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Dinâmica Evolutiva do Nicho Ecológico em Mamíferos

VICTOR HUGO MENDOZA RODRIGUEZ

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VICTOR HUGO MENDOZA RODRIGUEZ

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ATA DE DEFESA DE TESE

Ata nº 96 da sessão de Defesa de Tese de **Victor Hugo Mendoza Rodriguez**, que confere o título de **Doutor em Ecologia e Evolução**, na área de concentração em **Ecologia e Evolução**.

Aos **vinte e sete dias do mês de março de dois mil e vinte (27/03/2020)**, a partir das **14h00min**, por **videoconferência**, seguindo **portaria CAPES no. 36 de 16 de março de 2020 e recomendação da UFG**, realizou-se a sessão pública de Defesa de Tese intitulada **“Dinâmica evolutiva do nicho ecológico em mamíferos”**. Os trabalhos foram instalados pelo Orientador, **Professor Doutor Matheus de Souza Lima Ribeiro - PPGEE/ICB/UFG - Depto Ciências Biológicas/UFJ**, com a participação dos demais membros da Banca Examinadora: **Professora Doutora Levi Carina Terribile - PPGEE/ICB/UFG - Depto Ciências Biológicas/UFJ**, membro titular externo; **Professor Doutor João Carlos Nabout - CCET/Anápolis/UEG e PPGEE**, membro titular interno; **Professor Doutor Frederico Augusto Martins Valtuille Faleiro - DTI PosDoc - Dep. de Ecologia/UFG**, membro titular externo; e **Dra. Flávia de Figueiredo Machado - DocFix PosDoc - UFJ**, membro titular externo. Durante a arguição os membros da banca não fizeram sugestão de alteração do título do trabalho. A Banca Examinadora reuniu-se em sessão secreta a fim de concluir o julgamento da Tese, tendo sido o candidato **APROVADO** pelos seus membros. Proclamados os resultados pela **Professor Doutor Matheus de Souza Lima Ribeiro**, Presidente da Banca Examinadora, foram encerrados os trabalhos e, para constar, lavrou-se a presente ata que é assinada pelos Membros da Banca Examinadora, ao(s) **vinte e sete dias do mês de março de dois mil e vinte (27/03/2020)**.

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pelo apoio e amor infinito.

“No estudio por saber más, sino por ignorar menos”

“Eu não estudo para saber mais, mas para ignorar menos”

Juana Inés de Asbaje
(1648-1695)
Escritora mexicana
(Livre tradução)

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RESUMO

As diferentes condições ambientais e a história evolutiva de cada região impedem que as espécies estejam distribuídas homoganeamente pelo mundo todo, criando padrões de riqueza e diversidade. O que faz que duas espécies possam compartilhar o mesmo habitat? O que permite às espécies se estabelecerem em determinados locais do planeta? Nesta tese se contrastou a história filogenética com informação funcional em três escalas do nicho ecológico, correspondentes às escalas hierárquicas da biodiversidade do Robert H. Whittaker, α (local), β (regional) e γ (geográfica) para 4480 espécies de mamíferos atuais, tanto terrestres quanto marinhas do mundo todo. Assim, o Nicho α inclui as dinâmicas de competição. O nicho β , representa os filtros ambientais sobre as comunidades e o nicho γ está representado pelos reinos biogeográficos onde as espécies ocorrem. No primeiro capítulo particionei as três escalas do nicho com o intuito de avaliar a dinâmica evolutiva dentro de cada escala, esperando-se um conservadorismo evolutivo gradual, onde a escala α apresente a dinâmica mais lábil, e a escala γ a mais conservada. Levando em consideração para cada uma das espécies traços ecológicos na escala α , tolerâncias ambientais e tipos de habitat na escala β , e a região biogeográfica onde cada espécie ocorre na escala γ , estas informações foram correlacionadas com a distância filogenética, primeiramente para os mamíferos como um todo e posteriormente para dezessete ordens individuais. Contrário o esperado, a escala α mostrou alta convergência evolutiva, sugerindo a dinâmica mais conservada e a escala β a mais lábil. No segundo capítulo, analisei a dinâmica evolutiva das escalas α , β e γ do nicho em relação ao espaço geográfico global. Onde é esperado que as três escalas apresentem maior conservadorismo evolutivo nas latitudes tropicais e diminua ao se aproximar dos polos tanto nas espécies terrestres quanto nas espécies marinhas. Achei como esperado, este padrão para os mamíferos terrestres, porém, as espécies marinhas apresentaram um padrão oposto, pois as espécies com distribuição polar se apresentaram com o maior grau de conservadorismo. No terceiro capítulo, explorei a dinâmica evolutiva de cada uma das escalas do nicho com relação a variáveis climáticas críticas (temperaturas baixas, grandes elevações, baixa disponibilidade de água-energia) em comparação as regiões com condições estáveis. Esperando uma filtragem ambiental diferencial para as escalas α , β e γ , onde espécies com nichos similares co-ocorram sob condições ambientais similares. Finalmente, como quarto capítulo, fiz um mapeamento sistemático do Grande Intercambio Biótico Americano (*GABI* em inglês), analisando o comportamento espaciotemporal da literatura científica, identificando os países e instituições mais relevantes na produção científica para este tópico.

Palavras chave: dinâmica evolutiva, nichos α , β e γ , distância filogenética, distância funcional, mamíferos, Grande intercambio biótico americano, mapeamento sistemático.

ABSTRACT

The different environmental conditions and the evolutionary history of each region prevent a homogeneous species distribution worldwide, creating the observed richness and diversity pattern. What allows two species to share the same habitat? What allows species to settle in certain places than in others on the planet? At this thesis, I contrasted phylogenetic history versus functional information for 4480 terrestrial and marine species of extant mammals in three ecological niche scales that correspond to Robert H. Whittaker's hierarchical biodiversity scales: α (local), β (regional) and γ (geographic). Thus, Niche α includes the competition dynamics. Niche β , represents the environmental filters on the communities and niche γ is the geographical space represented by the biogeographical realms where species occur. In the first chapter, I partitioned the three niche scales to assess evolutionary dynamics within scales, expected an evolutionary gradient, with the α scale as the most evolutionary labile, and the γ scale as the most conserved. For all species, I gathered ecological traits of diet, diel activity, and strata use for the α scale, environmental tolerances, and habitat types, for the β scale, and for the biogeographic realm where each species occurs the γ scale. I correlated the traits at each scale with phylogenetic distance for all mammals and subsequently for seventeen individual orders. Contrary to expectations, the α scale showed higher evolutionary divergence, suggesting the most conservative dynamics and the β scale the most labile. In the second chapter, I analyzed how the evolutionary dynamics of the niche scales are structured in the global geographic space. I expected more evolutionary conservatism in tropical latitudes at all three scales and higher lability as they approach the poles, both in terrestrial and marine species. Terrestrial mammals exhibited the expected pattern; however, marine species showed the opposite pattern, with a higher conservatism in high latitudes. In the third chapter, I explored the evolutionary dynamics of niche scales concerning critical climatic variables (low temperatures, high elevations, and low availability of water energy) versus regions with stable conditions. I expected differential environmental filtering for α , β , and γ scales, where species with similar niches converge under similar environmental conditions. Finally, as a fourth chapter, I carried out a systematic mapping about the Great American Biotic Interchange (GABI), analyzing the Spatio-temporal trend of the scientific literature, identifying the most relevant countries and institutions in scientific production for this topic.

Key words: evolutionary dynamic, α , β and γ -niches, Phylogenetic distance, functional distance, mammals, Great American biotic interchange, systematic mapping study

INTRODUÇÃO GERAL

Atualmente, o conceito de nicho é considerado um eixo fundamental da ecologia, por ele tentar explicar por um lado, as necessidades das espécies para se estabelecerem e persistirem nos ecossistemas e por outro lado, o impacto que têm no funcionamento ecossistêmico por meio dos traços morfológicos, fisiológicos e comportamentais (Chase e Leibold 2003). Assim, o entendimento do comportamento destes traços no tempo e no espaço (conservadorismo, convergência ou divergência) permite explicar as regras de assembleia das comunidades, os padrões atuais de riqueza e distribuição das espécies, padrões de invasão biológica, resposta às mudanças climáticas, entre outros fatores (Diniz-Filho et al. 2010).

Chase e Leibold (2003) reconhecem um debate sobre a implementação e utilidade do conceito de nicho, quanto ao entendimento das interações locais que conformam as comunidades, assim como a relação com os padrões macro ecológicos que estabelecem a diversidade global. Segundo estes autores, a controversa deriva de duas correntes:

- 1) Pesquisas que seguem as ideias de Grinnell (1917) e Hutchinson (1957), baseadas numa escala ampla e relacionada com os requerimentos abióticos das espécies. Por exemplo Tingley et al. (2009), Rodder e Engler (2011), Larson et al. (2014), Peixoto, Villalobos e Cianciaruso (2017).
- 2) Trabalhos que estão fundamentados nas ideias de Elton (1927) e MacArthur e Levins (1967), que se relacionam com uma escala local, a partição de recursos, a influência de uma espécie sobre outra e como a performance das espécies afeta o funcionamento do ecossistema. Exemplos desta linha são os trabalhos de Araújo, Marcondes-Machado e Costa (2014) Comte, Cucherousset e Olden (2016), Manlick et al. (2018) ou Dehling e Stouffer (2018).

Assim, segundo Chase e Myers (2011), muitas pesquisas teóricas e empíricas inseridas na teoria do nicho estão atribuindo um papel central ao nicho, como gerador de padrões de biodiversidade. Este fato tem gerado um viés para com a corrente Grinnelliana, de acordo com Larson, Olden e Usio (2010), consequência principalmente da facilidade de acessar a informação climática e por funcionar em grandes escalas.

A diversidade de espécies tem uma relação direta com a escala espacial, qualquer mudança na escala, refletirá nos padrões observados de riqueza, diversidade taxonômica, e filogenética. As interações de competição são mais fortes em escalas menores; os filtros ambientais funcionam em escalas intermediárias limitando a dispersão das espécies, o conjunto destas interações vai escalando até chegar nos processos biogeográficos (Cavender-Bares et al. 2009). Nesta tese foram seguidas as ideias de Silvertwon et al. (2006a) que propõem uma correspondência nas escalas de biodiversidade de Robert H. Whittaker (1975), com uma estruturação hierárquica do hiper volume do nicho das espécies. Nesse sentido, o nicho α é onde ocorrem as interações interespecíficas que facilitam ou dificultam a coexistência local. O nicho β , correspondente ao(s) habitat(s) onde uma espécie pode estar presente; e o nicho γ representado pela distribuição da espécie e o reino biogeográfico onde a espécie ocorre (Silvertwon et al. 2006b). Duas espécies irmãs que co-ocorrem no mesmo local, experimentam uma diferenciação no uso de recursos durante o processo de especiação (diferenciação de nicho α), caso contrário aconteceria uma exclusão por competição (Ackerly et al. 2006). Por outro lado, a proximidade filogenética entre elas resulta em uma semelhança ecológica (Webb et al 2002), permitindo-lhes a ocorrência nos mesmos habitats (similaridade de nicho β). Essa diferenciação na escala α , mantendo similaridades na escala β , faz pensar com que cada escala dentro do nicho tem uma velocidade evolutiva diferente.

Entender o comportamento evolutivo do nicho ecológico das espécies é uma das perguntas centrais dentro da ecologia atual. Para responder a esta pergunta, Peterson (2011) considera necessário fazer uma abordagem adequada das escalas do nicho, separando-as nos seus componentes, mas incluindo todas as escalas. Para explorar e entender a dinâmica evolutiva do nicho, têm-se desenvolvido diferentes métricas correlacionando distância filogenética entre espécies com similaridade/dissimilaridade de traços funcionais na estrutura das comunidades (ver Cavender-Bades et al. 2003). Esta tese se baseou na proposta metodológica de Cadotte et al. (2013) para correlacionar diferentes informações ecológicas e biogeográficas à filogenia nos mamíferos atuais. Esta metodologia correlaciona a distância filogenética (PDist) e a distância funcional (FDist), mediante a equação: $FPDist = (aPDist + (1-a) FDist)^{1/p}$, estabelecendo assim uma relação euclidiana entre ambas as distâncias (FPDist) pelo parâmetro a . Altas taxas evolutivas podem ser representadas como $FDist > PDist$. Pelo contrário, $FDist < PDist$ significa uma baixa taxa de evolução. Assim, FPDist tenta refletir a convergência,

divergência ou conservadorismo evolutivo dos traços das espécies, pela contribuição relativa aportada pelas FDist e PDist, ajustada pelo parâmetro a que vai de 0 a 1. Valores de a próximos de zero, indicam divergência em FPDist, por uma PDist decrescente. Quando a se aproxima de 1, temos uma convergência em FPDist por uma PDist crescente (Ver detalhes em Cadotte et al. 2013).

Neste sentido, ainda foi explorada a dinâmica evolutiva dos nichos α , β e γ e como eles estão estruturados na taxonomia do grupo (capítulo 1), no espaço geográfico (capítulo 2) e como cada um dos nichos é influenciado pelo ambiente (capítulo 3), escritos no formato de artigo e em inglês. Por último, como um quarto capítulo, também na forma de artigo mas em português, integra-se o trabalho da minha qualificação de doutorado, onde fez-se um mapeamento sistemático da literatura relacionada com o Grande Intercambio Biótico Americano, o acontecimento de mistura das biotas da América do Norte e América do Sul, consequência da formação de uma ponte terrestre que interconectou ambas as massas continentais, anteriormente isoladas (Stehli e Webb). Ao final deste documento, evidencio aspectos gerais que pude concluir ao longo do trabalho.

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CAPÍTULO 1

Disentangling evolutionary dynamics on the hierarchical niche scale

Victor Hugo Mendoza Rodriguez^{1,2}, Frederico Valtuille Faleiro², Marcos Carlucci³, Matheus S. Lima-Ribeiro^{2*}

¹Programa de Pós-graduação em Ecologia & Evolução, Universidade Federal de Goiás, Goiânia, Brazil.

²Macroecology Lab., Universidade Federal de Jataí, Jataí, Brazil.

³ Programa de Pós-Graduação em Ecologia e Conservação, Universidade Federal do Paraná, Curitiba-PR, Brazil.

*Author for correspondence: muslima.ribeiro@gmail.com

Abstract

Community phylogenetic structure is influenced by temporal and spatial scales, that create differentiated niche scales whose evolutionary dynamics behave at different rates. Niche α represents the local scale and includes the competition dynamics. Niche β , as regional scale, represents the environmental filters on the communities and niche γ is the geographical space represented by the biogeographical realms where species occur. Here we analyze the niches α , β , and γ for a dataset of 4480 terrestrial and marine mammals, we also assess a subset of 432 species with physiological thermal tolerances and for seventeen orders, associating each niche scale to ecological, environmental and geographical traits. We found a higher evolutive rate in niche α in all dataset assessed except for the order Cetartiodactyla, conversely niches β and γ were exhibit a lower evolutive rate, strongly influenced by the phylogenetic history for all mammals but with a random behavior across the orders assessed. On the other hand, our Blomberg's K test exhibit a niche α with high phylogenetic signal mostly in all the datasets, niche β exhibited mostly the lowest values and niche γ showed a wandering pattern. We demonstrated the differential evolutive dynamics across the scales of the niche and how different methodologies influence the outputs.

Keywords: niches α , β , and γ , niche conservatism, niche evolution, phylo-functional distance, phylogenetic signal

1. Introduction

Afterwards Robert Whittaker proposed his spatial hierarchy for biodiversity (1975) because of niche differentiation, Pickett and Bazzaz (1978) adopted this idea and referred each hierarchy as niches α , β . Silvertown et al. (2006) revisited this idea, and suggested that the structure of phylogenetic trees could reflect this hierarchy configuration of niches.

The α niche represents the narrowest space of hypervolume a species occupies in a given time, which is determined by biotic interactions (i.e., the realized niche, Soberon and Peterson 2005). The long-term coexistence of identical species is not possible (Cushing et al. 2004) but is widely observed ecological similarity between sister species (Davies et al. 2007, Cavender-Bares et al. 2009), it is possible that the ecological divergence evolves at this α -scale, which permits the co-occurrence of congeneric species. Linking α niche to the phylogenetic tree structure, this scale could be placed among the tips, where the niche shifts tend to accumulate (Revell et al. 2008, Ogburn and Edwards 2015). The intermediate scale, the β niche, is related to habitat preferences and environmental tolerances of species (Silvertown et al. 2006). This niche represents a regional component and is linked to the fundamental (or potential) niche (Jackson and Overpack 2000). This scale establishes the composition and therefore differentiation among communities (Jackson and Blois 2015), which could be placed at a taxonomic level of family in the phylogeny (Silvertown et al. 2006).

It is now widely accepted that related phylogenetic species have ecological similarities (Webb et al. 2002). This similarity is determined in a wide way by the habitat preferences and environmental tolerances (β niche) during the speciation process (Leibold and Peek 2006: Tuomisto 2006). However, at a finer scale, the coexistence inside the communities is established by traits related to obtaining resources, such as diet (HilleRisLambers et al. 2012). This fine-scale dynamic of biodiversity corresponds to α niche. Hence, during the community assembly process, sister species can co-occur at a given community with similar β niche only as a consequence of ecological trait differentiation in the α niche level (Ackerly et al. 2006). Lastly, the γ niche refers to the spatial component derived from the interaction of the previous scales (Soberon, 2007), which it would determine the geographic range of species and their ability to share different biogeographic realms (Silvertown et al. 2006).

Nowadays, there is no a clear link between the functional traits and ecological niches (Mouquet et al. 2012), this create a lack of consensus about how ecology and phylogenetic processes influence the evolution of the niche scales at several temporal and spatial scales. This gap could be a consequence of an inadequate methodological approach. An example of this is the so-called McArthur's Paradox (see Chase and Myers, 2011), where the niche concept and its theoretical framework is applied differently depending on the phenomena and scale being studied.

Environmental heterogeneity establishes a distribution pattern of species traits, turning scale a determining factor in the configuration of the niche hypervolume. (D'Andrea and Ostling, 2016). Therefore, the hierarchical organization of the dimensions of the niche hypervolume impacts on different scales the ecosystem processes. Hence, a better partition of the different components of the niche would help to improve its comprehension. (Peterson, 2011; Mouquet et al. 2012).

To test the idea of a hierarchical structure in the niche, we selected different ecological traits, environmental tolerances and, geographic distribution integrated to phylogenetic information to assess the evolutionary dynamics of each of the niche scales in the extant mammals. We chose mammals for being an ecologically well-documented group with reasonably well-resolved phylogenetic information. Specifically, we expected a nested evolutionary dynamic for the niche, we predict a differential evolutionary dynamic with a more labile evolution on the local scale (niche- α), intermediate at the regional level (niche- β), and more conserved at the geographical level (niche- γ).

2. Methods

2.1 Phylogenetic data

To establish the phylogenetic relationship for our species, we used the 100 randomly solved phylogenies from Kuhn et al. (2011). From the original 5,020 species included in the phylogenetic tree, we excluded those species that lacked information of any functional traits, keeping a total of 4,080 species of marine and terrestrial extant mammals. Additionally, we pruned the original phylogeny for a dataset of thermal physiological tolerance of 432 species (see next section). Then, we proceed to estimate the cophenetic distance for these two phylogenies for subsequent analysis.

2.2 Species traits

Based on the idea that different traits are integrated at each scale of the niche, we gathered the information for competition and obtaining resources traits at the local scale (niche- α). At the regional scale (niche- β), we collected information for physiological and environmental tolerances; and at the geographical scale (niche- γ), we considered the biogeographic realm where the species occurs. (Table 1).

2.2.1 Niche- α

Following the idea that the niche- α occurs under the local competition scale for obtaining resources, we gathered the information for diet, activity, stratum, and body mass, these traits are recognized as relevant in the hypervolume of the mammalian niche (Safı et al. 2011). Additionally, we also collect information on population density, maximum longevity, weaning age.

Table 1. Ecological traits used to delineate the niches α , β , and γ .

Niche-α		
Trait	Levels	Source
Trophic guild	Herbivore, carnivore, omnivore	PanTheria (Jones et al. 2009)
Population	Population density, weaning age, and maximum longevity	PanTheria (Jones et al. 2009)
Diet (Proportion of food items)	Invertebrates, vertebrates (endotherms, ectotherms, fish, unknown), scavengers, and plant (fruit, seed, nectar, other)	EltonTraits Database (Wilman et al. 2014)
Activity	Diurnal, Crepuscular, Nocturnal	EltonTraits Database (Wilman et al. 2014)
Strata	ground, scansorial, aerial, arboreal and marine	EltonTraits Database (Wilman et al. 2014)
Niche-β		
Environmental Temperature	maximum and minimum (95%-5% quantiles)	WorldClim (Hijmans et al. 2005) and Marspec (Sbrocco and Barber 2013)
Fisiological Temperature	Low and Upper critical Temperature (LCT, UCT)	GlobalTherm (Bennet et al. 2018).
Altitude	Maximum (95% quantile)	--
Latitude	Tropical, temperate, and polar	--
Habitat	Forest, Savanna, Shrubland, Grassland, Wetlands, Rocky Areas, Caves & Subterranean Habitats, Desert, Marine Neritic, Marine Oceanic, Marine Intertidal, Marine Coastal, Artificial Terrestrial, Artificial Aquatic, Introduced Vegetation, Other and Unknown	IUCN (2018)
Niche-γ		
Wallace's biogeographical regions	Neartic, Neotropical, Palearctic, Ethiopian, Oriental, and Australian	Wallace (1876)
Holt's biogeographical regions	Afrotropical, Australian, Neartic, Neotropical, Madagascan, Oriental, Palearctic, Panamanian, Saharo-Arabian, and Sino-Japanese	Holt et al. (2013)
Marine biogeographical regions	Baltic sea, Black sea, NE and NW Atlantic and Mediterranean, Artic and North Pacific, Mid-tropical North Pacific, South-east Pacific, Mid-Atlantic, Pacific and Indian Oceans, North West Pacific and Southern Ocean	Castello et al. (2017)

2.2.2 Niche- β

We obtained environmental information for thermal tolerance, altitude, latitude, and habitat type to test the evolutive dynamic at this niche scale. We gathered the distribution map from the IUCN database for each of the species (IUCN, 2018). Then, we extracted thermal and altitudinal tolerances, utilizing RStudio V.3.6.1 (RStudio Team, 2016); by computing the maximum and minimum temperature (95% and 5% quantiles, respectively) and maximum altitude (95% quantile) from the geographical distributions of species. We obtained temperature and altitude information from the WorldClim database (www.worldclim.org; Hijmans et al. 2005), for terrestrial species, and marine temperature from the Marspec database (www.marspec.org; Sbrocco and Barber 2013); the altitude for marine species was set to the sea level (i.e., zero meters of elevation). Another β -trait was the latitude climatic zone at the species occur. We established three categories: Tropical (if 70% of the species range was within 24° North and South), temperate (if 70% of species range between 25° and 60 ° N or S) or polar (if 70% of the species range was above 60 °); the species could be considered in more than one category. Additionally, we also include at this scale the habitats explored by the species, gathered from the habitat classification by the IUCN (2017) (<https://www.iucnredlist.org/resources/habitat-classification-scheme>). Finally, we were interested in contrasting environmental thermal tolerance with physiological tolerance, so we used the information for 432 species that is provided in the GlobalTherm database (Bennet et al. 2018)

2.2.3 Niche- γ

For the broadest niche scale, we considered the biogeographic realms where species occur. If the geographic range of the specie comprised at least 30% within the biogeographic region, we considered it to belong to it, in such a way that a species could belong to more than one realm. For terrestrial species, we utilized the classical Wallace's classification, and the actual biogeographic proposal by Holt *et al.* (2011), for marine species we follow the proposal of Castelo et al. (2017).

2.3 Calculation of niche dynamic

We calculated a Phylogenetic Distance Matrix (PDist) for our 4,080 species of mammals, and for seventeen specific orders: Afrosoricida, Carnivora, Cetartiodactyla, Chiroptera, Cingulata, Dasyuromorphia, Didelphimorphia, Diprotodontia, Eulipotyphla, Lagomorpha, Macroscelidea, Peramelemorphia, Perissodactyla, Pilosa, Primata, Rodentia and, Scandentia. We calculated a Euclidean distance matrix for each niche scale using the traits within scales (FDist- α , FDist- β), for niche gamma, two matrices were estimated, one considering Wallace's realms + Marine realms (FDist- W) and another using Holt's realms + Marine realms (FDist- H). Additionally, we calculated PDist and FDist matrices for the 432 species in the GlobalTherm database, replacing in the FDist- β matrix the environmental thermal information for the physiological tolerances, and calculating for all niche scales. Because we have mixed categorical and continuous data, we estimated the Gower dissimilarity distance using the Gowdis function from the FD package (Laliberté, Legendre and Shipley, 2014) on R (R Core team) for all our variables.

Using our distance matrices, we followed Cadotte et al. (2013) framework, which permits to integrate functional and phylogenetic information in a functional-phylogenetic distance matrix (FPDis) as follow:

$$FPDist = [aPDist^p + (1 - a) FDist^p]^{1/p}.$$

where p works analogously to Euclidean distance and the parameter a tune the weight between a pure functional distance ($a=0$; overdispersion community) or pure phylogenetic distance ($a=1$; clustered community).

Because the traits exhibit a different evolutionary rate and the phylogeny may be more or less informative depending on the spatial scale considered, integrating both information allows maximizing the analysis of each of the niche scales and how is their evolutionary dynamics. (see Cadotte et al. 2013 and Gianuca et al. 2017 for details).

2.4 Phylogenetic signal

Additionally, we tested the strength of the phylogenetic signal in the traits in each niche, comparing the K-value (Blomberg et al. 2003) in each niche, with the information obtained from the FPDist matrices. In the same way that we did with the FPDist matrices, we initially measured the phylogenetic signal for all the mammals and later for the GlobalTherm database subset, and for the same seventeen orders. We used the function `phylosig` from the `phytools` package (Revell, 2017) on R for this purpose.

3. Results

3.1 *Niche- α*

The traits included analyzing the alpha niche for mammals explained 55% of the variation, tending to convergence by a higher informative FDist (Fig. 1). By considering only the subset of species from the GlobalTherm database, the convergent pattern is maintained, but an increase in phylogenetic influence is noticeable. Likewise, most of the orders analyzed individually present a similar pattern, with more information from FDist. Exceptions to this general pattern are Cetartiodactyla and Peramelemorphia, which showed a greater influence by the PDist, tending to divergence. Additionally, Pilosa exhibited conservatism for showing an intermediate tendency between FDist and PDist. In contrast with our PFDist matrices, we found a different tendency in the phylogenetic signal indicated by Blomberg's K (Blomberg, Garland and Ives 2003). We found the highest K values for niche- α , both, for all mammals in general and across orders, indicating that ecological traits for interspecific interactions have a higher phylogenetic signal. (Fig. 2). Among the traits- α for the whole group, three exhibited the highest signal: endothermic vertebrate diet ($K=1.2138$, $p=0.001$), nocturnal activity ($K=1.0253$, $p=0.001$), and scansorial stratum ($K=0.8603$, $p=0.001$). Individually, the orders that exhibited the highest phylogenetic signal in their niche- α were: Didelphimorphia, Diprotodontia, Eulipotyphla, Lagomorpha, Macroscelidea, Peramelemorphia, Perissodactyla, Pilosa and Scadentia.

3.2 Niche- β

Contrary to the pattern exhibited for the niche- α , the niche- β showed a greater influence on the PDist for all mammals, following a divergent pattern. This same trend is observed in the subset of data from the GlobalTherm database. Regarding the orders: Cetartiodactyla, Dasyuromorphia, Eulipotyphla, Lagomorpha, and Peramelemorphia followed the general pattern exhibited by all the mammals, with a higher phylogenetic correlation. On the other hand, orders that exhibited a higher correlation with FDist and therefore a convergent pattern were: Afrosoricida, Carnivora, Chiroptera, Cingulata, Didelphimorphia, Perissodactyla, Pilosa, Primata, Rodentia and Scandentia. Finally, Diprotodontia, Macroscelidea did not exhibit predominance by PDist or FDist, tending to conserve their traits- β . Conversely to niche- α , niche- β showed the lowest values in all cases, for the whole mammals' group and all the orders.

3.3 Niche- γ

The two combinations of biogeographic classifications used for the niche- γ (FPDist-W and FPDist-H) exhibited in both cases a divergent pattern (PDist > FDist). Similarly, the GlobalTherm database subset followed the same pattern, as did as the Carnivora, Cetartiodactyla, Eulipotyphla, Lagomorpha, Primates, and Rodentia orders. Afrosoricida, Cingulata, Dasyuromorphia, Didelphimorphia, Diprotodontia, Macroscelidea, Pilosa, Scandentia, on the other hand, had an opposite response, exhibiting a convergent pattern (FDist > PDist). Three orders exhibited a different behavior; Chiroptera showed different pattern in both gammas, tending to a conserved gamma_{WM} and exhibiting a more convergent gamma_{HM}. Peramelemorphia was convergent in gamma_{WM}, while in gamma_{HM} the pattern tended to be more conserved. Finally, the Perissodactyla order did not predominate for FDist or PDist, exhibiting a conservative niche gamma in both cases. Our phylogenetic signal test at this niche showed a variable behavior, displaying in a general way moderate K values between alfa and beta. Among the traits- γ , only the West Pacific realm exhibited a significance signal (K=1.1854, p= 0.001). Across the orders, Afrosoricida, Diprotodontia, Macroscelidea, Peramelemorphia and Scandentia exhibited high phylogenetic signal in their niche- γ .

4. Discussion

Recently, functional traits and phylogenetic information are used to understand community structure and assemblage rules. Most of the existing studies assessing niche evolution focus on one scale of the hypervolume of niche, ignoring the rest. Here, we gathered trait information and classified into the different scales of niche in order to capture the most possible portion of niche to enhance our macroevolutionary understanding for extant worldwide mammals. We addressed holistically the different levels (α , β and γ) in the hypervolume of niche, contrasting phylogenetic versus functional data for extant mammals. We started out the idea of a nested structure of α , β , and γ niche levels and expected a gradually degree of niche conservatism from niche α as the most labile, to the niche γ as the most conservative just as Silvertwon et al. (2006) proposed. Notwithstanding, our findings are not fitting with these ideas. The worldwide mammals' communities are phylogenetically structure by their biotic interactions more than by environmental variables. Even the phylogenetic signal analysis showed low values, with some exceptions.

It is recognized that phylogenetic community structure is scale-dependent, hence it is expected that phylogenetic composition changes following this rule, the greater the scale, the more clustered the phylogeny composition (Cavender-Bares et al. 2009). This is reflected in the output for niche alpha in our FPDist test that was the most phylogenetically repulsed maybe because includes the biotic interaction traits. This over-dispersed tendency was exhibit not only by the output slope for all species but also across the orders tested. Even when some of the characters included in the niche alpha are reported as highly labile, such as dietary niches (i.e. Price et al. 2012 and Cantalapiedra et al. 2013). Others, such as nocturnal activity or scansorial strata exhibited high K values, both traits are associated with the origin of mammals (Gerkema et al. 2013, Maor et al. 2017) and the Eutherians (Ji et al. 2002, Luo et al. 2011) respectively. Even when habitat structure is widely recognized as a key component in niche diversification (Stein et al. 2014), to our knowledge there is no any study assessing strata as a part of the niche hypervolume for mammals. For this study, scansorial strata exhibit the highest K-value(K-values not shown for traits separated), which attracts attention, as it is a characteristic identified since the origin of the Eutherians (Ji et al. 2002, Luo et al. 2011) which could indicate high conservatism for this trait along the mammal's evolution.

About β niche, our climatic variables did not exhibit significant values both, in the phylo-functional test and for phylogenetic signal. However, even with this low K-values, our outputs are in accordance with those found by Araujo et al. (2013) and Khaliq et al. (2015), where is reported higher phylogenetic conservatism for the upper limit of thermic niche, as well as here we found. However, Khaliq et al (2015) also remark the previous mentioned output, only when they considered a subset of tropical species, conversely at a global scale they report no phylogenetic influence, as we find in our phylo-functional test. Which could explain why the climatic variables do not exhibit high phylogenetic influence. Latitude exhibit higher phylogenetic signal for tropical species, this effect also widely recognized in mammals (Cooper, Freckleton and Jetz 2011), but as the other environmental variables, is highly influenced by functionality. Finally, for our environmental variables, the influence of altitude on mammals has been mainly addressed from the spatial point of view, permitting resource partition (i.e. Bocheres et al. 2011; Symes et al. 2013) on the one hand, or analyzing altitudinal diversity gradients on the other (i.e. Brown 2001; McCain 2005). Even when elevational niche conservatism has been reported in bats and rodents (Cisneros et al. 2014 and Dreiss et al. 2015 respectively) and other groups non-mammal groups (i.e. Kozak and Wiens 2010; Machac et al. 2010) in our study, altitude did not exhibit phylogenetic signal, however, it was the second highest K value after nocturnal activity. Safi et al. (2011) recognized temperature and altitude as relevant variables for species richness in mammals, but they also remark a lower effect on Phylo-fuctional diversity which could explain our results.

About the niche γ , is recognize a spatial effect on niche conservatism (i. e. Freckleton and Jetz, 2009; Cooper, Freckleton, and Jetz, 2011) due to species suffer dispersal constrains and tend to retain their center of origin (Cavender-Bares et al. 2009, Tamma et al. 2016). The pattern described by our FPDist outputs, exhibit a high phylogenetic influence when all mammal species are considered. Buckley et al. (2010) suggest that the actual distribution pattern for mammals and the environmental constraints were established in an early mammal radiation 80 Mya, with few distribution shifts since then. Nevertheless, even when is suggested a “within realm limited faunas”, the tendency of assemblages been phylogenetically clustered within a biogeographical realm (see Cantalapiedra et al. 2014), the outputs across the different orders showed both, under-dispersed (i. e. Lagomorpha, Rodentia, Eulipolyphla) and over-dispersed (i.e. Didelphimorphia, Afrosoricida, and Pilosa) behavior. Even the phylogenetic signal

showed for this niche low K- values, with some exceptions (i. e. Peramelemorphia). The different outputs displayed FPD1st and Blomberg's K could be associated with the specific phylogenetic history of each group. Cantalapiedra et al. (2014) highlight some factors that can influence on the expected under-dispersion that within the realm pattern should display, such as strong environmental pressure or the number of basal species and the phylogenetic distance among them.

Peixoto et al. (2017) report influence by taxonomic level on niche conservatism results, since when analyzing from species level, they did not detect phylogenetic signal. However, when they performed analyzes at family and order level phylogenetic signal was detected. We may have also some effect associated with the taxonomic level, however, differences observed between the all species-level test and the findings for the different orders exhibit differences that should be analyzed under the particular evolutionary history of each one.

As we mentioned in the introduction, most of the studies where niche conservatism is analyzed focus only on one niche level of the hypervolume, regardless of other components of niche. In this study we have attempted to encompass as much as possible the other components from the different levels in the niche at the species level. We have then assessed the relationship of each of niches with respect to each other: alpha, beta and gamma. A better understanding of the species niche in a holistic way of its components helps us to explain better the biodiversity of distribution and the co-occurrence patterns which determine the assemblage in the communities.

5. Literature

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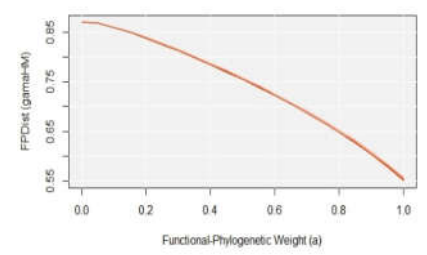
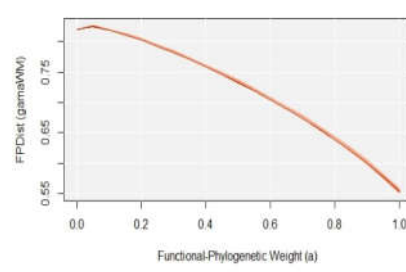
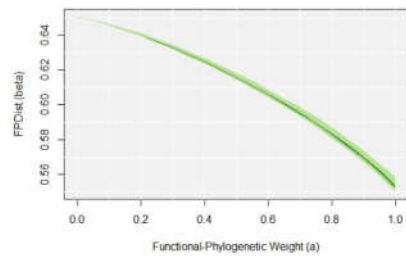
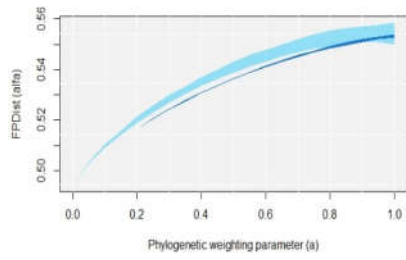
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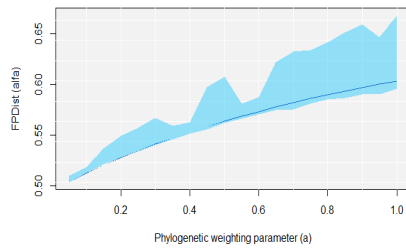
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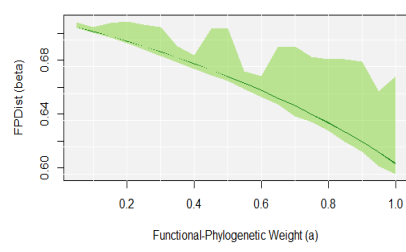
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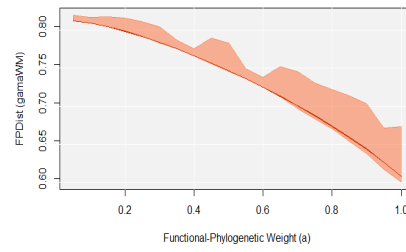
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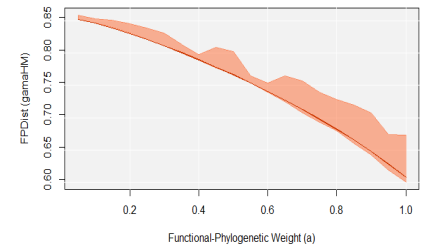
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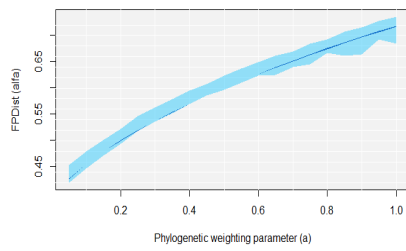
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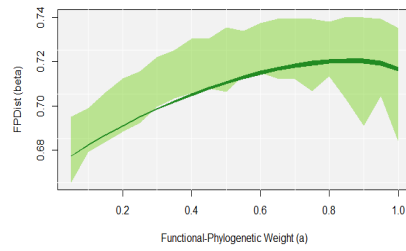
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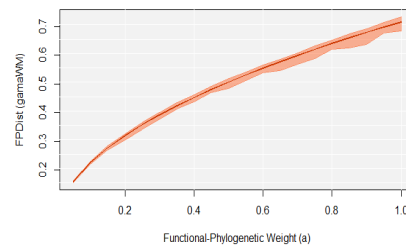
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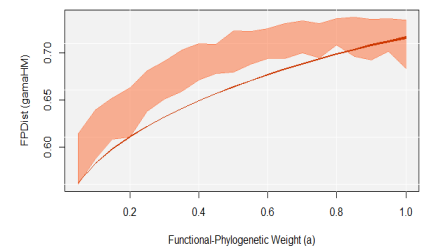
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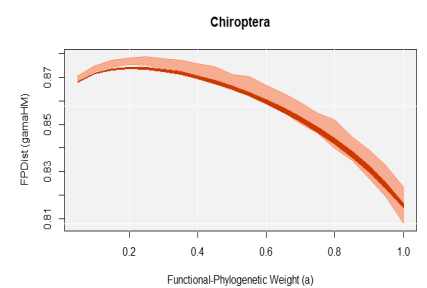
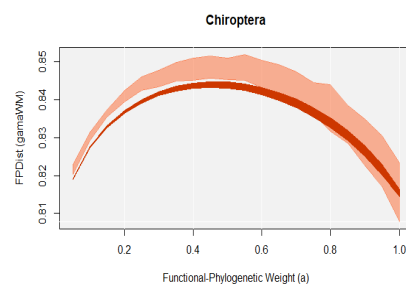
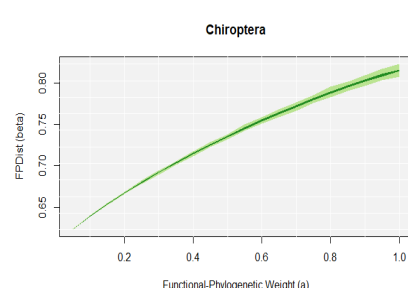
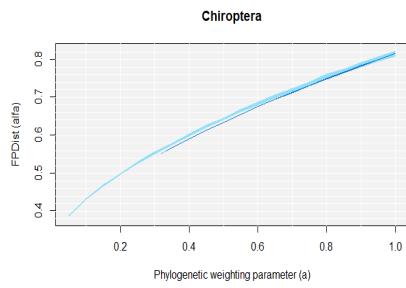
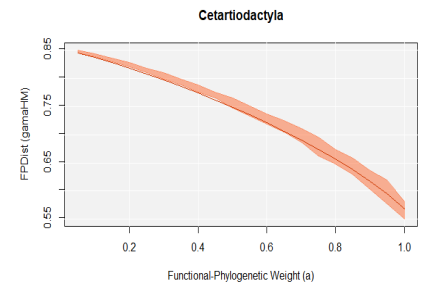
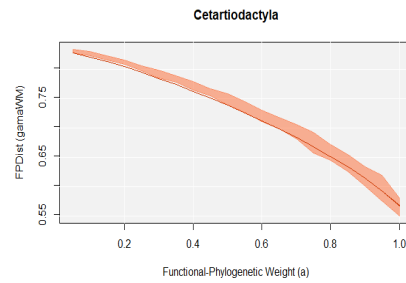
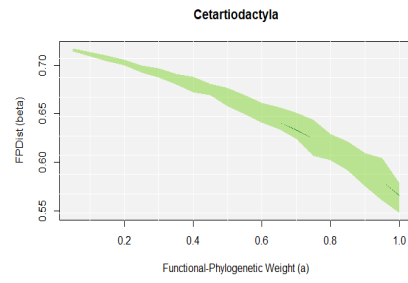
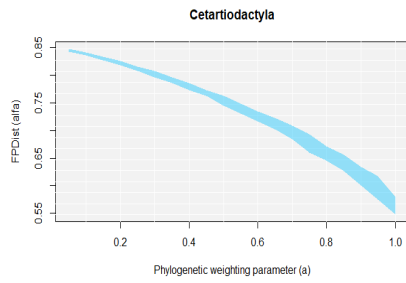
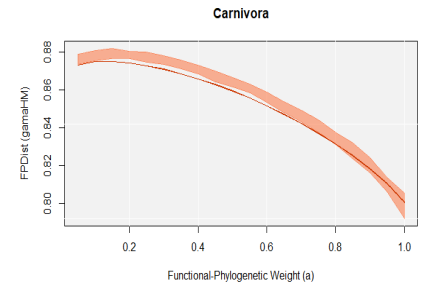
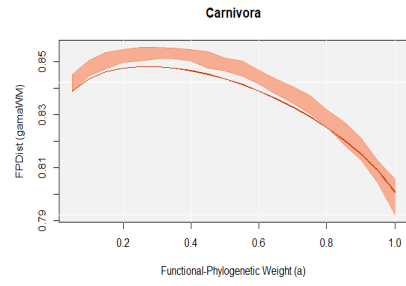
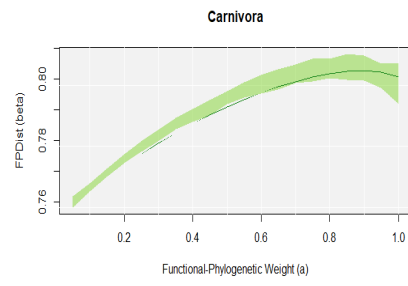
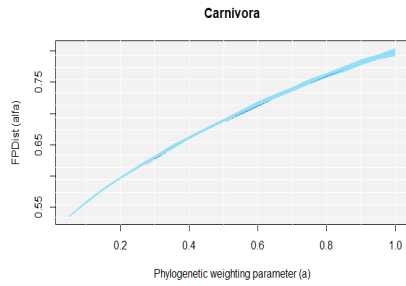


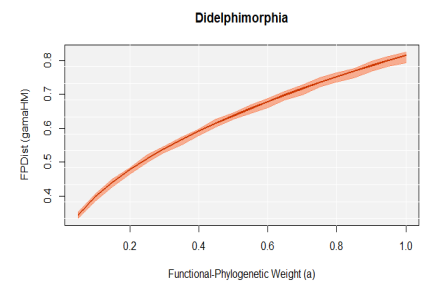
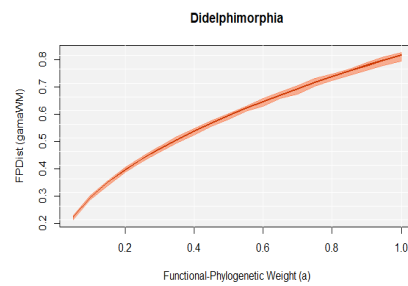
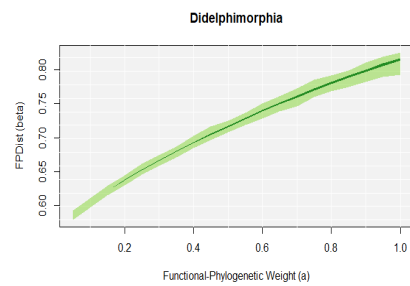
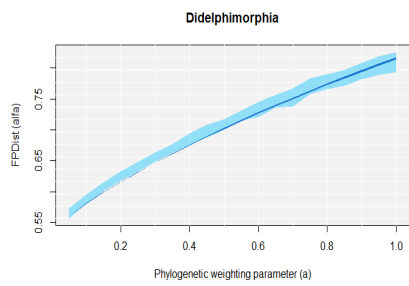
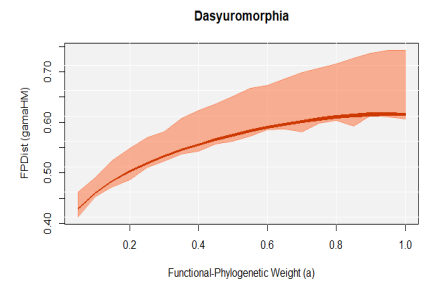
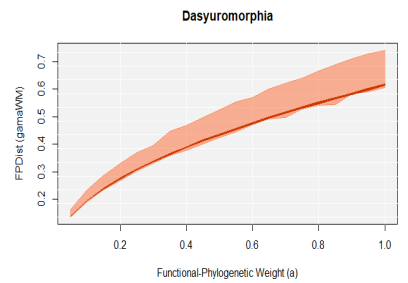
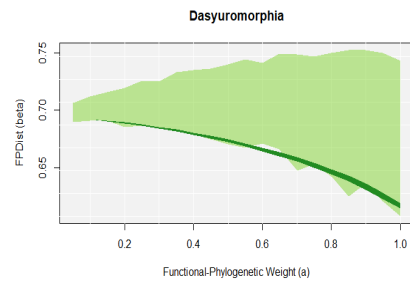
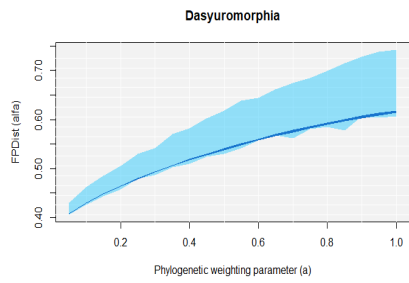
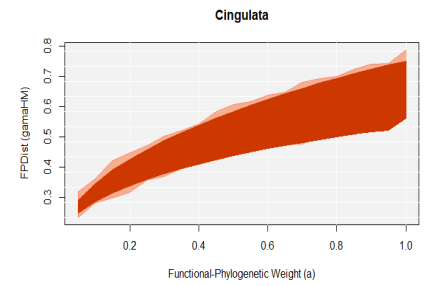
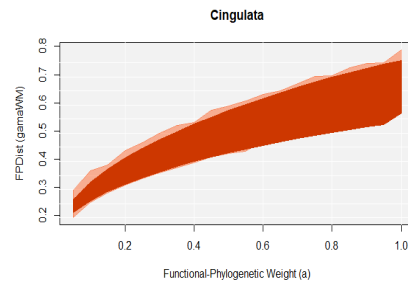
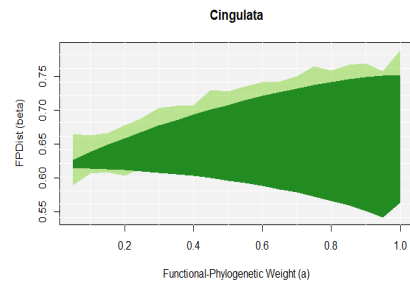
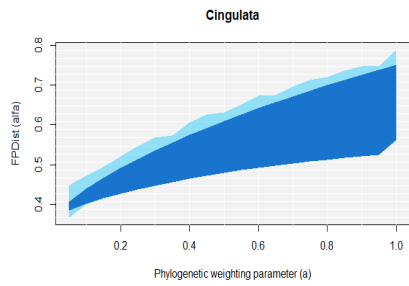
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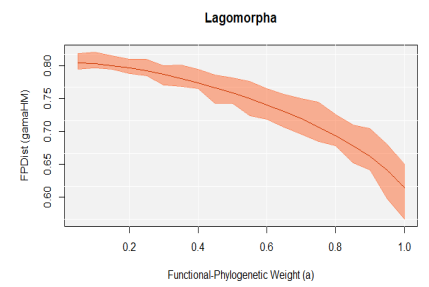
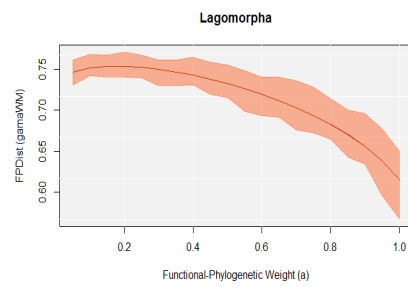
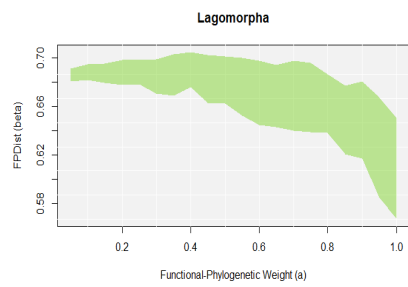
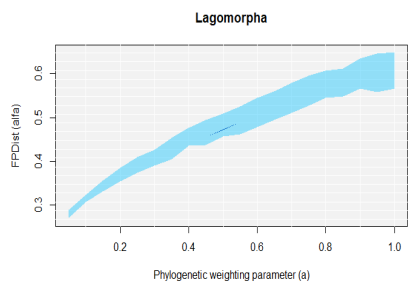
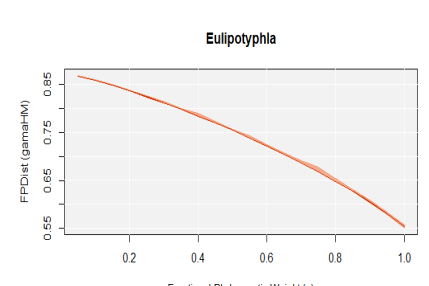
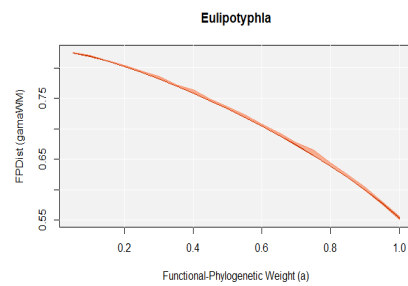
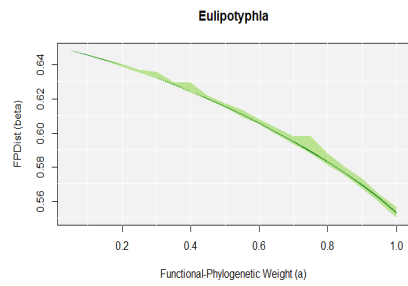
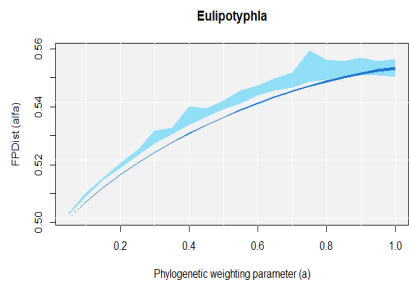
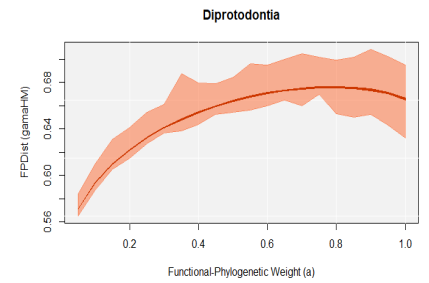
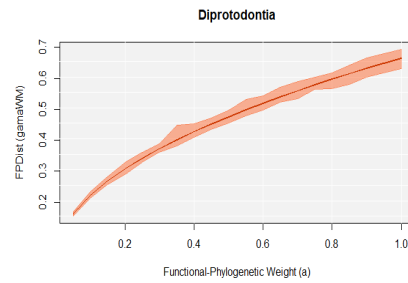
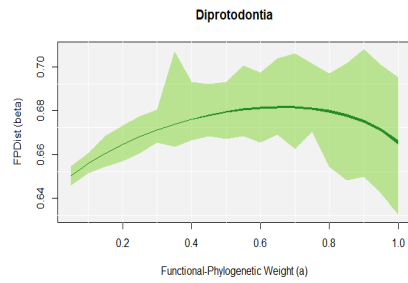
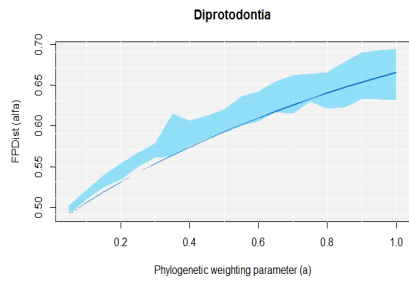


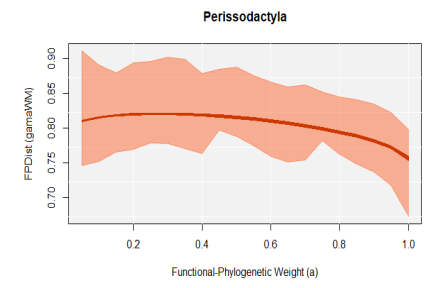
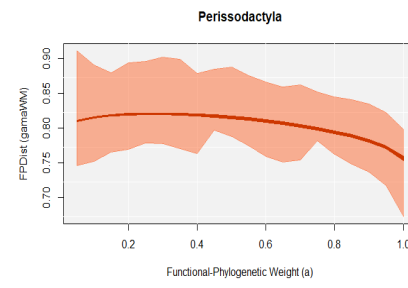
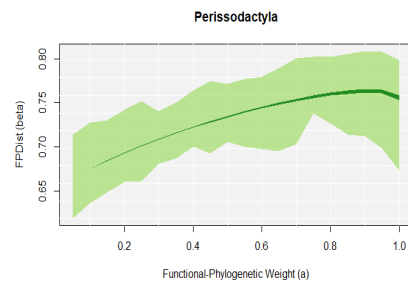
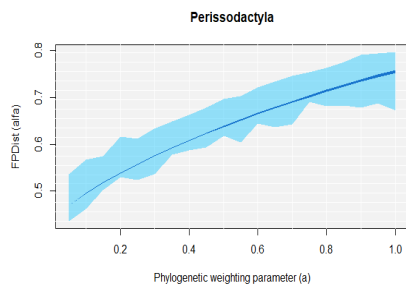
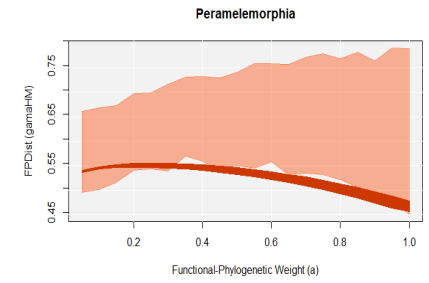
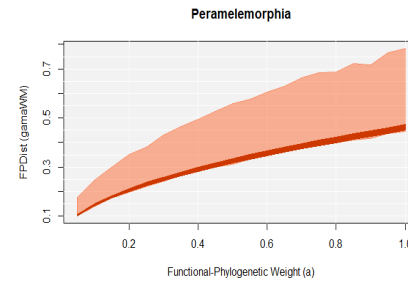
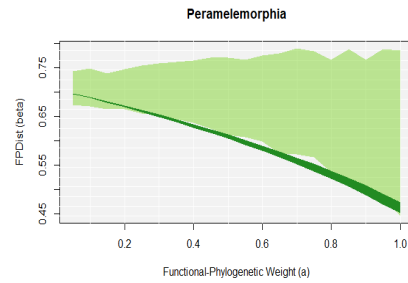
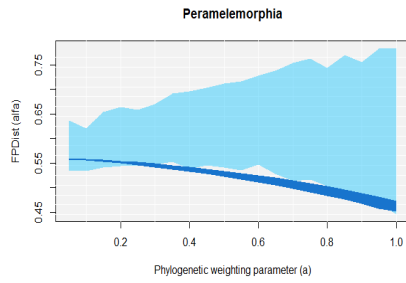
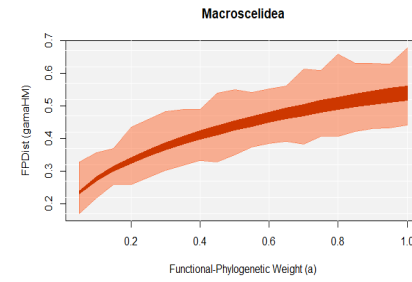
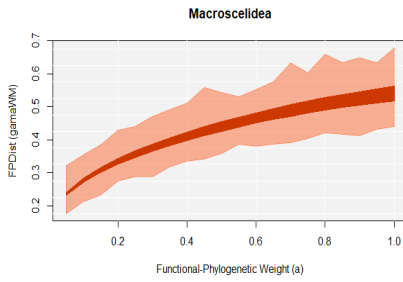
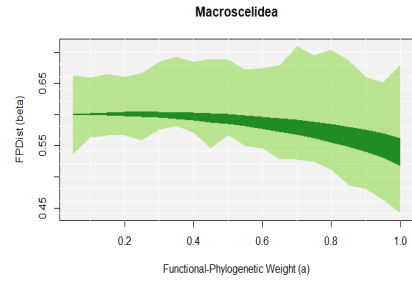
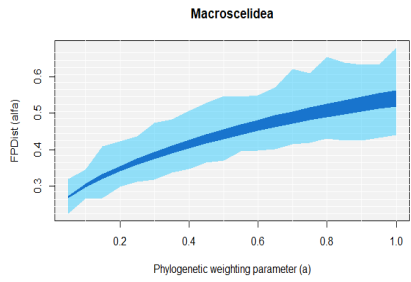
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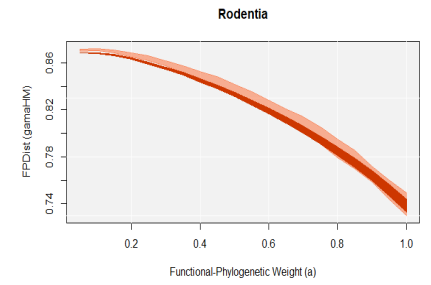
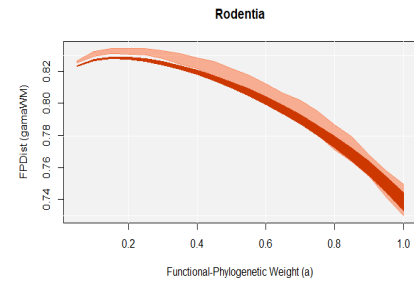
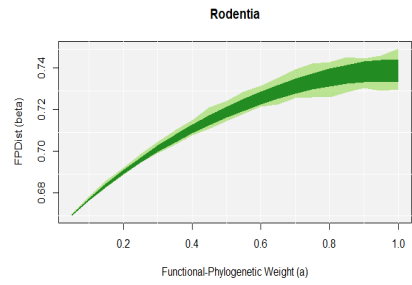
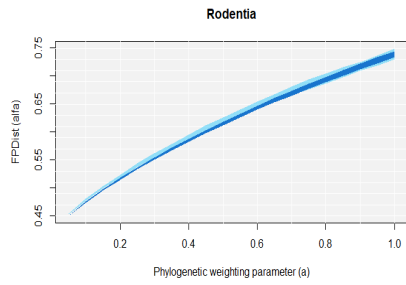
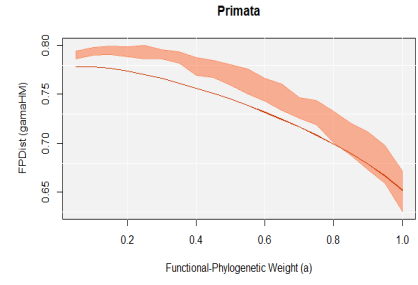
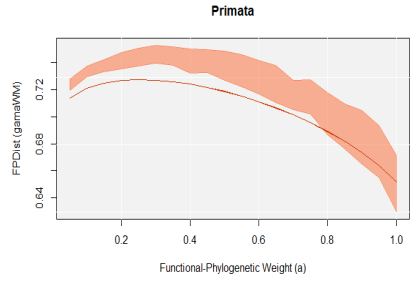
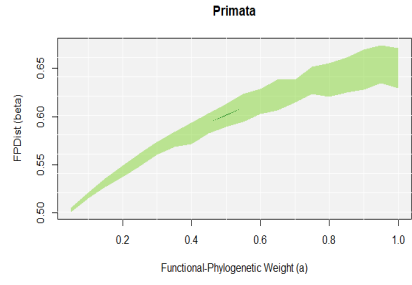
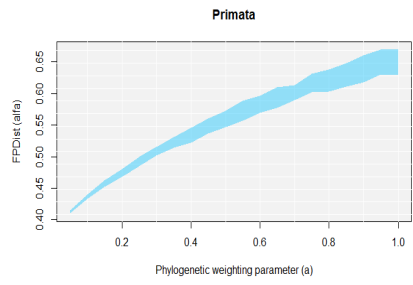
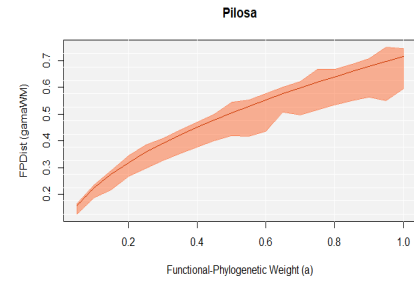
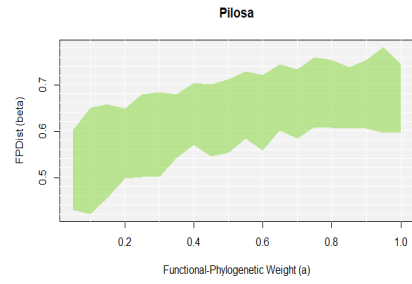
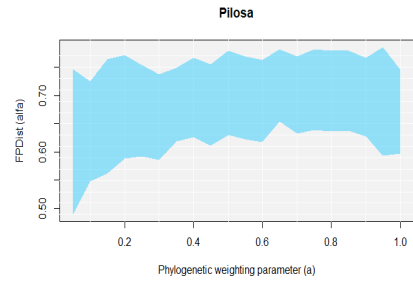












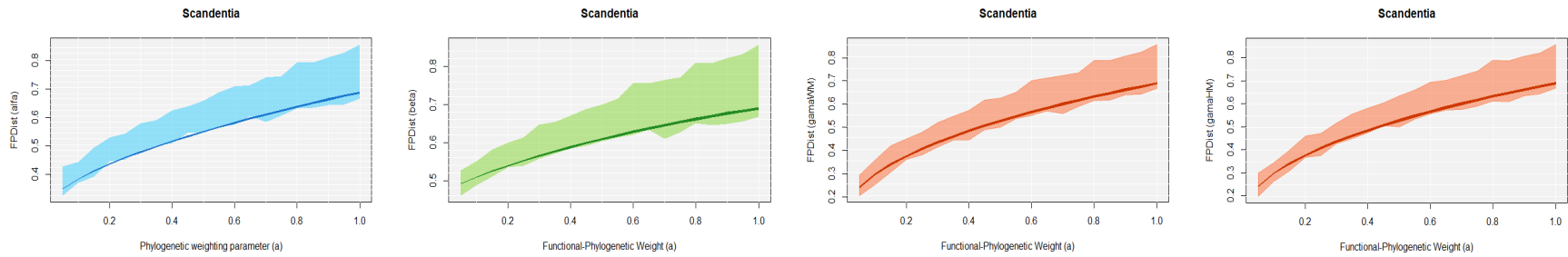
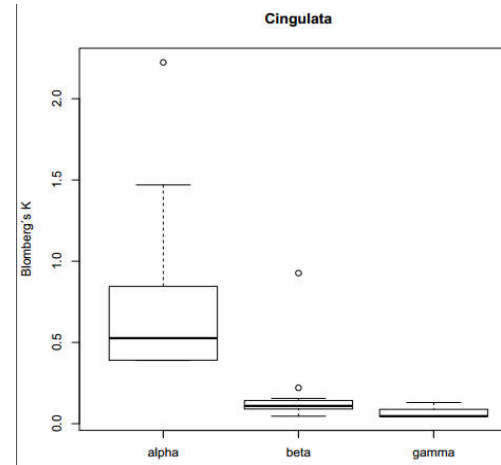
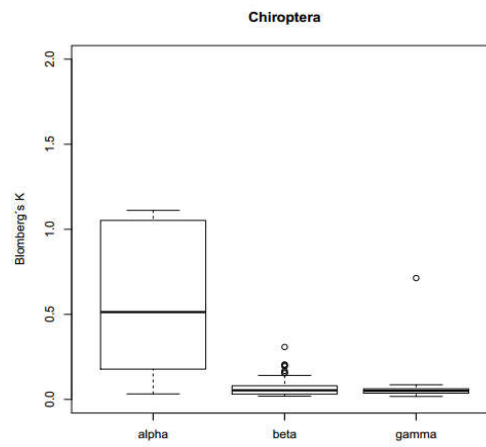
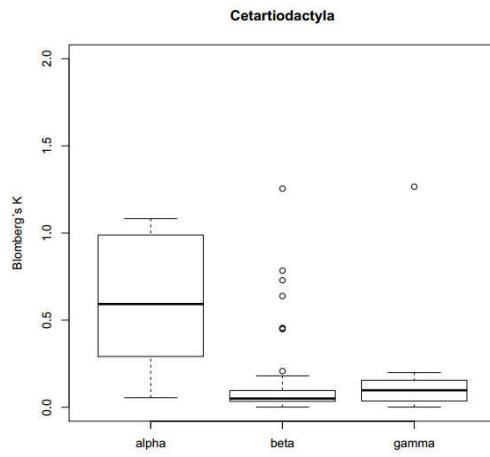
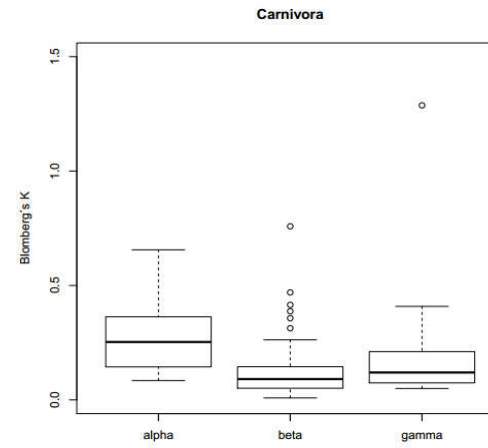
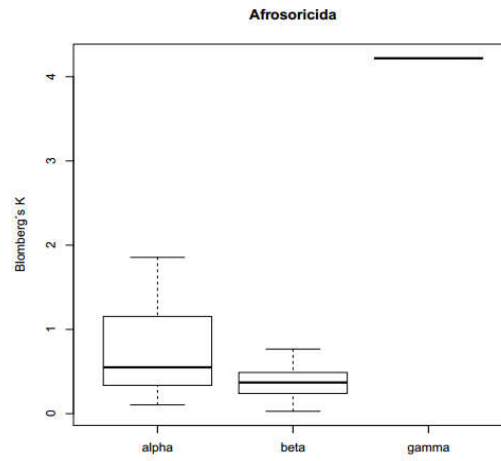
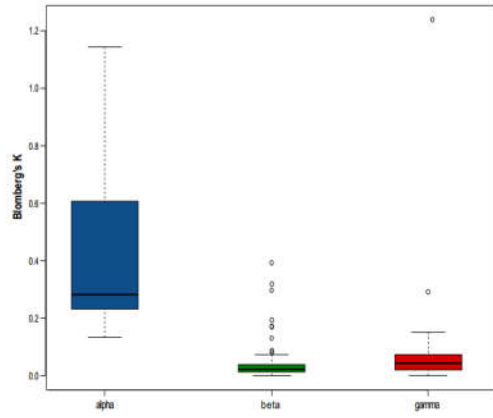
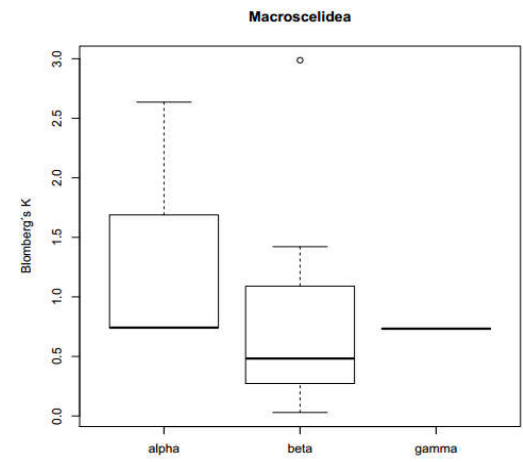
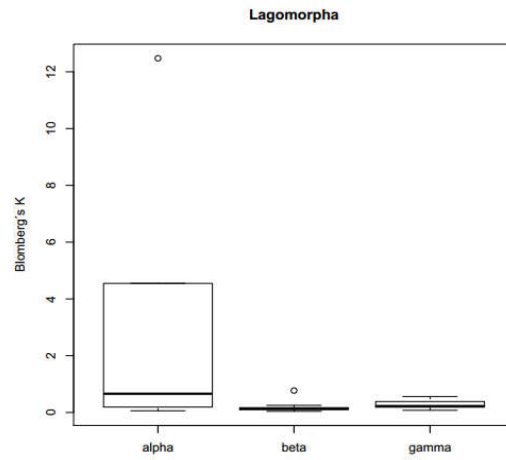
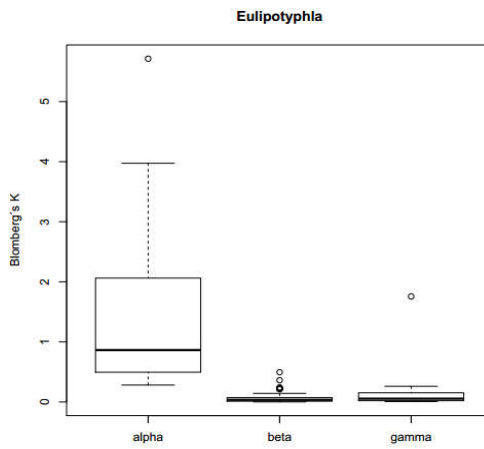
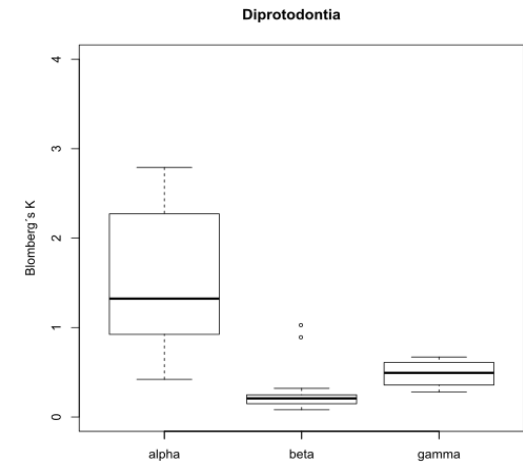
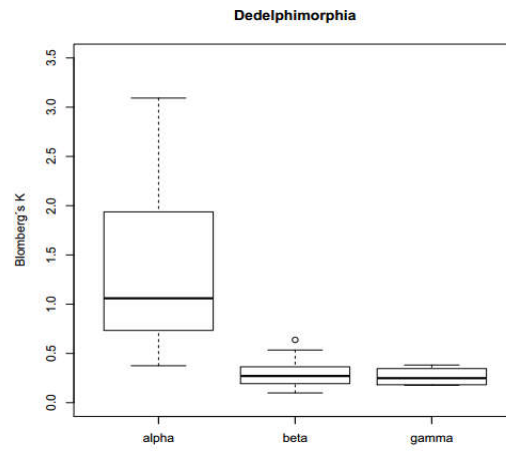
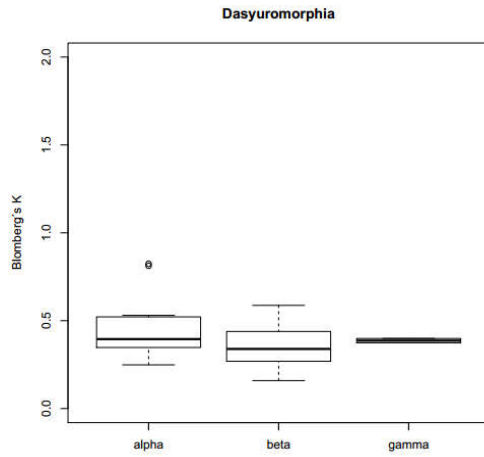


Figure.1 Mean functional phylogenetic distances contrasted to a-value parameter for niches α (blue), β (green), and γ (red: WM, follow Wallace’s classical biogeographic realms; HM follow Holt et al (2010) biogeographic realms) for 4480 extant mammal species, the TUC/TLC plot represent a subset of 432 species with physiological thermo neutral zone information in literature, and for 16 orders. Shaded regions represented the null distribution (5-95%). Solid line represented observed pairwise distances.





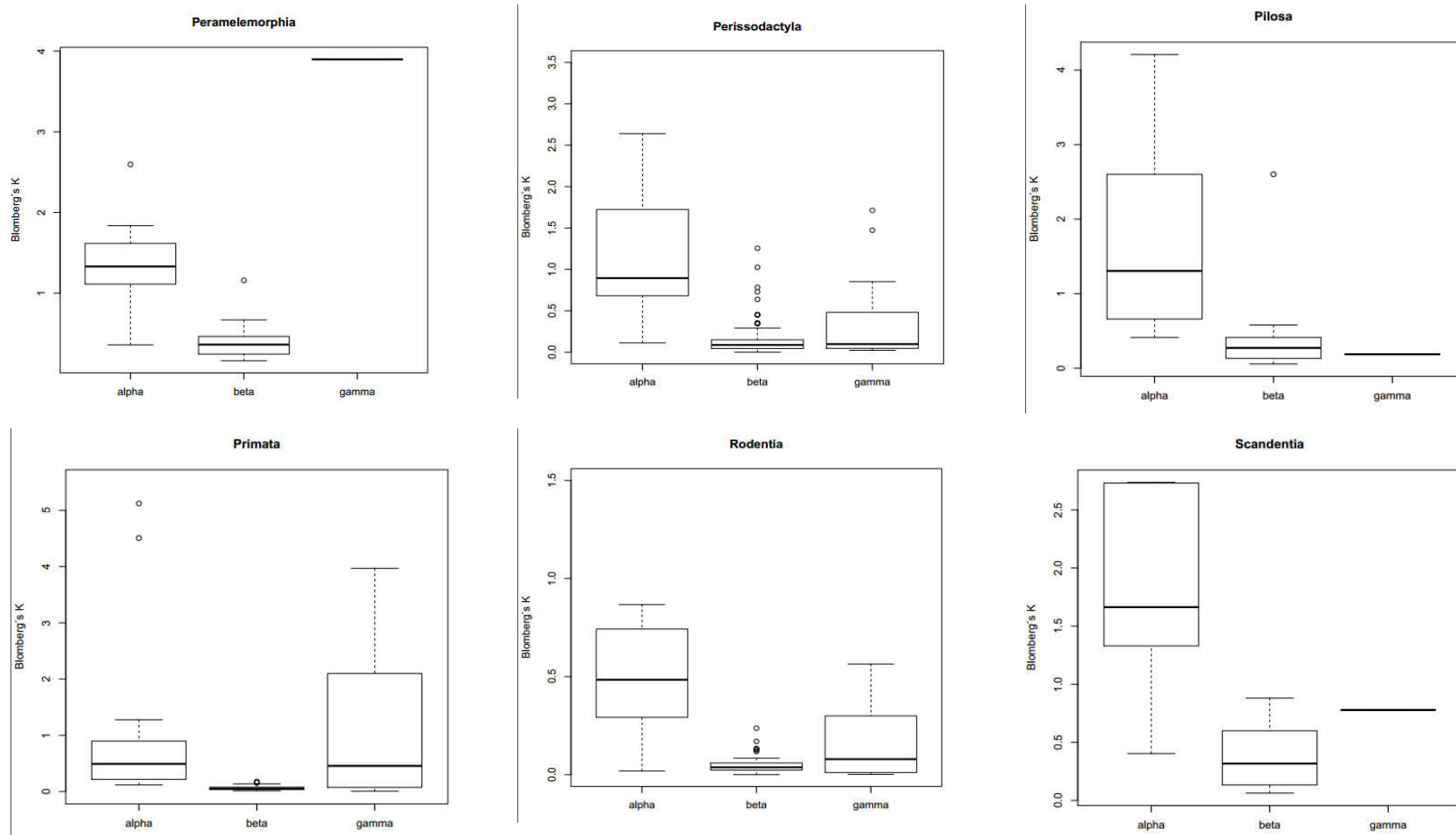


Figure. 2 Distribution of Blomberg's K statistical for niches α , β , and γ in extant mammals. Blomberg's K were calculated for ecological traits (diet, strata, activity) in alpha, environmental variables (elevation, maximum and minimum temperature, habitat type) in niche beta, and biogeographical realms where species occur in niche gamma.

CAPÍTULO 2

Spatial patterns of the hierarchical niche evolution in mammals

Victor Hugo Mendoza Rodriguez^{1,2}, Frederico Valtuille Faleiro², Marcos Carlucci³, Matheus S. Lima-Ribeiro^{2*}

¹Programa de Pós-graduação em Ecologia & Evolução, Universidade Federal de Goiás, Goiânia, Brazil.

²Macroecology Lab., Universidade Federal de Jataí, Jataí, Brazil.

³Programa de Pós-Graduação em Ecologia e Conservação, Universidade Federal do Paraná, Curitiba-PR, Brazil.

*Author for correspondence: mslima.ribeiro@gmail.com

Abstract

Niche hypervolume, the conditions where a species can establish and persist through the time, is hierarchically structured and determined by biotic interactions (α niche), environmental conditions (β niche) and the biogeographical realm where the species occur (γ niche). By analyzing the spatial pattern of niche evolution across 4480 species of extant mammals worldwide, the communities presented conserved niches (regardless if α , β or γ niche) at lower latitudes and throughout oceans. At high latitudes, the α and β niches showed convergent and divergent evolution, respectively. The α niche evolve under historical contingency, especially at harsh temperate and polar environments, resulting in communities with similar functional traits regardless of the species evolutionary history. The β niche present tropical conservatism and only rare descendants that diverge from its tropical relatives are able to colonize high latitudes. The γ niche is strongly spatially structured across landmasses, with the southern continents from Gondwana showing stronger niche convergences than the northern Laurasia continents. The spatial pattern of γ niche indicate that communities are mainly composed by species restrict to specific biogeographical realms, and reflect that mammals dispersed more easily across the Laurasia (less convergent) than across the Gondwana. Our results demonstrate the contrast of the geographic pattern among each of the hypervolume scales that compound the species niche.

Key-words: biotic interactions (α niche), environmental tolerances (β niche), geographical distribution (γ niche), niche conservatism, convergence or divergence.

1) Introduction

The concept of ecological niche has been guiding ecological research for nearly 100 years (Grinnell, 1917; Elton, 1927; Hutchinson, 1957; Chase & Leibold, 2003). In the last decades, the ecological niche conservatism has been hotly debated in the literature, with contrasting evidence regarding its evolutionary rates (Losos 2008; Peterson 2011). Considering the hierarchical evolutionary structure of the niche hypervolume as proposed by Silvertown *et al.* (2006), its most labile level, the α niche, encompasses the biotic forces acting at a local scale and represents the functional (phenotypic and behavioral) dimensions of the niche hypervolume. The β niche represents the regional processes where the abiotic forces act regulating the survival and reproductive rates of organisms through its environmental tolerances and would be more conserved across phylogenies. The interaction of all processes at α and β niches would establish the configuration for the distribution pattern observed across the biogeographic realms nested at γ niche, the most phylogenetically conserved dimensions.

Pulliam (2000) highlights in the relationship between the concept of niche and the distribution of species that there is not only a response to environmental variation, but that species also exerts changes in their environment, individually and by interacting among them. Keeping the previous in mind is that we can agree when Wiens (2011) states that niche concept is the best convergence point integrating ecological and biogeographic processes. The hierarchical structure for niche hypervolume proposed by Silvertown *et al.* (2006) represents this convergence given that the different processes which determining the community assemblage would be settled across spatial and temporal scales (see Wiens 2008).

Understand the community assembling pattern derived from the geographic distribution of species is considered an axial question for community ecology, biogeography, and macroecology (Pavoine and Bonsall, 2011; Hardy *et al.* 2012). The colonization and long-term interaction established by a pool of species across space are molded over time by evolutionary history. The slow and ancient process of continental drift, for example, isolates ancestors within biogeographic regions (γ niche), which are shared (conserved) by all descendants for long time due to dispersal limitations. If we consider the effect of the environmental conditions, it is expected that related species

show similar environmental tolerances (β niches) inherited from common ancestors, which enable them to co-occur in a given region into biogeographical realms (phylogenetic clustering across communities). However, ecological similarity through functional traits increases the possibility of competitive exclusion, making rarely possible that closely related and functionally similar species co-occur at the same place. Conversely, the filters by biotic forces would result in phylogenetic over-dispersed communities (Gerhold et al 2015).

The interaction among the biogeographic pool of species (γ niche), abiotic regional forces (β niche) and biotic local restrictions (α niche) drive the community assemblage and generate a patchy pattern of species distribution across space (Cheson, 2000). Thus, it is expected that evolutionary dynamic of ecological niche varies across geographic space (Mazel et al. 2017). Notwithstanding, species distribution and ecological niche conservatism is mostly defined as a function of environmental conditions only (the β niche; see a review of evidence in Peterson 2011) and the evolutionary dynamics of other niche dimensions, such as those that involve biotic interactions, remain largely unexplored or are explored in isolation. (see an example in Mazel et al. 2017 with α niche). Here we evaluate the spatial patterns of the hierarchical evolutionary dynamics in α , β and γ niches across 4840 mammals at global scale. We expect that mammals' communities exhibit species with more conserved niches (regardless if α , β or γ niche) at lower latitudes and throughout oceans species. Conversely, high latitudes species should exhibit more convergent niches.

2) Methods

To evaluate the evolutionary dynamic of ecological niche across geographic space, we gathered the geographical distribution of 4840 extant mammals from the IUCN database (IUCN, 2017), obtained the phylogenetic trees from Kuhn et al. (2011) and sampled specific traits that delineate the Silvertown's et al. (2006) α , β , and γ niches.

To access the α niche, we gathered foraging attributes from the PanTheria database (Jones et al 2009) and the EltonTraits database (Wilman et al. 2014) that are relevant to delineate biotic interactions into communities, such as trophic level, diet,

activity, strata, and population parameters (see details in Table 1). For β niche, we gathered the type of habitat that species explore according to the habitat classification of the IUCN (<https://www.iucnredlist.org/resources/habitat-classification-scheme>), as well as set the latitudinal climatic zone that each species occurs (tropical: $<30^\circ$ of latitude, temperate: between 30° and 60° , and polar: $>60^\circ$), and estimated its thermal and altitudinal tolerances (Table 1). We considered a species to occupy a given climatic zone if its geographical range covered at least 10% of that latitudinal band. The thermal and altitudinal tolerances were obtained by computing the maximum and minimum temperature (95% and 5% quantiles, respectively) and maximum altitude (95% quantile) from the geographical distributions of species. The temperature and elevation layers for continents were obtained from WorldClim database (www.worldclim.org; Hijmans et al. 2005), whereas the layers of marine temperature were obtained from the Marspec database (www.marspec.org; Sbrocco and Barber 2013); the altitude for every marine species was set to the sea level (i.e., zero meters of elevation). Finally, we set the biogeographic realms where species occur to delimitate the γ niche (Table 1). We considered the Wallace's biogeographical regions for continental mammals (Wallace 1876), and the marine biogeographical realms proposed by Costello et al. (2017) for marine mammals. We considered a species to occur in all biogeographical realms overlapping at least 10% of its geographical range.

Table 1. Ecological traits used to delineate the α , β , and γ niches.

Niche	Trait	Levels	Source
Alfa	Trophic	Herbivore, carnivore, and omnivore	PanTheria database
	Population	Population density, weaning age, and maximum longevity	Jones et al. 2009
	Diet	Proportion of food items in the diet: invertebrates, vertebrates (endotherms, ectotherms, fish, unknown), scavengers, and plant (fruit, seed, nectar, other)	EltonTraits database
	Activity	Nocturnal, diurnal, and crepuscular	(Wilman et al. 2014)
	Strata	Arboreal, ground, aerial, subsoil, and aquatic	
Beta	Temperature	maximum and minimum (95%-5% quantiles)	WorldClim and Marspec databases
	Altitude	Maximum (95% quantile)	
	Latitude	Tropical, temperate, and polar	-
	Habitat	Forest, Savanna, Shrubland, Grassland, Wetlands, Rocky Areas, Caves & Subterranean Habitats, Desert, Marine Neritic, Marine Oceanic, Marine Intertidal, Marine Coastal, Artificial Terrestrial, Artificial Aquatic, Introduced Vegetation, Other and Unknown	IUCN (2017)
Gamma	Wallace's biogeographical regions	Nearctic, Neotropical, Palearctic, Ethiopian, Oriental, and Australian	Wallace (1876)
	Marine biogeographical regions	Baltic sea, Black sea, NE and NW Atlantic and Mediterranean, Arctic and North Pacific, Mid-tropical North Pacific, South-east Pacific, Mid-Atlantic, Pacific and Indian Oceans, North West Pacific and Southern Ocean	Castello et al. (2017)

Next, we mapped the species occurrence in a grid of cells with spatial resolution of 2° lat/long covering the entire Earth's surface, resulting in 16,200 pixels. Ecological communities were delimited by including all species occurring in each of these pixels. The evolutionary dynamics of α , β , and γ niches were accessed for every community throughout the grid of cells by applying the approach proposed in Cadotte et al. (2013). We first estimated the functional-phylogenetic distance (FPDist) among all species pair, as follows:

$$FPDist = (aPDist^p + (1-a)FDist^p)^{1/p}$$

where PDist and FDist represent, respectively, the distances between species in the phylogenetic and trait spaces, “*a*” is the weighting parameter controlling the independent contribution of Pdist and Fdist to FPDist, and “*p*” combines them non-linearly (see details in Cadotte et al. 2013). We computed FPDist considering the *a*-weights ranging from zero (only FDist contributes) to one (only PDist contributes) at every 0.05 units, and obtained the Euclidean distance (*p*=2) from the combined functional and phylogenetic distances. Because the trait space delineating the α , β , and γ niches are composed by both continuous and categorical traits, we used the Gower dissimilarity coefficient from “*gowdis*” function {FD} (Laliberté and Legendre 2010; Laliberté et al. 2014) to estimate the FDist (Pavoine 2009). The PDist was computed by cophenetic distance along the phylogenetic tree by using the “*cophenetic*” function {stats} (R Core Team 2019).

To access niche dynamics at the community level, we computed the mean functional phylogenetic distance (MFPD) among FPDist from all pairs of species at every pixel (Cadotte et al. 2013). For each community, we obtained the slope from the relationship between MFPD and the *a*-weight, as well as the significance of such relationship along random samples of pairwise functional and phylogenetic distances. Because the non-linear combination between FDist and PDist, the MFPD was transformed to logarithmic scale before computing the slopes. The signal of this slope indicates if the pool of species present convergent (positive slopes), divergent (negative slopes) or conserved (null slopes) evolutionary dynamics, whereas its magnitude indicates the strength of the evolutionary mode. Additionally, the significance of the relationships indicates if communities are under-dispersed (similar species co-occurring: observed MFPD < random MFPD) or over-dispersed (dissimilar species co-occurring: observed MFPD > random MFPD). To evaluate the spatial patterns of the evolutionary niche dynamics, we mapped the slopes and the community assembly patterns (under/over-dispersed) across the Earth’s surface and related them against latitude. All procedures were implemented in the software R (R Core Team 2019).

3) Results

The mammals' communities presented species with more conserved niches (null slopes regardless if α , β or γ niches) at lower latitudes and throughout oceans (Figs. 1, 2). The α and β niches showed opposite evolutionary dynamics; whereas the α niche converge (positive slopes), the β niche diverge (negative slopes) among species into communities throughout the globe. The α niche showed stronger convergent evolution at higher latitudes for both continental (except Australia) and marine communities (Fig. 1a, b), whereas the β niche showed stronger divergent patterns at high continental latitudes, but at lower marine latitudes (Fig. 1c, d).

Contrary to α and β niches, the γ niche presents contrasting evolutionary modes between landmasses and oceans; the species from continental communities present convergent γ niches (positive slopes), whereas the marine communities present divergent γ niche (negative slopes) (Fig. 2). Additionally, the evolutionary dynamics of γ niche is spatially lesser structured along the latitudes than α and β niches, especially across the marine communities (Fig. 1e, f). Instead, the γ niche is strongly spatially structured across landmasses, with the southern Gondwana continents showing stronger γ niche convergences than the northern Laurasia continents.

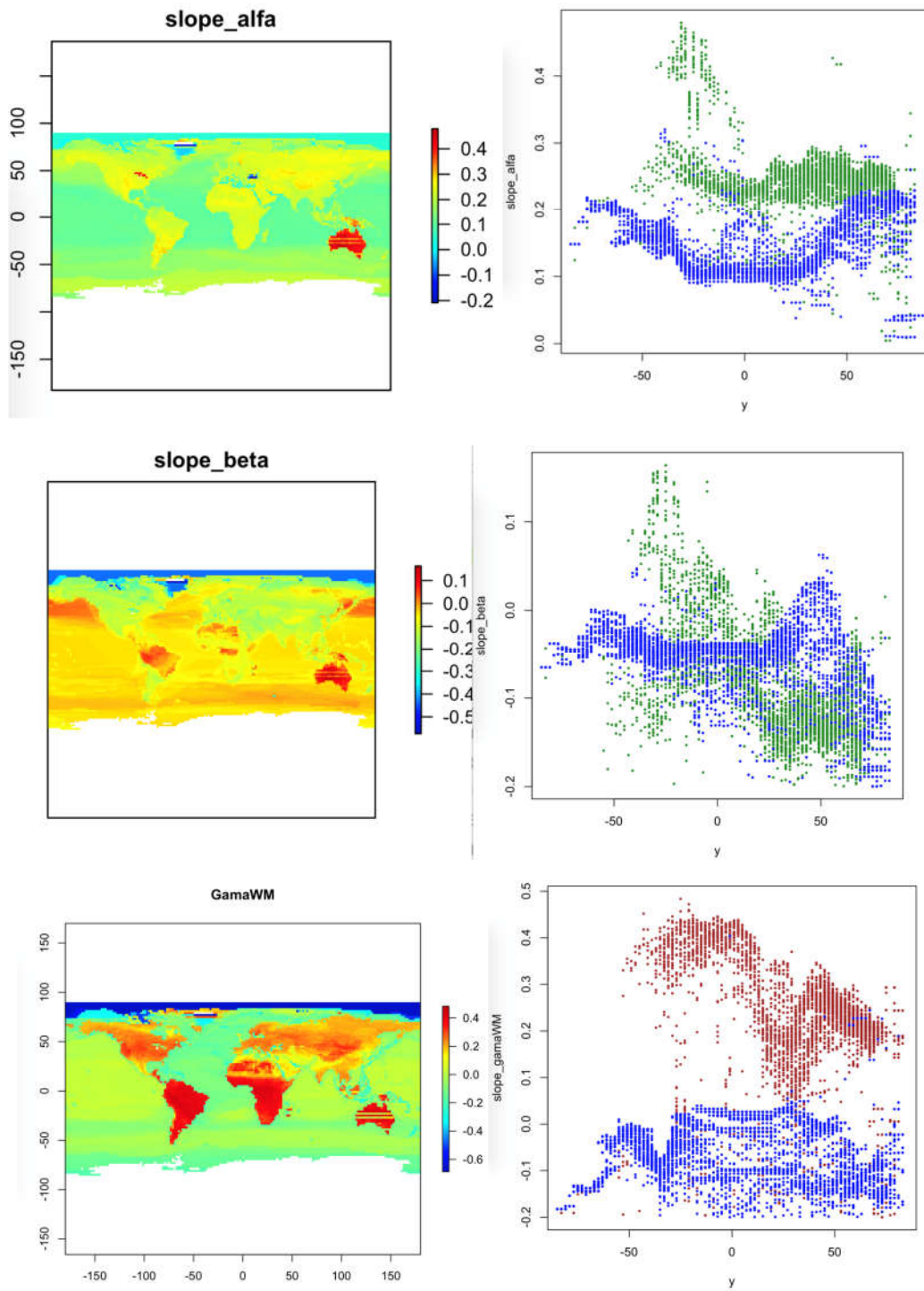


Figure 1. Spatial pattern of α , β , and γ niche evolution throughout the Earth surface (maps at left) and across latitude (right).

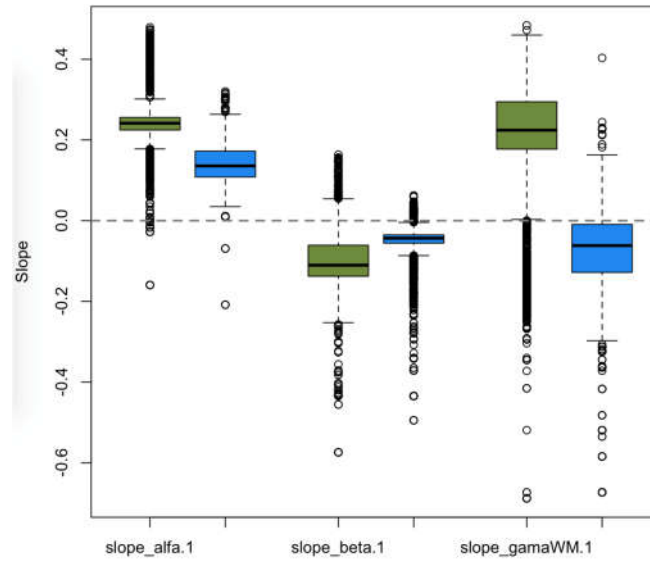


Figure 2. Magnitude and signal of slopes (MFPD x a-weights) across α , β , and γ niches from terrestrial (green) and oceanic (blue) mammal communities.

4) Discussion

In this study, we analyzed spatial patterns for α , β , and γ niches derived from phylogenetic and functional diversity interaction for all extant mammals worldwide. We generally expected the three niche scales would be globally more conserved in the tropics, both on the continents and in the ocean. However, although this was true for landmasses, the oceans showed greater conservatism in temperate zones. In turn, the α -niche showed a greater convergent tendency for all species showing a more pronounced influence by the phylogenetic history of the species. On the other hand, the β -niche showed a more divergent pattern, highlighting a greater relevance of functional traits on this scale. Our results demonstrate the contrast of the geographic pattern among each of the hypervolume scales that compound the species niche.

At high latitudes, the α and β -niches showed convergent and divergent evolution, respectively, opposing to our expectations. These findings indicate that α -niche evolve under historical contingency, especially at harsh temperate and polar environments, resulting in communities with similar functional traits regardless of the species evolutionary history. The β -niche present tropical conservatism and only some descendants that diverge from its tropical relatives might to colonize high latitudes. The

γ niche is strongly spatially structured across landmasses, with the southern continents from Gondwana showing stronger niche convergences than the northern Laurasia continents. The spatial pattern of γ niche indicate that communities are mainly composed by species restrict to specific biogeographical realms, and reflect that mammals dispersed more likely across the Laurasia (less convergent) than across the Gondwana.

Similarly, our findings showed a generalized evolutionary divergence of environmental tolerances (β -niche) among phylogenetically close mammals instead of convergence. This result corroborates other studies that suggest narrow niches in the stable tropical climatic conditions and wider niches in the more seasonal temperate latitudes (i.e. Quintero & Wiens 2013, Bonetti & Wiens 2014). This pattern makes sense about the area of origin and niche conservation as proposed by Wiens & Donogue (2004). When speciation occurs, the species maintain the environmental tolerances (β -niche) of their ancestors and continue to occupy in the same geographical regions as their close relatives. On the other hand, some species arose with evolutionary novelties and may tolerate environmental conditions that are different from their ancestors, allowing them to migrate and occupy other regions. The more conserved β -niche (slopes close to zero) at lower latitudes on continents suggests the origin of mammals in the tropics. Only species that differentiated their β -niche to bear colder climates may reach and persist at high latitudes. Thus, the niche β -divergence is higher in species occurring in temperate continental regions than in tropical ones.

Among all the latitudes, Australia stands out as it obtained the highest values for the three scales of the niche, indicating strong phylogenetic structuring in the species that occur there. This phenomenon could be explained by what was pointed out by Cooper et al. (2011), specialist species or species with restricted distribution tend towards niche conservatism. For example, Jones & Barmuta (2000) evaluate the niche differentiation in three dasyurid carnivorous species, finding strong overlap and competition at the trophic level, which in a similar way to the oceans, is attenuated by the preferences of stratum or vegetation type. In turn, our findings are consistent with those reported by Mazel et al. (2017), which highlighted a functional convergence for Australian communities, a consequence of in situ radiation, with other climatically similar regions in the world.

Based on the tropical conservatism suggested for terrestrial mammals (i.e. Buckley et al. 2010, Safi et al. 2011, Khaliq et al. 2014), we expected similar behavior in the oceans for the niche scales. Marine communities presented more conserved niches regardless of whether α , β or γ niche, however unlike the continents, temperate and polar zones are considered the most diverse (Kaschner et al. 2011, Pompa et al. 2011) and center of origin for these species (Berta et al. 2015). Thus, suggesting that a few species managed to invade the tropics, thus tending most species to maintain their environmental properties (β - niche) and their geographic distribution (γ -niche) as our results suggest. Some studies analyzing trophic niche in marine mammals (i.e. Pinela et al. 2010, Schick et al. 2011, Aurióles-Gamboa et al. 2013, Liu et al. 2015) found an influence of environmental conditions, such as distance from the line of coast, temperature, productivity or depth as determinants of diet partitioning, this coinciding with our results of a convergent alpha-niche and a divergent β -niche, this differentiation at the habitat level becomes more relevant when the competition for diet overlap is strong (Kashner et al. 2006).

Regarding the γ niche, our findings indicate that Gondwana's species hold their biogeographic realms in a higher proportion than Laurasia's species. This makes sense if we observe the history of the continental drift of these supercontinents, Laurasia continents always were more linked than Gondwana continents, which permitted species most likely migrate across the northern hemisphere. Conversely, after Gondwana split out, southern continents enter an isolation period keeping their species in the same areas they originated.

The mammals' communities presented an evident variation of α , β or γ niches evolution across the geographic space, although weakly support our predictions about the assembling pattern expected to each niche dimension. Instead a divergent α -niche, our findings showed a generalized evolutionary convergence of functional traits into mammals' communities worldwide. This pattern indicates that α -niche evolves under strong pressure by historical contingency. Because mammals have relatively limited combinations of functional traits (3 diet traits, 5 strata, and 3 activity), species have no option to randomly evolve these traits through time (i.e., by Brownian Motion).

Hence, regardless of when or where the species arose and evolved, phylogenetically distant species present similar α -niches. Reaffirming the importance of character differentiation in the beta scale to limit competitive exclusion, which is evident for both terrestrial and marine environments. most of the work focuses mainly on terrestrial species excluding marine mammals (ie. Olalla-Tarraga et al. 2011, Romdal, Araujo & Rahbek, 2013). This is one of the few works that includes both terrestrial and marine species trying to provide a more global overview for current mammalian species. Possibly the integration of palaeoenvironmental information and the interpretation of our dataset on a finer scale allows a more in-depth understanding of the geographical configuration of each of the niche scales.

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CAPÍTULO 3

Environmental filters, hierarchical niches, and mammals' community assembly

Victor Hugo Mendoza Rodriguez^{1,2}, Matheus S. Lima-Ribeiro^{2*}

¹Programa de Pós-graduação em Ecologia & Evolução, Universidade Federal de Goiás, Goiânia, Brazil.

²Macroecology Lab., Universidade Federal de Jataí, Jataí, Brazil.

*Author for correspondence: mslima.ribeiro@gmail.com

Abstract

The community assembly is a scale-dependent process, whose main driver is the interaction of competitive exclusion and environmental filtering. The α , β , and γ -niches are associated on a spatial scale and linked to the functional traits of the species. Therefore, contextualizing the ecological niche within the historical process of the community configuration will allow us to understand how obtaining resources and climate changes influence niche evolution. Here we explore the phylogenetic and functional relationships of α , β , and γ -niches in mammalian communities under global environmental gradients, attempting to identify a clustering or dispersal phylogenetic pattern within each of the niche scales by Environmental filtering, especially under harsh conditions. We divided the global geographic space into cells, and identified the mammalian species occurring in each one, we delimited the α , β , and γ -niches for each species with functional information, and we established the phylogenetic relationship for the community in each cell. We obtained environmental information of temperature, altitude, and evaporation for each cell in order to identify a differential environmental filtering on the three scales of the niche. Overall, the mammals' communities presented hierarchical niches slightly structured along the environmental gradients, especially with altitude. Altitude-only explain most of the variation in functional-phylogenetic distances among species (R^2 around 20%), but with an opposed effect than expected. Species are functionally and phylogenetically more similar at lower than at higher elevations with harsher environments. The under-dispersed communities at higher elevations indicate that the altitudinal filter select species with similar α and β -niche. We found a differentiated evolutionary response to altitude in each scale, showing the γ -niche to be phylogenetically more structured than β and α -niches, respectively. As expected, α -niche is labile and depends on ecological processes during community assembly. Our findings support the idea of a differential effect of environmental filtering on niche scales, with functional similar but phylogenetically distant species occupying similar environmental conditions and phylogenetically close species, tolerating similar environmental conditions

Keywords: α , β and γ niches, phylogenetic niche conservatism, environmental filters, mammal communities, scale, local assemblages.

1. Introduction

The niche conservatism has been an evolutionary process increasingly used to explain multiple ecological patterns (Wiens and Graham 2005) such as species richness and composition across communities (Lamana et al. 2014). It is widely recognized that the assembly processes of a community are determined, on the one hand, by competition and environmental filtering on the other. These processes can act on the species individually or jointly, establishing differentiation or convergence of traits for the local exploitation of resources (α -niche) or survival under certain environmental conditions (β -niche) (see Krasnov et al. 2014). However, different ecological traits may present different levels of conservatism (Olalla-Tárraga et al. 2011), and then affect community assemblage at different temporal and spatial scales. For example, the functional attributes related to the interspecific interactions (α -niche) present a labile (less conservative) pattern into communities resulting from competitive exclusions during the assemblage processes (Silvertwon et al. 2006). In contrast, the differences that results from evolutionary history and biogeographic scale, related to species distributions (γ -niche), present the most conservative pattern due to dispersal limitations through deep geological past (e.g. continental drift). In between, the traits related to the environmental tolerances and habitat preferences of species (β niche) present an intermediate level of conservatism in response to environmental changes over a nearer past (e.g. Quaternary glaciations) (Jackson & Overpack 2000; Silvertwon et al. 2006).

Species present in a region must possess the appropriate combination of characters to tolerate the specific conditions imposed by this region (Belmaker & Jetz, 2013). Thus, local variations in functionality and phylogenetic proximity determine co-existence or competitive exclusion within a community. On the one hand, environmental filters can promote trait clustering by the co-existence of functional similarity (convergent characters). On the other hand, ecological interactions such as competition, cause a phylogenetic repulsion to limit the functional similarity of closely related sympatric species. Belmaker & Jetz (2013) highlight the above as the best framework to explain trait under or overdispersion pattern. However, the complexity is that the observed pattern does not derive from a single process. The species co-occurrence is scale-dependent, at some point, functional similarity and phylogenetic relatedness become implicit within the community assembly process (ecological equivalence) (see Luza et al. 2015).

Overall, the biotic and abiotic filters affect the community assemblage by sorting species at different scales in accordance with their ecological characteristics (Silvertwon et al. 2006). It is expected that environmental filtering (β -niche) and dispersal barriers (γ -niche) would structure communities at biogeographical scales with more similar species than expected by chance (under-dispersion), whereas a high competition for biotic resources (α -niche) would define local communities and lead them toward over-dispersion (see Mayfield and Levine 2010). Additionally, the strength of this hierarchical filtering affecting community assembly vary at different points along the environmental gradients (Cavender-Bares & Wilczek 2003; de Bello et al. 2013). Considering that species are selected in accordance with the traits that allow them to tolerate environmental stresses (Spasojevic & Suding 2012), we wonder if such hierarchical filtering is potentiated under harsh environmental conditions and thus more strongly select for species with similar α , β and γ niches to co-occur into communities.

Here we addressed this question by exploring the differential conservatism of ecological traits associated to α , β and γ niches across mammals' communities and environmental gradients at a global scale. Specifically, we tested if climatically unstable regions, with cold temperatures, high elevation and low water-energy availability, filter species with more similar α , β and γ niches than noncritical conditions, both at the present time and for the last maximum glacial.

2. Methods

To evaluate the effect of environmental filtering on the community assembly, we obtained the geographical range, phylogeny and ecological traits for all extant species of terrestrial mammals worldwide, as well as raster layers for temperature, altitude, and potential evapotranspiration (PET) at a global scale. The species geographical range was obtained from the IUCN database (IUCN 2017), and the phylogenetic information from Kuhn et al. (2011). By comparing taxonomic synonymies between phylogenetic and geographic information, remained a total of 4725 extant terrestrial mammals. The layers for elevation and maximum, minimum and annual mean temperature were obtained from the WorldClim database (www.worldclim.org; Hijmans et al. 2005). We gathered temperature layers for the present and last glacial maximum (LGM, 21 ky ago). The layer for PET was obtained from Trabucco and Zomer (2019). All environmental layers were

upscaled to a grid of cells with spatial resolution of 2° lat/long using the functionalities of the “raster” package in the software R (Hijmans et al. 2016, R Core Team 2019).

The α , β and γ niches were delineated from distinct ecological traits in accordance with proposed in Silvertown et al. (2006). To delimit the α -niche, we gathered foraging attributes related to biotic interactions, such as trophic level, diet, strata, activity, population density, weaning age, and maximum longevity. All these functional traits were obtained from the PanTheria (Jones et al. 2009) and the EltonTraits databases (Wilman et al. 2014). The β -niche was delimited by setting the environmental conditions and habitat of species. We used the habitat classification from the IUCN (<https://www.iucnredlist.org/resources/habitat-classification-scheme>) to set the type of habitat that species explore. We also set the latitudinal climatic zone that each species occurs, named tropical (<30° of latitude), temperate (between 30° and 60°), and polar (>60°), and estimated its thermal and altitudinal tolerances. We considered that a species occupy a given climatic zone if its geographical range covered at least 10% of the respective latitudinal band. The thermal and altitudinal tolerances were obtained by the maximum and minimum temperature (95% and 5% quantiles, respectively) and maximum altitude (95% quantile) from the geographical distributions of species. Finally, γ -niche was set as the biogeographical realms where each species occurs. We followed the biogeographical realms delimited by Wallace (1976) and Costello et al. (2017) for terrestrial and marine species, respectively. We considered a species to occur in all biogeographical realms overlapping at least 10% of its geographical range.

We mapped the species occurrence in a grid of cells with spatial resolution of 2° lat/long, resulting in 16,200 pixels (considered here the communities) throughout the Earth’s surface. By using the functional-phylogenetic approach proposed by Cadotte et al. (2013), we estimated the functional-phylogenetic distance (FPDist) among all species pairs in each community, as follows: $FPDist = (aPDist^p + (1-a) FDist^p)^{1/p}$

where PDist and FDist represent, respectively, the distances between species in the phylogenetic and trait spaces, “ a ” is the weighting parameter controlling the independent contribution of Pdist and Fdist to FPDist, and “ p ” combines them non-linearly (see details in Cadotte et al. 2013). We computed FPDist considering the a -weights ranging from zero (only FDist contributes) to one (only PDist contributes) at every 0.05 units and obtained the Euclidean distance ($p=2$) from the combined functional and phylogenetic distances. Because the trait space delineating the α , β , and γ niches are composed by both continuous

and categorical traits, we used the Gower dissimilarity coefficient from “*gowdis*” function {FD} (Laliberté and Legendre 2010; Laliberté et al. 2014) to estimate the FDist (Pavoine 2009). The PDist was computed by cophenetic distance along the phylogenetic tree by using the “*cophenetic*” function {stats} (R Core Team 2019).

Next, we computed the mean functional-phylogenetic distance (MFPD) among FPDist from all pairs of species at every pixel in order to access the niche dynamics at the community level (Cadotte et al. 2013). Then, we related the MFPD from each α -value against annual mean temperature at the present (Tmean0) and LGM (Tmean21), climate stability (difference between Tmean0 and Tmean21, named ΔT), altitude and PET in a multiple regression. The best subset of predictors was determined by using the stepwise Akaike information criterion (stepAIC) (Yamashita et al., 2007). The predictors selected from best models represent the environmental filters that are relevant for α , β , and γ niches at a given functional-phylogenetic weight (a). Finally, we computed the individual R^2 for each environmental predictor selected by AIC procedure.

3. Results

We linked each scale in the niche to the main community assembly processes, α -niche to competition and β -niche to environmental filtering, except the climate stability (ΔT), all environmental variables integrated the best subset of predictors through the most models (Table S1). Climate stability (ΔT) was not selected in any model and, therefore, was omitted in the analyses. Overall, the mammals’ communities presented α , β , and γ -niches slightly structured along the environmental gradients; less than 25% of the total variation in MFPDs were explained by environmental variables (Fig. 1). Additionally, altitude-only explain most of the variation in MFPDs, whereas climatic variables (current and glacial temperature and PET) presented negligible coefficients of determination ($R^2 < 5\%$; Fig. 1). This indicates that the assembly process of mammals’ communities is more influenced by phylogenetic history and ecological interactions than by our environmental variables.

As we expected, the influence of phylogeny (higher a -values) increases gradually from α to β and γ niches (Fig. 2). Analyzing individually the environmental variables, altitude describes better this phylogenetic gradient from low to high a -values for the three niches. This could be interpreted as species more ecologically similar (same α -niche),

constrained by few α -traits but phylogenetically distant occupying regions of higher altitude. Altitude presented overall positive slopes, especially for relationships with α and β -niches (Fig. 3); these curves represent a conservatism in ecological interactions and environmental tolerances related to altitude, the MFPD increases with altitude throughout the functional-phylogenetic weighting (a-values) which reinforces the idea of functionally similar species, but phylogenetically distant. For γ -niche, the MFPD increases gradually and positively altogether with altitude across the a-values (Fig. 3), which means a higher phylogenetic structure when a bigger scale is considered.

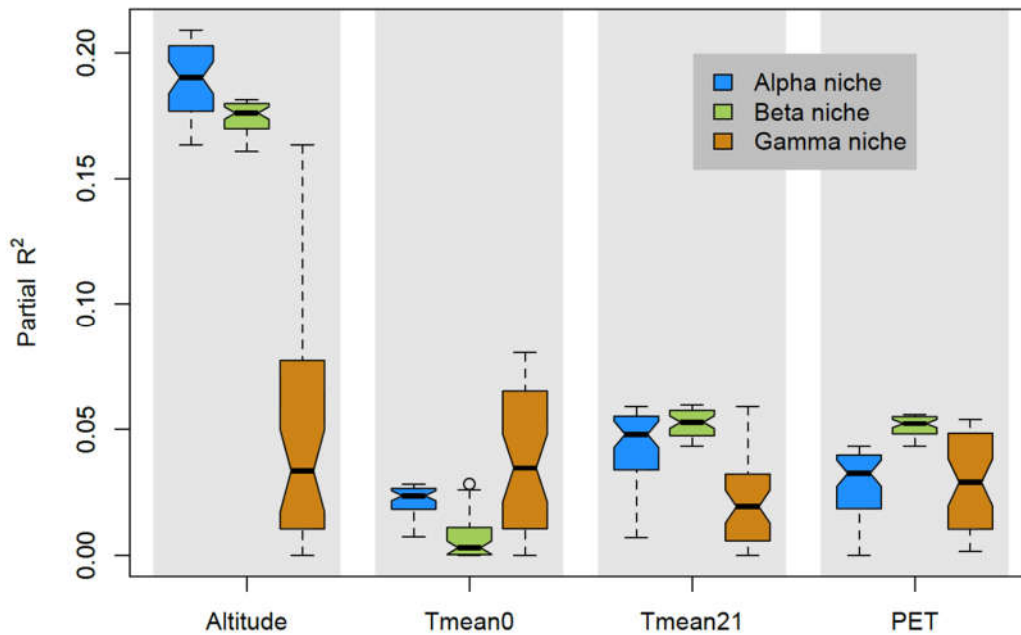


Figure 1. Partial coefficient of determination (R^2) from the relationships of MFPD against altitude, temperature at the present (T_{mean0}) and last glacial maximum - LGM (T_{mean21}), and potential evapotranspiration (PET). The MFPDs are represented for α (blue), β (green), and γ niches (brown).

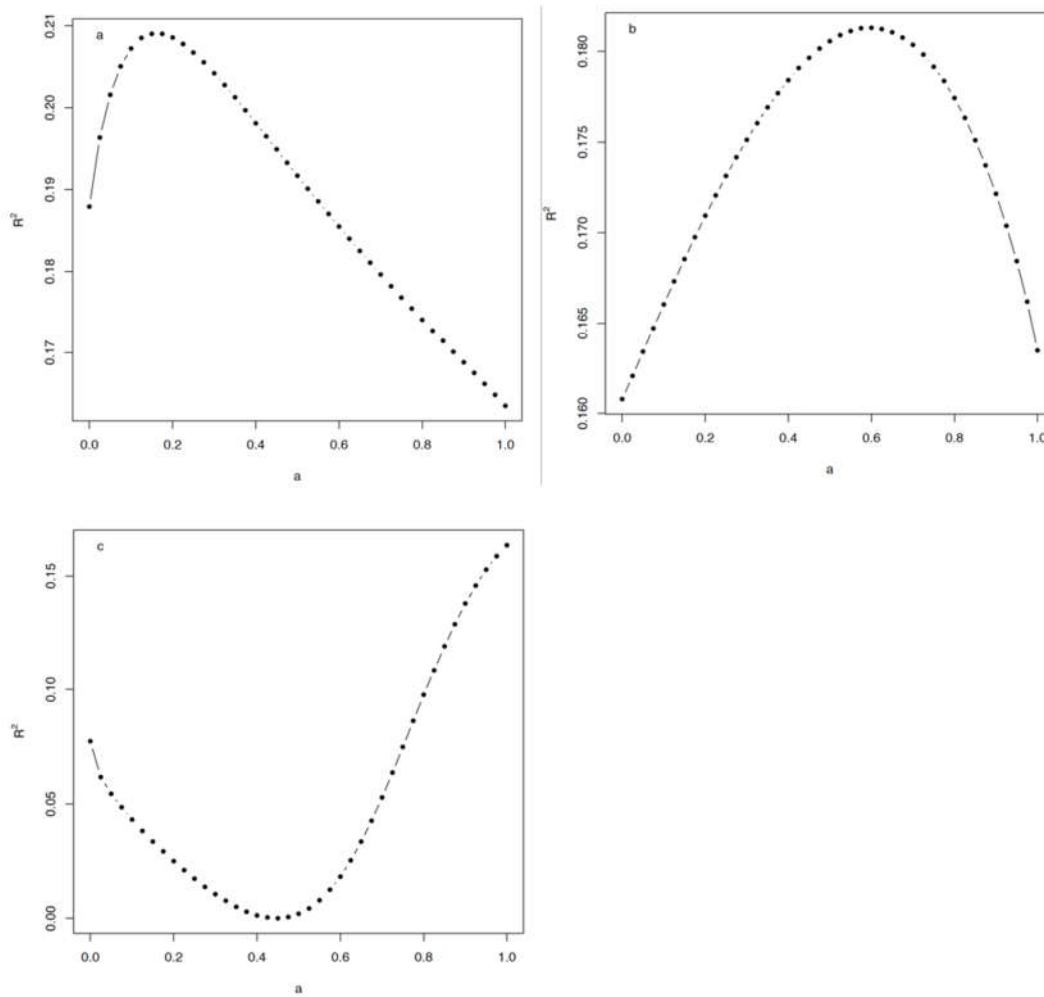


Figure 2. Proportion of total variation from α , β and γ niches explained by altitude-only across functional-phylogenetic weighing (a -values). Note that the higher R^2 for α , β and γ niches are obtained with low (~ 0.2), middle (~ 0.6), and high a -values (~ 1).

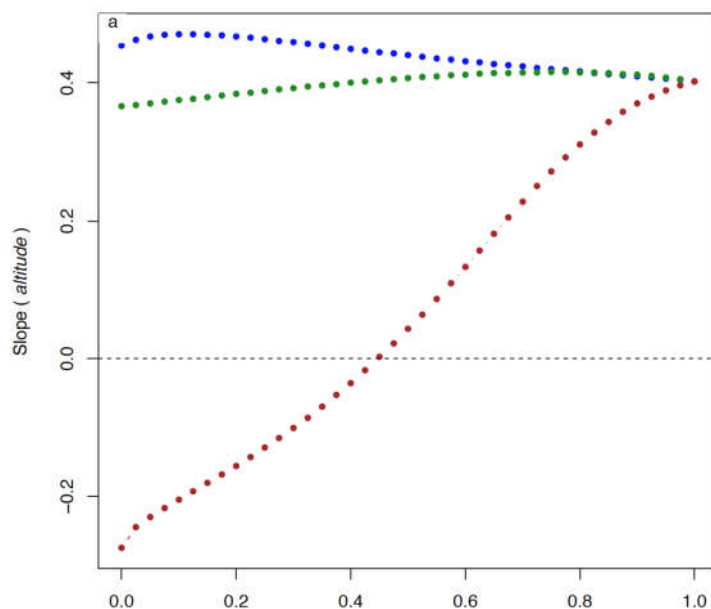


Figure 3. Slopes from the relationships of MFPD against altitude (a). The MFPDs are represented for α (blue), β (green), and γ niches (brown).

4. Discussion

The main goal of this work was to test the influence of environmental filtering on the hierarchical structure of the niche and its link with the assemblage of mammalian communities on a global scale. In this way, following the ideas of Silvertown et. al (2006), we expected at α -niche level, environmental factors contributed little to explain the phylogenetic community structure, because this scale is linked to the most labile scale of the niche hypervolume since it is at this scale where the ecological differentiation and competitive exclusion occur allowing close related species to occupy the same habitat. This idea is more clearly expressed by the pattern described in the curve of α -niche correlated to temperature, indicating overdispersion at low a-values, resulting from its high functional and phylogenetic distances.

On the other hand, the scale β represent the climate component in the niche hypervolume, so we expected the highest response to environmental filtering reflected at this scale, with phylogenetically clustered communities and similar β -niches that allow species to occupy harsh climatic regions. However, of all the variables we used, just altitude supported our hypothesis of a phylo-functional gradient structuring the niche scales, with the α -niche more determined by functionality, the intermediate β -niche, and

the γ -niche more structured in phylogeny. This finding agrees with the ideas of Luza et al (2015) that under harsh environmental conditions, environmental filtering allows the assembly of species with conserved physiological tolerances complemented by resource use strategies. The filter imposed under harsh environmental conditions, such as altitude, exerts a selection for species with specific traits capable of withstanding abiotic stress, which results in under-dispersed traits communities (Cadotte et al. 2013, Lamana et al. 2014). Thus, we observe an obvious phylogenetic arrangement on the elevation factor where phylogenetic dispersion gradually decreases from the over-dispersion in α to under-dispersion in γ . In other words, our findings are consistent with the idea of greater niche conservatism for extreme environmental values (see Olalla-Tárraga et al. 2011), at least in our elevation patterns at the three scales, like those findings reported for hummingbirds by Graham et al (2009, 2012 but see Kamilar et al. 2015)

Contrary to our findings for altitude, the other climatic variables do not support our hypothesis of a phylogenetic structuring gradient by environmental filtering, like that also reported in hummingbirds under dry climatic conditions (Graham et al 2009 and 2012). However, exist the idea that mammals do not have a high climate niche conservatism (see Cardillo 2011), this may be because mammalian communities have mostly exhibited a random and patternless phylogenetic distribution (Kamilar et al. 2015) and only at order taxonomic level for some regions have environmental filtering effects been reported manifested as a phylogenetic clustered assemblage, such as the case of ruminants for arid zones by Cantalapiedra and colleagues (2014). Therefore, if this were the case for our environmental variables, differential climate filtering may not be taking place at niche scales during community assembly, and only competitive exclusion would be acting as the main driver of establishment and coexistence. of species in a community delimited by geographic barriers and dispersal limits. Or on the other hand, evaluating how the niche scales respond when each order of mammals is analyzed individually.

The influence of the spatial scale during the community assembly process is a relevant factor to consider. Belmarker and Jetz (2013) highlight that the differentiation of characters and the operation of the assembly rules are highly scaled dependent, so the low values obtained for MPFD could be partly due to the scale used in our analyzes. In this sense, Cardillo (2011) suggests that it is easier to identify on local scales how competitive exclusion (α -niche) and environmental filtering (β -niche) act in the assembly process of communities. For example, Luza et al. (2015) identify a phylogenetic pattern of clustering

and repulsion structured on the spatial scale determined by environmental filtering, ecological interactions, and historical processes for the nonvolant small mammal community. Which agrees with our findings, at least for α -niche, with clustered functional traits under high altitude conditions, indicating that ecological interactions were important structuring assemblages at high elevation conditions. In addition of previously mentioned about the influence spatial scale, the abrupt decrease observed in the explanatory power for the rest of the environmental variables may be due to the functional traits considered within the alpha and beta niches and to the lack of phylogenetic signal in them. A detailed exploration analyzing by separating functional traits would allow a better interpretation of the effect of environmental gradients on communities, as mentioned by Gianuca et al. (2017).

Our findings support the idea of a differential effect of environmental filtering on niche scales, with functional similar but phylogenetically distant species occupying similar environmental conditions and phylogenetically close species, tolerating similar environmental conditions, at least for the altitude variable. Like other works have reported, a more detailed analysis in terms of phylogenetic and geographical scale may give us more substantial results that allow us to observe the differential action of the environment filtering on the α , β and γ scales of the niche.

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Supplementary Material

Table S1. Model selection with Akaike information criterion. The environmental variables with NA did not contribute to filter the species according their hierarchical niches across mammals' communities.

a	Alpha					Beta					Gamma				
	alt	Tmean0	Tmean21	deltaT	PET	alt	Tmean0	Tmean21	deltaT	PET	alt	Tmean0	Tmean21	deltaT	PET
0	1	1	1	NA	NA	1	NA	1	NA	1	1	1	1	NA	1
0.025	1	1	1	NA	1	1	NA	1	NA	1	1	1	1	NA	1
0.05	1	1	1	NA	1	1	NA	1	NA	1	1	1	1	NA	1
0.075	1	1	1	NA	1	1	NA	1	NA	1	1	1	1	NA	1
0.1	1	1	1	NA	1	1	NA	1	NA	1	1	1	1	NA	1
0.125	1	1	1	NA	1	1	NA	1	NA	1	1	1	1	NA	1
0.15	1	1	1	NA	1	1	NA	1	NA	1	1	1	1	NA	1
0.175	1	1	1	NA	1	1	NA	1	NA	1	1	1	1	NA	1
0.2	1	1	1	NA	1	1	NA	1	NA	1	1	1	1	NA	1
0.225	1	1	1	NA	1	1	NA	1	NA	1	1	1	1	NA	1
0.25	1	1	1	NA	1	1	NA	1	NA	1	1	1	1	NA	1
0.275	1	1	1	NA	1	1	1	1	NA	1	1	1	1	NA	1
0.3	1	1	1	NA	1	1	1	1	NA	1	1	1	1	NA	1
0.325	1	1	1	NA	1	1	1	1	NA	1	1	1	1	NA	1
0.35	1	1	1	NA	1	1	1	1	NA	1	1	1	1	NA	1
0.375	1	1	1	NA	1	1	1	1	NA	1	1	1	1	NA	1
0.4	1	1	1	NA	1	1	1	1	NA	1	1	1	1	NA	1
0.425	1	1	1	NA	1	1	1	1	NA	1	NA	1	1	NA	1
0.45	1	1	1	NA	1	1	1	1	NA	1	NA	1	1	NA	1

0.475	1	1	1	NA	1	1	1	1	NA	1	1	1	1	NA	1
0.5	1	1	1	NA	1	1	1	1	NA	1	1	1	1	NA	1
0.525	1	1	1	NA	1	1	1	1	NA	1	1	1	1	NA	1
0.55	1	1	1	NA	1	1	1	1	NA	1	1	1	1	NA	1
0.575	1	1	1	NA	1	1	1	1	NA	1	1	1	NA	NA	1
0.6	1	1	1	NA	1	1	1	1	NA	1	1	1	NA	NA	1
0.625	1	1	1	NA	1	1	1	1	NA	1	1	1	1	NA	1
0.65	1	1	1	NA	1	1	1	1	NA	1	1	1	1	NA	1
0.675	1	1	1	NA	1	1	1	1	NA	1	1	1	1	NA	1
0.7	1	1	1	NA	1	1	1	1	NA	1	1	1	1	NA	1
0.725	1	1	1	NA	1	1	1	1	NA	1	1	1	1	NA	1
0.75	1	1	1	NA	1	1	1	1	NA	1	1	1	1	NA	1
0.775	1	1	1	NA	1	1	1	1	NA	1	1	NA	1	NA	1
0.8	1	1	1	NA	1	1	1	1	NA	1	1	NA	1	NA	1
0.825	1	1	1	NA	1	1	1	1	NA	1	1	1	1	NA	1
0.85	1	1	1	NA	1	1	1	1	NA	1	1	1	1	NA	1
0.875	1	1	1	NA	1	1	1	1	NA	1	1	1	1	NA	1
0.9	1	1	1	NA	1	1	1	1	NA	1	1	1	1	NA	1
0.925	1	1	1	NA	1	1	1	1	NA	1	1	1	1	NA	1
0.95	1	1	1	NA	1	1	1	1	NA	1	1	1	1	NA	1
0.975	1	1	1	NA	1	1	1	1	NA	1	1	1	1	NA	1
1	1	1	1	NA	1	1	1	1	NA	1	1	1	1	NA	1

CAPÍTULO 4

Um olhar ao Grande Intercambio Biótico Americano desde a perspectiva do mapeamento literário sistemático

Victor Hugo Mendoza Rodriguez^{1,2}, Matheus S. Lima-Ribeiro^{2*}

¹Programa de Pós-graduação em Ecologia & Evolução, Universidade Federal de Goiás, Goiânia, Brazil.

²Macroecology Lab., Universidade Federal de Jataí, Jataí, Brazil.

Resumo

O Grande intercâmbio biótico americano (do inglês “*Great american biotic interchange*” GABI), permitiu o contato entre as biotas previamente isoladas da América do Norte e do Sul. Embora seja um tema pesquisado por mais de um século, ainda não está tudo dito com respeito ao GABI. Para o presente trabalho se efetuou uma busca de literatura científica em bases de dados especializadas, reunindo informação para um período de 40 anos. Com trinta países do mundo todo envolvidos na pesquisa ao redor do GABI, os mais destacados são os Estados Unidos, Argentina com o 31 e 18% da produção global. Assim mesmo, as instituições com maior destaque a nível mundial são a Universidad Nacional de La Plata da Argentina e a Universidad Nacional Autónoma de México. Dos trabalhos aqui analisados, os mamíferos emergem como o grupo de organismos mais estudado, principalmente carnívoros e xenarthras. Com a paleontologia e a phylogeografia como principais áreas de pesquisa e maioritariamente desenvolvidos na América do Sul. Existe uma relação entre o grupo estudado, a área de pesquisa e a data sugerida para a formação da conexão das Américas, com a paleontologia suportando datas mais recentes e a ecologia molecular que apoia um surgimento mais antigo. Preencher as lacunas de informação, principalmente dos países centro-americanos e acrescentar informação tanto paleontológica quanto molecular para outras taxa, ajudarão compreender melhor como aconteceu o GABI e as consequências na configuração da biota atual do Novo Mundo.

Palavras chave: *Mapeamento literário, Great American Biotic Interchange. Bases de dados*

1. Introdução

O Grande Intercambio Americano ou GABI (do inglês “*Great American Biotic Interchange*”) (Webb, 1985), também chamado de *Great American Faunal interchange* (Webb, 1976) é um evento já identificado desde a segunda metade do século XIX (Wallace 1876; von Ihenring, 1900). A mistura de elementos faunísticos da América do Norte e do Sul está amplamente documentada pelo registro fóssil, principalmente dos mamíferos, não são poucos os trabalhos que dão testemunha disso (ex. Marshall, 1985; Webb 2006; Woodburne, 2010 e referências).

Considerado como um evento único com relevância evolutiva (Perini et al. 2009), ecológica (McDonald, 2005) e biogeográfica (Cody et al. 2010) na história do planeta, um experimento biológico (Bacon et al. 2015) em macro escala, e inclusive denominado como uma “revolução” biológica pela consequência na reestruturação da biota (Defler, 2019). O GABI tem chamado muito a atenção da comunidade científica, por ser uma peça chave na configuração do

padrão de diversidade atual, que deu origem à região biogeográfica de maior diversidade biológica do mundo todo (Pelegrin et al. 2018).

O paradigma do GABI foi construindo-se desde a visão da paleontologia e a biogeografia dos mamíferos e desde os primeiros trabalhos (Simpson 1950 e 1980), é sugerido que os clados com origem na América do Norte se adaptaram melhor e conseguiram um melhor uso de recursos ao se estabelecer no Sul, outorgando-lhes uma sensação de superioridade competitiva quando comparados com os clados Sul-Americanos. Reforçando esta ideia o fato de não se observar uma ocupação territorial, substituição de espécies ou radiação semelhante na América do Norte por parte dos invasores do sul (Fariña et al. 2013). Assim, o GABI é descrito como um processo gradual constituído por diferentes etapas (proto-GABI e etapas do I-IV). Onde vários grupos taxonômicos, principalmente mamíferos, cruzaram o istmo do Panamá tanto com direção para o norte quanto para o sul durante os últimos 3,5Ma. Cada uma dessas etapas está detalhada em diversos trabalhos (Woodburne, 2010; Fariña et al. 2013, Cione et al. 2015 e Pelegrin et al. 2018).

Embora, mais famílias de mamíferos do Sul invadiram o Norte (21), em comparação com as 17 que se dispersaram no sentido oposto, segundo Webb (2006), muitas destas famílias desapareceram das latitudes neárticas durante a extinção da megafauna, restando poucas atualmente (Arroyo-Cabrales et al. 2010). Contrário ao acontecido nas regiões neárticas, os trópicos norte-americanos apresentam alto grau de endemismo derivado de organismos com origem no Sul, que faz pensar em processos de especiação similares com aqueles acontecidos com as famílias do norte na América do Sul. Assim, o GABI é considerado um evento dinâmico, bidirecional e recíproco (Carrillo et al. 2015). Contudo, não existe um saldo final para os diferentes grupos taxonômicos que participaram do GABI. Por exemplo, para psitacídeos (Eberhard e Bermingham, 2004), rãs (Pinto-Sanchez et al. 2011) e formigas (Winston, 2016) reporta-se um padrão de rápida dispersão e diversificação após o estabelecimento na América do Norte, processo similar com aquele observado na ordem Carnívora ao se estabelecer na América do Sul (Prevosti e Forasiepi, 2018).

O trabalho de Stehli e Webb (1985) incorporou para aquele momento o maior conhecimento do GABI, não focando apenas nos mamíferos, mas também incorporando o estado da arte para os outros grupos de vertebrados, estabelecendo o paradigma do GABI reconhecido por muitos anos e descrito previamente (Stehli e Webb, 1985 e referências). Porém, evidências aportadas por diversos autores na geologia (Montes et al. 2015, Jaramillo et al. 2017; Molnar 2017), na paleontologia (Campbell et al. 2009 e 2010, Rodriguez-Reyes et al. 2014, Prothero et al. 2014) e na filogeografia (Daza et al. 2009, Wilson et al. 2014, Wiston et al. 2016) colocam em dúvida a data estabelecida e propõem a existência de uma conexão entre as Américas há pelo menos 10 Ma. A aceitação ou rejeição destas evidências depende de cada autor e ainda causa controvérsia, que com um maior conhecimento irão se desvendando.

Os estudos cienciométricos, procuram elucidar a direção predominante na ciência, quantificando o desenvolvimento das disciplinas e os fatores mais frequentes presentes nestas disciplinas. Assim, é possível identificar informações uteis para identificar a obsolescência ou validade dos paradigmas estabelecidos e orientar o prosseguir dentro de uma linha de pesquisa (Spinak, 1998, mas ver Moraes e Giroldo, 2014)

Com base na visão da ciencimetria, o presente trabalho tem como objetivo avaliar a literatura científica relacionada ao Grande intercambio biótico americano, tanto em termos espaciais, identificando os países e as instituições mais produtivas, quanto em termos temporais. Assim, se busca caracterizar os linhas de pesquisa em questão de grupos taxonômicos, região geográfica, temporalidade geológica e enfoque ecológico. Identificar algumas hipóteses involucradas com o GABI, e finalmente avaliar a relação entre a idade sugerida para começo do GABI e o grupo taxonômico e a área de pesquisa.

2. Métodos

a) A busca

Foi realizada uma busca estruturada de literatura científica online nas bases de dados *SCOPUS* e *Web of Science* (WoS) na data 18 de setembro de 2019. A equação de busca utilizada na SCOPUS foi restrita com operadores booleanos para título, resumo e palavras chave (“TITLE-ABS-KEY”). No caso da WoS foi utilizada a busca avançada apenas com o operador booleano para tópico (“TS=”) (tabela 1). Os termos foram colocados entre aspas para indicar a busca da frase exata, excluindo palavras relacionadas. Com o intuito de abranger a maior quantidade disponível de literatura, a busca não foi restrita para um período específico em ambas as bases de dados.

Tabela 1. Estrutura da busca de literatura científica nas bases de dados especializadas utilizada neste trabalho.

Equações de busca	
<i>Scopus</i>	<i>Clarivate Web of Science</i>
TITLE-ABS-KEY (“Great American Interchange” OR “American Biotic Interchange” OR (“Great American Biotic Interchange” AND “GABI”) OR “American Faunal interchange” OR ‘Great American Faunal Interchange”).	TS=(“Great American Biotic Interchange” AND GABI) OR “Great American Biotic Interchange” OR “American Biotic Interchange” OR “American Faunal Interchange”

Com as planilhas obtidas das bases de dados, se fez uma primeira filtragem na literatura, eliminando os trabalhos duplicados entre ambas as bases comparando o *Digital Object Identifier* (DOI) para assim integrar uma base de dados única. Depois, fez-se uma segunda filtragem para os trabalhos remanescentes, onde foi conferido que cumpriam nosso quesito de busca, ter na secção do título, resumo ou palavras chave nossos termos de busca, desconsiderando os trabalhos sem este quesito. Para ambas as filtragens foi utilizado o RStudio V.3.6..1 (RStudio Team, 2016)

b) Diagramas bibliométricos

Após a filtragem, fizemos uma standardização de formato nos nomes das instituições e países de cada um dos coautores participantes de cada trabalho. Esta informação foi utilizada para construir um diagrama bibliométrico (redes de trabalho) por instituição e por país, com este intuito utilizei o software VOSviewer v1.6.13 (van Eck e Waltman, 2010)) que constrói esse tipo de diagramas, otimizando o peso da soma de quadrados das distâncias euclidianas entre todos os pares das categorias (van Eck e Waltman, 2013). Assim, atribui um peso dependente da frequência de cada item e gera agrupamentos baseados nas co-ocorrências nas publicações. No caso, foi definido um *threshold* mínimo de duas menções para considerar a inclusão do país e a instituição no diagrama bibliométrico.

c) Autores do GABI no tempo e no espaço

Separamos a informação de país de origem para o primeiro e último autor de cada trabalho e categorizamos em dois grupos, aqueles produzidos nos países latino-americanos e o resto do mundo (não latinos). Essa informação foi representada em um gráfico com as porcentagens anuais de trabalhos de cada grupo, e apresentado em um mapa para o total de países.

d) Palavras chave e diagramas foamtree

Para cada um dos artigos foram identificadas e extraídas as palavras chave, quando presentes, posteriormente foram classificadas em quatro grandes grupos: taxa, aspectos ecológicos, geográficos e geológicos. Depois de classificadas cada uma das palavras, foi construído um diagrama *foam tree* (Carrot Search FoamTree, 2019) para cada uma das cinco categorias estabelecidas. O diagrama *foam tree* divide o espaço em polígonos hierárquicos e assigna um peso proporcional para cada item dentro das categorias. No nosso caso, o peso de cada item foi determinado pela frequência com que apareceu cada uma das palavras chave no nosso total de artigos, desconsiderando aquelas palavras com menos de 3 menções.

e) PCA

Uma análise de componentes principais (PCA) foi aplicada correlacionando o grupo de organismos estudado, a área de pesquisa e a data proposta para a formação completa do istmo do Panamá. Assim, classificamos os organismos em: mamíferos, aves, vertebrados ectotérmicos

(anfíbios, répteis e peixes), artrópodes, parasitas (helmintos e nematódeos), plantas, e sem táxon (“*No taxa*”). Os trabalhos não focados em um grupo específico (ex. a flora ou a fauna na área de estudo), foram classificados como “comunidades” (ex.) Cada trabalho foi assignado dentro de uma área de pesquisa: geologia, paleontologia, ecologia de comunidades e ecologia molecular. Por último, os trabalhos foram classificados segundo a data do surgimento do Panamá em menor que 7 Ma, maior que 7 Ma ou sem data quando não era mencionada explicitamente (“*No Age*”). Esta data foi escolhida porque ocorre dentro do chamado proto-GABI (*sensu* Cione et al. 2015) quando os considerados primeiros organismos em cruzar o istmo (*heralds* ou *land-hoppers sensu* Webb 1985), aparecem em ambos os continentes, mas considerando que chegaram sem a existência da ponte terrestre.

f) *As teorias do GABI*

Finalmente, com aqueles artigos que tiveram uma ênfase na ecologia de comunidades, no sentido de explicar as consequências do GABI testando alguma teoria ecológica, ou aplicar o GABI como modelo para a explicação de alguma teoria, foram concentrados em uma tabela.

3. Resultados

Foram obtidos um total de 458 trabalhos, 201 da *Scopus* e 257 da WoS. Desse total foram removidos 168 duplicados e 72 artigos não cumpriram o quesito de conter os termos de busca no título, resumo ou palavras chave. Assim, o total de trabalhos incluídos nas análises foram $n=218$. Com um total de 30 países envolvidos na produção científica relacionada ao *Great American Biotic Interchange*, os cinco, mais destacados são: Estados Unidos (31%), Argentina (18%), Brasil (7%), México (7%) e Panamá (3%). Que geraram os maiores círculos no diagrama bibliométrico e agruparam ao redor de si os clusters de colaboração internacional (Fig. 1a).

O padrão anterior é suportado também quando se olha para as instituições mais produtivas em relação ao *GABI*. No caso de Argentina, México e Panamá, esta produção emerge maioritariamente de uma instituição só: A *Universidad Nacional de La Plata* (UNLP), a *Universidad Nacional Autónoma de México* (UNAM) e o *Smithsonian Tropical Research Institute*, respetivamente. Já no caso de Brasil e dos Estados Unidos, o volume da sua produção vem de múltiplas instituições, destacando-se a Universidade Federal do Rio de Janeiro e *The University of Florida* (Fig. 1b).

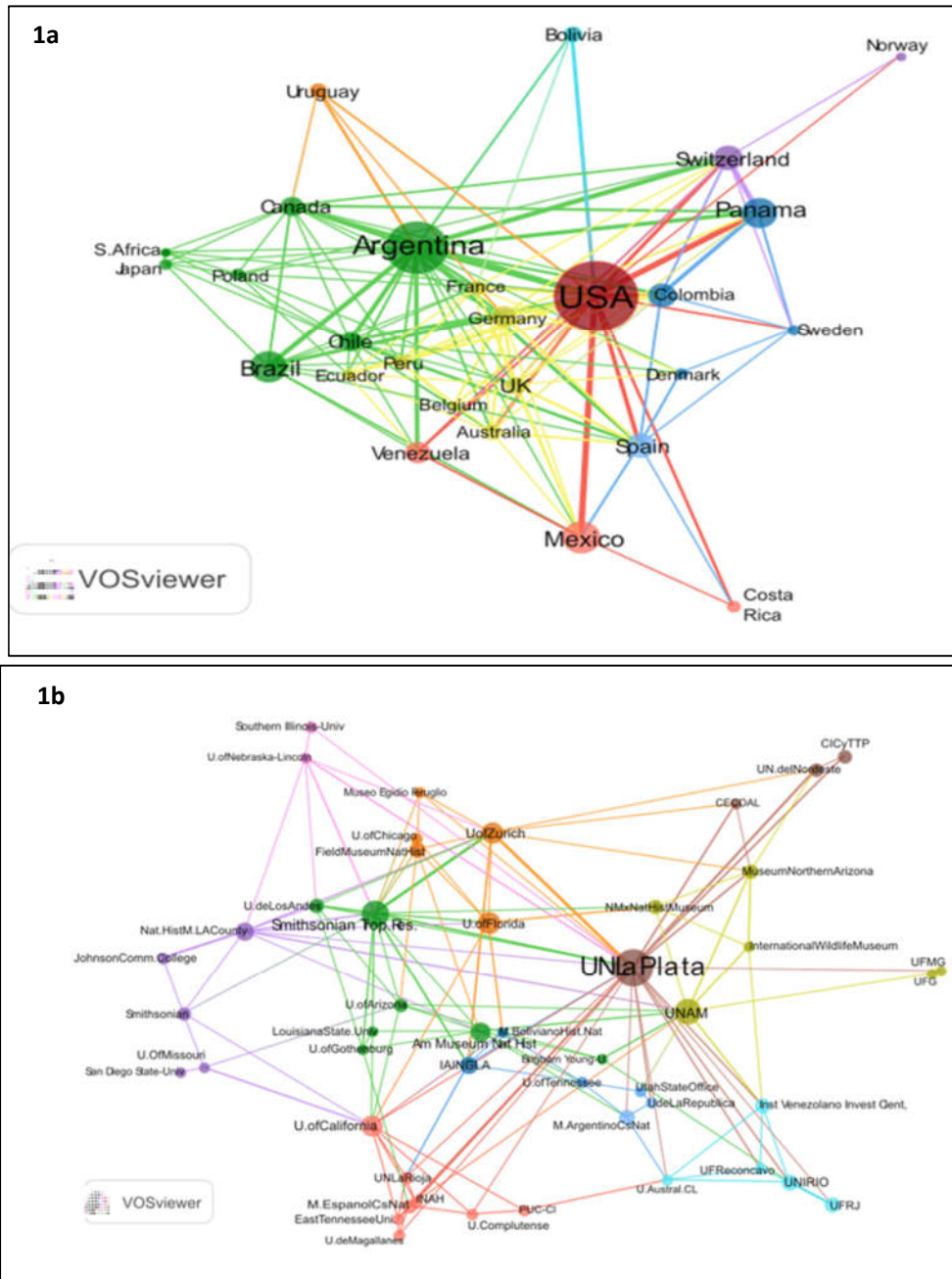


Figura 1. O tamanho dos círculos está determinado pela produtividade científica e as linhas representam vínculos cooperativos, quanto menor a distância maior o número de trabalhos conjuntos entre países (a) ou instituições (b). **a)** Rede global considerando a origem de todos os autores das publicações referentes ao GABI. Destacam três clusters principais, ao redor dos Estados Unidos (vermelho), da Argentina (verde) e do Panamá (azul). **b)** Network global de instituições agrupadas em nove principais clusters, liderados pela Universidad Nacional de La Plata (marrom), UNAM (amarelo), Smithsonian Tropical Research institute (verde). As instituições dos Estados Unidos ficam espalhadas no resto dos clusters, destacando-se The University of Florida (laranja).

A partir dos trabalhos mais antigos obtidos nesta busca (Marshall e Hecht, 1978 e Webb, 1978), se abrange um período de quatro décadas. Quando é considerada a origem do primeiro e último autor em cada trabalho, percebe-se que durante a década de 80 a produtividade foi liderada fora dos países latino-americanos. É a partir da década de 90 que aparecem os grupos de trabalho na região, aumentando pouco a pouco a produtividade na região, chegando a ser mais equilibrado na última década (Fig. 2a). No final, se consideramos o total global de primeiros e últimos autores, provêm de 30 países do mundo todo (Fig. 2b), sendo o 45% latino-americanos e 55% com origem fora da região.

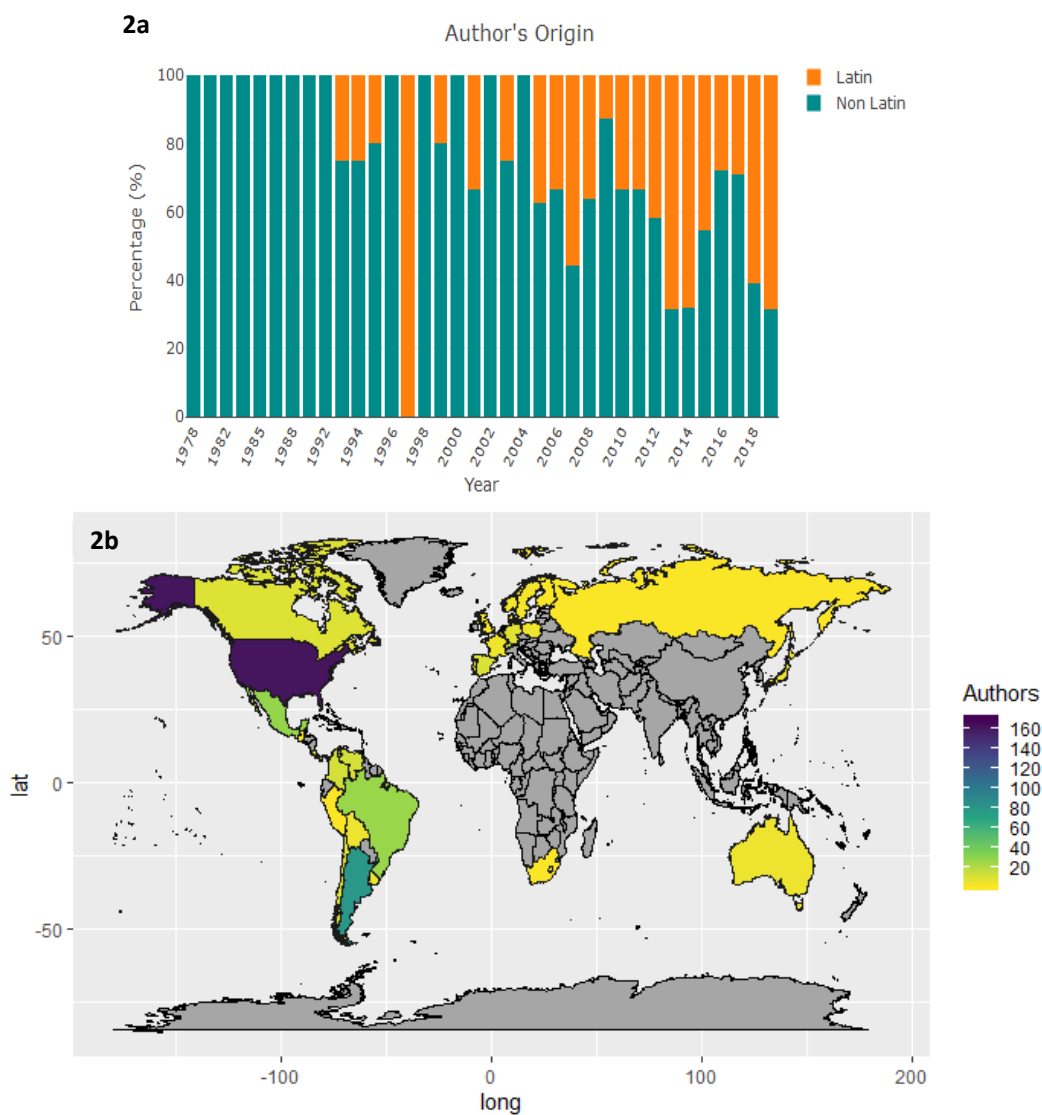


Figura 2: a) Porcentagem anual de trabalhos publicados para o período de 1978-2019 considerando apenas a origem do primeiro e último autor em cada publicação (Latino-americanos em laranja, não latino-americanos em verde). b) Distribuição mundial para primeiro e último autor.

a) As chaves do GABI

Extraímos um total de 861 palavras chaves, sendo o próprio termo “GABI” em todas suas variações, aquele que apresentou a maior frequência (n= 65). Do total de palavras, obtivemos 502 termos únicos que distribuídos nas cinco categorias estabelecidas da seguinte maneira: 152 táxons, 163 ecológicos, 74 geográficos e 113 geológicos (Tabela 2). A partir desses termos a estrutura dos meus diagramas *foamtree* foi determinada pela frequência e os termos englobados dentro de cada categoria.

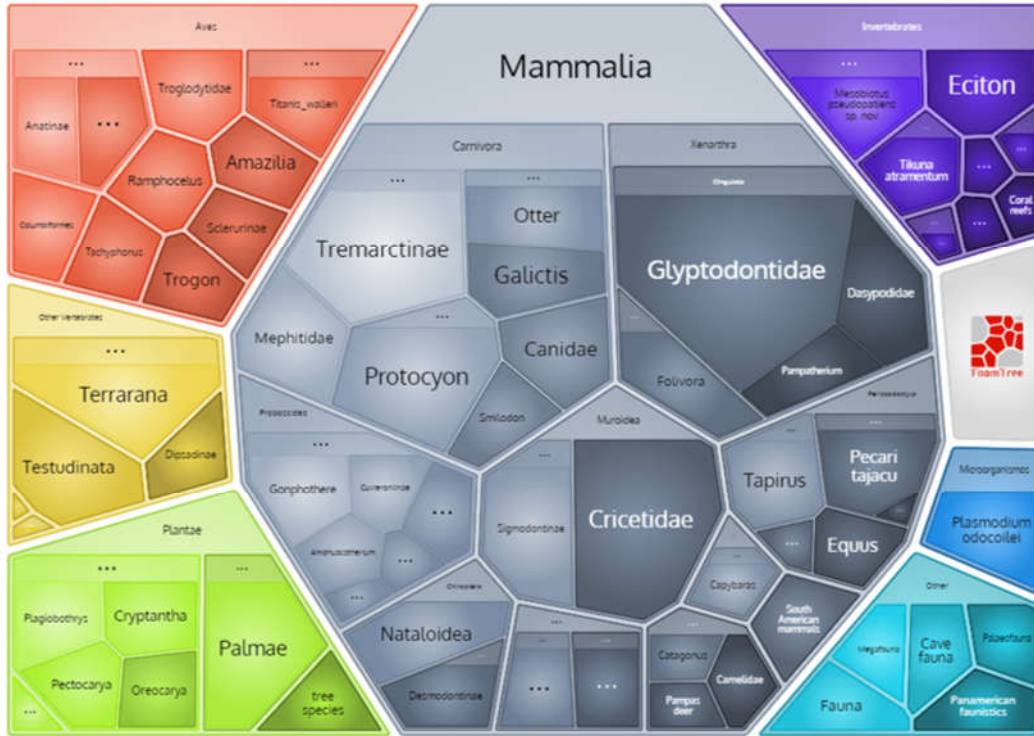
- Táxons: dentro deste diagrama foram criadas seis categorias cuja proporção espacial ficou distribuída da seguinte forma, mamíferos (53,7%), aves (15,7%), plantas (9,7%), invertebrados (9,7%), outros vertebrados (7,5%) e outros termos (3,7%) (Fig.3a).
- Ecologia: este diagrama foi estruturado com seis categorias, biodiversidade (46%) que incluiu processos, interações, traços, etc. Evolução (19%), Biogeografia (15,8%), Filogenia (11,4%), Ambiente (7%), Conservação (6%) e Macroecologia (2%) (Fig.3b).
- Geologia: este diagrama é integrado por oito categorias, Cenozoico (40%), Paleontologia (32%), Processos geológicos (20,8%), Mesozoico (4,6%), Isótopos (3,8%), Paleozoico (2,3%), Teoria do refúgio (2,3%) (Fig. 3c).
- Geografia: os critérios para conformar este diagrama foi baseado em critérios biogeográficos, ficando apenas três subcategorias abrangendo resto dos termos: Neotrópico (84,5%), Neártico (8,5%) e outros (7%) (Fig. 3d).

Tabela 2. Palavras chave com a maior frequência dentro das publicações científicas referentes ao GABI classificadas em quatro aspectos.

Palavras chave do GABI

Táxons	Ecologia	Geologia	Geografia
<i>Mammals</i> (n=13)	<i>Biogeography</i> (n=29)	<i>Pleistocene</i> (n=24)	<i>South America</i> (n=24)
<i>Carnivora</i> (n=11)	<i>Evolution</i> (n=13)	<i>Pliocene</i> (n=11)	<i>Neotropics</i> (n=16)
<i>Cingulata</i> (n= 5)	<i>Phylogeny</i> (n=12)	<i>Late Pleistocene</i> (n=6)	<i>Panamanian Isthmus</i> (n=11)
<i>Xenarthra</i> (n= 4)	<i>Taxonomy</i> (n=9)	<i>Quaternary</i> (n= 5)	<i>Central America</i> (n=5)

Figura. 3a



3b

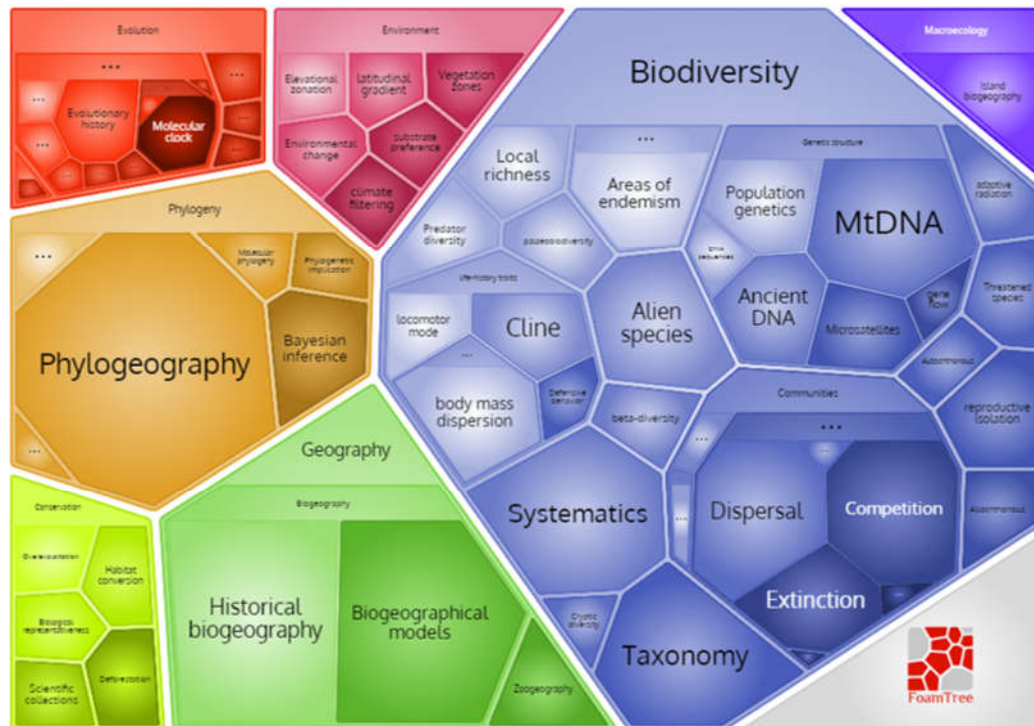
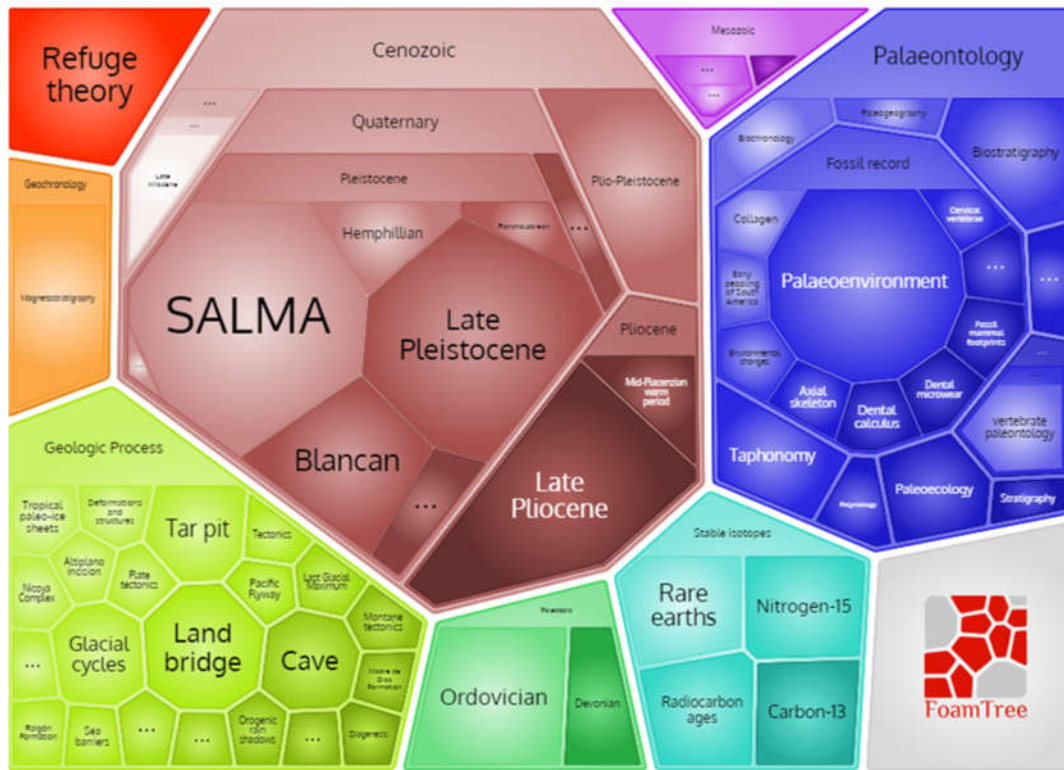


Figura 3. a) *Carrot foamtree* construído a partir da frequência das palavras chaves para os táxons do GABI. Os mamíferos representam o principal objeto de estudo (54%) destacando-se a ordem Carnívora e a superordem Xenarthra. b) *“Biogeography”* foi o termo mais frequente na literatura do GABI, embora *“biodiversity”* ocupe o maior espaço, isto é só derivado de agrupar a maioria dos termos sob sua influência.

3c



3d

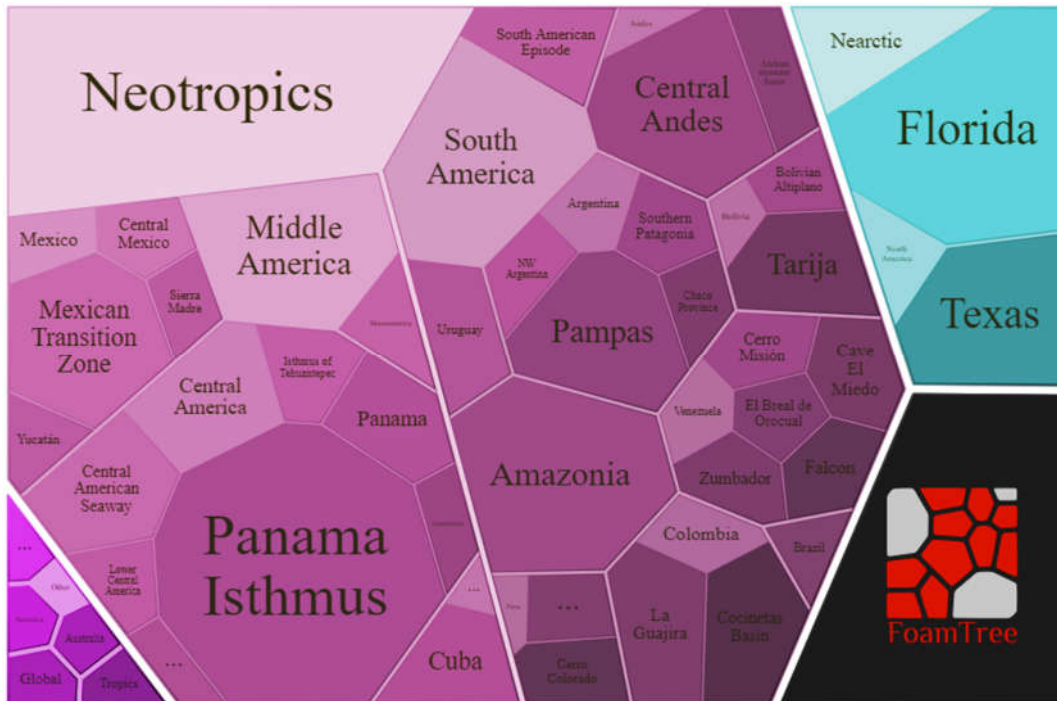
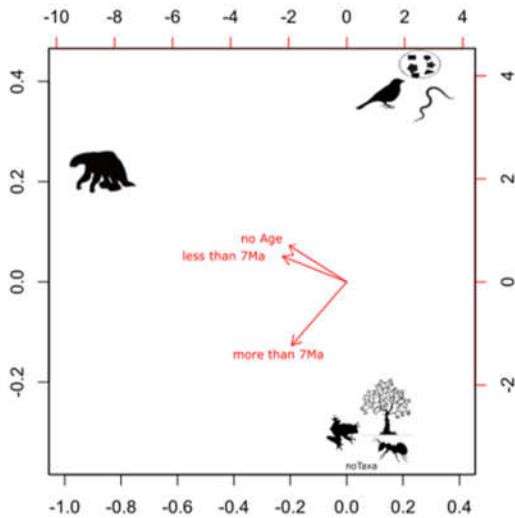


Figura 3. c) Embora a frequência de “*Quaternary*” não seja a maior, engloba “*Pleistocene*”. “*Paleontology*” ocupou um grande espaço do diagrama pelo número de termos incluídos dentro da categoria. d) Dentro dos termos geográficos, embora “*Neotropic*” foi o segundo mais frequente, foi colocado hierarquicamente acima do primeiro termo: “*South America*”.

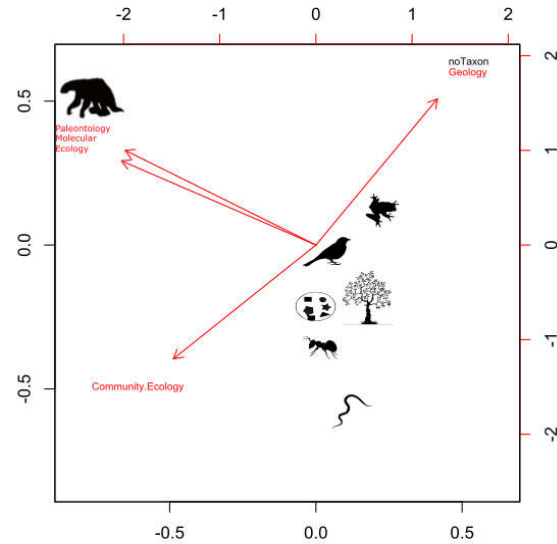
b) PCA

Os resultados obtidos na PCA indicam que a idade proposta para a formação da ponte terrestre entre as Américas e por tanto o começo do GABI depende do táxon estudado, os trabalhos realizados com mamíferos normalmente indicam uma idade mais recente (<7Ma), enquanto ectotermos (peixes, répteis e anfíbios), plantas e artrópodes indicam uma idade mais antiga (>7Ma) (Fig. 4a). Por outro lado, como já foi ressaltado pela análise das palavras chave, os mamíferos são o grupo mais estudado, especialmente pela paleontologia e ecologia molecular (Fig. 4b). Curiosamente, os mamíferos indicam idades contraditórias quando analisados em diferentes áreas de pesquisa, os mamíferos indicam uma idade recente ao serem analisados pelos paleontólogos, mas mais antiga quando submetidos a análises moleculares (Fig. 4c).

4a)



4b)



4c

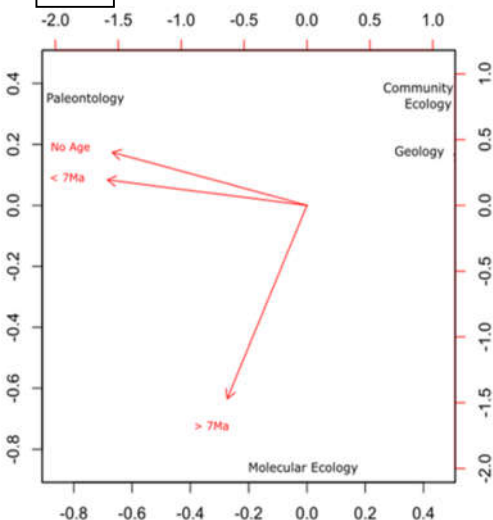


Figura 4. PCA correlacionando os diferentes táxons presentes na literatura do GABI: mamíferos, aves, vertebrados ectotérmicos (representados por uma rã), artrópodes (uma formiga), plantas, parasitas (helmintos e nematódeos) comunidades (representadas por figuras geométricas) ou sem táxon. 4a) correlação entre os organismos e três possíveis datas: <7Ma, >7Ma ou “No Age” quando os trabalhos não especificaram uma data da formação da ponte entre as Américas. 4b) correlação entre os diferentes grupos e quatro principais áreas de pesquisa: Geologia, Paleontologia, Ecologia molecular e ecologia de comunidades. 4c) Correlação das áreas de pesquisa com as datas previamente mencionadas.

c) Os experimentos do GABI

Embora o GABI seja considerado um grande experimento natural dentro da ecologia de comunidades, que pode permitir uma maior compreensão da dinâmica ecossistêmica, a proporção de trabalhos explorando aspectos de comunidade são os mínimos. A tabela 3 resume as publicações que tentam explicar os efeitos das correntes migratórias do *GABI* e seu efeito nas novas comunidades estabelecidas. Foram identificados 17 trabalhos, dos quais apenas dois foram aplicados na América Central (Pinto-Sánchez *et al.*, 2014 e Dick *et al.*, 2005) e mais três avaliaram ambas as Américas (Webb, 1991, Lessa *et al.* 1997, Stigall *et al.* 2017). Os restantes 11 trabalhos se focaram na América do Sul.

Tabela 3. Hipóteses relacionadas com o Grande intercambio biótico americano.

Fonte	Experimento	Resultado
Cassia-Silva and Sales (2019)	Conservadorismo de nicho por efeito restritivo das interações pós-GABI	Forças seletivas restringiram a evolução de traços de história de vida especialmente massa corporal.
López-Aguirre <i>et al.</i> (2017)	Fatores bióticos e abióticos como causa da extinção dos marsupiais carnívoros.	Interações não competitivas de tempo profundo junto com fatores abióticos derivaram na extinção deste grupo.
Stigall <i>et al.</i> 2017	Relação entre intercambio biótico e especiação com os padrões de diversidade.	Incremento na diversidade α , redução na diversidade β intercontinental e incremento final de diversidade γ .
Bacon <i>et al.</i> 2016	As mudanças climáticas da idade do gelo como desencadeante para o GABI nos mamíferos.	As mudanças climáticas e ambientais da idade de gelo formaram as condições de savana seca na América central que permitiram os mamíferos passar.
Yoshida and Tokita (2015)	Fragilidade estrutural dos ecossistemas permite invasões assimétricas.	Ecossistemas com taxas assimétricas de extinção têm cadeias alimentares curtas, maior proporção de espécies animais em relação a plantas e baixa proporção de carnívoros em relação a herbívoros.
Pinto-Sánchez <i>et al.</i> (2014)	Saturação de comunidades de Anfíbios na America Central.	Não existe evidência de saturação nas comunidades, pelo contrário um incremento dramático de riqueza regional.
Moreno-Bofarull <i>et al.</i> (2008)	Espécies generalistas tem menor especialização e taxa de extinção que especialistas (Hipótese de uso de recurso de Vrba)	A hipótese é suportada pela influência ecológica do GABI em combinação com as mudanças climáticas do passado como os modeladores evolutivos dos mamíferos na América do Sul

Tabela 3 (continuação) Hipóteses relacionadas com o Grande intercambio biótico americano.

Fonte	Hipótese	Conclusão
Dick <i>et al.</i> (2005)	Mistura equitativa de flora Norte e Sul-americana no Panamá e uma alta diversidade β , como consequência do <i>GABI</i> .	Não é possível explicar a diversidade β no Panamá desde a perspectiva histórica de colonização das espécies.
Croft (2001)	Reconstrução paleo-ambiental por meio de cenogramas.	A paleo-reconstrução pós GABI apresenta uma diversidade de predadores e ao mesmo tempo, mamíferos de porte maior ao esperado.
Rodríguez (2001)	Assimetria de vulnerabilidade nas invasões atuais, a fauna de origem norte-americano é mais resistente a invasores do que a de origem sul-americano.	Os táxons com maioria de espécies de origem sul-americano apresentam maior sensibilidade às invasões biológicas.
Lessa <i>et al.</i> (1997)	Extinção diferencial das Américas em função de massa corporal, nicho trófico e origem.	Não existe suporte para associar risco de extinção com nicho trófico e origem das espécies.
Vrba (1992)	A teoria do habitat como explicação do intercambio assimétrico de mamíferos.	Só migraram especialistas de ambientes abertos. A maioria das extinções foram de táxons de ambientes densos. E a diversidade orográfica sul-americana favoreceu a cladogênese.
Webb (1991)	Ecografia como explicação aos padrões atuais de distribuição dos mamíferos.	Os ciclos glaciais do Pleistoceno determinaram a migração entre as Américas, períodos quentes e húmidos favoreceram o fluxo S-N, períodos frios e secos o fluxo N-S.

Tabela 3. (Continuação) Hipóteses relacionadas com o Grande intercambio biótico americano.

Fonte	Hipótese	Conclusão
Marshall (1988)	Teoria do equilíbrio MacArthur-Wilson	A diferença na superfície dos continentes e a maior diversidade inicial da América do norte explicam o porquê do sucesso na invasão do Sul.
Marshall and Hecht (1978)	Mudanças climáticas e ecossistêmicas como origem do deslocamento das espécies na América do Sul	Não existe uma sobreposição de nicho entre as espécies do Norte e do Sul.
Webb (1978)	Existência de zonas adaptativas, com sobreposição de nicho.	Superioridade dos organismos holárticos na América do Sul e exclusão competitiva da fauna autóctone.

4. Discussão

Os resultados aqui obtidos apresentam os Estados Unidos (EUA) com a maior produção científica com respeito ao GABI, tanto em termos de trabalhos produzidos quanto de pesquisadores, instituições envolvidas e redes de trabalho com presença constante durante os quarenta anos abrangidos neste trabalho. Além disso, os trabalhos de pesquisadores de instituições dos EUA não estão apenas restritos ao seu próprio território (ex. Morgan e Lucas, 2003, Morgan e Emslie, 2010) como também no México e América Central (ex. Miller e Carranza-Castañeda, 2001, Tseng et al. 2017) e do Sul (ex. MacFadden et al. 1993, Croft, 2001, Shockey et al. 2007). Daí que ocupe o espaço central e o maior volume na rede de trabalho (Fig. 1a).

Embora durante a década de 80 a pesquisa sobre o GABI foi dominada pelos Estados Unidos, desde os primeiros anos da década de 90 outros países, principalmente da América latina, incrementaram pouco a pouco sua presença, passando a dirigir equipes de trabalho com ampla colaboração, não apenas regional, mas também global, modificando assim essa dominância. Destaca-se o caso da Argentina, quem equilibra a

balança para América lática e especialmente para a América do Sul. Ocupando o segundo lugar em produtividade, e assim como os EUA, a pesquisa argentina não está limitada dentro do seu território (ex. Castro et al., 2014, Perez et al., 2017 ou Boscaini et al., 2019).

Além da Argentina destacar como país, o padrão na network por instituições dá uma posição privilegiada para a *Universidad Nacional de La Plata* (UNLP), instituição que concentra a maior quantidade de pesquisa relacionada ao GABI (fig. 1b), marcando assim uma grande diferença com os EUA cuja pesquisa vem de numerosas instituições e está espalhada mais uniformemente pela network global.

No caso do Brasil e o México que ocupam a terceira e quarta posição e tem a mesma produção (7%) não é de estranhar sua posição na network, possivelmente influenciada pela sua localização geográfica, no caso do Brasil no mesmo cluster da Argentina, e o México no cluster dos EUA. Curiosamente o Brasil e o México apresentam uma analogia com Argentina e os EUA. No México uma instituição só, a UNAM, concentra a maioria das publicações, colocando-se na rede global como a segunda instituição, só após da UNLP. Já o Brasil, inclui mais organizações na network, decentralizando sua pesquisa.

Finalmente está o caso do Panamá, que pela sua produção tanto como países quanto como instituição (*The Smithsonian tropical research institute*) se ergue como o quinto país mais produtivo em termos de pesquisa e cooperação global, o que reflete com um cluster próprio no diagrama bibliométrico.

O protagonismo latino-americano, em cujo território se desenvolveram principalmente os acontecimentos do GABI vem se desenvolvendo gradualmente durante as últimas duas décadas. Embora a produção na região esteja concentrada desproporcionalmente na Argentina, Brasil e México, conforme se acrescentem novos países e mais descobrimentos ira-se integrando um melhor entendimento do *GABI*.

a) As chaves do GABI

Está amplamente reconhecido que o paradigma do GABI foi construído com um forte viés para com os mamíferos (Bacon et al. 2015, Pelegrin et al. 2018). Não é surpresa alguma então que olhando para os táxons das palavras chave, aqueles com a maior frequência estejam relacionadas aos mamíferos, o que também se reflete na configuração resultante no nosso diagrama *foamtree* (Fig. 3a). O termo “*Carnivora*” (e similares) ocupa

o maior espaço dentro do painel dos mamíferos, consequência da boa documentação paleontológica (ex. Verzi e Montalvo 2008 ou Wang e Carranza-Castañeda 2008, Rodrigues et al. 2016), molecular (ex. Koepfli et al. 2007) ou biogeográfica (ex. Wroe et al. 2004, Pedersen et al. 2014), isto pode estar relacionado com o fato de ser considerada a ordem que mais diversificou ao ter invadido a América do Sul experimentando uma radiação adaptativa explosiva (Prevosti e Forasiepi 2018).

O outro grupo destacado são os Xenarthra, ocupando o segundo maior painel dentro dos mamíferos, considerados os grandes protagonistas do GABI na América do Norte, por serem o grupo sul-americano com maior sucesso de colonização (McDonald, 2005; Webb, 2006), pela sua boa documentação, sua diversidade e ampla distribuição, tanto na América do Norte (ex. Gillette et al., 2016; McDonald et al., 2017) quanto na América do Sul (ex. Brandoni e Vezzosi, 2019; Moura et al., 2019) confere-lhes essa posição sobressaliente.

O GABI e a biogeografia sempre vieram se acompanhando, já reconhecido nos trabalhos de Wallace (Riddle e Hafner, 2010), que “*biogeography*” seja o termo mais frequente na literatura do GABI, ressalta esse vínculo e o grande interesse por explicar a história do padrão neotropical de diversidade e o papel cada vez mais importante que filogenia tem (“*phylogeny*” $n=12$) para desvendar esta história.

Desde os trabalhos de Simpson (1950 e 1980) na América do Sul, existe um grande interesse pelas consequências pós-GABI neste continente. Possivelmente este interesse, motiva pesquisadores de países e instituições de fora da região a trabalhar nele (ex. Shockey et al. 2009, Kaczmarek et al. 2016, Roberts et al. 2018), além do fato da América do Sul ter uma superfície maior e com mais países em comparação com América Central, que gera uma assimetria das pesquisas. Por exemplo, enquanto para América do Sul neste estudo registramos 133 autores, para América central (incluindo México) apenas 46.

b) PCA

Os resultados aqui apresentados indicam que a idade proposta para o GABI tem uma forte relação com a área de pesquisa. Em geral, a paleontologia indica idades mais recentes, enquanto a ecologia molecular sugere idades mais antigas. Isso é esperado, uma vez que essas áreas de pesquisa acessam diferentes evidências e indicam diferentes processos para o mesmo evento.

Os vieses inerentes à paleontologia podem ter contribuído com nossa concepção errada para a idade do *GABI*. Por exemplo, a probabilidade de fossilização, essencial para o estudo dos paleontólogos, é afetada pela idade do evento e tamanho populacional das espécies envolvidas (Kidwell e Flessa, 1995). Por passarem relativamente por menos intemperismo, eventos de fossilização mais recentes são mais bem preservados no registro fóssil (efeito “*the pull of the Recent*”; ver Fernandez-López, 2000) que pode ter enviesado a datação do GABI dada a grande quantidade de informação com idade menor do que 3,5Ma. Da mesma forma, por terem mais organismos possíveis de serem fossilizados, populações densas são mais prováveis de serem fossilizadas (Twitchett, 2001). Dessa forma, mesmo havendo migração entre os continentes durante ou anterior ao chamado proto-GABI (>7Ma), as pequenas populações de migrantes teriam uma chance muito pequena de serem fossilizadas e, portanto, acessadas pelos paleontólogos atualmente.

Por outro lado, temos a perspectiva da informação molecular. Já que a filogenia acessa à informação guardada no fluxo gênico, é possível a identificação de datas que escapam ao processo de fossilização. Assim, a evidência filogenética sugere deslocamentos mais antigos do que estabelece a informação paleontológica para diferentes grupos taxonômicos. Baseado no anterior, Bacon et al 2015 estabelece quatro correntes migratórias prévias à reconhecida para os mamíferos, 41Ma, 23.7Ma, 8.7Ma, e 5.2Ma (ver Jaramillo 2018).

c) Os experimentos do GABI

Diferentes experimentos ecológicos têm sido testados ao redor do *GABI* tentando explicar o processo de contato das biotas, principalmente do Norte no Sul e o resultado deste encontro. As teorias iniciais estavam fundamentadas apenas por interações bióticas (Webb, 1978) e pouco a pouco foram considerando outras variáveis que apenas a exclusão

competitiva. Além disso, tem se considerado não simplesmente uma perspectiva comunitária, mas também ecossistêmica. Assim temos hipóteses que incluem o fator climático (Marshall and Hecht, 1978; Webb, 1991; Bacon et al. 2016), traços funcionais (Lessa et al. 1997; Croft, 2001), história evolutiva (López-Aguirre et al. 2017; Cassia-Silva e Sales, 2019) ou aquelas hipóteses que testaram a estrutura ecossistêmica (Moreno-Bofarull et al. 2008; Yoshida e Tokita, 2015).

A literatura de ecologia de comunidades não escapa do padrão do GABI, fazendo do seu principal grupo de trabalho os mamíferos. Apenas um dos trabalhos avaliou um grupo animal diferente, anfíbios (Pinto-Sánchez et al, 2014) e mais um focou-se em comunidades vegetais (Dick et al. 2005). Assim, fica evidente a necessidade de incursionar nos outros grupos taxonômicos e avaliar o encontro Norte-Sul para essas biotas.

Finalmente, sob a premissa de uma idade mais antiga para a conexão terrestre das Américas e a proposta de existência de correntes migratórias alternadas por períodos de “estabilidade”, estabelece o desafio de entender esses novos cenários e testar novas hipóteses. Assim teremos um melhor entendimento da biogeografia do Novo Mundo.

5. Conclusão

O Grande intercâmbio biótico americano foi fundamental na configuração atual da biogeografia do Novo Mundo, porém é apenas uma das peças do quebra-cabeças que deu origem à região mais diversa do planeta. Conforme avança o conhecimento filogeográfico, a documentação do registro fóssil se amplia e o entendimento dos processos geológicos implicados no surgimento do Panamá melhoram, darão mais luz aos acontecimentos antes, durante e depois do *GABI*. Pela evidência geológica e molecular, tudo indica a uma idade mais antiga para a conexão das Américas e conseqüentemente para o fluxo migratório de organismos, fica por resolver, os fatores que impulsaram as diferentes correntes migratórias.

O foco do presente trabalho é o Grande intercambio biótico americano, e embora o surgimento do Istmo do Panamá esteja fortemente vinculado ao *GABI*, pois sem a ponte terrestre não teria a mesma magnitude ou não teria acontecido de fato. Ambos acontecimentos possuem uma literatura que merece ser analisada por si só e sem dúvida a maior informação e conhecimento do processo de formação do Panamá é chave no entendimento do *GABI*, porém, com os termos de busca aqui utilizados não é possível abranger uma visão panorâmica que integre o total da informação disponível para o processo geológico do surgimento da ponte, junto com o processo do *GABI*.

Este é o primeiro trabalho feito sobre o Grande intercambio biótico americano desde a perspectiva do mapeamento literário, até onde se sabe. A exploração de literatura derivada do manuseio de bases de dados poder ter algumas limitações, como pode ser a existência de falsos-negativos, porem alguns autores reconhecem que esse efeito pode ser amenizado contrastando as palavras chave com o título e o resumo (ver Sweileh et al. 2017) como realizado aqui.

Os resultados aqui apresentados foram obtidos a partir da exploração de bases que abrangem só revistas indexadas e completamente na língua inglesa, pelo que poderia representar um viés ou apenas uma fase da literatura total existente sobre o *GABI*. A busca e integração de literatura cinzenta espalhada nas instituições latino-americanas talvez jogariam um padrão distinto ao aqui apresentado que permitam um maior consenso e preenchimento das lacunas.

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CONSIDERAÇÕES FINAIS

Ao longo desta tese pude concluir que:

-O nicho α apresenta um padrão convergente para os mamíferos quando comparamos distância funcional e a distância filogenética. Já os nichos β e γ se apresentam como divergentes e mais influenciados pela filogenia;

-Diferente dos resultados filo-funcionais, o nicho alfa apresentou maior sinal filogenético contrário ao esperado. O nicho β também teve um resultado inesperado, apresentando o sinal mais baixo e γ valores intermediários entre α e β .

-Os nichos estão estruturados no espaço geográfico de forma oposta entre continentes e oceanos, demonstrando uma convergência continental com direção às altas latitudes, e em baixas latitudes nos oceanos;

-O nicho das comunidades mundiais de mamíferos recebe pouca influência das variáveis ambientais. Com relação às variáveis de altitude há uma forte influência filogenética, o que significa que poucos grupos de mamíferos possuem o nicho adequado para estas condições ambientais;

-Os Estados Unidos lideram por volume de pesquisadores e de instituições a produtividade científica com relação ao Grande Intercambio Biótico Americano. Embora esteja aumentando a participação latino-americana, a produtividade está concentrada em poucas instituições, da qual se destaca a Universidade Nacional de La Plata (Argentina), a Universidad Nacional Autónoma de México (México) e o Smithsonian (Panamá);

Em suma, nesta tese evidenciei a importância de explorar as diferentes escalas dentro do hipervolume do nicho. Cada escala apresenta um padrão evolutivo distinto, que não varia apenas pelas variáveis consideradas, mas também pela métrica utilizada. Para melhorar a percepção do nicho α , serão necessários refinamentos na escala geográfica, os quais devem incluir dados de profundidade para espécies marinhas, e avaliar a estruturação filogenética para outras variáveis ambientais, tais como precipitação ou potencial de evapotranspiração.