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Qual a importância de integrar diversas métricas de diversidade para a compreensão da estruturação e para fundamentar medidas de conservação de comunidades de anfíbios em biomas brasileiros?

Lilian Sayuri Ouchi de Melo

DOUTORADO

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apesar de nunca ter tido a oportunidade
de frequentar a sala de aula.

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"O maior obstáculo para a descoberta não é a
ignorância, é a ilusão do conhecimento" (D.J. Boorstion).

RESUMO

Atualmente estudos ecológicos têm expandido sua abordagem de maneira a enfocar padrões e processos que transitam entre a ecologia de comunidades, macroecologia e biogeografia. Ainda, é cada vez mais notável o direcionamento do conhecimento teórico gerado para estratégias voltadas à conservação da biodiversidade. Desta maneira, nesta tese buscamos revisar brevemente os grandes marcos dentro da ecologia de comunidades, como as diferentes dimensões da diversidade têm sido estudadas, e como vem sendo conduzida a integração das teorias em ecologia de comunidades com a macroecologia, biogeografia e conservação. No primeiro capítulo nosso principal objetivo foi selecionar áreas prioritárias para conservação baseadas em padrões de diversidade taxonômica, funcional e filogenética de anuros, em um bioma amplamente ameaçado pela expansão do cultivo de soja no Centro-Oeste brasileiro, o Cerrado. No segundo capítulo, buscamos elucidar os principais fatores climáticos (atuais e passados), geológicos e energéticos (e.g., produtividade), responsáveis pela distribuição da diversidade taxonômica, funcional e filogenética de anuros nos três maiores biomas brasileiros, Amazônia, Cerrado e Mata Atlântica. No primeiro capítulo, nossos resultados revelaram quatro áreas de maior interesse para a conservação no Cerrado que não foram detectadas quando consideramos apenas a riqueza de espécies. Isso indica que selecionar áreas prioritárias para conservação no Cerrado com base unicamente em métricas tradicionais de diversidade, como riqueza de espécies, que ignoram o grau de singularidade das espécies não é a estratégia mais adequada. Além das métricas tradicionais de diversidade não serem capazes de identificar padrões evolutivos, elas também não garantem a persistência das comunidades ao longo do tempo e, não permitem gerar predições a respeito das consequências das mudanças climáticas para o funcionamento ecossistêmico. No segundo capítulo, verificamos que cada tipo de domínio (florestado ou savânico) possui uma dinâmica própria na geração e manutenção dos padrões de diversidade nas três dimensões analisadas o que parece ser reflexo de um gradiente ambiental mais evidente em áreas florestadas e de uma maior heterogeneidade ambiental devido aos mosaicos de habitat presentes no Cerrado. Biomas florestados (Amazônia e Mata Atlântica) sofreram maior influência da estabilidade climática e da heterogeneidade de relevo, enquanto que o Cerrado não exibiu um padrão predominante, com ambas as variáveis influenciando em maior ou menor grau cada uma das dimensões de diversidade analisadas. Portanto, entender as peculiaridades de florestas e savanas pode ajudar a criar generalizações sobre como as diferentes dimensões da diversidade estão distribuídas ao redor do mundo.

Palavras-chave: América do Sul, dimensões da diversidade, domínios savânicos e florestais, Amazônia, Cerrado, Mata Atlântica, estabilidade climática.

ABSTRACT

Currently, ecological studies have been expanded their approach in order to discuss patterns and process that encompass community ecology, macroecology, and biogeography. Moreover, directing theoretical knowledge into biological conservation strategies is increasingly notable. Thus, in this thesis we seek to: i. briefly reviewing the community ecology biggest landmarks, ii. investigate how the different dimensions of diversity have been studied, iii. elucidate how community ecology theories are integrated to macroecology, biogeography, and conservation. In the first chapter, our main aim was to select priority areas for conservation based on anurans taxonomic, functional and phylogenetic diversity in in the Brazilian Cerrado savanna, a biome widely threatened by the expansion of soybean production. In the second chapter, we ought to elucidate the main climatic (current and past), geological and energetic (e.g., productivity) factors, responsible for the distribution of the taxonomic, functional and phylogenetic diversity of anurans in the three largest Brazilian biomes, the Amazon, the Cerrado and the Atlantic Forest. In the first chapter, our results revealed four areas of greater conservation interest in the Cerrado that had not been elucidated solely by species richness. This result indicates that selecting priority areas for conservation in the Cerrado based solely on traditional diversity metrics, such as species richness and endemism, that ignore the uniqueness of each species is not the most appropriate strategy. munBesides traditional metrics not being able to identify evolutionary patterns, they also do not ensure community persistence in the long term and, they do not allow us to make predictions about functional consequence of environmental changes. In the second chapter, we verified that each type of domain (forest or savanna) has its own dynamics in the generation and maintenance of the three diversity dimension, which seems to reflect a more evident environmental gradient in forested areas and greater environmental heterogeneity due to the habitat mosaics present in the Cerrado. Forested domains (Amazon and Atlantic

Rainforest) have presented greater influence of climatic stability and relief heterogeneity, while the Cerrado savanna had no predominant pattern, with both variables influencing in different degrees each one of the diversity dimensions analyzed. So, each type of domain has its own dynamic to generate and maintain the different forms of biodiversity, from taxonomic to functional and phylogenetic diversity. In this way, understanding the peculiarities of forests and savannas around the world might envision new insights and generalizations about diversity dimensions.

Keywords: South America, diversity dimensions, forest and savanna domains, Amazon, Cerrado, Atlantic Forest, climatic stability.

SUMÁRIO

GENERAL INTRODUCTION

Walking through important routes of community ecology

Target Journal: Theoretical Ecology

Walking through important routes of community ecology

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Abstract

Significant theoretical advances in community ecology have been helping us to comprehend not only community assembly and species coexistence but also what are the main drivers of the community diversity patterns. How ecology has evolved from 19 century until nowadays give us a panoramic view of species coexistence and diversity in local, regional and global scale. Furthermore, the advances of the last decades, including neutral perspectives, and phylogenetic and functional approaches into the community ecology field are bringing some insights of how evolutionary history and ecosystem functioning are inserted in and are essential to understanding the patterns of diversity in community ecology. Thus, here we draw some important landmarks of ecology history and try to bring some future directions of ecology according to the most recent studies.

Keywords: coexistence, community composition, species richness

1. Pinpointing some ecology landmarks

Ecological field studies started in about 18th century but it only came out as a science on the 19th century, when researchers began to do experiments and apply statistical tests to analyze environmental influence on species occurrence, community structure and the succession dynamics (Croker 1991; Brown 1999; Egerton 2007). Oecology was the first term coined by Ernest Haeckel in the 19th century being the kick-off mark to "ecology" emerge as a new study field. His proposal was a science capable of understanding the relationship between the organisms and its environment. However, in the 18th century when Darwin applied Malthus' essay to the natural world, one of the biggest approaches in the community ecology began to emerge, the importance of competition to species coexistence. By including the evolutionary changes as the main driver for the struggle for survival, Darwin could make feasible the idea of how one species, throughout enough time and shaped by selective pressures, could split into several new species.

At the beginning of 19th century Forbes (1887) published the paper "The lake as a microcosm" where he described the structure of lakes in Illinois, USA, regarding species composition, richness, and abundance of different taxa groups, from plants and algae to vertebrates and invertebrates. This paper is a milestone in ecology that affected earlier ecologists trying to tease apart how community is structured through time and space and what are the main drivers of species co-occurrence and biodiversity maintenance. In the beginning, predation and competition were attributed as the two main processes responsible for the maintenance of the community equilibrium (Gotelli 2009). Interestingly, these interspecific interactions are still at the core of contemporaneous discussion given their importance in shaping species niche breadth.

The switch of 1800 to 1900 century was marked by the development of ecology as a dynamic field, from Clements (1916) organismic definition of a community until Gleason (1926) individualistic concept. Clements organism definition of a community was based on local scale with few species of plants, where each species was complementary and imperative to the maintenance of the community functioning, as the organs in the organism. When some studies tried to apply Clements concept for tropical environments they started to find some incongruences and gaps in his ideas once the high resources availability allow the co-occurrence of many redundant species in the same area. Conversely, the individualistic concept could open the window to understand how species come into and live from a community based on their specific requirements. The conditions of an environment in the individualistic concept can favor (or harm) some species to occur in a community, which in turn determines interaction strength of co-occurring species.

By the way, Clements and Gleason definitions had a major influence in combining the effect of resource use and optimum condition to define the specific requirements of species, giving rise to a key concept in ecology, the niche. Niche theory started to be blooming and dominated the ecological discussions since Joseph Grinnell (1917), who was the first to address the niche concept based on a Californian bird (*Toxostoma redivivum*) as species' requirements regarding the place that the species occupies in the environment (Grinnell 1917), until nowadays (see McInerny and Etienne 2012a, b, c; Soberón 2014; Soberón and Arroyo-Peña 2017). Ten years later, Charles Elton (1927) introduced a functional concept of the niche, which describes the role of each species in the food web, instead of focusing in where they live. In 1934, Gause's axiom postulated that two species with the same niche requirements could not coexist (Gause 1934), being one of the start points to Hutchinson multidimensional niche space. Hutchinson (1957) synthesized the niche concept as a n-dimensional space or hypervolume. According to him, each resource, condition or biotic interaction is considered as an independent variable in an ordination. So, each axis of the ordination is one dimension of species niche and all together form a N-dimensional hypervolume which represents the fundamental niche of the species. Under the hypervolume area the species' requirement is completely attended, and the species can exist indefinitely (Hutchinson 1957). MacArthur and Levins (1967) include, explicitly, in their version of niche, the concept of limiting similarity., Which was considered as the competitive limits to the species similarity in the Lotka-Volterra model that allow species coexistence.

From nineties until nowadays niche theory has been revisited in many different ways from deterministic view to neutral theory. Chase and Leibold (2003) brought a remarkable theoretical approach about niche when they showed the impacts of how a species influence an ecological factor instead of just thinking about how an ecological factor influence species coexistence. Furthermore, they made a link between species interactions, mechanistic models of population regulation and the niche concept, focusing in measurable features of species (e.g., growth, consumption and death rates), and its application to the studies in community structure in local and regional scales (Chase and Leibold 2003). On the other hand, Hubbel's neutral theory assumes dispersal as a leading process driving community assembly, and not the species requirements or tolerances as those proposed by niche viewing (Hubbell 2001). As a result of random dispersal, the neutral dynamic is purely stochastic, spatial and individual based (Alonso et al. 2006). Based on that, the step ahead provided by the neutral theory is unifying the explanation and quantitative predictions for all the general macroecological patterns and downscale the influence of those dynamics for the local community assembly (Bell 2000; Hubbell 2001). In this way, neutral theory brought a dynamical formulation in which the community assembly is randomly defined according to the stochasticity of species origins, extinctions and dispersal, a completely opposite approach from niche theory. Now, the hot debate involves how the communities are assembled under deterministic (niche) and stochastic (neutral) mechanisms. Those are two complementary mechanisms acting together depending where, in an environmental gradient, the community is inserted in (see Adler et al. 2007; Fisher and Mehta 2014). Furthermore, as emphasized by Fisher and Mehta (2014), a community is not static, and it can transit from a selection-dominated regime (niche based) to a drift-dominated regime (neutral based) according to the environmental changes.

Linking niche and neutral theories, metacommunity concept came out bringing new insights for the community assembling at different spatial scales (Leibold et al. 2004). The step ahead provided by the metacommunity approach was to include dispersal effects as a dynamic driver of four different paradigms according to the environmental characteristics and species abundances in the community patches involved in the regional assembling. Since then, one of the most important achievements happened for the community ecology theory was exactly related to the inclusion of regional and large-scale process in the local community assembly by the frames provided by metacommunity theory (Logue et al. 2011).

Last but not least, the introduction of historical ecology, later on called ecophylogenetics, encompassed into community assembly both evolutionary process (e.g., adaptation and speciation), dispersal and colonization (Brooks and McLennan 1991). Those process would have led the current community structure to exhibit recent and historical patterns (Brooks and McLennan 1991). In the past two decades those ideas have gone through several theoretical advances. The ecophylogenetic is increasingly growing up since Webb et al. (2002), migrating from a dualist view of patterns, clustered and overdispersed communities and process, limiting similarity versus environmental filtering (Webb et al. 2002), to an emerging and integrated fusion of ecology, biogeography and macroevolution driving the community assembly process (Mouquet et al. 2012; Gerhold et al. 2015). Breaking up the dualist idea, Cavender-Bares et al. (2009) and Mayfield and Levine (2010) brought to the light that several different types of ecological and evolutionary process might be leading to the same community patterns in ecology. Progressively, the advances in evolutionary biology and phylogeny inferences are making feasible the blooming of this integrative approach in the community ecology as we can see in (Vellend 2010).

2. Does community ecology fit in a "closed" box?

Lawton (1999) was the first to call community ecology "a mess". According to him, it is hard to find useful generalizations due to the overwhelming emphasis on localness and, thus, ecological patterns and laws governing them are contingent. Some years later, Vellend (2010) emphasized the mess in the community ecology pointing how we could infer a lot of different processes (predation, competition, mutualism) just considering the basic model of Lotka-Volterra. Then, Vellend proposed a straightforward approach, based on the theoretical foundation of population genetics, organizing that "messy" research area in four main processes driving species diversity and composition at different scales: selection, speciation, drift, and dispersal. With this approach, Vellend did an articulation of a very general theory of community assembly dynamics. Even Vellend stated that *"all theoretical and conceptual models in community ecology can be understood with respect to their emphasis on these four processes"* and that *"empirical evidence exists for all of these processes and many of their interactions, with a predominance of studies on selection"*, due to these several other drivers of diversity it is an arduous work to draw a unified theory in ecology. Likewise, Diane Srivastava, a former PhD candidate of John Lawton, wrote a thoughtful essay arguing "*is perhaps chasing contingency we may discover general truths about the mechanisms of community ecology*" (Srivastava 2018). Emphasizing this discussion, Linquist et al. (2016) found contrasting patterns against Lawton's contingence argument, where in a meta-analyses the authors evidenced that yes, it is possible to have laws in community ecology. Specially by applying ecological generalization under a resilient view across taxonomy, habitat type, and scale (Linquist et al. 2016). In other words, take the borders of contingent ecological thinking out of the empirical hypothesis, is the way to a broad generalization in community ecology. So, the most important step ahead now seems to be the community assembly theory, which is increasingly being accepted as a framework for a unifying ecology. Community assembly theory states that species composition and relative abundance within a community is a result of hierarchical filters acting by impeding or allowing the occurrence of a new member in a community based on their functional traits (Keddy 1992; Pearson et al. 2018), which is a result of the evolutionary history of the regional species pool. Thus, community assembly theory is moving forward and seems able to integrate evolutionary and ecological concepts as neutral and niche process, and demographic process (Chesson 2000; Weiher et al. 2011; Kraft et al. 2015), moving into an integrative path to test community assembly in different spatial scales and under important types of drives.

3. Species diversity among spatial scales: an integrative view of processes and ecological thinking

The species diversity is structured by processes operating at different spatial and temporal scales. G. E. Hutchinson in his corollary 1959 paper, entitled "Homage to Santa Rosalia or Why are there so many kinds of animals", represented a landmark to the study of species diversity by focusing on the factors that control the number of different kinds of animals. In this paper, Hutchinson discussed the implications of food chains, natural selection, diversity of plants, the effect of size, niche requirements and environmental heterogeneity in driving animal diversity, but integrated with the trophic organization of the organisms present in a community. Furthermore, Hutchinson (1959) explains how diversified clades could promote new evolutionary opportunities easier than less diversified ones anticipating the current discussion of the phylogenetic community ecology field.

Hutchinson's thinking prevails until the beginning of 90's when most questions were centered in understanding drivers of species richness and composition at the local scale; indeed, there were comparatively few studies investigating how dispersal affects local communities (e.g., Cottenie et al. 2003; Cottenie and De Meester 2004). Many of 60 to 90 decades studies emphasized interspecific interaction as a potential driver of species coexistence and species diversity, which highlighted the importance of species interactions as a key process in ecological theories, e.g. coexistence mediated by predator (Paine 1966), assembly rules (Diamond 1975), limiting similarity (MacArthur and Levins 1967), etc. However, it has been demonstrated that a scale-dependent approach could address a better understanding of the maintenance of diversity patterns, once it can take into account both demographic stochasticity, environmental heterogeneity, and dispersal (Hart et al. 2017).

The first ecological theory to consider regional process in the community assembly process was the Equilibrium island biogeography theory (MacArthur and Wilson 1967). This theory considers island area and distance from the mainland as the main drivers of species richness equilibrium (Fattorini 2010) and emphasizes dispersal as the main process of community assembly and biodiversity. Besides, the authors link speciation and ecological drift as important process for local species adaptation and natural selection (Rosindell et al. 2011). The Theory of Island Biogeography predicts that larger islands and those close to the continent are more speciose. Bigger areas also comport bigger population and genetic diversity, reducing extinctions caused by bottleneck effects and potentially leading to sympatric speciation (Whittaker et al. 2008). The distance from the mainland represents the degree of isolation of each island; the farther is the distance the greater is the isolation, which decreases the probability of colonization (MacArthur and Wilson 1967; Fattorini 2010). Otherwise, as more connected are the islands lesser are speciation and extinction rates because of the continuous gene flow caused by individual's arrival (Fattorini 2010).

In the final of 1980, Robert Ricklefs shed light on how niche overlap and resource specialization determine species diversity at the local scale (Ricklefs 1987). Ricklefs focused on the idea of the saturation of the community in which local species interactions are limiting species richness, independently of regional species pool, resulting in niche spaces completely filled. On the other hand, if regional processes are driving local species richness, then there is niche space available for new colonization in this unsaturated community. In unsaturated communities, the addition of new species from the regional pool could result in an increase in local species richness, depending on the degree of niche overlap and how species are specialized in the resource use (Ricklefs 1987; Harrison and Cornell 2008). The framework of local species richness versus regional species richness represents one of the first multiscale theoretical approaches. It focused in evaluate the relative importance of processes acting at contrasting spatial scales in determining local species assembly (Ricklefs 1987). For example, Brooker et al. (2009) defended that local-scale processes could regulate both local and regional species diversity and coexistence. As a major concern, one of the crucial fragilities of those studies is how to define the local vs. regional scale, which at most of the time is defined arbitrarily. But, this issue still in a warm debate (e.g., Srivastava 1999; Hillebrand 2005; Gonçalves-Souza et al. 2013). In fact, defining a local community without properly considering the regional pool might result in the exclusion of potential source sites (i.e., metapopulation source-sink dynamics; Hanski and Gilpin 1991), which affects the comprehension of community assembling process.

Looking for an integrative spatial approach in community ecology, metacommunity theory emerged putting together metapopulation and island biogeographic theory as the background to explain community assembly through a dynamic approach. A metacommunity is a set of local communities within a landscape mosaic, linked by dispersal of potentially interacting species (Leibold et al. 2004). This theory elucidates how much emigration and immigration affect the dynamic of local communities and determine diversity patterns in both local and regional scales (Leibold et al. 2004). The arrival of a new individual could change interspecific relationship (Howeth and Leibold 2013) as well as evolutionary dynamics (Urban and Skelly 2006; Peres-Neto et al. 2012) and is affected by the environmental heterogeneity and distribution of habitat patches. There are four metacommunity paradigms that can be arranged through a dispersal rate and heterogeneity gradient among patch habitats: species sorting (efficient dispersal, high heterogeneity), patch dynamics (limited dispersal, low heterogeneity), mass effect (high dispersal, high heterogeneity), and neutral process (limited dispersal and no patch heterogeneity; Leibold et al. 2004; Winegardner et al. 2012). Therefore, the metacommunity concept comes expanding the ecology thinking for a regional scale encompassing neutral and niche-based process to understand what generate and maintain the species richness (e.g., Almeida et al. 2015), composition (e.g., Provete et al. 2014), and most recently, functional and phylogenetic diversity patterns (Gianuca et al. 2018).

Most studies with community ecology in the last two centuries focused in understanding three questions: (i) how resource partitioning, fluctuating environmental factors and frequency-dependent predation affect species coexistence (Chesson 2000); (ii) how local and regional process controls community and metacommunity assembly (Ricklefs and Schluter 1993; Holyoak et al. 2005); and (iii) how community ecology theories could be applied to macroecological goals, using evolutionary relationship among taxa combined with functional traits to infer evolutionary process (Gerhold et al. 2015), predict ecosystem properties (Mouquet et al. 2012; Díaz et al. 2013) and underline explanations for large-scale pattern of diversity (e.g., Wiens and Donoghue 2004; Winter et al. 2009; Diniz-Filho et al. 2009; Jetz et al. 2012; Fritz and Rahbek 2012).

4. Operationalization: diversity metrics to quantify different diversity facets

Several diversity metrics ensure a broad quantification of diversity in all its forms. Firstly, ecologists use species abundance and richness as the primary variables to understand community assembly. Studies on traditional diversity quantify diversity by summing up the species present in the sample (species richness), calculate diversity metrics that account for species richness and abundance (e.g., Shannon and Simpson index), account for species abundance (abundance curves) and, account for species abundance distribution across all species present in the sample unit (equitability indices). Since 70’s, several studies on traditional metrics have been developed, allowing the understanding of community structure and the anthropogenic impacts on ecological communities (e.g., Kushlan 1976; Hixon and Brostoff 1983). However, many criticisms have been made about diversity indices because they combine different parameters of community structure, as species richness and equitability, into a single value (Hurlbert 1971; Melo 2008). In addition, each one of the indices weights parameters in different ways, for example, for two communities (A and B), one index may indicate sample A as more diverse, while another index may indicate the opposite (Melo 2008). In this scenario, community ecologists have returned their focus on the traditional community structure parameters, such as species richness and species abundance distributions, due to the inherent low predictability of diversity indices. On the other hand, new theoretical frameworks and metrics have been developed as a result of the rapid advance of ecological theory and the need for complementary conservation prioritization approaches that better represent the evolutionary history and the role of the species in the ecosystem functioning (Tilman et al. 2001; Petchey and Gaston 2002; Webb et al. 2002).

Recently, several studies have been suggesting other biodiversity dimensions to improve our ability to tease apart the multiple drivers affecting species distribution (Villéger et al. 2008; Tucker et al. 2016). Among them, a lot of functional and phylogenetic diversity metrics has been created (see Schleuter et al. 2010; Tucker et al. 2016). Regarding to phylogenetic diversity approach, its first use was related to species conservation in 1990 by Robert May (May 1990). The idea behind it was to conserve an evolutionary unique species, *Sphenodon guntheri*, and to quantify how important this species should be, related to other reptile species considering the evolutionary relationship among them. Since then, community ecology and macroecology have incorporated phylogenetic relationship among species to explain patterns and elucidate process, as community assembly and biodiversity gradients, under the evolutionary view (e.g., Graham et al. 2009, 2016; Kraft and Ackerly 2010). For years, community ecology focused to explain phylogenetic cluster/overdispersion patterns as a result of environmental filtering or limiting similarity (e.g., Cavender-Bares et al. 2004; Verdú and Pausas 2007). With the advances of the field, many studies showed that this dichotomic approach was not appropriate because of the vast amount of process that could underline the same pattern (Cavender-Bares et al. 2009). Moreover, in the middle of the myriad of indices created (more than 70 according Tucker et al. 2016), choose the best one must be under concern of the questions addressed by the study.

Functional diversity metrics accounts for species morphological, behavioral, physiological and phenological traits, allowing to measure how much a species (or a group of species) contributes or responds to the ecosystem functioning (Violle et al. 2007). Moreover, some studies have demonstrated the importance of including species abundance and intraspecific variation to account, especially, for functional diversity (e.g., (Bolnick et al. 2011; Violle et al. 2012; Hart et al. 2017), once the variation among individuals is crucial to define the space occupied and the role of each species in the ecosystem function. Studies approaching functional diversity to underline questions related to ecosystem process and services as well as ecosystem resilience and the effects of environmental changes are recurrent (e.g., Hooper et al. 2005; Cianciaruso et al. 2012; Oliver et al. 2015). These kinds of studies are bringing important and valuable information about community structure and assembling process being able to guide effective restoration and conservation plans. Even though, functional approach has a big shortfall relying on the availability of good trait information especially regarding to express how functional is a functional trait.

Drawing and evaluating questions that one would like to address is the most fundamental step to incorporate both phylogenetic and functional analysis into ecological aims. However, even bringing advances into community ecology, phylogenetic and functional indices might be falling into the same unpredictability hole as traditional diversity ones, once more than put together species richness and abundance, they also combine species traits and evolutionary history which would increase the uncertainty of what the final value would mean. Thus, whether included cautiously and with keeping all the limitations in mind, analyzing biogeographical and evolutionary history, the whole played by the different species and how species are distributed in an area in a multidimensional context, may be an important criterion to use during the decision making.

5. The importance of multidisciplinary approaches in biodiversity conservation and sustainability

Despite all advances in theory and framework in the community ecology, few studies have implemented an integrative approach to prioritize areas deserving attention for conservation. An integration of different diversity facets could ensure the best prediction to protect better the diversity of species, traits, ecosystem functions and phylogenetic history (Devictor et al. 2010; De Palma et al. 2017). Recently, Pollock et al. (2017) improved the identification of the effectiveness of protected areas by combining multiple diversity dimensions with principles of spatial conservation for birds and mammals. Furthermore, they demonstrated how much diversity could be protected with the expansion of current protected areas and, how different diversity facets ensure alternative solutions for conservation. Besides this broad study, there are also, some efforts to conserve more local and regional diversity including a multi-faceted approach, as demonstrated for birds (Devictor et al. 2010), freshwater fishes (Strecker et al. 2011), spiders (Gonçalves-Souza et al. 2015) and frogs (Melo et al. 2018 in reviewing). Both approaches are important to address conservation actions in a broader scale, as continental and global.

However, before applying any global conservation strategy, first it is necessary to know how the diversity patterns are distributed in different areas/regions and what are the threats in each of them (which includes economic pressures, society struggles and political national and international relationship). Then, it is possible try to find the best way to deal with not just species richness loss, but to avoid ecosystem function decay and maintenance of evolutionary history, balancing economic costs and society benefits. However, the remaining question still persists: Is that enough for truly save species from the currently mass extinction? Besides all the academic efforts in theoretical and applied approaches, is crucial the inclusion of stakeholders, government and traditional communities during the decision making, as proposed by Systematic Conservation Planning since 2000's (e.g., Margules and Pressey 2000; Pressey and Bottrill 2008) in order to minimize the current mass extinction of species. On the other way, as more different parts of society are included, harder is the consensus about priorities in conservation, once different and maybe incongruent interests should be attended. Dealing with the conflicts of the inclusion of different actors in conservation planning is a challenge and requires all the parts views should be listened and considered during the decision-making framework (Brown 2003). This is not a trivial task but should be exercised and encouraged.

An interesting and powerful global initiative is the 2030 Agenda for Sustainable Development proposed by United Nations (UN) in 2015, which focus in 17 mainstream goals, signed by all the 193 members, to end poverty, ensure prosperity for all and protect the planet. To reach the goals, UN makes very clear the importance that everyone needs to do their part (governments, the private sector, civil society and us) and that there are three indivisible and integrated dimensions of sustainable development: the economic, social and environmental. As part of the scientific community of one of the signatory members, Brazil, we optimistically agree that this thesis might help elucidate new approaches and highlight important patterns related to the diversity of life on land (aim 15 of 2030 Agenda) and help to maintain the life forms in more than one type of diversity which helps to provide a good ecosystem functioning and lineages preservation through the time.

6. Concluding remarks

Community ecology has been presenting an enormous growth in the last two decades. One of the broadest discussions in the community ecology is about the absence of a unifying theory in the field. Even though, all the consolidate theories might be applied in a resilient way, taking out the borders of contingent ecological thinking from the hypothesis to be tested. As emphasized in recent studies, community ecology has general assembly process (Vellend 2010), which approximates it from a general theory, but a lot of ramifications are available given the spread abroad of different ecological questions. In this way, community assembly theory is moving into the "without borders" theory, by integrating several evolutionary and ecological concepts. Therefore, revisiting and integrating different areas of knowledge is the way to create new roads throughout the lens of ecology, guiding advances in community ecology into a step ahead in the frontier of knowledge and helping the world to reach the acclaimed sustainable development goals regarding life on land.

7. Glossary

Assembly theory (earlier called "assembly rules"): a theoretical framework developed to explain how natural communities are organized.

Biotic interaction: positive, negative or neutral interaction among individuals of the same or different species.

Coexistence: species coexistence occurs when species are already established in an area/community and any of them leads the others to extinction.

Co-occurrence: the occurrence of two or more species within the same area/community without necessarily establishing. Each species might be in the same place by change, for example, during a dispersal process, or, as have been accidentally carried to over there.

Community structure: emerging properties of ecological communities, as species richness (number of species), species composition and abundance distribution.

Ecological drift: random fluctuations in species population size related to stochastic process.

Environmental filtering: environmental conditions that select species from the regional pool that are able to survive and persist under especial conditions in a local scale.

Functional diversity: variation of traits within and among species. Can be estimated by different indices.

Limiting similarity: is defined as the maximum niche similarity that allows species coexistence.

Local pool: all the species present in a local/small area.

Niche breadth: is the range of environmental conditions and resources availability tolerated by a species.

Niche overlap: when two of more species share the same niche requirements.

Regional pool: all the species present in a regional/broad area. Often represents the potential species to colonize a specific habitat.

Phylogenetic diversity: is defined as a diversity measure of evolutionary relationships among species in an area.

Species functional traits: morphological, behavioral, physiological or phenological characteristics of an organism that can be measured and have an influence in species fitness.

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FIRST CHAPTER

Integrating phylogenetic and functional biodiversity facets to guide conservation: a case study using anurans in a global biodiversity hotspot

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Integrating phylogenetic and functional biodiversity facets to guide conservation: a case study using anurans in a global biodiversity hotspot

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Abstract

The Cerrado is one of the most threatened biomes in Brazil, with little spatial representation within the Protected Area network. Recently, proposed conservation plans worldwide have advocated for the use of multiple biodiversity facets to protect unique evolutionary and functional processes. Our aim was to identify areas with high biodiversity representativeness applying this multifaceted perspective, and propose conservation plans based on the joint analysis of taxonomic, functional and phylogenetic diversity. We used a database of the Brazilian National Program for Research in Biodiversity, which employs a standard protocol for sampling tadpoles. The Cerrado database includes samples from 165 water bodies spread over 15 localities, covering most of the Central Brazilian Cerrado. We selected four morphological traits to calculate functional diversity and used a dated phylogeny available in the literature to compute phylogenetic diversity. Our approach selected five priority areas for conservation, one of which is already protected. Our results highlighted the importance of four new areas which show high values of diversity, including original lineages and traits, and urgently need conservation prioritization. Furthermore, unlike the current protected network, our approach performs significantly better than random at protecting sites with high phylogenetic and functional diversity. We therefore discuss how the multifaceted indices considered can help protect key ecosystem functions and evolutionary legacy in anuran communities of the Brazilian Cerrado.

Keywords: Cerrado hotspot; multifaceted analysis; tadpoles; functional and phylogenetic diversity.

1 Introduction

Since the early 80's, different strategies have been applied to guide conservation decisions in a rational and systematic process, to conserve as much biological diversity as possible (Pressey et al. 2007). However, these approaches have been largely based on taxonomic diversity, namely the protection of individual species or the protection of hotspots of species richness (Margules and Pressey 2000; Myers et al. 2000; Rodrigues et al. 2006). While these approaches have certainly advanced greatly the field of conservation biology, they usually implicitly assume that the extinction or decline of one species or the other are equivalent (i.e., all species are phylogenetically and functionally equivalent) (Iknayan et al. 2014), and they usually focus on endemic and rare species as units of conservation (e.g., IUCN conservation categories; IUCN 2017). These simplifications may be problematic for two reasons. First, abundant and widespread species sometimes perform key or unique ecosystem functions or represent highly distinct evolutionary lineages (Lavorel et al. 1997; Devictor et al. 2010; Mouquet et al. 2012). Their decline or extinction would therefore have disproportionately important consequences for ecosystem function or for evolutionary distinctiveness. In this context, focusing solely on rarity, range size or population decline as criteria for prioritization may lead us to ignore potential tipping points for ecosystem functions. Second, regardless of the species range or abundance, not all species are equivalent. For example, keystone species may cause large shifts in ecosystem functions (Hooper et al. 2005). A growing body of literature suggests that species with different life history traits and ecological properties complement each other providing different ecosystem functions (i.e., the niche complementarity hypothesis: Cadotte 2017; Hautier et al. 2018). Conversely, the insurance hypothesis within the biodiversity ecosystem-function (BEF) framework predicts that some level of redundancy guarantees that the system resists to individual 1extinctions without compromising ecosystem processes (Reiss et al. 2009; Isbell et al. 2018). Furthermore, recent studies have shown that species that seem redundant when looking at one particular function, are not redundant when analyzing multiple functions at the same time (Reiss et al. 2009; Cadotte 2017; Hautier et al. 2018) or when compared through time (Loreau et al. 2003). All these lines of evidence point to the need to consider the maximization of species differences within an ecosystem as a suitable conservation goal if we are interested in the maintenance of ecosystem functions (e.g., Mace et al. 2012; Trindade-Filho et al. 2012).

Along the same lines, phylogenetic considerations may be relevant in conservation biology for several reasons (Mouquet et al. 2012). First, traits are sometimes highly conserved along evolutionary lineages. Because of this, phylogenies have been advocated as a proxy for functional composition (Cadotte et al. 2010; but see Venail et al. 2015). Indeed, given that we lack complete knowledge regarding the functional traits that are relevant for particular ecosystem functions, and given recent advances in molecular biology, phylogenies are sometimes more complete and of easier access than functional traits (Mouquet et al. 2012). Second, phylogenetic diversity and distinctiveness may be considered as conservation goals per se (Pavoine et al. 2005; Mouquet et al. 2012). For example, the extinction of a species from an old, species-poor clade will result in a greater loss of evolutionary information than the extinction of a less distinct species from a young and species-rich clade (Redding and Mooers 2006; Winter et al. 2013). On top of that, some species' extinctions can also cause evolutionary cascades, implying changes in the evolutionary paths of the remaining species (Dirzo et al. 2014). Finally, and more speculatively, it has also been proposed that phylogenetic diversity represents evolutionary potential during episodes of rapid environmental change, such as the one current climate change is imposing on ecosystems (Forest et al. 2007).

These recent developments also highlight the fact that there are at least four different dimensions of phylogenetic and functional composition that need to be considered to fully characterize the conservation value of a site within each facet. We will call them here functional or phylogenetic richness, divergence, regularity and originality (Table 1). Richness refers to the total number of species, or the total accumulated functional traits and evolutionary history represented in a community (Mason et al. 2005; Tucker et al. 2016); divergence refers to the average or overall phylogenetic or functional separation between species (Mason et al. 2003; Tucker et al. 2016); regularity is another type of divergence that focuses on how evenly spaced (phylogenetically or functionally) species within a community are (Mason et al. 2005; Tucker et al. 2016); and finally originality refers to how different one particular species is from all others (Pavoine et al. 2005). Notice that while richness, divergence and regularity are diversity measures and apply to the full community represented in a site, originality is species-specific and allows identifying species that are unique in either their functional or phylogenetic identities. Recent studies have shown that including functional and phylogenetic approaches into ecological studies ensure predictability on communities' sensitivity and resilience (e.g., Balvanera et al. 2006; Srivastava and Bell 2009; Mace et al. 2012). However, they have also shown that phylogenetic and functional diversity measures are often very highly correlated to taxonomic diversity (Meynard et al. 2011; Mouquet et al. 2012; Pardo et al. 2017). Therefore, the analysis of functional and phylogenetic diversity often requires comparing the observed diversity value to what would be expected solely from species richness (Laliberté and Legendre 2010; Vellend et al. 2011, Pardo et al. 2017). In other words, the conservation value of multiple sites need to be evaluated against what would be expected based on a random draw of the same number of species, potentially revealing areas with more trait functions or phylogenetic history than expected solely by the number of species present in that site.

The Cerrado biome is the richest savanna region in the world (Silva and Bates 2002; Silva et al. 2006) and comprises high species richness and endemism, therefore being considered as a global biodiversity hotspot (Myers et al. 2000). It is also one of the most endangered biomes of the world, threatened mainly by the expansion of the agricultural frontier (Strassburg et al. 2017). Amphibians, to which anurans belong, show a higher proportion of threatened species compared to other vertebrates, with 32.4% of all known species being in either the “threatened” or “extinct” categories (2,030 species out of 6,260 amphibians) (IUCN 2016). Large declines of amphibian populations have been documented, demanding urgent public and governmental efforts for effective amphibian conservation in Brazil (Becker and Loyola 2008). Anurans are highly dependent on the existence of high humidity and the persistence of water sources throughout their life cycles, resources that are limited in the Cerrado during the dry season. On top of their ecological vulnerabilities, adult anurans and tadpoles may fulfill important ecosystem functions in natural communities. For example, adult anurans and tadpoles feed on eggs (Bowatte et al. 2013), larval stages (Mokany 2007) and adult mosquitos (Raghavendra et al. 2008), some of which are important vectors of tropical diseases (e.g., *Aedes spp.*, *Anopheles spp.* and *Lutzomyia spp.*). They can therefore play a role controlling obnoxious populations and can help disease control (e.g., yellow fever, dengue fever, zika virus, malaria, leishmaniases; Raghavendra et al. 2008), especially in tropical areas. Most tadpoles also feed on microalgae, therefore playing an important role in the maintenance of water quality of ponds and streams by preventing water eutrophication (Ranvestel et al. 2004). Given this evidence, and although anuran functional roles have not been thoroughly studied and quantified, there is no question that their conservation has also functional implications at the ecosystem level. Loyola et al. (2008) identified priority areas for the conservation of endangered anurans in the Neotropics and found that species with an aquatic reproductive mode are often underrepresented in the conservation planning process. In fact, many protected forest remnants are isolated, meaning that forest habitats where adults spend most of their life, and water bodies where they reproduce, are often disconnected, a process called habitat splitting and which constitutes one of the greatest threats to amphibians (Becker et al. 2007). This makes anurans in the Cerrado a very highly vulnerable group of species.

In this study, we aimed at applying a taxonomic, phylogenetic and functional approach including as many of these different facets as possible to a highly vulnerable group of species, anurans, in a global biodiversity hotspot, the Cerrado biome in Brazil, to prioritize sites for conservation of water-dependent anurans. To our knowledge, this is the first integrative study using anurans’ taxonomic, phylogenetic and functional components to consider conservation recommendations in the Cerrado. We derive recommendations on highly valuable sites for conservation as well as focal species, highlighting the advantages and shortcoming of the multifaceted approach.

2 Methodology

2.1 Study area

The Cerrado is a Savannah biome, with a mosaic of savanna, grasslands and forests (Eiten 1972). The climate is tropical, with precipitation varying between 800 to 2000 mm/year, with a pronounced dry season from April to September (Peel et al. 2007), and average temperatures between 18°C to 28°C (Dias 1992). The Brazilian Cerrado is the second largest biome in South America, covering 2,036.448 km² (Ministério do Meio Ambiente 2017). Despite its biological importance, the Cerrado is the hotspot with the lowest percentage of fully protected areas in Brazil (Ministério do Meio Ambiente 2017). Although 8.21% of its territory is currently under some kind of legal protection, only 2.85% is under full protection, the other 5.36% being designated under sustainable use conservation units, including private reserves (Ministério do Meio Ambiente 2017).

2.2 Database

We used the database of the Brazilian National Program for Research in Biodiversity (SISBIOTA-Brazil) project that employed a standard protocol for sampling tadpoles in five Brazilian biomes. The Cerrado biome database gathers information on tadpoles from 165 waterbodies (ponds and streams), located in 15 distinct areas (Fig. 1). The sampling effort of the SISBIOTA focused on filling the gaps in tadpole inventories that were already existent, and is therefore appropriate to focus on the most vulnerable species, the ones that depend on waterbodies for reproduction (Lips et al. 2003; Bustamante et al. 2005). Additionally, to standardize and allow comparisons at large spatial scales from the SISBIOTA database, we considered only isolated lentic and lotic waterbodies, i.e., those without communication among them or with other types of waterbodies. The standard protocol consisted of sampling tadpoles with a hand dipnet (32 cm diameter and 1.5 mm² mesh) through all surface of each pond (Skelly and Richardson 2010) and along a 100 m transect in streams between November 2011 and May 2014. We sampled each water body during 1 hour, trying to maximize the total area covered as well as representing all types of microhabitats in each survey (Skelly and Richardson 2010). The total number of tadpoles per species for each water body was then considered as a reliable abundance estimate, which was subsequently used for the calculation of diversity indices requiring relative abundances. All the species included in our study present direct dependence of water bodies during some part of their life cycle. In our dataset there are two species that are generally considered as terrestrial or semi-terrestrial that are in fact dependent of water: *Ameerega flavopicta*, which exhibits parental care of the eggs, but where the adult males need to take the hatched tadpoles to nearby ponds associated to streams to complete their metamorphosis (Haddad and Martins 1994; Toledo et al. 2004); and *Thoropa* tadpoles, which present a semi-terrestrial development, but can only occur in rocks within or at the immediate proximity of streams (Caramaschi and Sazima 1984; Eterovick and Barros 2003).

2.3 Functional traits

We chose four morphological traits (total length, body compression, number of teeth rows and reproductive mode) available in the SISBIOTA database, which represent good predictors of the functional role of tadpoles on water ecosystems (Table S1). This database holds categorical and continuous morphological traits, determined in five to ten tadpoles per species, between 33 to 38 developmental stages (Gosner 1960). For species sampled out of this interval, we consulted the respective description papers or we made the measurements in tadpoles deposited in Brazilian scientific collections ("Coleção do Departamento de Zoologia e Botânica da UNESP de São José do Rio Preto", "Museu de Zoologia da Universidade Estadual de Campinas","Coleção Célio F. B. Haddad", "Coleção Zoológica da Universidade Federal de Goiás"). We excluded three species of our functional analysis because of the lack of information on all the four traits. The remaining species have complete information for all trait values.

2.4 Phylogeny

We constructed the phylogenetic topology for anuran species of the Cerrado based on Pyron (2014)'s dated phylogeny. Species unrepresented on that phylogeny were replaced with a congeneric species for which the same age was assumed. If no congeneric species was represented, we bound the species on the likely phylogenetic placement based on cladistics literature (Faivovich 2002; Faivovich et al. 2005, see topology in Fig. S1). Of the 67 species included in the analysis, 88% were represented in Pyron's phylogeny, 9% were added at the congeneric level, and 3% were bound based on the cladistics literature. We then used *bladj* (Branch Lenght Adjuster) on the software Phylocom 4.2 (Webb et al. 2008) to estimate the age of taxa that were bound on the Pyron's dated phylogeny. *bladj* sets the age of the nodes of unknown age by estimating the age of clade diversification from the branches of known age (see also Chamberlain et al. 2012). To calculate phylogenetic diversity, we considered the distance between species in millions of years.

2.5 Functional, phylogenetic and species diversity

We chose a variety of diversity indices to represent taxonomic, functional and phylogenetic richness, divergence and regularity, for the 15 sites studied, plus an index of species originality to identify functionally or phylogenetically unique species (Table 1). Among the indices considered, the Rao diversity index is the only one that can be calculated for taxonomic (TD), functional (FD) and phylogenetic diversity (PD), allowing comparisons between these three facets. All other indices are specific to either the taxonomic, functional or phylogenetic components (see Table 1 and Fig. 2 for details).

For functional and phylogenetic originality of species, we used the originality index proposed by Pavoine et al. (2005). This index is also based on the Rao quadratic entropy (QE), but specifically weights in the uniqueness of each species in different communities. We selected the top 5% of species with the highest originality values for further discussions.

2.6 Defining conservation priorities for protected areas

To identify priority areas for conservation of anuran species, we used a ranking method that integrates the different facets of diversity mentioned above. We did not consider spatial prioritization methods, such as systematic conservation planning, because we do not have continuous distribution information for the species or their habitats at the scale and resolution required, and optimization software commonly used to implement it are not currently well adapted to incorporate phylogenetic and functional diversity and their different variants. However, our dataset is the most complete in the region to include representation of early life-stages of anurans and evaluate important independent waterbodies. A score-based ranking method therefore seemed like a sensitive choice, given the good response regarding conservation prioritization in particular contexts (Volkmann et al. 2014; Chen et al. 2017). The ranking followed these steps:

(1) We computed Pearson's correlation among diversity indices, using the Bonferroni correction for significance levels (Table S2). When the indices were correlated to >0.8, we eliminated from further analysis one of them, prioritizing the index that represented more diversity dimensions and that was most used in the literature. A Principal Components Analysis (Legendre and Legendre 2012) complemented this analysis to visually assess the relationship among indices and the evidence of which one is representing the same diversity component (Fig. 3). This led us to remove four correlated diversity indices. Therefore, the rest of the ranking was carried out considering the remaining six diversity indices: Rao's Functional, Phylogenetic and Taxonomic diversities, species richness, functional divergence and evolutionary distance (Hed).

(2) We standardized each selected index with the following formula proposed by Maire et al. (2013):

$$Div_{stand} = \frac{\alpha_x - \alpha_{minx}}{\alpha_{\max x} - \alpha_{\min x}}$$

where α is the value of the index in each area x, and $\alpha_{\min x}$ and $\alpha_{\max x}$ are the lowest and highest values of the index α in the area x. Therefore, the standardized indices $Div_{stand(\alpha)}$ vary between 0 and 1within each of the 15 sampled areas.

(3) We calculated a synthetic index (SI) of conservation prioritization by summing up each of the standardized indices in each site (Maire et al. 2013). SI varies from a minimum value (different from zero, that represents the area with the lowest values for all indices) to six (the maximum value obtained if one area has the highest value for all indices).

(4) Finally, we ranked the areas based on their SI values. Sites with SI > 3.0 were considered as high priority, since those represent the highest diversity values for at least four of the six indices.

To ensure that the areas for conservation prioritization are representing singular sites that add new diversity to the previously selected ones, we estimated the cumulative percentage of Rao's functional and phylogenetic diversity when adding new sites. We implemented this by ranking the sites from the most to the least diverse (in terms of Rao FD and PD), and vice-versa, and calculated the pulled Rao FD and PD by aggregating the sites in order along the diversity gradient (Devictor et al. 2010). We compared these curves to a Whisker plot that represents the random expectation given the same species richness by randomly selecting areas for protection and calculating the accumulation of diversity sorting three sites each time and repeating the process 20 times. Finally, we performed a sample-based rarefaction analysis to verify if sample effort influenced our synthetic metric for prioritization of sites (Fig. S2). The classic rarefaction of species richness (Gotelli and Colwell 2001) has only been implemented to Rao's FD and PD (Ricotta et al. 2012), so we based this analysis only using Rao in all three facets.

2.7 Spatial Autocorrelation

We tested spatial autocorrelation using Moran's I correlograms for all biodiversity facets (Legendre and Legendre 2012). We choose a priori six distance classes, each one composed by similar number of samples and the significance test for autocorrelation was based in 1000 randomizations. Moran's I correlogram was calculated in the software *Spatial Analysis in Macroecology* (SAM; Rangel et al. 2006, 2010).

3 Results

We found 70 species of anurans distributed on 15 areas in the Brazilian Cerrado, but we eliminated three of them from the analysis because of lack of information on their functional traits (Table S3). Only the last distance class (around 850 Km) presents a low negative autocorrelation in functional diversity (FD), indicating that distant sites have different patterns of FD (Fig. S3). For the other five diversity indices, we found no spatial autocorrelation (Fig. S3).

The most phylogenetically original species was *Chiasmocleis albopunctata*, followed by two other Microhylidae frogs (*Dermatonotus muelleri* and *Elachistocleis cesarii*, Table S4). In fact, the originality analyses gave higher weights to Microhylidae species, which constitutes a largely isolated clade on our tree (Fig. S1). In terms of functional originality, the most original species was *Leptodactylus labyrinthicus*, followed by *Physalaemus marmoratus*, *L. gr. labyrinthicus* and *Physalaemus centralis* (Table S4). The functional originality analysis gave higher weights to Leptodactylidae frogs (the four most functionally original species).

Five areas presented high priority values according to the synthetic index. One of them, Lago Cedro Extractive Reserve (LAG, Table 2, Fig. 2), is already protected. The remaining four areas are not currently protected: Nova Roma (NOV), São Miguel do Araguaia (MIG), Pontalina (PON) and Jataí (JAT, Table 2, Fig. 2). The sample-based rarefaction analysis showed that the recommendation of JAT as high priority area was partly driven by sampling bias, whereas the other sites were robust to such biases. Indeed, when we rarefied the species richness, Rao’s FD and PD, JAT did not have the highest value of functional and phylogenetic diversity (Fig. S2). Conversely, even after rarefying these diversity dimensions, the other three areas still have the highest diversity values.

Related to the accumulation of functional and phylogenetic diversity, we found that our prioritization approach always does significantly better at representing the diversity facets as compared to choosing the sites randomly (Fig. 4). We also found that areas already protected fall within the range of the random selection, which means that those sites do not protect functionally and phylogenetically diverse sites more efficiently than a random draw of sites (Fig. 4).

4 Discussion

As hotly debated in the last decade (Mason et al. 2005; Tucker et al. 2016), we demonstrated that the use of species richness is not necessarily a good proxy for other biodiversity dimensions. Here, by combining different biodiversity dimensions into a synthetic metric, we were able to select five areas deserving high conservation priority for anurans in the Cerrado biodiversity hotspot. More importantly, four of these areas (Nova Roma - NOV, São Miguel do Araguaia - MIG, Pontalina – PON and Jataí – JAT: Figs 1 and 2) are not included in the current network of Brazilian protected areas (Ministério do Meio Ambiente 2004), highlighting the under-representation of phylogenetic and functional composition in the current protected area planning. Our results fall in line with other regions and taxonomic groups, such as birds (Devictor et al. 2010), fishes (Strecker et al. 2011), spiders (Gonçalves-Souza et al. 2015) and plants (Pardo et al. 2017), reinforcing the idea that there is a strong mismatch among different biodiversity facets, and that our current conservation planning system focusing on taxonomic units disregards the importance of community properties. This is well illustrated in our Fig. 4, which shows that by considering 4 to 9 sites for conservation (depending on the facet, Fig. 4a vs 4b), we would be doing a significantly better job than a random draw by systematically using a compound index such as the one used here. Conversely, that same analysis also shows that the areas that are currently protected do not do a better job as compared to a random selection, when considering functional and phylogenetic diversity.

The mismatch between taxonomic diversity, which is usually the only facet considered in conservation planning, and the other facets of diversity, can have important consequences in terms of the selection of sites of high priority (Devictor et al. 2010; Gonçalves-Souza et al. 2015). For instance, some areas could have high species richness but low phylogenetic diversity when there is geographic isolation and recent colonization with fast in situ diversification. Similarly, when species are functionally redundant, there is an incongruence between species richness and functional diversity (Gillespie 2004; Weinstein et al. 2014). Furthermore, phylogenetic and functional originality could also affect whether species richness will work properly as a proxy for other diversity dimensions (Swenson et al. 2007). When there is strong trait conservatism, sister groups will show similar traits; conversely, under low conservatism, traits can be more labile within a group of species. It is therefore the combination of evolutionary history as well as ecological mechanisms currently affecting community assembly, which will determine the interplay and relevance of taxonomic, phylogenetic and functional components in a conservation context. Therefore, and as others have done before us (Devictor et al. 2010; Gonçalves-Souza et al. 2015), we also recommend the use of complementary indices in conservation decisions. Our arguments are further reinforced by the recent study by Pollock et al. (2017), in which they demonstrated, at a global scale, that linking multifaceted biodiversity provides large conservation gains for birds and mammals by ensuring a rich array of further effects for the ecosystem functioning and human well-being.

4.1 Implications for the Brazilian protected network: the case of the Cerrado hotspot

Limited funding available for nature conservation usually jeopardizes our ability to protect biodiversity over large areas (Bruner et al. 2004). By using different approaches, and different diversity measures, we may avoid overlooking important features in deciding conservation prioritization. However, increasing human, social and academic effort to cover different conservation approaches is a double-edged sword, because it improves information assessment, but it increases conservation costs. The most common approach to identify conservation priority areas is to try to represent the maximum biodiversity while minimizing the total cost or area allocated to protected areas (Margules and Pressey 2000). Our approach uses different diversity facets, such as evolutionary history and functional traits, to increase the robustness of the selection of priority areas without significantly increasing conservation costs.

There are good reasons to create new protected areas in the Cerrado hotspot, including the small percent of land currently protected (only 2.85% of the Cerrado hotspot in integral protection conservation units) (Ministério do Meio Ambiente 2017) and the high deforestation rates, which make it one of the most threatened biomes on the South American continent (Silva and Bates 2002; Klink and Machado 2005). Interestingly, the areas JAT and NOV, were already defined as high priority areas for conservation in 2016 by the Brazilian Ministry of the Environment. These areas should be urgently protected because they have high anuran diversity in multiple facets (this study), as well as presence of traditional human communities, high esthetic value given by the caverns in the region, and presence of dry forests (Ministério do Meio Ambiente 2017). The other two areas, MIG and PON, were not included in this government document, and we argue that they should be added. On top of their high multifaceted biodiversity value, these two sites are located in areas under high agriculture and pasture pressure (Ministério do Meio Ambiente 2017), which cause water silting by soil erosion and contamination of water bodies, increasing the threats to anuran species.

4.2 Implications for anuran conservation

According to the IUCN red list (IUCN 2017), most of the anuran species present in our study area are not under any type of threat (excepted *Hypsiboas cipoensis*, which is considered "near threatened"). Thus, even if red lists are a useful and effective tool for conservation of vertebrates in general at large scales (Rodrigues et al. 2006), here they would not have added any useful insights regarding the conservation of anuran biodiversity. As Hidasi-Neto et al. (2013) have demonstrated, IUCN red lists are not able to capture on their own the ecological and evolutionary importance of species. This emphasizes the need of adding additional criteria to the IUCN red lists. Here, we argue that those lists should systematically include, both at the site level and at the species level, the value of phylogenetic and functional differences between species in reinforcing ecological processes.

In that context, an important criterion is species originality, which prioritizes species based on unique functional traits or evolutionary history (Pavoine et al. 2005). The pattern we have found suggests that some species contributing disproportionately to the functional or phylogenetic originality pattern of some areas deserve conservation attention, even if some of them are widespread. In the Cerrado hotspot, Microhylidae frogs, *Chiasmocleis albopunctata*, *Dermatonotus muelleri*, and *Elachistocleis cesarii* showed the most distinctive evolutionary history, which goes along the lines of Silvano et al. (2016) who had already characterized this group as evolutionary distinct in the Cerrado. This clade diversified about 70 million years ago during the late Cretaceous and early Tertiary, and has been an important source of diversification ever since (Roelants et al. 2007). Microhylidae frogs are fossorial species, and many of them present explosive breeding. Thus, these frogs only get out of the ground for reproduction, which occurs just once in a year (Wells 1977). These biological and behavioral characteristics allow them to deal with the severe dry season and frequent fires occurring in the Cerrado.

Opposite arguments regarding phylogenetically distinctiveness of groups have been made in the literature. On one hand it has been argued that recently diversified clades represent taxonomic groups that have higher evolutionary potential to adapt quickly to environmental changes, because they already show quick adapted evolutionary history (Erwin 1991; Mace et al. 2003). This would mean little phylogenetic originality at the species level would be compensated by high functional originality within a group and/or high phylogenetic and functional diversity at the community level. On the other hand, it has also been argued that older and more distinct clades carry high evolutionary potential to deal with stressful and stochastic events because of the accumulation of genetic diversification through time (Sgrò et al. 2011; Mouquet et al. 2012). This would mean that we should value phylogenetic originality over other diversity considerations. Despite these contradictions, two facts remain clear throughout both arguments. First, losing a species that represents an old and unique lineage is of conservation concern on itself, since its disappearance will eliminate a branch of evolutionary history that will remain unrepresented. In that context, highlighting the phylogenetic originality of these Microhylidae frogs can help us consider their conservation under a new perspective. And second, whether phylogenetic diversity represents on itself a desirable quality in conservation sites will depend on its relationship to functional properties of the ecosystems.

The four new areas identified here have at least one of these phylogenetic original species in their composition: *D. muelleri* (Microhylidae) and *E. cesarii* (Microhylidae) in NOV, *E. cesarii* in MIG, *D. muelleri* and *E. cesarii* in PON, and *E. cesarii* in JAT. Despite their functional originality, *L. labyrinthicus* and *P. centralis* were the only two functionally original species present in the selected areas, both were found in MIG, and *P. centralis* in JAT. These species exhibit traits that are making them unique in the sampled areas: the type of reproductive mode, the ability of their tadpoles to live in the bottom of ponds, and, in the case of *L. labyrinthicus*, reduced labial tooth rows (de Sousa et al. 2014). Their eggs are embedded in a foam nest, avoiding their desiccation (Zina 2006). The benthonic foraging of their free-living tadpoles and the foam nests of both species allow them to survive even when water volume decreases, a common event in a savanna biome. Although the functional roles of these species have not been thoroughly quantified in these ecosystems, tadpoles in general are crucial for nutrient cycling in water bodies because they affect the abundance and diversity of basal resources and primary consumers (Ranvestel et al. 2004), and abundant species are particularly important in influencing trophic links. Benthic tadpoles facilitate periphyton production by grazing, being key organisms for the food web dynamics and energy flow (Ranvestel et al. 2004). These kinds of traits seem to be associated with idiosyncratic functions that increase ecosystem functioning. Furthermore, as either functionally or phylogenetically original species have a significant contribution to the diversity of these high priority areas, losing these species in still unprotected areas could erode regional biodiversity. We therefore believe that future studies should focus on the role of these functionally unique species in maintaining water ecosystem health in the region.

5 Conclusions

In November 2016, the Brazilian Ministry of the Environment published a guide to enlarge, implement and consolidate the Brazilian national system of conservation units (SNUC) aiming to include new areas in the conservation system. Here we recommend that in a near future four areas in the Cerrado hotspot should be legally protected by Brazilian laws. More broadly, we strongly argue for the inclusion of phylogenetic and functional considerations in conservation planning. Selecting protected areas based on traditional biodiversity metrics that ignore the uniqueness of each species, such as species richness and endemism, disregards evolutionary and functional considerations that may be key for ecosystem resilience. Taxonomic criteria can be misleading because (i) they usually ignore evolutionary patterns, (ii) they do not ensure community persistence in the long term (Forest et al. 2007; Faith 2008) and, (iii) they do not allow us to make predictions about functional consequence of environmental changes (Díaz et al. 2007; Reiss et al. 2009). Ultimately, we can only guarantee the long-term maintenance of the community if we can protect key ecosystem functions, rather than species or sites selected at random or through rarity criteria, and we have to admit that species that are sometimes abundant or widespread may play key roles in the maintenance of ecosystems functions. One of the key advantages of our approach is that it allows incorporating such criteria, even without a full understanding of species evolutionary and functional roles within the community. One could argue that allocating limited conservation funds to species and sites that are unique on either one of these dimensions is a sensible investment for future resilience of ecosystems.

In addition, it is important to highlight that our study tried to fill the gap existing in anuran conservation regarding water-dependent larval stages. By conserving early developmental stages, we are increasing the probability that anurans reach their adult phase. Adult anurans exhibit an important role in mosquito control, the most common vectors of diseases in tropical systems.

Our study certainly has some potential limitations, such as the fact that we cannot tease apart the contribution of terrestrial, semi-terrestrial, and phytotelma species to ecosystem functioning, or how do species (and lineages) respond to different environmental habitats (e.g. ponds, streams). Thus, we encourage future studies to expand this approach to terrestrial and aquatic habitats. Also, there might be other more efficient ways to combine phylogenetic and functional information into a compound index, or even specific situations under which we might want to consider one or the other facet as more important for prioritization. However, this case study clearly demonstrates that the establishment of conservation strategies for anurans in the Cerrado can be improved by considering multiple biodiversity facets to maximize anuran protection. A major field that remains to be explored for a better assessment of the functional approach is the quantification of ecosystem services that are performed by anurans, including the key links to other trophic levels (e.g., how many mosquitos do they eat and what would happen with certain diseases if anurans disappear).

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Tables

Table 1. Dimensions of diversity (biodiversity facets), respective definition and diversity metrics used to quantify them. Species richness (SR), Rao’s taxonomic diversity ($\mathrm{TD}_{\mathrm{RAO}}$), Functional richness (FRic), Functional divergence (FDiv), Rao’s functional diversity ($\mathrm{FD}_{\mathrm{RAO}}$), Faith’s phylogenetic diversity (PD_{F}), Mean pairwise phylogenetic distance (MPD), Rao’s phylogenetic diversity ($\mathrm{PD}_{\mathrm{RAO}}$), Evolutionary distinctiveness (Hed and Haed).

Facet	Diversity			Originality
	Richness	Divergence	Regularity	
Taxonomic	Number of species: - SR	The degree of species similarities in a community: - $\mathrm{TD}_{\mathrm{RAO}}$ (Rao 1982)	The regularly distribution of species abundances in a community: - $\mathrm{TD}_{\mathrm{RAO}}$ (Rao 1982)	-
Phylogenetic	Total evolutionary history accumulated in a community: - PD_{F} (Faith 1992)	Mean phylogenetic distance of all species in a community: - $\mathrm{PD}_{\mathrm{RAO}}$ (Rao 1982) - MPD (Webb et al. 2002)	The regularly distribution of species in the phylogenetic tree in a community: - Rao's functional entropy (Rao 1982) - Hed and Haed (Cadotte et al. 2010)	How unique a species is according to its evolutionary history: - Phylogenetic Originality (Pavoine et al. 2005)
Functional	Total trait space accumulated in a community: - FRic (Villéger et al. 2008)	Mean divergence of functional characters in a community: - $\mathrm{FD}_{\mathrm{RAO}}$ (Rao 1982) - FDiv (Mason et al. 2003)	The regularly distribution of species traits abundances in a community: - $\mathrm{FD}_{\mathrm{RAO}}$ (Rao 1982)	How unique a species is according to its functional traits: Functional Originality (Pavoine et al. 2005)

Table 2. Conservation priority values for each area in the Brazilian Cerrado. Those in italic are already included in the Brazilian protected areas network and in bold are the areas identified as priorities for conservation. RESEX = Extractive Reserve, PE = State Park.

Areas	Synthetic Index
Nova Roma	4.11
São Miguel do Araguaia	4.07
RESEX Lago Cedro	4.07
Pontalina	3.41
Jataí	3.19
PE Lajeado	3.00
Alto Paraíso de Goiás	2.52
Pires do Rio	2.35
São João da Aliança	2.15
Caiapônia	2.08
Chapadão do Céu	1.76
Cristalina	1.52
PE Cerrado	1.43
PE Sempre Vivas	1.42
Serranópolis	1.14

Figures

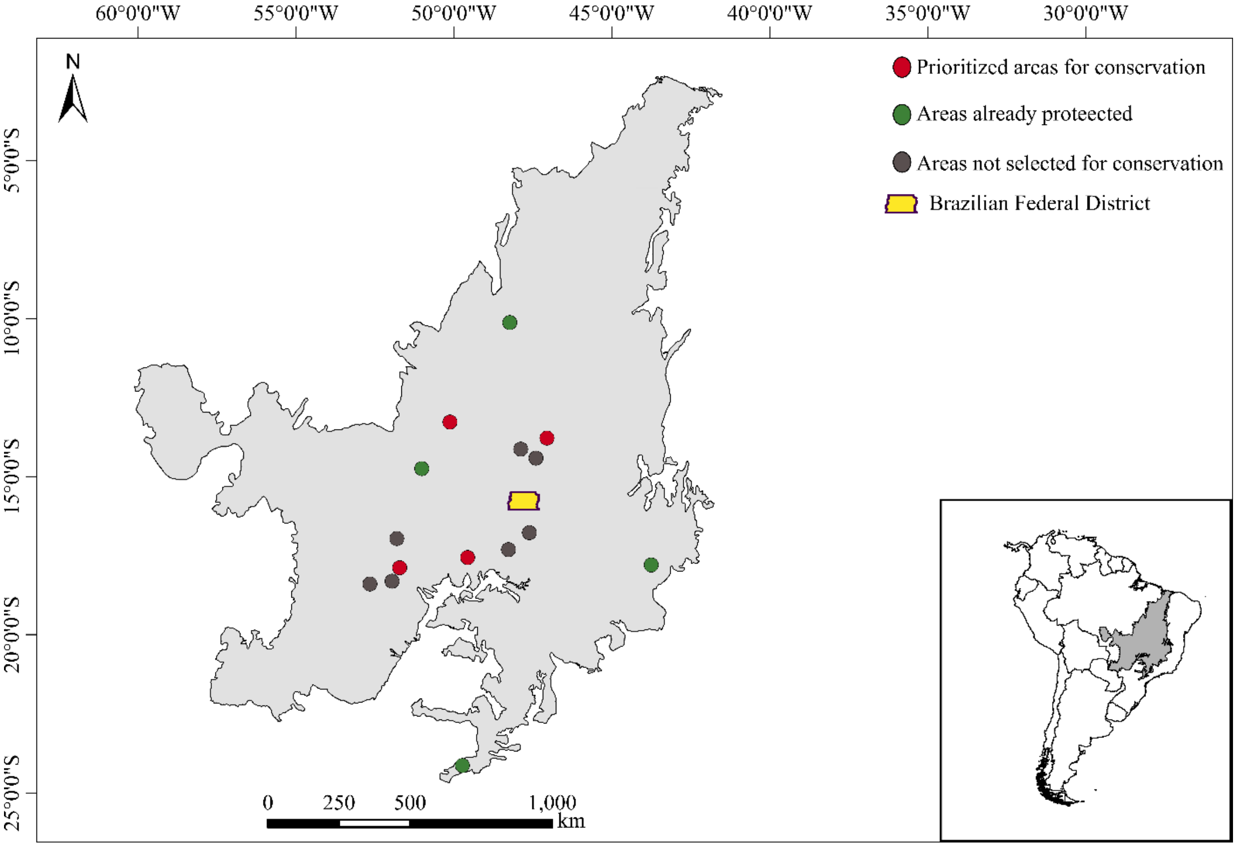
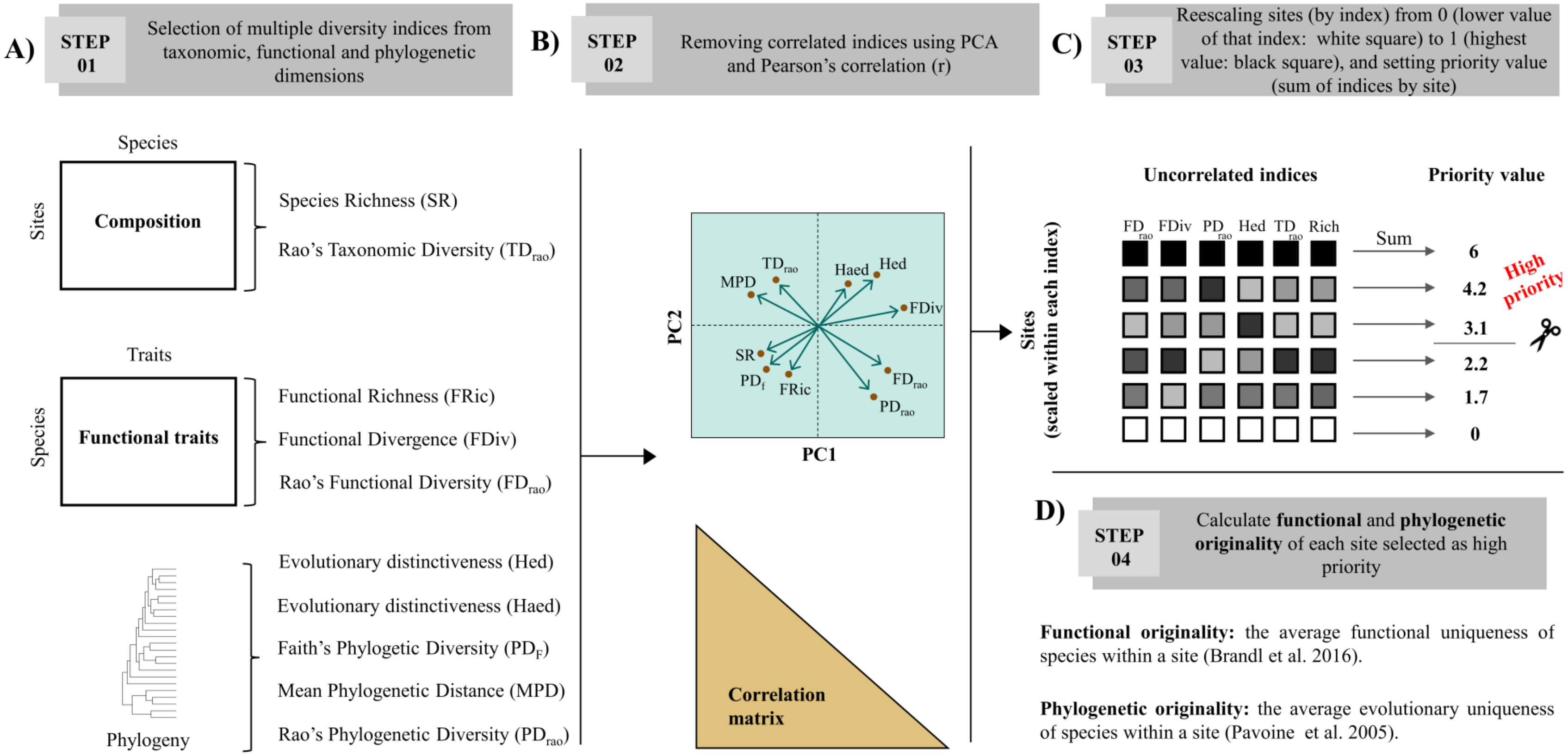


Fig 1. Distribution of 15 sampled areas in Brazilian Cerrado. Green dots represent already protected areas. Red dots are the areas selected by us as the priorities for conservation of multiple dimension of diversity. Gray dots are areas not selected as a priority in our conservation approach.



Functional originality: the average functional uniqueness of species within a site (Brandl et al. 2016).

Phylogenetic originality: the average evolutionary uniqueness of species within a site (Pavoine et al. 2005).

Fig 2. Main steps used in the prioritization for conservation in Cerrado. First, we performed the selection of multiple diversity indices using PCA (**Fig 3**) and Pearson's correlation corrected by Bonferroni criteria (Table S2). Second, we tested and removed the correlated indices. Third, we summed up the six indices selected for each area to obtain a synthetic index (SI) of conservation prioritization (Maire et al. 2013). SI varies from a minimum value (different from zero, that represents the area with the lowest values for all indices) to six (the maximum value obtained if one area has the highest value for all indices). We rank the areas based on their SI values and considered as areas with high priority for conservation those with SI > 3.0. Last, we calculated functional and phylogenetic originality.

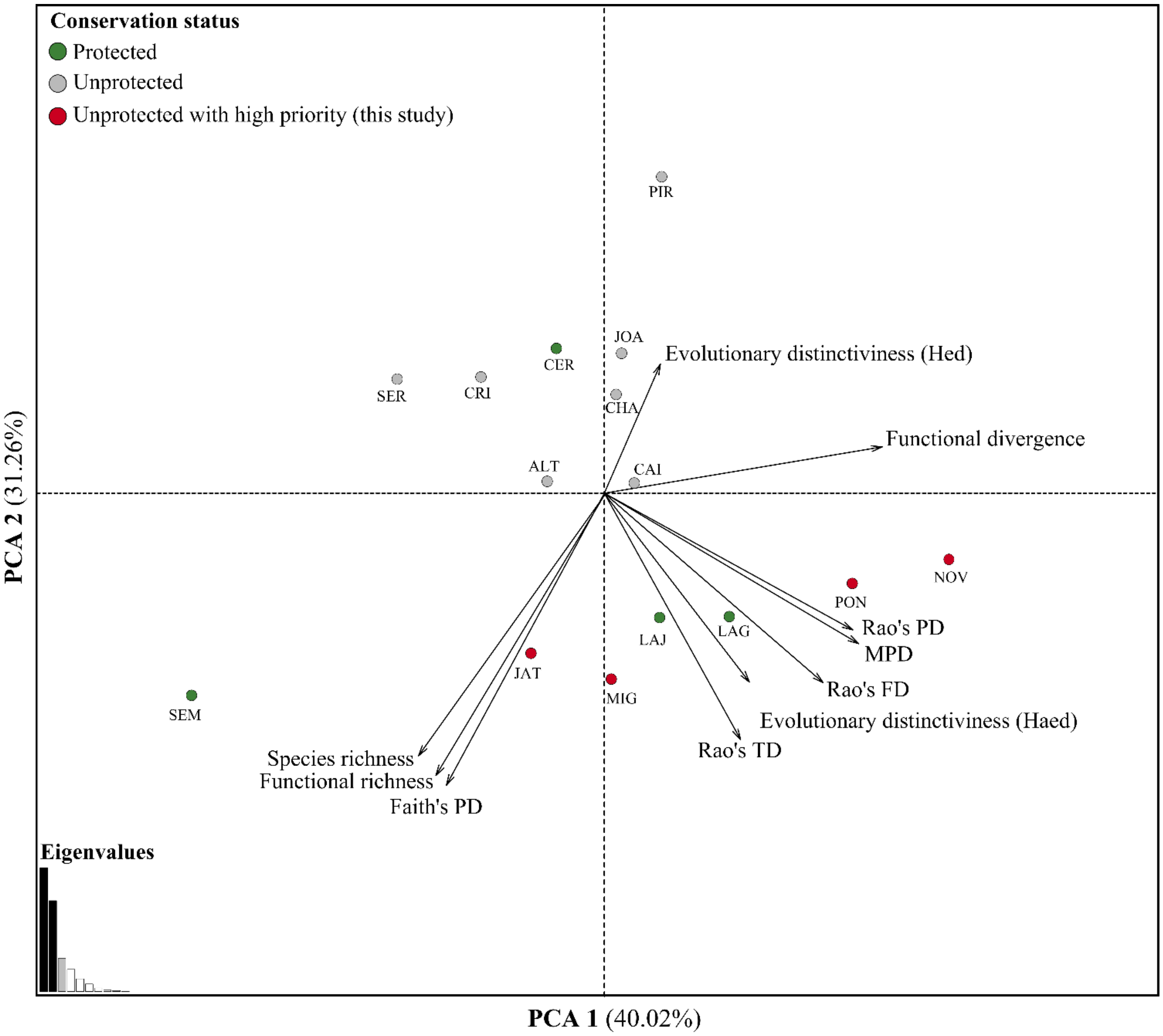


Fig 3. Principal component analysis of biodiversity indices. First axis explained 40.02% and second axis 31.26% of all data variation. Red circles represent sites with the lowest biodiversity values of all indices, excepted evolutionary distinctiveness (Hed). Abbreviations mean: CER (Cerrado State Park), LAJ (Lajeado State Park), LAG (Lago Cedro Extractive Reserve), SEM (Sempre Vivas State Park), JAT (Jataí), MIG (São Miguel do Araguaia), NOV (Nova Roma), PON (Pontalina), ALT (Alto Paraíso de Goiás), CAI(Caiapônia), CHA (Chapadão do Céu), CRI (Cristalina),JOA (São João da Aliança), SER (Serranópolis) and, PIR (Pires do Rio).

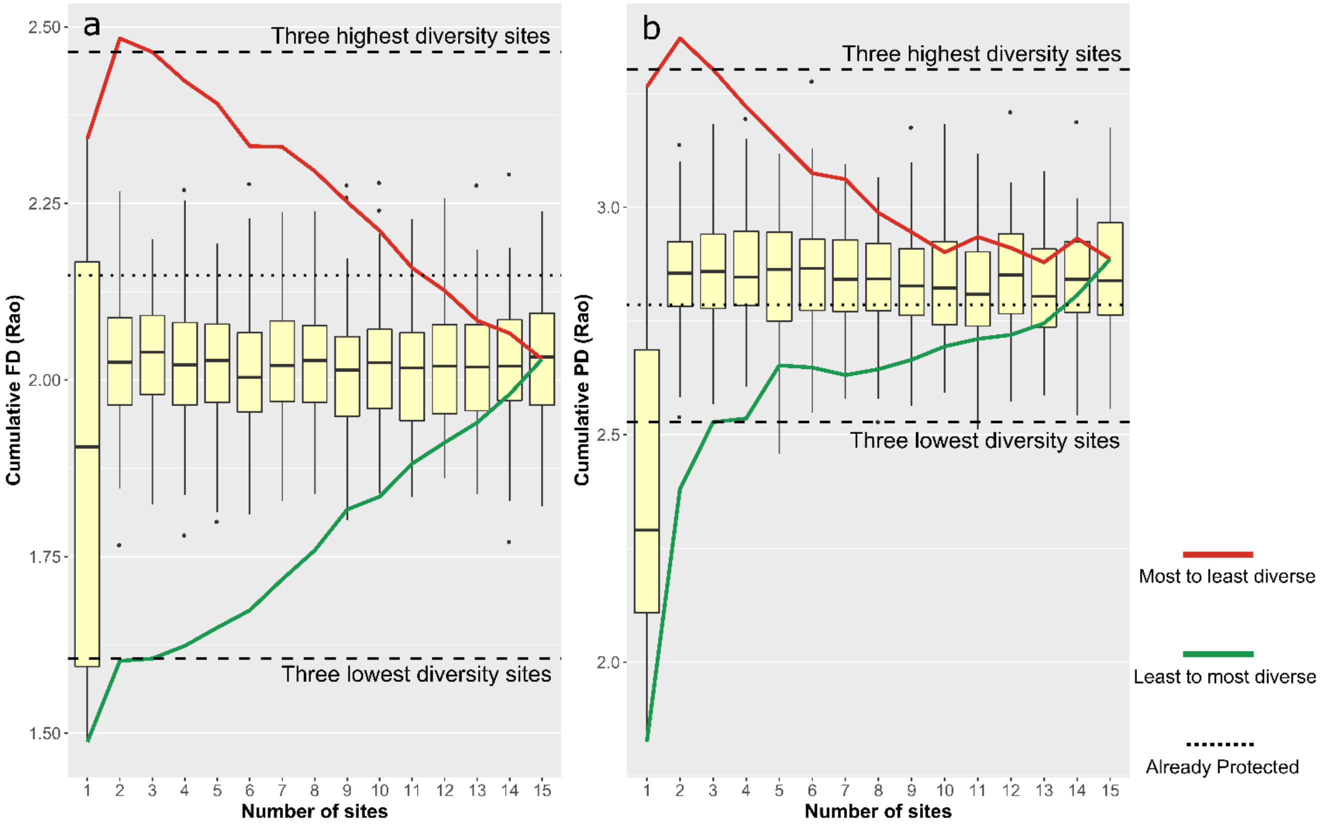


Fig 4. Diversity accumulation curves for (a) Functional Diversity (FD) and (b) Phylogenetic Diversity (PD) as calculated with Rao's index. Whisker boxes represent FD or PD for the same number of randomly selected sites. The red line represents the strategy where sites are added in order, from the most diverse to the least diverse. The green line represents the diversity if we added sites in the opposite order (from the least to the most diverse). The dotted line represents diversity in the sites already protected, and the two dashed lines represent cumulative diversity in the three sites containing either the highest or the lowest diversity. Therefore, the green line would represent adding sites in the least efficient possible way, whereas the red line is the most efficient way. Notice that the red line is above the whisker boxes (random expectation) and above the dotted line (already protected) until we have added almost all the sites to the protected area network, meaning that our strategy would, for any given number of protected sites, protect more functional and phylogenetic diversity than either the current protected areas or the least-to-most diversity strategy.

SUPPLEMENTARY MATERIAL

Integrating phylogenetic and functional biodiversity facets to guide conservation: a case study using anurans in a global biodiversity hotspot

L.S. Ouchi-Melo, Christine N. Meynard, T.Gonçalves-Souza and D.C.Rossa-Feres

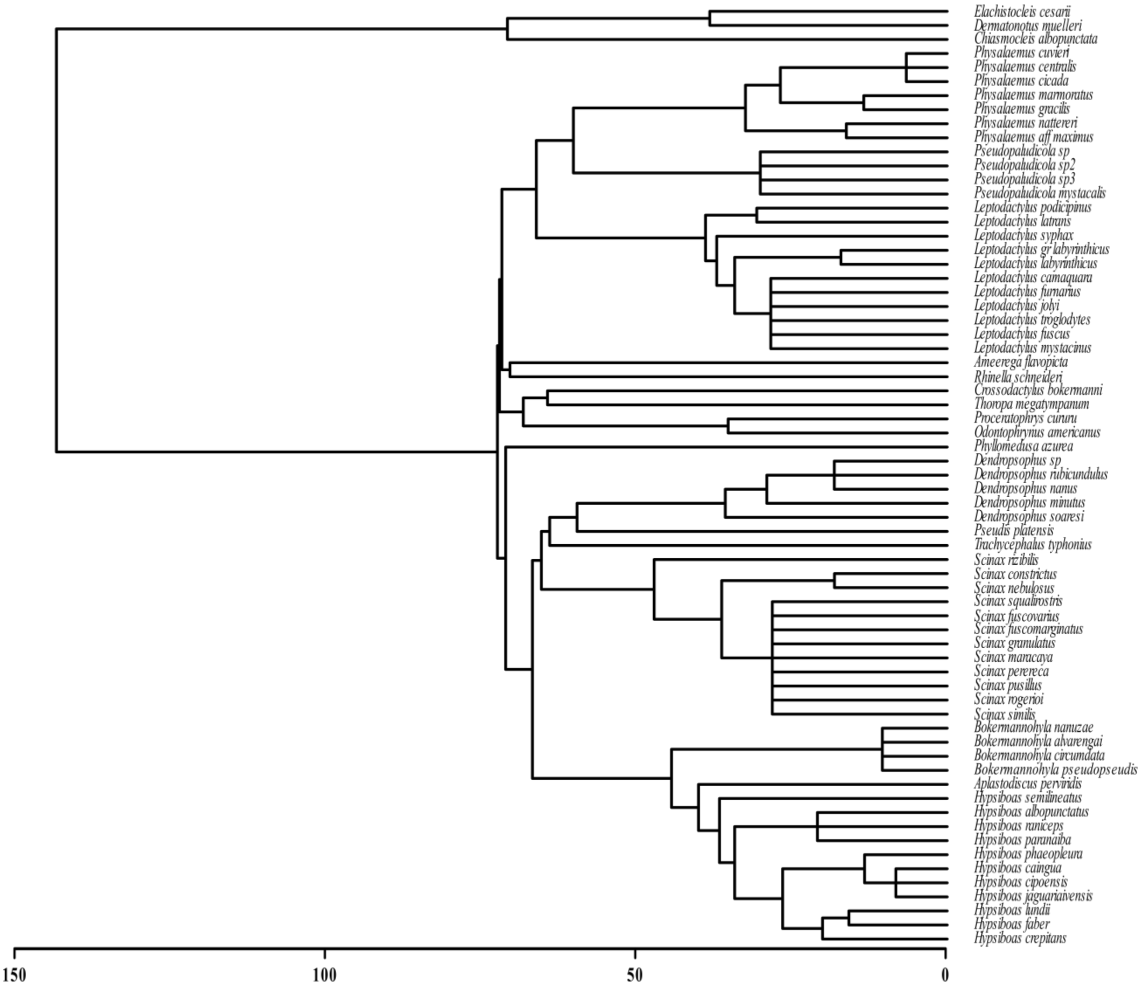


Figure S1. Phylogenetic relationships between Cerrado anuran species in millions of years.

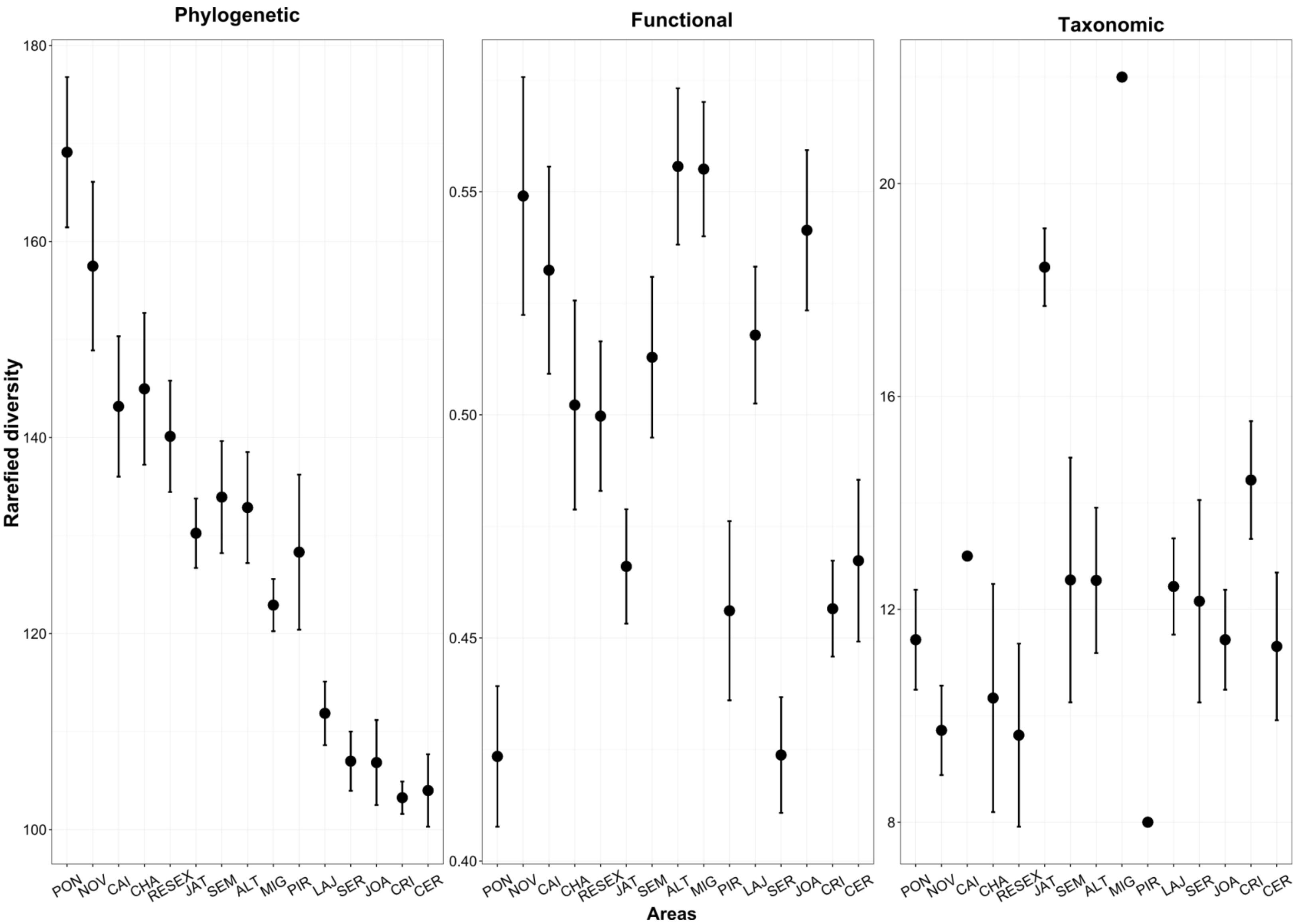
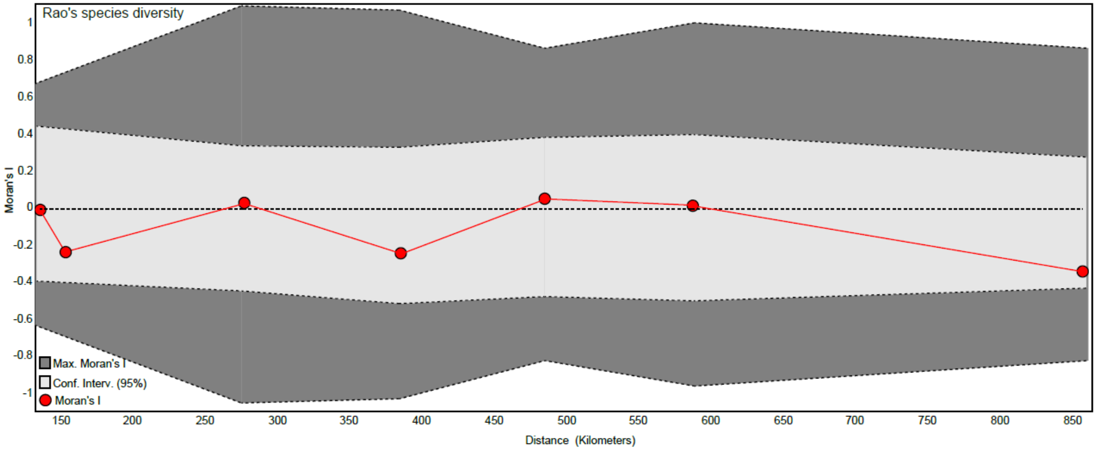
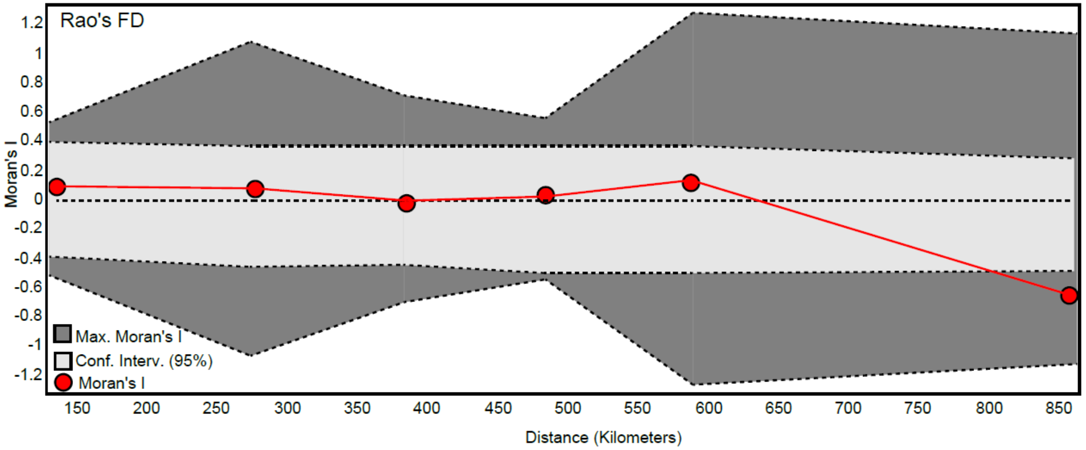
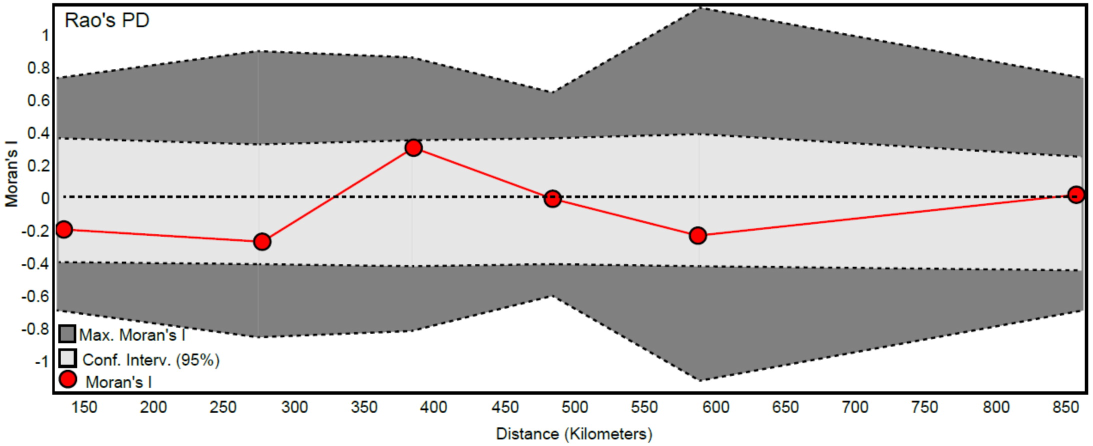
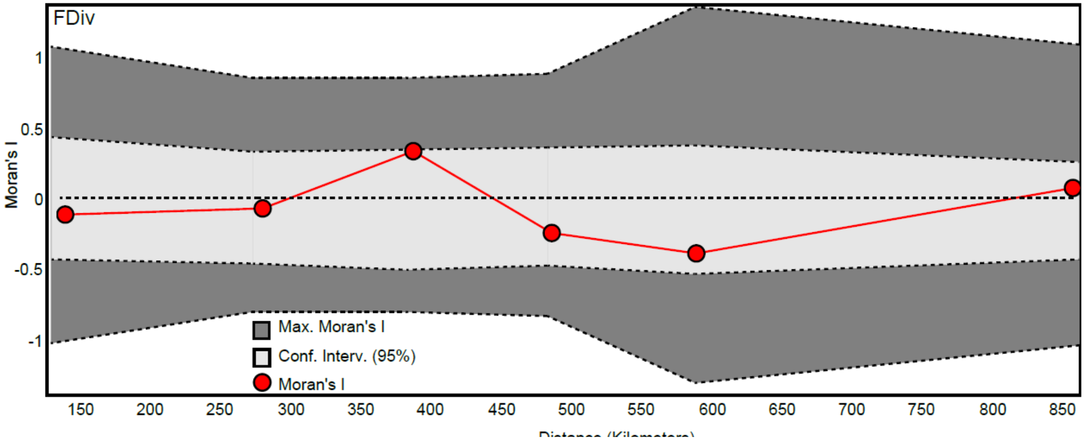


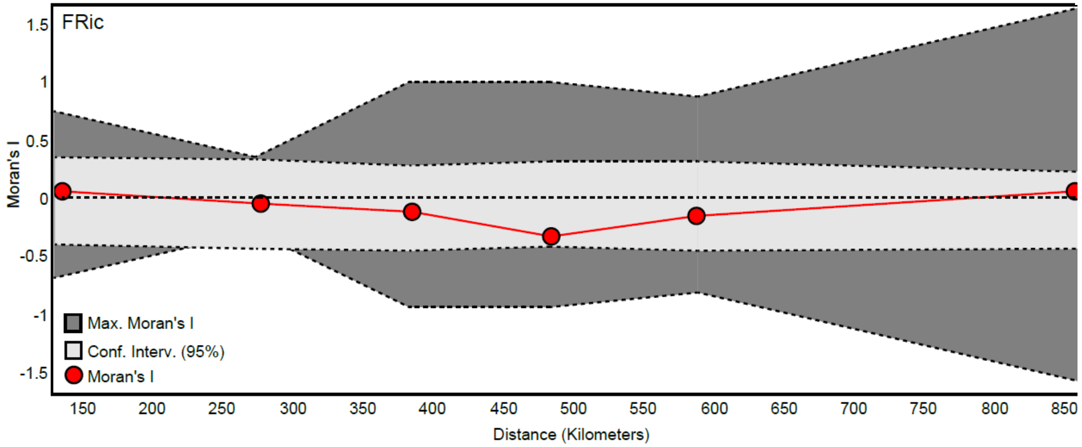
Figure S2. Rarefaction curves. Phylogenetic rarefaction, Functional rarefaction and, Taxonomic rarefaction (richness rarefaction) respectively.


Rao's species diversity
Moran's I
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
150
200
250
300
350
400
450
500
550
600
650
700
750
800
850
Distance (Kilometers)
▨ Max. Moran's I
☐ Conf. Interv. (95%)
● Moran's I


Rao's FD
Moran's I
1.2
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
-1.2
150
200
250
300
350
400
450
500
550
600
650
700
750
800
850
Distance (Kilometers)
▨ Max. Moran's I
☐ Conf. Interv. (95%)
● Moran's I


Rao's PD
Moran's I
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
150
200
250
300
350
400
450
500
550
600
650
700
750
800
850
Distance (Kilometers)
▨ Max. Moran's I
☐ Conf. Interv. (95%)
● Moran's I


FDiv
Moran's I
1
0.5
0
-0.5
-1
150
200
250
300
350
400
450
500
550
600
650
700
750
800
850
▨ Max. Moran's I
☐ Conf. Interv. (95%)
● Moran's I


FRic
Moran's I
1.5
1
0.5
0
-0.5
-1
-1.5
150
200
250
300
350
400
450
500
550
600
650
700
750
800
850
Distance (Kilometers)
▨ Max. Moran's I
☐ Conf. Interv. (95%)
● Moran's I

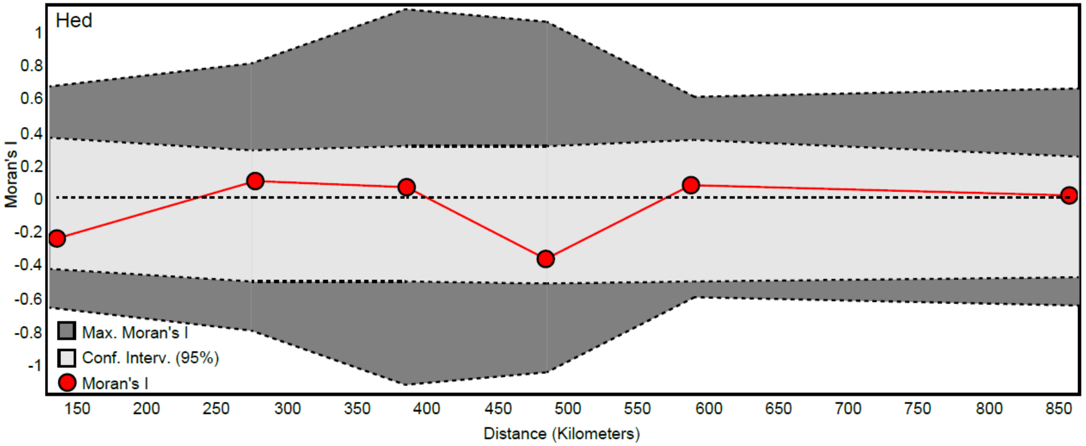

Hed
Moran's I
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
150
200
250
300
350
400
450
500
550
600
650
700
750
800
850
Distance (Kilometers)
▨ Max. Moran's I
☐ Conf. Interv. (95%)
● Moran's I

Table S1. Functional traits and their ecosystem function and the conservation expectation indicated by each one.

Functional trait	Function	Conservation expectation
Total length size (mm)	Survivorship ability (Smith, 1987)	Species with high total size tend to present greater survivorship ability than small ones (Smith, 1987). By consequence, less conserved environments tend to house larger species than preserved ones.
Body compression (body high in mm divided by body width in mm)	Position in water column (vertical preferences, (Altig, 2007; Queiroz et al., 2015)	Better conserved environments tend to house species with more variability than worst conserved ones. Environmental conserved habitats show better quality represented by deeper water column and food availability abundance, tending to house greater body compression diversity within the waterbody.
Number of teeth rows (categorical based on number of teeth rows)	Food acquisition (Venesky et al., 2010)	Environmental conserved habitats present high food availability (zooplankton and phytoplankton). By consequence species with great variability of number of teeth row tend to occur in conserved habitats (e.g. scrap feeder species have greater number of teeth rows than filter feeder species, and both tend to occur in preserved habitats).
Reproductive mode (categorical based on reproductive mode type)	Type of development (Haddad & Prado 2005)	A greater number of reproductive modes are expected in environmental conserved habitats, once they present high environmental heterogeneity than less conserved ones.

Table S2. Pearson's correlation among the diversity index: Rao's taxonomic diversity (TD), Rao's phylogenetic diversity (PD), Rao's functional diversity (FD), richness (Rich), functional richness (FRic), functional divergence (Fdiv), Faith's phylogenetic diversity (PDf), Mean pairwise distance (mpd), phylogenetic distinctiveness (Hed). The values above the diagonal are *P-values* adjusted by Bonferroni criteria. Values below diagonal are correlation values.

	TD	PD	FD	Rich	Fric	Fdiv	PDf	mpd	Haed	Hed
TD		1	0.16	1.00	1.00	1.00	1.00	0.64	1.00	1.00
PD	0.54		0.31	1.00	1.00	1.00	1.00	<0.001*	1.00	1.00
FD	0.70	0.66		1.00	1.00	0.17	1.00	0.12	1.00	1.00
Rich	0.23	-0.19	-0.15		<0.001*	1.00	<0.001*	1.00	1.00	1.00
Fric	0.16	-0.23	0.10	0.88		1.00	<0.001*	1.00	1.00	1.00
Fdiv	0.41	0.56	0.70	-0.50	-0.36		1.00	0.78	1.00	1.00
PDf	0.29	-0.09	0.02	0.94	0.90	-0.36		1.00	1.00	1.00
mpd	0.62	0.99	0.71	-0.18	-0.20	0.60	-0.08		1.00	1.00
Haed	0.27	0.32	0.51	0.04	0.11	0.40	0.15	0.35		1.00
Hed	-0.04	-0.03	0.11	-0.33	-0.14	0.42	-0.25	-0.03	-0.31	

* Asterisk indicatesignificative values of correlation.

Table S3. List of anuran species present at Cerrado sites with respective families and status of threaten according to International Union for Conservation of Nature (IUCN) red list. Red species were put out of our statistical analysis (see methodology).

Species list	Family	IUCN red list status
Amereega flavopicta	Bufonidae	Least concern
Aplastodiscus perviridis	Hylidae	Least concern
Bokermannohyla alvarengai	Hylidae	Least concern
Bokermannohyla circumdata	Hylidae	Least concern
Bokermannohyla nanuzae	Hylidae	Least concern
Bokermannohyla pseudopseudis	Hylidae	Least concern
Chiasmocleis albopunctata	Microhylidae	Least concern
Crossodactylus bokermanni	Hylodidae	Data deficient
Dendropsophus sp	Hylidae	-
Dendropsophus jimi	Hylidae	Least concern
Dendropsophus minutus	Hylidae	Least concern
Dendropsophus nanus	Hylidae	Least concern
Dendropsophus rubicundulus	Hylidae	Least concern
Dendropsophus soaresi	Hylidae	Least concern
Dermatonotus muelleri	Hylidae	Least concern
Elachistocleis cesarii	Microhylidae	Least concern
Physalaemus nattereri	Leptodactylidae	Least concern
Hypsiboas albopunctatus	Hylidae	Least concern
Hypsiboas caingua	Hylidae	Least concern
Hypsiboas cipoensis	Hylidae	Near thretened
Hypsiboas crepitans	Hylidae	Least concern
Hypsiboas faber	Hylidae	Least concern
Hypsiboas jaguariaivensis	Hylidae	Least concern
Hypsiboas lundii	Hylidae	Least concern
Hypsiboas paranaiba	Hylidae	Least concern
Hypsiboas pardalis	Hylidae	Least concern
Hypsiboas phaeopleura	Hylidae	Least concern
Hypsiboas prasinus	Hylidae	Least concern
Hypsiboas raniceps	Hylidae	Least concern
Hypsiboas aff semilineatus	Hylidae	-
Leptodactylus camaquara	Leptodactylidae	Data deficient
Leptodactylus furnarius	Leptodactylidae	Least concern
Leptodactylus fuscus	Leptodactylidae	Least concern
Leptodactylus jolyi	Leptodactylidae	Data deficient
Leptodactylus labyrinthicus	Leptodactylidae	Least concern

Leptodactylus gr labyrinthicus	Leptodactylidae	-
Leptodactylus latrans	Leptodactylidae	Least concern
Leptodactylus mystacinus	Leptodactylidae	Least concern
Leptodactylus podicipinus	Leptodactylidae	Least concern
Leptodactylus syphax	Leptodactylidae	Least concern
Leptodactylus troglodytes	Leptodactylidae	Least concern
Odontophrynus americanus	Odontophrynidae	Least concern
Phyllomedusa azurea	Hylidae	Data deficient
Physalaemus centralis	Leptodactylidae	Least concern
Physalaemus cicada	Leptodactylidae	Least concern
Physalaemus cuvieri	Leptodactylidae	Least concern
Physalaemus gracilis	Leptodactylidae	Least concern
Physalaemus marmoratus	Leptodactylidae	Least concern
Physalaemus aff maximus	Leptodactylidae	-
Proceratophrys cururu	Odontophrynidae	Data deficient
Pseudis platensis	Hylidae	Data deficient
Pseudopaludicola mystacalis	Leptodactylidae	Least concern
Pseudopaludicola sp	Leptodactylidae	-
Pseudopaludicola sp2	Leptodactylidae	-
Pseudopaludicola sp3	Leptodactylidae	-
Rhinella schneideri	Bufonidae	Least concern
Scinax constrictus	Hylidae	Least concern
Scinax fuscomarginatus	Hylidae	Least concern
Scinax fuscovarius	Hylidae	Least concern
Scinax granulatus	Hylidae	Least concern
Scinax maracaya	Hylidae	Data deficient
Scinax nebulosus	Hylidae	Least concern
Scinax perereca	Hylidae	Least concern
Scinax pusillus	Hylidae	Least concern
Scinax rizibilis	Hylidae	Least concern
Scinax rogerioi	Hylidae	-
Scinax similis	Hylidae	Least concern
Scinax squalirostris	Hylidae	Least concern
Thoropa megatympanum	Cycloramphidae	Least concern
Trachycephalus typhonius	Hylidae	Least concern

Table S4. QE based phylogenetic and functional originality values for 67 anuran species from Brazilian Cerrado. The values of species originality are organized in decreasing order to highlight the most original species.

Species	Phylogenetic originality	Species	Functional originality
Chiasmocleis albopunctata	0.180	***Leptodactylus labyrinthicus***	0.099
Dermatonotus muelleri	0.123	***Physalaemus marmoratus***	0.064
Elachistocleis cesarii	0.123	***Leptodactylus gr labyrinthicus***	0.064
Rhinella schneideri	0.039	***Physalaemus centralis***	0.056
Ameerega flavopicta	0.039	*Phyllomedusa azurea*	0.055
Phyllomedusa azurea	0.038	*Bokermannohyla pseudopseudis*	0.042
Thoropa megatympanum	0.034	*Hypsiboas semilineatus*	0.038
Crossodactylus bokermanni	0.034	*Dendropsophus soaresi*	0.037
Trachycephalus typhonius	0.025	*Dendropsophus minutus*	0.037
Odontophrynus americanus	0.025	*Trachycephalus typhonius*	0.035
Proceratophrys cururu	0.025	*Ameerega flavopicta*	0.031
Pseudis platensis	0.022	*Thoropa megatympanum*	0.031
Scinax rizibilis	0.015	*Leptodactylus latrans*	0.028
Dendropsophus soaresi	0.012	*Leptodactylus troglodytes*	0.027
Pseudopaludicola mystacalis	0.010	*Scinax nebulosus*	0.027
Pseudopaludicola sp3	0.010	*Bokermannohyla alvarengai*	0.022
Pseudopaludicola sp2	0.010	*Bokermannohyla nanuzae*	0.022
Pseudopaludicola sp	0.010	*Hypsiboas faber*	0.020
Aplastodiscus perviridis	0.010	*Chiasmocleis albopunctata*	0.015
Leptodactylus syphax	0.009	*Pseudopaludicola sp2*	0.015
Dendropsophus minutus	0.009	*Pseudopaludicola sp3*	0.015
Leptodactylus latrans	0.009	*Pseudopaludicola sp*	0.015
Leptodactylus podicipinus	0.009	*Pseudopaludicola mystacalis*	0.015
Physalaemus aff maximus	0.008	*Aplastodiscusper viridis*	0.013
Physalaemus nattereri	0.008	*Leptodactylus furnarius*	0.010
Hypsiboas semilineatus	0.008	*Leptodactylus mystacinus*	0.010
Physalaemus gracilis	0.007	*Leptodactylus syphax*	0.010
Physalaemus marmoratus	0.007	*Physalaemus cicada*	0.010
Scinax nebulosus	0.006	*Elachistocleis cesarii*	0.010
Scinax constrictus	0.006	*Hypsiboas lundii*	0.009
Dendropsophus nanus	0.005	*Hypsiboas crepitans*	0.009
Dendropsophus rubicundulus	0.005	*Leptodactylus jolyi*	0.008
Dendropsophus sp	0.005	*Leptodactylus podicipinus*	0.007
Leptodactylus labyrinthicus	0.005	*Physalaemus nattereri*	0.007
Leptodactylus gr labyrinthicus	0.005	*Physalaemus gracilis*	0.006
Bokermannohyla pseudopseudis	0.004	*Leptodactylus camaquara*	0.006
Bokermannohyla circumdata	0.004	*Leptodactylus fuscus*	0.006
Bokermannohyla alvarengai	0.004	*Dendropsophus sp*	0.006
Bokermannohyla nanuzae	0.004	*Dermatonotus muelleri*	0.006
Physalaemus cicada	0.004	*Hypsiboas raniceps*	0.005
Physalaemus centralis	0.004	*Dendropsophus nanus*	0.004
Physalaemus cuvieri	0.004	*Dendropsophus rubicundulus*	0.004
Leptodactylus mystacinus	0.004	*Physalaemus aff maximus*	0.004
Leptodactylus fuscus	0.004	*Bokermannohyla circumdata*	0.004

Leptodactylus troglodytes	0.004	*Rhinella schneideri*	0.003
Leptodactylus jolyi	0.004	*Hypsiboas cipoensis*	0.003
Leptodactylus furnarius	0.004	*Scinax granulatus*	0.002
Leptodactylus camaquara	0.004	*Scinax fuscovarius*	0.002
Hypsiboas paranaiba	0.004	*Scinax rizibilis*	0.002
Hypsiboas raniceps	0.004	*Physalaemus cuvieri*	0.002
Hypsiboas albopunctatus	0.004	*Hypsiboas paranaiba*	0.002
Hypsiboas crepitans	0.003	*Hypsiboas caingua*	0.002
Scinax similis	0.003	*Hypsiboas phaeopleura*	0.002
Scinax rogerioi	0.003	*Scinax maracaya*	0.001
Scinax pusillus	0.003	*Scinax perereca*	0.001
Scinax perereca	0.003	*Proceratophrys cururu*	0.001
Scinax maracaya	0.003	*Crossodactylus bokermanni*	0.001
Scinax granulatus	0.003	*Scinax squalirostris*	0.001
Scinax fuscomarginatus	0.003	*Scinax rogerioi*	0.001
Scinax fuscovarius	0.003	*Hypsiboas albopunctatus*	0.001
Scinax squalirostris	0.003	*Odontophrynus americanus*	0.001
Hypsiboas faber	0.002	*Scinax fuscomarginatus*	0.001
Hypsiboas lundii	0.002	*Scinax pusillus*	0.001
Hypsiboas phaeopleura	0.002	*Pseudis platensis*	0.001
Hypsiboas jaguariaivensis	0.001	*Hypsiboas jaguariaivensis*	0.001
Hypsiboas cipoensis	0.001	*Scinax constrictus*	0.001
Hypsiboas caingua	0.001	*Scinax similis*	0.001

SECOND CHAPTER

Ecological and historical drivers of spatial patterns of taxonomic, phylogenetic, and functional diversity in South American anurans

Target Journal: Global Ecology and Biogeography

Ecological and historical drivers of spatial patterns of taxonomic, phylogenetic, and functional diversity in South American anurans

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ABSTRACT

Aim: We aimed to investigate which factors (present-day climate, past climate, or topography) best explain distribution patterns of taxonomic, functional and phylogenetic diversity in savanna and rainforest domains, testing whether the importance of each of these factors is similar in different domains.

Location: South American Cerrado (savanna), Amazon (rainforest), and Atlantic Forest (rainforest) domains.

Time period: Present.

Major taxa studied: Anurans.

Methods: We used amphibian IUCN species range maps to estimate species richness and composition across the landscape under a spatial resolution (grid cell size) of 0.5° X 0.5°. We extracted current and past climate variables (derived by the Hadley Centre), productivity (ENVIREM) and elevation (Shuttle Radar Topography Mission) for each grid cell. We created domain stability maps over the past 120 kyr using a Random Forest machine learning algorithm. We calculated the Functional Dispersion index to represent functional diversity, Net Relatedness Index and Nearest Taxon Index to represent phylogenetic diversity of old and recent clades respectively, and species richness as an estimate of taxonomic diversity. To test the influence of predictor variables on each of these dimensions of biodiversity, we used Conditional Autoregressive Models (CAR).

Results: The importance of each predictor variable varied both across diversity dimensions and domains. Some response variables, such as phylogenetic and functional diversity, were significantly affected by spatial autocorrelation, with levels of spatial autocorrelation differing across regions for different biodiversity metrics. In the Cerrado savanna, each dimension of biodiversity was influenced by different sets of variables, such as precipitation, productivity and climatic stability. On the other hand, we found a major influence of productivity on all the three-diversity dimensions in the Atlantic Rainforest. Lastly, precipitation and relief slope were important predictors of all biodiversity metrics in the Amazon. Notwithstanding, the variables were not congruent in the direction of their influence in either forested domain, presenting a negative or positive domain-specific effect.

Main conclusions: Taxonomic, functional and phylogenetic diversity are shaped by distinct ecological drivers in different South American regions. Our findings suggest that rainforest and savanna domains have unique geographic and climatic configurations that affect biodiversity in different ways. However, common responses exist, such as the effect of climatic stability and topography on the biodiversity patterns of both rainforest domains (Amazon and Atlantic Rainforest).

KEYWORDS

Dimensions of biodiversity, functional diversity, phylogenetic diversity, biomes, savanna, forest, Amazon, Atlantic Forest, Cerrado, tropical system.

1 | INTRODUCTION

Understanding the processes that underscore richness and species distribution patterns at continental scales is key to advance the theory and practice of biological conservation. In the face of the challenges imposed by experimental studies over such large geographical areas, macroecology has emerged as a powerful field that seeks to identify large-scale biodiversity patterns and the global environmental correlates that explain these patterns. Notably, many hypotheses to explain well-known global patterns (e.g., the latitudinal diversity gradient) take into account environmental drivers, which has led to substantial progress in macroecology (Hawkins & Diniz-filho, 2004). For instance, previous studies have explored the potential roles of environmental heterogeneity, productivity and energy, as well as climate and geological history, as underlying processes dictating geographical gradients of species (e.g., Fraser, 1998; Currie, 2013; Vasconcelos *et al.*, 2014; Poorter *et al.*, 2017). Whereas there is compiling evidence linking these environmental predictors and large-scale diversity patterns for many different taxa, we still do not understand whether environmental correlates of taxonomic diversity (species richness) can be generalized to other biodiversity dimensions such as functional and phylogenetic diversity. In addition, few studies have asked whether these three diversity dimensions are being explained by a similar set of domain-specific environmental correlates.

Several studies have recently explored the correlates of specific dimensions of biodiversity within targeted domains. However, as domains have distinct climatic spaces (Jiang *et al.*, 2017), cross-domains comparisons can provide robust tests of macroecological patterns (e.g., Moncrieff *et al.*, 2015, 2016). In tropical regions, studies have often tested the effect of a single biodiversity dimension, or metric, in particular domains, especially for plants and vertebrates (e.g., Carnaval & Moritz, 2008; Wiens *et al.*, 2011; Neves *et al.*, 2017). While these contributions have tremendous value in guiding domain-focused studies and conservation efforts, they often differ in methodology and spatial scales, rendering synthesis difficult. In the biodiversity-rich and threatened Neotropical region, for instance, it is unknown whether similar environmental correlates can be enlisted to explain geographical patterns of accumulation of phylogenetic, trait, or taxonomic diversity, irrespectively of the studied domain. For example, whereas da Silva *et al.* (2012) found moisture reduced the number of anuran species and lineages in the Atlantic Rainforest, climatic variables did not explain taxonomic diversity in Amazonian treefrogs (Wiens *et al.*, 2011).

In this study, we explore the roles of energetic, climatic and topographic environmental variables in explaining the variation of taxonomic, functional and phylogenetic diversity across three key Neotropical domains: two hotspots of biodiversity in South America, the Atlantic Rainforest and the Cerrado savanna (Myers *et al.*, 2000), and the largest rainforest of the world, the Amazon. Despite hosting an exceptionally high number of species, biodiversity patterns in these geographic regions have rarely been compared. For example, there are no empirical tests comparing whether these three domains show similar patterns of species, evolutionary lineage, or trait diversity. This study focuses on answer the following questions: What (if any) environmental correlates best explain biodiversity patterns in each domain? Are similar environmental variables driving taxonomic, functional or phylogenetic biodiversity dimensions in different domains, or are the main drivers of biodiversity domain-specific?

Although there are several studies examining how climate influences taxonomic and functional diversity (e.g. Davidar *et al.*, 2007), the results are mixed. First, some studies have shown that temperature and precipitation positively affect both species (taxonomic) and functional diversity (Cadotte *et al.*, 2011). Conversely, climatic gradients can generate decoupled patterns of taxonomic and functional diversity, for instance due to functionally redundant species (Fonseca & Ganade, 2001). Moreover, topographic events (such as the uplift of the Andes) may have led to landscape shifts that may have impacted lineage diversification and the distribution of phylogenetic diversity (as in the Amazon basin; Hoorn *et al.*, 2010). In the Atlantic Forest, the uplift of the Serra do Mar and Serra da Mantiqueira likely had a similar influence. The high elevational plateaus in the Cerrado (ranging from 500 to 1700 m, Del'Arco & Bezerra, 1989; Silva, 1997), which were formed by tectonic events, may have affected biodiversity patterns, for instance through the maintenance of patches of stable habitats during the glaciation periods (Silva, 1997).

Our study focuses on the diversity of species, lineages, and traits of South American anurans. South America is the richest and most diverse region globally when it comes to frogs and toads (IUCN, 2017). Due to their strong habitat affiliation (Smith & Green, 2006; Gamble *et al.*, 2007), limited dispersal ability (Smith & Green, 2005), and sensitivity to environmental shifts (Beebee & Griffiths, 2005), amphibians are particularly well-suited for macroecological investigations. Global amphibian declines further render this group an appropriate one for biodiversity studies (Grant *et al.*, 2016). Environmental predictors are frequently reported as a limiting or determinant factor of anuran distribution patterns (Provete *et al.*, 2014; Cunningham *et al.*, 2015). We selected 11 environmental predictors related to topographic heterogeneity (as a proxy for geological history) as well as current and historical climate to ask whether and how they explain the distribution of phylogenetic, taxonomic and functional diversity of anurans in the Cerrado, the Atlantic Rainforest, and the Amazon. In cross-biome comparisons, we expect that current and past climate will be linked to increased taxonomic and decreased functional diversity by limiting species dispersal, while topographic heterogeneity increases phylogenetic diversity by favoring allopatric speciation (Figure 1g, 1h and 1i; detailed domain-specific predictions are provided in Figure 1 a-f). Based on our results, we discuss how comparisons between distinct domains can improve our understanding of the drivers of large-scale biodiversity patterns.

2 | METODOLOGY

2.1 | Domain overview

Our analyses focus on three of the largest and most diverse domains of South America: the Amazon, the Cerrado, and the Atlantic Rainforest (Figure 2). The Amazon is the largest rainforest domain of the world; it comprises nine countries, including Brazil, Peru, Bolivia, Colombia, Venezuela, Ecuador, Guyana, Suriname and French Guiana, with a total area of 6,700.00 km² (WWF, 2017). The Amazon is climatically heterogeneous, yet more than 90% of its extension is covered by humid tropical climate (Peel *et al.*, 2007), with a mean precipitation of 2130 mm/year (Costa & Foley, 1998). Although there is a predominance of humid tropical forest in this domain, it also encompasses a variety of other vegetation types, such as floodplain forests and savannas (WWF, 2017). The Amazon how it is nowadays dates from Late Miocene, after the onset of Andean tectonism (Hoorn *et al.*, 1995, 2010; Figueiredo *et al.*, 2009). Andean uplift was followed by an increase in sediment deposition, with the Andean region achieving its modern configuration during the Pliocene (~7 mya, Figueiredo *et al.*, 2009; Wesselingh *et al.*, 2010; Leite & Rogers, 2013).

The Cerrado is the second largest domain in South America, comprising an area of more than 2,000.00 km² (MMA, 2017). This domain, which occurs in central Brazil, is composed by a mosaic of dry forest, deciduous forest, and dense, open, and flooded savannas (Silva *et al.*, 2006). Vegetation heterogeneity, such as the presence of forest-savanna mosaics, contributes to high biodiversity in this region. The climate is tropical with a pronounced dry season (Peel *et al.* 2007). Precipitation in the Cerrado ranges from 800 to 2000 mm/year, and average temperatures range from 18°C to 28°C (Dias, 1992). The geological history of the Cerrado savanna includes old and young events of landscape formation, with old vast plateaus (ranging from 500 to 1700 m) and younger valley depressions (ranging from 100 to 500 m), which were formed during the Late Tertiary (Pliocene, 6 mya) and Early Quaternary (Pleistocene 1.6 mya) respectively (Ab'Saber, 1983; Silva, 1997).

The Atlantic Rainforest is located in South America's eastern coast, comprising an area of 1,300.00 km² along a pronounced latitudinal gradient (MMA, 2017). This domain extends from northeastern to southern Brazil; because of this latitudinal extent, the Atlantic Rainforest spans a variety of vegetational formations (e.g., restinga, coastal, dense, mixed and semi-deciduous forests; Oliveira-Filho & Fontes, 2000) and climate. Climate could be described as mostly tropical humid, turning to temperate in its southern most extent (Peel *et al.*, 2007). The Atlantic Rainforest extends through mountain chains such as the Serra do Mar and Serra da Mantiqueira, whose formation started in the Paleocene (65 mya), with important uplifts during the Miocene (23 mya, (Almeida & Carneiro, 1998).

To define the spatial extent of our target domains, we followed the boundaries recognized by the Brazilian Ministry of Environment for both the Atlantic Rainforest and the Cerrado (MMA, 2017), and the World Wildlife Fund for the Amazon (including all of the Amazon forest, beyond Brazilian borders; World Wildlife Fund 2018). In the Amazon, we restricted our analyses to the large extent of evergreen broadleaf forest to the east of the Andes, masking out marginal transitional areas such as the *babaçu* and seasonally dry forests.

2.2 | Present-day environmental data

To characterize present-day climatic conditions, we extracted predictor layers that reflect contemporary temperature and precipitation measurements. We used variables from the Hadley Centre Climate models (Singarayer & Valdes, 2010; Fuchs *et al.*, 2013), extracting the following bioclimatic descriptors: annual mean temperature (Bio 1), mean temperature of warmest quarter (Bio 10), mean temperature of the coldest quarter (Bio 11), annual precipitation (Bio 12), precipitation of wettest quarter (Bio 16) and precipitation of driest quarter (Bio 17). Additionally, we extracted potential evapotranspiration of the warmest quarter (PET) data from the ENVIREM database (Title & Bemmels, 2017), and converted them to a 0.5 x 0.5^{o} resolution.

2.3 | Topographic data

We downloaded Shuttle Radar Topography Mission (SRTM) digital elevation data from the Consortium for Spatial Information (Jarvis *et al.*, 2008) and used them to calculate three topographic variables that capture topographic heterogeneity in each 0.5 x 0.5° grid cell: slope (i.e., inclination of the mountain face), aspect (i.e., the direction that a slope faces), and roughness (i.e, irregularities of the soil surface). Slope and aspect were calculated according Horn (1981), and roughness according to Wilson *et al.* (2007). We calculated all the topographic variables in software R version 3.4.1, using the package raster (function *terrain*; Hijmans, 2016).

2.4 | Modeling habitat and climate stability over time

Stable areas formed during the glaciations events constituted areas of habitat refugia for animals and plants (Prance 1982; Graham *et al.*, 2010). The consequent isolation led to lineage and species diversification and the accumulation of genetic diversity (Carnaval *et al.*, 2009, 2014), contributing to increasing and maintaining species diversity over glaciations (Graham *et al.*, 2006; Araújo *et al.*, 2008). To estimate values of long-term historical climatic stability at each grid cell, we first used a Random Forest classification algorithm (Breiman, 2001) to perform a joint model of the distribution of the three domains under current climate based on bioclimatic descriptors. We used the centroid of each 0.5 x 0.5° grid cell as presence points of each domain, which resulted in 2128 points for the Amazon, 843 points for the Cerrado, and 502 points for the Atlantic Rainforest. By using a grid cell of 0.5 x 0.5°, we ensured that the distance between centroids was large enough for the Random Forest model to account for sampling bias while reducing the spatial autocorrelation of environmental data (Barratt *et al.*, 2017). The Random Forest classification performs a set of successive classifiers, with each one being independent from the previous ones, which helps avoid overfitting (Breiman, 2001). The algorithm computes the importance of each variable for the final model as the mean decrease in model accuracy. Variables that are more important for the classification model show higher values of the mean decrease in accuracy (Cutler *et al.*, 2007). To train our model, we created 3,288 random absence points from areas in South America that do not comprise any of the three domains included in this study. We implemented 500 classification trees in the model classification of all three domains and used the square root of the number of variables (a default parameter in the classification model) as the number of predictor variables randomly sampled as candidates at each split. To define climatic stability areas, we projected the resulting model of present-day habitat distributions to 31 time periods (with a time interval of 4 kyr) over the past 120 kyr, using the Hadley Centre Climate reconstructions (Singarayer & Valdes, 2010; Fuchs *et al.*, 2013). We then overlaid these 31 models of former habitat distribution to create a continuous layer of climatic stability, where the stability value of each grid cell varied from 0 to 31, which represents the maximum instability and stability, respectively. The results of the domain modeling and the stability map are available in the Appendix 1 (Table A1) and Supplementary Material (Figure S1, S2 and S3), respectively.

2.5 | Species ranges

Expert-drawn species range maps were used to estimate the number of species and composition under the same spatial resolution (0.5 x 0.5^{o} grid cell). Range maps were downloaded from the IUCN Global Amphibian Assessment, accessed in November 2014 (IUCN, 2017). Superimposed ranged maps were then used to extract species lists for each grid cell, using the package letsR (Vilela & Villalobos, 2015) in R, version 3.4.

To verify synonyms and check the taxonomic status of each species, we matched the species identity provided by IUCN against the Amphibians of the World Database (Frost, 2018; available at http://research.amnh.org/vz/herpetology/amphibia/amphib). Five species were excluded from downstream analyses: *Hyloxalus peruvianus*, *Ischnocnema bilineata*, and

Tepuihyla warreni due to phylogenetic and taxonomic uncertainty; *Rhinella pombali* because it is a hybrid between *R. crucifer* and *R. ornata* (Thomé *et al.*, 2010, 2012), and *Phrynomedusa fimbriata* because it is considered extinct by the IUCN. We provide the complete list of 1096 species used in our analyses as a Supplementary Material (Table S1).

2.6 | Phylogenetic diversity

To estimate anuran phylogenetic diversity at each cell, we used a consensus tree from the comprehensive phylogenetic study of Jetz & Pyron (2018). Briefly, Jetz & Pyron (2018) used the 2014 edition of the AmphibiaWeb (http://amphibiaweb. org) species list as the baseline taxonomy to gather GenBank DNA sequence data and to generate a comprehensive amphibian supermatrix-based phylogeny. To include species for which no genetic data are available, Jetz & Pyron (2018) used taxonomic knowledge to tentatively place unsampled taxa on the resulting molecular phylogeny, using the Bayesian approach Phylogenetic Assembly with Soft Taxonomic InferenceS (PASTIS; Jetz *et al.*, 2012; Thomas *et al.*, 2013). We ensured that all species considered in our study are (at least tentatively) placed in this phylogeny, which we used to estimate phylogenetic diversity. For the those species that were not present in Jetz and Pyron's (2018) phylogeny, we conservatively placed them within the clade that most likely includes their closely related species based on phenotypic attributes (in the form of a polytomy).

Old and recent lineage diversification can have different effects on spatial patterns of phylogenetic diversity. To account for both of these diversification timescales, we calculated phylogenetic diversity per grid using the net relatedness index (NRI) and the nearest taxon index (NTI) based on pairwise phylogenetic dissimilarity based on the phylogenetic tree (Webb *et al.*, 2002). NRI is a standardized measure of the mean pairwise phylogenetic distance between taxa in grids, relative to a phylogeny that includes the regional species pool. It quantifies the mean phylogenetic distance among all species pairs using the branch length or the number of nodes separating two taxa. NRI is appropriate to quantify the phylogenetic diversity related to early diverging clades. In turn, the NTI is a standardized measure of the phylogenetic distance to the nearest taxon for each taxon in the sample, and it quantifies the extent of terminal clustering, independently of deep level clustering (Webb *et al.*, 2002). NTI is specially affected by distances among terminal nodes, and it therefore better captures recent clade diversity. To avoid the problem of non-linearity of the evolutionary relatedness (Letten & Cornwell, 2015), we used the non-decoupled phylogenetic dissimilarity approach of de Bello *et al.* (2017) to calculate NTI and NRI; this method bypasses problems of linearity by implementing a square-root transformation on the phylogenetic distances.

2.7 | Trait data and functional diversity estimation

Using the scientific literature (especially taxonomic descriptions), books, and expert knowledge, we built a functional trait database for 1096 anuran species that occur in at least one of the three domains. We gathered data from three quantitative and two qualitative morphological and developmental traits; they relate to species dispersal capacity (tibia length), feeding (head width), survival (snout-vent length), type of development (direct/indirect), and type of tadpole (endotrophic: non-feeding larvae that can be non-hatched or free-swimming, with nutrition solely from parental sources; exotrophic: feeding larvae with energy sources coming from the habitat, larvae always free-swimming) (Table S2). For the missing quantitative data traits, we used Phylopars (Bruggeman *et al.*, 2009) to perform trait imputation (see Table S3 for the imputed trait data). To check whether missing data imputation did not change realized patterns of trait evolution on the phylogenetic tree, we tested for phylogenetic signal in the imputed and non-imputed continuous trait dataset by estimating the K statistic of Blomberg *et al.* (2003). In the case of the categorical trait data, phylogenetic signal was tested with the method of Maddison & Slatkin (1991), where the tree is fixed and traits are shuffled randomly. Additional details about the imputation method and results of both tests for phylogenetic signal are available in Appendix 2 (Tables A2, A3, A4 and A5).

Due to common ancestry, species are not independent units, with closely related species sharing more traits with each other than expected by chance. Because of this dependence, phylogenetic relatedness between species is being increasingly considered not only as a bias to be corrected, but as an potensignal allowing description of patterns and inference of processes at different evolutionary timescales (Cavender-Bares *et al.*, 2009; de Bello *et al.*, 2015; Gerhold *et al.*, 2015). Therefore, before estimating functional diversity, we accounted for evolutionary legacy in the functional traits following the method proposed by de Bello *et al.* (2017). With that, we identify functional diversity patterns with and without the influence of the degree of evolutionary relatedness. Briefly, the method creates a functional pairwise dissimilarity matrix, referred to as “non-decoupled trait dissimilarities”, which represents trait dissimilarity including the evolutionary legacy. It then employs a Principal Coordinate Analysis (PCoA) on the phylogenetic species pairwise dissimilarity (estimated base on the phylogeny) and uses the species scores (eigenvectors) as explanatory variables in a Redundancy Analysis (RDA) where the species traits are treated as response variables. The residuals of the RDA analysis correspond to the variation in species’ traits that are decoupled from the phylogeny, or the trait dissimilarity without the evolutionary legacy (de Bello *et al.*, 2017).

We calculated the functional diversity per grid cell with the functional dispersion index (FDis, Laliberté & Legendre, 2010) as a measure of functional trait diversity for both phylogenetic decoupled and non-decoupled trait data. FDis uses the uncorrected trait distance among species from a PCoA analysis. Because those distance values may produce negative eigenvalues, we applied a square root correction. We estimated FDis as the average distance from the centroid of the multivariate dispersion. FDis is not affected by the number of species and can handle any number and different types of traits (e.g., continuous, categorical, binary, etc.). Furthermore, this metric is not affected by outliers (Anderson, 2006; Laliberté & Legendre, 2010).

2.8 | Testing for multicollinearity and excluding autocorrelated variables

To exclude autocorrelated environmental predictors, we tested the presence of multicollinear variables using Variance Inflaction Factor (VIF, Table S4), considering a cut off threshold of < 3 (Zuur *et al.*, 2010) to keep the same predictor variables for the three domains. After performing VIF we standardized the remaining variables by scaling them to have the same range of variation (mean 0 and unit variance). After excluding the correlated data, we included the following predictor variables: climatic stability, PET of warmest quarter, precipitation of the driest quarter, relief slope and mountain aspect. The predictor and response variables are mapped for each domain in the Supplementary Material: Figures S1, S2, S3, S4, S5 and S6.

2.9 | Testing predictors of the multiple dimensions of diversity

Spatial autocorrelation can bias analyses of species-environment relationships because nearby sites are not independent from each other. Common methods like linear models can have an inflated type I error because spatially autocorrelated residuals violate the assumption of independent errors (Dormann *et al.*, 2007). Therefore, we used a Conditional Autoregressive (CAR) model to account for spatial autocorrelation and test the influence of the topographic, climatic and energetic predictor variables on three response variables: taxonomic (i.e., species richness), phylogenetic, and functional diversity. To account for the spatial structure, the CAR model incorporates spatial autocorrelation through neighborhood matrices, which specify the relationship between the response value at each location (i) and those at neighboring locations (j) (Haining, 2002; Lichstein *et al.*, 2002). This model fits a variance-covariance matrix based on the non-independence of spatial observations. The idea behind CAR is that the probability of values estimated at any given location is conditional on the level of neighboring values. This model allows the estimation of the contribution of the environmental factors excluding the spatial autocorrelation in the residuals (Dormann *et al.*, 2007). To perform the CAR model, we calculated an R^2 based on Kissling & Carl (2008). For the explanatory values of each environmental predictor and the ordinary least squares (OLS), we used the equations provided by Rangel *et al.* (2006).

3 | RESULTS

3.1 | Spatial patterns of the three biodiversity dimensions

Taxonomic, phylogenetic and functional diversity all have different spatial pattern distributions within each focal domain (Figures S4, S5 and S6). In all three domains, phylogenetically decoupled and non-decoupled functional diversities have completely inverse patterns of distribution: non-decoupled functional diversity patterns mirror those of phylogenetic diversity of recent taxa (NTI), whereas phylogenetically decoupled trait diversity shows high functional diversity in some areas coinciding with well-known ecotones areas. This pattern indicates that most differences in traits might be emerging in transitional zones (Figures S4, S5 and S6).

Regarding the spatial patterns of biodiversity metrics in the Atlantic Forest, there is a higher concentration of taxonomic diversity in the Serra do Mar region in the eastern Atlantic Brazilian cost. When functional traits are not phylogenetically corrected, the functional diversity pattern exhibits great similarity to the phylogenetic diversity based on both the more recent (NTI) and older clades (NRI, Figure S4). Functional non-decoupled diversity, NRI and NTI were also concentrated in the Serra do Mar region, with a gradient extending from the eastern Atlantic Rainforest into the northern portion of the domain. Conversely, we found high values of decoupled functional diversity in the south of the domain, which is a contact zone between the Atlantic Rainforest, Cerrado and Pampas (Figure S4).

In the Cerrado, higher values of NRI are more spread out in space, yet with a small concentration in the central-northern, southwestern and southeastern portions of the domain. In turn, NTI was concentrated in the western and southeastern portions of the domain. Regarding decoupled functional diversity, higher values were concentrated in the north, in a well-known transitional area between the Cerrado, the Amazon and the Caatinga known as the Cocais Forest. The non-decoupled functional diversity was more spread out in space, with higher values occurring on the northern to the southeastern Cerrado, as well as in the west (Figure S5).

In the Amazon, there is higher taxonomic and non-decoupled functional diversity, with higher NTI values concentrated in the northern and western regions. Non-decoupled diversity presents similar spatial patterns to NTI, while NRI also shows substantial diversity in the Amazon's central-eastern region (Figure S6). As in the Atlantic Rainforest and Cerrado, transitional zones along the Amazon edges present the highest values of decoupled functional diversity (Figure S6).

3.2 | Climatic, energetic and topographic predictors of biodiversity spatial patterns

3.2.1 | Spatial versus environmental variables importance

The response biodiversity metrics were influenced at different levels by each predictor variable. Moreover, some response variables were more affected by spatial autocorrelation than others as inferred by CAR models (Table 1). For instance, in all three domains, spatial variation in phylogenetic diversity (NRI and NTI) was higher than taxonomic and functional diversity, which might be a result of the presence of phylogenetic endemic species (Table 1). Moreover, levels of spatial autocorrelation differed across regions for all the biodiversity metrics (Table 1).

3.2.2 | Cross-domain and cross-dimension comparisons

In the Cerrado savanna, no single variable explains each of the biodiversity dimensions, with each metric being more influenced by a different set of variables (Table S5). On the other hand, we found a major influence of productivity on all the three diversity dimensions in the Atlantic Rainforest (TD: β= -9.703, $p<0.001$; NRI: β= -0.286, $p<0.001$; NTI: β= -0.389, $p<0.001$; FdisD: β= 0.006, $p<0.001$; FdisN: β= -0.011, $p<0.001$; Table S5). In the Amazon, precipitation and relief slope were the most important predictors of biodiversity (Precipitation, TD: β= 3.923, p<0.001; NRI: β= 0.409, p<0.001, NTI: β= 0.300, p<0.001, FdisD: β= -0.004, p<0.001, FdisN: β= 0.013, p<0.001; Relief slope, TD: β= -4.245, p<0.001; NRI: β= 0.356, p<0.001, NTI: β= 0.212, p<0.001, FdisD: β= -0.003, p<0.001, FdisN: β= 0.008, p<0.001; Table S5). Notwithstanding, each predictor variable was not congruent in how they influence biodiversity patterns in each forest domain, with both negative and positive effects (Table S5).

Climatic stability played a role in explaining both taxonomic diversity and NRI in all three domains. Precipitation of the driest quarter had a negative effect on the decoupled functional diversity, while PET had an important role in explaining non-decoupled functional diversity in all three domains (Table S5).

3.2.3 | Within-domain patterns

Once spatial structure was accounted for, one of the most prominent patterns was the influence of productivity (PET) as the main correlate of taxonomic (TD: β= -9.703, p<0.001), phylogenetic (NRI: β= -0.286, p<0.001; NTI: β= -0.389, p<0.001), and trait diversity (FdisD: β= 0.006, p<0.001; FdisN: β= -0.011, p<0.001) in the Atlantic Rainforest (Table S5). In this domain, PET negatively influenced all of the diversity dimensions, except functional decoupled diversity, on which PET had a positive influence. Moreover, we found no relationship between climatic stability and NTI (β= 0.032, p = 0.393), although a positive relationship was found between climatic stability and all the response variables (TD: β=3.486, p<0.001; NRI: β=0.114, p<0.001; FdisD: β=0.002, p<0.001; FdisN: β= 0.004, p<0.001). Taxonomic and functional diversity (decoupled and non-decoupled) were positively yet weakly influenced by relief slope (TD: β=, p<0.001) and mountain aspect (FdisD: β= 0.001, p<0.001; FdisN: β= 0.001, p<0.001), respectively (Table S5).

In the Cerrado savanna, the decoupled functional diversity was negatively associated with precipitation (β=-0.002, p<0.001, Table S5). Climatic stability had a negative effect in NRI (β= -0.082, p<0.001), NTI (β= -0.131, p<0.001), taxonomic (β= -1.108, p<0.001) and non-decoupled functional diversity (β= -0.002, p<0.001). The other dimensions of diversity were affected by each of the predictors in different ways.

In the Amazon, we found precipitation and relief slope to be the most important explanatory variables of all dimensions of diversity (Table S5). Precipitation had a consistent positive effect (TD: β= 3.923, p<0.001; NRI: β= 0.409, p<0.001; NTI: β= 0.300, p<0.001; FdisN: β= 0.013, p<0.001), except on decoupled functional diversity (β= -0.004, p<0.001). Relief slope was positively associated with non-decoupled functional diversity (β= 0.008, p<0.001) and both phylogenetic dimensions (NRI: β= 0.356, p<0.001, and NTI: β= 0.212, p<0.001), and negatively associated with taxonomic (β= -4.245, p<0.001) and decoupled functional diversity (β= -0.003, p<0.001). Mountain aspect, climatic stability and PET had little or no influence on biodiversity metrics in the Amazon (Table S5).

4 | DISCUSSION

4.1 | General patterns

Instead of demonstrating a pervasive role of single drivers of biodiversity patterns, we demonstrate that biological responses to ecological and historical factors are domain-specific, and, sometimes, also dimension-specific within a domain. Our results suggest that no single factor is responsible for spatial patterns of biodiversity across the Amazon, Cerrado, and Atlantic Rainforest, even when you analyze each dimension (taxonomic, phylogenetic, and functional) separately. Within the forested domains, a single or a couple of environmental factors can be important drivers of all dimensions of diversity (as is the case of productivity in the Atlantic Rainforest, and precipitation and slope in the Amazon) – but this does not occur in the savannahs of the Cerrado. Forest outcomes reinforces the findings of Weinstein *et al.* (2014), who uncovered found different roles of environmental and geographic factors in the spatial distribution of taxonomic, functional and phylogenetic diversity in Andean hummingbirds.

4.1.2 | Ecotones

A comparison of the spatial patterns of decoupled vs non-decoupled functional diversity revealed a striking pattern in ecotone areas, for all three domains. When the influence of phylogeny is removed from traits, these transitional areas emerge as the most diverse in trait variation. As predicted by de Bello *et al.* (2017), non-decoupled functional diversity appears to overemphasize trait variability in areas of lineage accumulation, hindering trait complementarity. This greater lineage richness is possibly resultant from intense diversification, especially in mountain areas such as the Atlantic Rainforest (Serra do Mar mountain, e.g., Firkowski *et al.*, 2016), and the Andes (e.g., Hughes & Eastwood, 2006; Fjeldsa *et al.*, 2012; Schwery *et al.*, 2015) – which appears to inflate uncorrected measures of functional diversity. To our knowledge, this study is the first one to elucidate a complementarity pattern emerging from functional diversity in ecotone areas – particularly between dry and forested domains – after decoupling the influence of phylogeny in the trait data. It is nonetheless consistent with previous findings of Nascimento *et al.* (2018), which demonstrated greater bird functional diversity for decoupled traits in areas where the vegetation strata and topographical complexity increases (similar to transitional areas). Hidasi-Neto *et al.* (2012) also reported an increase in functional diversity of birds in more disturbed areas.

Our finding has interesting implications for the way we interpret habitat transitions and peripheral areas of higher habitat instability over time. Repeatedly, studies have linked habitat stability (particularly in core refugia) and the accumulation of neutral (e.g. mitochondrial DNA) diversity. We here, however, find evidence that the less stable conditions at the edge of natural domains allow for the accumulation of adaptive (trait) diversity. Previous studies demonstrated higher species richness in ecotone regions (e.g., Risser, 1995; Lomolino, 2001; Kark *et al.*, 2007), attributing this to the fact that the latter comprise meeting areas among bordering domains or communities, each with a different regional pool. However, even in the absence of increased richness relative to other parts of the domains in question, our results demonstrate that ecotones allow for an accumulation of unique traits, favoring niche complementarity and ecosystem functioning. This renders these areas particularly relevant in the context of climate change mitigation and adaptation, as areas that hold trait variation.

4.2 | Cross-biome comparisons

4.2.1 | The effect of climate

In all three domains, we expected that current and past climates (in the form of climatic stability) would be associated with higher taxonomic diversity and lower functional diversity, while topographic heterogeneity would be linked to increased phylogenetic diversity (Fig. 1). However, we found a mixed, complexed and particular result where climatic stability increased taxonomic diversity in the Atlantic Rainforest only, while unexpectedly decreasing taxonomic diversity in the Amazon and Cerrado. Moreover, long-term climatic stability does not seem to be linked to levels of functional diversity in any of the three domains. Similar to long-term climatic stability, current climates often negatively affected functional diversity, in this case in all three domains. Specifically, current climates negatively affected decoupled functional diversity (without the influence of the degree of evolutionary relatedness) in all regions, as well as negatively affected non-decoupled functional diversity in the Cerrado. Yet, currents climates positively affected non-decoupled functional diversity in the Amazon. In this way, in general, we found an influence of climatic factors on taxonomic and functional diversity. However, this influence is completely related not just to the type of diversity but also to the intrinsic domain’s environmental characteristics. Bellow we detailed discussed these results according to each type of domain.

4.2.2 | The effect of topology

Regarding the effects of topography on levels of phylogenetic diversity, as we expected, both aspect and slope exhibited positive relationships with phylogenetic diversity of both recent and old clades. This result point to the importance of physical barriers to lineage diversification, presumably through allopatric speciation.

The terrain slope increases both metrics of phylogenetic diversity in the Amazon and only the diversity of recent clades in the Cerrado. Emphasizing the role of mountain in the evolutionary process. Surprisingly, instead of the terrain slope affects evolutionary history, the aspect has had a positive relationship in the Atlantic Rainforest, demonstrating that the face of the mountain is driving lineages diversification more than its slope. Depending on which direction the relief is facing, the solar energy irradiance, as well as net primary production and biomass accumulation varies (Lu *et al.*, 2002). Which seems to be determining the lineages accumulation and/or diversification in the Atlantic Rainforest.

Thus, based on the broad results for diversity dimensions, we can infer the diversity dimensions patterns in the Neotropical region are a result of ecological and evolutionary events acted since Neogene, especially by tectonic and paleogeographical events, and maintained by both the Pleistocene stable areas (Rull, 2011) and the current environmental conditions as primary productivity.

4.3 | Within-domain

4.3.1 | Drivers of biodiversity in Amazon

In the Amazon, the positive influence of precipitation, relief slope and stability in phylogenetic diversity of both old and recent (NRI and NTI) clades in the Amazon goes back to the biogeographic history of the domain. Most of the diversification of anuran lineages in the Amazon might have occurred driven by the topographic complexity created by Andes uplift (Santos *et al.*, 2009; Badgley, 2010) and landscape restructuration (Hoorn *et al.*, 2010). Moreover, the diversity of lineages was maintained until nowadays especially by the stable areas created during the last dry periods, and the high levels of precipitation. Unlike Wiens *et al.* (2011) findings for Hylidae in the Amazon, in which neither rates of diversification, climatic factors nor morphological variation have driven species richness, our results show that both historical and current variables have complementary roles in the diversification and lineages maintenance as also showed by Richardson *et al.* (2001), Antonelli *et al.* (2009) and Chaves *et al.* (2011). Our arguments find support in the biogeographic history of Amazon which is particularly marked by the Andean uplift, with most of the peaks built in the late middle Miocene until the early Pliocene (~7 to ~ 2 mya, Gregory-Wodzicki, 2000; Mora *et al.*, 2010). According to Hoorn *et al.* (2010), Andean uplift is the major driver changing the landscape of Amazon, which in turn, determine biodiversity patterns. Indeed, during the Pleistocene there were climatic changes in the Amazon which contributes to the formation of climatic stable areas (“refugia” areas) (Prance, 1982; Hooghiemstra & Hammen, 1998; Haffer, 2008). These refugia areas have prevented species to be driven to the extinction during the last dry period on Earth influencing the phylogenetic diversity. In addition, lots of lineages of Dendrobatidae (poison frogs) radiated and dispersed from the adjacent Andes to the forest (Santos *et al.*, 2009). Later, during the Miocene-Pliocene to the present, lineages have faced a rapid *in situ d*iversification (Santos *et al.*, 2009) as a result of the increased evolutionary rates especially within stable climatic areas (Fjeldsa & Lovett, 1997; Fjeldsa *et al.*, 1999; Cadena *et al.*, 2012). For example, Duellman (1982, 1997) demonstrated that isolation created by mountains could trigger diversification and speciation, because there is great environmental variation between montane and lowland habitats. On the other hand, the decoupled functional diversity shows that the decrease in precipitation and relief slope increase functional diversity. In this way, species adapted to both high and lowland, especially in areas with low precipitation can co-occur in lightening relief slope landscape facilitating species dispersal and favoring species with different trait types. However, the opposite pattern was found for non-decoupled Fdis. Non-decoupled Fdis reflected the NRI and NTI trend, which was nothing but the influence of the phylogenetic relationship into traits, which agrees with de Bello *et al.* (2017) arguments in the sense that it can hide the traits information when the evolutionary history underlie traits evolution.

4.3.2 | Drivers of biodiversity in the Atlantic Forest

We found that productivity and climatic stability were the main drivers of different diversity dimensions in Atlantic Rainforest. In general, the productivity had a negative impact on driving the diversity facets, except when we look for decoupled Fdis. So, we can raise some hypothesis about extrapolation of the hump-shaped productivity curve based on the well-known pattern of the decreasing in the TD after a given value of (Tilman, 1982; Abramsky & Rosenzweig, 1984)to phylogenetic diversity (and non-decoupled Fdis). High energy availability might increase species competition (especially among closely related species) reducing richness and phylogenetic diversity. In this way, we argue that there is probably an effect of interspecific interactions even in a high level of resource, limiting lineages and number of species while favoring the occurrence of distinct traits. Furthermore, as most of anurans present a complex life cycle and waterbodies within forested areas are less productive than waterbodies within dense forest (Skelly *et al.*, 2002), the competition might be occurring in the tadpoles level driving traits differentiation.

Relatively to the low (but recurrent) influence of climatic stable areas ("refugia") in four of the five facets of diversity analyzed, recent studies have presented a positive relationship of refugia with functional, phylogenetic and taxonomic diversity, evidencing the influence of climatic stable areas in the maintenance of evolutionary distinct lineages through the time and probably enhancing its diversification in Atlantic Rainforest formation (Carnaval *et al.*, 2009, 2014; da Silva *et al.*, 2014). Thus, we argue past diversification and lower extinction rates should be more important for frogs because of the low influence of recent stable areas in the diversity dimensions analyzed here, being these "refugia" areas have acted more intensely in the diversity maintenance. Contrary to our expectations, despite the uplift of the "Serra do Mar" and

"Serra da Mantiqueira" (southeastern Brazil) might have caused a vicariant process affecting lineage diversification due to allopatric speciation, we did not find the influence of relief slope in any dimension of diversity. Instead, there was evidence that the direction of the relief (aspect) is able to increase lineages and traits diversity once it does influence net primary production, solar energy irradiance, biomass accumulation (Lu *et al.*, 2002), and, by consequence, species distribution (Kappelle *et al.*, 1995).

4.3.3 | Drivers of biodiversity in the Cerrado

The geological history of Cerrado was marked by tectonic cycles of uplifts that have been resulted in the ancient plateaus and younger depressions (Ab'Saber, 1983; Del'Arco & Bezerra, 1989; Silva, 1997), dating from the late Tertiary until Quaternary. So, we were expecting the topographic heterogeneity would show a stronger pattern in determining diversity dimensions by its older historical influence in species diversification and maintenance than climatic stability. Against our expectations, even do not be the most important variable, the stable climatic areas, instead of topographic heterogeneity, was the most frequent driver of diversity dimensions pattern in the Cerrado savanna, predicting four of the five indices analyzed. This result agrees with some studies which have shown that areas of Cerrado plateaus (Ab'Saber, 1983; Silva, 1997; Werneck *et al.*, 2012) were climatically stable during the Quaternary period, being an important driver of species richness (e.g., Werneck *et al.*, 2012), genetic diversity (e.g., Vasconcellos et al. 2018 under review) and endemism (Azevedo *et al.*, 2016) for several taxonomic groups (i.e., birds, reptiles and amphibians). But, contrary to most of studies, climatic stable areas are influencing the diversity dimensions in a negative way. Based on some conceptual models proposed by Costa *et al.* (2017), we can raise some hypothesis mixing two scenarios of their study to explain the influence of stability in the Cerrado domain. This new scenario would have presented a first boost of vegetation recovery after the dry periods followed by periods with more stable and moderate vegetation recovery.

So, few climatic stability areas would have formed, and more recent lineages would occupy these stable patches leading to low taxonomic and phylogenetic diversity, with presence of few endemic species and more eco-generalists species (e.g., more general reproductive modes) that present high dispersal ability, resulting in low functional diversity present in the Cerrado. Precipitation and productivity also exhibited a negative relationship with diversity dimensions in the savanna domain. Species are already adapted to the dry climate (lineages and traits), so even with high precipitation levels it does not increase the present diversity over there, once more than arrive in an area species should establish and persist in the long term. Thinking about the influence of productivity, more than reflect the hump-shaped curve in the Cerrado, we argue that those adapted species occupy different niches in a scenario of resource limitation which would favor different lineages, species and, traits, especially in the driest areas, which might be a result of limiting similarity as argued by de Bello *et al.* (2017). On the contrary, when the availability of resources increases the species might expand their niches and the competition might be even greater than in a low-level resource, driving the dimensions of diversity down. Furthermore, due to its reproductive mode, most of the frogs in Cerrado are associated with ponds and not streams, for this reason, there are few species and lineages associated to areas with high productivity, which are mainly located along the rivers, being the reason why productivity is dropping some diversity dimensions down. Even with the explanations about the influence of stability, precipitation and productivity in diversity dimensions, Cerrado savanna was the most peculiar domain in the sense that no consistent pattern emerged related to the overall diversity dimension and variables importance. For doing so, even considered a savanna, Cerrado presents several degrees of vegetation heterogeneity and microclimate thought the domain (Silva *et al.*, 2006; Nogueira *et al.*, 2009), which might be causing the absence of a pattern among the diversity dimensions drivers. Furthermore, the hypothesis raised for each one of the predictors in the Cerrado are not mutually exclusive, suggesting that the heterogeneity found on the region, represented by a mosaic of forest, savanna and semiarid communities

(Silva *et al.*, 2006), might be leading to different factors acting at the same time and leading to the current diversity patterns. Complementarily, all the predictors used in our study are important to the current pattern of anuran diversity dimensions in the Cerrado as several other studies found for species richness (Hurlbert, 2004; Diniz-Filho & Bini, 2005; Costa *et al.*, 2007).

4.4 | Caveats

There is growing evidence demonstrating that spatial structure is the main parameter in macroecological studies, as a result of the influence of regional species pool (Kreft *et al.*, 2008), local speciation (Wiens & Donoghue, 2004) and species dispersal limitation (Padial *et al.*, 2014). Even several macroecological studies showing that structured spatial patterns in biodiversity are common to emerge when we look for patterns in broad scales (Ficetola *et al.*, 2017), the amount of spatial structure explaining our data was higher than we expected. As emphasized by several studies, the influence of spatial process in this scale is potentially related to allopatric speciation, niche conservatism, dispersion limitation and environmental filtering (Cavender-Bares *et al.*, 2004; Emerson & Gillespie, 2008; McCormack *et al.*, 2009; Pavoine & Bonsall, 2011; Swenson *et al.*, 2012). In this way, we would expect a great spatial influence exhibited by phylogenetic dimension whether the present lineages evolved retaining ancestral niche characteristics (niche conservatism, Wiens & Graham, 2005; Losos, 2008). Furthermore, niche conservatism is a common pattern in tropical areas (e.g., Graham *et al.*, 2006; Romdal *et al.*, 2013; Duchêne & Cardillo, 2015), making the species less liable to explore, spread and colonize a new environment (Wiens & Donoghue, 2004). Moreover, this pattern may be extended to taxonomic and functional diversity. Once the speciation leads to the increasing number of species in a region, and, most of the time, as a result of niche conservatism and environmental filtering, functionally similar species tend to occur close by each other, creating a strong spatial pattern in the data as mostly evidenced by functional decoupled results.

5 | CONCLUSION

The strong influence of spatial processes means they are responsible for most of the patterns in the geographical distribution of diversity dimensions in the three biggest biomes of South America. Basically, those patterns emerge mostly due to the species dispersal limitation determined by abiotic conditions, geographic isolation (due to environmental barriers), restricted niche evolution ability to spread over new ecological conditions (Wiens & Donoghue, 2004). Even though the low influence of the climatic and historical variables does not mean they were not important, but maybe they are more related to the levels of diversity we did not measure in our study, as genetic diversity and endemism. Herein, we verified that even with different strengths stability is an important factor to maintain the patterns of species diversity dimensions of anurans after the lineages diversification have been favored by mountain uplifts in the forested domains. We found support in the mountain-geobiodiversity hypothesis proposed by Mosbrugger *et al.* (2018), which advocates that the biodiversity patterns in mountain regions are influenced especially by the physical presence of alpine zones, montane and lowland, also climatic fluctuations that allowed mountains to act as species centers of diversification and, the environmental gradient created by the high-relief terrain which have slowed down migration during those climatic oscillations and provided stable areas for the species maintenance (refugia) and isolated them by creating geographical barriers that also enabled species survival and allopatric speciation. We also elucidated that complementary patterns in the functional diversity can emerge by integrating decoupled and non-decoupled functional diversity approaches which can ensure a better comprehension of the trait evolutionary history across climatic and geological gradients. As we observed, effects of environmental filtering, temporal niche dynamics as well as evolutionary process like sympatric speciation or character displacement might be leading to the increasing in species traits differences after taking phylogenetic relationship into account in the traits diversity. The big message that comes out here is each type of domain has its own dynamic to generate and maintain the different forms of biodiversity, from taxonomic to functional and phylogenetic diversity. So, understand the peculiarities of forests and savannas around the world might envision new insights and generalizations about diversity dimensions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found hereafter tables, figures and appendix in the supporting information tab for this article.

Figures

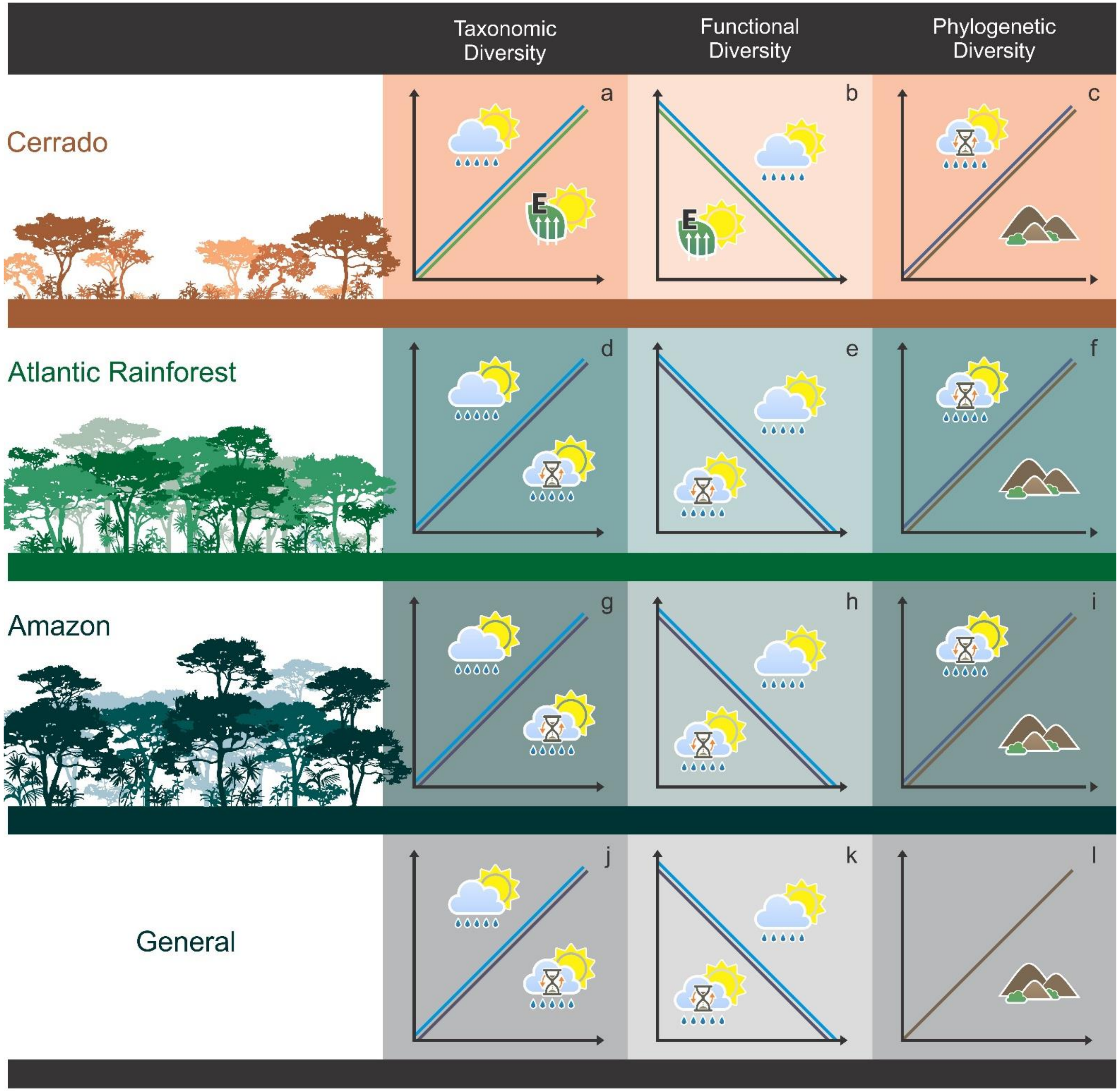

Figure 1. Expectations for the relationship between predictor variables and diversity dimensions. Cerrado: **a.** We expected that both current climate and energy would increase taxonomic diversity, due to higher energy availability and, also to species accumulation be favored by warmer temperatures and rainy weather. **b.** Instead, we expected that functional diversity would decrease in higher levels of energy availability, due to higher effects of species competition in high energetic environment which might lead to a homogenization of traits, and warmer temperature and rainy weather, once Cerrado species already passed through environmental filtering to deal with the dry climate and in a scenario with high temperature and precipitation more species would be present but holding redundant traits. **c.** Last, for phylogenetic diversity we were expecting to find a positive relationship among climatic stability and topographic heterogeneity (here, specially caused by Cerrado's plateaus) once topographic heterogeneity would favor species isolation and further allopatric diversification and stable areas would act in maintaining those new lineages until nowadays. Atlantic Rainforest and Amazon: **d/g.** We expected that both, current climate and climatic stability, would increase taxonomic diversity in both forests due to favor species co-occurrence and long-term species maintenance. **e.h.** Instead, we expected that current climate and climatic stability would decrease functional diversity in both forests due to favor species with trait similarities which were able to maintain themselves during the driest period, while nowadays the traits diversity would reflect the previous trait filtering. **f/i**. Last, for phylogenetic diversity we were also expecting to find a positive relationship among climatic stability and topographic heterogeneity (here, specially caused by mountain chains: Serra do Mar and Serra da Mantiqueira in the Atlantic Rainforest and, Andes in the Amazon), once topographic heterogeneity would favor species isolation and further allopatric diversification and stable areas would act in maintaining those new lineages un nowadays.

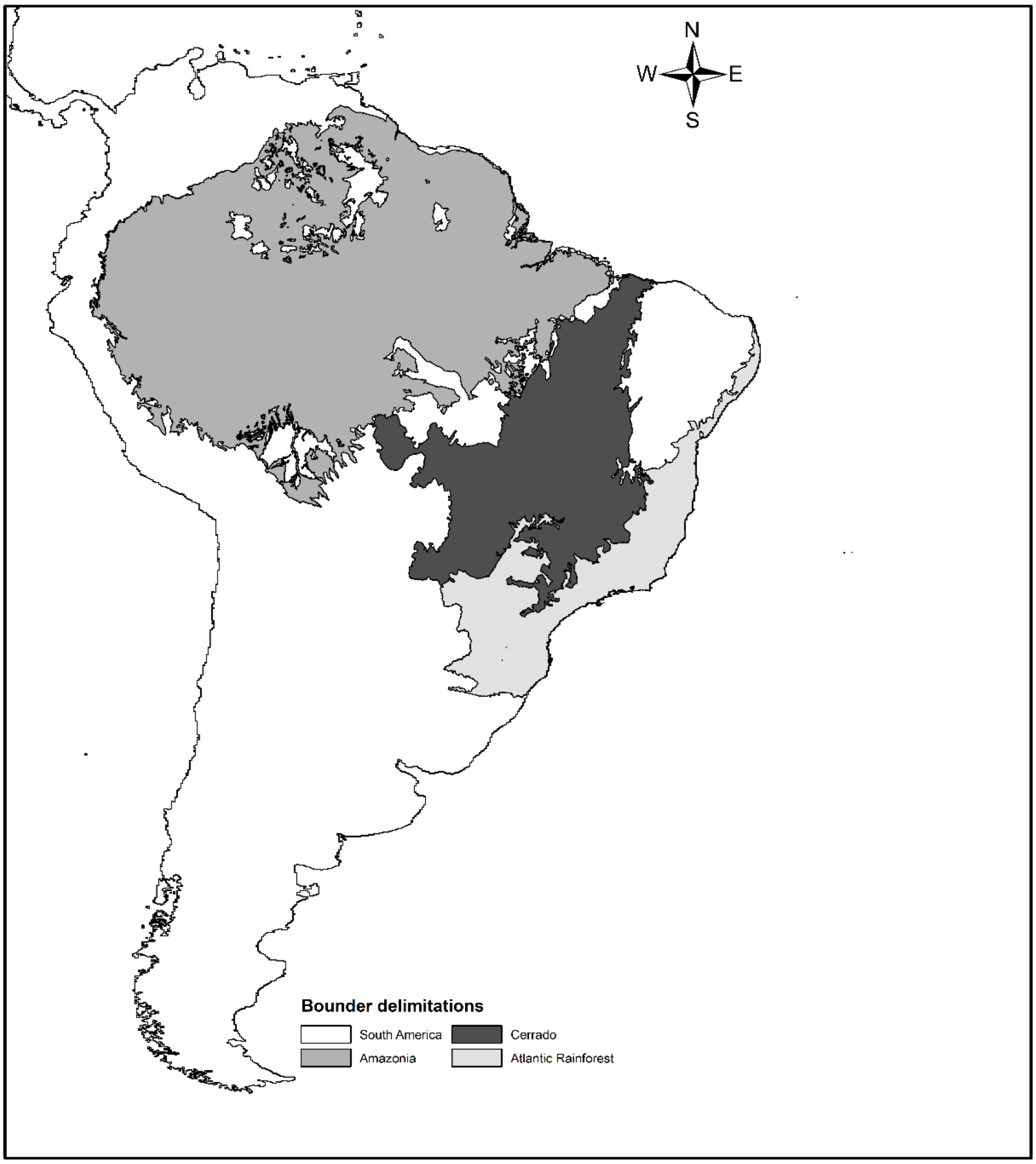

Figure 2. South America domains included in this study: Amazon, Cerrado and Atlantic Rainforest.

Tables

Table 1. Summary of CAR model results for the influence of the topographic heterogeneity (RELIEF), climatic stability (STABILITY), current climate variables (CLIMATE) in each biome diversity facets.

Biome	Model	Full model	Predictors r²	AIC	Significance
Atlantic Rainforest	Taxonomic Diversity ~ RELIEF + CLIMATIC STABILITY + CLIMATE	0.908	0.305	3682.8	$p < 0.001$
Cerrado	Taxonomic Diversity ~ RELIEF + CLIMATIC STABILITY + CLIMATE	0.875	0.194	3794.3	$p < 0.001$
Amazon	Taxonomic Diversity ~ RELIEF + CLIMATIC STABILITY + CLIMATE	0.960	0.209	11928.2	$p < 0.001$
Atlantic Rainforest	Functional diversity (decoupled) ~ RELIEF + CLIMATIC STABILITY + CLIMATE	0.852	0.382	-3864.9	$p < 0.001$
Cerrado	Functional diversity (decoupled) ~ RELIEF + CLIMATIC STABILITY + CLIMATE	0.874	0.093	-5712.2	$p < 0.001$
Amazon	Functional diversity (decoupled) ~ RELIEF + CLIMATIC STABILITY + CLIMATE	0.897	0.283	-15461.6	$p < 0.001$
Atlantic Rainforest	Functional diversity (non-decoupled) ~ RELIEF + CLIMATIC STABILITY + CLIMATE	0.885	0.284	-3209.2	$p < 0.001$
Cerrado	Functional diversity (non-decoupled) ~ RELIEF + CLIMATIC STABILITY + CLIMATE	0.858	0.147	-4725.0	$p < 0.001$
Amazon	Functional diversity (non-decoupled) ~ RELIEF + CLIMATIC STABILITY + CLIMATE	0.917	0.312	-11517.5	$p < 0.001$

Atlantic Rainforest	NRI ~ RELIEF + CLIMATIC STABILITY + CLIMATE	0.812	0.112	625.7	$p < 0.001$
Cerrado	NRI ~ RELIEF + CLIMATIC STABILITY + CLIMATE	0.765	0.05	389.1	$p < 0.001$
Amazon	NRI ~ RELIEF + CLIMATIC STABILITY + CLIMATE	0.877	0.300	2847.2	$p < 0.001$
Atlantic Rainforest	NTI ~ RELIEF + CLIMATIC STABILITY + CLIMATE	0.819	0.122	626.8	$p < 0.001$
Cerrado	NTI ~ RELIEF + CLIMATIC STABILITY + CLIMATE	0.864	0.08	881.7	$p < 0.001$
Amazon	NTI ~ RELIEF + CLIMATIC STABILITY + CLIMATE	0.884	0.183	1966.9	$p < 0.001$

APPENDICE

Appendix 1.

Domain classification modelling

The present-day domain classification modelling achieved through Random Forest was similar to present-day distribution maps of the Atlantic Rainforest, the Cerrado, and the Amazon (Figure A1). The mean prediction error of the present-day domain modeling was estimated as 22.02%. The model did not classify either the transitional area located between the Amazon and the Cerrado (*babaçu* forest), or the dry patches within the Amazon, as either Cerrado or Amazon. Yet, it classified the northern range of the coastal Atlantic Rainforest as belonging to the Amazon domain. So, we have taken out those mispredictions from the Atlantic Rainforest stability maps. Precipitation of the driest quarter, mean temperature of the coldest quarter, and the mean temperature of the warmest quarter were the most important variables guiding the final habitat classification model (Table A1).

Mapping habitat stability

When projected into the past and summed up the stability of each 4 kyr period, the final domain stability map showed stable areas are congruent with highlands (mountains and plateaus) in the Atlantic Rainforest and Cerrado. In contrast, the stable areas in the Amazon are associated with the lowland areas along the Amazon river basin.

In the Atlantic Rainforest and Cerrado we observed two widespread climatic stable areas with a narrow disjunction separating each of them. Both climatic stable areas showed low internal variation. In the Atlantic Rainforest, those separated stable areas are located in the central-south portion of the domain (Figure S1). The occurrence of the climatic stable areas in the Cerrado is associated with the central-southwestern and the central-northeastern plateaus (Figure S2), which even with the disjunction, preserved a small connection between them in the center of Cerrado. Besides the most climatic stable areas be present widespread along the both sides in the Amazon river without disjunction, they occurred from the base of the Andes following Marañón river course extending across the course of Amazon river until central-eastside of Amazon with low internal variation (Figure S3). Two portions of climatic stability are observed extending from the Amazon river to the north, and the only two disjunction portions of climatic stable areas are located south and north of the Amazon river downstream in the Atlantic Ocean (Figure S3).

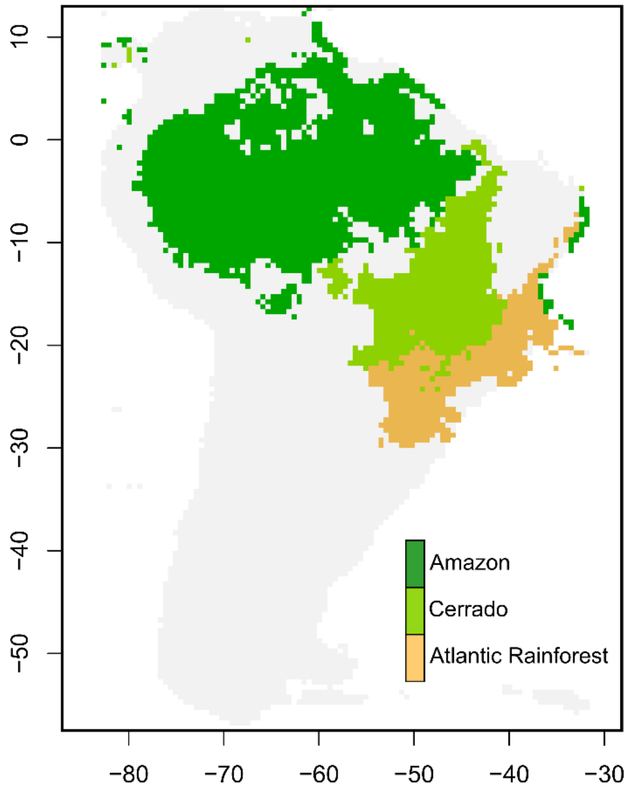

Figure A1. Present day random forest classification modelling for the Amazon, the Cerrado and Atlantic Rainforest.

Table A1. Variable importance contribution in terms of mean decrease in accuracy and of mean decrease in Gini Index. As higher is the Mean Decrease Accuracy greater is the importance of the variable.

Climatic variable	Mean Decrease Accuracy	Mean Decrease Gini
bio1	43.46	512.62
bio10	**58.81**	470.44
bio11	**58.9**	707.2
bio12	51.43	899.6
bio16	38.29	830.64
bio17	**129.47**	606

Appendix 2.

Testing differences between imputed and non-imputed trait data

Whenever continuous trait data were missing from a set of species, we used Phylopars (Bruggeman *et al.*, 2009) to perform trait imputation. Imputation of missing data has been shown to reduce error and improve estimation in macroecological and evolutionary studies (Penone *et al.*, 2014). To that end, Phylopars perform imputation based on the phylogenetic relationship among species, which has been demonstrated to improve estimation of missing trait values (e.g., Guénard *et al.*, 2013; Penone *et al.*, 2014; Swenson, 2014). For imputation, we represented the role of phylogeny by applying a Brownian motion evolutionary model. Brownian motion assumes an evolutionary model of constant change, with variance accumulation in species traits being proportional to the time of lineage splitting (Revell *et al.*, 2008). As showed by Penone *et al.* (2014), Phylopars has superior performance compared to other methods of trait imputation. Because it is impossible to apply the imputation analysis for species missing all the trait data, we excluded six species before performing the imputation. So, in the end, the computation of functional diversity was done for 1090 species instead of 1096. The imputation of missing data was performed in R version 3.4.1, package Rphylopars (function *phylopars*, Goolsby *et al.*, 2017). Approximately 10% of the continuous trait data, and 5% of the categorical trait data, were estimated through imputation (see imputed trait table in Table S3).

To be sure that the imputation of the missing data was not changing the evolutionary pattern of the phylogenetic tree, we tested for phylogenetic signal in the imputed and non-imputed continuous trait dataset by estimating the K statistic of Blomberg *et al.* (2003). Blomberg's K estimates the phylogenetic signal relatively to the number of evolutionary trait changes expected under Brownian motion (Blomberg *et al.*, 2003). In this approach, K < 1 indicates small phylogenetic signal in the data (i.e., closely-related species are less similar than expected by Brownian motion), K = 1 indicates that the trait evolution is happening according to the expected by Brownian motion, and K > 1 means high phylogenetic signal present in the data (i.e., closer species share more trait similarities than expected by Brownian motion). In the case of the categorical trait data, phylogenetic signal was tested with the method of Maddison & Slatkin, 1991, where the tree is fixed, but traits are reshuffled randomly. As in the case of Blomberg's K for continuous trait data, this method randomizes tree tips (taxa), and then compares the minimum number of character state changes (assuming maximum parsimony), with those under a null model, to estimate the minimum number of character-state transitions that account for the observed character distribution on the phylogeny. A significant phylogenetic signal is inferred when the randomized median is greater than the observed transition rates (Maddison & Slatkin, 1991). To estimate phylogenetic signal, we used 1,000 randomizations.

The strength of the phylogenetic signal emergent in the continuous data varied among domains, as shown by the values of Blomberg’s K (ranging from 0.048 to 0.062 in the Atlantic Rainforest, from 0.234 to 0.360 in the Cerrado, and from 0.3 to 0.394 in the Amazon; Table A2). For the continuous traits, in both imputed (Table A2) and non-imputed data (Table A3), there was less phylogenetic signal than expected under a Brownian Motion model. However, the opposite pattern is observed in the categorical trait data: all categorical traits exhibited significant phylogenetic signal in imputed (Table A4) and non-imputed data (Table A5).

Table A2. Phylogenetic signal of continuous imputed data in the three biomes. K: K statistics, PIC.variance.P: significance of K, PIC.variacence.Z: Z-score. Where k < 1 indicates small phylogenetic signal, k = 1 indicates that the trait evolution is happening according to the expected by Brownian motion, and k > 1 means high phylogenetic signal.

Biome	Trait	K	PIC.variance.P	PIC.variance.Z
Atlantic Forest	SVL	0.062	0.001	-1.0788357
	Head width	0.048	0.016	-0.9977475
	Tibia lenght	0.055	0.004	-1.1190054
Cerrado	SVL	0.345	0.001	-4.053306
	Head width	0.360	0.001	-4.233683
	Tibia lenght	0.234	0.001	-3.549059
Amazon	SVL	0.394	0.001	-5.278008
	Head width	0.383	0.001	-5.256102
	Tibia lenght	0.300	0.001	-5.054435

Table A3. Phylogenetic signal of continuous non-imputed data in the three biomes, taking out the missing data. K: K statistics, PIC.variance.P: significance of K, PIC.variance. Z: Z-score. Where k < 1 indicates small phylogenetic signal, k = 1 indicates that the trait evolution is happening according to the expected by Brownian motion, and k > 1 means high phylogenetic signal.

Biome	Trait	K	PIC.variance.P	PIC.variance.Z
Atlantic Forest	SVL	0.060	0.005	-1.0876163
	Head width	0.043	0.036	-0.9476158
	Tibia lenght	0.053	0.012	-1.0589323
Cerrado	SVL	0.463	0.001	-4.387820
	Head width	0.444	0.001	-4.037225
	Tibia lenght	0.332	0.001	-4.025540
Amazon	SVL	0.371	0.001	-4.154866
	Head width	0.367	0.001	-4.258878
	Tibia lenght	0.288	0.001	-4.094699

Table A4. Phylogenetic signal for imputed categorical data in the three biomes. The traits show phylogenetic signal when the observed number of changes in trait states is lower than the median null number of changes. *P* is the significance value.

Biome	Trait	Nº of trait states	Observed nº of changes	Median null nº of changes	*P*
Atlantic Rainforest	Reproductive mode	2	3	55	0
	Type of development	3	14	80	0
Cerrado	Reproductive mode	2	3	15	0
	Type of development	3	5	23	0
Amazon	Reproductive mode	2	13	138	0
	Type of development	3	20	150	0

Table A5. Phylogenetic signal for non-imputed categorical data in the three biomes, taking out the missing data. The traits show phylogenetic signal when the observed number of changes in trait states is lower than the median null number of changes. *P* is the significance value.

Biome	Trait	Nº of trait states	Observed nº of changes	Median null nº of changes	*P*
Atlantic Rainforest	Reproductive mode	2	3	55	0
	Type of development	3	13	66	0
Cerrado	Reproductive mode	2	3	13	0
	Type of development	3	5	19	0
Amazon	Reproductive mode	2	10	105	0
	Type of development	3	17	114	0

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SUPPORTING INFORMATION

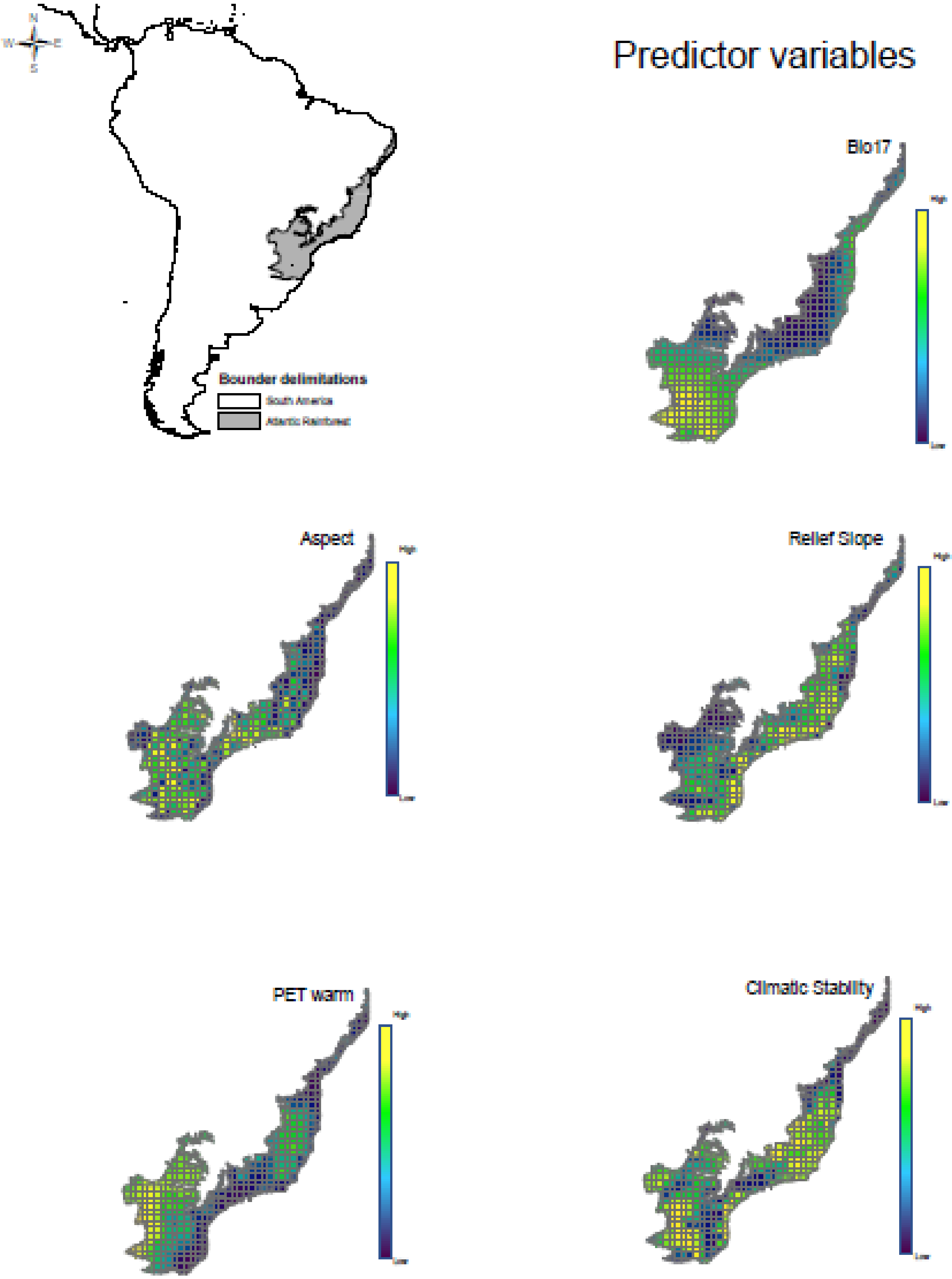

Figure S1. Maps of the Atlantic Rainforest predictor variables distribution. Precipitation of driest quarter (BIO17), Mountain Aspect (Aspect), Terrain slope (relief slope), Potential Evapotranspiration of the Warmest Quarter (PET warm), Climatic stability over the past 120,000 years (Climatic Stability).

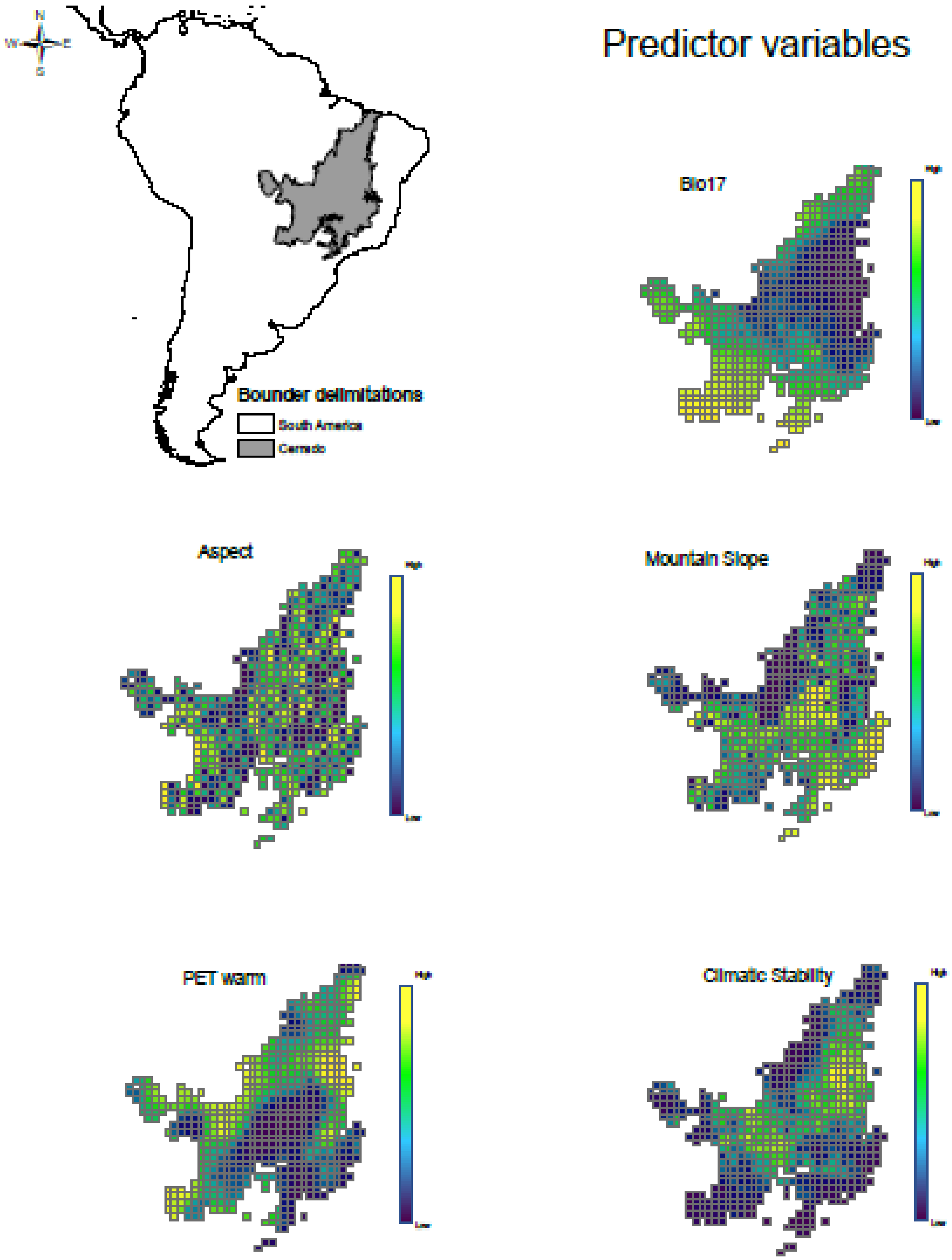

Figure S2. Maps of the Cerrado predictor variables distribution. Precipitation of driest quarter (BIO17), Mountain Aspect (Aspect), Terrain slope (relief slope), Potential Evapotranspiration of the Warmest Quarter (PET warm), Climatic stability over the past 120,000 years (Climatic Stability).

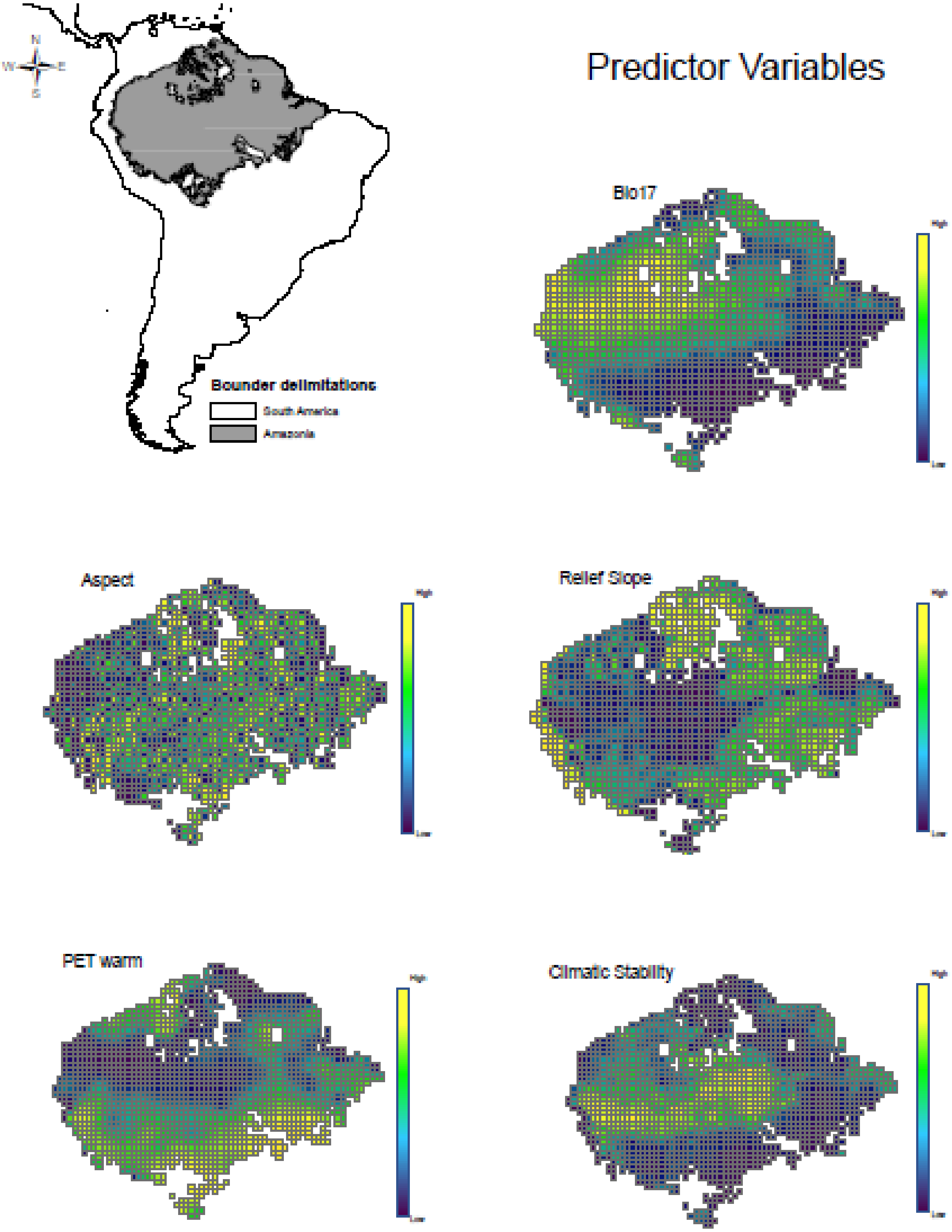

Figure S3. Maps of the Amazon predictor variables distribution. Precipitation of driest quarter (BIO17), Mountain Aspect (Aspect), Terrain slope (relief slope), Potential Evapotranspiration of the Warmest Quarter (PET warm), Climatic stability over the past 120,000 years (Climatic Stability).

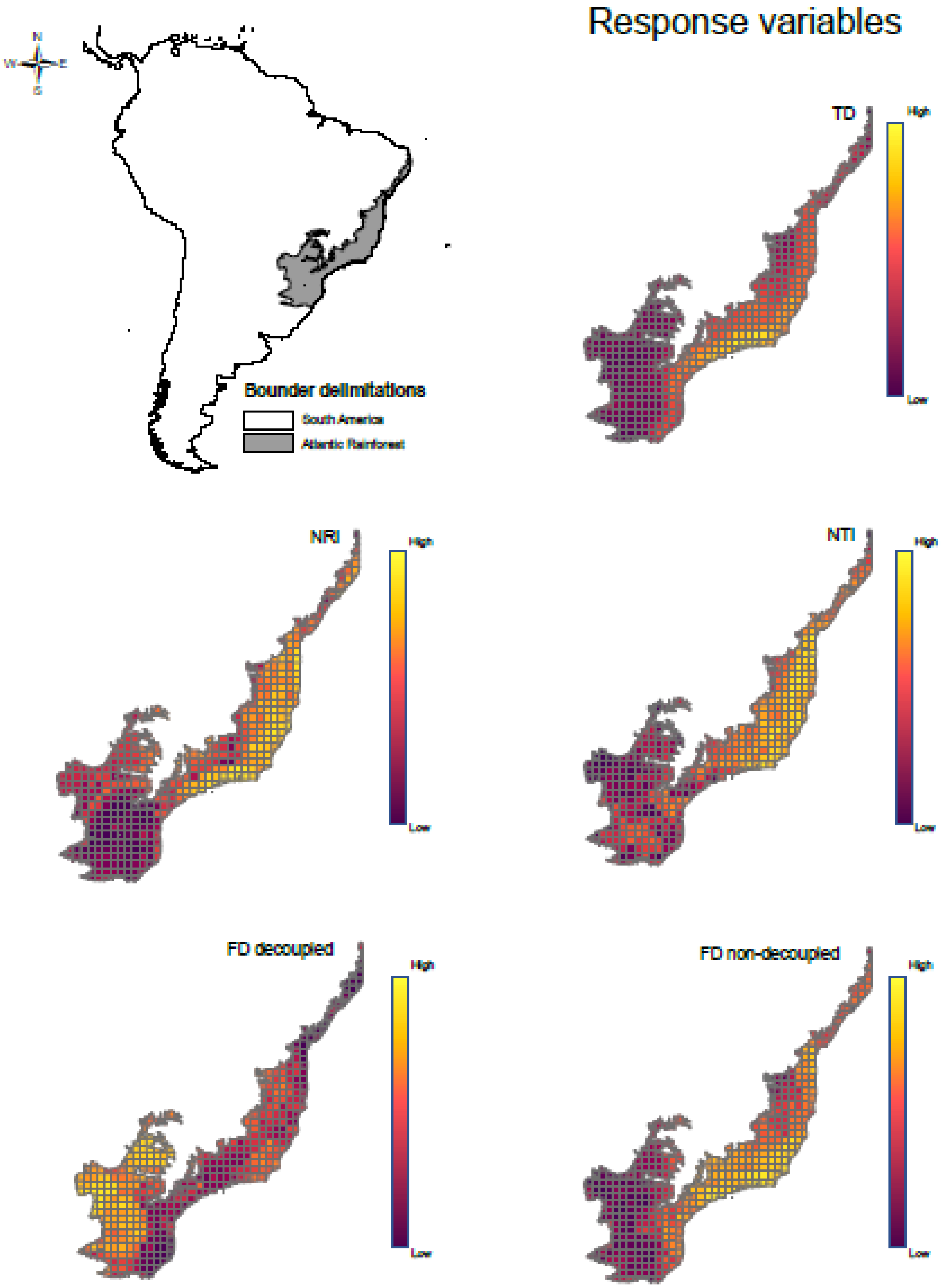

Figure S4. Maps of the Atlantic Rainforest response variables distribution. Taxonomic Diversity (TD), Phylogenetic diversity of early diverging clades (NRI), Phylogenetic diversity of recent diverging clades (NTI), Decoupled Functional Diversity (FD decoupled), Non-decoupled Functional Diversity (FD non-decoupled).

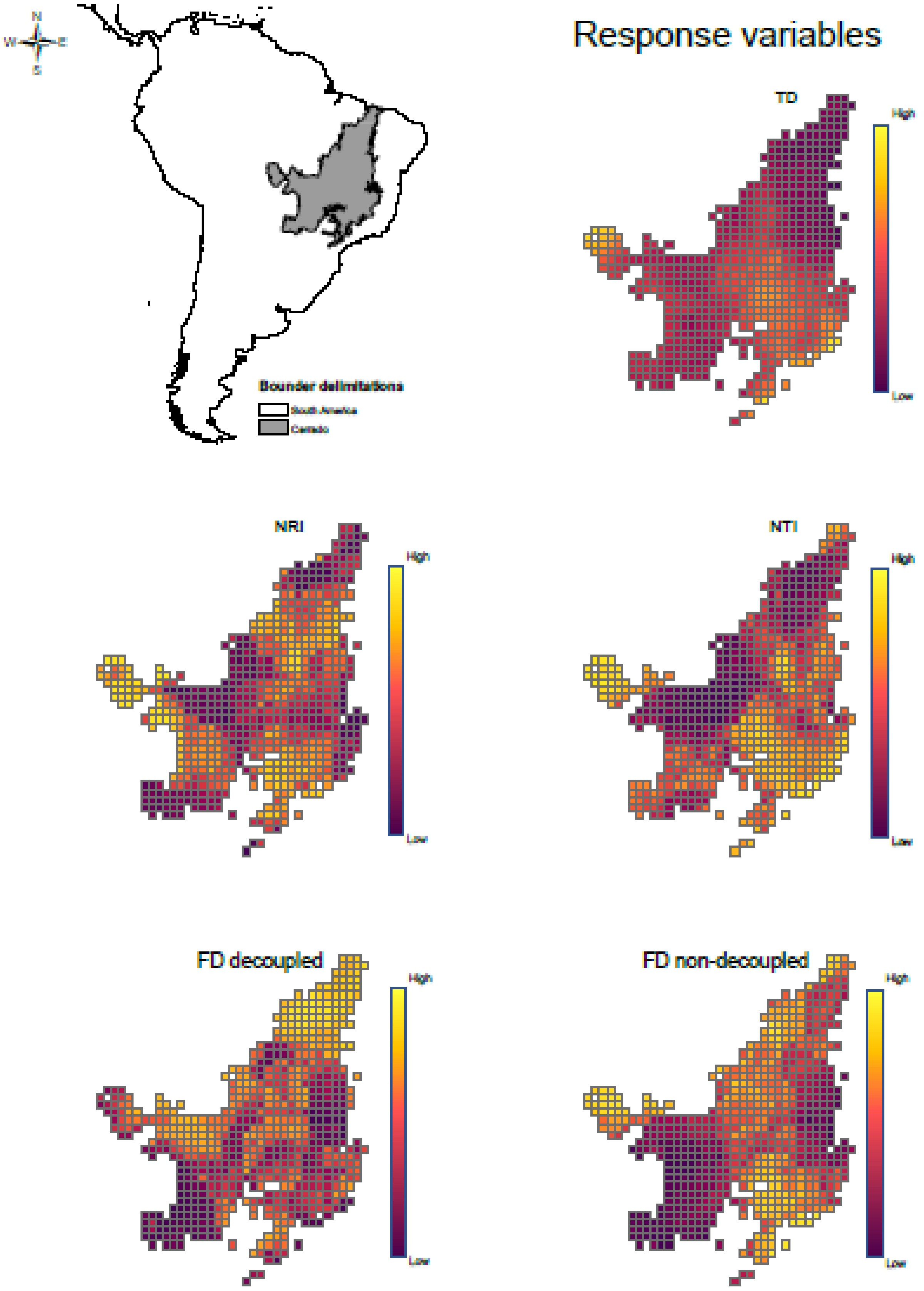

Figure S5. Maps of the Cerrado response variables distribution. Taxonomic Diversity (TD), Phylogenetic diversity of early diverging clades (NRI), Phylogenetic diversity of recent diverging clades (NTI), Decoupled Functional Diversity (FD decoupled), Non-decoupled Functional Diversity (FD non-decoupled).

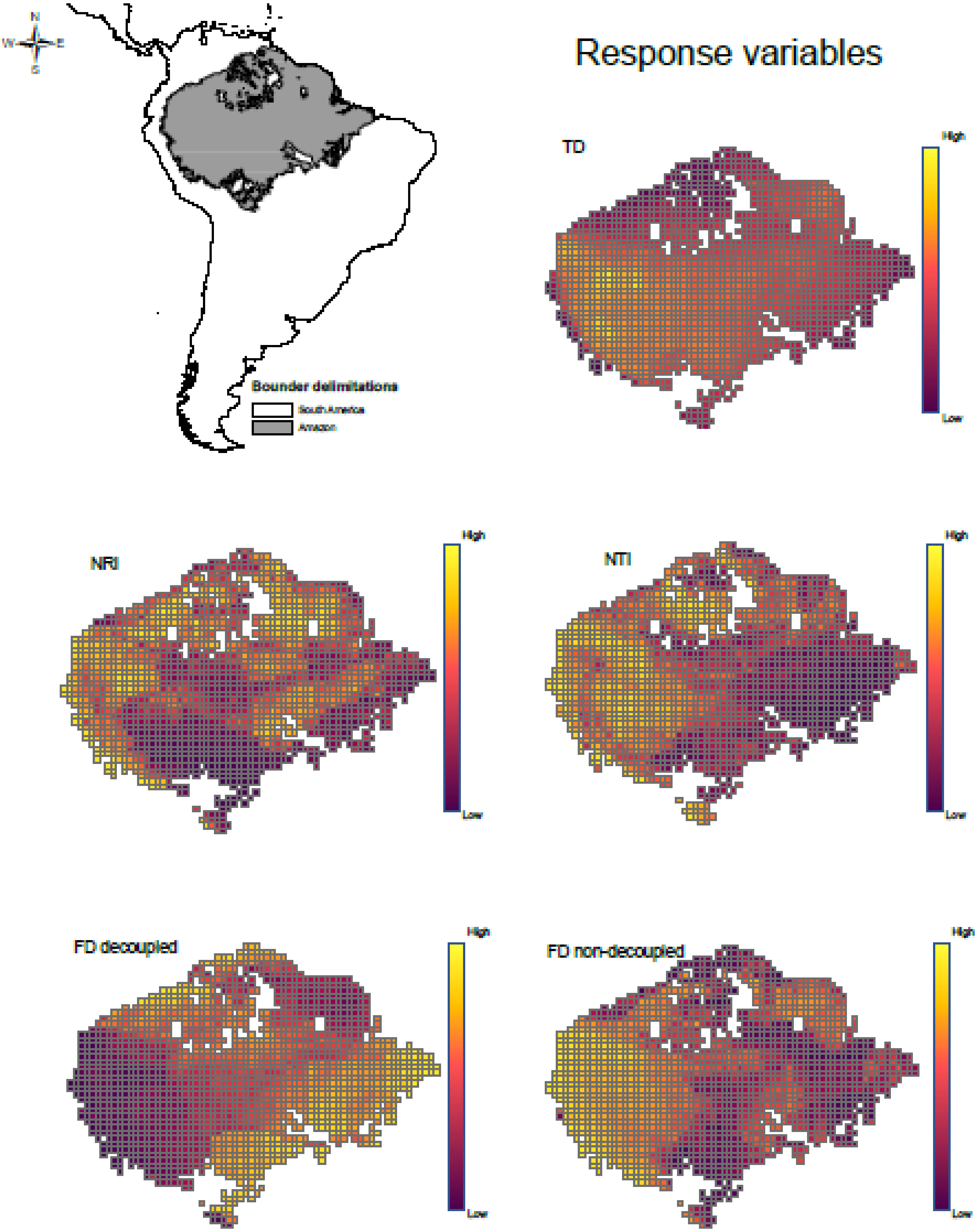

Figure S6. Maps of the Amazon response variables distribution. Taxonomic Diversity (TD), Phylogenetic diversity of early diverging clades (NRI), Phylogenetic diversity of recent diverging clades (NTI), Decoupled Functional Diversity (FD decoupled), Non-decoupled Functional Diversity (FD non-decoupled).

Table S1. Families and species included in diversity dimensions analyses and the authors responsible for the species description. Colors indicate the biome of species occurrence.

Family/Species	Amazonia	Cerrado	Atlantic Rainforest	Authors
Allophrynidae				
Allophryne ruthveni	🟩			Gaige, 1926
Alsodidae				
Limnomedusa macroglossa			🟨	(Duméril and Bibron, 1841)
Aromobatidae				
Allobates alessandroi	🟩			(Grant and Rodriguez, 2001)
Allobates brunneus	🟩	🟧		(Cope, 1887)
Allobates caeruleodactylus	🟩			(Lima and Caldwell, 2001)
Allobates conspicuus	🟩			(Morales, 2002)
Allobates crombiei	🟩			(Morales, 2002)
Allobates femoralis	🟩	🟧		(Boulenger, 1884)
Allobates fuscellus	🟩			(Morales, 2002)
Allobates gasconi	🟩			(Morales, 2002)
Allobates goianus		🟧		(Bokermann, 1975)
Allobates granti	🟩			(Kok, MacCulloch, Gaucher, Poelman, Bourne, Lathrop, and Lenglet, 2006)
Allobates insperatus	🟩			(Morales, 2002)
Allobates marchesianus	🟩	🟧		(Melin, 1941)
Allobates masniger	🟩			(Morales, 2002)
Allobates melanolaemus	🟩			(Grant and Rodriguez, 2001)
Allobates myersi	🟩			(Pyburn, 1981)
Allobates nidicola	🟩			(Caldwell and Lima, 2003)
Allobates olfersioides			🟨	(Lutz, 1925)
Allobates ornatus	🟩			(Morales, 2002)
Allobates paleovarzensis	🟩			Lima, Caldwell, Biavati, and Montanarin, 2010
Allobates subfolionidificans	🟩			(Lima, Sanchez, and Souza, 2007)
Allobates sumtuosus	🟩			(Morales, 2002)
Allobates trilineatus	🟩			(Boulenger, 1884)
Allobates undulatus	🟩			(Myers and Donnelly, 2001)
Allobates vanzolinius	🟩			(Morales, 2002)
Allobates zaparo	🟩			(Silverstone, 1976)
Anomaloglossus ayarzaguenai	🟩			(La Marca, 1997)
Anomaloglossus baeobatrachus	🟩			(Boistel and Massary, 1999)
Anomaloglossus beebei	🟩			(Noble, 1923)
Anomaloglossus degranvillei	🟩			(Lescure, 1975)
Anomaloglossus guanayensis	🟩			(La Marca, 1997)
Anomaloglossus kaiei	🟩			(Kok, Sambhu, Roopsind, Lenglet, and Bourne, 2006)
Anomaloglossus parimae	🟩			(La Marca, 1997)
Anomaloglossus parkerae	🟩			(Meinhardt and Parmalee, 1996)

Anomaloglossus shrevei	🟩			(Rivero, 1961)
Anomaloglossus stepheni	🟩			(Martins, 1989)
Anomaloglossus tamacuarensis	🟩			(Myers and Donnelly, 1997)
Anomaloglossus tepuyensis	🟩			(La Marca, 1997)
Anomaloglossus triunfo	🟩			(Barrio-Amorós, Fuentes-Ramos, and Rivas-Fuenmayor, 2004)
Anomaloglossus wothuja	🟩			(Barrio-Amorós, Fuentes-Ramos, and Rivas-Fuenmayor, 2004)
<u>Brachycephalidae</u>				
Amazophrynella bokermanni	🟩			(Izecksohn, 1994)
Amazophrynella minuta	🟩	🟧		(Melin, 1941)
Brachycephalus alipioi			🟨	Pombal and Gasparini, 2006
Brachycephalus brunneus			🟨	Ribeiro, Alves, Haddad, and Reis, 2005
Brachycephalus didactylus			🟨	Izecksohn, 1971
Brachycephalus ephippium			🟨	(Spix, 1824)
Brachycephalus ferruginus			🟨	Alves, Ribeiro, Haddad, and Reis, 2006
Brachycephalus hermogenesi		🟧	🟨	(Giaretta and Sawaya, 1998)
Brachycephalus izecksohni			🟨	Ribeiro, Alves, Haddad, and Reis, 2005
Brachycephalus nodoterga			🟨	Miranda-Ribeiro, 1920
Brachycephalus pernix			🟨	Pombal, Wistuba, and Bornschein, 1998
Brachycephalus pombali			🟨	Alves, Ribeiro, Haddad, and Reis, 2006
Brachycephalus vertebralis			🟨	Pombal, 2001
Ischnocnema bolbodactyla			🟨	(Lutz, 1925)
Ischnocnema epipeda			🟨	(Heyer, 1984)
Ischnocnema erythromera			🟨	(Heyer, 1984)
Ischnocnema gehrti			🟨	(Miranda-Ribeiro, 1926)
Ischnocnema gualteri			🟨	(Lutz, 1974)
Ischnocnema guentheri		🟧	🟨	(Steindachner, 1864)
Ischnocnema henselii			🟨	(Peters, 1870)
Ischnocnema hoehnei			🟨	(Lutz, 1958)
Ischnocnema holti			🟨	(Cochran, 1948)
Ischnocnema izecksohni		🟧	🟨	(Caramaschi and Kisteumacher, 1989)
Ischnocnema juipoca		🟧	🟨	(Sazima and Cardoso, 1978)
Ischnocnema lactea		🟧	🟨	(Miranda-Ribeiro, 1923)
Ischnocnema manezinho			🟨	(Garcia, 1996)
Ischnocnema nasuta		🟧	🟨	(Lutz, 1925)
Ischnocnema nigriventris			🟨	(Lutz, 1925)
Ischnocnema octavioi			🟨	(Bokermann, 1965)
Ischnocnema oea			🟨	(Heyer, 1984)
Ischnocnema paranaensis			🟨	(Langone and Segalla, 1996)
Ischnocnema parva			🟨	(Girard, 1853)

Ischnocnema penaxavantinho		🟧	🟨	Giaretta, Toffoli, and Oliveira, 2007
Ischnocnema pusilla			🟨	(Bokermann, 1967)
Ischnocnema randorum			🟨	(Heyer, 1985)
Ischnocnema sambaqui			🟨	(Castanho and Haddad, 2000)
Ischnocnema spanios			🟨	(Heyer, 1985)
Ischnocnema venancioi			🟨	(Lutz, 1958)
Ischnocnema verrucosa			🟨	Reinhardt and Lütken, 1862
Bufonidae				
Atelopus andinus	🟩			Rivero, 1968
Atelopus boulengeri	🟩			Peracca, 1904
Atelopus dimorphus	🟩			Lötters, 2003
Atelopus flavescens	🟩			Duméril and Bibron, 1841
Atelopus franciscus	🟩			Lescure, 1974
Atelopus pulcher	🟩			(Boulenger, 1882)
Atelopus seminiferus	🟩			Cope, 1874
Atelopus siranus	🟩			Lötters and Henzl, 2000
Atelopus spumarius	🟩			Cope, 1871
Atelopus tricolor	🟩			Boulenger, 1902
Dendrophryniscus berthalutzae			🟨	Izecksohn, 1994
Dendrophryniscus brevipollicatus			🟨	Jiménez de la Espada, 1870
Dendrophryniscus carvalhoi			🟨	Izecksohn, 1994
Dendrophryniscus krausae			🟨	Cruz and Fusinatto, 2008
Dendrophryniscus leucomystax			🟨	Izecksohn, 1968
Dendrophryniscus proboscideus			🟨	(Boulenger, 1882)
Dendrophryniscus stawiarskyi			🟨	Izecksohn, 1994
Frostius erythrophthalmus			🟨	Pimenta and Caramaschi, 2007
Frostius pernambucensis			🟨	(Bokermann, 1962)
Melanophryniscus admirabilis			🟨	Di-Bernardo, Maneyo, and Grillo, 2006
Melanophryniscus alipioi			🟨	Langone, Segalla, Bornschein, and de Sá, 2008
Melanophryniscus atroluteus			🟨	(Mertens, 1933)
Melanophryniscus cambaraensis			🟨	Braun and Braun, 1979
Melanophryniscus dorsalis			🟨	(Mertens, 1933)
Melanophryniscus fulvoguttatus			🟨	(Mertens, 1937)
Melanophryniscus macrogranulosus			🟨	Braun, 1973
Melanophryniscus moreirae			🟨	(Miranda-Ribeiro, 1920)
Melanophryniscus peritus			🟨	Caramaschi and Cruz, 2011
Melanophryniscus simplex			🟨	Caramaschi and Cruz, 2002
Melanophryniscus spectabilis			🟨	Caramaschi and Cruz, 2002

Melanophryniscus tumifrons			🟨	(Boulenger, 1905)
Oreophrynella cryptica	🟩			Señaris, 1995
Oreophrynella dendronastes	🟩			Lathrop and MacCulloch, 2007
Oreophrynella huberi	🟩			Diego-Aransay and Gorzula, 1990
Oreophrynella macconnelli	🟩			Boulenger, 1900
Rhaebo glaberrimus	🟩			(Günther, 1869)
Rhaebo guttatus	🟩	🟧		(Schneider, 1799)
Rhaebo nasicus	🟩			(Werner, 1903)
Rhinella abei			🟨	(Baldissera, Caramaschi, and Haddad, 2004)
Rhinella achavali			🟨	(Maneyro, Arrieta, and de Sá, 2004)
Rhinella acutirostris	🟩			(Spix, 1824)
Rhinella arenarum			🟨	(Hensel, 1867)
Rhinella bergi		🟧	🟨	(Céspedez, 2000)
Rhinella castaneotica	🟩			(Caldwell, 1991)
Rhinella ceratophrys	🟩			(Boulenger, 1882)
Rhinella cerradensis		🟧	🟨	Maciel, Brandão, Campos, and Sebben, 2007
Rhinella cristinae	🟩			(Vélez-Rodriguez and Ruiz-Carranza, 2002)
Rhinella crucifer			🟨	(Wied-Neuwied, 1821)
Rhinella dapsilis	🟩			(Myers and Carvalho, 1945)
Rhinella dorbignyi			🟨	(Duméril and Bibron, 1841)
Rhinella fernandezae			🟨	(Gallardo, 1957)
Rhinella festae	🟩			(Peracca, 1904)
Rhinella fissipes	🟩			(Boulenger, 1903)
Rhinella granulosa	🟩	🟧	🟨	(Spix, 1824)
Rhinella henseli			🟨	(Lutz, 1934)
Rhinella hoogmoedi		🟧	🟨	Caramaschui and Pombal, 2006
Rhinella humboldti	🟩			(Gallardo, 1965)
Rhinella icterica		🟧	🟨	(Spix, 1824)
Rhinella inca	🟩			(Stejneger, 1913)
Rhinella iserni	🟩			(Jiménez de la Espada, 1875)
Rhinella jimi		🟧	🟨	(Stevaux, 2002)
Rhinella lescurei	🟩			Fouquet, Gaucher, Blanc, and Vélez-Rodriguez, 2007
Rhinella magnussoni	🟩			Lima, Menin, and Araújo, 2007
Rhinella manu	🟩			Chaparro, Pramuk, and Gluesenkamp, 2007
Rhinella margaritifera	🟩	🟧	🟨	(Laurenti, 1768)
Rhinella marina	🟩	🟧		(Linnaeus, 1758)
Rhinella martyi	🟩			Fouquet, Gaucher, Blanc, and Vélez-Rodriguez, 2008
Rhinella nesiotes	🟩			(Duellman and Toft, 1979)
Rhinella ocellata	🟩	🟧		(Günther, 1858)
Rhinella ornata		🟧	🟨	(Spix, 1824)

Rhinella poeppigii	🟩			(Tschudi, 1845)
Rhinella proboscidea	🟩			(Spix, 1824)
Rhinella pygmaea			🟨	(Myers and Carvalho, 1952)
Rhinella roqueana	🟩			(Melin, 1941)
Rhinella rubescens	🟩	🟧	🟨	(Lutz, 1925)
Rhinella schneideri	🟩	🟧	🟨	(Werner, 1894)
Rhinella scitula		🟧		(Caramaschi and Niemeyer, 2003)
Rhinella spinulosa	🟩			(Wiegmann, 1834)
Rhinella stanlaii	🟩			(Lötters and Köhler, 2000)
Rhinella veraguensis	🟩			(Schmidt, 1857)
Rhinella veredas		🟧		(Brandão, Maciel, and Sebben, 2007)
Centrolenidae				
Centrolene azulae	🟩			(Flores and McDiarmid, 1989)
Centrolene bacatum	🟩			Wild, 1994
Centrolene durrellorum	🟩			(Cisneros-Heredia, 2007)
Centrolene medemi	🟩			(Cochran and Goin, 1970)
Chimerella mariaelenae	🟩			(Cisneros-Heredia and McDiarmid, 2006)
Cochranella croceopodes	🟩			(Duellman and Schulte, 1993)
Cochranella duidaeana	🟩			(Ayarzagüena, 1992)
Cochranella erminea	🟩			Torres-Gastello, Suárez-Segovia, and Cisneros-Heredia, 2007
Cochranella geijskesi	🟩			(Goin, 1966)
Cochranella resplendens	🟩			(Lynch and Duellman, 1973)
Cochranella riveroi	🟩			(Ayarzagüena, 1992)
Hyalinobatrachium cappellei	🟩			Van Lidth de Jeude, 1904
Hyalinobatrachium fleischmanni	🟩			(Boettger, 1893)
Hyalinobatrachium iaspidiense	🟩			(Ayarzagüena, 1992)
Hyalinobatrachium ruedai	🟩			Ruiz-Carranza and Lynch, 1998
Hyalinobatrachium taylori	🟩			(Goin, 1968)
Nymphargus bejaranoi	🟩			(Cannatella, 1980)
Nymphargus laurae	🟩			Cisneros-Heredia and McDiarmid, 2007
Nymphargus mariae	🟩			(Duellman and Toft, 1979)
Nymphargus mixomaculatus	🟩			(Guaysamin, Lehr, Rodríguez, and Aguilar, 2006)
Nymphargus ocellatus	🟩			(Boulenger, 1918)
Nymphargus phenax	🟩			(Cannatella and Duellman, 1982)
Nymphargus posadae	🟩			(Ruiz-Carranza and Lynch, 1995)
Nymphargus siren	🟩			(Lynch and Duellman, 1973)
Nymphargus truebae	🟩			(Duellman, 1976)

Rulyrana flavopunctata	🟩			(Lynch and Duellman, 1973)
Rulyrana mcdiarmidi	🟩			(Cisneros-Heredia, Venegas, Rada, and Schulte, 2008)
Rulyrana saxiscandens	🟩			(Duellman and Schulte, 1993)
Rulyrana spiculata	🟩			(Duellman, 1976)
Teratohyla adenocheira	🟩			(Harvey and Noonan, 2005)
Teratohyla amelie	🟩			(Cisneros-Heredia and Meza-Ramos, 2007)
Teratohyla midas	🟩			(Lynch and Duellman, 1973)
Vitreorana eurygnatha		🟧	🟨	(Lutz, 1925)
Vitreorana gorzulae	🟩			(Ayarzagüena, 1992)
Vitreorana parvula			🟨	(Boulenger, 1895)
Vitreorana ritae	🟩			(Lutz, 1952)
Vitreorana uranoscopa		🟧	🟨	(Müller, 1924)
Ceratophryidae				
Ceratophrys aurita		🟧	🟨	(Raddi, 1823)
Ceratophrys cornuta	🟩	🟧		(Linnaeus, 1758)
Ceratophrys cranwelli		🟧		Barrio, 1980
Craugastoridae				
Barycholos ternetzi	🟩	🟧	🟨	Miranda-Ribeiro, 1937
Ceuthomantis aracamuni	🟩			Barrio-Amorós and Molina, 2006
Ceuthomantis cavernibardus	🟩			(Myers and Donnelly, 1997)
Ceuthomantis duellmani	🟩			Barrio-Amorós, 2010
Euparkerella brasiliensis			🟨	(Parker, 1926)
Euparkerella cochranae			🟨	Izecksohn, 1988
Euparkerella robusta			🟨	Izecksohn, 1988
Euparkerella tridactyla			🟨	Izecksohn, 1988
Haddadus binotatus		🟧	🟨	(Spix, 1824)
Haddadus plicifer			🟨	(Boulenger, 1888)
Holoaden bradei			🟨	Lutz, 1958
Holoaden luederwaldti			🟨	Miranda-Ribeiro, 1920
Holoaden pholeter			🟨	Pombal, Siqueira, Dorigo, Vrcibradic, and Rocha, 2008
Hypodactylus dolops	🟩			(Lynch and Duellman, 1980)
Hypodactylus nigrovittatus	🟩			(Andersson, 1945)
Noblella lochites	🟩			(Lynch, 1976)
Noblella myrmecoides	🟩			(Lynch, 1976)
Oreobates crepitans		🟧		(Bokermann, 1965)
Oreobates cruralis	🟩			(Boulenger, 1902)
Oreobates heterodactylus		🟧		(Miranda-Ribeiro, 1937)
Oreobates lehri	🟩			(Padial, Chaparro, and De la Riva, 2007)
Oreobates quixensis	🟩			Jiménez de la Espada, 1872
Oreobates saxatilis	🟩			(Duellman, 1990)
Phrynopus bracki	🟩			Hedges, 1990
Pristimantis aaptus	🟩			(Lynch and Lescure, 1980)
Pristimantis acuminatus	🟩			(Shreve, 1935)

Pristimantis adiastolus	🟩		Duellman and Hedges, 2007
Pristimantis aureoventris	🟩		Kok, Means, and Bossuyt, 2011
Pristimantis albertus	🟩		Duellman and Hedges, 2007
Pristimantis altamazonicus	🟩		(Barbour and Dunn, 1921)
Pristimantis altamnis	🟩		Elmer and Cannatella, 2008
Pristimantis ardalonychus	🟩		(Duellman and Pramuk, 1999)
Pristimantis aureolineatus	🟩		(Guayasamin, Ron, Cisneros-Heredia, Lamar, and McCracken, 2006)
Pristimantis avius	🟩		(Myers and Donnelly, 1997)
Pristimantis bearsei	🟩		(Duellman, 1992)
Pristimantis bromeliaceus	🟩		(Lynch, 1979)
Pristimantis buccinator	🟩		(Rodriguez, 1994)
Pristimantis cantitans	🟩		(Myers and Donnelly, 1996)
Pristimantis carvalhoi	🟩		(Lutz, 1952)
Pristimantis chiastonotus	🟩		(Lynch and Hoogmoed, 1977)
Pristimantis citriogaster	🟩		(Duellman, 1992)
Pristimantis colonensis	🟩		(Mueses-Cisneros, 2007)
Pristimantis condor	🟩		(Lynch and Duellman, 1980)
Pristimantis conspicillatus	🟩		(Günther, 1858)
Pristimantis cosnipatae	🟩		(Duellman, 1978)
Pristimantis croceoinguinis	🟩		(Lynch, 1968)
Pristimantis cruciocularis	🟩		(Lehr, Lundberg, Aguilar, and von May, 2006)
Pristimantis danae	🟩		(Duellman, 1978)
Pristimantis delius	🟩		(Duellman and Mendelson, 1995)
Pristimantis dendrobatoides	🟩		Means and Savage, 2007
Pristimantis diadematus	🟩		(Jiménez de la Espada, 1875)
Pristimantis divnae	🟩		Lehr and von May, 2009
Pristimantis dundeei		🟧	(Heyer and Muñoz, 1999)
Pristimantis epacrus	🟩		(Lynch and Suárez-Mayorga, 2000)
Pristimantis eurydactylus	🟩		(Hedges and Schlüter, 1992)
Pristimantis exoristus	🟩		(Duellman and Pramuk, 1999)
Pristimantis fenestratus	🟩	🟧	(Steindachner, 1864)
Pristimantis frater	🟩		(Werner, 1899)
Pristimantis galdi	🟩		Jiménez de la Espada, 1870
Pristimantis gutturalis	🟩		(Hoogmoed, Lynch, and Lescure, 1977)
Pristimantis imitatrix	🟩		(Duellman, 1978)
Pristimantis infraguttatus	🟩		(Duellman and Pramuk, 1999)
Pristimantis inguinalis	🟩		(Parker, 1940)
Pristimantis inusitatus	🟩		(Lynch and Duellman, 1980)
Pristimantis jester	🟩		Means and Savage, 2007

Pristimantis kichwarum	🟩			Elmer and Cannatella, 2008
Pristimantis lacrimosus	🟩			(Jiménez de la Espada, 1875)
Pristimantis lanthanites	🟩			(Lynch, 1975)
Pristimantis librarius	🟩			(Flores and Vigle, 1994)
Pristimantis lindae	🟩			(Duellman, 1978)
Pristimantis lirellus	🟩			(Dwyer, 1995)
Pristimantis luscombei	🟩			(Duellman and Mendelson, 1995)
Pristimantis lythrodes	🟩			(Lynch and Lescure, 1980)
Pristimantis malkini	🟩			(Lynch, 1980)
Pristimantis marmoratus	🟩			(Boulenger, 1900)
Pristimantis martiae	🟩			(Lynch, 1974)
Pristimantis memorans	🟩			(Myers and Donnelly, 1997)
Pristimantis mendax	🟩			(Duellman, 1978)
Pristimantis minutulus	🟩			Duellman and Hedges, 2007
Pristimantis muscosus	🟩			(Duellman and Pramuk, 1999)
Pristimantis nebulosus	🟩			(Henle, 1992)
Pristimantis nephophilus	🟩			(Duellman and Pramuk, 1999)
Pristimantis nigrogriseus	🟩			(Andersson, 1945)
Pristimantis ockendeni	🟩			(Boulenger, 1912)
Pristimantis olivaceus	🟩			(Köhler, Morales, Lötters, Reichle, and Aparicio, 1998)
Pristimantis orcus	🟩			Lehr, Catenazzi, and Rodríguez, 2009
Pristimantis orphnolaimus	🟩			(Lynch, 1970)
Pristimantis paulodutrai			🟨	(Bokermann, 1975)
Pristimantis paululus	🟩			(Lynch, 1974)
Pristimantis pecki	🟩			(Duellman and Lynch, 1988)
Pristimantis percnopterus	🟩			(Duellman and Pramuk, 1999)
Pristimantis peruvianus	🟩			(Melin, 1941)
Pristimantis petersi	🟩			(Lynch and Duellman, 1980)
Pristimantis platydactylus	🟩			(Boulenger, 1903)
Pristimantis pruinatus	🟩			(Myers and Donnelly, 1996)
Pristimantis pseudoacuminatus	🟩			(Shreve, 1935)
Pristimantis pulvinatus	🟩			(Rivero, 1968)
Pristimantis quaquaversus	🟩			(Lynch, 1974)
Pristimantis ramagii			🟨	(Boulenger, 1888)
Pristimantis rhabdolaemus	🟩			(Duellman, 1978)
Pristimantis rufioculis	🟩			(Duellman and Pramuk, 1999)
Pristimantis saltissimus	🟩			Means and Savage, 2007
Pristimantis savagei	🟩			(Pyburn and Lynch, 1981)
Pristimantis skydmainos	🟩			(Flores and Rodriguez, 1997)
Pristimantis tantanti	🟩			(Lehr, Torres-Gastello, and Suárez-Segovia, 2007)
Pristimantis toftae	🟩			(Duellman, 1978)

Pristimantis variabilis	🟩			(Lynch, 1968)
Pristimantis ventrimarmoratus	🟩			(Boulenger, 1912)
Pristimantis versicolor	🟩			(Lynch, 1979)
Pristimantis vilarsi	🟩			(Melin, 1941)
Pristimantis vilcabambae	🟩			Lehr, 2007
Pristimantis vinhai			🟨	(Bokermann, 1975)
Pristimantis w.nigrum	🟩			(Boettger, 1892)
Pristimantis waoranii	🟩			(McCracken, Forstner, and Dixon, 2007)
Pristimantis yaviensis	🟩			(Myers and Donnelly, 1996)
Pristimantis zeuctotylus	🟩			(Lynch and Hoogmoed, 1977)
Pristimantis zimmermanae	🟩			(Heyer and Hardy, 1991)
Pristimantis zoilae	🟩			(Mueses-Cisneros, 2007)
Psychrophrynella usurpator	🟩			De la Riva, Chaparro, and Padial, 2008
Strabomantis cornutus	🟩			(Jiménez de la Espada, 1870)
Strabomantis sulcatus	🟩			(Lynch, 1976)
Yunganastes mercedesae	🟩			(Lynch and McDiarmid, 1987)
<u>Cycloramphidae</u>				
Cycloramphus acangatan			🟨	Verdade and Rodrigues, 2003
Cycloramphus asper			🟨	Werner, 1899
Cycloramphus bandeirensis			🟨	Heyer, 1983
Cycloramphus bolitoglossus			🟨	(Werner, 1897)
Cycloramphus boraceiensis			🟨	Heyer, 1983
Cycloramphus brasiliensis			🟨	(Steindachner, 1864)
Cycloramphus carvalhoi			🟨	Heyer, 1983
Cycloramphus catarinensis			🟨	Heyer, 1983
Cycloramphus cedrensis			🟨	Heyer, 1983
Cycloramphus diringshofeni			🟨	Bokermann, 1957
Cycloramphus dubius			🟨	(Miranda-Ribeiro, 1920)
Cycloramphus duseni			🟨	(Andersson, 1914)
Cycloramphus eleutherodactylus		🟧	🟨	(Miranda-Ribeiro, 1920)
Cycloramphus faustoi			🟨	Brasileiro, Haddad, Sawaya, and Sazima, 2007
Cycloramphus fuliginosus			🟨	Tschudi, 1838
Cycloramphus granulosus			🟨	Lutz, 1929
Cycloramphus izecksohni			🟨	Heyer, 1983
Cycloramphus juimirim			🟨	Haddad and Sazima, 1989
Cycloramphus lutzorum			🟨	Heyer, 1983
Cycloramphus migueli			🟨	Heyer, 1988
Cycloramphus mirandaribeiroi			🟨	Heyer, 1983
Cycloramphus ohausi			🟨	(Wandolleck, 1907)
Cycloramphus organensis			🟨	Weber, Verdade, Salles, Fouquet, and Carvalho-e-

			🟨	Silva, 2011
Cycloramphus rhyakonastes			🟨	Heyer, 1983
Cycloramphus semipalmatus			🟨	(Miranda-Ribeiro, 1920)
Cycloramphus stejnegeri			🟨	(Noble, 1924)
Cycloramphus valae			🟨	Heyer, 1983
Thoropa lutzi			🟨	Cochran, 1938
Thoropa megatympanum		🟧	🟨	Caramaschi and Sazima, 1984
Thoropa miliaris		🟧	🟨	(Spix, 1824)
Thoropa petropolitana			🟨	(Wandolleck, 1907)
Thoropa saxatilis			🟨	Cocroft and Heyer, 1988
Zachaenus carvalhoi			🟨	Izecksohn, 1983
Zachaenus parvulus			🟨	(Girard, 1853)
Dendrobatidae				
Adelphobates castaneoticus	🟩			(Caldwell and Myers, 1990)
Adelphobates galactonotus	🟩	🟧		(Steindachner, 1864)
Adelphobates quinquevittatus	🟩	🟧		(Steindachner, 1864)
Ameerega bassleri	🟩			(Melin, 1941)
Ameerega berohoka		🟧		Vaz-Silva and Maciel, 2011
Ameerega bilinguis	🟩			(Jungfer, 1989)
Ameerega braccata		🟧		(Steindachner, 1864)
Ameerega cainarachi	🟩			(Schulte, 1989)
Ameerega flavopicta	🟩	🟧	🟨	(Lutz, 1925)
Ameerega hahneli	🟩			(Boulenger, 1884)
Ameerega ingeri	🟩			(Cochran and Goin, 1970)
Ameerega macero	🟩			(Rodriguez and Myers, 1993)
Ameerega parvula	🟩			(Boulenger, 1882)
Ameerega petersi	🟩			(Silverstone, 1976)
Ameerega picta	🟩	🟧	🟨	(Tschudi, 1838)
Ameerega planipaleae	🟩			(Morales and Velazco, 1998)
Ameerega pongoensis	🟩			(Schulte, 1999)
Ameerega pulchripecta	🟩			(Silverstone, 1976)
Ameerega rubriventris	🟩			(Lötters, Debold, Henle, Glaw, and and Kneller, 1997)
Ameerega silverstonei	🟩			(Myers and Daly, 1979)
Ameerega simulans	🟩			(Myers, Rodriguez, and Icochea, 1998)
Ameerega smaragdina	🟩			(Silverstone, 1976)
Ameerega trivittata	🟩			(Spix, 1824)
Dendrobates leucomelas	🟩			Steindachner, 1864
Dendrobates nubeculosus	🟩			Jungfer and Böhme, 2004
Dendrobates tinctorius	🟩			(Cuvier, 1797)
Excidobates captivus	🟩			(Myers, 1982)
Hyloxalus azureiventris	🟩			(Kneller and Henle, 1985)
Hyloxalus bocagei	🟩			Jiménez de la Espada, 1870
Hyloxalus cevallosi	🟩			(Rivero, 1991)
Hyloxalus chlorocraspedus	🟩			(Caldwell, 2005)

Hyloxalus craspedoceps	🟩			(Duellman, 2004)
Hyloxalus eleutherodactylus	🟩			(Duellman, 2004)
Hyloxalus exasperatus	🟩			(Duellman and Lynch, 1988)
Hyloxalus faciopunctulatus	🟩			(Rivero, 1991)
Hyloxalus idiomelus	🟩			(Rivero, 1991)
Hyloxalus mittermeieri	🟩			(Rivero, 1991)
Hyloxalus nexipus	🟩			(Frogs, 1986)
Hyloxalus patitae	🟩			(Lötters, Morales, and Proy, 2003)
Hyloxalus pulchellus	🟩			(Jiménez de la Espada, 1875)
Hyloxalus sauli	🟩			(Edwards, 1974)
Hyloxalus shuar	🟩			(Duellman and Simmons, 1988)
Hyloxalus sordidatus	🟩			(Duellman, 2004)
Leucostethus argyrogaster	🟩			(Morales and Schulte, 1993)
Leucostethus fugax	🟩			(Morales and Schulte, 1993)
Ranitomeya amazonica	🟩			(Schulte, 1999)
Ranitomeya benedicta	🟩			Brown, Twomey, Pepper, and Sanchez-Rodriguez, 2008
Ranitomeya fantastica	🟩			(Boulenger, 1884)
Ranitomeya flavovittata	🟩			(Schulte, 1999)
Ranitomeya imitator	🟩			(Schulte, 1986)
Ranitomeya reticulata	🟩			(Boulenger, 1884)
Ranitomeya sirensis	🟩			(Aichinger, 1991)
Ranitomeya summersi	🟩			Brown, Twomey, Pepper, and Sanchez-Rodriguez, 2008
Ranitomeya uakarii	🟩			(Brown, Schulte, and Summers, 2006)
Ranitomeya vanzolinii	🟩			(Myers, 1982)
Ranitomeya variabilis	🟩			(Zimmermann and Zimmermann, 1988)
Ranitomeya ventrimaculata	🟩			(Shreve, 1935)
<u>Eleutherodactylidae</u>				
Adelophryne adiastola	🟩			Hoogmoed and Lescure, 1984
Adelophryne gutturosa				Hoogmoed and Lescure, 1984
Adelophryne pachydactyla			🟨	Hoogmoed, Borges, and Cascon, 1994
Adelophryne patamona	🟩			MacCulloch, Lathrop, Kok, Minter, Khan, and Barrio-Amoros, 2008
Eleutherodactylus johnstonei	🟩			Barbour, 1914
Phyzelaphryne miriamae	🟩			Heyer, 1977
<u>Hemiphractidae</u>				
Fritziana fissilis			🟨	(Miranda-Ribeiro, 1920)
Fritziana goeldii		🟧	🟨	(Boulenger, 1895)
Fritziana ohausi			🟨	(Wandolleck, 1907)
Gastrotheca albolineata			🟨	(Lutz and Lutz, 1939)

Gastrotheca andaquiensis	🟩			Ruiz-Carranza and Hernández-Camacho, 1976
Gastrotheca antoniiochoai	🟩			(De la Riva and Chaparro, 2005)
Gastrotheca carinaceps	🟩			Duellman, Trueb, and Lehr, 2006
Gastrotheca ernestoi			🟨	Miranda-Ribeiro, 1920
Gastrotheca excubitor	🟩			Duellman and Fritts, 1972
Gastrotheca fissipes			🟨	(Boulenger, 1888)
Gastrotheca flamma			🟨	Juncá and Nunes, 2008
Gastrotheca fulvorufa			🟨	(Andersson, 1911)
Gastrotheca longipes	🟩			(Boulenger, 1882)
Gastrotheca marsupiata	🟩			(Duméril and Bribon, 1841)
Gastrotheca microdiscus		🟧	🟨	(Andersson, 1910)
Gastrotheca nicefori	🟩			Gaige, 1933
Gastrotheca ochoai	🟩			Duellman and Fritts, 1972
Gastrotheca stictopleura	🟩			Duellman, Lehr, and Aguilar, 2001
Gastrotheca testudinea	🟩			(Jiménez de la Espada, 1870)
Gastrotheca weinlandii	🟩			(Steindachner, 1892)
Hemiphractus bubalus	🟩			(Jiménez de la Espada, 1870)
Hemiphractus helioi	🟩			Sheil and Mendelson, 2001
Hemiphractus johnsoni	🟩			(Noble, 1917)
Hemiphractus proboscideus	🟩			(Jiménez de la Espada, 1870)
Hemiphractus scutatus	🟩			(Spix, 1824)
Stefania ackawaio	🟩			MacCulloch and Lathrop, 2002
Stefania ayangannae	🟩			MacCulloch and Lathrop, 2002
Stefania breweri	🟩			Barrio-Amorós and Fuentes-Ramos, 2003
Stefania coxi	🟩			MacCulloch and Lathrop, 2002
Stefania evansi	🟩			(Boulenger, 1904)
Stefania ginesi	🟩			Rivero, 1968
Stefania goini	🟩			Rivero, 1968
Stefania marahuaquensis	🟩			(Rivero, 1961)
Stefania oculosa	🟩			Señaris, Ayarzagüena, and Gorzula, 1997
Stefania percristata	🟩			Señaris, Ayarzagüena, and Gorzula, 1997
Stefania riae	🟩			Duellman and Hoogmoed, 1984
Stefania roraimae	🟩			Duellman and Hoogmoed, 1984
Stefania satelles	🟩			Señaris, Ayarzagüena, and Gorzula, 1997
Stefania scalae	🟩			Rivero, 1970
Stefania schuberti	🟩			Señaris, Ayarzagüena, and Gorzula, 1997
Stefania tamacuarina	🟩			Myers and Donnolly, 1997
Stefania woodleyi	🟩			Rivero, 1968

Hylidae				
Aparasphenodon bokermanni			🟨	Pombal, 1993
Aparasphenodon brunoi			🟨	Miranda-Ribeiro, 1920
Aparasphenodon venezolanus	🟩			(Mertens, 1950)
Aplastodiscus albofrenatus			🟨	(Lutz, 1924)
Aplastodiscus albosignatus			🟨	(Lutz and Lutz, 1938)
Aplastodiscus arildae		🟧	🟨	(Cruz and Peixoto, 1985)
Aplastodiscus callipygius			🟨	(Cruz and Peixoto, 1985)
Aplastodiscus cavicola			🟨	(Cruz and Peixoto, 1985)
Aplastodiscus cochranae			🟨	(Mertens, 1952)
Aplastodiscus ehrhardti			🟨	(Müller, 1924)
Aplastodiscus eugenioi			🟨	(Carvalho-e-Silva and Carvalho-e-Silva, 2005)
Aplastodiscus flumineus			🟨	(Cruz and Peixoto, 1985)
Aplastodiscus ibirapitanga		🟧	🟨	(Cruz, Pimenta, and Silvano, 2003)
Aplastodiscus leucopygius		🟧	🟨	(Cruz and Peixoto, 1985)
Aplastodiscus musicus			🟨	(Lutz, 1949)
Aplastodiscus perviridis		🟧	🟨	Lutz, 1950
Aplastodiscus sibilatus			🟨	(Cruz, Pimenta, and Silvano, 2003)
Aplastodiscus weygoldti			🟨	(Cruz and Peixoto, 1987)
Boana albomarginata		🟧	🟨	(Spix, 1824)
Boana albopunctata	🟩	🟧	🟨	(Spix, 1824)
Boana atlantica			🟨	(Caramaschi and Velosa, 1996)
Boana balzani	🟩			(Boulenger, 1898)
Boana beckeri			🟨	(Caramaschi and Cruz, 2004)
Boana bischoffi		🟧	🟨	(Boulenger, 1887)
Boana boans	🟩	🟧		(Linnaeus, 1758)
Boana buriti		🟧		(Caramaschi and Cruz, 1999)
Boana caingua		🟧	🟨	(Carrizo, 1991)
Boana calcarata	🟩			(Troschel, 1848)
Boana cinerascens	🟩	🟧		(Spix, 1824)
Boana cipoensis		🟧	🟨	(Lutz, 1968)
Boana crepitans	🟩	🟧	🟨	(Wied-Neuwied, 1824)
Boana cymbalum			🟨	(Bokermann, 1963)
Boana dentei	🟩			(Bokermann, 1967)
Boana ericae		🟧		(Caramaschi and Cruz, 2000)
Boana exastis			🟨	(Caramaschi and Rodrigues, 2003)
Boana faber		🟧	🟨	(Wied-Neuwied, 1821)
Boana fasciata	🟩	🟧		(Günther, 1858)
Boana freicanecae			🟨	(Carnaval and Peixoto, 2004)
Boana geographica	🟩	🟧	🟨	(Spix, 1824)
Boana goiana		🟧	🟨	(Lutz, 1968)
Boana guentheri			🟨	(Boulenger, 1886)
Boana hobbsi	🟩			(Cochran and Goin, 1970)
Boana hutchinsi	🟩			(Pyburn and Hall, 1984)

Boana jimenezi	🟩			(Señaris and Ayarzagüena, 2006)
Boana joaquini			🟨	(Lutz, 1968)
Boana lanciformis	🟩	🟧		(Cope, 1871)
Boana latistriata			🟨	(Caramaschi and Cruz, 2004)
Boana lemai	🟩			(Rivero, 1972)
Boana leptolineata			🟨	(Braun and Braun, 1977)
Boana leucocheila	🟩			(Caramaschi and Niemeyer, 2003)
Boana liliae	🟩			(Kok, 2006)
Boana lundii		🟧	🟨	(Burmeister, 1856)
Boana marginata			🟨	(Boulenger, 1887)
Boana microderma	🟩			(Pyburn, 1977)
Boana multifasciata	🟩	🟧		(Günther, 1859)
Boana nympha	🟩			(Faivovich, Moravec, Cisneros-Heredia, and Köhler, 2006)
Boana ornatissima	🟩			(Noble, 1923)
Boana palaestes	🟩			(Duellman, De la Riva, and Wild, 1997)
Boana pardalis		🟧	🟨	(Spix, 1824)
Boana phaeopleura		🟧		(Caramaschi and Cruz, 2000)
Boana polytaenia		🟧	🟨	(Cope, 1870)
Boana pombali			🟨	(Caramaschi, Pimenta, and Feio, 2004)
Boana prasina		🟧	🟨	(Burmeister, 1856)
Boana pulchella			🟨	(Duméril and Bibron, 1841)
Boana punctata	🟩	🟧	🟨	(Schneider, 1799)
Boana raniceps	🟩	🟧	🟨	(Cope, 1862)
Boana rhythmica	🟩			(Señaris and Ayarzagüena, 2002)
Boana roraima	🟩			(Duellman and Hoogmoed, 1992)
Boana secedens			🟨	(Lutz, 1963)
Boana semiguttata			🟨	(Lutz, 1925)
Boana semilineata		🟧	🟨	(Spix, 1824)
Boana sibleszi	🟩			(Rivero, 1972)
Boana stellae			🟨	(Kwet, 2008)
Boana stenocephala			🟨	(Caramaschi and Cruz, 1999)
Boana tepuiana	🟩			(Barrio-Amorós and Brewer-Carias, 2008)
Boana xerophylla	🟩			(Duméril and Bibron, 1841)
Boana wavrini	🟩	🟧		(Parker, 1936)
Bokermannohyla ahenea			🟨	(Napoli and Caramaschi, 2004)
Bokermannohyla alvarengai		🟧	🟨	(Bokermann, 1956)
Bokermannohyla astartea			🟨	(Bokermann, 1967)
Bokermannohyla caramaschii			🟨	(Napoli, 2005)
Bokermannohyla carvalhoi			🟨	(Peixoto, 1981)
Bokermannohyla circumdata			🟨	(Cope, 1871)

Bokermannohyla claresignata			🟨	(Lutz and Lutz, 1939)
Bokermannohyla clepsydra			🟨	(Lutz, 1925)
Bokermannohyla gouveai			🟨	(Peixoto and Cruz, 1992)
Bokermannohyla hylax			🟨	(Heyer, 1985)
Bokermannohyla ibitiguara		🟧		(Cardoso, 1983)
Bokermannohyla ibitipoca			🟨	(Caramaschi and Feio, 1990)
Bokermannohyla izecksohni		🟧		(Jim and Caramaschi, 1979)
Bokermannohyla langei			🟨	(Bokermann, 1965)
Bokermannohyla lucianae			🟨	(Napoli and Pimenta, 2003)
Bokermannohyla luctuosa			🟨	(Pombal and Haddad, 1993)
Bokermannohyla martinsi		🟧	🟨	(Bokermann, 1964)
Bokermannohyla nanuzae		🟧	🟨	(Bokermann and Sazima, 1973)
Bokermannohyla pseudopseudis		🟧	🟨	(Miranda-Ribeiro, 1937)
Bokermannohyla ravida		🟧		(Caramaschi, Napoli, and Bernardes, 2001)
Bokermannohyla sagarana		🟧		Leite, Pezutti, and Drummond, 2011
Bokermannohyla saxicola		🟧	🟨	(Bokermann, 1964)
Bokermannohyla sazimai		🟧		(Cardoso and Andrade, 1982)
Bokermannohyla vulcaniae			🟨	(Vasconcelos and Giaretta, 2005)
Colomascirtus armatus	🟩			(Boulenger, 1902)
Corythomantis greeningi		🟧	🟨	Boulenger, 1896
Dendropsophus acreanus	🟩			(Bokermann, 1964)
Dendropsophus anataliasiasi	🟩	🟧		(Bokermann, 1972)
Dendropsophus anceps			🟨	(Lutz, 1929)
Dendropsophus aperomeus	🟩			(Duellman, 1982)
Dendropsophus araguaya		🟧		(Napoli and Caramaschi, 1998)
Dendropsophus berthalutzae			🟨	(Bokermann, 1962)
Dendropsophus bifurcus	🟩			(Andersson, 1945)
Dendropsophus bipunctatus			🟨	(Spix, 1824)
Dendropsophus bokermanni	🟩			(Goin, 1960)
Dendropsophus branneri	🟩	🟧	🟨	(Cochran, 1948)
Dendropsophus brevifrons	🟩			(Duellman and Crump, 1974)
Dendropsophus cerradensis		🟧		(Napoli and Caramaschi, 1998)
Dendropsophus cruzi		🟧	🟨	(Pombal and Bastos, 1998)
Dendropsophus decipiens		🟧	🟨	(Lutz, 1925)
Dendropsophus delarivai	🟩			(Köhler and Lötters, 2001)
Dendropsophus dutrai			🟨	(Gomes and Peixoto, 1996)
Dendropsophus elegans		🟧	🟨	(Wied-Neuwied, 1824)
Dendropsophus elianeae		🟧	🟨	(Napoli and Caramaschi, 2000)
Dendropsophus gaucheri	🟩			(Lescure and Marty, 2000)
Dendropsophus giesleri			🟨	(Mertens, 1950)

Dendropsophus haddadi			🟨	(Bastos and Pombal, 1996)
Dendropsophus haraldschultzi	🟩			(Bokermann, 1962)
Dendropsophus jimi		🟧	🟨	(Napoli and Caramaschi, 1999)
Dendropsophus joannae	🟩			(Köhler and Lötters, 2001)
Dendropsophus juliani	🟩			Moravec, Aparicio, and Köhler, 2006
Dendropsophus koechlini	🟩			(Duellman and Trueb, 1989)
Dendropsophus leali	🟩	🟧		(Bokermann, 1964)
Dendropsophus leucophyllatus	🟩	🟧		(Beireis, 1783)
Dendropsophus limai			🟨	(Bokermann, 1962)
Dendropsophus marmoratus	🟩	🟧		(Laurenti, 1768)
Dendropsophus mathiassoni	🟩			(Cochran and Goin, 1970)
Dendropsophus melanargyreus	🟩	🟧		(Cope, 1887)
Dendropsophus meridianus			🟨	(Lutz, 1954)
Dendropsophus microcephalus	🟩	🟧		(Cope, 1886)
Dendropsophus microps		🟧	🟨	(Peters, 1872)
Dendropsophus minimus	🟩			(Ahl, 1933)
Dendropsophus minusculus	🟩			(Rivero, 1971)
Dendropsophus minutus	🟩	🟧	🟨	(Peters, 1872)
Dendropsophus miyatai	🟩			(Vigle and Goberdhan-Vigle, 1990)
Dendropsophus nahdereri			🟨	(Lutz and Bokermann, 1963)
Dendropsophus nanus	🟩	🟧	🟨	(Boulenger, 1889)
Dendropsophus novaisi			🟨	(Bokermann, 1968)
Dendropsophus oliveirai			🟨	(Bokermann, 1963)
Dendropsophus parviceps	🟩	🟧		(Boulenger, 1882)
Dendropsophus pauiniensis	🟩			(Heyer, 1977)
Dendropsophus pseudomeridianus			🟨	(Cruz, Caramaschi, and Dias, 2000)
Dendropsophus reichlei	🟩			Moravec, Aparicio, Guerrero-Reinhard, Calderon, and Köhler, 2008
Dendropsophus rhea			🟨	(Napoli and Caramaschi, 1999)
Dendropsophus rhodopeplus	🟩			(Günther, 1858)
Dendropsophus riveroi	🟩			(Cochran and Goin, 1970)
Dendropsophus rossalleni	🟩			(Goin, 1959)
Dendropsophus rubicundulus	🟩	🟧	🟨	(Reinhardt and Lütken, 1862)
Dendropsophus ruschii			🟨	(Weygoldt and Peixoto, 1987)
Dendropsophus sanborni		🟧	🟨	(Schmidt, 1944)
Dendropsophus sarayacuensis	🟩			(Shreve, 1935)
Dendropsophus schubarti	🟩	🟧		(Bokermann, 1963)
Dendropsophus seniculus			🟨	(Cope, 1868)

Dendropsophus soaresi	🟩	🟧	🟨	(Caramaschi and Jim, 1983)
Dendropsophus studerae			🟨	(Carvalho-e-Silva, Carvalho-e-Silva, and Izecksohn, 2003)
Dendropsophus timbeba	🟩			(Martins and Cardoso, 1987)
Dendropsophus tintinnabulum	🟩			(Melin, 1941)
Dendropsophus triangulum	🟩			(Günther, 1869)
Dendropsophus tritaeniatus	🟩	🟧		(Bokermann, 1965)
Dendropsophus walfordi	🟩	🟧		(Bokermann, 1962)
Dendropsophus werneri		🟧	🟨	(Cochran, 1952)
Dendropsophus xapuriensis	🟩			(Martins and Cardoso, 1987)
Dryaderces inframaculata	🟩			(Boulenger, 1882)
Dryaderces pearsoni	🟩			(Gaige, 1929)
Hyloscirtus albopunctulatus	🟩			(Boulenger, 1882)
Hyloscirtus phyllognathus	🟩			(Melin, 1941)
Hyloscirtus torrenticola	🟩			(Duellman and Altig, 1978)
Itapotihyla langsdorffii		🟧	🟨	(Duméril and Bibron, 1841)
Julianus pnimus		🟧	🟨	(Bokermann and Sazima, 1973)
Julianus uruguayus			🟨	(Schmidt, 1944)
Lysapsus bolivianus	🟩	🟧		Gallardo, 1961
Lysapsus caraya	🟩	🟧		Gallardo, 1964
Lysapsus laevis	🟩			(Parker, 1935)
Lysapsus limellum		🟧	🟨	Cope, 1862
Myersiohyla aromatica	🟩			(Ayarzagüena and Señaris, 1994)
Myersiohyla kanaima	🟩			(Goin and Woodley, 1969)
Myersiohyla loveridgei	🟩			(Rivero, 1961)
Nyctimantis rugiceps	🟩			Boulenger, 1882
Ololygon agilis			🟨	(Cruz and Peixoto, 1983)
Ololygon albicans			🟨	(Bokermann, 1967)
Ololygon angrensis			🟨	(Lutz, 1973)
Ololygon arduous			🟨	(Peixoto, 2002)
Ololygon argyreornata			🟨	(Miranda-Ribeiro, 1926)
Ololygon ariadne			🟨	(Bokermann, 1967)
Ololygon atrata			🟨	(Peixoto, 1989)
Ololygon belloni			🟨	(Faivovich, Gasparini, and Haddad, 2010)
Ololygon berthae		🟧	🟨	(Barrio, 1962)
Ololygon brieni			🟨	(De Witte, 1930)
Ololygon canastrensis		🟧		(Cardosoand Haddad, 1982)
Ololygon carnevallii			🟨	Caramaschi and Kisteumacher, 1989
Ololygon catharinae			🟨	(Boulenger, 1888)
Ololygon centralis		🟧		(Pombal and Bastos, 1996)
Ololygon faivovichi			🟨	(Brasileiro, Oyamaguchi, and Haddad, 2007)
Ololygon flavoguttata			🟨	(Lutz and Lutz, 1939)
Ololygon heyeri			🟨	Peixoto and Weygoldt, 1986

Ololygon hiemalis		🟧	🟨	(Haddad and Pombal, 1987)
Ololygon humilis			🟨	(Lutz and Lutz, 1954)
Ololygon insperata			🟨	(Silva and Alves-Silva, 2011)
Ololygon jureia			🟨	(Pombal and Gordo, 1991)
Ololygon kautskyi			🟨	Carvalho-e-Silva and Peixoto, 1991
Ololygon littoralis			🟨	(Pombal and Gordo, 1991)
Ololygon littoreus			🟨	Peixoto, 1988
Ololygon longilinea		🟧	🟨	(Lutz, 1968)
Ololygon luizotavioi		🟧	🟨	Caramaschi and Kisteumacher, 1989
Ololygon machadoi		🟧	🟨	(Bokermann and Sazima, 1973)
Ololygon melloi			🟨	Peixoto, 1989
Ololygon obtriangulata		🟧	🟨	(Lutz, 1973)
Ololygon perpusilla			🟨	(Lutz and Lutz, 1939)
Ololygon ranki			🟨	(Andrade and Cardoso, 1987)
Ololygon rizibilis		🟧	🟨	(Bokermann, 1964)
Ololygon trapicheiroi			🟨	(Lutz and Lutz, 1954)
Ololygon v.signatus			🟨	(Lutz, 1968)
Osteocephalus alboguttatus	🟩			(Boulenger, 1882)
Osteocephalus buckleyi	🟩			(Boulenger, 1882)
Osteocephalus cabrerai	🟩			(Cochran and Goin, 1970)
Osteocephalus castaneicola	🟩			Moravec, Apaaricio, Guerrero-Reinhard, Calderón, Jungfer, and Gvozdík, 2009
Osteocephalus deridens	🟩			Jungfer, Ron, Seipp, and Almendáriz, 2000
Osteocephalus fuscifacies	🟩			Jungfer, Ron, Seipp, and Almendáriz, 2000
Osteocephalus heyeri	🟩			Lynch, 2002
Osteocephalus leoniae	🟩			Jungfer and Lehr, 2001
Osteocephalus leprieurii	🟩	🟧		(Duméril and Bribon, 1841)
Osteocephalus mimeticus	🟩			(Melin, 1941)
Osteocephalus mutabor	🟩			Jungfer and Hödl, 2002
Osteocephalus oophagus	🟩			Jungfer and Schiesari, 1995
Osteocephalus planiceps	🟩			Cope, 1874
Osteocephalus subtilis	🟩			Martins and Cardoso, 1987
Osteocephalus taurinus	🟩	🟧		Steindachner, 1862
Osteocephalus verruciger	🟩			(Werner, 1901)
Osteocephalus yasuni	🟩			Ron and Pramuk, 1999
Phyllodytes acuminatus			🟨	Bokermann, 1966
Phyllodytes brevirostris			🟨	Peixoto and Cruz, 1988
Phyllodytes edelmoi			🟨	Peixoto, Caramaschi, and Freire, 2003
Phyllodytes gyrinaethes			🟨	Peixoto, Caramaschi, and Freire, 2003
Phyllodytes kautskyi			🟨	Peixoto and Cruz, 1988

Phyllodytes luteolus			🟨	(Wied-Neuwied, 1824)
Phyllodytes maculosus			🟨	Cruz, Feio, and Cardoso, 2007
Phyllodytes melanomystax			🟨	Caramaschi, Silva, and Brito-Pereira, 1992
Phyllodytes punctatus			🟨	Caramaschi and Peixoto, 2004
Phyllodytes tuberculosus			🟨	Bokermann, 1966
Phyllodytes wuchereri			🟨	(Peters, 1873)
Pseudis bolbodactyla		🟧	🟨	Lutz, 1925
Pseudis cardosoi			🟨	Kwet, 2000
Pseudis fusca		🟧	🟨	Garman, 1883
Pseudis minuta			🟨	Günther, 1858
Pseudis paradoxa	🟩	🟧	🟨	(Linnaeus, 1758)
Pseudis platensis		🟧	🟨	Gallardo, 1961
Pseudis tocantins		🟧		Caramaschi and Cruz, 1998
Scarthyla goinorum	🟩			(Bokermann, 1962)
Scinax acuminatus		🟧	🟨	(Cope, 1862)
Scinax alter			🟨	(Lutz, 1973)
Scinax auratus			🟨	(Wied-Neuwied, 1821)
Scinax baumgardneri	🟩			(Rivero, 1961)
Scinax blairi	🟩			(Fouquette and Pyburn, 1972)
Scinax boesemani	🟩			(Goin, 1966)
Scinax cabralensis		🟧		Drummond, Baêta, and Pires, 2007
Scinax caldarum		🟧	🟨	(Lutz, 1968)
Scinax camposseabrai		🟧	🟨	(Bokermann, 1968)
Scinax cardosoi			🟨	(Carvalho-e-Silva and Peixoto, 1991)
Scinax chiquitanus	🟩			(De la Riva, 1990)
Scinax constrictus		🟧		Lima, Bastos, and Giaretta, 2005
Scinax cretatus			🟨	Nunes and Pombal, 2011
Scinax crospedospilus			🟨	(Lutz, 1925)
Scinax cruentomma	🟩			(Duellman, 1972)
Scinax curicica		🟧	🟨	Pugliese, Pombal, and Sazima, 2004
Scinax cuspidatus			🟨	(Lutz, 1925)
Scinax danae	🟩			(Duellman, 1986)
Scinax duartei		🟧	🟨	(Lutz, 1951)
Scinax eurydice	🟩	🟧	🟨	(Bokermann, 1968)
Scinax exiguus	🟩			(Duellman, 1986)
Scinax funereus	🟩			(Cope, 1874)
Scinax fuscomarginatus	🟩	🟧	🟨	(Lutz, 1925)
Scinax fuscovarius	🟩	🟧	🟨	(Lutz, 1925)
Scinax garbei	🟩			(Miranda-Ribeiro, 1926)
Scinax granulatus		🟧	🟨	(Peters, 1871)
Scinax hayii		🟧	🟨	(Barbour, 1909)
Scinax ictericus	🟩			Duellman and Wiens, 1993

Scinax iquitorum	🟩			Moravec, Tuanama, Pérez-Peña, and Lehr, 2009
Scinax jolyi	🟩			Lescure and Marty, 2000
Scinax karenanneae	🟩			(Pyburn, 1993)
Scinax kennedyi	🟩			(Pyburn, 1973)
Scinax lindsayi	🟩			Pyburn, 1992
Scinax maracaya		🟧		(Cardoso and Sazima, 1980)
Scinax nasicus	🟩	🟧	🟨	(Cope, 1862)
Scinax nebulosus	🟩	🟧		(Spix, 1824)
Scinax oreites	🟩			Duellman and Wiens, 1993
Scinax pachycrus		🟧	🟨	(Miranda-Ribeiro, 1937)
Scinax pedromedinae	🟩			(Henle, 1991)
Scinax perereca		🟧	🟨	Pombal, Haddad, and Kasahara, 1995
Scinax proboscideus	🟩			(Brongersma, 1933)
Scinax rostratus	🟩			(Peterns, 1863)
Scinax ruber	🟩	🟧		(Laurenti, 1768)
Scinax similis			🟨	(Cochran, 1952)
Scinax squalirostris		🟧	🟨	(Lutz, 1925)
Scinax tigrinus		🟧		Nunes, Carvalho, and Pereira, 2010
Scinax wandae	🟩			(Pyburn and Fouquette, 1971)
Scinax x.signatus	🟩	🟧	🟨	(Spix, 1824)
Sphaenorhynchus bromelicola			🟨	Bokermann, 1966
Sphaenorhynchus caramaschii		🟧	🟨	Toledo, Garcia, Lingnau, and Haddad, 2007
Sphaenorhynchus carneus	🟩			(Cope, 1868)
Sphaenorhynchus dorisae	🟩			(Goin, 1957)
Sphaenorhynchus lacteus	🟩	🟧		(Doudin, 1800)
Sphaenorhynchus mirim			🟨	Caramaschi, Almeida, and Gasparini, 2009
Sphaenorhynchus orophilus			🟨	(Lutz and Lutz, 1938)
Sphaenorhynchus palustris			🟨	Bokermann, 1966
Sphaenorhynchus pauloalvini			🟨	Bokermann, 1973
Sphaenorhynchus planicola			🟨	(Lutz and Lutz, 1938)
Sphaenorhynchus prasinus			🟨	Bokermann, 1973
Sphaenorhynchus surdus			🟨	(Cochran, 1953)
Tepuihyla edelcae	🟩			(Ayarzagüena, Señaria, and Gorzula, 1993)
Tepuihyla exophthalma	🟩			(Smith and Nooman, 2001)
Tepuihyla rodriguezi	🟩			(Rivero, 1968)
Tepuihyla tuberculosa	🟩			(Boulenger, 1882)
Trachycephalus atlas			🟨	Bokermann, 1966
Trachycephalus coriaceus	🟩			(Peters, 1867)
Trachycephalus dibernardoi			🟨	Kwet and Solé, 2008
Trachycephalus hadroceps	🟩			(Duellman and Hoogmoed, 1992)
Trachycephalus imitatrix		🟧	🟨	(Miranda-Ribeiro, 1926)

Trachycephalus lepidus			🟨	(Pombal, Haddad, and Cruz, 2003)
Trachycephalus mesophaeus		🟧	🟨	(Hensel, 1867)
Trachycephalus nigromaculatus		🟧	🟨	Tschudi, 1838
Trachycephalus resinifictrix	🟩	🟧		(Goeldi, 1907)
Trachycephalus typhonius	🟩	🟧	🟨	(Linnaeus, 1758)
Xenohyla eugenioi			🟨	Caramaschi, 1998
Xenohyla truncata			🟨	(Izecksohn, 1959)
<u>Hylodidae</u>				
Crossodactylus aeneus		🟧	🟨	Müller, 1924
Crossodactylus bokermanni		🟧		Caramaschi and Sazima, 1985
Crossodactylus caramaschii		🟧	🟨	Bastos and Pombal, 1995
Crossodactylus cyclospinus			🟨	Nascimento, Cruz, and Feio, 2005
Crossodactylus dantei			🟨	Carcerelli and Caramaschi, 1993
Crossodactylus dispar			🟨	Lutz, 1925
Crossodactylus gaudichaudii			🟨	Duméril and Bibron, 1841
Crossodactylus grandis			🟨	Lutz, 1951
Crossodactylus lutzorum			🟨	Carcerelli and Caramaschi, 1993
Crossodactylus schmidti			🟨	Gallardo, 1961
Crossodactylus trachystomus			🟨	(Reinhardt and Lütken, 1862)
Hylodes amnicola			🟨	Pombal, Feio, and Haddad, 2002
Hylodes asper		🟧	🟨	(Müller, 1924)
Hylodes babax			🟨	Heyer, 1982
Hylodes cardosoi			🟨	Lingnau, Canedo, and Pombal, 2008
Hylodes charadranaetes			🟨	Heyer and Croft, 1986
Hylodes dactylocinus			🟨	Pavan, Narvaes, and Rodrigues, 2001
Hylodes fredi			🟨	Canedo and Pombal, 2007
Hylodes glaber			🟨	(Miranda-Ribeiro, 1926)
Hylodes heyeri			🟨	Haddad, Pombal, and Bastos, 1996
Hylodes lateristrigatus			🟨	(Baunmann, 1912)
Hylodes magalhaesi			🟨	(Bokermann, 1964)
Hylodes meridionalis			🟨	(Mertens, 1927)
Hylodes mertensi			🟨	(Bokermann, 1956)
Hylodes nasus			🟨	(Lichtenstein, 1823)
Hylodes ornatus			🟨	(Bokermann, 1967)
Hylodes otavioi		🟧	🟨	Sazimai and Bokermann, 1983
Hylodes perplicatus			🟨	(Miranda-Ribeiro, 1926)
Hylodes phyllodes			🟨	Heyer and Croft, 1986
Hylodes pipilans			🟨	Canedo and Pombal, 2007
Hylodes regius			🟨	Gouvêa, 1979

Hylodes sazimai			🟨	Haddad and Pombal, 1995
Hylodes uai		🟧	🟨	Nascimento, Pombal, and Haddad, 2001
Hylodes vanzolinii			🟨	Heyer, 1982
Megaelosia apuana			🟨	Pombal, Prado and Canedo, 2003
Megaelosia bocainensis			🟨	Giaretta, Bokermann, and Haddad, 1993
Megaelosia boticariana			🟨	Giaretta and Aguiar, 1998
Megaelosia goeldii			🟨	(Baunmann, 1912)
Megaelosia jordanensis			🟨	(Heyer, 1983)
Megaelosia lutzae			🟨	Izecksohn and Gouvêa, 1987
Megaelosia massarti			🟨	(De Witte, 1930)
<u>Leptodactylidae</u>				
Adenomera ajurauna			🟨	(Berneck, Costa, and Garcia, 2008)
Adenomera andreae	🟩	🟧		(Müller, 1923)
Adenomera araucaria			🟨	Kwet and Angulo, 2002
Adenomera bokermanni		🟧	🟨	(Heyer, 1973)
Adenomera diptyx	🟩	🟧	🟨	(Boettger, 1885)
Adenomera heyeri	🟩			Boistel, Massary, and Ângulo, 2006
Adenomera hylaedactyla	🟩	🟧	🟨	(Cope, 1868)
Adenomera lutzi	🟩			Heyer, 1975
Adenomera marmorata		🟧	🟨	Steindachner, 1867
Adenomera martinezi	🟩	🟧		(Bokermann, 1956)
Adenomera nana			🟨	(Müller, 1922)
Adenomera thomei			🟨	(Almeida and Angulo, 2006)
Crossodactylodes bokermanni			🟨	Peixoto, 1983
Crossodactylodes izecksohni			🟨	Peixoto, 1983
Crossodactylodes pintoi			🟨	Cochran, 1938
Edalorhina nasuta	🟩			Boulenger, 1912
Edalorhina perezi	🟩			Jiménez de la Espada, 1870
Engystomops freibergi	🟩	🟧		(Donoso-Barroso, 1969)
Engystomops petersi	🟩			Jiménez de la Espada, 1872
Engystomops pustulosus	🟩			(Cope, 1864)
Hydrolaetare dantasi	🟩			(Bokermann, 1959)
Hydrolaetare schmidti	🟩	🟧		(Cochran and Goin, 1959)
Leptodactylus bolivianus	🟩	🟧		Boulenger,1898
Leptodactylus bufonius		🟧		Boulenger, 1894
Leptodactylus caatingae		🟧	🟨	Heyer and Juncá, 2003
Leptodactylus camaquara		🟧	🟨	Sazima and Bokermann, 1978
Leptodactylus chaquensis	🟩	🟧	🟨	Cei, 1950
Leptodactylus colombiensis	🟩			Heyer, 1994
Leptodactylus cunicularius		🟧	🟨	Sazima and Bokermann, 1978
Leptodactylus cupreus			🟨	Caramaschi, Feio, and São Pedro, 2008

Leptodactylus didymus	🟩			Heyer, García-Lopez, and Cardoso, 1996
Leptodactylus diedrus	🟩			Heyer, 1994
Leptodactylus discodactylus	🟩			Boulenger, 1884
Leptodactylus elenae	🟩	🟧	🟨	Heyer, 1978
Leptodactylus flavopictus			🟨	Lutz, 1926
Leptodactylus fragilis	🟩			(Brocchi, 1877)
Leptodactylus furnarius		🟧	🟨	Sazima and Bokermann, 1978
Leptodactylus fuscus	🟩	🟧	🟨	(Schneider, 1799)
Leptodactylus gracilis		🟧	🟨	(Duméril and Bibron, 1840)
Leptodactylus griseigularis	🟩			(Henle, 1981)
Leptodactylus hylodes			🟨	(Reinhardt and Lütken, 1862)
Leptodactylus jolyi			🟨	Sazima and Bokermann, 1978
Leptodactylus knudseni	🟩	🟧		Heyer, 1972
Leptodactylus labyrinthicus	🟩	🟧	🟨	(Spix, 1824)
Leptodactylus latinasus		🟧	🟨	Jiménez de la Espada, 1875
Leptodactylus latrans	🟩	🟧	🟨	(Steffen, 1815)
Leptodactylus lauramiriamae		🟧		Heyer and Crombie, 2005
Leptodactylus leptodactyloides	🟩			(Anderson, 1945)
Leptodactylus lithonaetes	🟩			Heyer, 1995
Leptodactylus longirostris	🟩			Boulenger, 1882
Leptodactylus marambaiae			🟨	Izecksohn, 1976
Leptodactylus myersi	🟩			Heyer, 1995
Leptodactylus mystaceus	🟩	🟧	🟨	(Spix, 1824)
Leptodactylus mystacinus	🟩	🟧	🟨	(Burmeister, 1861)
Leptodactylus natalensis			🟨	Lutz, 1930
Leptodactylus notoaktites		🟧	🟨	Heyer, 1978
Leptodactylus paraensis	🟩			Heyer, 2005
Leptodactylus pentadactylus	🟩	🟧		(Laurenti, 1768)
Leptodactylus petersii	🟩	🟧		(Steindachner, 1864)
Leptodactylus plaumanni			🟨	Ahl, 1936
Leptodactylus podicipinus	🟩	🟧	🟨	(Cope, 1862)
Leptodactylus pustulatus	🟩	🟧		(Peters, 1870)
Leptodactylus rhodomystax	🟩	🟧		Boulenger, 1884
Leptodactylus rhodonotus	🟩			(Günther, 1869)
Leptodactylus rhodostima	🟩			(Cope, 1874)
Leptodactylus riveroi	🟩			Heyer and Pyburn, 1983
Leptodactylus rugosus	🟩			Noble, 1923
Leptodactylus sabanensis	🟩			Heyer, 1994
Leptodactylus sertanejo		🟧	🟨	Giaretta and Costa, 2007
Leptodactylus spixi		🟧	🟨	Heyer, 1983
Leptodactylus stenodema	🟩	🟧		Jiménez de la Espada, 1875
Leptodactylus syphax	🟩	🟧	🟨	Bokermann, 1969
Leptodactylus tapiti		🟧		Sazima and Bokermann, 1978

Leptodactylus troglodytes	🟩	🟧	🟨	Lutz, 1926
Leptodactylus validus	🟩			Garman, 1888
Leptodactylus vastus	🟩	🟧	🟨	Lutz, 1930
Leptodactylus viridis			🟨	Jim and Spirandeli Cruz, 1973
Leptodactylus wagneri	🟩			(Peters, 1862)
Lithodytes lineatus	🟩	🟧		(Schneider, 1799)
Paratelmatobius cardosoi			🟨	Pombal and Haddad, 1999
Paratelmatobius gaigeae			🟨	(Cochran, 1938)
Paratelmatobius lutzii			🟨	Lutz and Carvalho, 1958
Paratelmatobius mantiqueira			🟨	Pombal and Haddad, 1999
Paratelmatobius poecilogaster			🟨	Giaretta and Castanho, 1990
Physalaemus aguirrei			🟨	Bokermann, 1966
Physalaemus albifrons		🟧	🟨	(Spix, 1824)
Physalaemus albonotatus	🟩	🟧	🟨	(Steindachner, 1864)
Physalaemus angrensis			🟨	Weber, Gonzaga, and Carvalho-e-Silva, 2006
Physalaemus atlanticus			🟨	Haddad and Sazima, 2004
Physalaemus barrioi			🟨	Bokermann, 1967
Physalaemus biligonigerus	🟩	🟧	🟨	(Cope, 1861)
Physalaemus bokermanni			🟨	Cardoso and Haddad, 1985
Physalaemus caete			🟨	Pombaland Madureira, 1997
Physalaemus camacan			🟨	Pimenta, Cruz, and Silvano, 2005
Physalaemus centralis	🟩	🟧	🟨	Bokermann, 1962
Physalaemus cicada		🟧	🟨	Bokermann, 1966
Physalaemus crombiei			🟨	Heyer and Wolf, 1989
Physalaemus cuvieri	🟩	🟧	🟨	Fitzinger, 1826
Physalaemus deimaticus		🟧	🟨	Sazima and Caramaschi, 1988
Physalaemus ephippifer	🟩	🟧		(Steindachner, 1864)
Physalaemus erikae			🟨	Cruz and Pimenta, 2004
Physalaemus erythros			🟨	Caramaschi, Feio, and Guimarães, 2003
Physalaemus evangelistai		🟧	🟨	Bokermann, 1967
Physalaemus fischeri	🟩			(Boulenger, 1890)
Physalaemus gracilis		🟧	🟨	(Boulenger, 1883)
Physalaemus henselii			🟨	(Peters, 1872)
Physalaemus insperatus			🟨	Cruz, Cassini, and Caramaschi, 2008
Physalaemus irroratus			🟨	Cruz, Nascimento, and Feio, 2007
Physalaemus jordanensis			🟨	Bokermann, 1967
Physalaemus kroyeri		🟧	🟨	(Reinhardt and Lütken, 1862)
Physalaemus lisei			🟨	Braun and Braun, 1977
Physalaemus maculiventris		🟧	🟨	(Lutz, 1925)
Physalaemus marmoratus		🟧	🟨	(Reinhardt and Lütken, 1862)

Physalaemus maximus			🟨	Feio, Pombal and Caramaschi, 1999
Physalaemus moreirae			🟨	(Miranda-Ribeiro, 1937)
Physalaemus nanus			🟨	(Boulenger, 1888)
Physalaemus nattereri	🟩	🟧	🟨	(Steindachner, 1863)
Physalaemus obtectus			🟨	Bokermann, 1966
Physalaemus olfersii		🟧	🟨	(Lichtenstein and Martens, 1856)
Physalaemus riograndensis			🟨	Milstead, 1960
Physalaemus rupestris			🟨	Caramaschi, Carcerelli, and Feio, 1991
Physalaemus signifer			🟨	(Girard, 1853)
Physalaemus soaresi			🟨	Izecksohn, 1965
Physalaemus spiniger			🟨	(Miranda-Ribeiro, 1926)
Pleurodema bibroni			🟨	Tschudi, 1838
Pleurodema brachyops	🟩			(Cope, 1869)
Pleurodema diplolister		🟧	🟨	(Peters, 1870)
Pleurodema marmoratum	🟩			(Duméril and Bibron, 1840)
Pseudopaludicola boliviana	🟩	🟧		Parker, 1927
Pseudopaludicola canga	🟩			Giaretta and Kokubum, 2003
Pseudopaludicola ceratophryes	🟩			Rivero and Serna, 1985
Pseudopaludicola falcipes		🟧	🟨	(Hensel, 1867)
Pseudopaludicola llanera	🟩			Lynch, 1989
Pseudopaludicola mineira		🟧	🟨	Lobo, 1994
Pseudopaludicola mystacalis	🟩	🟧	🟨	(Cope, 1887)
Pseudopaludicola saltica		🟧	🟨	(Cope, 1887)
Pseudopaludicola ternetzi		🟧	🟨	Miranda-Ribeiro, 1937
Scythrophrys sawayae			🟨	(Cochran, 1953)
Microhylidae				
Adelastes hylonomos	🟩			Zweifel, 1986
Arcovomer passarellii			🟨	Carvalho, 1954
Chiasmocleis alagoanus			🟨	Cruz, Caramaschi, and Freire, 1999
Chiasmocleis albopunctata	🟩	🟧	🟨	(Boettger, 1885)
Chiasmocleis anatipes	🟩			Walker and Duellman, 1974
Chiasmocleis antenori	🟩			(Walker, 1973)
Chiasmocleis atlantica			🟨	Cruz, Caramaschi, and Izecksohn, 1997
Chiasmocleis avilapiresae	🟩	🟧		Peloso and Sturaro, 2008
Chiasmocleis bassleri	🟩			Dunn, 1949
Chiasmocleis capixaba			🟨	Cruz, Caramaschi, and Izecksohn, 1997
Chiasmocleis carvalhoi	🟩		🟨	(Nelson, 1975)
Chiasmocleis centralis		🟧		Bokermann, 1952
Chiasmocleis cordeiroi			🟨	Caramaschi and Pimenta, 2003
Chiasmocleis crucis			🟨	Caramaschi and Pimenta, 2003
Chiasmocleis devriesi	🟩			Funk and Cannatella, 2009

Chiasmocleis gnoma			🟨	Canedo, Dixo, and Pombal, 2004
Chiasmocleis hudsoni	🟩			Parker, 1940
Chiasmocleis leucosticta		🟧	🟨	(Boulenger, 1888)
Chiasmocleis magnova	🟩			Moravec and Köhler, 2007
Chiasmocleis mantiqueira			🟨	Cruz, Feio, and Cassini, 2007
Chiasmocleis mehelyi		🟧		Caramaschi and Cruz, 1997
Chiasmocleis sapiranga			🟨	Cruz, Caramaschi, and Napoli, 2007
Chiasmocleis schubarti			🟨	Bokermann, 1952
Chiasmocleis shudikarensis	🟩			Dunn, 1949
Chiasmocleis tridactyla	🟩			(Duellman and Mendelson, 1995)
Chiasmocleis ventrimaculata	🟩			(Anderson, 1945)
Ctenophryne barbatula	🟩			Lehr and Trueb, 2007
Ctenophryne carpish	🟩			Lehr, Rodriguezn and Córdova, 2002
Ctenophryne geayi	🟩	🟧		Mocquard, 1904
Dasypops schirchi			🟨	Miranda-Ribeiro, 1924
Dermatonotus muelleri	🟩	🟧	🟨	(Boettger, 1885)
Elachistocleis bicolor		🟧	🟨	(Guérin-Méneville, 1838)
Elachistocleis bumbameuboi		🟧		Caramaschi, 2010
Elachistocleis carvalhoi	🟩	🟧		Caramaschi, 2010
Elachistocleis erythrogaster			🟨	Kwet and Di-Bernardo, 1998
Elachistocleis helianneae	🟩	🟧		Caramaschi, 2010
Elachistocleis matogrosso		🟧		Caramaschi, 2010
Elachistocleis ovalis	🟩	🟧	🟨	(Schneider, 1799)
Elachistocleis piauiensis		🟧		Caramaschi and Jim, 1983
Elachistocleis surinamensis	🟩			(Daudin, 1802)
Elachistocleis surumu	🟩			Caramaschi, 2010
Hamptophryne alios	🟩			(Wild,1995)
Hamptophryne boliviana	🟩	🟧		(Parker, 1927)
Myersiella microps			🟨	(Duméril and Bibron,1841)
Otophryne pyburni	🟩			Campbell and Clarke, 1998
Otophryne robusta	🟩			Boulenger, 1900
Otophryne steyermarki	🟩			Rivero, 1968
Stereocyclops histrio			🟨	(Carvalho, 1954)
Stereocyclops incrassatus			🟨	Cope, 1870
Stereocyclops parkeri			🟨	(Wettstein, 1934)
Synapturanus mirandaribeiroi	🟩			Nelson and Lescure, 1975
Synapturanus rabus	🟩			Pyburn, 1977
Synapturanus salseri	🟩			Pyburn, 1975
<u>Odontophynidae</u>				
Macrogenioglottus alipioi		🟧	🟨	Carvalho, 1946
Odontophrynus americanus		🟧	🟨	(Duméril and Bibron, 1841)
Odontophrynus carvalhoi		🟧	🟨	Savage and Cei, 1965
Odontophrynus cultripes		🟧	🟨	Reinhardt and Lütken, 1862

Odontophrynus salvatori		🟧		Caramaschi, 1996
Proceratophrys appendiculata			🟨	(Günther, 1873)
Proceratophrys avelinoi		🟧	🟨	Mercadal de Barrio and Barrio, 1993
Proceratophrys bigibbosa			🟨	(Peters, 1872)
Proceratophrys boiei		🟧	🟨	(Wied-Neuwied, 1824)
Proceratophrys brauni			🟨	Kwet and Faivovich, 2001
Proceratophrys concavitympanum	🟩			Giaretta, Bernarde, and Kokubum, 2000
Proceratophrys cristiceps		🟧	🟨	(Müller, 1883)
Proceratophrys cururu		🟧	🟨	Eterovick and Sazima, 1998
Proceratophrys goyana		🟧		(Miranda-Ribeiro, 1937)
Proceratophrys laticeps			🟨	Izecksohn and Peixoto, 1981
Proceratophrys melanopogon			🟨	(Miranda-Ribeiro, 1926)
Proceratophrys moehringi			🟨	Weygoldt and Peixoto, 1985
Proceratophrys moratoi		🟧		(Jim and Caramaschi, 1980)
Proceratophrys palustris			🟨	Giaretta and Sazima, 1993
Proceratophrys paviotii			🟨	Cruz, Prado, and Izecksohn, 2005
Proceratophrys phyllostomus			🟨	Izecksohn, Cruz, and Peixoto, 1999
Proceratophrys schirchi			🟨	(Miranda-Ribeiro, 1937)
Proceratophrys subguttata			🟨	Izecksohn, Cruz, and Peixoto, 1999
Proceratophrys vielliardi		🟧		Martins and Giaretta, 2011
<u>Phyllomedusidae</u>				
Agalychnis buckleyi	🟩			(Boulenger, 1882)
Agalychnis hulli	🟩			(Duellman and Mendelson, 1995)
Callimedusa atelopoides	🟩			(Duellman, Cadle, and Cannatella, 1988)
Callimedusa baltea	🟩			(Duellman and Toft, 1979)
Callimedusa tomopterna	🟩	🟧		(Cope, 1868)
Cruziohyla craspedopus	🟩			(Frankhouser, 1957)
Hylomantis aspera			🟨	(Peters, 1873)
Hylomantis granulosa			🟨	(Cruz, 1989)
Phasmahyla cochranae		🟧	🟨	(Bokermann, 1966)
Phasmahyla exilis			🟨	(Cruz, 1980)
Phasmahyla guttata			🟨	(Lutz, 1924)
Phasmahyla jandaia		🟧	🟨	(Bokermann and Sazima, 1978)
Phasmahyla spectabilis			🟨	Cruz, Feio, and Nascimento, 2008
Phasmahyla timbo			🟨	Cruz, Napoli, and Fonseca 2008
Phyllomedusa bahiana			🟨	Lutz, 1925
Phyllomedusa bicolor	🟩	🟧		(Boddaert, 1772)
Phyllomedusa boliviana	🟩	🟧		Boulenger, 1902
Phyllomedusa burmeisteri		🟧	🟨	Boulenger, 1882
Phyllomedusa camba	🟩			De la Riva, 1999

Phyllomedusa coelestis	🟩			(Cope, 1874)
Phyllomedusa distincta		🟧	🟨	Lutz, 1950
Phyllomedusa iheringii			🟨	Boulenger, 1885
Phyllomedusa sauvagii		🟧	🟨	Boulenger, 1882
Phyllomedusa tarsius	🟩	🟧		(Cope, 1868)
Phyllomedusa tetraploidea		🟧	🟨	Pombal and Haddad, 1992
Phyllomedusa vaillantii	🟩	🟧		Boulenger, 1882
Pithecopus ayeaye		🟧	🟨	Lutz, 1966
Pithecopus azureus	🟩	🟧	🟨	(Cope, 1862)
Pithecopus centralis		🟧		(Bokermann, 1965)
Pithecopus hypochondrialis	🟩	🟧	🟨	(Daudin, 1800)
Pithecopus megacephalus			🟨	(Miranda-Ribeiro, 1926)
Pithecopus nordestinus		🟧	🟨	(Caramaschi, 2006)
Pithecopus oreades		🟧		(Brandão, 2002)
Pithecopus palliatus	🟩			(Peters, 1873)
Pithecopus rohdei			🟨	(Mertens, 1926)
Phrynomedusa appendiculata			🟨	(Lutz, 1925)
Phrynomedusa bokermanni			🟨	Cruz, 1991
Phrynomedusa marginata			🟨	(Izecksohn and Cruz, 1976)
Phrynomedusa vanzolinii			🟨	Cruz, 1991
Pipidae				
Pipa arrabali	🟩			Izecksohn, 1976
Pipa aspera	🟩			Müller, 1924
Pipa carvalhoi			🟨	(Miranda-Ribeiro, 1937)
Pipa pipa	🟩	🟧		(Linnaeus, 1758)
Pipa snethlageae	🟩			Müller, 1914
Ranidae				
Lithobates palmipes	🟩	🟧	🟨	(Spix, 1824)
Telmatobiidae				
Telmatobius hintoni	🟩			Parker, 1940
Telmatobius macrostomus	🟩			Peters, 1873

Table S2. Species traits selected and included in the functional analises per 0.5 x 0.5 grid for the Amazon, the Cerrado and the Atlantic Rainforest. We provided the biological interpretation of each trait as well as its ecological function for a clearer interpretation of the reason why to include each one of them.

Type of development	**Trait**	**Biological interpretation**	**Ecological function**	**Type of metric**
Adult	Snout vent length	Higher values represent a greater dispersion ability	Survival (Cabrera-Guzmán et al. 2013), Dispersal ability (Jenkins et al. 2007)	Continuous
	Head width	Small values reflect more specific prey consumption	Diet-Prey consuption (Duellman & Trueb 1994), nutrient cycling (Cortéz-Gomez et al. 2016)	Continuous
	Tibia length	Higher values represent a greater dispersion ability	Dispersal ability (Cortéz-Gomez et al. 2016)	Continuous
	Reproductive mode	Reflect the type of reproduction	Anuran development (Duellman & Trueb 1994; Haddad & Prado 2005)	Categorical
Tadpole	Tadpoles type of development	*Exotrophic*: environmental role in nutrient cycling *Endotrophic*: absence of environmental nutrient cycling	Nutrient cycling (Whiles et al. 2006; Cortéz-Gomez et al. 2015, 2016)	Categorical

Table S3. Imputed trait dataset according to Brownian evolutionary model for 1090 species present in the Amazon, the Atlantic Rainforest and the Cerrado. Snout-vent length (SVL), head width and tibia length are represented in millimeter.

Species	SVL	Head width	Tibia lengh
Adelastes hylonomos	28.9	8.8	10
Adelophryne adiastola	14.6	4.64	6.2
Adelophryne gutturosa	13	4.5	6
Adelophryne pachydactyla	11.1	4.32	5.46
Adelophryne patamona	21.5	8.5	11
Adelphobates castaneoticus	21.9	7.03	8.78
Adelphobates galactonotus	34.7	12.05	15.27
Adelphobates quinquevittatus	18.98	6.09	8.5
Adenomera ajurauna	19.03	7.09	8.15
Adenomera andreae	21	9	13.04
Adenomera araucaria	19.9	6.7	9.34
Adenomera bokermanni	24	7.9	10.4
Adenomera diptyx	22	7.61	10.27
Adenomera heyeri	25.8	10.3	10.8
Adenomera hylaedactyla	23.48	8.61	10.92
Adenomera lutzi	30.1	11.2	14.6
Adenomera marmorata	21.9	6.69	9.2
Adenomera martinezi	23	7	11.09
Adenomera nana	18.9	6.09	8.88
Adenomera thomei	23.21	6.75	10.17
Agalychnis buckleyi	52.4	17	26.8
Agalychnis hulli	37.1	14.1	18.6
Allobates alessandroi	22	7.6	10.2
Allobates brunneus	18	5.5	8.5
Allobates caeruleodactylus	16.1	5.2	7.5
Allobates conspicuus	16	5.4	8
Allobates crombiei	17.7	6.2	9.1
Allobates femoralis	25	8	12
Allobates fuscellus	17.5	5.7	8
Allobates gasconi	13.9	5	6.1
Allobates goianus	18	6	8.09
Allobates granti	16.8	5.29	7.63
Allobates insperatus	16.7	6.1	8.1
Allobates marchesianus	15.85	5.2	7.6
Allobates masniger	19	6.5	8.6
Allobates melanolaemus	22.7	7.3	10.6
Allobates myersi	32.8	10.5	15
Allobates nidicola	20.2	6.7	8.5
Allobates olfersioides	16.9	5.1	7.27
Allobates ornatus	17.3	5.3	8.7

Allobates paleovarzensis	20.06	5.85	9.21
Allobates subfolionidificans	17.6	6.4	8.3
Allobates sumtuosus	15.6	5.6	7.5
Allobates trilineatus	17.2	6	8
Allobates undulatus	22.2	6.8	10.1
Allobates vanzolinius	21.8	7.1	9.8
Allobates zaparo	28	9.35	13.28
Allophryne ruthveni	21	7	10.28
Amazophrynella bokermanni	22	7	10.5
Amazophrynella minuta	19.7	5.82	8.44
Ameerega bassleri	37.5	12.19	17.43
Ameerega berohoka	23	7	10.6
Ameerega bilinguis	30.78	9.52	14.32
Ameerega braccata	20.19	6.26	10.12
Ameerega cainarachi	27.85	8.2	14.65
Ameerega flavopicta	26.66	8.03	12.99
Ameerega hahneli	19.02	5.76	9.33
Ameerega ingeri	27.5	8.5	12
Ameerega macero	28.59	9	14.38
Ameerega parvula	28.5	8.75	12.87
Ameerega petersi	28	8.3	14.39
Ameerega picta	22.2	6.38	10.75
Ameerega planipaleae	26.5	7.89	12.1
Ameerega pongoensis	28.59	8.78	12.94
Ameerega pulchripecta	26	7.11	12.34
Ameerega rubriventris	21.1	6.6	9.9
Ameerega silverstonei	38.3	10.1	18.3
Ameerega simulans	27	7.7	12
Ameerega smaragdina	26.5	7.69	13.77
Ameerega trivittata	43.5	12	20.5
Anomaloglossus ayarzaguenai	26.6	9.2	13.6
Anomaloglossus baeobatrachus	17.6	5.5	7.9
Anomaloglossus beebei	17.8	6.1	8
Anomaloglossus degranvillei	20.1	7.8	9.9
Anomaloglossus guanayensis	21.5	8	11.5
Anomaloglossus kaiei	18.9	6.6	8.8
Anomaloglossus parimae	22	7.6	10.7
Anomaloglossus parkerae	17	6.4	9.9
Anomaloglossus shrevei	19.3	7.3	9.6
Anomaloglossus stepheni	16.63	5.97	7.98
Anomaloglossus tamacuarensis	22.4	8	11.7
Anomaloglossus tepuyensis	28.3	9.7	14
Anomaloglossus triunfo	19.7	6.55	9.65
Anomaloglossus wothuja	21.7	6	10.3
Aparasphenodon bokermanni	71.1	21.2	34
Aparasphenodon brunoi	49.16	20.5	25.64

Aparasphenodon venezolanus	49.82	14.24	22.2
Aplastodiscus albofrenatus	39.3	12.97	19.26
Aplastodiscus albosignatus	41.5	13.28	21.58
Aplastodiscus arildae	38.7	12.6	18.7
Aplastodiscus callipygius	48	16	23.2
Aplastodiscus cavicola	33.2	11.6	17.3
Aplastodiscus cochranae	43.56	16.65	20.69
Aplastodiscus ehrhardti	33.7	10.38	17.27
Aplastodiscus eugenioi	37.5	13	19.8
Aplastodiscus flumineus	45.1	14.3	23.6
Aplastodiscus ibirapitanga	41.3	13.3	19.3
Aplastodiscus leucopygius	42	13.8	20.5
Aplastodiscus musicus	47	16	22.64
Aplastodiscus perviridis	39.66	14.97	18.88
Aplastodiscus sibilatus	31.8	10.4	15.9
Aplastodiscus weygoldti	41.7	13.7	20.8
Arcovomer passarellii	16	3.44	4.04
Atelopus andinus	28	8	12.3
Atelopus boulengeri	51	15.5	22.44
Atelopus dimorphus	31.3	7.1	13.9
Atelopus flavescens	28.92	8.31	13.03
Atelopus franciscus	30.69	8.56	13.71
Atelopus pulcher	34.07	9.1	15.47
Atelopus seminiferus	40	9	16.73
Atelopus siranus	23.5	6.3	10.4
Atelopus spumarius	34.6	9.6	15.4
Atelopus tricolor	20.82	6.18	9.7
Barycholos ternetzi	30.4	10.2	17.2
Boana albomarginata	56	21	30
Boana albopunctata	58	17.4	31.9
Boana atlanticus	38.32	13.83	18.3
Boana balzani	48.5	16.6	26
Boana beckeri	32.8	10.5	16.3
Boana bischoffi	42.8	19.24	30.9
Boana boans	105	40	58.5
Boana buriti	30	7.7	15.1
Boana caingua	33.1	8.32	17.45
Boana calcarata	48.2	17.6	28.8
Boana cinerascens	35.3	12.24	18.21
Boana cipoensis	34.35	11.88	18.44
Boana crepitans	65	23	36
Boana cymbalum	47	14.75	25.1
Boana dentei	50	18	25.49
Boana ericae	31.8	10.8	16.9
Boana exastis	86.5	30.2	50.1
Boana faber	99.2	40.48	58.13

Boana fasciata	35.4	11.39	20.07
Boana freicanecae	40	15.3	21.7
Boana geographica	49	18	24
Boana goiana	33	10.93	18.71
Boana guentheri	36	10.4	16.74
Boana hobbsi	42.5	14.7	21.3
Boana hutchinsi	43	15.8	21.8
Boana jimenezi	30.9	11.43	16.69
Boana joaquini	50.86	16.69	27.33
Boana lanciformis	63.2	19.8	44.2
Boana latistriata	44.8	13.7	22
Boana lemai	31.5	12.3	16.7
Boana leptolineata	30	8.6	15.2
Boana leucocheila	75.4	22.6	46
Boana liliae	35.15	12.85	19.23
Boana lundii	72.4	24.5	37.5
Boana marginata	46.3	15.6	24.3
Boana microderma	31.7	11.1	16.2
Boana multifasciata	50.2	15.7	29.2
Boana nympha	32.7	11.5	17.3
Boana ornatissima	40.8	13.79	23.34
Boana palaestes	49	14.8	23.7
Boana pardalis	68.7	23.36	35.04
Boana phaeopleura	32.7	10	17.4
Boana polytaenia	38.1	11.81	19.05
Boana pombali	58.1	19.2	30.2
Boana prasina	44.7	13.86	22.8
Boana pulchella	43.5	14.01	22.07
Boana punctata	35.7	12.5	18.9
Boana raniceps	69	22	40
Boana rhythmica	32.9	11.3	17.3
Boana roraima	45.5	15.7	25.2
Boana secedens	56.4	17.46	26.8
Boana semiguttatus	43.1	14.3	22.7
Boana semilineata	68.3	24.43	34.8
Boana sibleszi	32.9	12.17	17.11
Boana stellae	46.56	15.17	24.64
Boana stenocephala	28.3	7.7	14
Boana tepuiana	42.8	14.8	21.3
Boana wavrini	78	29.63	40.68
Boana xerophylla	57	19.8	32.2
Bokermannohyla ahenea	52.1	18.1	26.4
Bokermannohyla alvarengai	76	32	37.88
Bokermannohyla astartea	40.4	15.88	25.58
Bokermannohyla caramaschii	62.85	22.47	32.56
Bokermannohyla carvalhoi	61	23	33

Bokermannohyla circumdata	60	21.6	30
Bokermannohyla claresignata	61	23	33
Bokermannohyla clepsydra	53	18.75	27.75
Bokermannohyla gouveai	68	23.9	36
Bokermannohyla hylax	58.5	20.4	29.8
Bokermannohyla ibitiguara	40.48	15.18	20.72
Bokermannohyla ibitipoca	39.5	14.1	20
Bokermannohyla izecksohni	44.9	16.3	24.6
Bokermannohyla langei	66	23	32.92
Bokermannohyla lucianae	47.6	17.2	24.4
Bokermannohyla luctuosa	53.75	18.6	27.3
Bokermannohyla martinsi	56	21	28.66
Bokermannohyla nanuzae	41	20.5	20.5
Bokermannohyla pseudopseudis	43.5	102.3	23.68
Bokermannohyla ravida	42.1	16	22.1
Bokermannohyla sagarana	48.9	18.3	25.7
Bokermannohyla saxicola	50.1	17.69	25
Bokermannohyla sazimai	57.23	10.74	16.33
Bokermannohyla vulcaniae	46.75	17.1	24.98
Brachycephalus alipioi	15.3	6.8	6.8
Brachycephalus brunneus	10.2	3.9	3.3
Brachycephalus didactylus	10.2	4	4.3
Brachycephalus ephippium	19	7.5	7.5
Brachycephalus ferruginus	13.8	5.5	4.4
Brachycephalus hermogenesi	10	3.38	4.46
Brachycephalus izecksohni	11.1	4.5	3.8
Brachycephalus nodoterga	12.4	5.1	4.5
Brachycephalus pernix	14.9	5.94	4.15
Brachycephalus pombali	15	6	5.1
Brachycephalus vertebralis	12.9	5.3	4.5
Callimedusa atelopoides	42.5	16.3	16.3
Callimedusa baltea	63.5	21.8	29.4
Callimedusa tomopterna	55.5	19.63	24.26
Centrolene azulae	27.5	10	16.2
Centrolene bacatum	20.3	7.2	12.2
Centrolene medemi	26.1	10.3	18.7
Ceratophrys aurita	149	83.44	55.13
Ceratophrys cornuta	94	63	37.5
Ceratophrys cranwelli	83	48	28
Ceuthomantis aracamuni	18.2	6.2	11
Ceuthomantis cavernibardus	28.8	10.9	16.8
Ceuthomantis duellmani	24.3	8.6	14
Chiasmocleis alagoanus	26.8	7	10.2
Chiasmocleis albopunctata	32.6	8	10.3
Chiasmocleis anatipes	18.97	4.21	8.76
Chiasmocleis antenori	12.3	4.2	6

Chiasmocleis atlantica	30.6	8.1	12.3
Chiasmocleis avilapiresae	31.9	7.9	13.7
Chiasmocleis bassleri	25.6	6.6	11.9
Chiasmocleis capixaba	20.2	5.7	7.5
Chiasmocleis carvalhoi	20.2	5.6	7.9
Chiasmocleis centralis	23.6	6.8	8.72
Chiasmocleis cordeiroi	22.1	6.5	9
Chiasmocleis crucis	19.9	6.1	8.6
Chiasmocleis devriesi	42.2	12.5	15.4
Chiasmocleis gnoma	15.9	5.2	6.4
Chiasmocleis hudsoni	21.5	5.5	10.2
Chiasmocleis leucosticta	23.6	6.4	10.3
Chiasmocleis magnova	17.75	5.45	7.75
Chiasmocleis mantiqueira	21.5	6	10
Chiasmocleis mehelyi	19	5.5	6.4
Chiasmocleis sapiranga	23.5	6.4	9.5
Chiasmocleis schubarti	28.7	8	11.9
Chiasmocleis shudikarensis	26.7	6.9	11.9
Chiasmocleis tridactyla	12.4	4	5.1
Chiasmocleis ventrimaculata	25.5	5.4	10.5
Chimerella mariaelenae	19	7.4	10.8
Cochranella duidaeana	21.46	8.22	12.91
Cochranella erminea	23.4	7.6	13.6
Cochranella geijskesi	36.1	12.6	17
Cochranella resplendens	27.3	9.5	14.61
Cochranella riveroi	25	10.9	13.6
Colomascirtus armatus	64.3	21.8	34.2
Corythomantis greeningi	48	19.6	25.31
Crossodactylodes bokermanni	15.3	5.7	7.2
Crossodactylodes izecksohni	14.3	6	5.8
Crossodactylodes pintoi	17	7	7
Crossodactylus aeneus	31	10	14
Crossodactylus bokermanni	23.8	7.8	12.2
Crossodactylus caramaschii	24.5	7.94	12.69
Crossodactylus cyclospinus	29.4	8.8	13.3
Crossodactylus dantei	21.7	8	11.4
Crossodactylus dispar	26.9	9.5	12.4
Crossodactylus gaudichaudii	21.8	7.63	10.03
Crossodactylus grandis	34.5	12.7	15.8
Crossodactylus lutzorum	23.2	7.7	11.7
Crossodactylus schmidti	29	10	14
Crossodactylus trachystomus	24.2	7.8	11.8
Cruziohyla craspedopus	73	27.24	34.41
Ctenophryne barbatula	26.6	10.2	10
Ctenophryne carpish	33.7	12.6	11.7
Ctenophryne geayi	43.3	16.78	16.78

Cycloramphus acangatan	46.8	19.9	14.8
Cycloramphus asper	49.4	20.75	22.23
Cycloramphus bandeirensis	33.1	14.58	14.11
Cycloramphus bolitoglossus	39.8	17.11	13.53
Cycloramphus boraceiensis	55.4	23.18	24.79
Cycloramphus brasiliensis	68.9	28.94	33.07
Cycloramphus carvalhoi	58.8	27.1	18.7
Cycloramphus catarinensis	37.5	16	15.5
Cycloramphus cedrensis	40.5	17.3	18.7
Cycloramphus diringshofeni	30.6	12.24	15.3
Cycloramphus dubius	52.4	23.06	25.15
Cycloramphus duseni	38.4	15.74	18.43
Cycloramphus eleutherodactylus	46.2	19.5	23.32
Cycloramphus fuliginosus	54.7	23.52	24.07
Cycloramphus granulosus	37.8	15.74	15.88
Cycloramphus izecksohni	34.9	14.5	17.3
Cycloramphus juimirim	37.27	16.2	14.3
Cycloramphus lutzorum	45.1	19.2	22.1
Cycloramphus migueli	42.1	19.2	14
Cycloramphus mirandaribeiroi	60.2	27	29.7
Cycloramphus ohausi	36.2	15.56	15.56
Cycloramphus organensis	32.34	11.19	12.44
Cycloramphus rhyakonastes	42.2	17.8	21.6
Cycloramphus semipalmatus	45.5	20.55	21.51
Cycloramphus stejnegeri	49.6	20.83	16.86
Cycloramphus valae	36.2	13.4	16.3
Dasypops schirchi	52.28	9.95	19.86
Dendrobates leucomelas	33.8	10.39	14.75
Dendrobates nubeculosus	24.5	8	10.3
Dendrobates tinctorius	39	10.75	17.14
Dendrophryniscus berthalutzae	22	6.35	9.79
Dendrophryniscus brevipollicatus	21.2	7.52	11.5
Dendrophryniscus carvalhoi	18.5	5	8.51
Dendrophryniscus krausae	22.6	6.3	9.9
Dendrophryniscus leucomystax	25	7.5	10.3
Dendrophryniscus proboscideus	41.3	12.2	17.3
Dendrophryniscus stawiarskyi	22	6.71	9.69
Dendropsophus acreanus	33.25	10.75	16.83
Dendropsophus anataliasiasi	19.4	5.46	9.25
Dendropsophus anceps	42	14	22
Dendropsophus aperomeus	25	8.2	13.4
Dendropsophus araguaya	19.8	6	9.9
Dendropsophus berthalutzae	20	7	11.14
Dendropsophus bifurcus	25.7	8.68	13.98
Dendropsophus bipunctatus	24.5	8.5	12.5
Dendropsophus bokermanni	23.48	6.88	11.6

Dendropsophus branneri	18.5	6.06	10
Dendropsophus brevifrons	21.68	6.53	10.25
Dendropsophus cerradensis	18.9	6	9.6
Dendropsophus cruzi	22.9	6.6	11.9
Dendropsophus decipiens	19	7	10
Dendropsophus delarivai	26.6	9.1	14.6
Dendropsophus dutrai	38.1	10.7	18.93
Dendropsophus elegans	31.6	9.8	16.7
Dendropsophus elianeae	25.75	7.58	12.11
Dendropsophus gaucheri	19.2	6.73	11.94
Dendropsophus giesleri	25	8.72	13.18
Dendropsophus haddadi	22.6	7.5	11.34
Dendropsophus haraldschultzi	21.33	7	31.33
Dendropsophus jimi	21.5	6.35	10.45
Dendropsophus joannae	17.2	5.2	8.8
Dendropsophus juliani	20.7	7.5	10.3
Dendropsophus koechlini	28	8.8	13.6
Dendropsophus leali	20	6	12.58
Dendropsophus leucophyllatus	27	9	14
Dendropsophus limai	19	6.5	9.36
Dendropsophus marmoratus	35.5	11.7	21.5
Dendropsophus mathiassoni	21.4	6.6	10.2
Dendropsophus melanargyreus	37	11	18
Dendropsophus meridianus	24	8.13	13.39
Dendropsophus microcephalus	22.8	29.4	52.9
Dendropsophus microps	22.5	8.5	14.36
Dendropsophus minimus	23.26	8.5	14.03
Dendropsophus minusculus	20	6.5	9.7
Dendropsophus minutus	21.1	6.75	10.97
Dendropsophus miyatai	17.34	5.93	9.51
Dendropsophus nahdereri	41	14.73	21.18
Dendropsophus nanus	20	6	9.5
Dendropsophus novaisi	39	11.5	19.18
Dendropsophus oliveirai	17.8	5.8	8.16
Dendropsophus parviceps	23.45	6.75	11.87
Dendropsophus pauiniensis	20.2	6.8	9.9
Dendropsophus pseudomeridianus	21.8	6.8	10.7
Dendropsophus reichlei	21.5	7.6	11.6
Dendropsophus rhea	19	5.9	9.46
Dendropsophus rhodopeplus	27.3	9.28	14.5
Dendropsophus riveroi	20	6.4	10.4
Dendropsophus rossalleni	22.8	8.3	12.53
Dendropsophus rubicundulus	22	7	10
Dendropsophus ruschii	27.9	8.7	13.8
Dendropsophus sanborni	20	5.5	10
Dendropsophus sarayacuensis	25.6	9.1	14.6

Dendropsophus schubarti	18.66	6.09	11.19
Dendropsophus seniculus	37.7	12.44	18.85
Dendropsophus soaresi	30.9	9	13.5
Dendropsophus studerae	28.2	9.4	15.4
Dendropsophus timbeba	22.5	7.5	11.3
Dendropsophus tintinnabulum	20	6.27	11.23
Dendropsophus triangulum	27.6	9.61	14.96
Dendropsophus tritaeniatus	22	6.5	13.49
Dendropsophus walfordi	19.5	6.5	9.96
Dendropsophus werneri	20.5	6.5	10
Dendropsophus xapuriensis	16.69	5.96	9.74
Dermatonotus muelleri	54.3	17.85	21.7
Dryaderces inframaculata	51.9	16.67	27.18
Dryaderces pearsoni	54.7	18.93	28.01
Edalorhina nasuta	38	13.78	17.35
Edalorhina perezi	22	7.5	10
Elachistocleis bicolor	42.5	11.82	15.69
Elachistocleis bumbameuboi	37.4	8.6	12.9
Elachistocleis carvalhoi	35.2	8.4	13.2
Elachistocleis erythrogaster	35.46	7.2	11.68
Elachistocleis helianneae	31.7	7.3	11.8
Elachistocleis matogrosso	30.6	7.1	10.65
Elachistocleis ovalis	36	9	12.5
Elachistocleis piauiensis	22.5	5.8	8.2
Elachistocleis surinamensis	37.44	9.71	13.27
Elachistocleis surumu	25.6	6.65	8.9
Eleutherodactylus johnstonei	29.1	10.5	11.3
Engystomops freibergi	27.5	8	14
Engystomops petersi	30	10	14.85
Engystomops pustulosus	30	10	12
Espadarana durrellorum	25.7	8.7	14.6
Euparkerella brasiliensis	20.5	8.5	8
Euparkerella cochranae	15	6	6.5
Euparkerella robusta	17	6.5	6.7
Euparkerella tridactyla	22	9.5	8
Excidobates captivus	14.16	4.68	6.57
Fritziana fissilis	22.9	8.24	12.6
Fritziana goeldii	32.5	11	15.5
Fritziana ohausi	32.1	10.59	15.41
Frostius erythrophthalmus	23.4	8.3	9.2
Frostius pernambucensis	20.17	7.05	7.25
Gastrotheca albolineata	55	21.6	25.4
Gastrotheca andaquiensis	73.7	28.35	47.5
Gastrotheca antoniiochoai	27.8	8.9	15.1
Gastrotheca carinaceps	79.7	29	44
Gastrotheca ernestoi	63	23	33.48

Gastrotheca excubitor	37.1	14.02	18.92
Gastrotheca fissipes	67.2	25.9	30.8
Gastrotheca flamma	55.3	20.3	27.9
Gastrotheca fulvorufa	68.8	25.54	38.14
Gastrotheca longipes	55.7	21.4	35.1
Gastrotheca marsupiata	46.5	16.38	24.82
Gastrotheca microdiscus	70	26	39
Gastrotheca nicefori	65.3	25.7	36.4
Gastrotheca ochoai	33.4	11.72	17.6
Gastrotheca stictopleura	68.3	23.1	34.1
Gastrotheca testudinea	76.67	27.5	36.5
Gastrotheca weinlandii	90	36	48.6
Haddadus binotatus	57.4	22.39	32.14
Hamptophryne alios	49.5	20.5	16.6
Hamptophryne boliviana	39	14.61	13.4
Hemiphractus bubalus	60.7	27	33.7
Hemiphractus helioi	52.7	27	27.3
Hemiphractus johnsoni	45.5	23.3	26.5
Hemiphractus proboscideus	44.4	25.5	25
Hemiphractus scutatus	48	23.55	22
Holoaden bradei	30.8	11.7	11
Holoaden luederwaldti	39.6	16.2	15.9
Holoaden pholeter	44.6	16.3	19
Hyalinobatrachium cappellei	23	8.7	13.2
Hyalinobatrachium fleischmanni	19.2	7	10.8
Hyalinobatrachium iaspidiense	22.7	8.8	12.5
Hyalinobatrachium ruedai	21.2	7.82	11.8
Hyalinobatrachium taylori	20.84	7.34	11.25
Hydrolaetare dantasi	84.3	36.4	35.2
Hydrolaetare schmidti	82	34.6	36.3
Hylodes amnicola	28.8	8.9	15.4
Hylodes asper	45.5	15.02	25.03
Hylodes babax	30.6	9.7	17.2
Hylodes cardosoi	42.4	14	23.2
Hylodes charadranaetes	34.4	10.4	17.3
Hylodes dactylocinus	25.4	8.1	12.7
Hylodes glaber	38.8	12.5	21.7
Hylodes heyeri	45	13.5	23.4
Hylodes lateristrigatus	39	12.5	21
Hylodes magalhaesi	33	10.5	19.2
Hylodes meridionalis	41.7	13.6	21.2
Hylodes mertensi	51.5	17.6	28.1
Hylodes nasus	38	13	20
Hylodes ornatus	24.9	7.5	13.1
Hylodes otavioi	32.46	9.8	18.56
Hylodes perplicatus	38.6	13	22.7

Hylodes phyllodes	31.8	9.54	13.99
Hylodes pipilans	25.1	7.8	13.8
Hylodes regius	35.6	11.6	19.1
Hylodes sazimai	27.6	9.2	14.4
Hylodes uai	32.7	11.2	17.5
Hylodes vanzolinii	29	9.5	16.9
Hylomantis aspera	41.7	15.5	20.4
Hylomantis granulosa	37.4	14.5	17.2
Hyloscirtus albopunctulatus	41.5	14	21.7
Hyloscirtus phyllognathus	36.87	12.13	18.25
Hyloscirtus torrenticola	34.9	12.11	17.24
Hyloxalus azureiventris	27	9.11	13.04
Hyloxalus bocagei	27.3	9.5	12.8
Hyloxalus cevallosi	18.2	6.2	10.1
Hyloxalus chlorocraspedus	28.2	8.9	14
Hyloxalus craspedoceps	19.5	7	8.8
Hyloxalus eleutherodactylus	22.7	7.3	10.3
Hyloxalus exasperatus	20.5	7	9.4
Hyloxalus faciopunctulatus	23.83	8.97	10.87
Hyloxalus idiomelus	25.3	8.1	12.2
Hyloxalus mittermeieri	25.03	8.48	12.32
Hyloxalus nexipus	21.4	7.58	10.79
Hyloxalus patitae	22.6	7.91	11.07
Hyloxalus pulchellus	20.4	6.6	9.2
Hyloxalus sauli	22.41	8.52	11.47
Hyloxalus shuar	26.5	11.1	13.2
Hyloxalus sordidatus	33	11.2	15.5
Hypodactylus dolops	57.6	24.2	34.1
Hypodactylus nigrovittatus	21.1	8.27	9.58
Ischnocnema bolbodactyla	20.4	6.5	9.8
Ischnocnema epipeda	20.5	6.9	10.9
Ischnocnema erythromera	23.6	8.5	14.9
Ischnocnema gehrti	21.54	7.35	11.2
Ischnocnema gualteri	29.1	15.68	19.73
Ischnocnema guentheri	36.1	13	23.1
Ischnocnema henselii	33.4	11.8	20.7
Ischnocnema hoehnei	29.4	9.41	18.82
Ischnocnema holti	25.6	9.2	12.5
Ischnocnema izecksohni	43.5	16	25.8
Ischnocnema juipoca	25.1	9.4	13.7
Ischnocnema lactea	33	11	15
Ischnocnema manezinho	33.06	12.59	19.31
Ischnocnema nasuta	33	11	20
Ischnocnema nigriventris	19	6.84	9.12
Ischnocnema octavioi	31.25	12	17.57
Ischnocnema oea	17.7	6	11.1

Ischnocnema paranaensis	17.7	6.1	8.6
Ischnocnema parva	19.7	7.49	9.26
Ischnocnema penaxavantinho	20.3	7.2	11
Ischnocnema pusilla	16	6.5	11.62
Ischnocnema randorum	16.6	5.64	7.97
Ischnocnema sambaqui	36.89	13.96	19.16
Ischnocnema spanios	21.4	7.28	11.13
Ischnocnema venancioi	25.5	7.5	12
Ischnocnema verrucosa	22.1	9.3	12
Itapotihyla langsdorffii	74.9	21.72	40.45
Julianus pinimus	29	9.6	13.3
Julianus uruguayus	24.6	8.3	12.8
Leptodactylus bolivianus	89.3	30.9	43.8
Leptodactylus bufonius	53.6	18.28	21.33
Leptodactylus caatingae	35.3	12.7	14.1
Leptodactylus camaquara	32	15	11.04
Leptodactylus chaquensis	77	28.33	35.5
Leptodactylus colombiensis	46.3	15.5	21.3
Leptodactylus cunicularius	40	15	22
Leptodactylus cupreus	52.4	18	26.1
Leptodactylus didymus	46.7	15.8	25.1
Leptodactylus diedrus	34.3	12.4	16.9
Leptodactylus discodactylus	35	13.65	17.15
Leptodactylus elenae	43.5	14.3	20.6
Leptodactylus flavopictus	131.6	55.27	61.85
Leptodactylus fragilis	34.2	11.39	15.6
Leptodactylus furnarius	35.4	11.6	11.98
Leptodactylus fuscus	45.5	15.93	23.66
Leptodactylus gracilis	43	13.63	24.64
Leptodactylus griseigularis	46.6	15.84	21.44
Leptodactylus hylodes	25.3	8.7	12.1
Leptodactylus jolyi	45.4	17	34.05
Leptodactylus knudseni	132	48.84	54.12
Leptodactylus labyrinthicus	141.8	56.72	62.39
Leptodactylus latinasus	34	11.5	14
Leptodactylus latrans	96.8	32.91	46.46
Leptodactylus lauramiriamae	31.2	11.6	11.5
Leptodactylus leptodactyloides	46.3	15.74	21.76
Leptodactylus lithonaetes	71.4	27.4	31.5
Leptodactylus longirostris	41.8	13.96	22.03
Leptodactylus myersi	109.4	41.38	43.76
Leptodactylus mystaceus	43.6	14.91	22.54
Leptodactylus mystacinus	57.3	20.06	24.07
Leptodactylus natalensis	39.9	13.57	17.96
Leptodactylus notoaktites	56.1	18.4	31.5
Leptodactylus paraensis	128.7	49.9	54

Leptodactylus pentadactylus	148.1	57.76	66.65
Leptodactylus petersii	39.1	13.69	17.2
Leptodactylus plaumanni	41.93	14.17	25.53
Leptodactylus podicipinus	38.8	12.8	15.91
Leptodactylus pustulatus	51	17.85	22.44
Leptodactylus rhodomystax	76.5	29.07	33.66
Leptodactylus rhodonotus	75	27.75	31.5
Leptodactylus rhodostima	69.68	26.2	31.09
Leptodactylus riveroi	62.8	23.2	29.9
Leptodactylus rugosus	68.2	26.6	30.69
Leptodactylus sabanensis	51	17.34	24.99
Leptodactylus sertanejo	54.3	14.8	35.1
Leptodactylus spixi	43	14.5	21.5
Leptodactylus stenodema	91.1	32.8	35.53
Leptodactylus syphax	79.7	29.1	30
Leptodactylus tapiti	32	12	8.68
Leptodactylus troglodytes	49.9	16.92	19.81
Leptodactylus validus	36.9	11.81	16.97
Leptodactylus vastus	151.1	60.14	62.4
Leptodactylus viridis	66.4	23.8	29.7
Leptodactylus wagneri	65.5	22.27	33.41
Leucostethus argyrogaster	22.1	6.87	9.81
Leucostethus fugax	20.1	5.99	9.05
Limnomedusa macroglossa	48	19	33
Lithobates palmipes	75	28.5	38
Lithodytes lineatus	54	17.5	25
Lysapsus bolivianus	18	7	12
Lysapsus caraya	16.5	3	11.5
Lysapsus laevis	21	6.43	13.4
Lysapsus limellum	17	6	12
Macrogenioglottus alipioi	72	50	32
Megaelosia apuana	92.2	38.6	45.1
Megaelosia bocainensis	66.7	27	32.6
Megaelosia boticariana	74.9	34.45	39.7
Megaelosia goeldii	89.98	34.83	45.15
Megaelosia jordanensis	47	20.6	23
Megaelosia lutzae	90	35.1	40.5
Megaelosia massarti	115.43	47.9	56.1
Melanophryniscus admirabilis	35.53	10.4	13.04
Melanophryniscus alipioi	21.06	6.81	7.58
Melanophryniscus atroluteus	21	5.08	7.81
Melanophryniscus cambaraensis	34.2	10.4	14.2
Melanophryniscus dorsalis	23.95	7.55	8.35
Melanophryniscus fulvoguttatus	27.1	7.9	8.7
Melanophryniscus macrogranulosus	33.58	9.57	11.79
Melanophryniscus moreirae	27.4	7.42	9.22

Melanophryniscus peritus	39.3	9.3	11.7
Melanophryniscus simplex	28.6	8.9	10.1
Melanophryniscus spectabilis	33.6	10.4	11.7
Melanophryniscus tumifrons	30	8.8	11.5
Myersiella microps	15	4.65	6.15
Myersiohyla aromatica	44.5	16	24.4
Myersiohyla kanaima	47.6	16.1	24.2
Myersiohyla loveridgei	42	15	22
Noblella lochites	14.9	5.2	7
Noblella myrmecoides	13.6	4.75	6.4
Nyctimantis rugiceps	61.3	22.31	32.18
Nymphargus bejaranoi	24.4	8.18	13.81
Nymphargus laurae	19.9	7.4	11.7
Nymphargus mariae	30	10.4	16.6
Nymphargus mixomaculatus	26.3	8.8	14.9
Nymphargus ocellatus	29	10.4	18.15
Nymphargus phenax	22.1	7.82	12.8
Nymphargus posadae	31.2	10.23	19.83
Nymphargus siren	20.7	7.18	11.86
Nymphargus truebae	23.3	8.46	15.56
Odontophrynus americanus	44.6	18.91	11.73
Odontophrynus carvalhoi	67.9	29.2	23.7
Odontophrynus cultripes	58.6	22.85	16.58
Odontophrynus salvatori	27.3	12.25	10.6
Ololygon agilis	16	6	9
Ololygon albicans	38	12.5	19.16
Ololygon angrensis	28.5	9.51	14.14
Ololygon arduous	26.2	8.38	13.67
Ololygon argyreornata	20.48	6.68	11.05
Ololygon ariadne	43	15	23.83
Ololygon atrata	19.4	7.2	8.9
Ololygon belloni	28.4	10.4	15.3
Ololygon berthae	18.1	6	9
Ololygon brieni	34.5	11.39	17.6
Ololygon canastrensis	28.78	8.93	16.9
Ololygon carnevallii	24.5	8.3	13.6
Ololygon catharinae	45	15.3	22.39
Ololygon centralis	19.74	6.53	10.73
Ololygon faivovichi	19.9	6.3	10.6
Ololygon flavoguttata	42	15	21
Ololygon heyeri	36.6	12.41	19.38
Ololygon hiemalis	28.17	9.39	14
Ololygon humilis	31.5	9.91	15.77
Ololygon insperata	23.8	8.5	13.1
Ololygon jureia	29.3	9.5	16.1
Ololygon kautskyi	28.6	9.5	15.7

Ololygon littoralis	28.9	9	16.5
Ololygon littoreus	19.3	4.95	9.65
Ololygon longilinea	48	17	25
Ololygon luizotavioi	24.1	7.7	12.2
Ololygon machadoi	24.3	9	10
Ololygon melloi	18.7	6.23	9.16
Ololygon obtriangulatus	24.5	7.46	12.35
Ololygon perpusilla	19.8	6.53	10.1
Ololygon ranki	27.15	9.25	14.95
Ololygon rizibilis	34	10	16.79
Ololygon trapicheiroi	40	13.75	21.08
Ololygon v.signata	25.7	7.7	12.8
Oreobates crepitans	32	11.5	16.07
Oreobates cruralis	29.3	10.1	14.5
Oreobates heterodactylus	26.77	9.42	13.4
Oreobates lehri	24.4	9.3	15.7
Oreobates quixensis	58	25	32.66
Oreobates saxatilis	51.5	20.3	31.4
Oreophrynella cryptica	20.8	7.1	7.7
Oreophrynella dendronastes	33.9	11.8	13.3
Oreophrynella huberi	19	7	7
Oreophrynella macconnelli	22	7.54	8.25
Osteocephalus alboguttatus	45	15.55	24.13
Osteocephalus buckleyi	61.7	21.47	34.12
Osteocephalus cabrerai	52.7	19.2	31.8
Osteocephalus castaneicola	57.6	18.4	31.9
Osteocephalus deridens	47.8	16.18	26.92
Osteocephalus fuscifacies	53.2	19.7	27.5
Osteocephalus heyeri	42.8	14.3	21.9
Osteocephalus leoniae	40.1	13.8	21.5
Osteocephalus leprieurii	56.52	19.05	30.9
Osteocephalus mimeticus	34	12	23
Osteocephalus mutabor	48.3	18.1	25.9
Osteocephalus oophagus	52.16	16.25	28.75
Osteocephalus planiceps	63.2	20.4	36.6
Osteocephalus subtilis	37.23	13.23	20.37
Osteocephalus taurinus	82.5	26.41	43.6
Osteocephalus verruciger	64.5	23.09	35.15
Osteocephalus yasuni	52.7	17.8	31
Otophryne pyburni	56.3	18.7	18.6
Otophryne robusta	51.7	18.3	11.8
Otophryne steyermarki	35.1	11.6	14.6
Paratelmatobius cardosoi	21.75	8.14	9.8
Paratelmatobius gaigeae	16.7	5.5	7.08
Paratelmatobius lutzii	23	8	9
Paratelmatobius mantiqueira	16.8	6.31	6.81

Paratelmatobius poecilogaster	26.05	10.1	11.9
Phasmahyla cochranae	31.25	11.25	15.31
Phasmahyla exilis	34.5	11	18.5
Phasmahyla guttata	35	11	17
Phasmahyla jandaia	30.4	11.5	15.52
Phasmahyla spectabilis	45.6	15.1	22.2
Phasmahyla timbo	35.2	12.8	17.3
Phrynomedusa appendiculata	37.4	12.71	18.33
Phrynomedusa bokermanni	46	16	23
Phrynomedusa marginata	28	11	13
Phrynomedusa vanzolinii	36	12.9	17.8
Phrynopus bracki	19.8	7.81	7.4
Phyllodytes acuminatus	24.5	11	12.29
Phyllodytes edelmoi	26.2	9.5	13.8
Phyllodytes gyrinaethes	26	9.7	13
Phyllodytes kautskyi	38	13.9	18.6
Phyllodytes luteolus	23	8.15	10.94
Phyllodytes maculosus	49.5	18.6	22.1
Phyllodytes melanomystax	24.5	8.9	11.7
Phyllodytes tuberculosus	23	8.6	11.2
Phyllodytes wuchereri	26.66	9.93	12.57
Phyllomedusa bahiana	75	23	27
Phyllomedusa bicolor	110.4	43.7	46.1
Phyllomedusa boliviana	62.6	21.8	32.4
Phyllomedusa burmeisteri	35	11	17
Phyllomedusa camba	81.46	27.29	35.23
Phyllomedusa coelestis	64.8	22.8	31.4
Phyllomedusa distincta	70	21	28
Phyllomedusa iheringii	74	24	26
Phyllomedusa sauvagii	70	23.16	29.18
Phyllomedusa tarsius	95.5	32.5	45.1
Phyllomedusa tetraploidea	59.05	19.5	24.23
Phyllomedusa vaillantii	44	16.43	18.65
Physalaemus aguirrei	30	9.5	14.09
Physalaemus albifrons	34	11.05	16.63
Physalaemus albonotatus	30.2	9.61	13.63
Physalaemus angrensis	19.73	6.2	9.88
Physalaemus atlanticus	22.4	7.1	10.7
Physalaemus barrioi	26.67	8.56	13.07
Physalaemus biligonigerus	37.5	12.61	17.04
Physalaemus bokermanni	16.22	6	8.02
Physalaemus caete	24.54	9.1	12.31
Physalaemus camacan	23.3	7.4	11.1
Physalaemus centralis	43	13	18.4
Physalaemus cicada	27.5	8	12.81
Physalaemus crombiei	21.8	8.5	10.46

Physalaemus cuvieri	30.6	9.18	13.16
Physalaemus deimaticus	24.3	7.9	10.25
Physalaemus ephippifer	28.5	8.1	15.1
Physalaemus erikae	23.1	7.4	11.6
Physalaemus erythros	26.6	8.1	10.8
Physalaemus evangelistai	21.5	6	10.47
Physalaemus fischeri	33	9.3	13.6
Physalaemus gracilis	30	9.93	14.34
Physalaemus henselii	19	5.12	8.5
Physalaemus insperatus	26.2	7.5	12.23
Physalaemus irroratus	22.9	7.6	10.2
Physalaemus jordanensis	24	7.2	11.66
Physalaemus kroyeri	32	10.29	14.51
Physalaemus lisei	25.04	7.21	13.1
Physalaemus maculiventris	22.33	6.52	10.95
Physalaemus marmoratus	41.8	12.5	16.2
Physalaemus maximus	46.3	14.1	21.9
Physalaemus moreirae	25.4	8.8	11.9
Physalaemus nanus	18	3.53	6.85
Physalaemus nattereri	40.65	13.69	19.71
Physalaemus obtectus	26	8	12.12
Physalaemus olfersii	31.9	9.89	14.67
Physalaemus riograndensis	18.6	5.84	8.91
Physalaemus rupestris	17.8	5.2	7.1
Physalaemus signifer	21.5	6.5	10.5
Physalaemus soaresi	24	6.9	10.5
Physalaemus spiniger	21.1	6.3	10.2
Phyzelaphryne miriamae	19.6	7	8.9
Pipa arrabali	40	10.5	18.5
Pipa aspera	45	11	20.6
Pipa carvalhoi	57.7	15.1	23.4
Pipa pipa	134	54	53.5
Pipa snethlageae	89	27.5	31
Pithecopus ayeaye	39.17	12.5	15.67
Pithecopus azureus	43.1	12.1	16.6
Pithecopus centralis	42	14.5	12.84
Pithecopus hypochondrialis	35	11.8	16.3
Pithecopus megacephalus	43.7	14.4	17
Pithecopus nordestinus	41.1	12.1	16.5
Pithecopus oreades	36.48	12.21	14.54
Pithecopus palliata	43.6	14.26	18.6
Pithecopus rohdei	42	13.77	19.34
Pleurodema bibroni	31	13	14
Pleurodema brachyops	36	14.5	15
Pleurodema diplolister	33.8	13.3	13.6
Pleurodema marmoratum	31.8	10.5	10.9

Pristimantis aaptus	22.9	8.2	12.5
Pristimantis acuminatus	24	9.04	13.09
Pristimantis adiastolus	28	8.9	17.3
Pristimantis albertus	20.2	7	10.45
Pristimantis altamazonicus	27.9	10.35	13.62
Pristimantis altamnis	27.6	10.8	15.2
Pristimantis ardalonychus	27.4	10.4	13.7
Pristimantis aureolineatus	27.5	11.1	14.5
Pristimantis aureoventris	26.8	10.4	14.9
Pristimantis avius	33	13.1	17.9
Pristimantis bearsei	38.4	15.7	19.3
Pristimantis bromeliaceus	40.2	14.1	19.5
Pristimantis buccinator	28.2	9.6	16.1
Pristimantis cantitans	33	13.3	17.8
Pristimantis carvalhoi	17	6	10
Pristimantis chiastonotus	38.4	12.3	21.15
Pristimantis citriogaster	45.2	20	30.8
Pristimantis colonensis	18.65	6.75	10.36
Pristimantis condor	55.5	20.7	36
Pristimantis conspicillatus	49	18.5	29
Pristimantis cosnipatae	25.1	9.3	13.6
Pristimantis croceoinguinis	20.2	7.35	11.03
Pristimantis cruciocularis	20.3	7.6	10.5
Pristimantis danae	34	12.8	19.6
Pristimantis delius	30.9	12.3	16.8
Pristimantis dendrobatoides	29.5	10.2	23
Pristimantis diadematus	39.8	15.36	19.73
Pristimantis divnae	23.1	8.6	11.55
Pristimantis dundeei	23.6	7.9	13.3
Pristimantis epacrus	39.2	14.78	19.38
Pristimantis eurydactylus	34.7	13.1	17
Pristimantis exoristus	23.4	9	12.5
Pristimantis fenestratus	41.5	14.25	22.43
Pristimantis frater	21.5	8	10.5
Pristimantis galdi	21.4	8	13.2
Pristimantis gutturalis	30.4	9.9	17.3
Pristimantis imitatrix	15.8	5.6	8.4
Pristimantis infraguttatus	22.9	8.9	10.7
Pristimantis inguinalis	27	10.31	14.14
Pristimantis inusitatus	24	9.5	12.2
Pristimantis jester	21.2	8.4	11.86
Pristimantis kichwarum	20.2	7.6	12.3
Pristimantis lacrimosus	22.5	8.65	12.39
Pristimantis lanthanites	36.4	13.4	21.4
Pristimantis librarius	24.9	9.1	12.7
Pristimantis lindae	39.2	15.3	19.2

Pristimantis lirellus	21.5	8.2	11.8
Pristimantis luscombei	26.1	10.3	13.7
Pristimantis lythrodes	16.8	5.9	9.2
Pristimantis malkini	33.8	12.5	18.3
Pristimantis marmoratus	22	8	11
Pristimantis martiae	22.2	7.8	10.3
Pristimantis memorans	31.5	12.5	17.8
Pristimantis mendax	23	9.3	12.9
Pristimantis minutulus	17	6	9.6
Pristimantis muscosus	46.1	18.3	23.1
Pristimantis nebulosus	26.3	10.63	14.28
Pristimantis nephophilus	29.7	11.6	15.9
Pristimantis nigrogriseus	26.15	10.36	14.02
Pristimantis ockendeni	26.5	10.07	14.07
Pristimantis olivaceus	19.8	7.2	9.5
Pristimantis orcus	34	13	15.7
Pristimantis orphnolaimus	33.4	13.7	16.1
Pristimantis paulodutrai	35	10	19.75
Pristimantis paululus	19.4	7.1	9.6
Pristimantis pecki	17.8	7.2	9.3
Pristimantis percnopterus	25.9	10.2	14.1
Pristimantis peruvianus	41.5	17.9	23.28
Pristimantis petersi	19.9	7.4	10.2
Pristimantis platydactylus	30	11	14.2
Pristimantis pruinatus	26.8	12.9	12.9
Pristimantis pseudoacuminatus	20	6.76	13.56
Pristimantis pulvinatus	26.1	9.8	14.1
Pristimantis quaquaversus	26.1	10.4	13.8
Pristimantis ramagii	22	7.63	13.06
Pristimantis rhabdolaemus	29.7	10.2	17.3
Pristimantis rufioculis	20.6	7.7	11.5
Pristimantis saltissimus	22.5	8.6	12.42
Pristimantis savagei	21.2	7.8	11.5
Pristimantis skydmainos	30.5	12.5	18.3
Pristimantis tantanti	20.75	7	11.1
Pristimantis toftae	21.1	7.3	12.4
Pristimantis variabilis	24.35	8.21	13.02
Pristimantis ventrimarmoratus	36.9	14.05	18.05
Pristimantis versicolor	22.2	8.7	12.4
Pristimantis vilarsi	38.11	13.33	20.2
Pristimantis vilcabambae	22.1	8.1	10.4
Pristimantis vinhai	25	9	12.1
Pristimantis w.nigrum	59	20.5	38
Pristimantis waoranii	29.76	13.57	15.77
Pristimantis yaviensis	28.1	12	14.4
Pristimantis zeuctotylus	25.4	10	14.2

Pristimantis zimmermanae	19.1	6.9	9.5
Pristimantis zoilae	28.39	10.98	14.78
Proceratophrys appendiculata	48.5	25.8	21.6
Proceratophrys avelinoi	33.58	15.33	11.25
Proceratophrys bigibbosa	53.4	23.8	16.8
Proceratophrys boiei	62.1	31.4	23.9
Proceratophrys brauni	39.8	19.2	14.1
Proceratophrys concavitympanum	54	24.97	19.4
Proceratophrys cristiceps	44.7	19.7	16.1
Proceratophrys cururu	50.45	23.2	19.15
Proceratophrys goyana	59.3	26.3	21.9
Proceratophrys laticeps	71.5	42.5	24.5
Proceratophrys melanopogon	52.2	26.3	19
Proceratophrys moehringi	60	33	25.2
Proceratophrys moratoi	35.7	15	12.5
Proceratophrys palustris	29.83	14.95	10.4
Proceratophrys paviotii	51	23.6	18.4
Proceratophrys phyllostomus	55.4	27.6	19
Proceratophrys schirchi	46	17	20
Proceratophrys subguttata	47.3	26.7	17.8
Proceratophrys vielliardi	40.3	18	15.4
Pseudis bolbodactyla	43.1	16.2	24
Pseudis cardosoi	42.2	14.87	21.42
Pseudis fusca	43.45	16.65	25.4
Pseudis minuta	45.8	15.78	25.23
Pseudis paradoxa	56	19	32
Pseudis platensis	50	16	25
Pseudis tocantins	36.8	15.4	22.6
Pseudopaludicola boliviana	13.4	4.6	7.1
Pseudopaludicola canga	18.2	6.1	8.3
Pseudopaludicola ceratophyes	13	4.5	7.9
Pseudopaludicola falcipes	14.95	5.2	7.25
Pseudopaludicola llanera	15.9	5.2	7.4
Pseudopaludicola mineira	17.4	6.3	8
Pseudopaludicola mystacalis	18.9	6.63	10
Pseudopaludicola saltica	20.2	7.29	14
Pseudopaludicola ternetzi	19.9	6.7	10.25
Psychrophrynella usurpator	24.1	7.4	10
Ranitomeya amazonica	17.5	5.59	8.17
Ranitomeya benedicta	17.2	5.5	8.3
Ranitomeya fantastica	20	6.56	9.07
Ranitomeya flavovittata	18.1	6.01	7.31
Ranitomeya imitator	19	6	7
Ranitomeya reticulata	17	5.61	7.78
Ranitomeya sirensis	16.8	5.4	6.4
Ranitomeya summersi	19.5	6.3	8.5

Ranitomeya uakarii	15.39	5.08	7
Ranitomeya vanzolinii	17.5	6	7.3
Ranitomeya variabilis	26.8	9.03	14.1
Ranitomeya ventrimaculata	16	5	7
Rhaebo glaberrimus	66.4	22.3	26.2
Rhaebo guttatus	174.3	63.6	65.7
Rhaebo nasicus	66.5	24.82	32.59
Rhinella abei	81.9	29.1	17.1
Rhinella achavali	119	43.9	29.31
Rhinella acutirostris	57	19.84	20.92
Rhinella arenarum	66.03	24.7	21.6
Rhinella bergi	49.93	16.62	16.39
Rhinella castaneotica	39.5	13	14
Rhinella ceratophrys	93.9	31.1	44.8
Rhinella cerradensis	114.5	41.4	41.6
Rhinella cristinae	55.1	19.5	22.1
Rhinella crucifer	81.63	30.98	34.72
Rhinella dapsilis	77	27	31
Rhinella dorbignyi	55.58	19.15	16.23
Rhinella fernandezae	57.01	19.03	17.7
Rhinella festae	37	13.04	11.16
Rhinella fissipes	38.4	12	11.5
Rhinella granulosa	52.89	16.99	18.4
Rhinella henseli	58.27	19.87	26.69
Rhinella hoogmoedi	47.9	17.7	19.3
Rhinella humboldti	41	15	14.5
Rhinella icterica	137.3	53.55	49.43
Rhinella inca	39	14	20
Rhinella iserni	38.75	14	14.36
Rhinella jimi	133.8	48.63	45.37
Rhinella lescurei	43.7	15.95	18.45
Rhinella magnussoni	45.9	14.8	16.3
Rhinella manu	38.18	11.84	13.86
Rhinella margaritifera	68.9	25.88	29.36
Rhinella marina	97.5	36	38
Rhinella martyi	66.5	28	27.42
Rhinella nesiotes	29	11.7	11.2
Rhinella ocellata	59	20	19
Rhinella ornata	63.57	22.79	29.21
Rhinella poeppigii	123.78	45.55	45.67
Rhinella proboscidea	50.5	18.04	19.36
Rhinella pygmaea	40.76	13.84	12.46
Rhinella roqueana	74.5	28.06	31.06
Rhinella rubescens	120	45.53	40.58
Rhinella schneideri	250	95.32	104.07
Rhinella scitula	48	16.9	18.1

Rhinella spinulosa	80	30	30
Rhinella stanlaii	58.3	21.05	21.95
Rhinella veraguensis	55	19.21	20
Rhinella veredas	101.9	34.2	21.9
Rulyrana flavopunctata	24.9	9.01	14.31
Rulyrana mcdiarmidi	29.03	10.9	17.06
Rulyrana saxiscandens	22	7.7	12.9
Rulyrana spiculata	26.1	9.49	15.5
Scarthyla goinorum	20	6	12.18
Scinax acuminatus	45	16.14	21.06
Scinax alter	28.3	9.3	14.1
Scinax auratus	22.8	7.4	13
Scinax baumgardneri	29	9	13.5
Scinax blairi	32.3	10.17	14.9
Scinax boesemani	31.4	11	15.5
Scinax cabralensis	23.7	8.5	11.9
Scinax caldarum	28	8.82	16
Scinax camposseabrai	31.2	7.9	13.1
Scinax cardosoi	19.6	6.1	10
Scinax chiquitanus	33.5	10	17.2
Scinax constrictus	31.93	10.67	17.64
Scinax cretatus	30.7	10.5	15.8
Scinax crospedospilus	31	9.92	15.81
Scinax cruentomma	28	8.9	13.4
Scinax curicica	30.4	9.8	14.7
Scinax cuspidatus	27	9	15.5
Scinax danae	26.2	8.91	13.1
Scinax duartei	37	11	18
Scinax eurydice	42	14	23
Scinax exiguus	19.8	6.14	9.31
Scinax funereus	35	11.4	17.9
Scinax fuscomarginatus	20.4	5.7	9.9
Scinax fuscovarius	42.5	12.5	22
Scinax garbei	41.3	12.8	23.9
Scinax granulatus	34	12	18
Scinax hayii	48	15.84	24.96
Scinax ictericus	32	10.3	16.2
Scinax iquitorum	38.5	12.7	18.9
Scinax jolyi	124.19	49.05	61.99
Scinax karenanneae	30.5	10.3	15.8
Scinax kennedyi	37.3	11.5	20.3
Scinax lindsayi	26.3	8.4	13.3
Scinax maracaya	27.58	8.75	15.25
Scinax nasicus	31	10.02	15.55
Scinax nebulosus	37.5	12.84	19.81
Scinax oreites	36.5	11.4	18.7

Scinax pachycrus	33	10	19
Scinax pedromedinae	29.4	9.3	15.8
Scinax perereca	42.2	13.2	20
Scinax proboscideus	37.4	12.81	20.26
Scinax rostratus	42	14.1	24.2
Scinax ruber	40.3	12.7	20.5
Scinax similis	35	11	16.5
Scinax squalirostris	27	9	14
Scinax tigrinus	29.6	9.4	15.9
Scinax wandae	24.9	7.7	12
Scinax x.signatus	42.5	13.6	21.25
Scythrophrys sawayae	17.5	6	9
Sphaenorhynchus bromelicola	28	9	14.05
Sphaenorhynchus caramaschii	27.67	8.38	13
Sphaenorhynchus carneus	15.8	5.5	8.62
Sphaenorhynchus dorisae	27.5	9.1	12.34
Sphaenorhynchus lacteus	42.6	14.81	19.36
Sphaenorhynchus mirim	17.2	5.2	7.2
Sphaenorhynchus orophilus	30.3	8.79	13.33
Sphaenorhynchus palustris	34	11	16.37
Sphaenorhynchus pauloalvini	20	6.4	8.88
Sphaenorhynchus planicola	24	7	12
Sphaenorhynchus prasinus	31	9.8	13.94
Sphaenorhynchus surdus	25.78	7.75	12.53
Stefania ackawaio	46.48	18.15	31.14
Stefania ayangannae	44.67	18	30.82
Stefania breweri	49.6	18.5	32.5
Stefania coxi	67.23	27.16	43.03
Stefania evansi	63.9	26.89	39.81
Stefania ginesi	55	23	33
Stefania goini	92.2	40.5	60
Stefania marahuaquensis	27	10	15.9
Stefania oculosa	55.3	22.6	33.1
Stefania percristata	39.6	15	23.9
Stefania riae	59	21.77	34.57
Stefania roraimae	46	17.63	28.88
Stefania satelles	56.6	21.2	29.5
Stefania scalae	49.8	20.71	31.87
Stefania schuberti	76	33.8	42
Stefania tamacuarina	50	20	30
Stefania woodleyi	60	21.5	34
Stereocyclops histrio	35.9	13.5	13.7
Stereocyclops incrassatus	41	15.5	17.5
Stereocyclops parkeri	37.15	13.01	14.82
Strabomantis cornutus	56.5	27	29
Strabomantis sulcatus	42	18.98	21.64

Synapturanus mirandaribeiroi	32.9	7.81	10.94
Synapturanus rabus	19	4.8	6.7
Synapturanus salseri	25.1	6.9	10.5
Telmatobius hintoni	80.6	35.66	36.59
Telmatobius macrostomus	65.03	29.47	29.39
Tepuihyla edelcae	34.5	11.6	17.8
Tepuihyla exophthalma	32.7	12	17.3
Tepuihyla rodriguezi	37	12.14	18.8
Tepuihyla tuberculosa	85.7	29.2	45.6
Teratohyla adenocheira	22.4	9.4	12.4
Teratohyla amelie	18.2	6.6	11.1
Teratohyla midas	22.7	8.17	13.1
Thoropa lutzi	27.5	10.5	15.5
Thoropa megatympanum	43.2	18.7	21.2
Thoropa miliaris	71.1	28.44	39.11
Thoropa petropolitana	21	7.5	12
Thoropa saxatilis	57.5	23.9	33.9
Trachycephalus atlas	98	30	27.13
Trachycephalus coriaceus	57.5	18.63	29.48
Trachycephalus dibernardoi	77.58	25.38	39.47
Trachycephalus hadroceps	53.9	19.6	25.8
Trachycephalus imitatrix	53	16	26
Trachycephalus lepidus	58.7	20.1	33.1
Trachycephalus mesophaeus	67	21	32
Trachycephalus nigromaculatus	86	26	36
Trachycephalus resinifictrix	80	25	37
Trachycephalus typhonius	88.6	29.24	38.63
Vitreorana eurygnatha	22	8	11
Vitreorana gorzulae	21.4	8.7	12.9
Vitreorana parvula	17	6.06	9.11
Vitreorana ritae	19	7.5	11.5
Vitreorana uranoscopa	25	9	14
Xenohyla eugenioi	42.5	13.25	16.85
Xenohyla truncata	39.78	11.83	15.42
Yunganastes mercedesae	44.8	16.95	31.2
Zachaenus carvalhoi	35	14	16
Zachaenus parvulus	20.5	9.5	9

Table S4. Variables selected for the final model using VIF to exclude autocorrelated variables. Nine of the 20 input variables had collinearity problem (Bio1, Bio10, Bio11, Bio12, roughness, PET of the driest quarter, CVbio1, CVbio10, CVbio12). So, we selected five variables according to our predictions to be included in the final CAR model.

Predictor Variable	VIF
Bio 16	**1.792344**
Bio 17**	**2.490485**
PET of coldest quarter	**2.084837**
PET of warmest quarter**	**2.198103**
Annual PET wet	**2.560582**
Aspect**	**1.094310**
Mountain slope**	**1.221094**
CVbio11	**1.021612**
CVbio16	**1.250076**
CVbio17	**2.320962**
Stability**	**1.211727**

****Variables included in the CAR model.**

Table S5. Importance (beta) and significance values of each predictor variable included the CAR model for diversity dimensions in the Amazon, Cerrado, and Atlantic Rainforest. Taxonomic diversity (TD), Phylogenetic diversity of early diverging clades (NRI), Phylogenetic diversity of recent diverging clades (NTI), Decoupled Functional Diversity (FD decoupled), Non-decoupled Functional Diversity (FD non-decoupled).

Biome	Diversity Dimension	Variables	Beta	Significance (p)
Atlantic Rainforest	TD	Precipitation	1.7922	0.0953
		PET	-9.7029	0.0000
		Relief Aspect	0.8558	0.1532
		Relief Slope	3.2301	0.0000
		Stability	3.4856	0.0000
	NRI	Precipitation	-0.0707	0.1491
		PET	-0.2856	0.0000
		Relief Aspect	0.0648	0.0177
		Relief Slope	0.0045	0.8897
		Stability	0.1138	0.0003
	NTI	Precipitation	0.0796	0.1847
		PET	-0.3888	0.0000
		Relief Aspect	0.0159	0.6341
		Relief Slope	-0.0350	0.3769
		Stability	0.0325	0.3937
	FD decoupled	Precipitation	-0.0013	0.0156
		PET	0.0056	0.0000
		Relief Aspect	0.0007	0.0258
		Relief Slope	-0.0004	0.2442
		Stability	0.0019	0.0000
	FD non-decoupled	Precipitation	-0.0001	0.9165
		PET	-0.0105	0.0000
		Relief Aspect	0.0014	0.0110
		Relief Slope	0.0004	0.5329
		Stability	0.0039	0.0000
Cerrado	TD	Precipitation	0.2157	0.5443
		PET	-2.8302	0.0000
		Relief Aspect	-0.0437	0.7768
		Relief Slope	0.9608	0.0000
		Stability	-1.1078	0.0012
	NRI	Precipitation	-0.1467	0.0000
		PET	-0.0505	0.0862
		Relief Aspect	0.0442	0.0006
		Relief Slope	-0.0087	0.6442
		Stability	-0.0822	0.0038
	NTI	Precipitation	-0.0470	0.2669
		PET	-0.1939	0.0000
		Relief Aspect	0.0242	0.1873
		Relief Slope	0.0629	0.0192
		Stability	-0.1311	0.0013

	FD decoupled	Precipitation	-0.0024	0.0000
		PET	0.0003	0.4141
		Relief Aspect	-0.0001	0.6230
		Relief Slope	-0.0003	0.1181
		Stability	0.0000	0.9736
	FD non-decoupled	Precipitation	-0.0052	0.0000
		PET	-0.0057	0.0000
		Relief Aspect	0.0001	0.6914
		Relief Slope	-0.0011	0.0103
		Stability	-0.0022	0.0015
Amazon	TD	Precipitation	3.9227	0.0000
		PET	0.4953	0.1598
		Relief Aspect	-0.0041	0.9797
		Relief Slope	-4.2447	0.0000
		Stability	-0.9978	0.0169
	NRI	Precipitation	0.4090	0.0000
		PET	-0.1598	0.0000
		Relief Aspect	-0.0219	0.1122
		Relief Slope	0.3562	0.0000
		Stability	0.1679	0.0000
	NTI	Precipitation	0.2993	0.0000
		PET	-0.0180	0.4445
		Relief Aspect	-0.0120	0.2695
		Relief Slope	0.2121	0.0000
		Stability	0.0597	0.0321
	FD decoupled	Precipitation	-0.0038	0.0000
		PET	-0.0005	0.0192
		Relief Aspect	0.0002	0.0168
		Relief Slope	-0.0025	0.0000
		Stability	-0.0002	0.4026
	FD non-decoupled	Precipitation	0.0127	0.0000
		PET	0.0031	0.0000
		Relief Aspect	-0.0011	0.0001
		Relief Slope	0.0079	0.0000
		Stability	0.0005	0.4509

FINAL CONSIDERATIONS

- The establishment of conservation strategies for anurans in the Cerrado hotspot should consider multiple biodiversity facets to maximize anuran protection as elucidated by five prioritization areas in our study. Selecting protected areas based on traditional biodiversity metrics that ignore the uniqueness of each species, such as species richness and endemism, is not the most inclusive conservation strategy because it usually does not identify evolutionary patterns, it does not ensure community persistence in the long term and, it does not allow us to make predictions about functional consequence of environmental changes.
- Besides considering different biodiversity dimensions in the prioritization decision making, researches should do an extra effort to build solid databases to enhance a better understanding of species geographic distribution, lineages and the role of each species in the ecosystem functioning.
- The geographical distribution of diversity dimensions in the Amazon, the Cerrado and Atlantic Rainforest, are strongly influenced by spatial processes. Those patterns have emerged mostly due to the species dispersal limitation determined by abiotic conditions, geographic isolation (due to environmental barriers), restricted niche evolution ability to spread over new ecological conditions. There is growing evidence demonstrating that spatial structure is the main parameter in macroecological studies, as a result of the influence of regional species pool, local speciation, and species dispersal limitation.
- We found support that biodiversity patterns in high elevational regions are influenced especially by the geographical barriers created by the physical presence of alpine zones. Also, climatic fluctuations would have allowed mountains to act as species centers of diversification. Therefore, both the environmental gradient created by mountain uplift, which probably have

slowed down migration during climatic oscillations periods and provided stable areas for the species maintenance (refugia), enabling species survival and allopatric speciation.

- We found a striking pattern that emerges when comparing functional decoupled and non-decoupled diversity, especially related to ecotone areas. When we take the influence of phylogenetic relatedness out, we are able to evaluate the pure variation of the traits. Instead, the non-decoupled functional diversity might be overemphasizing the trait variability in some areas (i.e., Andes), hindering traits complementarity. So, it seems that harsher conditions do favor species with different traits (independent of their phylogenetic relationship) to explore different niche conditions and avoid negative interspecific interactions which emphasizes the higher functional diversity in ecotones areas.