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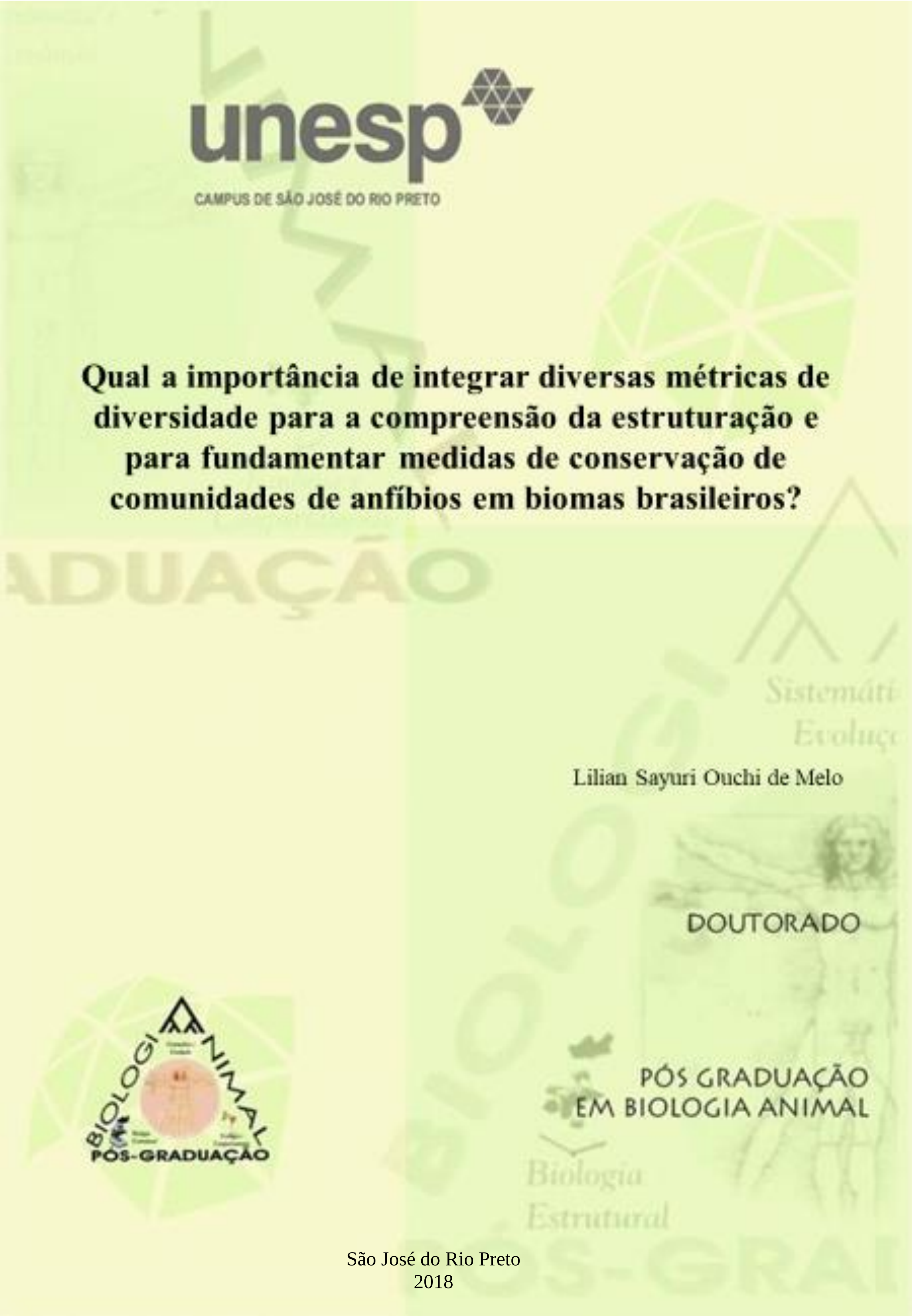

CAMPUS DE SÃO JOSÉ DO RIO PRETO

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

PÓS GRADUAÇÃO
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São José do Rio Preto
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Dedico esta tese à minha querida avó, Shime
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a maior incentivadora dos meus estudos
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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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.