not Evaluated	Vulnerable	58,350	14,825
Ololygon angrensis	Not Evaluated	Endangered	10,075	2,000
Ololygon arduous	Not Evaluated	Endangered	675	825
Ololygon argyreornata	Not Evaluated	Non-threatened	266,525	137,300
Ololygon ariadne	Not Evaluated	Endangered	9,250	2,400
Ololygon aromothyella	Not Evaluated	Extinct	1,050	0
Ololygon belloni	Not Evaluated	Extinct	550	0
Ololygon brieni	Not Evaluated	Vulnerable	83,125	16,150
Ololygon carnevalli	Not Evaluated	Vulnerable	58,400	8,175
Ololygon catharinae	Not Evaluated	Non-threatened	81,500	44,700
Ololygon cosenzai	Not Evaluated	Extinct	1,300	0
Ololygon flavoguttata	Not Evaluated	Non-threatened	220,400	95,775
Ololygon heyeri	Not Evaluated	Endangered	4,525	2,450

Ololygon hiemalis	Not Evaluated	Non-threatened	85,575	22,725
Ololygon humilis	Not Evaluated	Non-threatened	91,800	34,725
Ololygon insperata	Not Evaluated	Extinct	550	0
Ololygon kautskyi	Not Evaluated	Critically Endangered	125	50
Ololygon litoralis	Not Evaluated	Endangered	22,575	3,200
Ololygon littoreus	Not Evaluated	Endangered	18,700	2,350
Ololygon longilinea	Not Evaluated	Vulnerable	78,700	7,350
Ololygon luizotavioi	Not Evaluated	Vulnerable	104,500	15,650
Ololygon machadoi	Not Evaluated	Endangered	66,800	3,825
Ololygon obtriangulata	Not Evaluated	Non-threatened	158,975	30,075
Ololygon peixotoi	Critically Endangered	Critically Endangered	6,400	50
Ololygon perpusilla	Not Evaluated	Non-threatened	110,950	45,925
Ololygon ranki	Not Evaluated	Extinct	6,750	0
Ololygon rizibilis	Not Evaluated	Non-threatened	167,050	64,975
Ololygon strigilata	Not Evaluated	Critically Endangered	23,450	75
Ololygon v-signata	Not Evaluated	Non-threatened	74,150	28,475
Phasmahyla cochranae	Not Evaluated	Vulnerable	109,700	17,075
Phasmahyla exilis	Not Evaluated	Vulnerable	53,600	5,000
Phasmahyla guttata	Not Evaluated	Non-threatened	108,500	36,925
Phasmahyla jandaia	Not Evaluated	Endangered	21,125	925
Phasmahyla spectabilis	Not Evaluated	Endangered	19,100	350
Phasmahyla timbo	Not Evaluated	Extinct	475	0
Phrynomedusa marginata	Not Evaluated	Non-threatened	89,100	36,650
Phyllodytes acuminatus	Not Evaluated	Vulnerable	79,700	13,000
Phyllodytes edelmoi	Not Evaluated	Critically Endangered	10,275	25
Phyllodytes gyrinaethes	Critically Endangered	Extinct	6,100	0
Phyllodytes kautskyi	Not Evaluated	Vulnerable	61,675	11,000
Phyllodytes luteolus	Not Evaluated	Non-threatened	178,050	145,100
Phyllodytes maculosus	Not Evaluated	Endangered	35,000	750
Phyllodytes melanomystax	Not Evaluated	Vulnerable	51,825	10,400
Phyllodytes punctatus	Not Evaluated	Endangered	200	775
Phyllodytes tuberculosus	Not Evaluated	Extinct	3,175	0
Phyllodytes wuchereri	Not Evaluated	Endangered	37,750	2,800
Pseudis bolbodactyla	Not Evaluated	Non-threatened	240,950	175,800
Pseudis cardosoi	Not Evaluated	Endangered	28,600	2,450
Pseudis fusca	Not Evaluated	Endangered	23,300	925
Pseudis minuta	Not Evaluated	Non-threatened	73,500	26,800
Pseudis paradoxa	Not Evaluated	Non-threatened	157,900	142,325
Scinax alter	Not Evaluated	Non-threatened	363,050	219,000
Scinax auratus	Not Evaluated	Non-threatened	84,475	72,025

Scinax caldarum	Not Evaluated	Vulnerable	100,975	11,875
Scinax cretatus	Not Evaluated	Extinct	4,650	0
Scinax crospedospilus	Not Evaluated	Non-threatened	82,700	26,075
Scinax cuspidatus	Not Evaluated	Non-threatened	250,225	115,225
Scinax duartei	Vulnerable	Vulnerable	78,175	7,750
Scinax eurydice	Not Evaluated	Non-threatened	327,675	269,475
Scinax fuscomarginatus	Not Evaluated	Non-threatened	694,300	566,050
Scinax fuscovarius	Not Evaluated	Non-threatened	927,300	618,925
Scinax granulatus	Not Evaluated	Non-threatened	301,975	104,825
Scinax hayii	Not Evaluated	Non-threatened	229,000	97,475
Scinax imbegue	Not Evaluated	Extinct	1,500	0
Scinax juncae	Not Evaluated	Extinct	1,875	0
Scinax pachychrus	Not Evaluated	Non-threatened	84,575	122,525
Scinax perereca	Not Evaluated	Non-threatened	322,775	136,400
Scinax similis	Not Evaluated	Vulnerable	54,125	17,575
Scinax squalirostris	Not Evaluated	Non-threatened	847,425	413,275
Scinax trapicheiroi	Not Evaluated	Vulnerable	26,950	5,850
Scinax tymbamirim	Not Evaluated	Extinct	1,200	0
Scinax uruguayus	Not Evaluated	Vulnerable	146,825	7,175
Scinax x-signatus	Not Evaluated	Non-threatened	791,625	699,525
Sphaenorhynchus botucudo	Not Evaluated	Extinct	1,800	0
Sphaenorhynchus caramaschii	Not Evaluated	Non-threatened	79,350	33,850
Sphaenorhynchus mirim	Not Evaluated	Endangered	900	225
Sphaenorhynchus orophilus	Not Evaluated	Non-threatened	94,325	28,425
Sphaenorhynchus palustris	Not Evaluated	Non-threatened	131,125	69,200
Sphaenorhynchus pauloalvini	Not Evaluated	Endangered	42,075	350
Sphaenorhynchus planicola	Not Evaluated	Non-threatened	87,975	28,200
Sphaenorhynchus prasinus	Not Evaluated	Non-threatened	198,225	130,075
Sphaenorhynchus surdus	Not Evaluated	Non-threatened	98,325	31,725
Trachycephalus atlas	Not Evaluated	Non-threatened	22,575	25,150
Trachycephalus dibernadoi	Not Evaluated	Non-threatened	79,550	24,800
Trachycephalus imitatrix	Not Evaluated	Non-threatened	286,675	92,225
Trachycephalus lepidus	Not Evaluated	Extinct	400	0
Trachycephalus mesophaeus	Not Evaluated	Non-threatened	532,025	445,900
Trachycephalus nigromaculatus	Not Evaluated	Non-threatened	351,075	191,600
Trachycephalus typhonius	Not Evaluated	Non-threatened	457,275	434,650
Vitreorana eurygnathum	Not Evaluated	Non-threatened	417,000	177,600
Vitreorana uranoscopa	Not Evaluated	Non-threatened	498,725	200,875
Xenohyla truncata	Endangered	Vulnerable	34,125	8,425
Hylodidae				
Crossodactylus aeneus	Not Evaluated	Non-threatened	134,675	55,975
Crossodactylus bokermani	Not Evaluated	Endangered	300	650
Crossodactylus caramaschii	Not Evaluated	Non-threatened	60,000	20,700
Crossodactylus dantei	Endangered	Extinct	200	0

Crossodactylus dispar	Not Evaluated	Non-threatened	107,400	22,450
Crossodactylus gaudichaudii	Not Evaluated	Non-threatened	115,475	45,875
Crossodactylus grandis	Not Evaluated	Endangered	18,875	1,975
Crossodactylus schmidti	Not Evaluated	Non-threatened	23,500	29,775
Hylodes amnicola	Not Evaluated	Extinct	650	0
Hylodes asper	Not Evaluated	Non-threatened	126,300	42,475
Hylodes babax	Not Evaluated	Endangered	3,150	4,225
Hylodes cardosoi	Not Evaluated	Endangered	8,050	350
Hylodes charadranaetes	Not Evaluated	Endangered	13,300	1,900
Hylodes dactylocinus	Not Evaluated	Endangered	2,800	150
Hylodes heyeri	Not Evaluated	Vulnerable	28,725	9,450
Hylodes lateristrigatus	Not Evaluated	Non-threatened	122,975	46,250
Hylodes magalhaesi	Not Evaluated	Critically Endangered	6,650	50
Hylodes meridionalis	Not Evaluated	Endangered	9,900	1,075
Hylodes nasus	Not Evaluated	Non-threatened	166,425	75,425
Hylodes ornatus	Not Evaluated	Endangered	25,550	1,375
Hylodes otavioi	Not Evaluated	Extinct	350	0
Hylodes perere	Not Evaluated	Extinct	2,075	0
Hylodes perplicatus	Not Evaluated	Endangered	9,700	4,175
Hylodes phyllodes	Not Evaluated	Vulnerable	49,375	8,400
Hylodes pipilans	Not Evaluated	Extinct	475	0
Hylodes regius	Not Evaluated	Critically Endangered	5,300	50
Hylodes sazimai	Not Evaluated	Endangered	16,950	225
Megaelosia apuana	Not Evaluated	Endangered	400	2,675
Megaelosia bocainensis	Not Evaluated	Extinct	500	0
Megaelosia goeldii	Not Evaluated	Vulnerable	52,075	14,825
Megaelosia massarti	Not Evaluated	Extinct	4,250	0
Leptodactylidae				
Adenomera ajurauna	Not Evaluated	Extinct	4,200	0
Adenomera araucaria	Not Evaluated	Critically Endangered	7,225	50
Adenomera bokermani	Not Evaluated	Non-threatened	285,575	101,300
Adenomera engelsi	Not Evaluated	Extinct	4,600	0
Adenomera marmorata	Not Evaluated	Non-threatened	271,550	85,600
Adenomera nana	Not Evaluated	Vulnerable	23,450	7,050
Adenomera thomei	Not Evaluated	Vulnerable	30,925	7,825
Crossodactylodes bokermanni	Not Evaluated	Endangered	3,925	1,475
Crossodactylodes izecksohni	Not Evaluated	Extinct	425	0
Leptodactylus cupreus	Not Evaluated	Extinct	850	0
Leptodactylus flavopictus	Not Evaluated	Non-threatened	128,075	58,600
Leptodactylus furnarius	Not Evaluated	Non-threatened	348,725	227,725
Leptodactylus fuscus	Not Evaluated	Non-threatened	958,100	785,450
Leptodactylus gracilis	Not Evaluated	Non-threatened	368,900	152,550

Leptodactylus jolyi	Not Evaluated	Extinct	675	0
Leptodactylus labyrinthicus	Not Evaluated	Non-threatened	482,250	380,975
Leptodactylus latrans	Not Evaluated	Non-threatened	942,525	731,225
Leptodactylus macrosternum	Not Evaluated	Non-threatened	824,975	541,625
Leptodactylus mystaceus	Not Evaluated	Non-threatened	55,600	25,300
Leptodactylus mystacinus	Not Evaluated	Non-threatened	960,700	703,175
Leptodactylus natalensis	Not Evaluated	Non-threatened	242,950	220,200
Leptodactylus noaktites	Not Evaluated	Non-threatened	226,600	55,250
Leptodactylus plaumanni	Not Evaluated	Non-threatened	205,050	94,625
Leptodactylus podicipinus	Not Evaluated	Non-threatened	260,575	232,200
Leptodactylus spixi	Not Evaluated	Non-threatened	389,350	376,850
Leptodactylus troglodytes	Not Evaluated	Non-threatened	114,275	127,475
Leptodactylus vastus	Not Evaluated	Non-threatened	58,500	37,875
Leptodactylus viridis	Not Evaluated	Endangered	24,250	1,300
Paratelmatobius cardosoi	Not Evaluated	Extinct	3,150	0
Paratelmatobius gaigeae	Not Evaluated	Extinct	625	0
Paratelmatobius lutzii	Critically Endangered	Critically Endangered	475	25
Paratelmatobius poecilogaster	Not Evaluated	Extinct	4,700	0
Paratelmatobius yepiranga	Not Evaluated	Extinct	2,200	0
Physalaemus aguirrei	Not Evaluated	Non-threatened	99,750	24,650
Physalaemus atlanticus	Not Evaluated	Extinct	100	0
Physalaemus barrioi	Not Evaluated	Extinct	1,000	0
Physalaemus bokermanni	Not Evaluated	Extinct	475	0
Physalaemus camacan	Not Evaluated	Extinct	100	0
Physalaemus crombiei	Not Evaluated	Non-threatened	121,425	33,900
Physalaemus cuvieri	Not Evaluated	Non-threatened	957,400	743,075
Physalaemus erikae	Not Evaluated	Endangered	27,850	900
Physalaemus feioi	Not Evaluated	Endangered	33,675	350
Physalaemus jordanensis	Not Evaluated	Endangered	38,200	1,450
Physalaemus kroyeri	Not Evaluated	Non-threatened	94,400	129,100
Physalaemus lateristriga	Not Evaluated	Endangered	17,675	2,875
Physalaemus lisei	Not Evaluated	Vulnerable	69,050	11,975
Physalaemus maculiventris	Not Evaluated	Non-threatened	171,625	56,050
Physalaemus maximus	Vulnerable	Extinct	11,825	0
Physalaemus moreirae	Not Evaluated	Endangered	9,925	775
Physalaemus nanus	Not Evaluated	Vulnerable	52,125	12,600
Physalaemus obtectrus	Not Evaluated	Non-threatened	75,375	22,525
Physalaemus olfersii	Not Evaluated	Non-threatened	266,900	118,425
Physalaemus signifer	Not Evaluated	Non-threatened	191,100	74,775
Physalaemus soaresi	Critically Endangered	Extinct	475	0
Physalaemus spiniger	Not Evaluated	Vulnerable	25,050	5,900
Pseudopaludicola falcipes	Not Evaluated	Non-threatened	558,200	256,450

Scythrophrys sawayae	Not Evaluated	Vulnerable	22,625	9,675
Microhylidae				
Arcomover passareli	Not Evaluated	Non-threatened	95,175	36,450
Chiasmocleis alagoanus	Endangered	Extinct	525	0
Chiasmocleis atlantica	Not Evaluated	Vulnerable	67,425	17,525
Chiasmocleis capixaba	Not Evaluated	Endangered	44,475	1,200
Chiasmocleis carvalhoi	Not Evaluated	Vulnerable	88,375	15,400
Chiasmocleis crucis	Not Evaluated	Extinct	100	0
Chiasmocleis gnoma	Not Evaluated	Extinct	100	0
Chiasmocleis leucosticta	Not Evaluated	Non-threatened	141,450	48,000
Chiasmocleis mantiqueira	Not Evaluated	Extinct	650	0
Chiasmocleis schubarti	Not Evaluated	Non-threatened	139,075	67,700
Dasypops schirchi	Not Evaluated	Critically Endangered	18,775	25
Elachistocleis bicolor	Not Evaluated	Non-threatened	350,925	137,450
Elachistocleis cesarii	Not Evaluated	Non-threatened	690,200	525,425
Elachistocleis erythrogaster	Not Evaluated	Extinct	4,950	0
Myersiella microps	Not Evaluated	Non-threatened	147,975	56,300
Stereocyclops histrio	Not Evaluated	Endangered	1,100	100
Stereocyclops incrassatus	Not Evaluated	Non-threatened	215,875	113,325
Stereocyclops parkeri	Not Evaluated	Vulnerable	37,725	6,425
Odontophrynidae				
Macrogenioglottus alipioi	Not Evaluated	Non-threatened	287,400	201,200
Odontophrynus americanus	Not Evaluated	Non-threatened	879,800	440,400
Odontophrynus carvalhoi	Not Evaluated	Non-threatened	70,725	114,550
Odontophrynus maisuma	Not Evaluated	Non-threatened	825,000	538,125
Proceratophrys appendiculata	Not Evaluated	Non-threatened	158,725	67,575
Proceratophrys avelinoi	Not Evaluated	Non-threatened	236,550	131,700
Proceratophrys bigibbosa	Not Evaluated	Vulnerable	67,450	12,225
Proceratophrys boiei	Not Evaluated	Non-threatened	530,725	432,500
Proceratophrys brauni	Not Evaluated	Endangered	38,425	2,875
Proceratophrys cristiceps	Not Evaluated	Non-threatened	73,625	34,775
Proceratophrys cururu	Not Evaluated	Extinct	100	0
Proceratophrys laticeps	Not Evaluated	Non-threatened	121,375	34,525
Proceratophrys melanopogon	Not Evaluated	Vulnerable	60,000	13,525
Proceratophrys minuta	Not Evaluated	Vulnerable	350	7,375
Proceratophrys paviotti	Not Evaluated	Extinct	325	0
Proceratophrys renalis	Not Evaluated	Non-threatened	153,000	105,850
Proceratophrys sanctarictae	Critically Endangered	Vulnerable	1,325	7,775
Proceratophrys schirchi	Not Evaluated	Non-threatened	163,325	49,075
Proceratophrys subguttata	Not Evaluated	Vulnerable	31,250	13,350
Pipidae				
Pipa carvalhoi	Not Evaluated	Non-threatened	231,175	184,175

Phyllomedusidae				
Hylomantis aspera	Not Evaluated	Vulnerable	17,400	5,200
Hylomantis granulosa	Vulnerable	Endangered	26,700	1,675
Phyllomedusa bahiana	Not Evaluated	Endangered	30,325	1,050
Phyllomedusa burmeisteri	Not Evaluated	Non-threatened	479,175	425,725
Phyllomedusa distincta	Not Evaluated	Non-threatened	148,775	62,550
Phyllomedusa iheringii	Not Evaluated	Extinct	5,650	0
Phyllomedusa nordestina	Not Evaluated	Non-threatened	188,975	218,000
Phyllomedusa rohdei	Not Evaluated	Non-threatened	217,475	91,650
Phyllomedusa tetraploidea	Not Evaluated	Non-threatened	314,425	206,850
Ranidae				
Lithobates catesbeianus	Not Evaluated	Non-threatened	131,525	103,250
Lithobates palmipes	Not Evaluated	Endangered	27,225	600

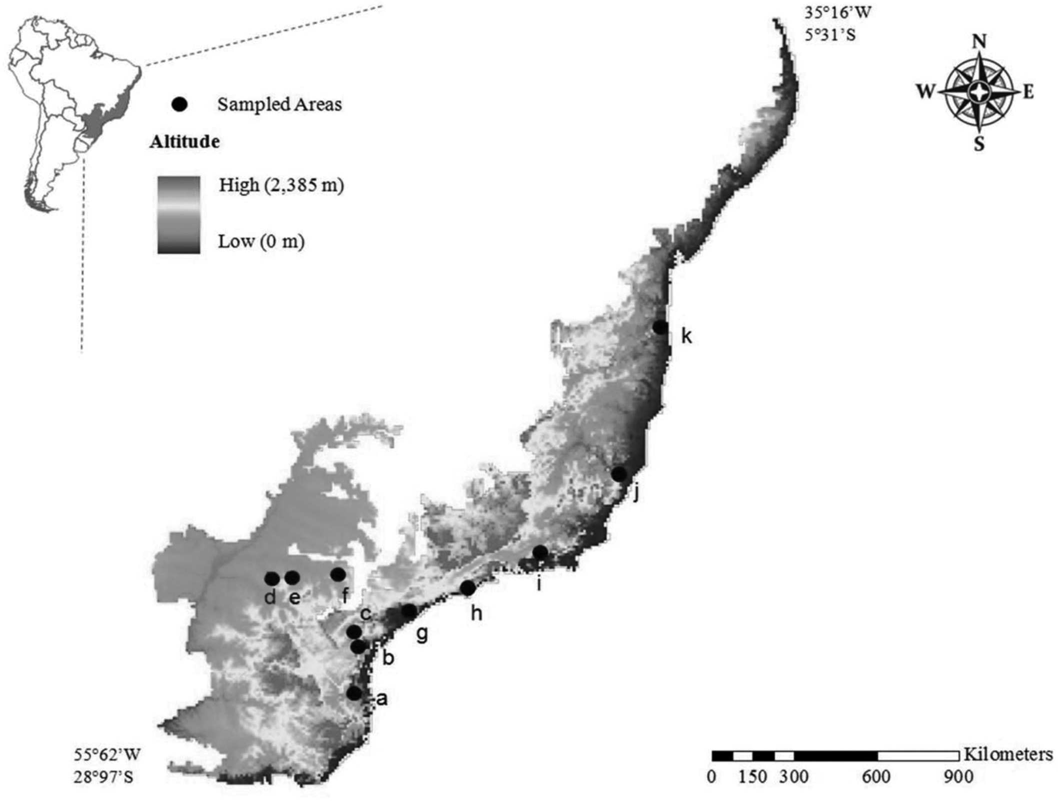

Figure S1. Map of the Brazilian Atlantic Forest hotspot (in gray) in South American territory and complementary fieldwork areas (black dots). (a) Parque Ecológico Spitzkopf, SC, (b) Parque Estadual Pico do Marumbi, PR, (c) Parque estadual de Campinhos, PR, (d) Parque municipal das Perobas, PR, (e) Parque Estadual Mata dos Godoy, PR, (f) Refúgio municipal da vida Silvestre, Horto Florestal de Jacarezinho, PR, (g) Estação Ecológica de Juréia-Itatins, SP, (h) Parque Estadual da Serra do Mar Núcleo Caraguatatuba, SP, (i) Parque Nacional da Serra dos Órgãos, RJ, (j) Reserva Biológica Augusto Ruschi, ES, (k) Reserva Biológica de Una, BA. We sampled amphibians using acoustic and visual nocturnal and diurnal surveys (Crump and Scott Jr., 1994; Zimmerman, 1994). We searched at the margins of water bodies, streams, and along 2,000 m forest transects in each sampled area.

Part IV

Evolutionary Ecology

Back Cover: *Rhinella henseli* (Lutz, 1934)
– Photo by Felipe S. Campos

Chapter 7

Functional trait evolution in amphibian phylogenetic relationships

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Functional trait evolution in amphibian phylogenetic relationships

Evolución de los rasgos funcionales en relaciones filogenéticas de anfibios. Los patrones actuales de biodiversidad de anfibios neotropicales son el resultado de sus relaciones funcionales y filogenéticas. Comprender las asociaciones entre similitud ecológica y evolutiva de las especies ayuda a formular una hipótesis sobre el impacto de los cambios evolutivos en la ecología funcional. En este estudio, evaluamos los estados de carácter ancestrales de los rasgos funcionales de anfibios y su historia evolutiva en el Bosque Atlántico brasileño. Utilizamos 12 genes (11.906 pb) para reconstruir una filogenia de 207 especies de anfibios y la relacionamos con ocho rasgos funcionales con respecto a su morfología, historia de vida y características de comportamiento. Revelamos evidencia de la relación entre la filogenia y los rasgos funcionales, lo que sugiere que estos rasgos están impulsados por la historia filogenética. A pesar de la alta tasa de endemismo de los anfibios del Bosque Atlántico, nuestros hallazgos dependen en gran medida de buenos estudios en linajes filogenéticos completos para superar las limitaciones biogeográficas potenciales. Sugerimos que las especies relacionadas filogenéticamente pueden tener diferentes rasgos funcionales y la fuerza de las señales filogenéticas cambia a través de los grupos taxonómicos. Este estudio destaca el uso de la señal filogenética en caracteres descriptivos y puede ayudar a avanzar en el conocimiento sobre la evolución adaptativa en diferentes linajes filogenéticos.

– Spanish Abstract (Resumen)

Functional trait evolution in amphibian phylogenetic relationships

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KEYWORDS

Anura
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Evolutionary change
Phylogenetic signal
Ecological traits

ABSTRACT

Current biodiversity patterns of Neotropical amphibians are the result of their functional and phylogenetic relationships. Understanding the associations between ecological similarity and phylogenetic relatedness among species helps in the formulation of a hypothesis about the impact of evolutionary changes on functional ecology. Here, we assess the ancestral character states of amphibian functional traits and their evolutionary history in the Atlantic Forest Hotspot. We use 12 genes (11,906 bp) to reconstruct a phylogeny for 207 amphibian species and relate it to eight functional traits regarding their morphology, life-history and behavioural features. We reveal evidence of a relationship between phylogeny and functional traits, suggesting that these traits are driven by phylogenetic history. Despite the high endemism rate of Atlantic Forest amphibians, our findings heavily rely on good studies on complete amphibian phylogenetic lineages to overcome potential biogeographical constraints. We suggest that phylogenetically related species may have different functional traits and the strength of the phylogenetic signals change across amphibian taxonomic groups. This study highlights the use of phylogenetic signal in descriptive characters and may help to move forward the knowledge on adaptive evolution at different phylogenetic lineages.

INTRODUCTION

Functional trait evolution is the evolutionary history of ecological interactions that addresses fundamental aspects on species' morphology, life-history and behaviour, according to their phylogenetic relationships (Wiens & Graham 2005; McGill et al., 2006; Kraft et a., 2007; Violle et al., 2007). Despite the assumption that closely related species can be ecologically similar (Losos, 2008), many functional traits are conserved enough to show strong phylogenetic signals (Freckleton et al., 2002; Webb et al., 2002; Moles et al., 2005; Donoghue, 2008). In this context, a central question is how similar do traits need to be to qualify as conserved (Pyron et al., 2015).

The use of phylogenetic signals can provide the degree to which closely related species tend to have similar traits (Blomberg et al., 2003). Empirical evidence shows that within a major clade, some lineages have strong phylogenetic signals in functional traits, whereas others are likely to show predominantly divergent traits (Diniz-Filho et al., 2010). A single ecological trait can show different values of phylogenetic signal in relation to which node is considered to evaluate it (Swenson & Enquist, 2009). Therefore, systematic measures that allow evaluating how closely related species tend to retain more similar traits than distantly related ones can respond to a set of descriptive variables, which may be useful to describe evolutionary processes behind ecological patterns (Duarte et al., 2012).

One of the main challenges in evolutionary biology is to explain the relation of the functional traits in the organisms, and how these traits can change multiple times (Gomez-Mestre et al., 2012). Another challenge which has yet to be addressed is to understand how the evolutionary traits are related with the long-term maintenance of ancestral characters and the multiple origins of common ancestral states (e.g., Hansen & Houle, 2004; Uyeda et al., 2011). The key strategy to address these challenges is assessing the relationships between functional and phylogenetic traits (Cadotte et al., 2008; Gravel et al., 2011). Understanding the associations between ecological similarity and phylogenetic relatedness is an essential step to reveal biodiversity assembly mechanisms and ecosystem functioning (Hof et al., 2010; Bello et al., 2017).

Current patterns of diversity and distribution of tropical amphibians is a consequence of their functional and phylogenetic traits (Pyron & Wiens, 2013). Evolutionary processes involving amphibians at a macroscale have been widely explored in previous research (e.g., Wiens, 2007; Hof et al., 2010; Ernst et al., 2012; Fritz & Rahbek, 2012; Duarte et al., 2014; Trakimas et al., 2016). Some studies also highlight a tendency of amphibians to evolve some degree of phylogenetic signal in their ecological traits (Wiens et al., 2006; Wollemberg et al., 2008; Moen et al., 2009). Inferring evolutionary processes in community ecology suggests that patterns of correlated trait evolution can reveal which traits are critical for environmental filtering (Cavender-Bares & Wilczek, 2003), as well as trait convergence across environmental gradients (Ernst et al., 2012). This means, the relationships between evolutionary history and ecological traits on the assembly rules of amphibians may not be as simple as it seems (Duarte et al., 2014).

How can evolutionary biologists determine what is the best method to test phylogenetic signal of functional traits? In an attempt to answer this question, some studies suggest that phylogenetic signal alone can provide enough evidence for it (Münkemüller et al., 2012), whereas others highlight that phylogenetic conservatism is only existing when phylogenetic signals are stronger than those predicted under Brownian evolution model (Losos, 2008; Wiens, 2008; Cooper et al., 2010; Wiens et al., 2010; Pyron et al., 2015). Here, we evaluated the tendency for amphibian species to resemble functional traits each other more than they resemble species drawn by chance in an amphibian phylogeny for the Atlantic Forest Hotspot. Under such a scenario, we assessed the ancestral character states of amphibian functional traits and their evolutionary histories, addressing the relationships among the diversity of ancestral states at different taxonomic levels. Given that species inherit their functional traits from their ancestors, interspecific changes have accumulated slowly over time under random walk or Brownian evolution model (Olalla-Tárraga et al., 2017). To address this question, we calculated phylogenetic signals of functional traits and showed evidence that these traits follow a Brownian evolution model. We determined whether amphibian functional traits can be potentially driven by phylogenetic relationships. Our findings revealed that phylogenetically related species may have different ecological functions and the strength of the phylogenetic signals can vary across orders, families and subfamilies.

MATERIALS AND METHODS

Study Area

The Atlantic Forest is one of the five most important biodiversity hotspots on Earth (Myers et al., 2000). Originally, it covered around 1 500,000 km^2 of which only about 12% (~ 195 km^2) remains in Brazil, Paraguay and Argentina (Ribeiro et al., 2009), corresponding to around 100,000 km^2 of Brazilian forest remnants (Tabarelli et al., 2005). These forest remnants face a high rate of habitat loss (Teixeira et al., 2009), which is one of the main factors driving amphibian populations to extinction (Stuart et al., 2004; Becker et al., 2007; Ferreira et al., 2016). Despite this, the Atlantic Forest is still considered the leader biome in amphibian diversity in Brazil (Haddad et al., 2013), accounting for more than 50% of all amphibian species listed for Brazil (Haddad et al., 2013). Their geographical characteristics with wide altitudinal range have favoured high species richness and levels of endemism, including more than 543 recognized amphibian species (Haddad et al., 2013). Here, we used the term Atlantic Forest according to the vegetation remnant map produced by the SOS Mata Atlântica/INPE (2015).

Data Acquisition

We obtained the spatial data on amphibian species from a joint research through three procedures types. First, we built a dataset with all the species distributed in the Atlantic Forest according to their functional traits, as proposed by Haddad et al. (2013); second, we conducted a complementary fieldwork in seven protected areas located in the major Atlantic Forest remnants of Brazil (Fig. S1), in order to supplement the available dataset with additional distribution and observed functional traits; and third, we obtained the molecular data through 207 species nucleotide sequences obtained from GenBank (Benson et al., 2013), provided by the National Center for Biotechnology Information (NCBI). We led the fieldwork in seven protected areas across the Serra do Mar Coastal Forests and the Central Corridor of the Atlantic Forest, stretching from the South to the Northeast of the country (see Fig. S1). In all localities, we conducted the survey using acoustic and visual nocturnal/diurnal assessments (Crump & Scott Jr., 1994; Zimmerman, 1994), through an active search around water bodies, streams and along 2,000 m forest transects for each protected area sampled. According to the American Society of Ichthyologist and Herpetologist (ASIH, 2004), we euthanized the collected species with hydrochloride benzocaine (≥ 250 mg/l), under the national biological sampling between 2015-2018 (ICMBio-SISBIO; license #30344/44755).

Functional Traits

We characterized 207 amphibian species according to eight functional traits that determine different dimensions of the amphibians' ecological niches in relation to their morphology, life-history and behaviour. We used the following traits according to Haddad et al. (2013), with some additional complements obtained in the fieldwork: 1. Activity (nocturnal; diurnal; nocturnal and diurnal); 2. Body size (small < 3cm; medium 3-10 cm; large > 10cm); 3. Calling site (without calling; bamboo groove; swamp and pond; bromeliad; forest floor; tree crown; cave and burrow; stream and rivulet; river; low vegetation; leaf titter; swamp, pond, stream and rivulet); 4. Toxicity (unknow; toxic; unpalatable; non-toxic); 5. Habit (arboreal; terrestrial; cryptic; fossorial; rheophilic; semi-aquatic; aquatic; arboreal and cryptic; arboreal and aquatic; fossorial and aquatic; arboreal and terrestrial); 6. Habitat (forest; open area; forest and open area); 7. Developmental mode (direct; indirect); 8. Members (apod; tetrapod). Such functional traits primarily contribute to ecosystem supporting services through direct and indirect changes on the ecosystem functions and processes

(Hocking & Babbitt, 2014). These functions can be structural (habitat and habit) and ecological (body size, members, activity, toxicity, calling site, and developmental mode). For further details, see the Supporting Information (Table S1), where we showed the specific ecosystem function of each amphibian functional traits assessed in the Brazilian Atlantic Forest (Duellman & Trueb, 1994; Wells, 2007; Toledo et al., 2007; Haddad et al., 2013; Hocking & Babbitt, 2014).

Phylogenetic Tree

According to the protocol proposed by Pyron & Wiens (2011) in an extant amphibian phylogeny, we used 12 genes to produce a novel phylogeny estimate for the Atlantic Forest amphibians (i.e., 11 906 bp for each species), through three mitochondrial (i.e., Cyt-b, 12s and 16s) and nine nuclear genes (i.e., CXCR4, H3A, NCX1, POMC, RAG1, ROHD, SIA, SLC8A3 and TYR). For the length-variable regions, we performed multiple pairwise comparisons by the online version of MAFFT v.6.8 and the G-INS-i algorithm (Katoh & Toh, 2008). After, we put together alignments of all genes in the same alignment using the software SequenceMatrix 1.7.7 (Vaidya et al., 2011) to concatenate the supermatrix previously produced.

We conducted the phylogenetic relationships with Bayesian analyses in software BEAST 1.7 (Drummond et al., 2012). We performed the phylogeny based on the combined data matrix through a HKY model of sequence evolution for one partition for all genes, using a Yule speciation process as the tree prior and an uncorrelated relaxed clock. We run the Yule process for 100 million generations, ensuring that the number of generations convergence were sufficient assessed with Tracer 1.6 (Rambaut et al., 2014), removing a conservative 10% burn-in fraction for the final tree. We combined these results with the use of LogCombiner 1.8 (Rambaut & Drummond, 2013a).

We conducted additional phylogenetic estimations based on 100 stochastic trees to account for the phylogenetic uncertainty of the single reconstructed phylogenetic tree for our 207 species assessed. Given these 100 random simulations, we built the maximum clade credibility tree (summary tree) with the use of TreeAnnotator 1.8 (Rambaut & Drummond, 2013b). To account the node uncertainty on the reconstructed trees, we used the average posterior probability distribution by the relative frequency of posterior nodes in accordance with the 100 stochastic trees assessed. We considered the nodes strongly supported if they received posterior probability ≥ 0.95. To edit the final phylogenetic tree, we used the package 'ape' (Paradis, 2012), in the R software (R Development Core Team, 2017).

Our reconstructed phylogenetic trees were based on taxonomic reviews that incorporated the newly obtained phylogenetic information by imposing the smallest possible change on the existing classification. We did not consider low node supports of the phylogenetic trees provided by the Bayesian analyses. We only used species from one geographic region, which in case of low node supports (not shown), could be a result of an incomplete lineage sorting and thus the lack of information in the sequence data. Finally, we revealed a wide-ranging phylogenetic relationship across two orders, 17 families and 15 subfamilies (Fig. 1).

Reconstruction of ancestral character states

We reconstructed the ancestral character states using maximum-likelihood estimations under stochastic character mapping analysis (SIMMAP; Bollback, 2006), by 1,000 simulations for discrete characters based on the functional-trait matrix (Table S3). We compared the likelihood estimations with a value of lambda = 1 for providing a standardized method to draw the reconstructed phylogenies onto the functional-space plot, accounting the phylogenetic uncertainty for the ancestral character states. We also used null simulations across the tips of the reconstructed trees indicating the expected variances on ancestral states among species under Brownian motion. We performed the stochastic character mapping analysis and the null simulations in the R software (R Development Core Team, 2017), using the “make.simmap” and “fastBM” functions of the package “phytools” (Revell, 2012).

Given that the ancestral characters may originate at the root of a phylogenetic tree or may converge to the tips of the tree (Pavoine et al., 2010), we assessed the relationships among the diversity of ancestral states at different taxonomic levels. To reduce the uncertainty behind the evolutionary origin of the functional traits, we used an additive partitioning of diversity based on the ancestral states observed and expected for the taxonomic levels “species”, “subfamilies”, “families”, and “orders”. For each taxonomic level, a value of alpha diversity was associated. Therefore, $\alpha1$ represented the alpha diversity in the lower taxonomic level (species), so that $\alpha2$, $\alpha3$ and $\alpha4$ corresponded to alpha diversity in the three subsequent levels (subfamilies, families and orders). According to the protocol proposed by Crist et al. (2003), we tested the statistical significance of each diversity component using a null model under a 95% confidence interval with 999 randomizations. We used expected diversity partitions through the null model implemented in the “r2dtable” function, which is based on the Patefield algorithm for generating random matrices (see Blüthgen et al., 2008). We performed all analyses for the additive partitioning of diversity in the R software (R Development Core Team, 2017), using the algorithms "boot" and "mass" through the “adipart” function of the package “vegan” (Oksanen et al., 2013).

We evaluated the ancestral traits for the following "nodes" from the original tree: Orders – Gymnophiona and Anura; Families – Typhlonectidae, Siphonopidae, Microhylidae, Leptodactylidae, Pipidae, Ranidae, Aromobatidae, Hylodidae, Cycloramphidae, Bufonidae, Craugastoridae, Brachycephalidae, Eleutherodactylidae, Odontophrynidae, Hemiphractidae, Phyllomedusidae and Hylidae; and Subfamilies – Gastrophryninae, Paratelmatobiinae, Leiuperinae, Leptodactylinae, Allobatinae, Craugastorinae, Holoadeninae, Ceuthomantinae, Phyzelaphryninae, Hemiphractinae, Scinaxinae, Pseudinae, Lophyohylinae, Dendropsophinae and Cophomantinae. We followed Frost (2016) for the taxonomic nomenclature of families, subfamilies and species (Fig. 1).

Phylogenetic signal

We assessed the phylogenetic signal of each functional trait using a robust test proposed by Abouheif (1999). The Abouheif's Cmean test uses the Geary's C and Moran's I indices, providing a phylogenetic proximity matrix that does not relate to branch length but focuses on topology of the tree and has a non-zero diagonal values (see Pavoine et al., 2008). We estimated Abouheif's Cmean with 999 randomizations using the package "adephylo" (Jombart et al., 2010), in the R software (R Development Core Team, 2017).

In order to test what functional traits follow a stochastic Brownian evolution model, we used a measure based on the maximum likelihood of phylogenetic signals, called lambda (λ), developed by Pagel (1999). This metric refers to a tree transformation parameter that gradually eliminates the phylogenetic structure ranging from 1 to 0, where λ equal to 1 correspond to the Brownian evolution model, whereas λ equal to 0 correspond to the complete absence of phylogenetic signal (Münkemüller et al., 2012). The strongest argument for using Pagel's λ is that it provides a reliable effect size measure besides testing for phylogenetic signal for both continuous and discrete traits (e.g., Gumm & Mendelson, 2011; Münkemüller et al., 2012; Best & Stachowicz, 2013). For this analysis, we used the "phylosig" function of the package "phytools" (Revell, 2012), in the R software (R Development Core Team, 2017).

The main reason behind our choice by the Abouheif's Cmean and the Pagel's λ tests is their high annalistic power to provide a reliable effect size measure for discriminating between more complex models of trait evolution performed well and substantially better than Fritz and Purvis' D, and Blomberg's K (Münkemüller et al., 2012). Fritz and Purvis' D test is a statistic approach to measure phylogenetic signal strength only in binary traits, which are not the encountered in our case study. Given that our categorical dataset is based on multiple and discrete traits, we had to opt for a robust index that could be able to response our functional questions. In this context, we followed the guidelines proposed by Münkemüller et al. (2012) to better assess phylogenetic signal and distinguish it from random trait distributions.

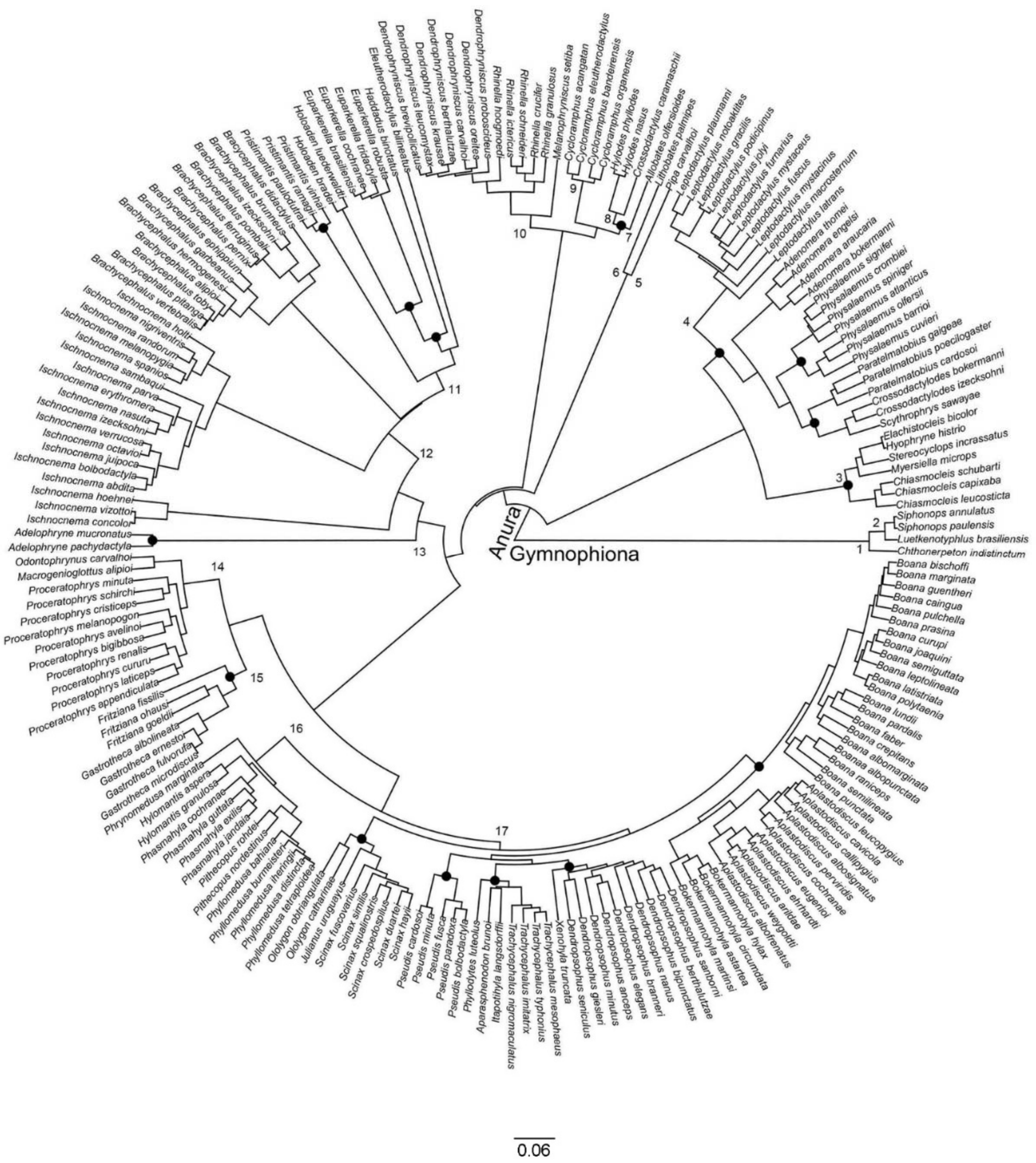

Fig. 1. Reconstructed phylogenetic tree for 207 amphibian species of the Atlantic Forest based on Pyron & Wiens (2011) and Duellman et al. (2016). Numbers indicate nodes of Families, and circles indicate nodes of Subfamilies. Average posterior probability is strongly supported by random samplings (i.e., > 0.95; Fig. S2). 1. Typhlonectidae; 2. Siphonopidae; 3. Microhylidae (Gastrophryninae); 4. Leptodactylidae (Paratelmatobiinae, Leiuperinae, Leptodactylinae); 5. Pipidae; 6. Ranidae; 7. Aromobatidae (Allobatinae); 8. Hylodidae; 9. Cycloramphidae; 10. Bufonidae; 11. Craugastoridae (Craugastorinae, Holoadeninae, Ceuthomantinae); 12. Brachycephalidae; 13. Eleutherodactylidae (Phyzelaphryninae); 14. Odontophrynidae; 15. Hemiphractidae (Hemiphractinae); 16. Phyllomedusidae; 17. Hylidae (Scinaxinae, Pseudinae, Lophyohylinae, Dendropsophinae, Cophomantinae).

Given that Pagel's λ is most valuable for discrete traits that follow Brownian motion (Best & Stachowicz, 2013), we fitted the reconstructed phylogenetic trees to a model selection approach based on the corrected Akaike criterion (AICc) for three evolutionary models (i.e., BM = Brownian-motion model; EB = Early-burst model; White = White-noise model). We performed these models of character trait correlated evolution using the "fitDiscrete" function of the "geiger" package (Harmon et al., 2008), in the R software (R Development Core Team 2017).

In addition to the measures described above, we created a traitgram to visualize the phylogenetic signal and rate change for the functional traits across the nodes of the reconstructed phylogeny, using the "phenogram" function of the package "phytools" (Revell, 2012), in the R software (R Development Core Team, 2017). Time scales analysis of the multigene dataset are congruent with previous studies (San Mauro et al., 2005; Roelants et al., 2007; Wiens, 2007; Blackburn et al., 2010; Roelants et al., 2011) and support anuran radiation episodes in the Triassic/Early Jurassic (basal anuran radiation).

RESULTS

Maximum-likelihood ancestral state reconstructions showed different evolutionary patterns onto functional-space plots, fitting the Brownian-motion evolution model (Fig. 2). Activity trait indicated the "nocturnal" ancestral state as a symplesiomorphic character shared by orders Anura and Gymnophiona, and the "diurnal" ancestral state as a homoplastic character shared by the families Aromobatidae, Hylodidae and Brachycephalidae (Fig. 2a). Body size indicated the "large (> 10cm)" ancestral state as a symplesiomorphic character shared by orders Anura and Gymnophiona, and the "medium (3-10 cm)" and "small (< 3cm)" ancestral states as homoplastic characters for the order Anura (Fig. 2b). Calling site and Toxicity were considered as autapomorphic traits for order Anura due to emerged independently through different ancestors (Figs. 2c-d). Habit trait indicated the "aquatic" state as a synapomorphic character (subfamily Pseudinae) and the "arboreal" state as homoplastic characters (families Hylidae, Hemiphractidae and Phyllomedusidae), whereas Habitat trait indicated all ancestral states as symplesiomorphic characters (Figs. 2e-f). Developmental mode indicated the "direct" and "indirect" states as symplesiomorphic characters (Fig. 2g). Members indicated the "apodal" state as an apomorphic character for order Gymnophiona, and the "tetrapod" state as a synapomorphic character for order Anura (Fig. 2h).

Additive partitioning of diversity showed the greatest number of ancestral states in the lower taxonomic level (i.e., species), indicating that 97% of total observed ancestral states was converged to the tips of the tree (Fig. 3). Comparing

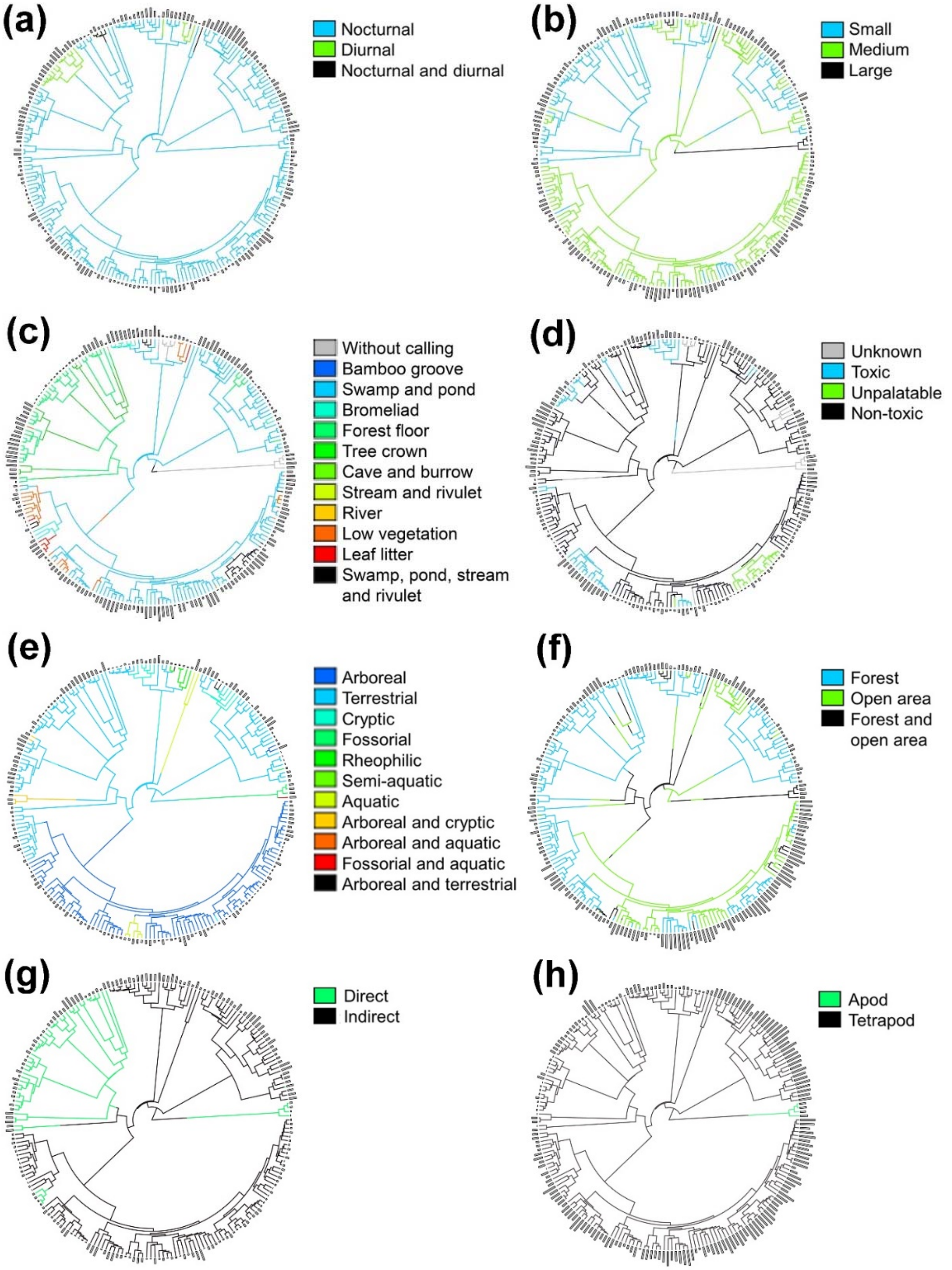

Fig. 2. Maximum-likelihood ancestral state reconstruction for the amphibian functional traits of the Atlantic Forest (N = 207 species). Reconstructed phylogenetic trees show discrete traits through stochastic character mapping (SIMMAP), based on 1,000 simulations. Vertical bars across the tips of the trees indicate the expected variances on ancestral states among species under the Brownian-motion evolution model.

with the expected diversity provided by the null model, only the levels "species" and "families" showed significant values ($P < 0.05$). However, the levels "subfamilies", "families" and "orders" did not show relevant diversity values, together accounting for less than 3% of the total diversity of ancestral states evaluated.

Overall, Abouheif's Cmean and Pagel's λ tests indicated that all functional traits showed significant phylogenetic signals against random expectations. Results of the model selection approach based on the corrected Akaike criterion (AICc) support the Brownian-motion as the best fitted model for our trait evolution approach (Table 1).

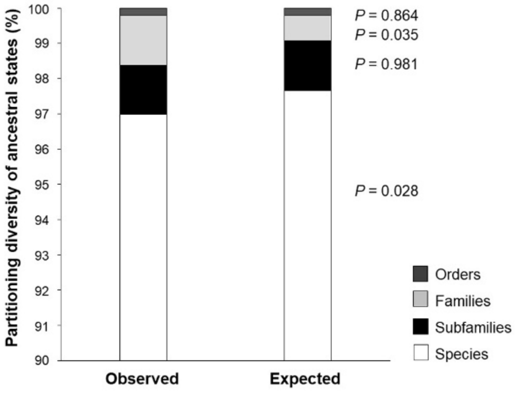

Fig. 3. Additive partitioning diversity of ancestral states observed and expected at different taxonomic levels (species, subfamilies, families, and orders), according to the reconstructed phylogenetic tree based on 207 amphibian species of the Atlantic Forest. Random expectations are based on a null model under a 95% confidence interval with 999 randomizations. Bars are organized from lower (species) to higher (orders) taxonomic levels.

According to Abouheif's Cmean, the traits that had the highest values were developmental mode (Cmean = 0.891, $P < 0.001$), members (Cmean = 0.753, $P < 0.001$) and habit (Cmean = 0.704, $P < 0.001$). Abouheif's simulations represented the distribution of the statistical Cmean calculated from each functional trait along the phylogeny evaluated (Fig. 4).

Results of Pagel's λ also indicated the highest values of the maximum likelihood for the traits developmental mode and members ($\lambda > 1.00$, $P < 0.001$), totally supporting a Brownian evolution model. The traits body size, toxicity, activity and calling site also had high λ values ($\lambda > 0.900$, $P < 0.001$), showing close relations to the Brownian evolution model. However, the traits habit and habitat showed moderate phylogenetic signals under this same model ($\lambda > 0.600$, $P < 0.001$).

Table 1. Phylogenetic signal of functional traits according to the Abouheif's Cmean and the Pagel's λ tests for the Atlantic Forest amphibians. Results of fitting the corrected Akaike criterion (AICc) are calculated under three evolutionary models by using λ = 1: BM = Brownian-motion model; EB = Early-burst model; White = White-noise model (i.e., no phylogenetic signal).

Functional traits	Abouheif's C_{mean}^{*}	Pagel's λ^{*}	BM (AICc)	EB (AICc)	White (AICc)
Activity	0.546	0.928	92.286	94.147	194.069
Body size	0.600	0.956	232.844	233.050	339.822
Calling site	0.345	0.915	532.064	533.668	767.113
Toxicity	0.627	0.939	187.080	188.051	405.864
Habit	0.704	0.688	399.962	401.506	627.706
Habitat	0.296	0.620	327.294	329.802	363.913
Developmental mode	0.891	1.006	45.951	51.318	237.532
Members	0.753	1.006	13.282	13.719	41.513

* All p-values < 0.001

The traitgram illustrated an evidence for phylogenetic signal and rate change in the functional traits across the nodes of the reconstructed phylogeny (Fig. 5), spreading through the functional trait space estimated from the basal anuran radiation in the Triassic and Early Jurassic periods (i.e., about 200 million years ago). Through this traitgram, we showed a horizontal dimension of evolutionary divergence time visualizing a quantitative trait evolution for multiple ancestral characters.

DISCUSSION

Our results showed a strong tendency to retain ancestral functional traits in Atlantic Forest amphibians, which might in turn imply a lower functional adaptability of species to current and future climate change, corroborating with the findings of Urban et al. (2014). Given the partitioning diversity of reconstructed ancestral states at taxonomic levels, we found a high diversity at the species level. We suggest the additive partitioning of ancestral states as a complementary approach for the stochastic character mapping, in an attempt to reduce the uncertainty behind the evolutionary origin of the functional traits among taxonomic groups. Despite this, phylogenetic characteristics of some species can be influenced or directly affected by other not phylogenetically related species. Under similar ecological pressures, some species are reinforced to exhibit the same functional traits, due to the high phenotypic plasticity of amphibians (Lawler, 1989; Horat & Semlitsch, 1994; Relyea, 2001; Urban et al., 2014).

We highlighted Developmental mode and Members as the most ancestral traits across the long sequence of changes in the basal amphibian radiation at the Atlantic Forest. Indirect development characters seem to represent terminal stages that are retained for tens of millions of years without proceeding to direct development (e.g., Phyllomedusidae and Hylidae families). Although we have shown high levels of homoplasy, some lineages do not seem to have been hampered in their diversification. Many specialization modes can be evolving with variations in different functional traits related to behaviour, habitat and developmental modes (Roelants et al., 2011).

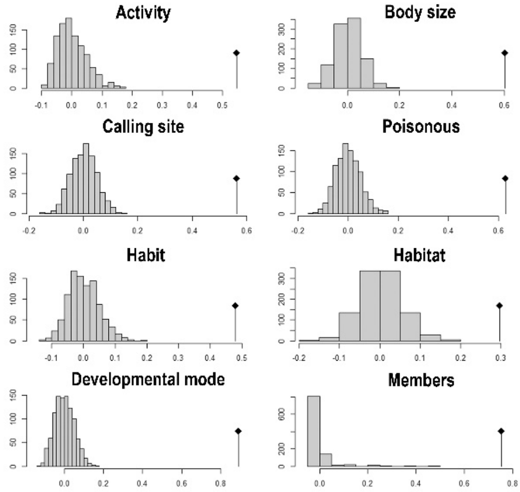

Fig. 4. Phylogenetic signal simulations according to the Abouheif's test calculated for each functional trait across the reconstructed phylogeny of amphibians of the Atlantic Forest (N = 207 species). Black diamonds indicate the position of the observed mean distributions in relation to the Cmean randomizations. All p-values < 0.001.

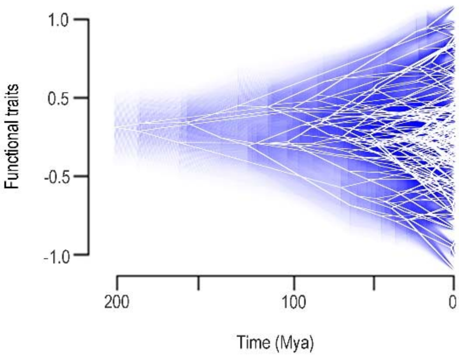

Fig. 5. Traitgram showing the phylogenetic signal and rate change for the functional traits across the nodes of the reconstructed phylogeny of amphibians of the Atlantic Forest (N = 207 species). Y-axis represents the phylogenetic signal for the functional trait values (log10-transformed). X-axis represents the relative time (millions of years) and the length of the branches represents a surrogate of time. Transparent blue stain represents 95% of confidence interval. All p-values < 0.001.

The development of the same functional traits using different evolutionary mechanisms cannot be distinguished by our results. However, most of specialization modes behind the functional traits assessed can have been widespread with homoplasy across parallel evolutions (see Bossuyt & Milinkovitch, 2000).

Despite an overall and robust observed trend of detection of phylogenetic signals in functional traits, we found large variation in ancestral character histories among taxonomic groups. Both measures used to determine the strength of the phylogenetic signals were highly significant, suggesting that they are following a Brownian evolution model. This was supported by the length of the branches (a surrogate of time), as expected of characters evolving under a random walk model (Gingerich, 2009; Hunt, 2012; Hunt & Rabosky, 2014). However, low phylogenetic signals in functional traits (i.e., Cmean < 0.6) also showed exceptions from the random walk model, especially in the terminal branches. These exceptions may indicate that ecological condition changes could be fast in these taxonomic bifurcation points and not in the overall reconstructed tree. On one hand, mapping trait evolution on reconstructed phylogenies allows estimating where the phylogenetic nodes connect the species trait values to the trait values of their potential ancestors (Ackerly, 2009; Kembel et al., 2010; Revell, 2012). On the other hand, the phylogenetic relationships of species showed by the traitgram can be difficult to understand, mainly when species in different parts of the phylogeny have similar functional traits (Revell, 2013). In this context, Campos et al. (2017) revealed a high congruence of functional and phylogenetic patterns of amphibian biodiversity, providing potential trade-offs for ecological and evolutionary processes in the Brazilian Atlantic Forest.

Some other studies stated a doubt if the establishing of the existence of a phylogenetic signal is a useful approach for ecology and evolution (Wiens & Graham, 2005; Wiens, 2008). However, there is an ongoing demand for further evidence to identify phylogenetic signals in different communities (Losos, 2008). The attempts to assess the existence of a phylogenetic signal are very relevant to researches of biodiversity gradients and species distribution models for climate change predictions (Hof et al., 2010), while the fact of its generality is still under discussion.

We observed that many functional traits are conserved enough to show strong phylogenetic signals when closely related species have similar traits, whereas convergence has occurred when species from different lineages have similar ecological characters. Conserved traits have been observed in different amphibian lineages, at least within lower clades such as families or genera (Wiens et al., 2006; Wollemberg et al., 2008; Algar et al., 2009; Moen et al., 2009). Among these clades, the Hylidae family showed to be generally conserved across the evolutionary history of the group in relation to climatic factors (Wiens et al., 2006). This association with speciation rates can be explained by latitudinal diversity gradient (Wiens et al., 2011). Some salamanders of the genera *Plethodon* and *Desmognathus* also showed relationships between speciation and endemism rates with conserved traits across the phylogeny (Kozak & Wiens, 2006).

Widespread conservatism hypothesis is supported by phylogenetic clusters based on ecological niche constraints (Pianka et al., 2017) and their geographic location (Wiens et al., 2006). However, we need to take into account that most associations between phylogenetic and functional traits are scarcely based on an entire phylogenetic tree (Diniz-Filho et al., 2010). Therefore, some phylogenetically conserved traits apparently attributed to regional amphibian clades can be underestimated due to history-related biogeographical constraints on different phylogenetic lineages (Hof et al., 2010; Ernst et al., 2012).

We showed a promising approach in how amphibian functional traits can recover significant phylogenetic signals in the Atlantic Forest. However, our findings heavily rest on good studies on complete amphibian phylogenetic lineages to overcome potential biogeographical constraints. Our study includes basically all Atlantic Forest amphibian species with available data on both phylogenetic and functional features, highlighting how badly more basic research is needed to provide empirical data for testing evolutionary and ecological questions. We provide evidence in support of the idea that phylogenetically related species may have different functional traits, even though the strength of the phylogenetic signal varied considerably across amphibian orders, families and subfamilies. In summary, this is the first study investigating reconstructed ancestral states under maximum likelihood and phylogenetic signals across an entire class of organisms in the Atlantic Forest, nevertheless accounting variation at different taxonomic levels. Despite the potential biogeographical constraints of our assumptions, our results address how the functional trait evolution of amphibians can be informative to describe regional phylogenetic patterns based on multiple and discrete characters. A starting point to address questions related to conservatism hypothesis and biogeographical constraints of different phylogenetic lineages may help to describe the evolutionary patterns that may be important for environmental filtering. This work has sought to move forward the use phylogenetic signals as a proxy for ecological similarities, supporting conservation studies that explore functional drivers of phylogenetic loss in biodiversity hotspots.

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APPENDIX. Supporting Information

Supplementary files:

Table S1. Ecosystem functions and references for the amphibian functional traits assessed in the Brazilian Atlantic Forest.

Fig. S1. Atlantic Forest remnants (grey spots) and complementary fieldwork areas (black dots) sampled in the Brazilian coastal region. 1. Parque Ecológico Spitzkopf, SC; 2. Parque Estadual Pico do Marumbi, PR; 3. Estação Ecológica de Juréia-Itatins, SP; 4. Parque Estadual da Serra do Mar Núcleo Caraguatatuba, SP; 5. Parque Nacional da Serra dos Órgãos, RJ; 6. Reserva Biológica Augusto Ruschi, ES; 7. Reserva Biológica de Una, BA.

Fig. S2. Average posterior probability and relative frequency of posterior nodes in accordance with 100 nodes stochastic trees for 207 amphibian species of the Atlantic Forest.

Table S1. Ecosystem functions and references for the amphibian functional traits assessed in the Brazilian Atlantic Forest.

Functional traits	Ecosystem functions	References
Activity	Dispersal ability, predator-prey relationships, sexual selection	Duellman and Trueb 1994, Wells 2007, Haddad et al. 2013, Hocking and Babbitt 2014
Body size	Hunting tolerance, dispersal ability, predator-prey relationships, sexual selection	Duellman and Trueb 1994, Wells 2007, Toledo et al. 2007, Haddad et al. 2013, Hocking and Babbitt 2014
Calling site	Dispersal ability, predator-prey relationships, sexual selection	Duellman and Trueb 1994, Wells 2007, Haddad et al. 2013, Hocking and Babbitt 2014
Toxicity	Hunting tolerance, predator-prey relationships	Duellman and Trueb 1994, Wells 2007, Haddad et al. 2013, Hocking and Babbitt 2014
Habit	Dispersal ability, predator-prey relationships	Duellman and Trueb 1994, Wells 2007, Haddad et al. 2013, Hocking and Babbitt 2014
Habitat	Dispersal ability, predator-prey relationships	Duellman and Trueb 1994, Wells 2007, Haddad et al. 2013, Hocking and Babbitt 2014
Developmental mode	Dispersal ability, predator-prey relationships, sexual selection	Duellman and Trueb 1994, Haddad and Prado 2005, Wells 2007, Haddad et al. 2013, Hocking and Babbitt 2014
Members	Dispersal ability, predator-prey relationships	Duellman and Trueb 1994, Wells 2007, Haddad et al. 2013, Hocking and Babbitt 2014

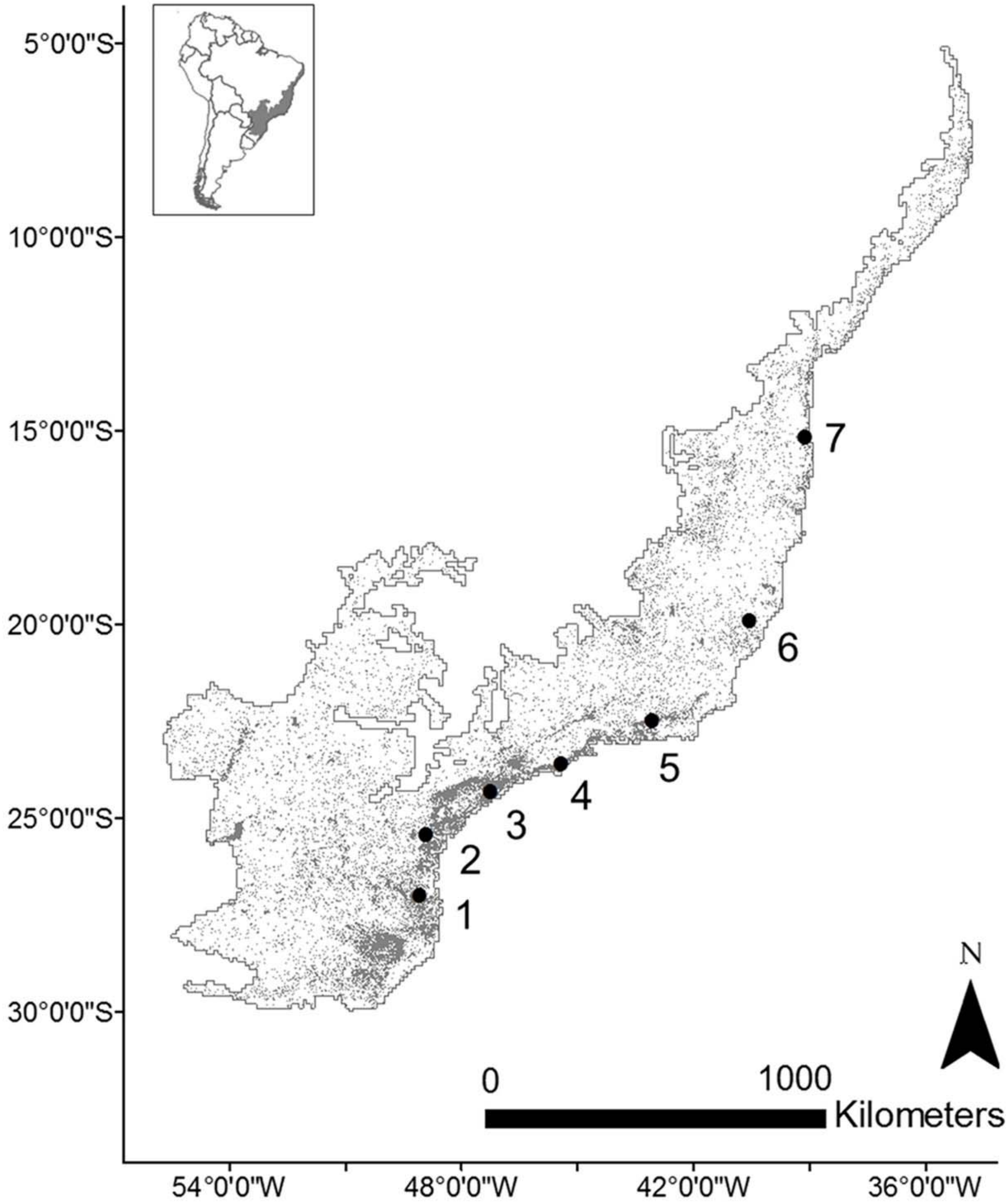

Fig. S1. Atlantic Forest remnants (grey spots) and complementary fieldwork areas (black dots) sampled in the Brazilian coastal region. 1. Parque Ecológico Spitzkopf, SC; 2. Parque Estadual Pico do Marumbi, PR; 3. Estação Ecológica de Juréia-Itatins, SP; 4. Parque Estadual da Serra do Mar Núcleo Caraguatatuba, SP; 5. Parque Nacional da Serra dos Órgãos, RJ; 6. Reserva Biológica Augusto Ruschi, ES; 7. Reserva Biológica de Una, BA.

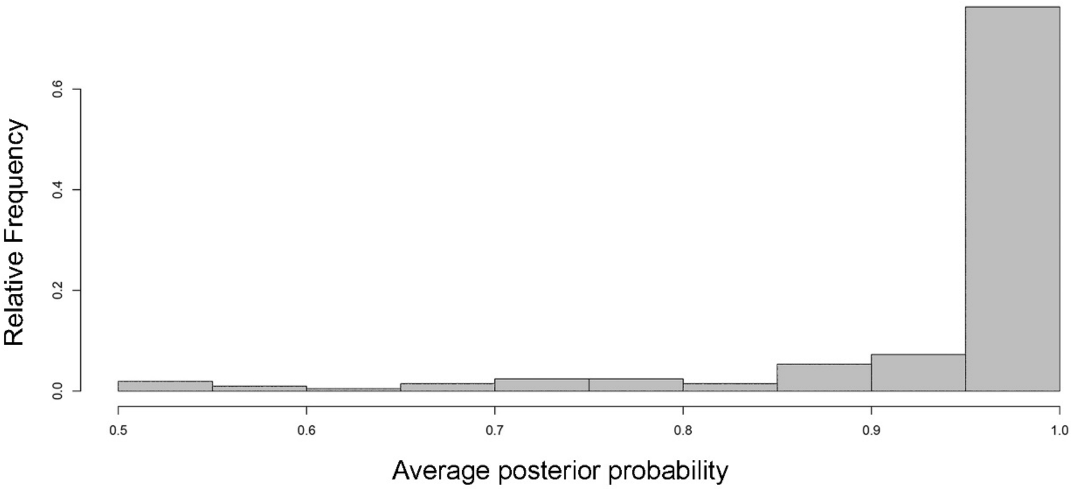

Fig. S2. Average posterior probability and relative frequency of posterior nodes in accordance with 100 nodes stochastic trees for 207 amphibian species of the Atlantic Forest. The node distribution mean is strongly supported by random samplings (i.e., > 0.95), accounting for the phylogenetic uncertainty and the maximum clade.

Chapter 8

Evolutionary history of amphibian antipredator mechanisms

Article Submitted to Animal Behaviour
Status: Under Review

Evolutionary history of antipredator mechanisms of amphibians

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Historia evolutiva de los mecanismos anti-depredadores de anfibios. Comprender las estrategias defensivas de las especies es crucial en cualquier estudio etológico con el objetivo de distinguir y clasificar comportamientos observados en diferentes categorías. Los mecanismos anti-depredadores pueden originarse en adaptaciones evolutivas, presiones ecológicas, o por la unión de ambos procesos. Los anfibios tienen alta plasticidad adaptativa y sufren fuerte presión ambiental, principalmente en relación a sus diversos depredadores. En este estudio, se investigó el origen de los mecanismos anti-depredadores de 115 especies de anfibios en el Bosque Atlántico brasileño. Los orígenes evolutivos fueron analizados con base a características genéticas, diversidad de comportamientos defensivos y características ecológicas funcionales (rasgos de historia de vida). Los resultados mostraron que muchos mecanismos provienen de forma independiente en diferentes familias y subfamilias. El mecanismo de producción de secreciones, por ejemplo, ha demostrado un origen puramente filogenético y puede estar asociado al desarrollo de otras estrategias defensivas. Las características funcionales que exponen los anfibios a la depredación actúan como una fuerte presión evolutiva en los procesos adaptativos de las especies. Las especies que tienden a tener una mayor diversidad de mecanismos anti-depredadores también tienden a aumentar su rango de distribución geográfica. Los resultados observados presentan nuevas perspectivas sobre mecanismos anti-depredadores de anfibios y establecen un enfoque innovador para describir sus relaciones evolutivas en el Bosque Atlántico brasileño.

– Spanish Abstract (Resumen)

Evolutionary history of antipredator mechanisms of amphibians

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Anura
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Defensive behaviour
Phylogenetic signal

ABSTRACT

Understanding the antipredator mechanisms is one of the main tasks to describe the diversity and dispersal of species. The origin of antipredator mechanisms can be through of random evolution, ecological pressures (biotic and abiotic) or by the union of both. Amphibians have strong phenotypic plasticity and are often affected by environmental pressure mainly due to predation processes. In this paper, we investigate the origin of antipredator mechanisms of 115 amphibian species of the Atlantic forest. We analyse the evolutionary origins of species based on genetic characteristics and their relationships among the diversity of antipredator mechanisms and functional traits. Our results show that many mechanisms have origin independently in different families and subfamilies. Antipredator mechanism of production secretions is a purely phylogenetic mechanism and follow an evolution model Brownian that can direct adjustment or development of new mechanisms. Functional traits that exposes amphibians susceptible to predation act as strong evolutionary pressure in adaptive processes. Species with a greater diversity of antipredator mechanisms tend to increase their geographical ranges. Our findings present new perspectives on the antipredator mechanisms of amphibians and set an innovative approach to describe their evolutionary relationships in the Brazilian Atlantic Forest.

Submitted to Animal Behaviour - Under Review

INTRODUCTION

One of the main drivers of evolution is the predator-prey race. This evolutionary process is generally associated with adaptive selection to stabilize specific phenotypes through natural selection (Darwin, 1859). Predators affect prey directly by consumption, and indirectly by the induction of energetically costly antipredator responses (Alcock, 2011). These responses can include changes in prey behavioural, morphological or developmental traits (Petranka et al., 1987; Smith & Van Bus-kirk, 1995; Lima, 1998; Podjasek et al., 2005; Preisser et al., 2005; Verheggen et al., 2009). Antipredator mechanisms are essential for survival of prey (Ruxton et al., 2004). However, both sides (predator and prey) do not have control of these adaptations (Alcock, 2011), and sometimes the predator comes out ahead of this evolutionary run (Brodie, 1999). Therefore, the evolution and adjustment of behaviour in response to predation can be faster in some generations (Juliano & Gravel, 2002).

The success of an antipredator mechanism will allow further evolution (Vermeij, 1982). Correlations between antipredator mechanisms are particularly important for understanding natural selection on mechanism (Brodie, 1992). Preys with weak behavioural responses to predators could avoid predation processes through effective morphological or chemical defences (Dewit et al., 1999). Evolutionary origin of behaviour is directly related to the adaptive success of the species and may reflect new defensive strategies or simply the adjustment of an existing mechanism (Dewit et al., 1999; Juliano & Gravel, 2002).

Behaviour and morphology can be mechanically independent and often used to produce antipredator responses (Dewit et al., 1999). Phylogenetically related species share similar behavioural characteristics due to common ancestry (Harvey & Pagel, 1991), leading them to explore and settle in similar environments. This phenotypic similarity between related species is known as phylogenetic signal and describes the tendency of a particular characteristic to be conserved (Harvey & Pagel, 1991; Blomberg & Garland, 2002). However, the diversity of phenotypic characteristics can have different directions, and will depend on their evolutionary history. Phenotypic traits may depend upon for root of a phylogenetic tree, or may converge to their tips (Pavoine et al., 2010). Moreover, the evolution of these characteristics can be explained by Brownian motion, a process of random genetic drift at a constant rate of evolution and non-directional selection (Felsenstein, 1985; Lynch, 1990; Martins, 1994; Pagel, 1997; Diniz-Filho & Vieira, 1998).

Functional traits can strongly influence the capacity of distribution of many species (Brown & Maurer, 1989; Gaston, 1990; Lawton, 1993). These features can driver the prey species, which should adjust their antipredator strategy depending on the current threat imposed by potential predators (Sih, 1986; Harvell, 1990; Bronmark & Miner, 1992; Smith & Van Bus-kirk, 1995; Relyea 2001; Ferrari et al., 2010; Higginson et al., 2012; Brown et al., 2013). In consequence, evasive and defensive behaviours are expected to exhibit phenotypic flexibility in response to the level of predation risk (Kats & Dill, 1998; Lass & Spaak, 2003; Ferrari et al., 2010; Higginson et al., 2012; Brown et al., 2013).

Diversity of antipredator adaptations in amphibians is probably more complex than that of any other terrestrial vertebrate group (Lourenço-de-Moraes et al., 2016). This may be the case because amphibians are prey for numerous arthropods, including insects, spiders, and centipedes, and nearly all vertebrate groups, from fish to mammals (Toledo, 2005; Zug et al., 2001). Thus, selective pressure driving the evolution of antipredator mechanisms in amphibians is likely strong. Defensive behaviours reduce the chance of a species being consumed by a predator, either by reducing the likelihood of being detected or by reducing the chances of being consumed, once an encounter takes place (Wells, 2007).

The high predation pressure on amphibian species is a natural phenomenon of great ecological and evolutionary significance (Toledo, 2005; Wells, 2007). Considering the several antipredator mechanisms developed by amphibians, Toledo et al. (2011) listed more than 30 different behavioural defensive strategies. Many amphibian species exhibit these behaviours synergistically (Lourenço-de-Moraes et al. 2014a; Figueiredo et al., 2017), or in an escalated sequence (Lourenço-de-Moraes et al., 2014b; 2016). However, the phylogenetic origin of most antipredator mechanisms of amphibians remains unknown. Understanding the evolution of correlated traits can answer key questions about the advantages and disadvantages of a particular trait in relation to its potential distribution (Lande & Arnold, 1983; Price & Langen, 1992). Therefore, the study of antipredator mechanism can provide some of the most fascinating answers to ecological and evolutionary questions regarding species struggle for existence (Zug et al., 2001). Using Atlantic Forest amphibians as our object of study, we hypothesize the following: (1) ancestral antipredator mechanisms are explained by phylogenetic relationships; (2) ecological specialization influences the diversity of antipredator mechanisms; (3) species with a greater diversity of antipredator mechanism have higher geographical ranges. Through these considerations, we used reconstructed phylogenetic trees for understanding the evolutionary history of antipredator mechanisms and their ecological relationships.

MATERIALS AND METHODS

Study Area

Our analyses focused on species from the Atlantic Forest biodiversity hotspot (Myers et al., 2000), which originally covered around 150 million ha with heterogeneous environmental conditions provided by a wide range of climatic belts and vegetation formations (Tabarelli et al., 2005; Ribeiro et al., 2009) (Fig. 1).

Data Collection

We led the survey in eleven Protected Areas (PAs), stretching from the South to the Northeast of the Brazilian Atlantic Forest (Fig. 1). We sampled each area for 10 days between January 2015 and March 2016. We sampled the species using acoustic and visual surveys (Heyer et al., 1994), searching around ponds, streams, burrows, bromeliads, and leaf litters along 2,000 m forest transects in each PA.

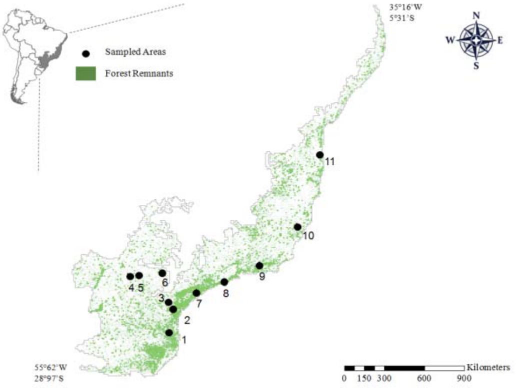

Fig. 1. Map showing the sampled areas and the forest remnants in the Atlantic Forest. 1. Parque Ecológico Spitzkopf, SC; 2. Parque Estadual Pico do Marumbi, PR; 3. Parque estadual de Campinhos, PR; 4. Parque municipal das Perobas, PR; 5. Parque Estadual Mata dos Godoy, PR; 6. Refúgio municipal da vida Silvestre, Horto Florestal de Jacarezinho, PR; 7. Estação Ecológica de Juréia-Itatins, SP; 8. Parque Estadual da Serra do Mar Núcleo Caraguatatuba, SP; 9. Parque Nacional da Serra dos Órgãos, RJ; 10. Reserva Biológica Augusto Ruschi, ES; 11. Reserva Biológica de Una, BA.

Beyond the field data, we determinate the geographical ranges for each species according to the IUCN Red List of Threatened Species database (IUCN, 2017). We used ArcGIS 10 software (ESRI, 2011) to build presence/absence matrices from the species distribution data by superimposing a grid system of cells of 0.1 latitude/longitude degrees, creating a network of 10,359 grid cells. The geographical ranges covered by our grid system was measured for each species.

Antipredator Mechanisms

We assessed 115 amphibian species across the forest remnants surveyed in the Brazilian Atlantic Forest. We simulated the predator attack according to the method “Finger only-stimuli”, proposed by Lourenço-de-Moraes et al. (2016). In this method, the researcher’s fingers are used to stimulate the frogs to display defensive behaviours, considering humans as possible predators. We defined 13 mechanisms based on the two extant literature reviews on amphibian antipredator mechanisms (see Dodd, 1976; Toledo et al. 2011). According to these classification systems and our field observations, we used the following mechanisms: (1) production of secretions; (2) camouflage; (3) immobility; (4) contracting; (5) body inflation; (6) body elevation; (7) stretched legs; (8) escape; (9) aposematism; (10) cloacal discharge; (11) gaped mouth; (12) defensive vocalizations; and (13) fighting back (Table 1).

Table 1. Antipredator mechanisms of amphibians and their respective variations in the Atlantic Forest.

Antipredator Mechanisms	Variations of the mechanisms
Production of secretions	0= Absence; 1=Odoriferous; 2=Adhesive; 3=Poisonous; 4=Slippery; 5 = Distastefull
Camouflage	0= Absence; 1= Presence
Immobility	1= Motionless flatten; 2= Motionless alert; 3= Thanatosis
Contracting	0= Absence; 1= Contracting; 2= Pragmosis; 3= Crouching down; 4= Chin-tuckin; 5=Eye protection
Body inflation	0= Absence; 1= Presence
Body elevation	0= Absence; 1= Legs stretched vertically; 2= Legs stretched laterally; 3= Elevation; 4= Elevation laterally
Stretched legs	0= Absence; 1= Presence
Escape	1= Only jump; 2= Varius jump; 3= Hide
Aposematism	0= Absence; 1= Total; 2= Partial
Cloacal Discharge	0= Absence; 1= Liquid; 2= Solid
Gaped mouth	0= Absence; 1= Presence
Defensive vocalizations	0= Absence; 1= Distress call; 2= Alarm call
Fighting back	0= Absence; 1= Erratic movements; 2=Fighting; 3=Spine agression; 4=Charging; 5= Head hinting; 6=Biting

Phylogenetic Data

According to the protocol proposed by Pyron & Wiens (2011) in an extant amphibian phylogeny, we used 12 genes to produce a novel estimate phylogeny for the Atlantic Forest amphibians (i.e. 11,906 bp for each species), through three mitochondrial (i.e. Cyt-b, 12s and 16s) and nine nuclear genes (i.e. CXCR4, H3A, NCX1, POMC, RAG1, ROHD, SIA, SLC8A3 and TYR). For the length-variable regions, we performed multiple pairwise comparisons by the online version of MAFFT v.6.8 and the G-INS-i algorithm (Katoh & Toh, 2008). After, we put together alignments of all genes in the same alignment using the software SequenceMatrix 1.7.7 (Vaidya, 2011) to concatenate the supermatrix previously produced. We based the phylogenetic relationships on 115 amphibian species (Fig. 2), through nucleotide sequences obtained from the GenBank database (Benson et al., 2013).

We conducted the phylogenetic relationships with Bayesian analyses in the software BEAST 1.8 (Drummond & Rambaut, 2007). We performed the phylogeny based through a HKY model of sequence evolution for one partition for all genes, using a Yule speciation process as the tree prior and an uncorrelated relaxed clock. We run the Yule process for 100 million generations, ensuring that the number of generations convergence were sufficiently assessed with the Tracer 1.6 (Rambaut et al., 2014), removing a conservative 10% burn-in fraction for the final tree. We combined these results using the LogCombiner 1.8 (Rambaut & Drummond, 2013a).

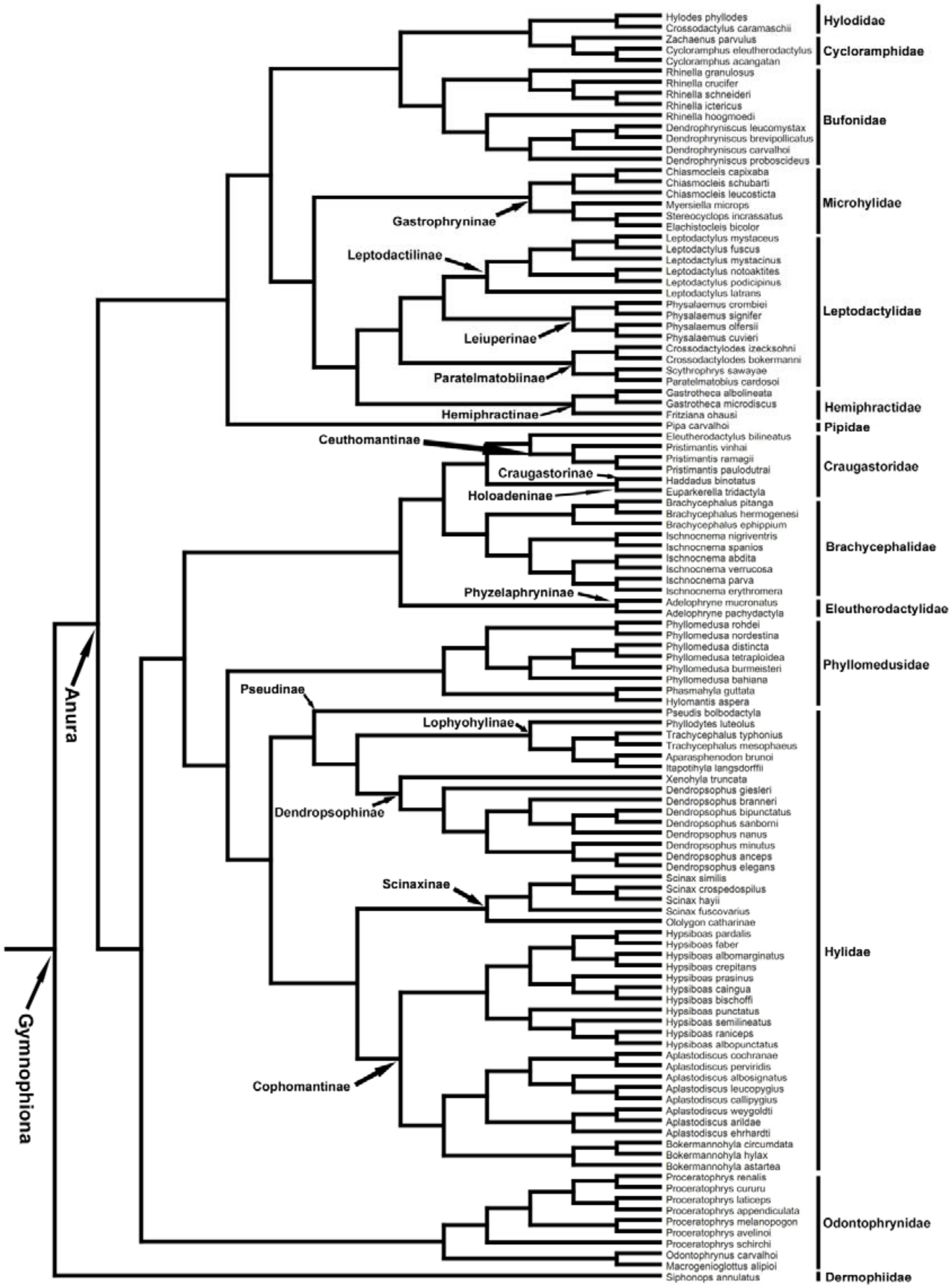

Fig. 2. Original tree based on Pyron & Wiens (2011) and Duellman et al. (2016). The nomenclature of species follows Frost (2016). Orders, Families and Subfamilies are indicated in the tree.

We conducted additional phylogenetic estimations based on 100 stochastic trees to account for the phylogenetic uncertainty of the single reconstructed phylogenetic tree for our 115 species assessed. Given these 100 random simulations, we built the maximum clade credibility tree (summary tree) with the use of the software TreeAnnotator 1.8 (Rambaut & Drummond, 2013b).

We considered the nodes strongly supported if they received posterior probability ≥ 0.95. To edit the new phylogenetic tree, we used the package 'ape' (Paradis, 2012), in the R software (R Development Core Team, 2017). The reconstructed phylogenetic tree provided a revised taxonomic classification that incorporated the newly obtained phylogenetic information by imposing the smallest possible change on the existing classification. We did not consider the low node supports from the reconstructed phylogenetic tree provided by the Bayesian analyses. We only used species from one geographic region, which in case of low node support (not shown) could be a result of an incomplete lineage sorting, and thus the lack of information in the sequence data.

Functional Traits

We characterized 115 amphibian species according to five functional traits that determine different dimensions of the amphibians' ecological niches in relation to their morphology, life-history and behaviour. We used the following traits according to Haddad et al. (2013), with some additional complements obtained in the fieldwork: (1) body size (small < 3cm, medium 3-10 cm, large > 10cm); (2) development mode (direct or indirect); (3) habitat (forested areas, open areas, and both open and forested areas); (4) activity (nocturnal, diurnal, and both), and (5) habit (arboreal, phytotelmate, terrestrial, cryptozoic, fossorial, rheophilic, and aquatic).

Reconstruction of Ancestral States

We reconstructed the ancestral character states through maximum-likelihood estimations under stochastic character mapping analysis (SIMMAP; Bollback, 2006), using 1,000 simulations for discrete characters based on the matrix data of antipredator mechanisms (Table S1). We compared the likelihood estimations with a value of lambda = 1 for providing a standardized method to draw the reconstructed phylogenies onto the antipredator mechanisms plot, accounting the phylogenetic uncertainty for the ancestral character states. We also used null simulations across the tips of the reconstructed trees indicating the expected variances on ancestral states among species under Brownian motion. We performed the stochastic character mapping analysis and the null simulations in the R software (R Development Core Team, 2017), using the "make.simmap" and "fastBM" functions of the package "phytools" (Revell, 2012). We followed Frost (2016) for the amphibian nomenclature.

Phylogenetic Signal

To estimate the phylogenetic signals, we used a robust measure proposed by Abouheif (1999). Abouheif's test turns out to be a Moran's test, but Abouheif's matrix of phylogenetic proximities has a non-zero diagonal. These proximities are based both on Moran's I and Geary's c tests (Legendre & Fortin, 1989). The exact test was performed. We used the Abouheif's test implemented in the "adephylo" package with 999 randomizations (Pavoine et al 2008) in the R software (R Development Core Team, 2017).

In order to test what antipredator mechanism follows a stochastic Brownian evolution model, we used a maximum-likelihood based measurement of phylogenetic signal, through lambda (λ) model, as developed by Pagel (1997). This metric corresponds to a tree transformation parameter which gradually eliminates phylogenetic structure when varying from 1 to 0. Lambda transformation is performed by multiplying the off-diagonal elements of the variance/covariance matrix describing the tree topology and the branch lengths (Münkemüller, et al. 2012). Lambda values of 1 correspond to a Brownian evolution model, whereas at the other extreme a lambda value of 0 corresponds to a complete absence of phylogenetic structure (star-like phylogeny). Estimated lambda can be compared to zero by computing a likelihood ratio and comparing it to a chi-square distribution with one degree of freedom (Münkemüller, et al. 2012). Hence testing for a significant phylogenetic signal relative to phylogenetically unstructured data. We used the 'phylosig' function from the package 'phytools' (Revell, 2012) in the R software (R Development Core Team, 2017).

Antipredator Mechanisms vs. Functional Traits

In order to evaluate the response of the diversity of antipredator mechanisms of each species to the predicted body size, development mode, habit, habitat and activity. We used permutation multivariate analysis of variance (PERMANOVA), with 999 permutations based on a Euclidean distance matrix through the "adonis" function of the package 'vegan' (Oksanen et al., 2013) in the R software (R Development Core Team, 2017). In addition, we used Boxplots to visualize the traits that better explained the diversity of antipredator mechanisms.

Spatial Range vs. Antipredator Mechanisms

To associate the diversity of antipredator mechanisms to the species' distribution ranges, we used correlation matrices comparing the diversity of antipredator mechanisms of species and their distribution ranges, through simple linear regression models. We used these correlations for all mechanisms and their variations (see Table 1). We performed these analyses using the package 'vegan' (Oksanen et al., 2013) in the R software (R Development Core Team, 2017).

RESULTS

Ancestral States

Our results showed that the antipredator mechanisms camouflage, immobility, fighting back, and escape have common ancestral states for Anura and Gymnophiona (simplesiomorphic) based on 115 species, two Orders, 14 Families and 12 Subfamilies (Fig. 3). Fighting back mechanism did not appear as ancestral state only to the families Dermophiidae, Hemiphractidae, Phyllomedusidae and Odontophrynidae. The escape mechanism showed two apomorfics variations in anurans' "only jump" and "various jump", and "various jump" is a homologous feature for Brachycephalidae and Eleutherodactilidae (Ceuthomantinae), evolving independently in Leptodactilinae (homoplasy).

Body inflation showed apomorphic states in different ancestors, and homoplastic states in the Bufonidae, Microhylidae (synapomorphy of Gastrophryninae), Leptodactylidae (synapomorphy of Leptodactiilinae and Leiuperinae), Craugastoridae (synapomorphy of Holoadeninae), Hylidae (synapomorphy of Cophomantinae) and Cycloramphidae.

The mechanism of producing secretions, despite being simplesiomorfic state, appeared in Anura as homoplastic way with different specializations or adjustments throughout its evolution. Two subfamilies of Hylidae (synapomorphy of Scinaxinae and Cophomantinae) had production of odoriferous secretion as homologous. Slippery mechanism present in the Hylidae family and subfamily Leptodactylinae is a homoplasy, and poisonous in Bufonidae and Phyllomedusidae (homoplasy).

Contracting mechanism showed an apomorfic and emerged independently, considering a homoplasy in Bufonidae, Hemipractidae, Phyllomedusidae, Odontophrynidae and in the subfamily Comophantinae. The mechanism gaped mouth showed an apomorfic state, homologous in Terrarana (Craugastoridae, Brachycephalidae and Eleutherodactylidae) and it can be regarded as synapomorphy for the Terrarana group. The mechanisms body elevation, stretched legs and defensive vocalizations did not show ancestral states to any taxa (Fig. 3; see Table S1).

Phylogenetic Signal

Aboufe's results indicated that most antipredator mechanisms have significant

Table 2. Phylogenetic signal of antipredator mechanisms according to the Pagel's λ tests and the Abouheif's Cmean for the Atlantic Forest amphibians.

Antipredator mechanisms	Pagel's λ	*P*	Abouheif's C-mean	*P*
Production of secretions	1.0145	0.0000	0.4273	0.001
Camouflage	0.8200	0.0008	0.1707	0.031
Immobility	0.7897	0.0000	0.4204	0.001
Contracting	0.0680	0.3834	0.0800	0.063
Body inflation	0.0001	1.0000	0.2192	0.099
Body elevation	0.0001	1.0000	0.3337	0.011
Stretched legs	0.5073	0.0001	0.2323	0.001
Escape	0.7729	0.0001	0.2465	0.001
Aposematism	0.5052	0.0001	0.2973	0.003
Cloacal discharge	0.6911	0.0000	0.2667	0.001
Gaped mouth	0.7310	0.0000	0.1950	0.001
Defensive vocalizations	0.2065	0.3236	0.3278	0.006
Fighting back	0.6304	0.0086	0.4273	0.001

phylogenetic signals. These results showed strong phylogenetic signals for the mechanisms production of secretions (C-mean = 0.43, $p < 0.05$), immobility (C-mean = 0.42, $p < 0.05$), fighting back (C-mean = 0.33, $p < 0.05$), and stretched legs (C-mean = 0.33, $p < 0.05$). The mechanism contracting (C-mean = 0.11, $p > 0.05$) and body inflation (C-mean = 0.08, $p > 0.05$) showed no significant phylogenetic signals (Table 2; see Fig. S1).

The results obtained from the Pagel's lambda (λ) indicated the mechanisms production of secretion ($\lambda = 1.01$, $p < 0.001$), camouflage ($\lambda = 0.82$, $p < 0.001$) and immobility ($\lambda = 0.79$ $p< 0.001$) showed values close to 1, fitting a Brownian evolution model. Contracting ($\lambda = 0.07$, $p > 0.001$), body inflation ($\lambda = 0.00$, $p > 0.001$) and body elevation ($\lambda = 0.00$, $p > 0.001$) showed no significant values (Table 2; see Fig. S2).

Antipredator Mechanisms vs. Functional Traits

The PERMANOVA results revealed that the functional traits explained 40.4% of the diversity of antipredator mechanisms (Table S2). Habit was main trait responsible for this explained variation (25.1%), following by body size (5.2%), activity (5.0%) and habitat (4.9%). Development mode did not show any significance relation with the diversity of antipredator mechanisms. The boxplot illustrated which functional traits had the greatest diversity of antipredator mechanisms (e.g. nocturnal, arboreal, fossorial, medium, large, and open areas; see Fig. S3).

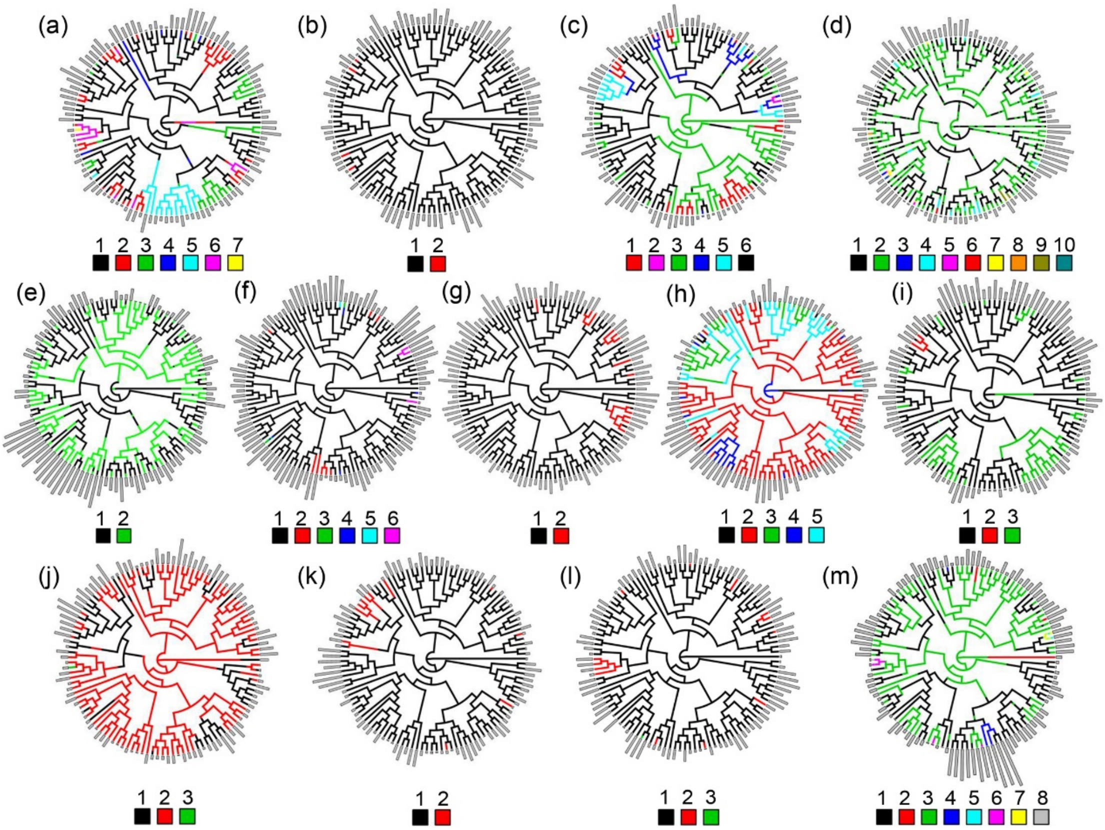

Fig. 3. Maximum-likelihood ancestral state reconstructions for 13 amphibian antipredator mechanisms in the Atlantic Forest (N = 115 species). Vertical bars across the tips of the trees indicate the expected variances on ancestral states among species under Brownian-motion. (a) Production of secretions: 0= absence, 1= odoriferous, 2= adhesive, 3= poisonous, 4= slippery, 5= distasteful; (b) Camouflage: 0= absence, 1= presence; (c) Immobility: 1= motionless flatten, 2= motionless alert, 3= thanatosis; (d) Contracting: 0= absence, 1= contracting, 2= pragmosis, 3= crouching down, 4= chin-tuckin, 5= eye protection; (e) Body inflation: 0= absence, 1= presence; (f) Body elevation: 0= absence, 1= legs stretched vertically, 2= legs stretched laterally, 3= elevation, 4= elevation laterally; (g) Stretched legs: 0= absence, 1= presence; (h) Escape: 1= only jump, 2= various jump, 3= hide; (i) Aposematism: 0= absence, 1= total, 2= partial; (j) Cloacal Discharge: 0= absence, 1= liquid, 2= solid; (k) Gaped mouth: 0= absence, 1= presence; (l) Defensive vocalizations: 0= absence, 1= distress call, 2= alarm call; (m) Fighting back: 0= absence, 1= erratic movements, 2=fighting, 3=spine aggression,4= charging, 5= head hinting, 6= biting.

Spatial Range vs. Antipredator Mechanisms

The relation between the diversity of antipredator mechanisms and species distributions indicated significant values ($r^2 = 0.15$, $p < 0.001$), showing that amphibian species with more defensive behaviours can have greater spatial ranges (see Fig. S4).

DISCUSSION

Our results indicated some ancestral mechanisms with strong phylogenetic signal (e.g. production secretions and immobility). However, these mechanisms showed simplesiomorphic and homoplatic ancestral states, which suggest some independent evolutionary histories. Our findings revealed that the evolution of these mechanisms follows a stochastic Brownian evolution model.

The mechanism of camouflage did not show a strong phylogenetic signal but fitted to the Brownian evolution model. We found simplesiomorphic states between Gymnophiona and Anura (e.g. camouflage and immobility), suggesting some basal defensive mechanisms in Amphibians. On the camouflage mechanism, we observed only a little change in few fully aposematic species, while on the immobility mechanism, we found more recent changes (e.g. thanatosis). Both mechanisms (camouflage and immobility) have strong phylogenetic signal, suggesting ecological influences as evolutionary pressures.

According to Brodie (1983), the production of secretions mechanism can be directly related to the diversity of antipredator strategies in amphibians. Our findings showed that species that produce secretions also can influence the evolution other behavioural traits in synergy with ecological pressures. We observed that clades with toxic species generally have contracting mechanisms acting in synergy. In Phyllomedusidae for example, there are several passive antipredator mechanisms that render no aggressive contact with predator species. Phyllomedusid frogs have a combination of production of toxic substances, partial aposematism, immobility, camouflage and contracting, which suggest an evolutionary success of ecological pre-predator processes. Moreover, the production of slippery secretions leads species to develop synergistic post-predator behaviours (e.g. fight, escape "various jump", camouflage and immobility).

Contracting is used in synergy with other defensive strategies to produce secretions that may cause or provide the regurgitation of the prey by predator (Sazima, 1974; Toledo et al., 2010). We showed ancestral states in the contracting mechanism for the families Bufonidae, Phyllomedusidae, Odontophrynidae and Hemipractidae, as well as in the subfamily Cophamantinae (synapomorphic state), suggesting an evolutionary convergence at different taxonomic levels, mainy concentrated on the tips of the trees. Although not having significant phylogenetic signals, the evolutionary history of this mechanism seems to be associated to the mechanism to produce toxic or unpalatable secretions.

The mechanism of stretched legs presented a significant phylogenetic signal but with a week signal of random evolution (Brownian motion model). This mechanism showed homoplastic states in the Cycloramphidae, Bufonidae, Microhylidae (synapomorphy in Gastrophryninae), Leptodactylidae (synapomorphy in Paratelmatobinae) and Odontophrynidae. Its evolution seems to be recent emerging independently (homoplastic) in different families and subfamilies of anurans (apomorphic).

According to Gingras & Ficth (2013), advertisement call has strong phylogenetic relationship among genera in anurans. However, our results did not show this pattern for defensive call. Defensive vocalization is a apomorfic state with homologous origin in the Cycloramphidae, Bufonidae, Microhylidae (Gastrophryninae), Leptodactylidae (Leiuperinae) and Hylidae (Scinaxinae and Cophomantinae). Recent studies suggest that defensive vocalizations may have ethological origins in response to antipredator mechanisms that are fundamental for the species survival (Toledo et al., 2015; Lourenço-de-Moraes et al., 2016; Forti et al., 2018). We showed that the mechanism of defensive vocalizations is an autopomorfic state in the subfamilies Comophantinae and Hemiphractinae.

We defined the mechanism of gaped mouth as an apomorfic state with a homologous origin in the Terrarana group (Brachycephalidae, Craugastoridae and Eleutherodactylidae). This group has diminutive species and their main predators are arthropods (Toledo, 2005). The origin of this mechanism may have influenced the miniaturization of the species of this group (Hedges et al., 2008; Clemente-Carvalho et al., 2011). However, this behaviour can be also observed in families of larger species as Hemiphractidae (Lourenço-de-Moraes et al., 2016). The presence of this behaviour in large species appears in synergy with the mechanisms of body inflation, biting, defensive vocalization, and fighting back (see Toledo et al., 2011; Lourenço-de-Moraes et al., 2016). In diminutive species of Terrarana group, these mechanisms do not appear in synergy with other behaviours (Lourenço-de-Moraes et al., 2014b), suggesting evolutionary histories with distinct origins (Homology).

Mechanisms with no phylogenetic signals (body inflation, body elevation and contracting) did not follow a model of random evolution. These mechanisms evolved independently and seems to be more recent in evolutionary terms. However, appear as ancestral mechanisms of homoplasy in some amphibian families and subfamilies. The emergence of recent evolutionary histories suggests ethological origins of antipredator mechanisms. The ability to memorize a certain defensive feature that may help the animal to maintain a certain behaviour, is present even in invertebrates (Punzo, 2004). Demonstrating learning ability in response to a threat stimulus is necessary to the prey survival.

Our results revealed that fighting back mechanism had a weak phylogenetic signal and a low value for a Brownian evolution. Toledo et al. (2011) and Lourenço-de-Moraes et al. (2016) suggested that biting behaviour may be related to parental care strategies. Figueiredo et al. (2017) recorded a pregnant female *Ischnocnema henseli* performing biting. Other Terrarana species also have been found performing parental care strategies (Hedges et al., 2008; Ryan et al., 2010). It is possible that this mechanism has ethological origin based on ecological pressures according to their ancestral characteristics.

The ecological specializations of amphibian species showed a strong evolutionary pressure in relation to their defensive characteristics. Our results showed that functional traits can explain 40.4% of the diversity of antipredator mechanisms, mainly explained by the functional trait "habit". In addition, functional traits also can be related to the potential distribution of species (Diaz et al. 2007; Gomes-Rodrigues, 2015).

On one hand, species with exposed habitats (i.e. arboreal species) have a greater diversity of predators such as birds, reptiles, mammals and invertebrates (Toledo, 2005, Toledo et al., 2007; Pombal Jr., 2007). Thus, it is expected that this ecological pressure influences a rapid and effective responses to the survival of the species in the predator-prey race. On the other hand, fossorial species has reduced posterior limbs adapted to excavation (Haddad et al., 2013), and because of this, they lost their key defensive strategies of terrestrial species such as jumping behaviours. Therefore, they were selectively adapted to develop other defensive strategies (Haddad et al., 2013). Our results showed that species with medium and large body sizes have greater diversity of antipredator mechanisms. We suggest that medium and large species are more exposed than small species, and because of this, they tend to develop more defensive strategies according to their habitat preferences.

It is widely documented that functional traits such as body size can influence the species dispersal processes (Bell, 2001). Our results confirmed the hypothesis suggested by Lourenço-de-Moraes et al. (2016), which species with greater diversity of antipredator mechanisms have greater geographical distribution. The high predation pressure on amphibian species associated to their limited dispersal abilities renders a constant evolutionary selection of effective antipredator mechanisms.

Although there are several differences of defensive behaviours among anuran populations (Toledo et al., 2007), genetic characteristics of the species can influence their evolutionary histories. Under similar ecological pressures, different antipredator mechanisms can be developed according to the high phenotypic plasticity of amphibians (Lawler, 1989; Horat & Semlitsch, 1994; Relyea, 2001).

Our results showed that the evolutionary history of antipredator mechanisms of amphibians can be highly plastic and fast. Amphibian antipredator mechanisms may have purely phylogenetic origin or may have only ecological origins in response to possible predators in the past. The different defensive behaviours that exists across the amphibian tree of life provides a great antipredator strategy, which can be directly associated to the species dispersal abilities. Specialization processes driven by functional traits is a strong selective pressure on amphibian species struggle for existence. Our work advanced the understanding on the ecology and evolution of defensive behaviours in amphibians, which have been shown to be diverse and complex (Zelick et al., 1999; Wells, 2007; Toledo et al., 2015). In this context, our findings provide new perspectives on the evolutionary and ecological plasticity of amphibians in a changing environment.

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APPENDIX. Supporting Information

Supplementary files:

Table S1. Ancestral antipredator mechanisms for each Order, Family and Subfamily of 115 amphibian species assessed in the Brazilian Atlantic Forest.

Table S2. Results from the PERMANOVA on the relation between the functional traits and the diversity of antipredator mechanisms of amphibians assessed in the Brazilian Atlantic Forest.

Fig. S1. Simulations of C-mean statistics calculated for the antipredator mechanisms data along the tips of the phylogeny. Black circles indicate the position of the observed mean C-statistic relative to the null hypothesis. P-value of the observed mean C-statistic is statistically significant at an alpha of 0.05.

Fig. S2. Traitgrams indicated Pagel's lambda (λ). Axis 'y' showed the traces of antipredator mechanisms, and 'x' the scale of time in millions of years. The P-value of the lambda (L) test is statistically significant at an alpha of 0.001.

Fig. S3. Boxplot showing the relation between the functional traits and the diversity of antipredator mechanisms by the selection of the significant PERMANOVA results.

Fig. S4. Linear regression between the antipredator mechanisms and the geographical ranges of 115 amphibian species in the Brazilian Atlantic Forest ($r^2 = 0.15$, $P < 0.001$).

Table S1. Ancestral antipredator mechanisms for each Order, Family and Subfamily of 115 amphibian species assessed in the Brazilian Atlantic Forest.

Order/Family/ Subfamily	Production of secretions	Camouflage	Immobility	Contracting	Body inflation	Body elevation	Stretched legs	Escape	loacal Discharge	Gaped mouth	Defensive vocalizations	Fighting back
Gymnophiona	Absence / Poisonous	Presence	Motionless	Absence	Absence	Absence	Absence	Hide	Absence	Absence	Absence	Erratic movements
Dermophiidae	Absence	Presence	Motionless	Absence	Absence	Absence	Absence	Absence	Absence	Absence	Absence	Absence
Anura	Absence	Presence	Motionless	Absence	Absence	Absence	Absence	Only jump	Absence	Absence	Absence	Fighting
Bufonidae	Poisonous	Presence	Motionless	Contracting	Presence	Absence	Absence	Only jump	Liquid	Absence	Absence	Fighting
Brachycephalidae	Absence	Presence	Motionless	Absenc	Absence	Absence	Absence	Various jump	Absence	Absence / Presence	Absence	Fighting
Craugastoridae	Absence	Presence	Motionless	Absence	Absence	bsence	Absence	Only jump	Absence	Absence / Presence	Absence	Fighting
Ceuthomantinae	Odoriferous	Presence	Motionless	Absence	Absence	Absence	Absence	Various jump	Liquid	Absence	Absence	Fighting
Craugastorinae	Absence	Presence	Motionless	Absence	Absence	Absence	Absence	Only jump	Absence	Presence	Absence	Fighting
Cycloramphidae	Absen	Presence	Motionless / Thanatosis	Absence	Presence	Absence	Absence	Only jump	Liquid	Absence	Absence	Fighting / Biting
Eleutherodactylidae	Absence	Presence	Motionless	Absence	Absence	bsence	Absence	Only jump	Absence	Absence / Presence	Absence	Fighting
Phyzelaphryninae	Absence	Presence	Motionless	Absence	Absence	bsence	Absence	Only jump	Absence	Absence / Presence	Absence	Fighting
Hemiphractidae	Absence	Presence	Motionless	Contracting	Absence	bsence	Absence	Only jump	Liquid	Absence	Absence	Absence
Hylidae	Absence	Presence	Motionless	Absence	Absence / Presence	Absence	bsence	Only jump	Liquid	Absence	Absence	Fighting
Comophantinae	Odoriferous	Presence	Motionless	Absence / Contracting	Absence / Presence	Absence	Absence	Only jump	Liquid	Absence	Absence	Fighting
Dendropsodinae	Absence	Presence	Motionless	Absence	Absence / Presence	Absence	Absence	Only jump	Liquid	Absence	Absence	Fighting
Lophyohylinae	Absence	Presence	Motionless	Absence	Absence / Presence	Absence	bsence	Only jump	Liquid	Absence	Absence	Fighting
Pseudinae	Absence	Presence	Motionless	Absence	Absence	Absence	bsence	Only jump	Absence	bsence	Absence	Fighting
Scinaxinae	Odoriferous	Presence	Motionless	Absence	Absence / Presence	Absence	bsence	Only jump	Liquid	Absence	Absence	Fighting
Hylodidadae	Slippery	Presence	Motionless / Thanatosis	Absence	Presence	Absence	Absence	Only jump	Liquid	Absence	Absence	Fighting
Leptodactylidae	Absence	Presence	Motionless	Absence	Absence	Absence	Absence	Only jump	Liquid	Absence	Absence	Absence / Fighting
Leiuperinae	Absence	Presence	Motionless	Absence	bsence	Absence	Absence	Only jump	Liquid	Absence	Absence	Fighting
Leptodactyliniae	Absence / Slippery	Presence	Motionless	Absence	Presence	Absence	Absence	Various jump	Liquid	Absence	Absence	Fighting
Paratelmatobiinae	Absence	Presence	Motionless	Absence	Absence	Absence	bsence	Only jump	Liquid	Absence	Absence	Absence / Fighting
Microhylidae	Odoriferous	Presence	Motionless	Absence	Absence	Absence	Absence	Only jump	Liquid	Absence	Absence	Fighting
Odontophrynidae	Absence	Presence	Motionless	Absence / Contracting	Absence	Absence	bsence	Only jump	Absence	bsence	Absence	Absence
Pipidae	Absence	Presence	Motionless	Absence	Absence	Absence	bsence	Only jump	Absence	bsence	Absence	Fighting
Phyllomedusidae	Poisonous	Presence	Motionless	Contracting	Absence	Absence	Absence	Only jump	Absence	Absence	Absence	Absence

Table S2. Results from the PERMANOVA on the relation between the functional traits and the diversity of antipredator mechanisms of amphibians assessed in the Brazilian Atlantic Forest.

Variables	**df**	***F* model**	***R*²**	***P* value**
Activity	1	9.463	0.05060	0.002
Body size	1	9.857	0.05271	0.001
Habit	1	47.100	0.25187	0.001
Habitat	1	9.306	0.04976	0.001
Development mode	1	2.275	0.01217	0.108
Residuals	109		0.58289	–
Total	114	–	1.00000	–

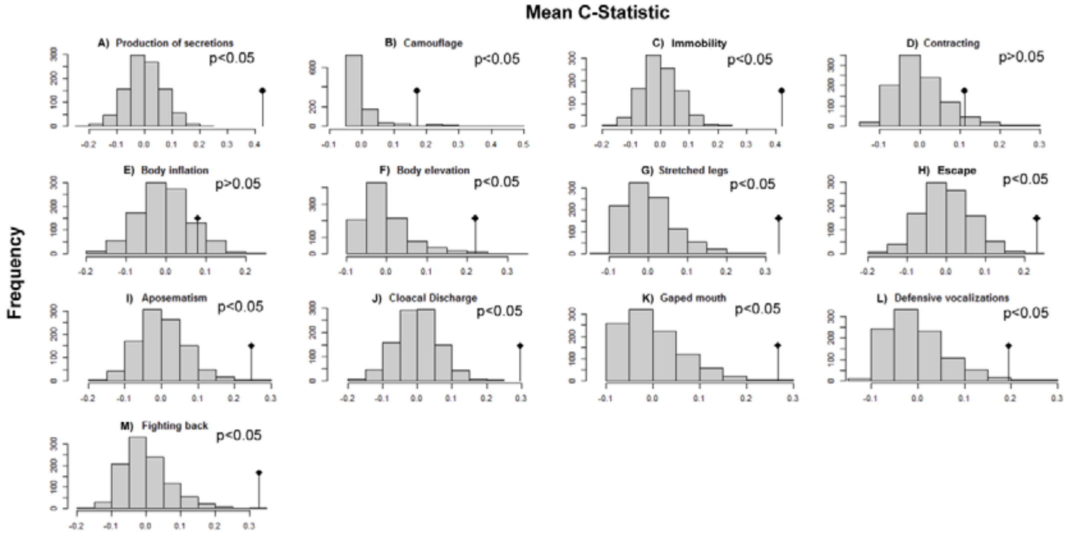

Fig. S1. Simulations of C-mean statistics calculated for the antipredator mechanisms data along the tips of the phylogeny. Black circles indicate the position of the observed mean C-statistic relative to the null hypothesis. P-value of the observed mean C-statistic is statistically significant at an alpha of 0.05.

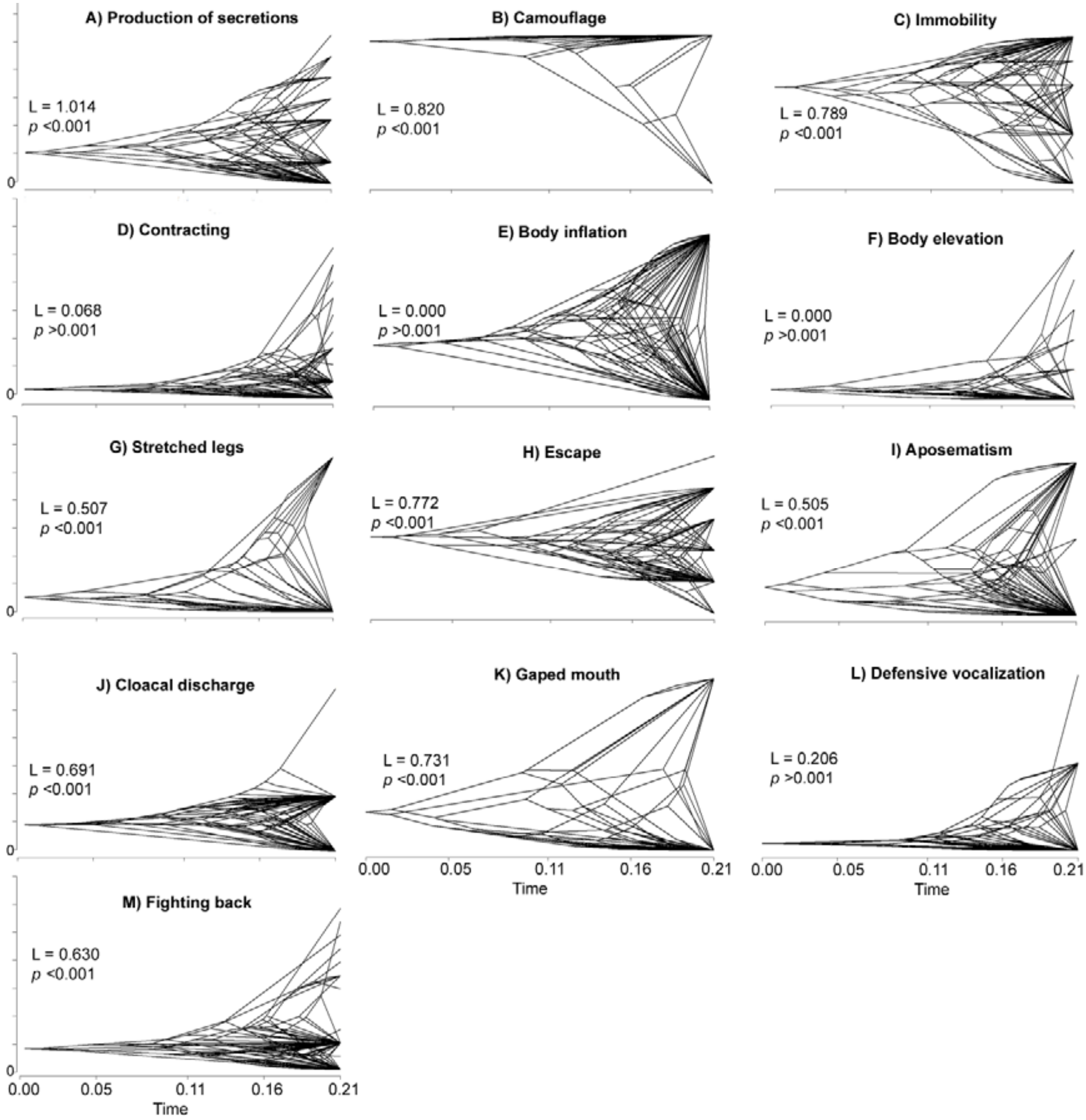

Fig. S2. Traitgrams indicated Pagel's lambda (λ). Axis 'y' showed the traces of antipredator mechanisms, and 'x' the scale of time in millions of years. The P-value of the lambda (L) test is statistically significant at an alpha of 0.001.

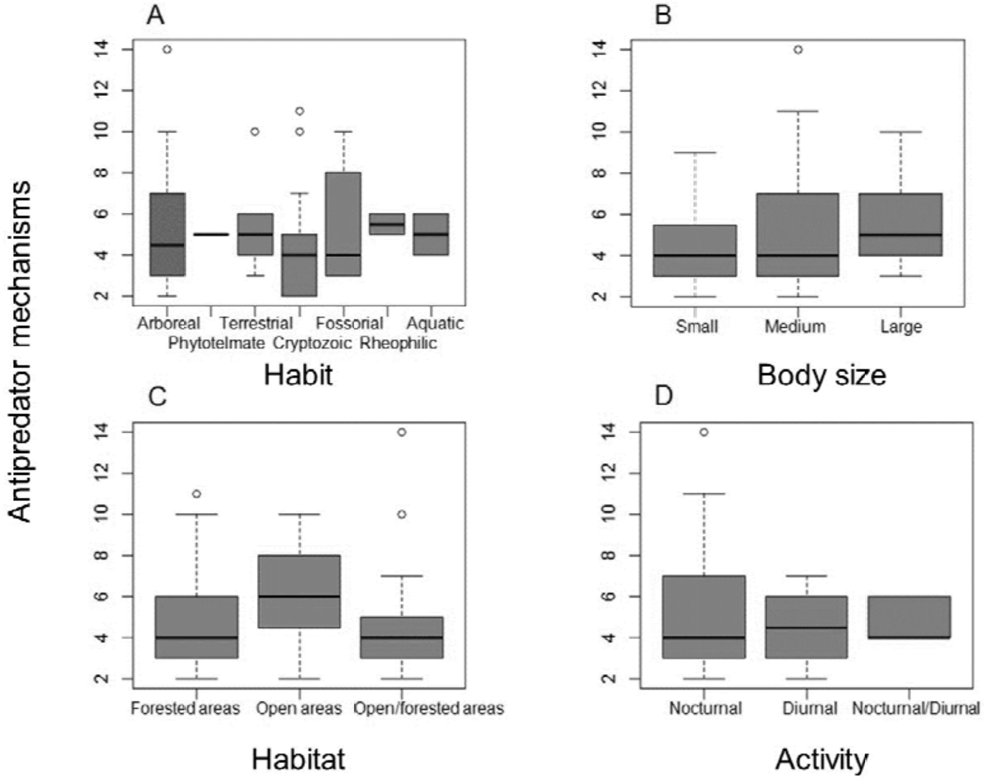

Fig. S3. Boxplot showing the relation between the functional traits and the diversity of antipredator mechanisms by the selection of the significant PERMANOVA results.

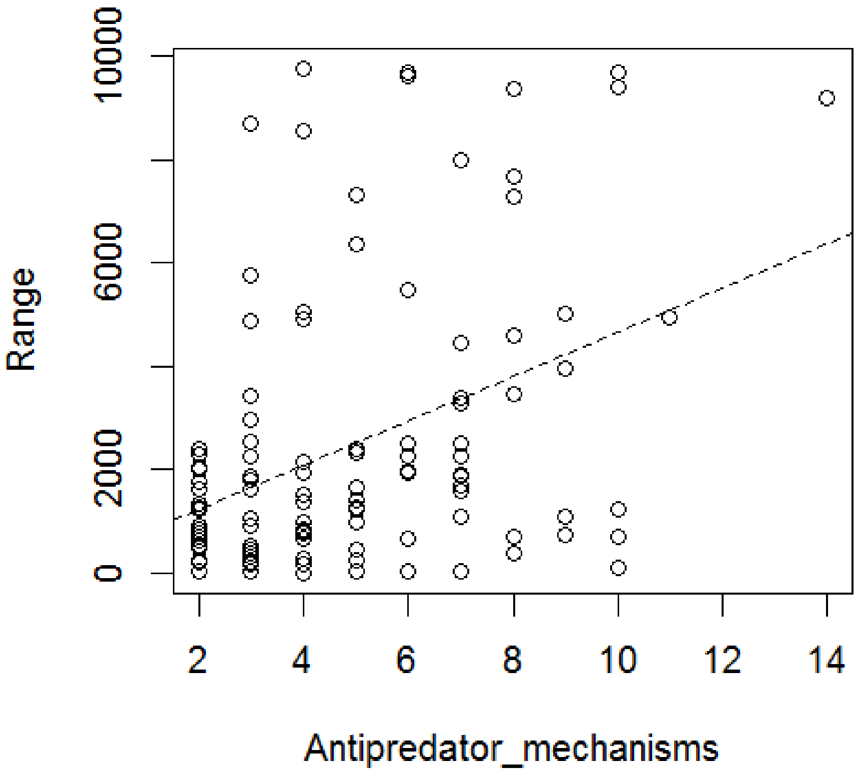

Fig. S4. Linear regression between the antipredator mechanisms and the geographical ranges of 115 amphibian species in the Brazilian Atlantic Forest ($r^2 = 0.15$, $P < 0.001$).

Part V

Biodiversity Conservation

Back Cover: *Boana albomarginata* (Spix, 1824)
– Photo by Mirco Solé

Chapter 9

The efficiency of indicator groups for the conservation of amphibians in the Brazilian Atlantic Forest

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The efficiency of indicator groups for the conservation of amphibians in the Brazilian Atlantic Forest

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La eficiencia de los grupos de indicadores para la conservación de anfibios en el Bosque Atlántico brasileño. La selección adecuada de grupos indicadores de biodiversidad es clave en las estrategias de conservación. Sin embargo, estas evaluaciones difieren en las escalas espaciales, en los métodos utilizados y en los grupos seleccionados como indicadores, lo que generalmente produce resultados contradictorios. La congruencia espacial entre riqueza de especies y la complementariedad de grupos taxonómicos es un paso fundamental para identificar eficientes grupos indicadores de biodiversidad. El objetivo principal de este estudio fue evaluar el rendimiento y la eficiencia de ocho grupos taxonómicos (familias) que representan la más alta diversidad de anfibios en el Bosque Atlántico brasileño. Las rutinas de optimización basadas en el concepto de complementariedad se aplicaron para verificar el rendimiento de cada grupo indicador seleccionado en relación con la representatividad de los anfibios, a través del uso del software MARXAN. Además, se aplicaron valores estimados del coste de la tierra requerida por cada grupo evaluado. Algunos grupos han sido sustancialmente más efectivos que otros con respecto a la representación de anfibios. Leiuperidae fue considerado como el mejor grupo indicador entre las familias analizadas, representando el 71% de las especies de anfibios en el Bosque Atlántico brasileño (es decir, 290 especies). En este sentido, este estudio promueve la comprensión de cómo los patrones de diversidad de anfibios pueden ser informativos para las decisiones de conservación en diferentes escalas espaciales.

– Spanish Abstract (Resumen)

Ecology and Evolution

Open Access

The efficiency of indicator groups for the conservation of amphibians in the Brazilian Atlantic Forest

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Amphibians, Atlantic Forest, biodiversity indicators, representativeness, surrogates, systematic conservation planning.

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Abstract

The adequate selection of indicator groups of biodiversity is an important aspect of the systematic conservation planning. However, these assessments differ in the spatial scales, in the methods used and in the groups considered to accomplish this task, which generally produces contradictory results. The quantification of the spatial congruence between species richness and complementarity among different taxonomic groups is a fundamental step to identify potential indicator groups. Using a constructive approach, the main purposes of this study were to evaluate the performance and efficiency of eight potential indicator groups representing amphibian diversity in the Brazilian Atlantic Forest. Data on the geographic range of amphibian species that occur in the Brazilian Atlantic Forest were overlapped to the full geographic extent of the biome, which was divided into a regular equal-area grid. Optimization routines based on the concept of complementarily were applied to verify the performance of each indicator group selected in relation to the representativeness of the amphibians in the Brazilian Atlantic Forest as a whole, which were solved by the algorithm "simulated annealing," through the use of the software MARXAN. Some indicator groups were substantially more effective than others in regard to the representation of the taxonomic groups assessed, which was confirmed by the high significance of the data ($F = 312.76$; $P < 0.01$). Leiuperidae was considered as the best indicator group among the families analyzed, as it showed a good performance, representing 71% of amphibian species in the Brazilian Atlantic Forest (i.e., 290 species), which may be associated with the diffuse geographic distribution of their species. In this sense, this study promotes understanding of how the diversity standards of amphibians can be informative for systematic conservation planning on a regional scale.

Introduction

Increased rates of habitat loss and human occupation are creating demands for more adequate strategies to maximize efforts for biodiversity conservation (Diniz-Filho et al. 2008). One of the conservation strategies mostly used to preserve threatened species is the establishment of protected areas (Lawler and White 2008). The selection of sites for the protection of biological communities and the maintenance of ecosystem processes, within the context of systematic conservation planning (see Margules and Pressey 2000), is an extremely efficient tool to preserve species and habitats (Clemens et al. 1999; Myers et al. 2000; Kati et al. 2004; Rodrigues and Brooks 2007; Loucks et al. 2008). However, the resources available for the creation of protected areas are limited (Loucks et al. 2008). Therefore, it is no surprise that the inclusion of the economic costs into conservation planning can result in more feasible conservation strategies on the ground (Naidoo et al. 2006).

A central issue in systematic conservation planning is the identification of targets to be conserved (Margules and Pressey 2000; Groves et al. 2002; Cowling and Pressey 2003;

Sarkar 2004). Protected area networks are often selected to protect species of distinct taxonomic groups, communities of high biological relevance, or combinations of different abiotic conditions favorable to local ecosystems, with the assumption that such sites will also protect a wider range of biodiversity (Lawler and White 2008). Therefore, conservation planners should count on surrogates, or indicator groups, to represent the largest possible part of local biodiversity in reserve selection (Kremen 1992; Raven and Wilson 1992; Flather et al. 1997). The validity of this hypothesis depends on how well the chosen indicator group represents a wider array of biodiversity (Lawler and White 2008). In this way, the adequate selection of indicator groups is fundamental for the consistency of successful systematic conservation planning (Margules and Pressey 2000; Margules and Sarkar 2007).

Most conservation plans are based on the biodiversity surrogates (e.g., Loiselle et al. 2003; Stoms et al. 2005; Margules and Sarkar 2007; Rodrigues and Brooks 2007). These surrogates are generally based on the species, such as keystone species, umbrella species, or flagship species (Andelman and Fagan 2000; Mace et al. 2007; Grantham et al. 2010). Additionally, these surrogates may also be based on other parameters, such as vegetation structure, soil coverage, and environmental gradients (Faith and Walker 1996a,b; Sarkar et al. 2005; Trakhtenbrot and Kadmon 2005), even though it is known that surrogates based on the species are more efficient than those based on environmental proxies (Rodrigues and Brooks 2007).

Quantifying the spatial congruence between species richness and complementarity among different taxonomic groups is a fundamental step to identify potential indicator groups (Howard et al. 1998; van Jaarsveld et al. 1998; Pinto et al. 2008). However, these evaluations differ in spatial scale, in the methods used and in the groups that are tested, which generally produces contradictory results (e.g., Schmit et al. 2005; Bani et al. 2006; Lamoreux et al. 2006; Chiarucci et al. 2007; Rodrigues and Brooks 2007; Grantham et al. 2010; Lewandowski et al. 2010). In spite of the importance and usefulness of systematic investigations about the consistency of indicator groups to guide conservation actions and decision-making processes, only a few studies have explicitly evaluated this aspect (e.g., Araújo et al. 2001; Manne and Williams 2003; Bani et al. 2006; Lawler and White 2008; Trindade-Filho and Loyola 2011).

There is a trend in the scientific literature in relation to studies on organisms that indicate habitat quality (Lima 2001). In this sense, amphibians have been identified as potential biological indicators due to their naked skin and their use of aquatic and terrestrial habitats, which makes them extremely vulnerable to environmental disturbances (Blaustein and Wake 1995; Tocher et al. 1997; Cosson et al. 1999; Kwet and Di-Bernardo 2002; DeGarady and Halbrook 2006; Lebboroni et al. 2006). However, these previous studies did not clearly evaluate which characteristics might make amphibians a good indicator group across different taxa (Sewell and Griffiths 2009). This suggests that some taxa previously highlighted as good indicators could have appeared so simply because they harbored many species, instead of really exhibiting good indicator qualities (Larsen et al. 2009). In order to use a straightforward approach to improve this concept, the main purpose of this study was to assess the performance of amphibian families as potential indicator groups to represent overall amphibian diversity in the Brazilian Atlantic Forest.

Materials and Methods

Study area

The Brazilian Atlantic Forest was chosen as our case study because it is one of the 34 global biodiversity hotspots for conservation priorities (Mittermeier et al. 2004), having high rate of habitat loss (Teixeira et al. 2009), which is one of the main factors that driving amphibians to extinction (Stuart et al. 2004; Becker et al. 2007). This biome originally covered approximately 150 million hectares, but it is now reduced to only 11.4–16.0% of its pristine cover (Ribeiro et al. 2009). The majority of the forest remnants cover less than 100 hectares (Ranta et al. 1998) and are isolated from each other, representing forests at early and middle succession stages (Viana et al. 1997; Metzger 2000; Metzger et al. 2009). The remaining large fragments are located in hilly terrain, hindering human occupation (Silva et al. 2007). Yet, the ranges of different altitudinal and latitudinal gradients where these remnants are found have favored a high biodiversity as compared to other biomes in Brazil (Ribeiro et al. 2009).

The Atlantic Forest is the leader biome in amphibian diversity in Brazil, comprising about 400 species (i.e., about 50% of all amphibian species within Brazil, Haddad et al. 2008). This high species richness is explained by the high diversity of habitats and microhabitats, which favor endemisms (Haddad 1998).

Data

Data on the geographic range of Atlantic Forest amphibian species were obtained from the IUCN Red List of Threatened Species database (IUCN 2012). The software ArcGIS 9.3 (ESRI 2008) was used to overlap the species ranges to the full geographic extent of the biome, which was divided into a regular equal-area grid containing cells with spatial resolution of 0.5° (i.e., about 50 km^2), providing a network of 436 cells. The total land area covered by this grid was based on the atlas of the remaining Atlantic Forest (SOS Mata Atlântica and Instituto Nacional de Pesquisas Espaciais 2008).

Presence–absence data matrices were designed for 408 amphibian species occurring in the Brazilian Atlantic Forest in such a way that a given species was considered as present when its area of occurrence included any section of the grid system.

Species were divided into eight potential indicator groups, which were based on the different taxonomic groups represented by the families Brachycephalidae, Bufonidae, Cycloramphidae, Hylidae, Hylodidae, Leiuperidae, Leptodactylidae, and Microhylidae. Amphibian families with less than 20 species were excluded from the analyses because of their small sample size. These families included the Allophrynidae, Aromobatidae, Caeciliidae, Centrolenidae, Ceratophryidae, Craugastoridae, Dendrobatidae, Eleutherodactylidae, Hemiphractidae, Pipidae, Ranidae, Plethodontidae, Rhinatrematidae, and Strabomantidae. The taxonomy adopted for the families followed the classification proposed by Blackburn and Wake (2011).

Analyses

In order to evaluate the performance of indicator groups (amphibian families), the smallest set of grid cells needed to represent all species of each indicator group was selected to solve a problem known as "minimum set coverage" (Underhill 1994). Then, the species representation was maximized with the lowest possible number of cells (Church et al. 1996; Andelman et al. 1999; Cabeza and Moilanen 2001). Thus, a set of eight cells was chosen as the lowest number of cells needed to represent all species among the potential indicator groups assessed.

After that, the 20 best sets of solutions to maximize the representation of each indicator group within eight cells were selected, solving the problem known as "maximal representation problem" (Church et al. 1996). The best spatial solutions to represent the maximum number of species in each group were encountered, with the condition that these solutions do not exceed a set of eight cells in the grid system. This was necessary to evaluate the effectiveness of the selected indicator groups (i.e., the percentage of diversity represented), so they could be compared without biases related to the number of cells contained in each group (see Lawler and White 2008).

Optimization routines based on the concept of complementarity (Vane-Wright et al. 1991; Howard et al. 1998; Cabeza and Moilanen 2001) were then used to verify the performance of each indicator group in regard to the representativeness of overall amphibian species. This concept assumes a nonoverlapping representation of natural features (Cabeza and Moilanen 2001), providing a measure of the contribution of an area to the full complement of biodiversity features assessed (Margules and Sarkar 2007), which implies that the conservation benefits that follow from a particular conservation action at a site depend on the regional context of the site and conservation actions taken elsewhere (Moilanen 2008). Optimization problems were solved by the algorithm "simulated annealing" (Kirkpatrick et al. 1983; Possingham et al. 2000), which was run 10,000 times for each group, using the software MARXAN, version 2.43 (Ball et al. 2009). This is a nonsequential algorithm that looks for optimal solutions (minimum number of cells) by comparing entire sets of areas. Initially, the algorithm selects a random network of cells and, at each iteration (in this case, 10,000 iterations), it randomly changes the system by adding, deleting, and/or switching cells (Possingham et al. 2000) and thus compares the changes resulting in a cost equation (Kelley et al. 2002). The increased acceptable cost decreases at each iteration (Andelman et al. 1999). Therefore, at each step, the new solution is compared with the former solution and the best one is maintained (Kirkpatrick et al. 1983; Possingham et al. 2000).

The average conservation percentage of target species represented a measure of the performance of each indicator group selected. For comparison, 20 solutions were tested with the smallest set of grid cells required to represent all species of each indicator group based on a random collection of species, assessing their effectiveness in relation to all studied species. These sets were built to evaluate whether the performance of the selected indicator groups was higher, similar, or lower than that expected randomly, extrapolating the representation of a null model.

In addition, land cost-effective relationships were calculated according to the number of grid cells required to represent all species from each indicator group assessed. The land cost-effective values were based on the model proposed by Bode et al. (2008), which established an economic cost of 68,733 dollars by each km^2 of Brazilian Atlantic Forest. Thus, it was possible to provide an economic cost estimation of the minimum effective land coverage of each indicator group.

The relationship between the number of species and the representativeness of each indicator group evaluated was correlated by linear regression analyses, using the software Ecosim 7.72 (Gotelli and Entsminger 2005). Subsequently, the average representation percentage of each indicator group was compared through an analysis of variance (ANOVA), using the software STATISTICA, version 8.0 (StatSoft, Inc 2007), where the effectiveness in capturing biodiversity represented by the relative number of species recorded was the response variable. The significance level of this analysis was 1% because even though the sets of solutions for each indicator group are unique, there may be a large overlay of the cells regarded as important, therefore reducing the independence of solutions (Lawler and White 2008). Diminishing the significance level to a more conservative value may be a way to reduce the effects of spatial autocorrelation when specific methods to control this phenomenon are not applicable or are simply unnecessary (Diniz-Filho et al. 2003; Kubota et al. 2007; Loyola 2009; Trindade-Filho and Loyola 2011).

Results

Spatial patterns of species richness

The geographical distribution of the eight potential indicator groups showed different spatial patterns of species richness among them (Fig. 1). There was greater species richness in the southeastern Brazil, mainly for Brachycephalidae, Cycloramphidae, Hylidae, Hylodidae, and Microhylidae. However, Hylidae, Leiuperidae, and Leptodactylidae also were well represented within the southern and northeastern regions (Fig. 1), so that Bufonidae was more distributed in the southern and southeastern Brazil (Fig. 1).

Performance and efficiency of indicator groups

The use of families as overall amphibian diversity indicators represented more species than the random choice for representative areas of amphibian diversity in the Brazilian Atlantic Forest (Fig. 2). All amphibian family groups analyzed were considered as potential indicators and showed a good spatial congruence in relation to their representativeness, because all the groups considered individually accounted for more than 50% of the species pool assessed (Fig. 2, Table 1). However, some indicator group indicators were more effective than others in regard to the representation of the taxonomic groups assessed ($F = 312.76$; $P < 0.01$). Leiuperidae was considered as the best indicator group, as it showed a good performance and cost-effective, representing 71% of amphibian species in the Brazilian Atlantic Forest (i.e., 290 species) from only eight grid cells, being based on a group with a relatively low number of species (i.e., 31 species; Fig. 2, Table 1). Species richness within the indicator groups was not correlated with the mean representativeness among them ($r = 0.40$; $P > 0.15$; see Table 1).

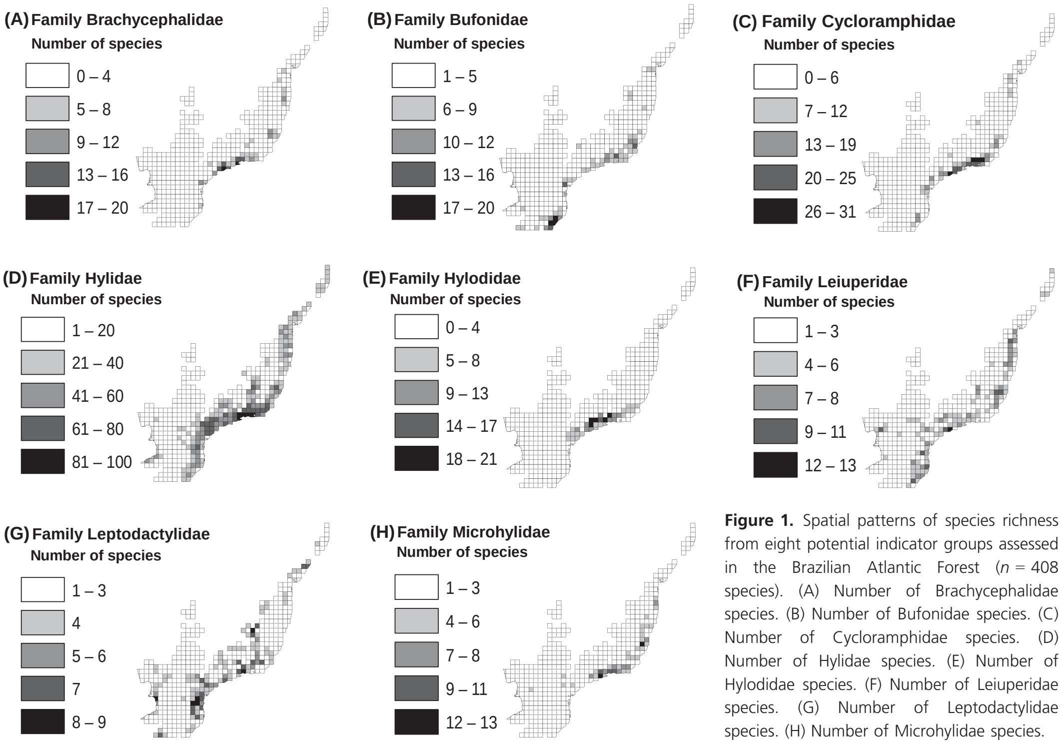

Figure 1. Spatial patterns of species richness from eight potential indicator groups assessed in the Brazilian Atlantic Forest ($n = 408$ species). (A) Number of Brachycephalidae species. (B) Number of Bufonidae species. (C) Number of Cycloramphidae species. (D) Number of Hylidae species. (E) Number of Hylodidae species. (F) Number of Leiuperidae species. (G) Number of Leptodactylidae species. (H) Number of Microhylidae species.

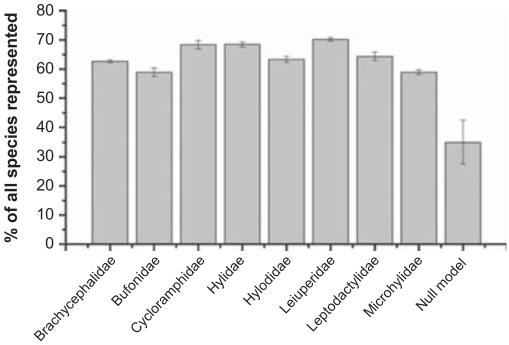

Figure 2. Efficiency of indicator groups to represent the amphibian species in the Brazilian Atlantic Forest. Gray bars represent the mean percentages among the 20 best solutions to represent all species as from the smallest set of grid cells necessary for each indicator group. Error bars denote standard deviations of the means.

Discussion

One of the biggest challenges for tropical conservation biology is to develop precise methods for conservation planning (Becker et al. 2010). Our results indicate that sites selected from potential indicator groups can include a large part of the diversity of amphibians in the Brazilian Atlantic Forest. Similar conclusions were obtained using similar methodologies applied to other taxonomic groups (e.g., Lawler et al. 2003; Loyola et al. 2007; Lawler and White 2008; Pinto et al. 2008; Larsen et al. 2009; Trindade-Filho and Loyola 2011; Trindade-Filho et al. 2012), even though their results can be considered controversial (see Lawler et al. 2003). Some authors have argued that the efficient use of indicator groups requires the selection of large extensions of land, so that the majority of the target species can be represented (see Howard et al. 1998). However, our results showed that good indicator groups can effectively represent biodiversity from a relatively small area.

A species taxonomic group can be considered a good indicator when its geographic distribution spatially coincides with the distribution of the other groups in a given region (Gaston 1996; Flather et al. 1997; Virolainen et al. 2000). In regard to amphibians, although they have been widely promoted as indicators of environmental quality, rigorous complementarity tests are still lacking (Sewell and Griffiths 2009). In large spatial scales, the objective is not to identify areas for protected areas, but to identify regions of high value for conservation that are important in the scale in question (Moore et al. 2003). Besides representing all conservation targets, the regions selected by complementarity are constituted by the lowest possible pool of cells (i.e., minimum of resources) (Lawler et al. 2003).

The performance observed for Leiuperidae as an indicator group may be associated with the diffuse geographic distribution of their species, the lower number of grid cells required to represent all of the species of each indicator group, and the low number of species which compose this group in comparison with the other groups evaluated (see Table 1). Leiuperidae species cover a wide range of different environmental conditions (Grant et al. 2006), representing a great spatial heterogeneity. These species co-occur in common habitats as much for generalist species as for specialist species, providing the occurrence of complementary groups, which favors a greater beta diversity (Loyola et al. 2007; Lawler and White 2008; Pinto et al. 2008; Larsen et al. 2009; Trindade-Filho and Loyola 2011). However, some authors argue that only species with restricted distribution exhibit congruent geographic standards compared with other species distributed in wide spatial scales (Lamoreux et al. 2006).

Our results are relatively optimistic, because they consist of a representation of species in at least one grid cell. This is a limitation, because restricting species occurrence

Table 1. Number of species, number of grid cells required to represent all species, percentage of species represented, and land cost-effective by each indicator group assessed in the Brazilian Atlantic Forest.

Indicators Groups (IG)	Number of species per IG	Number of grid cells required to represent all species from each IG	Percentage of species represented by IG (%)	Land cost-effective by IG ($)
Brachycephalidae	35	9	63	30,929,850
Bufonidae	33	9	59	30,929,850
Cycloramphidae	41	11	69	37,803,150
Hylidae	184	26	69	89,352,900
Hylodidae	33	13	65	44,676,450
Leiuperidae	31	8	71	27,493,200
Leptodactylidae	30	11	65	37,803,150
Microhylidae	21	8	59	27,493,200

to a single site is similar of the old adage of putting all your eggs on a single basket (see Ricketts et al. 2005). Conservation outcomes were most sensitive to uncertainty in the land cost data, because the use of species extents of occurrence overestimates their real geographic ranges (Rondinini et al. 2006), which in turn increase the effectiveness of indicator groups whose distribution was based on such maps. One possible solution would be the utilization of species distribution modeling methods currently available (Araújo and New 2007). However, these models are known have other sources of uncertainties (Loiselle et al. 2003; Wilson et al. 2005; Diniz-Filho et al. 2009a,b, 2010). Nevertheless, as we are not proposing the creation of protected areas, but suggesting that the use of indicator groups to operate as a shortcut for mapping biodiversity, the use of species extents of occurrence may still be considered a possible solution to investigate the efficacy of indicator groups (e.g., Lawler et al. 2003; Loyola et al. 2007; Rodrigues and Brooks 2007; Lawler and White 2008; Pinto et al. 2008; Larsen et al. 2009; Grantham et al. 2010; Trindade-Filho and Loyola 2011; Trindade-Filho et al. 2012).

For this purpose, future studies on species inventories could be concentrated on the groups scientifically proven as indicators of biodiversity. This suggests that taxonomists tend to concentrate their efforts in the localities that guarantee success in the collection of as many species as possible (Sastre and Lobo 2009). Optimal solutions of complementarity based on different biodiversity analyses have been successful in conservation planning at the global level (Csuti et al. 1997), including for amphibians (Diniz-Filho et al. 2006). The use of taxonomic subgroups as potential indicators of biodiversity has also been a common practice in conservation studies (e.g., Simberloff 1998; Caro and O'Doherty 1999; Andelman and Fagan 2000). In this context, biodiversity surrogate groups and indicator groups have been utilized in different ways to guide conservation strategies (Caro and O'Doherty 1999). Yet, there is an ample spectrum of circumstances that define the relative complexity of conservation planning based on the use of indicator groups (Stoms et al. 2005). Indicator groups should follow predictors of complementarity performance, such as variability between extents of occurrence, occupation of different ecoregions, variability of records of geographic distribution, and average body size in relation to the species pool considered in the analyses (Manne and Williams 2003).

Nevertheless, when we try to choose a specific target to protect other biodiversity aspects than species richness, we create a challenge to the conservation biologists. Here, we are proposing that the use of amphibian families as indicator groups of biodiversity can be a straightforward strategy to maximize the conservation value of small spatial scales. Usually, we must allocate conservation efforts to areas with higher diversity than expected by chance. However, this depends on the purpose of the conservation plan as well on the nature of the ecosystem we are interested in protect. In practice, our results carry a great deal of interest, not only because they are novel, but also because they reveal that a taxonomically defined group (i.e., Leiuperidae) can be used as a conservation shortcut of amphibian biodiversity in the Brazilian Atlantic Forest.

Even though the indicator groups presented in this study had a good performance in representing amphibian diversity in the Brazilian Atlantic Forest, it is important to note that our analyses evaluated efficacy based on a single measurement of diversity. Therefore, we did not incorporate other important aspects, such as population viability (see Carroll et al. 2003), functional diversity, and phylogenetic relationships (see Carvalho et al. 2010; Devictor et al. 2010; Trindade-Filho et al. 2012). However, this was due to the limited knowledge about the majority of the species of our data group. A recent analysis showed that the data-deficient species also seems to reflect a spatial knowledge deficiency (Brito 2010). This lack of knowledge underscores the urgent need for the development of strategies toward systematic conservation planning, which may contribute directly to the stability of the ecosystems and long-term evolutionary processes (Trindade-Filho et al. 2012). In this sense, this study helps in understanding how the spatial patterns of amphibians can be informative for the conservation planning at regional scales.

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Conflict of Interest

None declared.

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Chapter 10

Cost-effective conservation of amphibian ecology and evolution

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Cost-effective conservation of amphibian ecology and evolution

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Conservación rentable de la ecología y evolución de los anfibios. La pérdida de hábitat es la amenaza más importante para la supervivencia de las especies, y la selección eficiente de áreas prioritarias es fundamental para una buena planificación sistemática para la conservación de biodiversidad. Utilizando anfibios como objeto de conservación, se ha propuesto una estrategia innovadora para demonstrar que los modelos de priorización pueden ir más allá de la capacidad de protección de especies amenazadas. Además de incorporar las diversidad funcional, filogenética y taxonómica, el nuevo protocolo considera el coste ecónomico de la tierra. Fueron seleccionados nuevos sitios clave para la conservación de anfibios dentro del Bosque Atlántico de Brasil, revelando una congruencia de patrones ecológicos y evolutivos. El estudio sugiere un esquema de pago por servicios ecosistémicos en terrenos privados desprotegidos, estableciendo una compensación ambiental por los procesos ecológicos y evolutivos que fornecen los anfibios (en concreto, 13.273 dólares por kilómetro cuadrado). En comparación con las actividades agrarias brasileñas, este valor corresponde al 24,13 % del lucro medio de una tierra agrícola local. Los resultados obtenidos destacan la importancia de mantener los remanentes de la cubierta forestal en el Bosque Atlántico y proporcionan una representación máxima de la biodiversidad con el menor costo económico posible. Este nuevo enfoque de economía ambiental también puede aplicarse a otras regiones ricas en biodiversidad donde habitan especies en peligro de extinción.

– Spanish Abstract (Resumen)

CONSERVATION ECOLOGY

Cost-effective conservation of amphibian ecology and evolution

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Habitat loss is the most important threat to species survival, and the efficient selection of priority areas is fundamental for good systematic conservation planning. Using amphibians as a conservation target, we designed an innovative assessment strategy, showing that prioritization models focused on functional, phylogenetic, and taxonomic diversity can include cost-effectiveness–based assessments of land values. We report new key conservation sites within the Brazilian Atlantic Forest hot spot, revealing a congruence of ecological and evolutionary patterns. We suggest payment for ecosystem services through environmental set-asides on private land, establishing potential trade-offs for ecological and evolutionary processes. Our findings introduce additional effective area-based conservation parameters that set new priorities for biodiversity assessment in the Atlantic Forest, validating the usefulness of a novel approach to cost-effectiveness–based assessments of conservation value for other species-rich regions.

INTRODUCTION

Ecosystem functioning and evolutionary processes are usually linked, carrying a series of short-term implications for ecological and human well-being (*1*). The consequences of human activities go beyond species loss, with various studies also reporting losses of functional traits and evolutionary history in various human-influenced landscapes (*2*). These losses are increasing demands for effective strategies on biodiversity conservation (*3*), which have been also subject to the incorporation of economic costs with the objective of providing more feasible conservation strategies on the ground (*4*). Given that habitat loss is the most important threat to species survival, the protected sites chosen by decision makers determine what species and how many of these will be able to survive in nature (*5*). The effectiveness of these selected sites in achieving conservation goals depends on how well the ecological diversity is represented in a given area (*6*). Several studies have focused on spatial prioritization to represent taxonomic diversity (TD), not highlighting the importance of capturing other biodiversity components, such as functional diversity (FD) and phylogenetic diversity (PD) (*7*). Moreover, to date, their conservation strategies have been blind to the functions these other components perform in a cost-effective conservation policy.

FD is a biodiversity dimension that represents the extent of functional differences among species based on the distinction of their morphological, physiological, and ecological traits (*8*). PD adds value to theoretical and applied ecology studies by distinguishing species according to their evolutionary histories (*9*), reflecting the time and mode of divergence across the tree of life (*10*). In addition, FD and PD can better predict ecosystem function and stability than TD (*11*, *12*). However, using TD, FD, and PD in a simultaneous approach can help predict differential effects of competition and environmental filtering on the community assembly (*13*). Nonetheless, consistency in the relationships between TD, FD, and PD can provide insights into the extent to which community assembly is driven by deterministic versus stochastic processes (*14*).

A central question in community ecology and conservation biology is related to determining how biodiversity patterns can influence ecosystem functioning (*15*–*17*). The key strategy to address this issue is to assess the relationships between functional and phylogenetic biodiversity components of the ecosystem (*11*, *18*). Understanding the associations between ecological similarity and phylogenetic relatedness among species helps in the formulation of a hypothesis about the impact of evolutionary changes on functional ecology (*19*). Focusing on both functional and phylogenetic traits of a community can improve our understanding of the consequences of biodiversity loss (*20*). However, to describe how environmental actions can protect multiple dimensions of biodiversity, comparative methods on the consequences of species extinction in relation to ecological and evolutionary traits still need to be applied (*21*).

Approaches to setting conservation priorities recommend ranking ecosystems on several criteria, including level of endangerment and metrics of species value such as evolutionary distinctiveness, ecological importance, and social significance (*21*). On the other hand, these approaches have not yet been implemented in practice and therefore remain as theoretical studies, not applied effectively in ecological landscape planning (*22*). Although the role of protected areas (PAs) in conserving biological communities is essential for natural systems (*23*), conservation planning needs to include the ecological functions performed by species that occur not only inside PAs but also throughout the biome (*24*). In this context, environmental set-asides on private land have been shown to be a promising strategy for conservation of species and ecological functions across farmlands (*25*). Nevertheless, set-asides of private land for conservation generally come with economic costs to the landowners (*26*). Therefore, environmental strategies that incorporate payment for ecosystem services (PES) can provide an efficient tool for increasing landowner participation in conservation programs (*25*). This strategy's feasibility is reflected in the ever-increasing number of PES projects around the world (*27*, *28*). Despite this trend, most PES projects are relatively local initiatives that may not adequately represent the full range of conservation needs and economic issues observed throughout biodiversity hot spots (*28*). On the other hand, many environmental organizations are developing systematic planning tools to help identify opportunities that offer the greatest return on investment in biodiversity protection (*29*). In a conservation context, this investment can be indicated by cost-effectiveness–based estimates of land values, that is, the trade-off between biodiversity gains and economic costs of paying landowners to participate in set-aside programs (*26*).

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A conservation dilemma arises from the question of how much cost and which biodiversity components should be chosen in large-scale conservation programs. This context suggests a need for development of conservation plans that optimally balance economic costs and ecological constraints (*30*). However, effective conservation plans should also take into account the maintenance of functional and evolutionary processes as a justification for investments, mainly in biodiversity hot spots (*31*–*33*). Here, we explore how FD, PD, and TD are distributed in the most endangered biodiversity hot spot on Earth—the Brazilian Atlantic Forest (*34*)—focusing on the most threatened vertebrate group worldwide, amphibians (*35*). Given that spatial patterns of diversity and distribution of tropical amphibians are a consequence of their ecological and phylogenetic relations (*36*), we conducted a spatial prioritization of conservation management for the biodiversity components FD, PD, and TD, concerning threatened species (TS), PAs, and their respective land cost-effective values. We centered our land cost-effective estimations on the average PES values of $13,273 for each square kilometer given annually to the private forest landowners in the Brazilian Atlantic Forest (*26*, *28*). We aimed to incorporate the functions that amphibians perform with cost-effective considerations, exploring adequate conservation models that can allow us to preserve endangered species at a low cost. Therefore, we report for the first time that the selection of priority sites based on PD and FD can be extended to include not only high species richness and threatened taxonomic groups but also land cost-effective outcomes.

RESULTS

Our results revealed a high FD and PD in the eastern Atlantic Forest, with the highest rates in the east central region rising to the northeast (Fig. 1, A and B). We found high correlations between TD with FD and PD ($r^2 = 0.86$, $P < 0.001$ and $r^2 = 0.82$, $P < 0.001$, respectively) (fig. S1, A and B). However, we observed that the values of FD and PD significantly differ from the random expectation of the null models ($P < 0.001$). Moreover, using paired *t* tests to validate these differences, we found highly significant differences between the observed distributions of FD and PD and the null models ($P < 10^{-16}$, *t* test). When we compared FD, PD, and TD with TS, we found low but significant correlations ($r^2 = 0.31$, $P < 0.001$; $r^2 = 0.26$, $P < 0.001$; and $r^2 = 0.33$, $P < 0.001$, respectively) (fig. S1, D to F). Mapping these relationships, we revealed important spatial mismatches and congruencies among these biodiversity components (Fig. 1, A to D). Our spatial analysis revealed a wide disparity among the biodiversity these various measures of biodiversity: We observed a

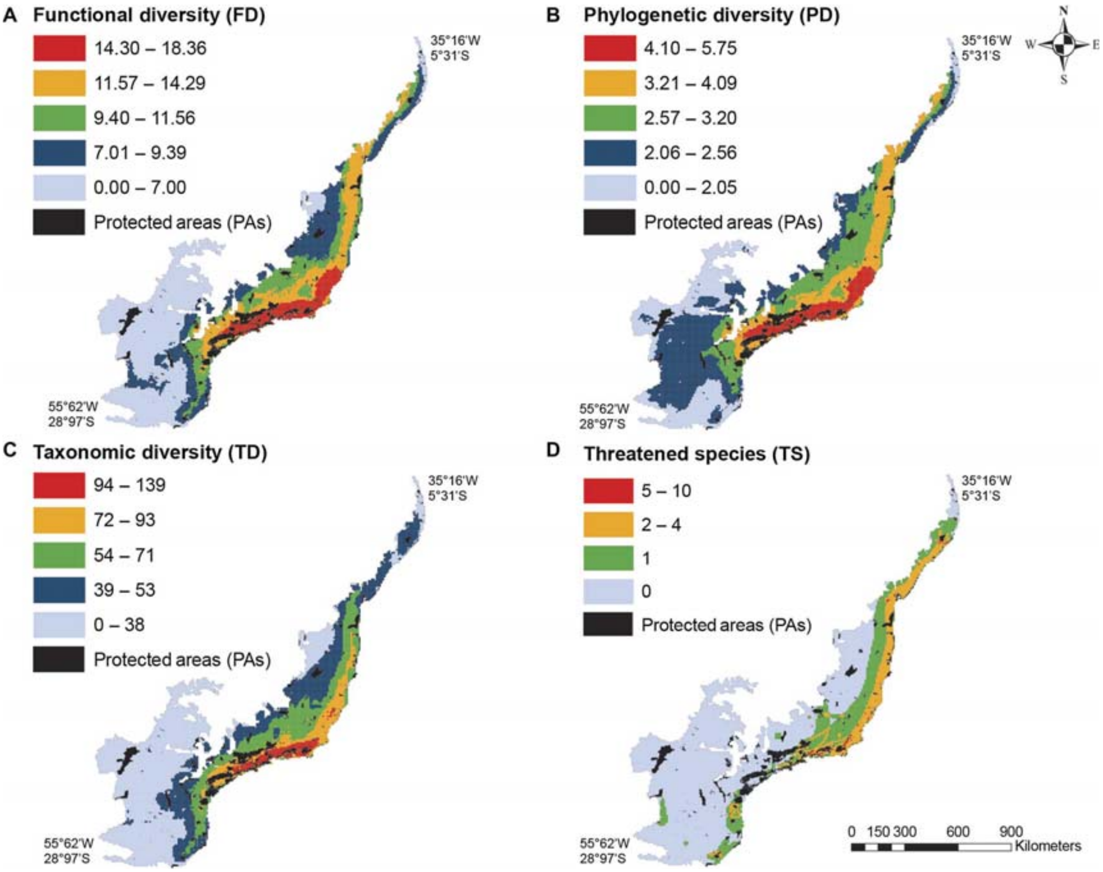

Fig. 1. Spatial distribution of FD (Petchey and Gaston's FD), PD (Faith's PD), TD, and TS of amphibians in the Brazilian Atlantic Forest.

proportional difference of 5% between FD and PD, 14% between FD and TD, 12% between PD and TD, 44% between FD and TS, 42% between PD and TS, and 29% between TD and TS (fig. S2).

Through mapping and calculating the spatial data of the PAs, we found that a 9309.15-km^2 protected area in the Brazilian Atlantic Forest corresponded to only 9% of the region's entire area, comprising 2316.74 km^2 of strict protection areas and 6992.41 km^2 of sustainable use areas. This PA network comprises ~10% of FD, PD, and TD and almost 30% of TS, according to their spatial distributions across the Brazilian Atlantic Forest (Table 1). In total, we found 38 TS, corresponding to 17 critically endangered, 10 endangered, and 11 vulnerable species, with ~70% of their total geographical range distributed outside the PAs (Table 1). Incorporating cost-effectiveness assessments of land values into evaluation of PAs and non-PAs, we showed the amount of investment needed for proportional values of FD, PD, TD, and TS of amphibians in the Brazilian Atlantic Forest (Table 1). Permutational multivariate analysis of variance (PERMANOVA) results reveal that cost-effectiveness assessment of land values can be considered as a strong predictor for those biodiversity attributes assessed as conservation targets (table S1).

Our three prioritization models illustrate several scenarios for integrative assessments of FD, PD, TD, and TS attributes (Fig. 2). However, model 1 best represents the highest-priority regions for conservation (Table 2). Alternatively, models 2 and 3 show larger land areas, which also require higher investment. Although our results are area-dependent (square kilometers), we found a mismatch between percentage forest cover and overall land area in each model (Table 2). We recommend model 1 as the best cost-effective strategy, which has a greater capability to safeguard larger forest areas in addition to being the cheapest alternative (figs. S3 to S5). Moreover, model 1 has the lowest presence of PAs, which reinforces the urgent need to develop conservation efforts in these sites (Table 2). We also note that the priority sites indicated by this model corroborate the two larger climatic refuges for Neotropical species during the late Pleistocene [see the study of Carnaval *et al.* (*37*) for details], located in the central corridor of the Atlantic Forest and the Serra do Mar coastal forests.

DISCUSSION

Our findings provide different optimization scenarios for the conservation of amphibian diversity aspects. FD and PD indices have been proposed as effective techniques for capturing potential niche complementarity in a community (*11*, *38*). Some studies have highlighted the potential role of PD as a proxy for FD, yet this association is premised on the assumption that phylogenetic diversity generates ecological trait diversification, which in turn can result in greater niche complementarity (*20*). Despite the increasing evidence for positive correlations between taxonomic, functional, and phylogenetic attributes and ecosystem stability (*39*), the mismatch among TD, FD, and PD (*7*) is creating a conservation impasse, which demands a practical approach to assessing relative conservation values of these components of biodiversity. From a conservation viewpoint, FD and PD can be considered as two key attributes of diversity for safeguarding ecosystem goods and services (*40*), as well as for representing evolutionary processes and features of conservation interest (*41*). Therefore, measuring each of these biodiversity components in a complementary way is crucial for understanding the composition and dynamics of natural communities (*10*).

Mason *et al.* (*42*) showed that the FD component may reveal changes in community assembly processes along an environmental gradient, suggesting that this index may be a strong predictor of complex processes structuring communities. A multifaceted framework of the FD metrics behind these assembly processes facilitates the development of predictive models and more adequate tools for understanding how community structure is related to ecosystem functioning (*43*). In this context, the FD index can provide a potentially efficient power analysis to differentiate assembly rules for different degrees of species richness (*43*). On the other hand, null model approaches provide a robust means to test whether species with similar functional traits are more or less probable to occur together than expected at random (*44*). Therefore, use of the FD index associated with null models has shown to be the approach that best relates to community functioning and ecosystem processes (*8*, *43*).

Considering the role of amphibian species in community functioning, the ecological contributions of these species can affect aquatic and terrestrial ecosystems as a whole, as well as the flux between these ecosystems (*45*). Amphibians have varied and significant roles in ecosystems, from soil bioturbation and nutrient cycling to pest control and ecosystem engineering (*46*). Some studies suggest that the loss of amphibians from stream ecosystems can alter primary production, algal community structure, faunal food chains (from aquatic insects up to riparian predators), and reduce energy transfers among diverse ecosystems through their role in nutrient cycling (*45*–*47*). Amphibians have frequently been cited as potential biological indicators of environmental change due to their permeable skin, high rates of contaminant bioaccumulation, climate-sensitive breeding cycles, and the fact that many species are dependent on both terrestrial and aquatic habitats during their life cycle (*48*–*51*). In addition, some amphibian taxa from small areas within the Atlantic Forest have been identified as potential indicators of general biodiversity (*52*).

Although a particular individual diversity component could be used as a surrogate for other biological attributes, biodiversity assessment should benefit from integrative approaches connecting evolutionary and functional ecology (*40*). Using integrative conservation strategies, we showed a congruence of ecological and evolutionary processes in the proposed models, yet they also revealed mismatches between land area and priority rank. Because of the large area considered for conservation, economic costs become an obstacle; but if insufficient land area is set aside, biological gains are weak (*26*). Our results thus demonstrate that local conservation policies for the Brazilian Atlantic Forest PAs do not guarantee the survival of most amphibian species in this region (~90% of TD). Moreover, the current PA network effectively protects only less

Table 1. Land cost-effectiveness and percent land covered by PAs and non-PAs, according to the spatial distribution of the FD (Petchey and Gaston's FD), PD (Faith's PD), TD, and TS of amphibians in the Brazilian Atlantic Forest.

	FD	PD	TD	TS
PAs				
Land cost-effectiveness (million dollars)	159.49	152.71	127.86	36.36
Land covered (%)	11.60	11.10	9.38	29.37
Non-PAs				
Land cost-effectiveness (million dollars)	1215.45	1222.32	1245.97	87.07
Land covered (%)	88.40	88.90	90.62	70.63

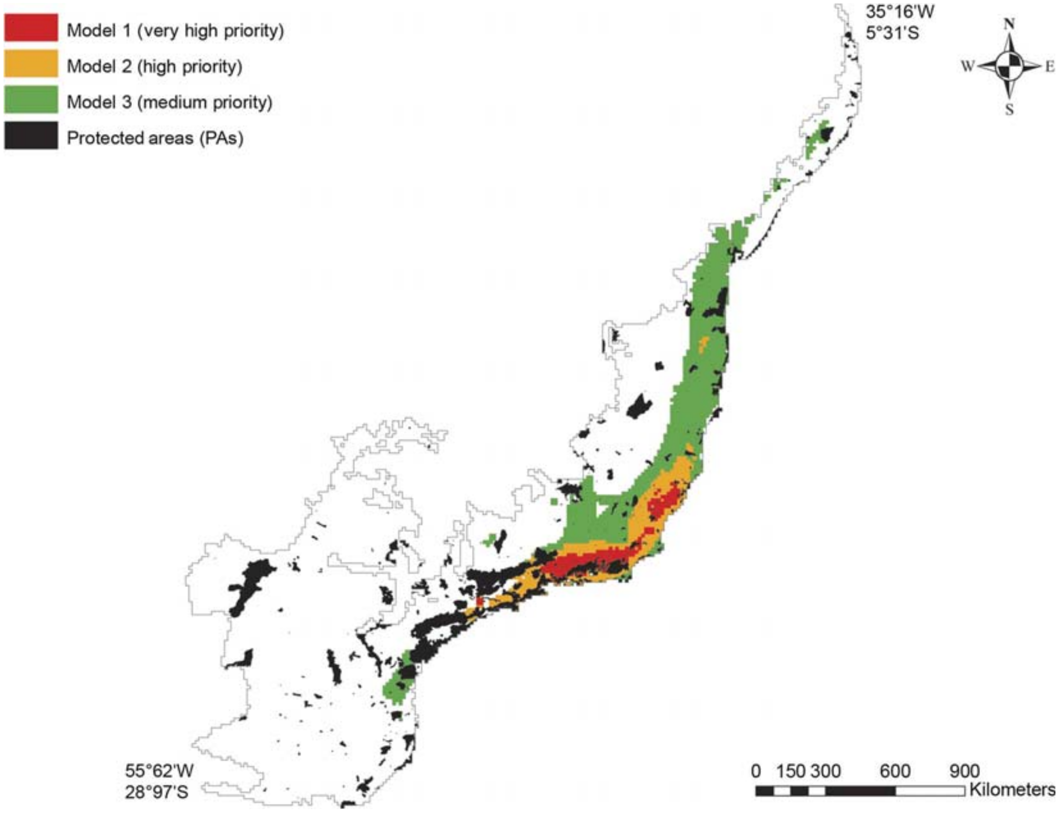

Fig. 2. Spatial distribution of the PAs and the three prioritization models proposed to amphibian conservation in the Brazilian Atlantic Forest.

Table 2. Area, excluded PAs, forest cover, and land cost-effectiveness by three priority scenarios to amphibian conservation in the Brazilian Atlantic Forest. Model 1, very high priority; model 2, high priority; model 3, medium priority.

Priority scenarios	Area (km^2)	Excluded PAs (km^2)	Forest cover (%)	Land cost-effectiveness/year (million dollars)
Model 1	1,995.28	293.62	24.25	26.48
Model 2	4,555.12	934.02	15.30	60.46
Model 3	13,213.50	1406.28	11.86	175.38

than 10% of the total Atlantic Forest remnants (*53*). Although this reduced PA area seems inadquate, our results revealed that 28% of this network does nevertheless safeguard important eco-evolutionary processes, represented by those areas showing a ≥50% FD, PD, and TD value of the total observed.

The selection of PAs is normally aimed to preserve species of different taxonomic groups, communities of high biological relevance, or combinations of different abiotic conditions favorable to local ecosystems, assuming that these sites will protect a wider range of biodiversity (*54*). However, many case studies reveal the inadequacy of the PA network in representing species diversity (*55*). In north-eastern Brazil, Campos *et al.* (*56*) showed that the size of the PAs along the geographical range of threatened amphibian species does not necessarily safeguard their persistence, a finding also observed in this study. Moreover, it is predicted that the number of amphibian species of the Brazilian Atlantic Forest will decline within the PA network due to changing climate conditions (*57*). This network faces an additional risk because of its location within the economic center of Brazil (*53*), with a high human population density (~70% of the total Brazilian population) (*58*) and the presence of mining and logging industries in the region (*57*). To make matters worse, a recent mining dam burst on 5 November 2015 destroyed one of the main river basins of the central corridor of Atlantic Forest, leading to the worst environmental disaster in the history of Brazil (*59*), which further accentuates the urgency for implementation of conservation strategies in this region. The federal and state Brazilian governments have sued the mine's owner companies with $5 billion in damages (*59*), which have been said to be designated for funding of conservation plans aimed to restore this highly degraded ecosystem.

We centered our prioritization models on a return-on-investment framework to simulate how limited conservation funds could be spent on biodiversity protection, which were not based on agriculture land values, in accordance with the suggestions proposed by Sutton *et al.* (*29*). Our study demonstrates how the cost-effectiveness–based methods for assessing land values developed by our models could work as a functional PES, which, in comparison with agrarian activities, corresponds to 24.13% of the median yearly gross profit per square kilometer of agricultural land distributed in the Atlantic Forest domain (*26*). However, considering that only 12.30% of the total area covered by our models is represented by forest remnants, we recommend active reforestation practices in the nonforest areas (degraded livestock lands and abandoned agricultural lands). These practices would require an additional cost of up to $500,000/km^2 for the first 3 years of restoration in the most degraded sites [see the study of Melo *et al.* (*60*) and Brancalion *et al.* (*61*) for details], corresponding to 0.02% of the Brazilian gross domestic product (*26*). On the other hand, most areas would follow natural regeneration simply by stopping the drivers of disturbance (*60*), taking into account that at least 20% of the area considered for restoration needs some active reforestation practice (*61*).

Considered individually, no single forest remnant reaches the minimum land values proposed by the Aichi Biodiversity Target 11, which concluded that the terrestrial PAs should be expanded to at least 17% by 2020 (*62*). In this context, models 1, 2, and 3 rise to about 5, 7, and 16%, respectively, from the current Brazilian Atlantic Forest PAs. We draw attention to the critical need for amphibian conservation efforts in Atlantic Forest, and to the critical fact that ~90% of FD, PD, and TD remain outside the PAs. Conservation strategies such as PES are essential to maintain the ecological and evolutionary process. Although the strength of this study is its innovative approach to incorporating biodiversity components into considerations of cost-effectiveness in conservation, our results rest heavily on good research in ecosystem service provisioning. According to the environmental message reported by Naeem *et al.* (*17*), we also highlight the precautionary principle, in which "biodiversity conservation ensures ecosystem functions that in turn ensure ecosystem services benefiting humanity." Although we know that some ecosystem services cannot be subject to pricing, they should be considered on the basis of their biological value. Stakeholders and decision makers are key actors whose contribution is essential to putting these reports into practice. This situation demands political will and improved environmental services based on cost-effective designations of the highest-priority conservation areas, to reduce extinction risk and avoid species loss. Our research highlights the importance of maintaining the forest cover remnants in the Atlantic Forest, to provide a maximum representation of biodiversity components with the lowest economic cost. This innovative approach is not only amphibian-specific but can also be used in conservation plans for other taxonomic groups. This work has advanced knowledge of the analytical methods that can be used to plan effective environmental actions to protect multiple biodiversity components with limited resources.

MATERIALS AND METHODS

Study area

Considered as the most threatened biodiversity hot spots on Earth (*34*), the Atlantic Forest had an original of area around 1,500,000 km^2, of which only about 12.9% (~194,500 km^2) still remains in Brazil, Paraguay, and Argentina (*53*), corresponding to about 100,000 km^2 of Brazilian forest remnants (*63*). The large fragments are located in hilly terrain, which hinder human occupation (*64*). Moreover, the ranges of different altitudinal and latitudinal gradients where these remnants were found have favored high biodiversity and endemic species compared to other biomes in Brazil (*53*).

Although having a high rate of habitat loss (*65*), which is one of the main risk factors for amphibian extinction (*35*), the Atlantic Forest is the leader biome in amphibian diversity in Brazil, with 543 described species, comprising ~90% endemics and corresponding to more than 50% of all amphibian species of the entire country (*66*). However, despite the legal restrictions on deforestation in the Brazilian Atlantic Forest, vegetation is still extracted illegally, representing a mean rate of forest loss of around 0.15%/year (*67*). Here, we used the term Brazilian Atlantic Forest with regard to the vegetation remnant map reported by the SOS Mata Atlântica/Instituto Nacional de Pesquisas Espaciais in 2015 (*67*).

Data acquisition

We obtained spatial data on amphibian species with three procedural approaches. First, we built a data set with all the species distributed in the Atlantic Forest according to Haddad *et al.* (*66*); second, we included maps of geographical ranges for each species from the International Union for Conservation of Nature (IUCN) Red List of Threatened Species database (*68*); and third, we conducted complementary fieldwork comprising the major Atlantic Forest remnants of Brazil, to supplement the data set with additional data on distribution and observed functional traits (body size, reproductive mode, habitat, activity, poison patterns, habit, and calling site).

We led the survey in seven Brazilian PAs located in the central corridor of the Atlantic Forest and the Serra do Mar coastal forests, stretching from the south to the northeast of the country (fig. S6). We sampled each area for 10 days between January and March 2015 (wet season), which are the months of highest activity of amphibians in the Atlantic Forest (*69*). In all localities, we conducted the survey using acoustic and visual nocturnal/diurnal assessments (*70*, *71*), through an active search around water bodies, streams, and along 2000 m of forest transects for each assessed PA.

Next, we used ArcGIS 10.1 software (*72*) to build presence/absence matrices from the species distribution data by superimposing a grid system with cells of 0.1° latitude/longitude, creating a network with 10,359 grid cells for the Brazilian Atlantic Forest. We also used spatial data on the Atlantic Forest PAs through the Brazil's Ministry of Environment database (*73*), including their categories (IUCN categories I to IV) and land coverage.

Data analyses

We characterized 453 amphibian species through eight functional traits from 56 categories that determine different dimensions of the amphibians' ecological niches regarding morphology, life history, and behavior. We used the trait categories reported by Haddad *et al.* (*66*), with some additional complementary data obtained in our fieldwork (see data file S1). Data file S1 describes the functional traits and their references for 453 amphibian species sampled in the Brazilian Atlantic Forest:

(i) body size (millimeter), (ii) members (apodal and tetrapod), (iii) activity (nocturnal, diurnal, and both), (iv) toxicity (toxic, nontoxic, unpalatable, or bad odor), (v) habitat (forested area, open area, and both), (vi) habit (arboreal, phytotelmate, terrestrial, cryptozoic, fossorial, rheophilic, semiaquatic, and aquatic), (vii) calling site (bamboo grove, swamp or lake, bromeliad, forest floor, tree canopy, caves or burrows, rock wall, backwater river, stream, river, shrubs, grasslands, and not sings), and (viii) reproductive mode [1 to 39 modes; see the study of Haddad and Prado (*74*)]. These functional traits primarily contribute to ecosystem-supporting services through direct and indirect changes on ecosystem functions and processes (*46*). These functions can be structural (habitat and habit) and ecological (body size, members, activity, poisonous, calling site, and reproductive mode). For further details, see the Supplementary Materials (table S2), where we show the specific functions and the ecosystem-supporting services of each one of the functional traits assessed (*46*, *66*, *74*–*77*).

To calculate the FD, we followed the protocol proposed by Petchey and Gaston (*8*): (i) construction of a species-trait matrix, (ii) conversion of species-trait matrix into a distance matrix, (iii) clustering distance matrix into a UPGMA (Unweighted Pair-Group Method with Arithmetic Average) dendrogram, and (iv) calculating FD by summing dendrogram branch lengths of species community. According Petchey and Gaston (*8*), FD is the functional metric that best relates to the functioning of communities. To create the distance matrices, we used the method proposed by Pavoine *et al.* (*78*), through the Gower distance. We constructed the dendrograms using a hierarchical clustering, where only the species found in both the functional trait data set and the amphibian occurrence database were considered. To verify whether FD was influenced by species richness, we used independent swap null models (*79*), according to the protocol proposed by Swenson (*80*). The values provided by these models are more sensitive in preserving both site diversity and species frequency of occurrence while randomizing the pairs of species/sites, which ensure that patterns of trait assembly do not simply reflect differential occurrence of particular species (*80*, *81*). We tested whether the observed FD was higher, equal, or lower than that expected by chance for each grid cell, assuming a random distribution in which every species could occupy any grid cell in the biome. For this, we computed 1000 random replicates of the remaining FD, allowing us to obtain a *P* value of FD as compared to the distribution of the random replicates. Although observed and null FD metrics indicate very similar responses (*43*, *80*), the values generated by these metrics do not necessarily represent redundant information. Observed FD is highly correlated with species richness, whereas its null model is totally independent of the species richness of an assemblage (*80*), which provides expected values at different species richness levels (*43*). In addition, we compared relative changes of observed and null FD distributions using paired *t* test. Given their different ability to discriminate community assembly rules, where the predictive accuracy of null FD is clearly better than the observed FD (*43*, *80*), we used the null model approach to detecting patterns in the overlap among species in functional character space. Therefore, we used the term FD with regard to the null FD distributions in all further comparisons. We performed all analyses using the packages "ade4," "picante," "FD," and "vegan" through the R software (*82*).

For PD, we used the Faith's PD index (*83*), comprising the sum of the lengths of the branches from the phylogenetic tree of all species assessed. We based the phylogenetic distance on 207 species nucleotide sequences obtained from GenBank (data file S2) [see the study of Benson *et al.* (*84*)], provided by the National Center for Biotechnology Information. Following the protocol proposed by Pyron and Wiens (*85*) in an extant amphibian phylogeny, we used 12 genes to produce a novel phylogeny estimate for the Atlantic Forest amphibians (11,906 base pairs for each species), through three mitochondrial (Cyt-b, 12s, and 16s) and 9 nuclear (CXCR4, H3A, NCX1, POMC, RAG1, ROHD, SIA, SLC8A3, and TYR) genes. For length-variable regions, we performed multiple pairwise comparisons using the online version of MAFFT 6.8 with the G-INS-i algorithm (*86*). Next, we put together alignments of all genes in the same alignment, using the software Sequence Matrix 1.7.7 (*87*) to concatenate the supermatrix previously produced.

We reconstructed phylogenetic relationships with Bayesian analyses using BEAST 1.8 (*88*). We performed the phylogenetic analysis based on the combined data matrix through the Hasegawa, Kishino, and Yano (HKY) model of sequence evolution for one partition for all genes, using a Yule speciation process as the tree prior under an uncorrelated relaxed clock. We ran the Yule process for 100 million generations, ensuring that the number of generations convergence was sufficiently assessed with Tracer 1.6 (*88*), removing a conservative 10% burn-in fraction for the final tree. We combined these results with the use of LogCombiner 1.8.1 and TreeAnnotator 1.8.1 (*88*). We considered the nodes strongly supported if they received a posterior probability of ≥0.95. To edit the new phylogenetic tree, we used R software (*82*), from the package "ape" (*89*), using the Mesquite software 3.04 (*90*) as an additional viewing tool. As provided on the functional metrics, we also built null models to PD according to the same protocol used to obtain the null FD expectations (*80*). Therefore, we computed 1000 random replicates of remaining PD, obtaining a *P* value of PD as compared to the distribution of the random replicates. We also compared relative changes of observed and null PD distributions using paired *t* test. As proposed in the FD analyses and considering the predictive accuracy of the null PD compared with the observed PD, we used the term PD with regard to the null PD distributions in all further comparisons. We performed the null model analyses using the packages ade4, picante, and vegan through the R software (*82*).

In addition, we calculated the TD and the number of TS present in each grid cell, correlating with the values obtained by the FD and PD indices through simple linear regression models. We also plotted the mismatches among the relative values of these biodiversity components in a spatial representation to show where the greatest disparity might be would be, which is also of interest. We classified TS according to the National Red List categories, using the official list of TS of the Brazilian fauna (*91*). We calculated the cost-effectiveness values according to the area required to represent each biodiversity component assessed (FD, PD, TD, and TS). Following Banks-Leite *et al.* (*26*), we based our cost-effectiveness analyses on the average value of PES across the Brazilian Atlantic Forest remnants, which corresponds to $13,273 for each square kilometer given annually to the private forest landowners (*28*). In addition, to provide a comparative estimate of cost-effectiveness–based land values of PAs and non-PAs, we performed a gap analysis (*92*), measuring the amount of FD, PD, TD, and TS covered both by PAs and non-PAs. Thus, to assess the response of cost-effectiveness against the predicted variables FD, PD, TD, and TS, we used PERMANOVA, with 1000 permutations based on a Euclidean distance matrix, through the "adonis" function in the vegan R package (*93*). Finally, we provide three prioritization models based on different levels of complementary scenarios calculated as

$$\text{Model 1 (90\%)} = \left\{\text{FD} \geq \left[\left(0.9\left(\left(\sum\nolimits_{\text{i}=0}^{\text{n}}\text{FD}\right)/\text{N}\right)\right)/0.5\right] + \text{PD} \geq\right.$$

$$\left[\left(0.9\left(\left(\sum\nolimits_{i=0}^{n}\text{PD}\right)/N\right)\right)/0.5\right] + \text{TD} \geq$$

$$\left[\left(0.9\left(\left(\sum_{i=0}^{n}\mathrm{TD}\right)/N\right)\right)/0.5\right] + \mathrm{TS} \geq 1\Big\}\text{-PAs}$$

$$\text{Model 2 (70\%)} = \Big\{\mathrm{FD} \geq \left[\left(0.7\left(\left(\sum_{i=0}^{n}\mathrm{FD}\right)/\mathrm{N}\right)\right)/0.5\right] + \mathrm{PD} \geq \left[\left(0.7\left(\left(\sum_{i=0}^{n}\mathrm{PD}\right)/N\right)\right)/0.5\right] + \mathrm{TD} \geq \left[\left(0.7\left(\left(\sum_{i=0}^{n}\mathrm{TD}\right)/N\right)\right)/0.5\right] + \mathrm{TS} \geq 1\Big\}\text{-PAs}$$

$$\text{Model 3 (50\%)} = \Big\{\mathrm{FD} \geq \left[\left(\sum_{i=0}^{n}\mathrm{FD}\right)/\mathrm{N}\right] + \mathrm{PD} \geq \left[\left(\sum_{i=0}^{n}\mathrm{PD}\right)/N\right] + \mathrm{TD} \geq \left[\left(\sum_{i=0}^{n}\mathrm{TD}\right)/N\right] + \mathrm{TS} \geq 1\Big\}\text{-PAs}$$

where model 1 refers to very high priority, and values of FD, PD, and TD are ≥90% of the total observed (N); model 2 refers to high priority, where values of FD, PD, and TD are ≥70% of the total observed (N); and model 3 refers to a medium priority, where values of FD, PD, and TD are ≥50% of the total observed (N). We did not consider areas with FD, PD, and TD values lower than the average conservation targets assessed (FD, PD, and TD, <50% of the total observed). The main reason for this approach was to establish prioritization models that indicate areas from medium to very high priority, leaving out areas with low priority. In these three models, we considered only areas containing at least one TS (TS, ≥1) and excluded all the PAs available, analyzing only non-PAs (areas under no protection). Under our prioritization approach, we assumed that areas that are already protected, such as PAs, do not have priority for additional conservation efforts.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/3/6/e1602929/DC1

fig. S1. Plots of the relationships between FD (Petchey and Gaston's FD), PD (Faith's PD), TD, and TS of amphibians in the Brazilian Atlantic Forest.

fig. S2. Mismatch maps among FD (Petchey and Gaston's FD), PD (Faith's PD), TD, and TS of amphibians in the Brazilian Atlantic Forest.

fig. S3. Spatial distribution of the PAs, the forest remnants outside of the PAs, and the very high priority sites covered by the proposed model 1 to amphibian conservation in the Brazilian Atlantic Forest.

fig. S4. Spatial distribution of the PAs, the forest remnants outside of the PAs, and the high-priority sites covered by the proposed model 2 to amphibian conservation in the Brazilian Atlantic Forest.

fig. S5. Spatial distribution of the PAs, the forest remnants outside of the PAs, and the medium-priority sites covered by the proposed model 3 to amphibian conservation in the Brazilian Atlantic Forest.

fig. S6. Forest remnants and complementary fieldwork areas sampled in the Brazilian Atlantic Forest.

table S1. Results from the PERMANOVA on the land cost-effectiveness by the FD (Petchey and Gaston's FD), PD (Faith's PD), TD, and TS of amphibians in the Brazilian Atlantic Forest.

table S2. Specific functions, ecosystem-supporting services, and references related to the amphibian functional traits assessed in the Brazilian Atlantic Forest.

data file S1. Functional traits and references for 453 amphibian species sampled in the Brazilian Atlantic Forest (.xlsx as a separate file).

data file S2. GenBank accession numbers for 207 amphibian species sampled in the Brazilian Atlantic Forest (.xlsx as a separate file).

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Supplementary Materials for

Cost-effective conservation of amphibian ecology and evolution

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The PDF file includes:

- fig. S1. Plots of the relationships between FD (Petchey and Gaston's FD), PD (Faith's PD), TD, and TS of amphibians in the Brazilian Atlantic Forest.
- fig. S2. Mismatch maps among FD (Petchey and Gaston's FD), PD (Faith's PD), TD, and TS of amphibians in the Brazilian Atlantic Forest.
- fig. S3. Spatial distribution of the PAs, the forest remnants outside of the PAs, and the very high priority sites covered by the proposed model 1 to amphibian conservation in the Brazilian Atlantic Forest.
- fig. S4. Spatial distribution of the PAs, the forest remnants outside of the PAs, and the high-priority sites covered by the proposed model 2 to amphibian conservation in the Brazilian Atlantic Forest.
- fig. S5. Spatial distribution of the PAs, the forest remnants outside of the PAs, and the medium-priority sites covered by the proposed model 3 to amphibian conservation in the Brazilian Atlantic Forest.
- fig. S6. Forest remnants and complementary fieldwork areas sampled in the Brazilian Atlantic Forest.
- table S1. Results from the PERMANOVA on the land cost-effectiveness by the FD (Petchey and Gaston's FD), PD (Faith's PD), TD, and TS of amphibians in the Brazilian Atlantic Forest.
- table S2. Specific functions, ecosystem-supporting services, and references related to the amphibian functional traits assessed in the Brazilian Atlantic Forest.

Other Supplementary Material for this manuscript includes the following:
(available at advances.sciencemag.org/cgi/content/full/3/6/e1602929/DC1)

- data file S1 (Microsoft Excel format). Functional traits and references for 453 amphibian species sampled in the Brazilian Atlantic Forest (.xlsx as a separate file).
- data file S2 (Microsoft Excel format). GenBank accession numbers for 207 amphibian species sampled in the Brazilian Atlantic Forest (.xlsx as a separate file).

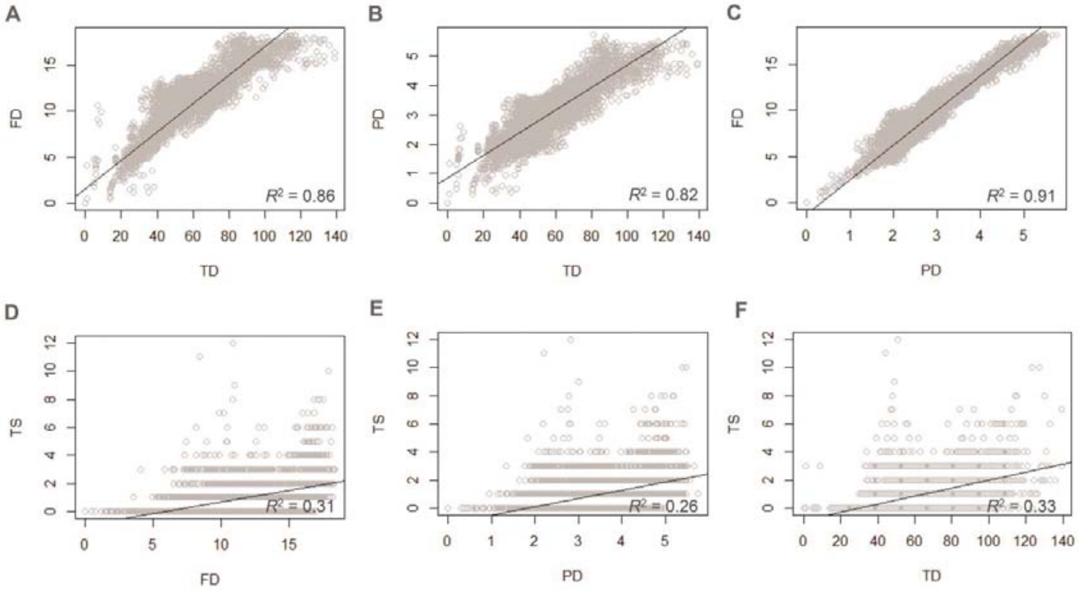

fig. S1. Plots of the relationships between FD (Petchey and Gaston's FD), PD (Faith's PD), TD, and TS of amphibians in the Brazilian Atlantic Forest. (**A**) Linear regression between FD and TD. (**B**) Linear regression between PD and TD. (**C**) Linear regression between FD and PD. (**D**) Linear regression between TS and FD. (**E**) Linear regression between TS and PD. (**F**) Linear regression between TS and TD.

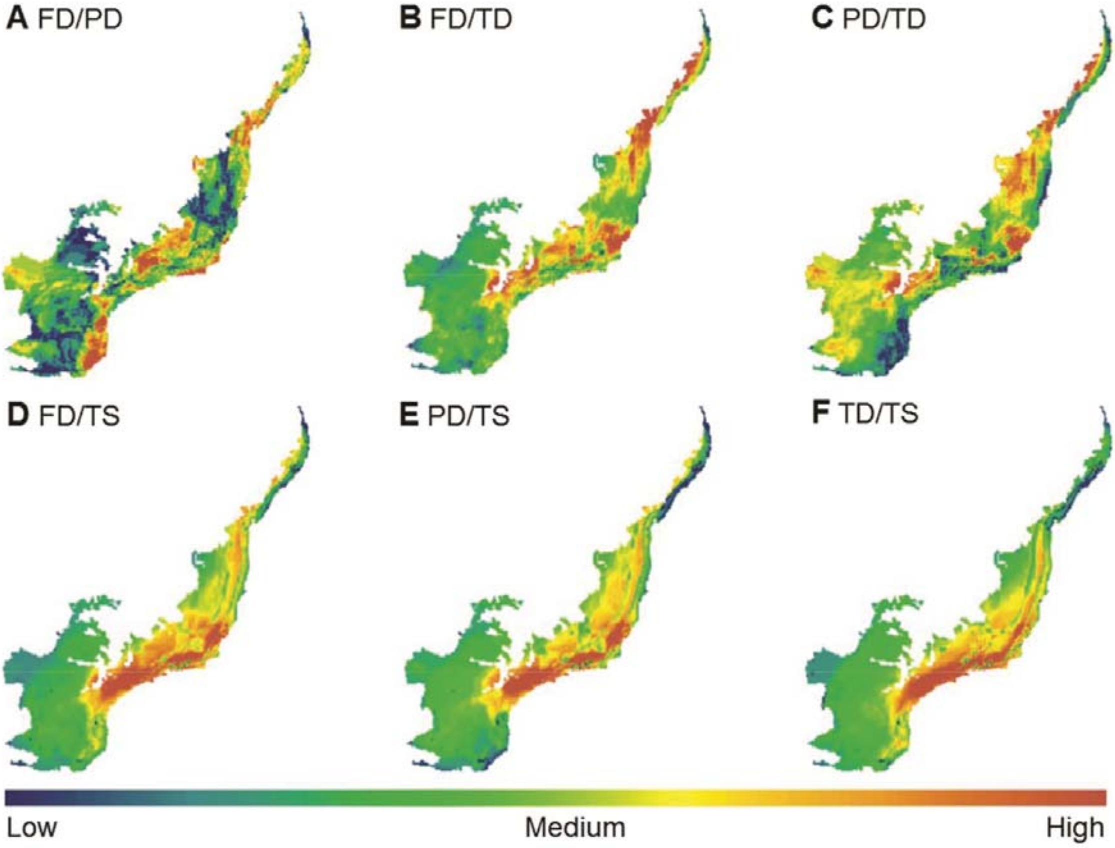

fig. S2. Mismatch maps among FD (Petchey and Gaston's FD), PD (Faith's PD), TD, and TS of amphibians in the Brazilian Atlantic Forest. (**A**) Mismatch map between FD and PD (5% of disparity). (**B**) Mismatch map between FD and TD (14% of disparity). (**C**) Mismatch map between PD and TD (12% of disparity). (**D**) Mismatch map between FD and TS (44% of disparity). (**E**) Mismatch map between PD and TS (42% of disparity). (**F**) Mismatch map between TD and TS (29% of disparity).

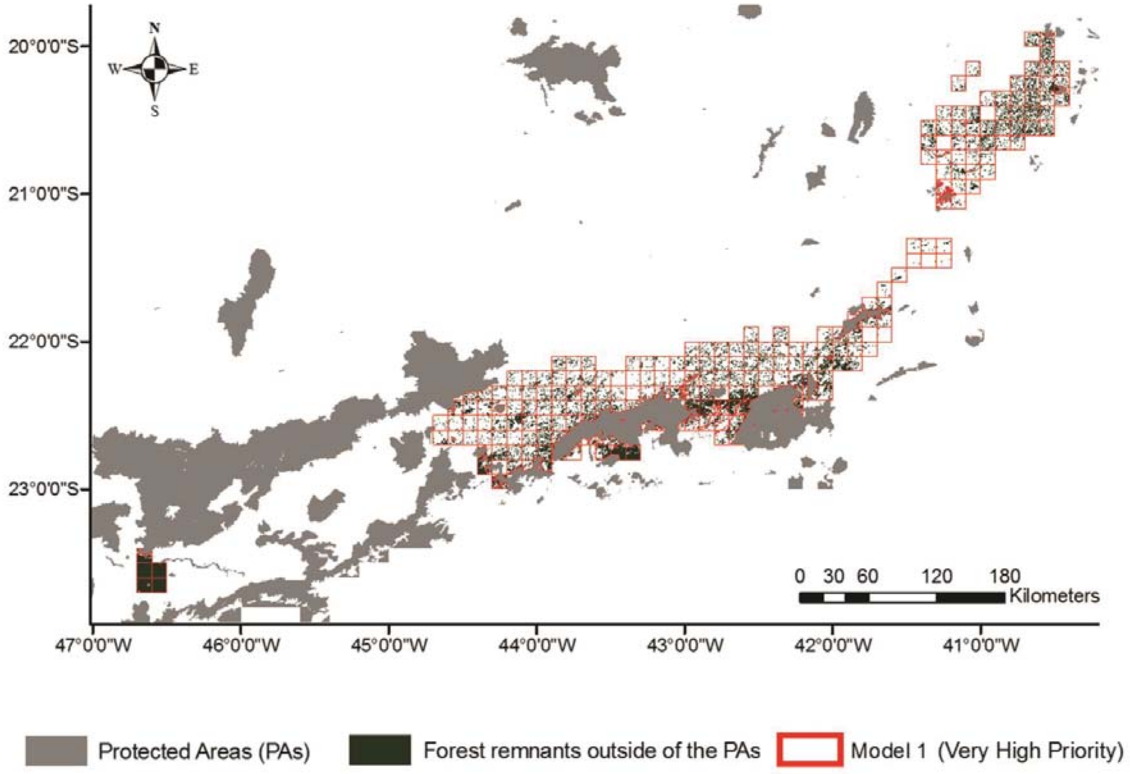

fig. S3. Spatial distribution of the PAs, the forest remnants outside of the PAs, and the very high priority sites covered by the proposed model 1 to amphibian conservation in the Brazilian Atlantic Forest.

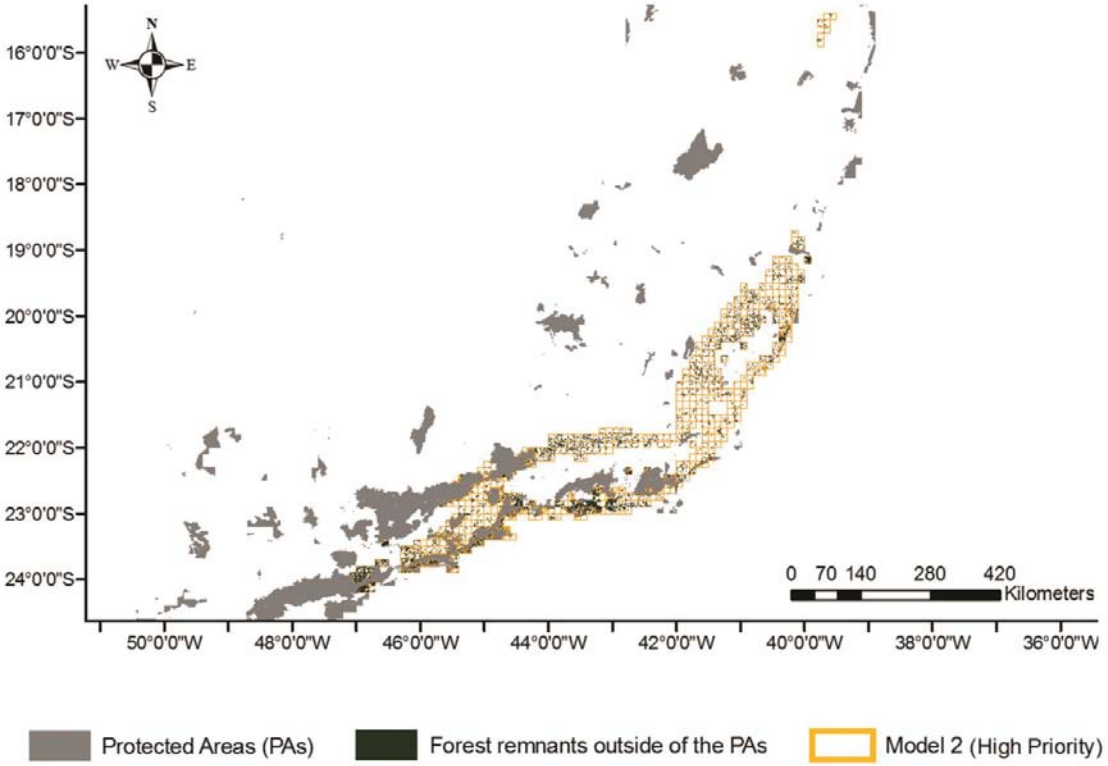

fig. S4. Spatial distribution of the PAs, the forest remnants outside of the PAs, and the high-priority sites covered by the proposed model 2 to amphibian conservation in the Brazilian Atlantic Forest.

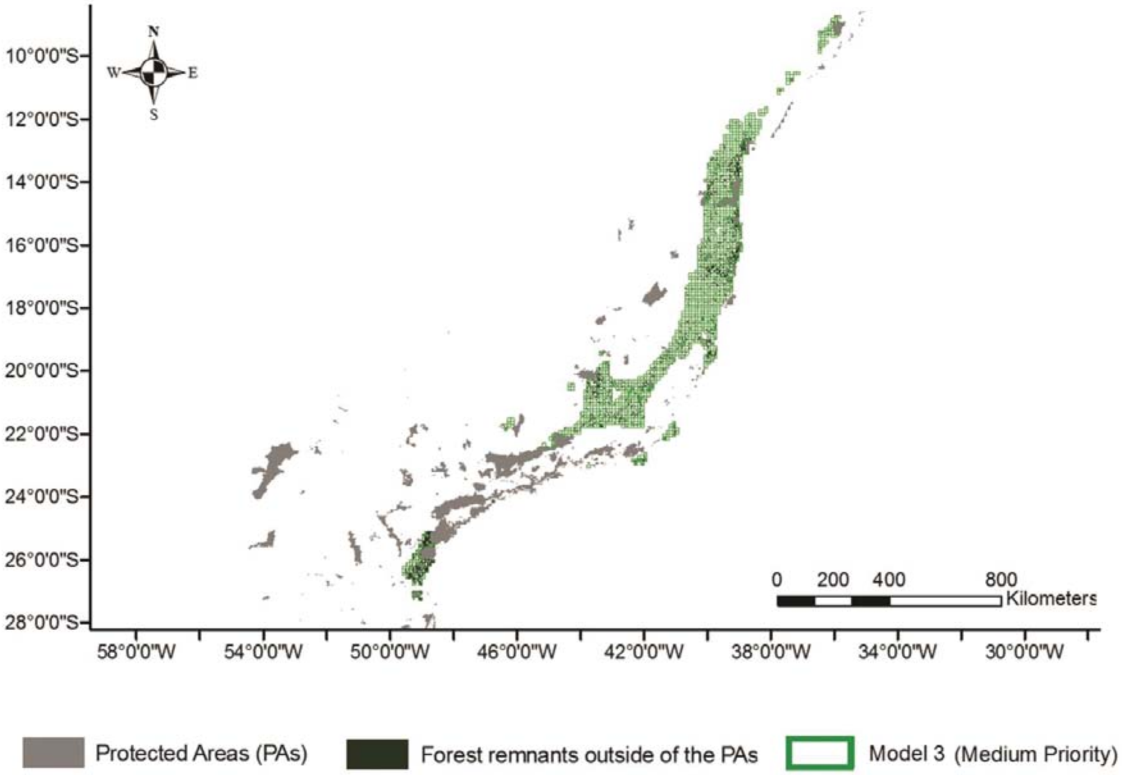

fig. S5. Spatial distribution of the PAs, the forest remnants outside of the PAs, and the medium-priority sites covered by the proposed model 3 to amphibian conservation in the Brazilian Atlantic Forest.

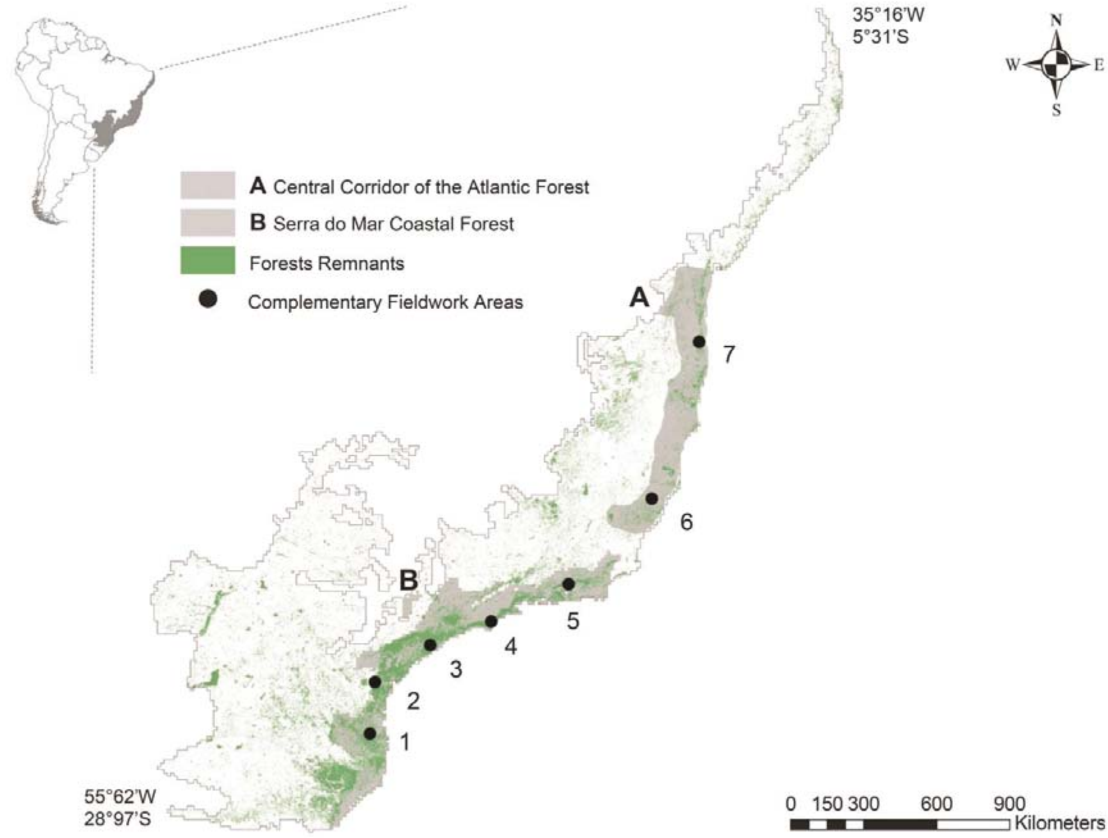

fig. S6. Forest remnants and complementary fieldwork areas sampled in the Brazilian Atlantic Forest. (**A**) Central Corridor of the Atlantic Forest. (**B**) Serra do Mar Coastal Forests, Brazil. 1. Parque Ecológico Spitzkopf, SC; 2. Parque Estadual Pico do Marumbi, PR; 3. Estação Ecológica de Juréia-Itatins, SP; 4. Parque Estadual da Serra do Mar Núcleo Caraguatatuba, SP; 5. Parque Nacional da Serra dos Órgãos, RJ; 6. Reserva Biológica Augusto Ruschi, ES; 7. Reserva Biológica de Una, BA.

table S1. Results from the PERMANOVA on the land cost-effectiveness by the FD (Petchey and Gaston's FD), PD (Faith's PD), TD, and TS of amphibians in the Brazilian Atlantic Forest.

Attributes	**df**	***F* model**	R^2	***P* value**
FD	1	334.15	0.03	0.001
PD	1	297.62	0.02	0.001
TD	1	511.00	0.04	0.001
TS	1	105.28	0.01	0.001
Residuals	10354	–	0.90	–
Total	10358	–	1.00	–

table S2. Specific functions, ecosystem-supporting services, and references related to the amphibian functional traits assessed in the Brazilian Atlantic Forest.

Functional traits	Specific functions	Ecosystem supporting services	References
Body size (mm)	Hunting tolerance, dispersal ability, predator-prey relationships, sexual selection	Trophic transfer, nutrient cycling, protection of primary productivity by controlling herbivores	*46, 66, 75–77*
Members (apodal and tetrapod)	Dispersal ability, predator-prey relationships	Trophic transfers, nutrient cycling, soil bioturbation, ecosystem engineering	*46, 66, 75, 76*
Activity (nocturnal, diurnal, and both)	Dispersal ability, predator-prey relationships, sexual selection	Trophic transfer, nutrient cycling	*46, 66, 75, 76*
Toxicity (toxic, non-toxic, unpalatable, or bad odor)	Hunting tolerance, predator-prey relationships	Trophic transfer, nutrient cycling	*46, 66, 75, 76*
Habitat (forested area, open area, and both)	Dispersal ability, predator-prey relationships	Trophic transfer, faunal food chains, nutrient cycling, soil bioturbation, ecosystem engineering	*46, 66, 75, 76*
Habit (arboreal, phytotelmate, terrestrial, cryptozoic, fossorial, rheophilic, semi-aquatic, and aquatic)	Dispersal ability, predator-prey relationships	Trophic transfer, faunal food chains, soil bioturbation, ecosystem engineering, decomposition (tadpoles), nutrient cycling	*46, 66, 75, 76*
Calling site (bamboo grove, swamp or lake, bromeliad, forest floor, tree canopy, caves or burrows, rock wall, backwater river, stream, river, shrubs, grasslands and not sings)	Dispersal ability, predator-prey relationships, sexual selection	Trophic transfer, faunal food chains, nutrient cycling, soil bioturbation, ecosystem engineering,	*46, 66, 75, 76*
Reproductive mode (1 to 39 modes)	Dispersal ability, predator-prey relationships, sexual selection	Trophic transfer, faunal food chains, nutrient cycling, soil bioturbation, decomposition (tadpoles), ecosystem engineering	*46, 66, 74–76*

General Discussion

GENERAL DISCUSSION

In this thesis, we provided a unique database with timely results, which will extend the current scientific literature on setting priorities for biodiversity conservation aims, linking their ecological, evolutionary and economic aspects. Using the Brazilian Atlantic Forest as study area, we designed an innovative approach showing efficient prioritization models based on functional, phylogenetic and taxonomic diversity of amphibians. Such models are needed as a reference point for evaluating ecological and evolutionary processes as results of conservation strategies. In the development of this scientific effort, we advanced issues that have not yet been implemented in practice and not applied effectively in ecological landscape planning. We believed that our study has moved forward the ecology-based knowledge to promote useful strategies in decision-making regarding amphibian conservation, validating the usefulness of our approach for other species-rich regions, which can also be used for other taxonomic groups. Taking into account the extensive data and the variety of topics addressed in this thesis, we defined an integrative conservation strategy using spatial distribution, threatened species, climate change, evolutionary ecology, and biodiversity conservation.

Spatial distribution

Amphibian spatial distribution patterns are not well understood, mainly because of incomplete information on taxonomy and distribution of many species, especially in Neotropical regions (Vieites et al., 2009). Regarding Atlantic Forest amphibians, the knowledge on biogeography and taxonomy is recent, because several species are often revalidated (e.g., Pimenta et al., 2015), and mainly because every year new species have been discovered (e.g., Lourenço-de-Moraes et al., 2014; Ferreira et al., 2015; Bornschein et al., 2016; Malagoli et al., 2017). Despite this, high numbers of undescribed amphibians have been estimated to occur in poorly studied tropical regions (Fouquet et al., 2007). Many of these species could be facing extinction but are not including in the scope of conservation actions, due to the absence of adequate sampling across species-rich regions (Campos et al., 2014a).

Studies aimed to represent amphibian species composition are essential to understand effects of local scales such as density-dependent interactions, habitat selection, and community assembly processes (Haddad, 1998; Dias et al., 2014). Despite the increased availability of spatial data on species distribution, basic species inventories are crucial to inform local biodiversity conservation aims at broad environmental scales. Our complementary fieldwork highlights the importance of maintaining forest remnants towards a straightforward representation of the amphibian species composition in the major and best well-preserved Atlantic Forest remnants from Brazil – the mountain chain Serra do Mar (**Chapter 1**). Furthermore, we showed multiple spatial scales for understanding biogeographic patterns in the entire Brazilian Atlantic Forest, incorporating observed functional traits into amphibian species distributions (**Chapter 2**). Our findings revealed that the species of open areas tend to disperse from west to east regions, drawing inferences regarding the variation in species turnover and nestedness across the biome.

Geographical records on spatial species occurrence provided by field inventories are crucial for answering central questions in biogeography (Lomolino & Heaney, 2004), ecology (Brown et al., 1996) and evolutionary biology (Holt, 2003), besides taxonomic gaps. Such information is also necessary for the effective allocation of conservation efforts over broad spatial extents and at fine spatial grains (Boitani et al., 2011). Moreover, species occurrence databases obtained from fieldworks are required to study species' responses to environmental change (Boakes et al., 2010), and for policy-relevant indices of biodiversity change (Butchart et al., 2010). Therefore, in the case of Atlantic Forest, further investments in basic research regarding the collection of field data from species inventories are critical to better understand its extraordinary amphibian species richness (Verdade et al., 2012).

Given that our incomplete taxonomic knowledge hampers our attempts to conserve biodiversity, innovative studies in the classification of species and their interactions are needed to guide conservation prioritization (Wilson, 2017). Compiling data about species distribution ranges also is an important step in planning conservation actions (Hurlbert & Jetz, 2007), which has been shown in some studies on Brazilian amphibian communities (e.g., Trindade-Filho et al., 2012; Verdade et al., 2012; Morais et al., 2013; Campos et al., 2014b; Campos et al., 2017). Species distribution is amongst the most studied topics by macroecologists and biogeographers worldwide (Ricklefs, 1987; Oberdorff, 1997; Svenning & Skov, 2007; Carnaval & Moritiz, 2008; Carnaval et al., 2009; Baselga et al., 2012; Silva et al., 2014). Despite the constant increase in the number of conservation scientists in last decades, this is still not enough to solve the biodiversity conservation demands in species-rich regions (Lawler et al. 2006), which is even more relevant in the case of Brazilian amphibians (Urbina-Cardona, 2008; Campos et al., 2014a). Amphibian researchers agree that local species richness, taxonomy, geographic ranges, natural history and population status are vastly understudied in Brazil (Pimenta et al., 2005; Silvano & Segalla, 2005; Verdade et al., 2012). Some research biases also have been detected for amphibian species that are more common and more widely distributed, as well as the trends observed at a global scale (Brito, 2008). These trends shown that most amphibian conservation actions are directed at areas dominated by non-threatened species. According to Schiesari et al. (2007), these biases when present, may reflect important consequences for declining populations, and the threat intensity may be inversely related to the species' abundance and geographical ranges.

Threatened species

Taxonomists generally describe widespread and locally abundant species before small-ranged and locally scarce ones (Collen et al., 2004). But how many species are unknown to science? Even in well-known taxonomic groups, there may be several unknown species, which can be rare and threatened with extinction (Pimm et al., 2010). However, uncertainties about where species are may be more limiting than not knowing how many species there are. Some studies on conservation priority setting usually assume that we know the species to be conserved as well as where they occur (Pimm et al., 2014). In general, the number of threatened species matches the number of small-ranged species. This helps to determine where currently threatened species occur and where species may become threatened in the future (Schipper et al., 2008). Combining a minimum number of small-ranged species and sufficiently high habitat loss, Myers et al. (2000) highlighted that habitat destruction is greatest where there are highest concentrations of small-ranged species, which make them potentially threatened. In this context, identifying threatened species has been a successful approach for setting conservation priorities, since it enables practitioners to target those species known to be at highest risk of extinction (Mace et al., 2008).

The knowledge on amphibian species with small geographical ranges in the Atlantic Forest is particularly incomplete and very recently acquired (Campos et al., 2014a). The best-known species have large geographical ranges and are often common within them. Conservation-relevant knowledge is still accumulating quickly, even for the best-known taxonomic groups. Specialists should follow the accumulation of new knowledge carefully, improving the challenges to protect threatened species. Uncertainties about where species are distributed may be more warning than not knowing how many species there are (Pimm, 2014). Among the several uncertainties in projecting future extinction rates, a particularly important one is the effect that conservation actions might have in reducing them (Waldron et al., 2013).

The Red List of Threatened Species from the International Union for Conservation of Nature (IUCN), is the most important mechanism for classifying species based in their extinction risk (Rodrigues et al., 2006; Hoffmann et al., 2008). However, when the data available in the assessments is not adequate to determine the threat category, species are classified as Data Deficient (IUCN, 2012). More than one decade has passed since the results of the Global Amphibian Assessment (GAA) have been published, conveying the high proportion of amphibians listed as Data Deficient (Stuart et al., 2004). Threatened amphibian species have received frequent attention in the conservation literature (Stuart et al., 2004; Stuart et al., 2005; Morais et al., 2012; Campos et al., 2016; Campos et al., 2017), whereas Data Deficient species have received sparse attention so far (e.g., Brito, 2010; Isaac et al., 2012; Trindade-Filho et al., 2012; Moraes et al., 2013).

Population declines also have been reported in Data Deficient species (Lips et al., 2005), where habitat loss, diseases, climate change, and pollution are identified as potential threat factors (Lips et al., 2005; Pounds et al., 2006; Eterovick et al., 2005; Verdade et al., 2012). These factors generally increase the species vulnerability, which could be linked to the lack of capacity to cope and adapt to environmental changes. Despite there is no currently scientific consensus regarding the definition of the term “vulnerability” (i.e., including both exposition and sensitivity), it is generally agreed that there is not a single cause (IPCC, 2014). In a comprehensive review, Pacifici et al. (2015) described different approaches to assess the vulnerability of species concerning on data availability. These approaches can be correlative, mechanistic, trait-based or a combination of them. In this context, the conservation of threatened species is more effective when supported by knowledge, not just on species themselves, but on the threats affecting species and the most effective measures needed for addressing those threats (Murray et al., 2011).

Some studies on biogeographic and range size patterns of amphibians suggest that the Atlantic Forest harbors a high diversity of restricted range-species, which are poorly represented by protected areas, especially in the northeastern region (Whitton et al., 2012; Villalobos et al., 2013; Campos et al., 2013). Our findings highlighted that the size of protected areas in the Atlantic Forest along the geographical range of threatened amphibians do not necessarily safeguard their persistence (**Chapter 3**; **Chapter 4**). We did not provide quantitative estimates of species extinction risk. However, we showed evidence of inefficient protection for the threatened amphibian species that are covered by the current protected network.

Atlantic Forest reserves close to urban ecosystems are also failing to protect amphibians (Lourenço-de-Moraes et al., 2018). Even in good environmental conditions, if amphibian distribution is not incorporated into protected areas, the discontinuity between suitable habitats does not ensure species dispersal (Becker et al., 2010; Nori et al., 2015). Given that it is expected that species vulnerability increases with temperature (Pacifici et al., 2015), long-term threats imposed by climate change jeopardize threatened species persistence, which may significantly affect amphibian conservation actions in the Atlantic Forest remnants.

Climate change

Anticipating climate change is one of the main threats to global biodiversity (Thomas et al., 2004; Pereira et al., 2010). This threat is highly related to anthropogenic causes and their effects are continuously promoting changes in physiological and ecological processes, which directly affect the distribution and persistence of species (Stenseth et al., 2002; Huey et al., 2009). Several species have already responded to climatic shifts over multiple scales and accurate predictions suggest that climate-induced changes in habitats will commit 15–37% of species to extinction (Thomas et al., 2004).

The science of global warming has reached a consensus on environmental impacts driven by ambitious targets of urbanization, agriculture and livestock (Nordhaus et al., 2010). These rapid changes and dynamic responses offer a new challenge to the scientific community – they forecast what would be the future patterns of environmental conditions to prevent further extinctions.

In the **Chapter 5**, we use an approach based on landscape connectivity and climate change models, showing that ecological connectivity is directly related to how species are affected by spatio-temporal dynamics under forecast climate scenarios. Our results indicate that predicted climate change can reduce 75% of the forest remnants that in turn may reduce the amphibian dispersion. Species dispersal can affect the ecological connectivity and play an important role in determining the probability of species persistence in suitable landscapes across space and time (Martensen et al., 2017). We highlight the importance of maintaining forest remnants in the main Atlantic Forest biodiversity corridor (i.e., the Central Corridor), suggesting implications for amphibian conservation planning and providing new approaches on ecological connectivity in different climatic conditions.

Studies modeling ecological responses to climate change are increasing and contributing to a better understanding of how threatened persistence and diversity of species are (Maclean & Wilson, 2011). Eight out of ten models predict at least 20% loss of vertebrate species under lower emission scenarios at tropical and temperate regions of the western hemisphere due to loss of areas with suitable conditions (Lawler et al., 2009). Previous studies also have predicted that amphibians will be more susceptible to global warming than birds or mammals (Blaustein et al., 1994), with a predicted net loss for many species in range size under the lower emissions scenario (Lawler et al., 2009). This high amphibians' susceptibility to climate change is associated with their microhabitats, hydrological regimes, infectious diseases, and limited dispersal ability (Pounds et al., 2006; Early & Sax, 2011), which can also act in synergy.

Focusing on the Atlantic Forest, our findings highlight that 60% of amphibian species can become threatened by 2080 (**Chapter 6**). We show that the most likely impact of climate change should occur in the western edge and on the northeastern edge of the biome. Although our data predict a dramatic reduction of species ranges, we suggest that species may have suitable habitat in higher latitudes and altitudes areas. Species with access to mountainous regions may migrate to higher altitude areas, which have lower temperatures (Colwell et al., 2008), and retain greater humidity due to better-preserved forests cover (Ribeiro et al., 2009). Taking this into account, we recommend new conservation efforts in highlands as a more effective strategy to alleviate the effects of climate change on this region.

Using climate-based models, Carnaval et al. (2009) proposed three climatic refuges for amphibians during the late Pleistocene: 1. Southern Bahia state (located in the Central Corridor of the Atlantic Forest); 2. Pernambuco state; 3. North-east region of São Paulo (i.e., Serra do Mar). For future climatic conditions (i.e., by 2080), we showed that species tend to disperse towards areas with milder temperatures (i.e., high latitudes/altitudes), coinciding with those areas proposed as refuges during the late Pleistocene, supporting Carnaval et al. (2009) hypothesis. In addition, we suggest new climatic refuges in the Espírito Santo state, the Serra da Mantiqueira region in the south of Minas Gerais state, and the south of Serra do Mar in the east of Paraná state. At a broader level, the congruence between amphibian-climate refuges and suitable habitat models in a world of ever-accelerating environmental changes can help to predict patterns of phylogeography and guide research on ecology and evolution.

Evolutionary ecology

Evolutionary dynamics of ecological processes are often related to biogeographic patterns, macroevolutionary rate shifts, and the relative ability of species to respond to global change (Saupe et al., 2017). Widespread niche convergence to ecosystem functions is constantly changing over evolutionary and ecological timescales in response to changing environmental conditions (Pianka et al., 2017). In this context, functional and phylogenetic diversity offer different and complementary information about ecological and evolutionary traits among species, providing an essential step to reveal biodiversity assembly mechanisms and their feedbacks to ecosystem functions (Bello et al., 2017). Therefore, species-specific traits may be important for responses to habitat disturbance in determining which species can be able to persist over environmental changes (Devictor et al., 2008; Newbold et al., 2014).

In this thesis, we use an innovative design based on the ancestral character states of the amphibian functional traits and their evolutionary history in the Atlantic Forest (**Chapter 7**). We address how these relations ensure species composition patterns and how they can support hypothesis about evolutionary changes on functional traits. In summary, we suggest that these traits are potentially driven by phylogenetic conservatism, although they heavily rely on good studies on complete amphibian phylogenetic lineages to overcome potential biogeographic constraints.

Our study highlights evidence-based questions on the niche conservatism dynamics to increase the sensitivity in the detection of adaptive evolution on large-scale phylogenetic relationships. We report for the first time an empirical study exploring reconstructed ancestral states under maximum parsimony and phylogenetic signals across an entire class of organisms in the Atlantic Forest, accounting variation at different taxonomic levels. Our results reveal that phylogenetically related species may have different functional traits and the strength of the phylogenetic signals can vary across orders, families and subfamilies. Furthermore, we show that amphibians' functional traits can drive more than 40% of the diversity of antipredation mechanisms (**Chapter 8**). Given that amphibians have high adaptive plasticity and suffer strong predatory pressure (Relyea, 2001; Urban et al., 2014), we highlight some defensive behaviors as outcomes of interactions through evolutionary adaptation to different predators. In this context, we advance the knowledge on phylogenetic relationships of functional traits in amphibian communities and help to describe the evolutionary patterns that ensure ecological community structures.

Overall, the use of phylogenetic metrics in ecology has been suggested as a relevant tool for conservation science, which can be related to processes such as extinction (Purvis et al., 2000, Jetz & Pyron, 2018), biotic invasion (Winter et al., 2009), ecosystem functioning (Srivastava et al., 2012), and ecosystem services (Faith et al., 2010). Evidence on evolutionary traits mediating ecological functions usually come from metrics such as functional and phylogenetic diversity in studies assessing the impact of anthropogenic activities (e.g., Diaz et al., 2007; Flynn et al., 2009; Thuiller et al., 2014; Campos et al., 2017). The evolutionary history can be used as a predictor or outcome of ecological processes (Tucker et al., 2017). Still the utility of phylogeny for conservation aims depends on the question addressed and the available data

(Winter et al., 2013). Therefore, the interplay of past diversification and evolutionary history provides complementary tools for conserving the amphibian tree of life (Jetz & Pyron, 2018).

Biodiversity conservation

A multifaceted framework of biodiversity components is key to ensure functioning ecosystems that provide social and ecological services in changing landscapes (Pollock et al., 2017). Although biodiversity has been considered integral to the sustainable development agenda (Adams et al., 2004; Sachs et al., 2009; Griggs et al., 2013), its potential to improve human well-being has not been systematically explored (Naeem et al., 2016). Biodiversity conservation can be launched by multiple actors and sectors, from governments, academia and non-governmental organizations to businesses and other stakeholders (Seddon et al., 2016). Environmental challenges facing humanity require a new approach to biodiversity conservation (Corlett, 2015). A plausible option is to incorporate values of biodiversity into decision-making using economic advantages (Atkinson et al. 2012), however this pathway remains controversial (McCauley, 2006; Neuteleers & Engelen, 2015; Silvertown, 2015). In a world where conservation action is often constrained by land use costs, the inclusion of economic considerations is crucial to determine effective priorities for benefit-targeting conservation.

The exponential growth of human activities is a real threat to biodiversity and human well-being. Conservation efforts are limited by time and money (Mace, 2005; Loucks et al., 2008; Naeem et al., 2016). Management responses to the global biodiversity crisis are demanding efficient approaches for conserving multiple biodiversity components with limited resources. Considering data availability and scarcity of resources for conservation, the use of indicator groups as shortcuts for spatial biodiversity patterns is crucial to define conservation priorities (Rondinini et al., 2006; Lawler & White, 2008; Grantham et al., 2010). Taxonomic groups can be considered useful biodiversity surrogates when their geographic distribution ranges spatially coincide with the distribution of several other groups in a limited region (Gaston, 1996; Flather et al., 1997; Virolainen et al., 2000). Using a complementary approach in the Atlantic Forest, we showed the effectiveness and consistency of amphibian taxonomic groups from small geographic ranges as potential surrogates of biodiversity (**Chapter 9**). Our findings indicate that sites selected from indicator groups can represent more than 70% of the amphibian species from the Atlantic Forest, supporting conservation actions and reducing time for decision-making. We also showed a practical suggestion to represent taxonomic groups aiming at economic cost estimations. Whenever supported by ecological theory, the use of biodiversity surrogates associated with land cost-effective values provides fundamental scientific basis for conservation decisions, which validates the extension of this work to further taxonomic groups and key biodiversity regions.

Many environmental organizations are developing landscape planning tools able to offer economic returns on investment in biodiversity protection (Sutton et al., 2016). Such investments can be indicated by cost-effectiveness–based estimates of land values and suggest a trade-off between biodiversity gains and economic costs for applied purposes of conservation planning (Silvertown, 2015). Because of the large area considered for benefit-targeting conservation, economic costs become an obstacle, but if insufficient land area is set aside, biological gains are weak (Banks-Leite et al., 2014). The most important criterion for conservation decisions should be to achieve maximum representation of biodiversity with the smallest possible cost (Margules & Pressey, 2000). To identify possible solutions, we designed a framework for understanding the foundational role of amphibian ecology and evolution in sustaining payment for ecosystems services. This framework allows to highlight new directions for a practical conservation planning.

We suggest a comprehensive ecological-economic modeling through a trade-off between biological conservation gains and the cost of paying landowners, by using private lands to protect amphibians and their habitats (**Chapter 10**). The economic costs attributed in our models can work as an effective mechanism of annual payments for environmental services in the Atlantic Forest hotspot. Compared to Brazilian agrarian activities, the ecological compensation proposed in our study (i.e., specifically 13.273 dollars per square kilometer) corresponds to a quarter of the average value a farmer of these regions could get from traditional farming activities. Our study provides three complementary models on economic estimations to represent the biodiversity components – functional, phylogenic and taxonomic diversity – in relation to their threats and protection status. Such models are needed as a reference for evaluating ecological and evolutionary processes as results of cost-effective conservation strategies, predicting potential effects of environmental filtering in face of socio-ecological challenges. In this study, we suggested that an area equivalent to the city of São Paulo and US $ 25 million per year could save the Atlantic Forest amphibians through a systematic conservation planning. The key innovative insight we bring is going beyond traditional biological concerns, but incorporating cost-benefit relationships from an ecological economics perspective.

In most cases, the relationships between biodiversity services and environmental economics, requires interdisciplinary approaches and science-based policies for achieving sustainable development, balancing economic and ecological goals (Frank & Schlenker, 2016; Naeem et al., 2016; Seddon et al., 2016). In an attempt to warrant conservation attention, payments for ecosystem services are increasingly being implemented on the local and national scales (Banks-Leite et al., 2014). The concept of ecosystem services defines nature in an anthropocentric term (Silvertown, 2015). As a development of anthropocentrism, the monetization of ecosystem services has been associated into ecological thinking as a practical pathway to connect environmental concerns in the policy-making agenda (McCauley, 2006; Kallis et al., 2013; Adams, 2014; Schroter et al., 2014). Considering the dominant neoliberal ideology, the strategic plan of the global Convention on Biological Diversity calls for biodiversity values to be integrated into national and local development, poverty reduction strategies and planning processes (CBD, 2010). However, effective conservation planning should safeguard taxonomic, phylogenetic, and functional diversity to ensure biodiversity persistence in a changing world (Pressey et al., 2007). Efforts to secure the future of these biodiversity dimensions rely on cost-effectiveness–based assessments of conservation values (Banks-Leite et al., 2014). In this context, our findings present a new conservation strategy that incorporates functional, phylogenetic, and taxonomic diversity for improved cost-effective outcomes.

Thinking about the economic benefits of preserving amphibians may seem strange, but the fact is that such species are relevant environmental service providers (Whiles et al., 2006), and their diversity presence help to maintain different aspects of the environment that are fundamental to human well-being. In addition to controlling insect populations and vector diseases, amphibians have varied and significant environmental functions (Hocking & Babbitt, 2014). Amphibian biodiversity can affect the nutrient cycling at the ecosystem level, which can also be related to the quality of drinking water (e.g., Blaustein & Wake, 1995; DeGarady & Halbrook, 2006; Lebboroni et al., 2006; Whiles et al., 2006; Hopkins, 2007; Hocking & Babbitt, 2014; Meredith et al., 2016). These and other provisional services provided by amphibian species and their habitats motivated the idea of payment for ecosystem services. According to this logic, rural producers and private land owners who keep forest remnants in good conditions could be financially compensated for them to remain so, without overturning, planting or grazing. It is key to note that we are not talking about forest restoration in these areas, which would be much more expensive. Therefore, the idea is just to keep what already exists. By crossing the data with integrative approaches connecting evolutionary and functional ecology aspects, it was possible to establish which sites would more broadly cover the diversity of amphibians in the Atlantic Forest and could help to protect them.

The key areas identified along this thesis can be used as a biological foundation for amphibian conservation planning, which also would have to account for other factors such as opportunity costs, social/political considerations, and funding for land investments based on biodiversity values. On the economic perspective of sustainable development, there is a critical need for using empirical data to estimate the effects of compensating a decline in ecosystem functions with human-made benefits (Naeem et al., 2016). Biodiversity values are widely based on the variability among living organisms including taxonomic, phylogenetic, and functional diversity, and mainly on the ecological complexes of which they are part (CBD, 2005). Therefore, conserving biodiversity beyond species distinctiveness is essential to warrant the provision of ecosystem services and their contribution to human well-being, the evolutionary potential for species adaptation, and the extraordinary biodiversity dimensions that exists across taxonomic lineages.

Conclusions

CONCLUSIONS

Our study has advanced knowledge of the analytical methods that can be used for setting amphibian conservation planning across the Brazilian Atlantic Forest, highlighting seven main conclusions:

1. Functional traits ensure the species' ability to disperse. We showed evidence of the relationship between morphological, physiological, and ecological features with amphibian dispersal. While there is increasing distribution data, we still need more boots on the ground. Field-based approaches are crucial to obtain life-history traits that answer general questions in ecology, evolution and conservation.

2. The use of functional assessments into conservation policy is key to protect species in endangered ecosystems. However, the current Brazilian protected network is unable to conserve the most threatened species. Beyond the crisis faced by unprotected amphibians, we also sounded the alarm regarding the species covered by protected areas.

3. Atlantic Forest reserves are expected to be less effective in a near future, where forest connectivity losses will reduce amphibian dispersal. For improved conservation outcomes, we recommend some landscape paths with low resistance values, drafting a blueprint for functional biodiversity corridors.

4. The response of amphibians to anticipated declines depend on local climatic conditions. Regarding adaptation to climate change, we showed that species tend to disperse towards high altitude areas as potential climate refuges, safeguarding ecological and evolutionary processes.

5. Despite the potential biogeographical constraints of our assumptions, we revealed that amphibian functional traits are driven by phylogenetic history. However, the strength of the phylogenetic signals change across taxonomic

groups. We found evidence that functional traits explain the evolutionary history of antipredator mechanisms. Our work also supports conservation studies aimed to explore interactions between functional trait evolution and phylogenetic loss.

6. Given the rapid rate of human–induced species losses, we suggest a shortcut for conservation planning using indicator groups to represent amphibian biodiversity. In this sense, we showed that restricted-range species can be used as potential biodiversity surrogates at broad spatial scales. In addition, we applied these estimates in cost-effectiveness–based assessments of land values.

7. Finally, we introduced a new conservation strategy that incorporates functional, phylogenetic and taxonomic diversity for improved cost-effective outcomes. In an attempt to explain why amphibians matter, we showed a multifaceted framework of biodiversity components proposed as strong drivers of ecosystem functioning and services. One of the possible recommendations with low pollical cost could be payment for biodiversity–ecosystem services. This would to bring market value on realistic scales, where stakeholders are expecting positive returns.

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Supporting Information

SUPPORTING INFORMATION

– Supplementary files:

- **Data file S1.** Functional traits and references for 453 amphibian species sampled in the Brazilian Atlantic Forest (.xlsx as a separate file).

- **Data file S2.** GenBank accession numbers for 207 amphibian species sampled in the Brazilian Atlantic Forest (.xlsx as a separate file).

Database available at:

http://advances.sciencemag.org/content/suppl/2017/06/19/3.6.e1602929.DC1

– Additional research efforts:

- **Other published papers.** List of Additional Publications in Scientific Journals (Appendix I)

– Media coverage/Science communication:

- **Info & Metrics.** Attention Score by Altmetric on behalf of Science (AAAS). Available at: http://advances.sciencemag.org/content/3/6/e1602929/tab-article-info

- **Press office – Universitat de Barcelona.** Overview of media attention for the article published in Science Advances, 2017 (Appendix II).

List of Additional Publications in Scientific Journals:

1. Mônico, A. T., Zocca, C. Z., Lourenço-de-Moraes, R., **Campos, F. S**., Ferreira, R. B. (2016). *Myersiella Microps*. Antipredator Mechanisms. *Herpetological Review*, *47*, 644–645.
2. **Campos, F. S.**, Solé, M. (2015). Taxonomic Changes: An Attempt to Overcome the Linnean Shortfalls for Brazilian Amphibians. *Froglog - Newsletter of the IUCN/SSC Amphibian Specialist Group (ASG), 23*, 17.
3. **Campos, F. S.**, Brito, D., Solé, M. (2014). Diversity patterns, research trends and mismatches of the investigative efforts to amphibian conservation in Brazil. *Annals of the Brazilian Academy of Sciences (Print), 86*, 1873–1886.
4. **Campos, F. S.**, Trindade-FIlho, J., Brito, D., Llorente, G. A., Solé, M. (2014). Recent Publications: Conservations and Ecology – The efficiency of indicator groups for the conservation of amphibians in the Brazilian Atlantic Forest (Abstract). *Froglog – Newsletter of the IUCN/SSC Amphibian Specialist Group (ASG*), *22*(4), 57.
5. **Campos, F. S.**, Lage, A. R. B. (2013). Checklist of amphibians and reptiles from the Nova Roma Ecological Station, in the Cerrado of the State of Goiás, central Brazil. *Herpetology Notes, 6*, 431–438.
6. **Campos, F. S.**, Lage, A. R. B., Ribeiro, P. H. P. (2013). Diversity of medium and large sized mammals in a Cerrado fragment of central Brazil. *Journal of Threatened Taxa, 5*, 4994–5001.
7. **Campos, F. S**., Brito, D., Solé, M. (2013). Recent Publications: Conservations and Ecology – Threatened amphibians and their conservation status within the protected area network in northeastern Brazil (Abstract). *Froglog – Newsletter of the IUCN/SSC Amphibian Specialist Group (ASG)*, *21*(4), 68.
8. Lourenço de Moraes, R., **Campos, F. S.**, Toledo, L. F. (2012). The tadpole of *Dendropsophus haddadi* (Bastos & Pombal 1996) (Hylidae: Hylinae). *Zootaxa (Auckland. Print), 3476*, 86–88.
9. **Campos, F. S.**, Lourenço de Moraes, R., Pereira, C. S. A. (2011). New state record of *Mesoclemmys perplexa* Bour and Zaher, 2005 (Reptilia: Chelidae) in Brazil. *Herpetology Notes, 4*, 263–264.
10. **Campos, F. S.**, Vaz-Silva, W. (2010). Temporal and spatial distribution of anuran fauna in different environments in Hidrolândia, Goiás State, Central Brazil. *Neotropical Biology & Conservation*, *5*, 179–187.

UNIVERSITAT DE BARCELONA

Cost-effective conservation of amphibian ecology and evolution

Science Advances, 2017

Science Magazine @sciencemagazine
New research in @ScienceAdvances describes a cost-effective strategy to help save the frogs of Brazil

Cost-effective conservation could save Brazilian amphibians

An economic strategy to protect a threatened biodiversity hot spot

Área de São Paulo e US$ 25 mi por ano salvariam anfíbios da mata atlântica

Mata Atlântica: estudo indica onde investir para conservar melhor

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UNIVERSITY OF BARCELONA

Ricardo Lourenço-de-Moraes
FEDERAL UNIVERSITY OF GOIÀS

Mirco Solé
STATE UNIVERSITY OF SANTA CRUZ, BAHIA

PRESS OFFICE
July, 2017

«Cost-effective conservation of amphibian ecology and evolution»

Conservation Ecology, 2017

Un nou estudi sobre economia ambiental ajuda a millorar la conservació dels amfibis a la Mata Atlântica brasilera
http://www.ub.edu/web/ub/ca/menu_eines/noticies/2017/07/004.html

Un nuevo estudio sobre economía ambiental ayuda a mejorar la conservación de los anfibios en la selva atlántica brasileña
http://www.ub.edu/web/ub/es/menu_eines/noticies/2017/07/004.html

A new study on environmental economy helps improving the preservation of amphibians in the Brazilian Atlantic Forest
http://www.ub.edu/web/ub/en/menu_eines/noticies/2017/07/004.html

Un nou estudi sobre economia ambiental ajuda a millorar la conservació dels amfibis a la Mata Atlântica brasilera
http://www.ub.edu/noticies/cgi/event.pl?id=103930&noticiaub=BIOLOGIA

Economia ambiental ajuda a millorar la conservació dels amfibis a la Mata Atlânt
http://www.ub.edu/irbio/CAnoticia.php?id=568

Economía ambiental ayuda a mejorar la conservación de los anfibios en la selva atlántica brasileña
http://www.ub.edu/irbio/ESnoticia.php?id=568

Environmental economy helps improving the preservation of amphibians in the Brazilian Atlantic Fores
http://www.ub.edu/irbio/ENnoticia.php?id=568

Un nuevo estudio sobre economía ambiental ayuda a mejorar la conservación de los anfibios en la selva atlántica brasileña
http://www.alphagalileo.org/ViewItem.aspx?ItemId=177029&CultureCode=es

A new study on environmental economy helps improving the preservation of amphibians in the Brazilian Atlantic Forest
http://www.alphagalileo.org/ViewItem.aspx?ItemId=177029&CultureCode=en

Um novo estudo sobre economia ambiental ajuda a melhorar a conservação dos anfíbios na Mata Atlântica brasileira
http://www.alphagalileo.org/ViewItem.aspx?ItemId=177029&CultureCode=pt

Mata Atlântica: estudo indica onde investir para conservar melhor
http://www.oeco.org.br/noticias/mata-atlantica-estudo-indica-onde-investir-para-conservar-melhor/

Mata Atlântica: estudo indica onde investir para conservar melhor
http://www.retecresiduos.com.br/noticias/mata-atlantica-estudo-indica-onde-investir-para-conservar-melhor/

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http://www.tbsambiental.com.br/noticias/mata-atlantica-estudo-indica-onde-investir-para-conservar-melhor/

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http://www.diretodaciencia.com/2017/06/22/boletim-de-noticias-22jun-mec-permitira-curso-a-distancia-para-faculdades-que-nao-oferecem-presencial/

Área de São Paulo e US$ 25 mi por ano salvariam anfíbios da mata atlântica
http://www1.folha.uol.com.br/ambiente/2017/06/1894719-area-de-sao-paulo-e-us-25-mi-por-ano-salvariam-anfibios-da-mata-atlantica.shtml

Área de São Paulo e US$ 25 milhões por ano salvariam anfíbios
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http://www.vidambiental.com.br/noticias

Bolsista da Capes participa de artigo destacado em publicação internacional
http://portal.mec.gov.br/index.php?option=com_content&view=article&id=50981

Estudo de bolsista revela custo para preservação de anfíbios da Mata Atlântica
http://www.capes.gov.br/sala-de-imprensa/noticias/8447-estudo-de-bolsista-da-capes-revela-custo-para-preservacao-de-anfibios-da-mata-atlantica

Bolsista da Capes participa de artigo destacado em publicação internacional
http://www.correiobraziliense.com.br/app/noticia/eu-estudante/ensino_ensinosuperior/2017/07/03/ensino_ensinosuperior_interna,606882/bolsista-da-capes-participa-de-artigo-destacado-em-publicacao-internac.shtml

Mata Atlântica: estudo indica onde investir para conservar melhor
http://www.sintemamt.org.br/noticias/exibir.asp?id=1860&noticia=Mata_Atlantica_estudo_indica_onde_investir_para_conservar_melhor

Área de São Paulo e US$ 25 mi por ano salvariam anfíbios da mata atlântica
http://brazil.shafaqna.com/PT/BR/3367742

Improving the preservation of amphibians in the Brazilian Atlantic Forest
https://www.sciencedaily.com/releases/2017/07/170704094106.htm

Improving the preservation of amphibians in the Brazilian Atlantic Forest
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Improving the preservation of amphibians in the Brazilian Atlantic Forest
https://www.longroom.com/discussion/564864/improving-the-preservation-of-amphibians-in-the-brazilian-atlantic-forest

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Improving the preservation of amphibians in the Brazilian Atlantic Forest
http://www.newsnow.co.uk/h/Science/Zoology
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Economía ambiental para la conservación de anfibios en la selva atlántica brasileña
http://www.agenciasinc.es/Noticias/Economia-ambiental-para-la-conservacion-de-anfibios-en-la-selva-atlantica-brasilena

El 90% de la biodiversitat en amfibis de la selva atlàntica brasilera està fora de protecció
http://www.vilaweb.cat/noticies/el-90-de-la-biodiversitat-en-amfibis-de-la-selva-atlantica-brasilera-esta-fora-de-proteccio/

El 90% de la biodiversitat en amfibis de la selva atlàntica brasilera està fora de protecció
http://www.aldia.cat/gent/noticia-90-biodiversitat-amfibis-selva-atlantica-brasilera-fora-proteccio-20170704182701.html

Un nuevo estudio sobre economía ambiental ayuda a mejorar la conservación de los anfibios en la selva atlántica brasileña
http://noticiasdelaciencia.com/not/24984/un-nuevo-estudio-sobre-economia-ambiental-ayuda-a-mejorar-la-conservacion-de-los-anfibios-en-la-selva-atlantica-brasilena/

UB alerta sobre amenaza que sufren anfibios de la Mata Atlántica brasilera
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https://es.makemefeed.com/2017/07/04/un-nou-estudi-sobre-economia-ambiental-ajuda-a-millorar-la-conservacio-dels-amfibis-a-la-mata-atlantica-brasilera-6732859.html

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