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Dissertação de Mestrado

Discriminando múltiplos fatores determinantes da partição de nicho em pequenos mamíferos sul-americanos

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Porto Alegre, Abril de 2013

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"Da liberdade de explorar vem a alegria de aprender. Do conhecimento adquirido pela iniciativa pessoal advém o desejo de obter mais conhecimentos. Cultivar um naturalista é como cultivar um músico ou um atleta: excelência para os talentosos, prazer por toda a vida para os demais, benefício para toda a humanidade".

Edward O. Wilson

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RESUMO

A estruturação em comunidades biológicas sugere que há fatores que determinam quais espécies poderão ocorrer juntas. Os pequenos mamíferos sul-americanos (marsupiais e roedores cricetídeos) apresentam um padrão de dispersão no continente sul-americano bastante distinto. Os marsupiais chegaram ao continente há cerca de 100 milhões de anos e os roedores cricetídeos o colonizaram apenas na formação do Istmo do Panamá em aproximadamente 2,5 milhões de anos. Atualmente esses dois grupos ocupam nichos bastante diversos e também específicos. O objetivo geral desta dissertação é explorar padrões funcionais entre pequenos mamíferos sul-americanos, apresentando uma nova métrica de análise e discriminando os principais mecanismos que estruturam esses padrões. Assim, ela está dividida em dois capítulos: o primeiro apresenta uma nova abordagem analítica para o cálculo de divergência funcional entre clados coocorrentes na mesma comunidade; o segundo trata de avaliar os principais determinantes da divergência funcional entre marsupiais e roedores cricetídeos sul-americanos. A métrica desenvolvida no primeiro capítulo foi adaptada da abordagem de diversidade beta funcional, entretanto, ao invés de compararmos pares de comunidades, comparamos pares de clados que coocorrem na mesma comunidade, distinguindo o quanto similiar ou diferente funcionalmente esses clados são. No segundo capítulo, verificamos que fatores ambientais, funcionais, históricos e evolutivos influenciam a divergência funcional entre os dois clados aqui estudados. Além disso, nós encontramos uma tendência de aumento da diferenciação de nicho entre marsupiais e roedores cricetídeos em direção ao norte do continente sul-americano. Nós podemos inferir que a porta de entrada da colonização dos roedores cricetídeos no continente determina, ainda hoje, padrões de funcionalidade dos ambientes, além de outros fatores importantes como o clima.

Palavras-chave: divergência funcional, pequenos mamíferos, diferenciação de nicho, América do Sul

ABSTRACT

The existence of structure in biological communities suggests that there are factors that determine which species may occur together. Small mammals of South America (marsupials and cricetid rodents) show a pattern of dispersal in this continent quite different and interesting. Marsupials arrived on South American continent about 100 million years and cricetid rodents only colonized it in the formation of the Isthmus of Panama, approximately 2.5 million years. Currently, these two groups occupy several and specific niches. The major goal of this thesis is to explore functional patterns among small mammals in South America, presenting an analytical novelty and discriminating mechanisms that driving these patterns. Thus it is divided into two chapters: the first presents a new functional approach for the calculation of functional divergence among clades co-occurring in the same community; the second evaluates the main drivers of functional divergence between marsupials and cricetid rodents in South America. The metric developed in the first chapter was adapted from the approach of functional beta diversity, however, instead of comparing pairs of communities, we compared pairs of clades co-occurring in the same community, discriminating how functionally similar or different these clades are. In the second chapter, we found that environmental, functional, evolutionary and historical factors determine the functional divergence among two clades studied here. Furthermore, we found a trend of increased niche differentiation between marsupials and cricetid rodents northward South American continent. We may infer that the gateway of cricetid rodents already determines patterns of functionality in environments nowadays, beyond other important factors, like climate.

Key-words: functional divergence, small mammals, niche differentiation, South America

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Capítulo 2.

Figure 1 Steps to obtaining the mean functional distance between marsupials and cricetids within each community. We obtain the Gower's distance matrix from the trait matrix and, then, the functional dendrogram. C1 represents community 1 containing four species (two marsupials and two cricetids). 1 e 2 represent sum of branch lengths that connect one cricetid to marsupials; 3 e 4 represent sum of branch lengths that connect the other cricetid to marsupials. The mean of these sums will be the MFD observed.

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Capítulo 1.

Table 1: Results of functional divergence for the scenario 1 (trait 1) and 2 (trait 2) for community 1 (C1) and community 2 (C2). It shows the same structure of function output file in R environment. ‘N taxa A’ corresponds to species number in clade A;’ N taxa B’ corresponds to species number in clade B; ‘MFD_{obs}’ corresponds to mean functional distance between two clades; ‘$MFD_{Random.mean}$’ corresponds to the mean null mfd values; ’$MFD_{Random.sd}$’ corresponds to standard deviation of mean MFD_{Null}; ‘$SES.MFD_{obs}$’ corresponds to standardized effect size of MFD (ses.mfd); ‘MFD_{obs} p’ corresponds to probability of MFD_{Obs} being generated by chance.

Introdução Geral

Perspectivas ecológicas e a Macroecologia

A existência de estrutura em comunidades biológicas sugere que há fatores que determinam quais espécies poderão ocorrer juntas. A compreensão dos fatores que explicam a variação nos padrões de riqueza e diversidade observados dentro e entre comunidades é um dos principais objetivos em ecologia de comunidades (Kraft *et al*. 2007). Esses padrões têm sido explicados principalmente pelos mecanismos relacionados às interações com o ambiente e com outras espécies, como filtros ambientais e diferenciação de nicho, ou ainda por processos estocásticos, nos quais o papel das interações entre as espécies é considerado pouco relevante (Hubbell 2001). No início da década de 1990, os estudos ecológicos começaram a direcionar sua atenção para outra dimensão da estruturação de comunidades: o componente histórico da relação entre as espécies (Ackerly e Donoghue 1995).

A integração de uma perspectiva histórica no contexto da ecologia de comunidades vem sendo cada vez mais utilizada, pois a forma como as comunidades se estruturam no presente também é um reflexo das histórias evolutivas das espécies que compõem essas comunidades (Webb *et al*., 2002). Desta forma, os padrões de diversidade são influenciados tanto por fatores ecológicos locais quanto por circunstâncias históricas e geográficas (Rickfles & Schluter, 1993). Processos regionais podem influenciar tanto a diversidade regional quanto a diversidade local e, portanto, torna-se imprescindível entender as comunidades locais através dessas perspectivas históricas (Ricklefs & Schluter, 1993). Apesar da dimensão histórica ter sido incorporada nas análises ecológicas apenas nas últimas décadas, Darwin (1859) já havia constatado que as espécies mais próximas (filogeneticamente) sofreriam uma competição mais intensa entre si do que com espécies mais distantes.

A disciplina de macroecologia, proposta por Brown e Maurer (1989), surgiu da necessidade dos ecólogos de incorporar simultaneamente perspectivas históricas e geográficas em estudos visando compreender mais completamente a abundância local, distribuição e diversidade de espécies nas comunidades ecológicas. Visto por outro ângulo, a macroecologia se utiliza de uma perspectiva ecológica a fim de compreender a história e a composição das biotas continentais e regionais (Brown, 1995). Ou seja, ela surgiu como uma forma de explorar a interface entre as tradicionais disciplinas da biogeografia e da ecologia de comunidades e, pode também ser vista, como uma forma de estudar as relações entre os organismos e seu ambiente, caracterizando e explicando padrões estatísticos de abundância, distribuição geográfica e diversidade (Brown, 1995).

Se por um lado, estudos biogeográficos têm há muito analisado os efeitos de condições ambientais do passado e do presente sobre a distribuição geográfica das espécies e a associação entre a história da vida na Terra e as relações filogenéticas entre os organismos, estudos de ecologia de comunidades têm como objetivo analisar os processos que regulam a abundância, distribuição e diversidade de espécies em comunidades locais (Brown, 1995). Além disso, a ecologia de comunidades se propõe a investigar a natureza das interações entre os organismos, suas origens e suas consequências ecológicas e evolutivas (Cavender-Bares *et al*., 2009). A integração entre estas duas abordagens permite-nos analisar até que ponto padrões geográficos de distribuição das espécies e sua interação com fatores ambientais explicam porque as comunidades são como são, explorando as interações funcionais entre as espécies.

A análise de padrões de organizações de comunidades, através da integração dos atributos das espécies que ali coocorrem, pode ajudar a entender processos relacionados a interações biológicas entre as espécies. Interações interespecíficas também são muito importantes na estruturação das comunidades. A forma como as espécies interagem

entre si (por competição, por exemplo) determina também como elas respondem às restrições ecológicas (Mouilott *et al.*, 2007). Por sua vez, tanto gradientes ambientais quanto a história evolutiva de diferentes clados filogenéticos podem afetar a variação de atributos ecológicos nas espécies que compõem as comunidades (Cavender-Bares *et al*., 2009; Swenson & Enquist, 2009) e interferir na forma como essas espécies coocorrem. Assim, é possível avaliar a variação destas características a partir de métricas de diversidade funcional das comunidades (Pavoine & Bonsall, 2010).

Medidas de diversidade funcionais geralmente expressam a comunidade como um todo, seja dentro ou entre comunidades. Assim, a comunidade é tida como uma unidade fechada e única. Integrar alguma medida que avalie diferenças funcionais entre grupos dentro de uma mesma comunidade é muito relevante para que possamos analisar outro ângulo da comunidade: as relações funcionais entre espécies (ou grupos de espécies) que coocorrem em uma mesma comunidade. Mais interessante ainda é poder relacionar diferentes clados com diferentes histórias evolutivas, nos quais podem expressar distintos padrões de funcionalidade do ecossistema e ainda mostrar processos de partição de nicho entre diferentes grupos.

O conceito de nicho, tão fundamental dentro da Ecologia, é um dos pontos centrais nessa abordagem funcional, pois nos permite entender quais espécies coexistem (Emery *et al*., 2012; Ackerly *et al*., 2006). Tanto as diferenças entre os nichos das espécies (Chesson, 2000) quanto suas habilidades competitivas (Mayfield *et al.*, 2010) são fundamentais para que haja coexistência entre elas. Uma abordagem bastante interessante é relacionar o nicho aos padrões de distribuição amplos descritos acima, como gradiente latitudinal de riqueza e diversidade, por exemplo. Vázquez & Stevens (2004) apresentam a hipótese da amplitude de nicho, na qual os nichos das espécies se tornam mais estreitos em direção aos trópicos.

Pequenos mamíferos não voadores sul-americanos

Os pequenos mamíferos não voadores sul-americanos são bastante interessantes para explorar a relação de funcionalidade com questões históricas e geográficas pois possuem histórias biogeográficas bastante distintas. Eles são representados principalmente pelas famílias Didelphidae (entre os marsupiais) e Cricetidae (entre os roedores) que podem apresentar tanto espécies com ampla distribuição quanto aquelas com distribuição restrita (Cáceres *et al*., 2008).

Os marsupiais constituíram-se em um dos mais importantes elementos faunísticos ao longo do Terciário sul-americano (Oliveira & Goin, 2012). Sugere-se uma origem norte-americana para os marsupiais, provavelmente a cerca de 100 milhões de anos (Oliveira & Goin, 2012), quando a América do Sul ainda era parte do supercontinente Gonduana. A família Didelphidae é a mais diversa dentre as famílias de marsupiais viventes no Novo Mundo (Braun *et al*., 2005), ocupando uma variedade de nichos, tanto alimentares quanto espacias (Delciellos & Vieria, 2006).

Os roedores tiveram duas principais colonizações na América do Sul: os roedores Hystricognathi ou Caviomorpha são bem representados do final do Eoceno (cerca de 40 milhões de anos) até o presente; os roedores Sigmodontines da América do Sul (Família Cricetidae) derivam de uma série de invasões, nas quais foram mais acentuadas no Plioceno (Eisenberg & Redford, 1989). Certamente, uma das mais importantes influências externas na história da biota sul-americana desde o Paleoceno foi o intercâmbio entre os continentes americanos, o Istmo do Panamá, há aproximadamente 2,5 milhões de anos (Eisenberg & Redford, 1989).

Os roedores cricetídeos da subfamília Sigmodontinae formam o grupo com maior diversidade de espécies dentre os mamíferos do Novo Mundo (D´Elia *et al*., 2006). Os sigmondontines estão distribuídos predominantemente na América do Sul

(cerca de 60 genêros endêmicos), embora eles também alcancem as Américas Central e Norte (D´Elia, 2003). Os roedores da família Cricetidae apresentam uma enorme variedade de grupos ecomorfológicos, tais como: terrícolas, arborícolas, semiaquáticos e fossoriais (Reis *et al*., 2011).

Considerando as ideias propostas até o momento, esta dissertação está dividida em dois capítulos. O primeiro capítulo tem o objetivo de descrever um método proposto para avaliar a divergência funcional entre dois clados coocorrentes na mesma comunidade. Ele apresenta a descrição detalhada do método, exemplifica-o. O segundo capítulo tem o objetivo de avaliar os principais determinantes da divergência funcional entre marsupiais e roedores cricetídeos sul-americanos, avaliando fatores relacionados à história biogeográfica dos clados, a gradientes ambientais e à funcionalidade de cada um dos grupos.

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Abstract

Many functional metrics have been described over the last years. Incorporating some metric evaluating the functional variation within communities enable us to estimate the degree of niche partitioning between co-occurring species belonging to different lineages within a community. We propose a metric that allows us to estimate the amount of functional divergence between groups of co-occurring species belonging to different lineages. To calculate the functional divergence between two clades we need three matrices: a matrix describing species occurrences or abundances across an array of communities, a matrix describing each species by a set of functional traits (that it will be transformed in a trait distance matrix), and a matrix defining the clade to which each species belong. We calculated the mean functional distance (MFD) between the species belonging to each phylogenetic clade and compare this value to a null model (SES.MFD). Positive values indicate high degree of niche partitioning because clades are very functionally different. On the other hand, negative values indicate niche overlap because the clades are very similar to each other in such set of traits considered. This metric benefits ecologists wishing to understand how clades co-occur in determined community, inferring niche based-processes.

Key-words community functionality, functional difference, niche partitioning, mean functional distance between two clades

Introduction

Historically, ecologists describe community structure using biodiversity indices based on species occurrences or abundances (Pavoine & Bonsall 2010). However, recently, studies have focused on other components of biodiversity, incorporating concepts like functional and phylogenetic diversity (Petchey & Gaston 2006; Webb et al. 2002). Functional diversity is usually described by three kinds of indices that express different parts of the functional component: functional richness, functional evenness and functional diversity (or, according to Schleuter et al. 2010, functional divergence). These indices describe "how much of the functional niche space is filled by the existing species (functional richness) and how niche space is filled (functional evenness and functional divergence/variance)" (Schleuter et al. 2010). The metric called functional divergence by Schleuter et al. (2010) also incorporates measures of functional diversity. Indeed, functional metrics allow us to look at communities from another angle, since they express the ways organisms are influenced by and/or determine the ecosystem functioning and dynamics (Tilman 2001). Mason et al. (2005) highlighted that functional difference between species within a community received more attention in last decade. In this study, we define functional divergence as the functional variation among two clades co-occurring in the same community.

Many functional metrics have been described over the last years; some reviews of methodological novelties regarding the assessment of functional diversity can be verify in Schleuter et al. (2010), Pavoine & Bonsall (2010), Petchey & Gaston (2006) and Ricotta (2005). Functional metrics usually express the community as a whole (alpha diversity) or values between communities (beta diversity). Thus, the community remains like a closed unit. Although Mason et al. (2005) have also incorporated the concept of functional divergence in their study, the methodological approach proposed

by them still considers all species together within the community. Now, incorporating some metric enabling us to evaluate the functional variation among clades within the communities is very relevant because it show us one more angle of community: the functional relationship between the co-occurring species that compose it. Still more interesting, it might represent an opportunity to understand how clades carrying divergent evolutionary histories might co-occur and change ecosystem functionality. This is a central topic in ecology currently.

Here, we propose a metric of functional divergence between pairs of phylogenetic clades co-occurring within a single community. For this, we adapted a framework underlying the concept of functional beta diversity to assess functional divergence between pairs of phylogenetic clades co-occurring in a single community, instead of comparing pairs of communities as a whole. Such metric allows us to estimate the amount of niche partitioning between different groups of co-occurring species lineages.

Material e Methods

Description of Functional Divergence

In order to calculate the metric of functional divergence, we need three matrices: a matrix describing species occurrences or abundances across an array of communities, a matrix describing each species by a set of functional traits, and a matrix defining the clade to which each species belong (each species must belong to any of two clade-defined groups). The trait matrix may contain only one or several traits.

The first step is to obtain a distance matrix between species directly from the species-by-traits matrix or from a functional dendrogram (Petchey & Gaston 2002). If you choose to obtain the distances from a dendrogram, the functional distance among

species will be based on the branch lengths of the dendrogram, following the same approach used by Petchey & Gaston (2002) to measure of functional diversity (FD). FD is defined as the sum of branch lengths of the functional dendrogram necessary to connect all the species present in a local community (Petchey & Gaston (2002).

To obtain an estimate of functional divergence between two phylogenetic clades in each community, we calculated the mean functional distance (MFD) among species belonging to each phylogenetic clades. The MFD metric provides a measure of dispersion of functional traits among species belonging to different clades and co-occurring within the same community. The basic idea underlying the MFD metric was adapted directly from a widely known metric developed to measure the mean phylogenetic distance between species occurring in two different communities, the *comdist* function from Picante package in R environment (Kembel *et al*. 2010).

To evaluate the probability of an observed MFD value (MFD_{Obs}) being generated by chance, we built a null model in which taxa vectors were randomly shuffled across the functional distance matrix used to calculate MFD_{Obs}. Label shuffling was repeated for a given number of times (say 999). At each label shuffling, a null MFD (MFD_{Null}) was computed. To calculate the probability of MFD_{Obs} being generated by chance, we counted the number of MFD_{Null} values $\geq MFD_{Obs}$/ 999+1. Furthermore, in order to make MFD_{Obs} comparable among communities, we computed a standardized effect size (SES.MFD) as follows:

$$\text{SES.MFD} = \frac{\text{MFD}_{Obs} - \text{Mean MFD}_{Null}}{\text{Standard deviation MFD}_{Null}}$$

Positive values of SES.MFD indicate high functional divergence between two phylogenetic clades occurring in the community; in other words, clades show high degree of niche partitioning, for a given p-value of functional divergence being

generated by chance. On the contrary, negative values indicate that clades co-occurring in a community show functionally similar species, which indicates niche overlap. P values less than 0.025 or more than 0.975 indicate functional divergence more and less, respectively, than expected by chance, for an alpha value of 0.05.

We performed all measurements in R environment (R Core Team 2013). The complete function is available in the supplementary material 1 and 2.

Results

Example: Simulated communities

We built simulated communities to test the use of MFD metric. The regional species pool contains ten species; five belonging to clade A and five belonging to clade B (Fig. 1). We created two communities, one containing all species and other containing only six species (Figure 1). Trait 1 variability is small in the species belong to clade A and large in those belonging to clade B (T1 in Figure 1). Trait 2 is large or small, independently of the clade to which species belong (T2 in Figure 1). To facilitate the metric understanding, we used one trait individually (T1 or T2), however we would use a trait matrix with several traits together. For each simulated community we computed SES.MFD, considering trait 1 or 2 separately.

The function output file in R environment contains the following information: 1) species number of each clade; 2) mean functional distance between two clades (MFD_{Obs}); 3) mean null MFD values (MFD_{Null}); 4) standard deviation of Mean MFD_{Null}; 5) ranking of MFD_{Obs} in relation to the number of MFD_{Null} values; 6) standardized effect size of MFD (SES.MFD) and probability of MFD_{Obs} being generated by chance.

In the first scenario (T1 in Figure 1), species belonging to a given clade are very similar to each other, but functionally different from species belonging to the other

clade. And since the number of species change (C1 and C2 in Table 1), the trend is the same because the species in each clade maintain very functionally different to the other clade. SES.MPD values are positive, showing that clades present high functional divergence (Table 1), and ultimately, high niche partitioning. In the second scenario (T2 in Figure 1), species trait varies among species independently of the clade to which species belong. In this case, SES.MFD values are lower than those observed in T1 (Table 1), also showing negative values (that could imply in niche overlapping among groups.

Conclusion

This new approach allows us to evaluate how different groups of organisms are related to, evoking niche-based processes. Further, this benefits ecologists that wish understanding how the species, or groups of species, co-occur in determined community. Actually, what the functional relationship among them is. It can be also used to understand biogeographical patterns because different clades with distinct evolutionary histories can present several functional patterns.

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TABLE

Table 1: Results of functional divergence for the scenario 1 (trait 1) and 2 (trait 2) for community 1 (C1) and community 2 (C2). It shows the same structure of function output file in R environment. 'N taxa A' corresponds to species number in clade A;' N taxa B' corresponds to species number in clade B; 'MFD_{obs}' corresponds to mean functional distance between two clades; '$MFD_{Random.mean}$' corresponds to the mean null mfd values; '$MFD_{Random.sd}$' corresponds to standard deviation of mean MFD_{Null}; '$SES.MFD_{obs}$' corresponds to standardized effect size of MFD (ses.mfd); 'MFD_{obs} p' corresponds to probability of MFD_{Obs} being generated by chance.

	N taxa A	N taxa B	MFD_{obs}	$MFD_{Random.mean}$	$MFD_{Random.\ sd}$	$SES.MFD_{obs}$	MFD_{obs} p
Trait 1							
C 1	5	5	7.2	4.347	0.489	5.829	0.996
C 2	3	3	7	4.355	0.921	2.871	0.967
Trait 2							
C 1	5	5	3.56	3.941	0.439	-0.868	0.092
C 2	3	3	0.78	3.929	0.868	-3.632	0.003

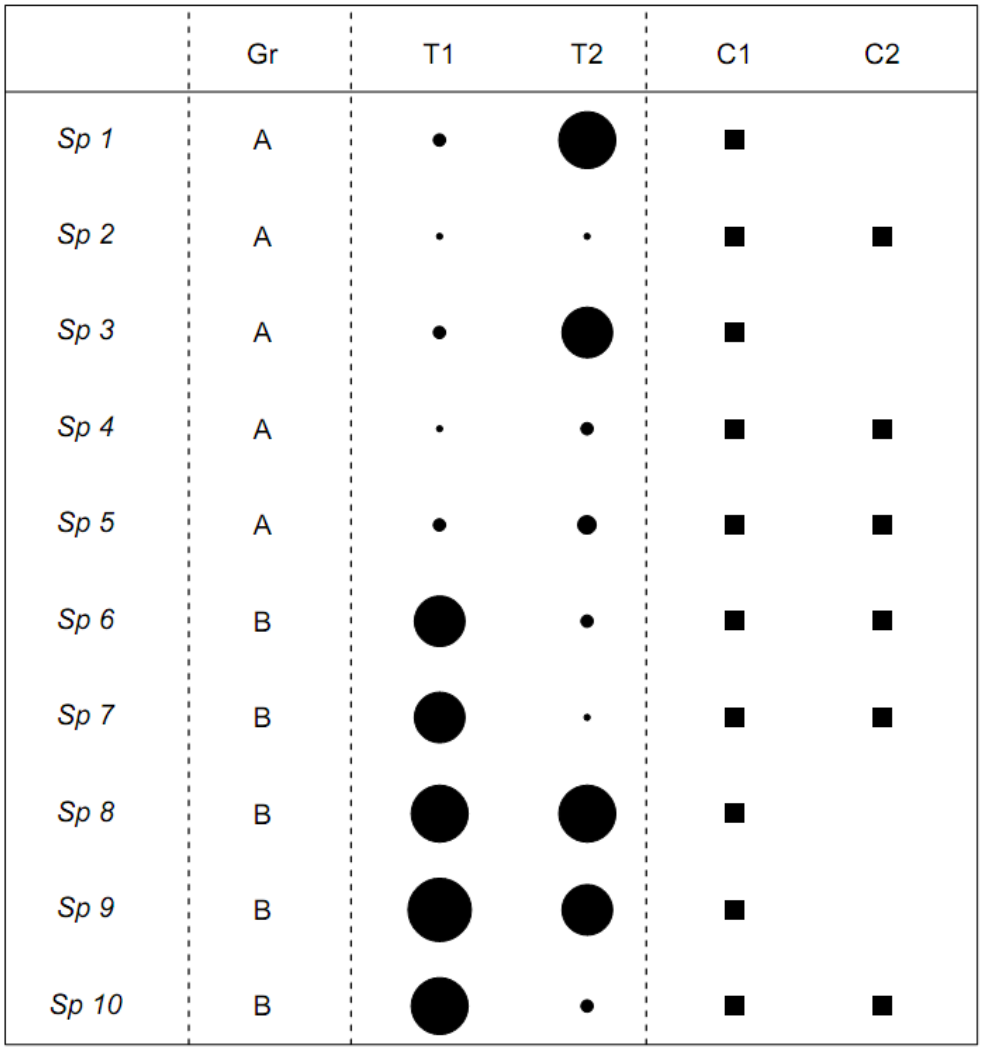

Figure 1: Example of simulated communities for understanding the metric of functional divergence. Species are represented by Sp 1 to Sp 10; Gr corresponds clades to which species belong (A and B); T1 corresponds to trait 1; T2 corresponds to trait 2; two communities are represented by C1 and C2. Circle sizes represent different values of traits. Similar sizes correspond to similar values of traits and represent species that are functional more similar. Squares represent presence of each species in communities.

SUPPORTING INFORMATION

Supporting Information 1: Descriptive manual of functional divergence function in R environment.

Supporting Information 2: Function for usage in R environment.

Supplementary material 1: Descriptive manual of functional divergence function (ses.mfd.groups) in R environment.
Function name: ses.mfd.groups
Title: Calculates mean functional distance among two groups within community
Description: Calculates mean functional distance separating two taxa groups into the same community, a measure of functional divergence among groups

Usage: ses.mfd.groups(comm, dis, groups,abundance.weighted = FALSE, permutations=999)

Arguments:

- comm = Community data with species as columns and sampling units as rows.
- dis = Interspecific distance matrix.
- groups = Factor giving the groups for each species, with species as rows.
- abundance.weighted = considering species abundances in mean pairwise distances separating two taxa groups within communities (Default abundance.weighted = FALSE)
- permutations = Number of randomizations

Values:

- groups = The levels in groups.
- results = A data frame containing the number of taxa in each group, the observed mean functional distance between two groups within each community, the mean and standard deviation of null mean functional distance values, the rank of mean functional distance observed, the standardized effect size of mean functional distance and probability of mean functional distance observed being generated by chance.

Notes:

- If any community does not have species of the one group, results of observed values will be zero and the function will not calculate standardized effect size of mean functional distance between two groups within each community, returning a 'NA'.
- The names of species must be presented in rows of 'group' argument, columns of 'comm' argument and rows and columns of 'dis' argument.

Dependent packages:

- Vegan
- Picante
- Ape

Example:

```
comm<-matrix(NA,2,10)
colnames(comm)=colnames(comm,FALSE,"sp_")
rownames(comm)=rownames(comm,FALSE,"com_")
comm[1,]=1
comm[2,]=c(1,1,0,1,1,0,1,1,1,1)
comm
```

```
spp<-matrix(NA,10,1)
colnames(spp)=colnames(spp,FALSE,"T")
rownames(spp)=rownames(spp,FALSE,"sp_")
spp[,1]=c(2,2,2,2,2,6,6,6,6,6)
spp
dis<-vegdist(spp,method="euclidean")
dis

groups<-matrix(NA,10,1)
rownames(groups)=rownames(groups,FALSE,"sp_")
colnames(groups)=c("Gr")
groups[,1]=c(rep("A",5),rep("B",5))
groups

ses.mfd.groups(comm,dis,groups)
```

Supplementary material 2: Comdist.groups function for usage in R environment.

```
#####################################################################
#####################################################################

## Function

ses.mfd.groups<-function (comm, dis, groups,abundance.weighted = FALSE,
permutations=999)
{
        comm<-as.matrix(comm)
        dis<-as.matrix(dis)
        groups<-as.matrix(groups)
        rownames(comm)=rownames(comm,do.NULL=FALSE,prefix="comm_")
        colnames(groups)=colnames(groups,do.NULL=FALSE)
        if (!abundance.weighted) {
        comm <- decostand(comm, method = "pa")
        }
        if (is.null(colnames(dis))) {
                stop("\n Error in column names of dis\n")
        }
        if (is.null(rownames(dis))) {
                stop("\n Error in row names of dis\n")
        }
        if (is.null(rownames(groups))) {
                stop("\n Error in row names of groups\n")
        }
        if (is.null(colnames(comm))) {
                stop("\n Error in column names of comm\n")
        }
        if(length(which((sort(colnames(comm))==sort(rownames(groups)))=="FALSE")
)>0|dim(comm)[2]!=dim(groups)[1]){
                stop("\n Colnames in comm do not match with row names of groups\n")
        }
        if(length(which((sort(colnames(comm))==sort(rownames(dis)))=="FALSE"))>0
|dim(comm)[2]!=dim(dis)[1]){
        stop("\n Colnames in comm do not match with row names of dis\n")
        }
        if(length(which((sort(colnames(comm))==sort(colnames(dis)))=="FALSE"))>0|
dim(comm)[2]!=dim(dis)[2]){
        stop("\n Colnames in comm do not match with column names of groups\n")
        }
        GG<-unique(groups[,1])
        if(length(GG)!=2){
                stop("Error in groups: groups must contain exactly two levels")
        }
        group_1<-ifelse(groups[colnames(comm),]==GG[1],1,0)
        group_2<-ifelse(groups[colnames(comm),]==GG[2],1,0)
        N <- dim(comm)[1]
        n_taxa_group_1<-matrix(NA,nrow=N,ncol=1)
```

```
        n_taxa_group_2<-matrix(NA,nrow=N,ncol=1)
        comm_groups<-matrix(NA,dim(comm)[1]*2,dim(comm)[2])
        rownames(comm_groups)=rownames(comm_groups,do.NULL=F)
        for (j in 1:N){
                com<-cbind(comm[j,])
                com_group_1<-ifelse(com>0 & group_1>0,1,0)
                com_group_2<-ifelse(com>0 & group_2>0,1,0)
                n_taxa_group_1[j,1]<-sum(com_group_1)
                n_taxa_group_2[j,1]<-sum(com_group_2)
                comm_groups[(j*2)-1,]<-as.numeric(com_group_1)
                comm_groups[j*2,]<-as.numeric(com_group_2)
                rownames(comm_groups)[(j*2)-
1]=paste(rownames(comm)[j],GG[1],sep="_")

        rownames(comm_groups)[(j*2)]=paste(rownames(comm)[j],GG[2],sep="_")
        }
        colnames(comm_groups)=colnames(comm)
   dat <- match.comm.dist(comm_groups, dis)
   dat_comm <- dat$comm
   dat_dis <- as.matrix(dat$dist)
   dat_comm <- decostand(dat_comm, method = "total", MARGIN = 1)
   mfd <- matrix(nrow = N*2, ncol = N*2)
        LL<-c()
        KK<-c()
        for (l in 1:N){
                LL<-c(LL,((l*2)-1))
                KK<-c(KK,l*2)
        }
   for (l in LL) {
      for (k in KK) {
        mfd[k, l] <- sum(dat_dis * outer(as.vector(t(dat_comm[k,])),
as.vector(t(dat_comm[l, ]))))
      }
   }
        obs_mfd<-matrix(NA,N,1)
        for (l in 1:N){
                obs_mfd[l,1]<-mfd[l*2,(l*2)-1]
        }
        if(permutations!=0){
        mfd_null<-matrix(NA, permutations,N)
        for (i in 1: permutations){
                dist_null<-dis
                randomization<-sample(colnames(dist_null))
                colnames(dist_null)=randomization
                rownames(dist_null)=randomization
                dat_A <- match.comm.dist(comm_groups, dist_null)
           dat_comm_A <- dat_A$comm
        dat_dis_A <- as.matrix(dat_A$dist)
        dat_comm_A <- decostand(dat_comm_A, method = "total", MARGIN = 1)
           mfd_A <- matrix(nrow = N*2, ncol = N*2)
```

```
        for (l in LL) {
        for (k in KK) {
                mfd_A[k, l] <- sum(dat_dis_A * outer(as.vector(t(dat_comm_A[k,])),
as.vector(t(dat_comm_A[l, ]))))
              }
        }
                obs_mfd_A<-matrix(NA,N,1)
                for (l in 1:N){
                        obs_mfd_A[l,1]<-mfd_A[l*2,(l*2)-1]
                }
                mfd_null[i,]<-as.numeric(obs_mfd_A)
        }
        mfd.rand.mean <- apply(X = mfd_null, MARGIN = 2, FUN = mean, na.rm =
TRUE)
        mfd.rand.sd <- apply(X = mfd_null, MARGIN = 2, FUN = sd, na.rm = TRUE)
        mfd.obs.z <- (as.numeric(obs_mfd) - mfd.rand.mean)/mfd.rand.sd
        mfd.obs.rank <- apply(X = rbind(as.numeric(obs_mfd), mfd_null), MARGIN =
2, FUN = rank)[1, ]
        mfd.obs.rank <- ifelse(is.na(mfd.rand.mean), NA, mfd.obs.rank)
        mfd.obs.p<-mfd.obs.rank/(permutations + 1)
        Res_mfd<-matrix(NA,N,7)
        Res_mfd<-
cbind(n_taxa_group_1,n_taxa_group_2,obs_mfd,mfd.rand.mean,mfd.rand.sd,mfd.obs.z,
mfd.obs.p)
        colnames(Res_mfd)=c(paste("n_taxa",GG[1],sep="_"),paste("n_taxa",GG[2],se
p="_"),"mfd_obs","mfd_rand_mean","mfd_rand_sd","mfd_obs_z","mfd_obs_p")
rownames(Res_mfd)=rownames(comm,do.NULL=FALSE)
        }
        else{
                Res_mfd<-cbind(n_taxa_group_1,n_taxa_group_2,obs_mfd)
                rownames(Res_mfd)=rownames(comm,do.NULL=FALSE)

        colnames(Res_mfd)=c(paste("n_taxa",GG[1],sep="_"),paste("n_taxa",GG[2],se
p="_"),"mfd_obs")
        }
        Res<-list(call = match.call(),groups=GG,results=Res_mfd)
   return(Res)
}

#########################################################################
#########################################################################
```

Capítulo 2[2]

Article type: Research article

Historical and environmental factors drive niche differentiation among small mammals in South America

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Running Title Drivers of niche differentiation in small mammals

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ABSTRACT

Aim Distinguishing the main drivers of niche differentiation among small mammals in South America, considering their historical arrival at the continent, evolutionary histories and current environmental gradients.

Location South American continent.

Methods Occurrence of marsupial and cricetid rodent species in 103 communities across South America was described, and life history traits of all species were compiled. For each community we calculated functional redundancy within each clade and functional divergence between clades. The influence of environmental, functional redundancy and historical-evolutionary variables on the functional divergence between marsupials and cricetid rodents was evaluated using path analysis and model selection based on AIC.

Results Functional divergence showed a latitudinal gradient across South America. Marsupials and cricetids showed higher niche differentiation northwards. Functional redundancy of marsupials was mostly determined by climate and distance of the Isthmus of Panama, whereas functional redundancy of cricetid rodents was mostly determined by the evolutionary age of cricetid species. Different factors drove functional divergence: both–climate and functional variables as well as historical and evolutionary ones.

Main Conclusions Niche differentiation between marsupials and cricetid rodents across the South American continent was determined by a set of interconnected historical, evolutionary and environmental factors. The basal clade (marsupials) was more important than the derived clade (cricetids) for directly determining functional divergence. Marsupials might have maintained their functional characteristics, showing niche conservatism. Current functional patterns are still influenced by the biotic

invasion occurred about 3 million years ago which culminated with the formation of the Isthmus of Panama.

Keywords niche partitioning, South America, marsupials, cricetid rodents, functional redundancy, functional divergence

Introduction

Patterns of biodiversity distribution have been well studied by ecologists and the causes of these patterns have challenged them for many years. The variation of biological communities along environmental gradients, either gradually or abruptly, is well known. Latitudinal gradient is the most clearly recognized pattern worldwide (Willig *et al.,* 2003) and different factors have been suggested to be important drivers of variation in species richness along both latitudinal and elevational gradients (McCain, 2004; Willig et al., 2003). Groups of organisms show distribution patterns driven by different factors (Wu *et al.,* 2012) and even within a large group (like mammals or birds), different taxa can have divergent patterns as a consequence of their individual evolutionary trajectories, like basal or derived clades (Hawkins *et al.,* 2011).

For a long time, community ecologists explained the structure of communities through current environmental factors or interactions. Nonetheless, the integration of historical perspectives in the community ecology context has been widely used nowadays, once the current community structure is partly a reflection of the evolutionary histories of species that compose these communities (Webb *et al*., 2002). This historical perspective may be incorporated into ecological analyses by phylogenetic or geographical methods that can help us understand the evolution of biological communities in large regions (Buckley *et al.,* 2010; Ricklefs, 2006; Leiobold *et al.,* 2010). Moreover, since regional processes influence both local and regional species composition, it has become indispensable to understand the distribution of local communities across biogeographic gradients (Ricklefs & Schluter, 1993).

Ecological and evolutionary processes that generate and maintain species diversity also act on species traits through space and time (Swenson & Enquist, 2009). Incorporating species traits to understand ecological structure of communities might

help us to elucidate processes related to biotic interactions among species. Interspecific interactions are also relevant in shaping communities, as the manner in which species interact with others (as competitors for example) determine how they will respond to environmental constraints (Mouilott *et al.*, 2007). This functional approach incorporates the concept of niche that is a fundamental concept in ecology for understanding where species live and which species can coexist (Emery *et al*., 2012; Ackerly *et al*., 2006). Niche differences among species are essential for species coexistence (Chesson, 2000) and the niche of a species can be determined by its phylogenetic history (Wiens & Graham, 2005). Niche differences and competitive ability differences may drive the coexistence of different species in competitive communities (Mayfield *et al.*, 2010) and niche breadth can also be related to the above-cited latitudinal gradient, by the hypothesis that niche become narrower towards the Tropics (Vázquez & Stevens, 2004).

Small mammal species (rodents, marsupials and bats) represent the majority of mammal species (Cáceres *et al*., 2008). Non-volant small mammals, mainly the Cricetidae (among rodents) and Didelphidae families (among marsupials), have interesting and unique histories of colonization in the South American continent. The marsupials constituted, among mammals, one of the most important faunal elements along the South American Tertiary (Oliveira & Goin, 2012). The available evidence suggests a North American origin for neotropical marsupials about 100 million years ago (Oliveira & Goin, 2012), when South America was still part of the supercontinent Gondwana (Eisenberg & Redford, 1989). From the end of the Cretaceous period, marsupials might have started their dispersal into South America (Oliveira & Goin, 2012). The family Didelphidae is the most diverse among the families of marsupials living in the New World (Braun *et al.*, 2005), occupying a variety of niches (Delciellos & Vieira, 2006). Neotropical marsupials are described as predominantly arboreal in

their morphology (Delciellos & Vieira, 2006). Differences in locomotory performance may stem from differences in body size, but phylogenetic effects and arboreal specific adaptations also have an important role, since some lineages are clearly associated with differences in body size and the use of forest strata (Delciellos & Vieria, 2006).

Rodents had two main colonization events in South America: Hystricognathi rodents are likely to have come from Africa about 40 million years ago (currently represented by echimyid rodents among the small species); and Sigmodontine rodents (represented by cricetid rodents) which came from North America more recently when the Isthmus of Panama was formed (Eisenberg & Redford, 1989). Regarding the Paleocene, the most important external influence in the history of South American biota by far was the interchange between the American continents, through the Isthmus of Panama, approximately 2.5 million years ago (Webb, 1991). Cricetid rodents of the subfamily Sigmodontinae form the group with the highest species diversity among the New World mammals (D'Elia *et al.*, 2006). Sigmondontines are distributed predominantly in South America (about 60 endemic genera), although they also reach the North and Central Americas (D'Elia, 2003). They have a huge variety of ecomorphological groups, such as terrestrial, arboreal, fossorial and semi-aquatic (Reis *et al.*, 2011).

According to the biogeographical context, marsupials and sigmodontines rodents started their colonization in South America from the north of continent, although it happened in a different time scale. Taking these ideas into consideration, we hypothesized that these two groups of small mammals show some pattern of niche differentiation along the South American continent because of their biogeographical histories and their ecological characteristics. Therefore, the main questions of this study are: *Is there niche differentiation between marsupials and sigmodontine rodents along a latitudinal*

gradient in South America? Historical and evolutionary drivers are more important than environmental ones to determine this relationship? In this study we aimed at evaluating the main drivers of niche differentiation between small mammals in South America considering their arrival at the continent, evolutionary histories and the current environment.

Methods

Small mammals from South America

We compiled 103 communities of small mammals data across South America (Appendix S1) and the occurrence of marsupial and cricetid rodent species was described for each of these communities. All species registered were reviewed by a specialist (NCC) and, whenever possible, incorrect taxonomic identifications and synonymies were corrected. We considered each survey delimited by its geographic coordinates as a community (a sampling unit). With this procedure we obtained our species composition matrix of communities.

All communities considered were surveyed using traps and included at least 1000 trap-nights of sampling effort. The influence of the trap type and sampling effort used in each study on the species composition of each community was evaluated using Mantel Test, instead of the previous criteria. Furthermore, we evaluated the spatial autocorrelation with the response variables through spatial correlogram based on Moran's I coefficient multiple distance classes (Sokal & Oden, 1978; Legendre & Legendre, 1998). Species composition was not sampling method and effort dependent (Mantel Test - Ro=0.02; p=0.65). We did not find spatial autocorrelation (Moran's I < 0.2 for first distance class; other classes showed values close to zero), which means that

the response variables are not structured by space and, thus, a spatial variable was not included in the analysis.

Ecological traits

We compiled a species-level database of functional traits of marsupials and cricetid rodents (Appendix S2). Life history traits included in the analysis were weight, head-body length, tail length, diet and form of locomotion. Dietary categories were insectivore, herbivore, granivore, omnivore, frugivore, piscivore, seed predator and leaf predator, which were treated as binary traits. Species could be allocated in more than one diet category because they may eat more than one type of food. Modes of locomotion considered were terrestrial, semifossorial, semiaquatic, arboreal and scansorial, also treated as binary.

Species diversity, functional diversity and functional divergence within communities

We calculated Simpson's species diversity for each community based on the species composition matrix. Functional diversity was based on Rao's quadratic entropy (Botta-Dukát, 2005) with the trait matrix for each group (marsupials and cricetid rodents) after Gower dissimilarity using the SYNCSA software (available on http://ecoqua.ecologia.ufrgs.br/ecoqua/SYNCSA.html). Considering these variables, we obtained the functional redundancy metrics (FR) by subtracting of functional diversity from species diversity:

$$FR = Simpson's\ species\ diversity - Rao's\ quadratic\ entropy$$

We defined Functional Redundancy for each group (marsupials and cricetid rodents). These measures indicate how species in the same community are functionally similar or different within each group (de Bello *et al*., 2007; Pillar *et al*., 2013).

To obtain a variable describing the functional difference between marsupials and cricetid rodents within each community, we used the new approach described by Gonçalves *et al*., (in prep.). This metric adapted a phylogenetic metric between communities using the *comdist* function at Picante package in R software (Kembel *et al*., 2010) and calculated mean functional distance (mfd) between marsupials and cricetids within each community. We called such variable as functional divergence. We computed functional divergence within each community based on a hierarchical dendrogram (Ward clustering method) generated from a Gower's distance matrix, following the description in Fig 1. Observed values of functional divergence were compared to patterns expected under a null model of random shuffling of taxa vectors across the functional distance matrix and measures of standardized effect size (ses.mfd) were calculated:

$$\text{SES. MFD} = \frac{\text{MFD}_{Obs} - \text{Mean MFD}_{Null}}{\text{Standard deviation MFD}_{Null}}$$

Positive values of functional divergence (SES.MFD) represent a high functional turnover between marsupial and cricetid rodent species, demonstrating that the two groups are very different and could indicate niche partitioning. On the opposite, negative values indicate that groups have pairs of species very functionally similar suggesting niche overlap.

Environmental variables

In order to assess the environmental drivers of functional divergence between marsupials and cricetid rodents, we chose climatic, topographic and land cover variables to describe the current environment. Annual mean temperature, temperature seasonality, annual precipitation and precipitation seasonality were the climatic variables and altitude was the topographic variable used. All of them were obtained from Worldclim 1.4 at the resolution of 2.5 arc-minute (Hijmans et al., 2005) and were grouped in what we called climatic predictors. We extracted these variables from a radius of 0.042° (around 4,7km) for each geographic coordinate and used altitude range and the mean values of other climatic variables inside this radius. These land cover variables were obtained from the GLC2000 database which was produced using multi-sensor satellite observations at a spatial resolution of 1km (Global Land Cover 2000 database). Land cover variables were synthesized in six land cover groups. Using zonal tabulate area tool in PatchAnalyst for ArcGis 9.3 software, we calculated the proportion for each group in the same radius used for climatic predictors. The land cover groups were: Tree cover, Shrub and herbaceous cover, Cultivated and managed areas Cover, Mosaic areas Cover, Bare areas/water bodies Cover and Artificial surfaces Cover. Bare areas are represented primarily by non-vegetated areas containing less than four percent of the vegetation during at least 10 months a year and included areas like bare rock and sands. Artificial areas consisted of built up areas and mosaic areas represented mixed patches that contain several other natural cover types.

Historical factors

In order to describe the historical influence on functional divergence, we used the geographic distance (geodesic distance) of each community to a point in the Isthmus

of Panama (9°N, -80°W), which played an important role in the colonization of South America and represented a reference point for the position of the biota gateway. We called this variable biogeographical history. We also incorporated an evolutionary variable to elucidate the biogeographical history. We calculated the evolutionary age of marsupials and cricetid rodents in each community and hypothesized that more basal clades would be expected to be found northwards, independently of the current environment. Furthermore, we expected that such relationship would be clearer for cricetid rodents, as they colonized the South American continent more recently when compared to marsupials.

Phylogenetic relationships were assessed from mammalian phylogeny of Bininda-Emonds *et al.* (2007). For a better phylogenetic resolution of rodents we used the phylogenetic hypothesis proposed by Fabre *et al*. (2012), which is well resolved up to species level. We added only one genus and seven species that lacked in Fabre et al.'s phylogenetic tree. *Drymoreomys* was included as sister group of *Eremoryzomys* according to Percequillo *et al*. (2011). All missing species were included as soft polytomies within the respective genera, even if genera were all resolved. We transformed the rodent phylogeny in a topologic tree and replaced it in the topologic original mammal phylogeny (Bininda-emonds et al., 2007). As a result, we had a topologic mammal phylogeny with better resolved rodent clade. Furthermore, we included *Cryptonanus*, a marsupial genus lacked in the original mammal tree. Its position in the tree was defined based on Voss et al. (2005). After that, we inserted divergence time estimates available in Bininda-Emonds et al. (2007) and Fabre et al. (2012) in the tree through the BLADJ module of Phylocom 4.2 software (Webb et al., 2008). The tree branch lengths were based on divergence time estimates in millions of years (my). We obtained a phylogenetic tree with the marsupial and cricetid species

recorded in South America using the Phylomatic module of Phylocom 4.2 (Webb et al., 2008) showed in Fig 2.

We took the length of the terminal branch of each species, which means the age (my) of the last node that represents the divergence of this species. Age was used as a species trait and we calculated the mean evolutionary age of species for each group (marsupials or cricetid rodents) in each community through the species composition matrix and the age of each species.

Data Analysis

We performed a correlation analysis between redundancy or functional divergence and latitude to elucidate a possible latitudinal gradient in these variables. Evolutionary age of each group was related to latitude through regression analysis. The influence of environment, historical variables and redundancy of marsupials or cricetids on the functional divergence between marsupials and cricetids was evaluated using path analysis (Shipley, 2000). We followed the hypothetical model showed in Fig 3A, establishing all possible connections between variables. From this hypothetical model, we built the path model in several steps using the model selection based on Akaike's information criterion (AIC, Burnham & Anderson, 2002) following the same approach used by Brum *et al*. (2012). First, we employed model selection to find the predictor variables (x_1, x_2, x_n) that directly explained functional divergence. After finding such predictors, we ran a new model selection for each previously detected predictor variables (x_1, x_2, x_n), which became the response variables in model selection, in order to find their respective predictors (z_1, z_2, z_n), and so on. Such iterative approach followed the causal relationships previously established in the hypothetical model (Fig 3B). The best models were selected based on the lowest AIC values. After that, with the

predictors selected for each variable, we performed several multiple regressions to evaluate the strength of each relation. All analyses were performed using SAM v4.0 (Rangel *et al.*, 2010).

Results

We found 129 cricetid rodent and 46 marsupial species distributed across 103 communities. Species and their phylogenetic relationship are shown in Fig 3. Both the redundancy of marsupials and cricetid rodents did not demonstrate a correlation to latitude, however functional divergence was positively correlated with latitude ($r=0.28$; $p=0.004$; Fig 4). As hypothesized, evolutionary age of cricetid rodents showed a latitudinal gradient (Fig 5) and more basal clades were more represented in the northern portion of the South American continent ($R^2=0.14$; $p<0.001$). The evolutionary age of marsupials did not demonstrate any association with latitude ($R^2=0.02$; $p=0.13$).

Historical, environmental and functional variables were important to explain the functional divergence ($R^2= 0.47$; $p<0.001$) according to the model (Fig 6). Biogeographical history (distance of the Isthmus of Panama) showed a negative association with functional divergence. It means that functional divergence increases towards the north of South America. Although, this increase was not totally clear in Figure 4. Evolutionary age of marsupials showed a positive association with functional divergence. That is to say those communities containing younger marsupials species showed lower functional divergence between marsupials and cricetids. Historical variables were also indirectly important in driving functional divergence. Evolutionary age of cricetid rodents presented an indirect relationship with functional divergence through cricetid rodents functional redundancy (Fig 6). It also means that communities containing younger cricetids showed a lower functional redundancy for this group.

Beyond the functional divergence, biogeographical distance was also relevant to determine climatic variables and functional redundancy of marsupials. The more distant from the Isthmus of Panama, the greater the redundancy of marsupials within the communities. It is interesting that the redundancy for each group was influenced by different historical factors. Functional redundancy of marsupials was determined by biogeographical history and functional redundancy of cricetid rodents was determined by the evolutionary age of their clades.

Climatic variables (precipitation and annual mean temperature) were more important than land cover variables to explain this functional relationship among groups. Other climatic variables, such as precipitation seasonality and temperature seasonality, showed indirect relationship to functional divergence through marsupials functional redundancy. Land cover variables showed little importance in the model as a whole. Functional variables related both to marsupials and cricetid rodents were important in determining functional divergence, presenting a positive association among these variables. Greater redundancies within each group, that is, species of each group that are more similar, determine a greater difference between groups, i.e. the groups are more different to each other.

Discussion

Our findings suggest that there is a pattern of niche differentiation between marsupials and cricetid rodents along the South American continent (Fig 4). Niche differentiation was determined by a set of interconnected historical and environmental factors, despite of environmental factors (mainly climatic variables) being often evoked to explain community assembly patterns worldwide (Hawkins *et al.*, 2003). For instance, Meserve (1981) found a niche overlap in small mammal communities in

Chilean semiarid region indicating lower levels of competition for resources among small mammals including cricetid species and one marsupial. In that study, environmental factors were more important than evolutionary and biogeographical characteristics to explain patterns of resource utilization in the Chilean small mammal fauna (Meserve, 1981). The overlap between historical and environmental factors has been pointed out by some studies in different groups of organisms (Duarte *et al*., 2009; Duarte *et al*., 2013; Eiserhardt *et al.,* 2013). Such interplay between different kinds of drivers (historical and environmental) likely occurs because of historical, environmental and ecological processes might act on distinct temporal and spatial scales (Ghaham & Fine, 2008; Cardillo, 2011; Emery *et al*., 2012; Villalobos *et al.,* 2013).

While ecological processes occur more specifically at the local scale, acting directly upon individuals (Webb *et al*., 2002), historical and evolutionary processes are more related to the regional scale, affecting whole clades and/or generating broad scale species pools (Wiens & Donoghue, 2004). For instance, the formation of the Isthmus of Panama allowed the invasion of a totally different biota into the South American continent (Webb, 1978) and, according to our results, still determines current functional biodiversity patterns.

In this study we found higher niche partitioning towards the north of the South American continent. This is consistent with the niche breadth hypothesis, which predicts species with narrower niches distributed toward the tropics (Vázquez & Stevens, 2004). Thus, species could be less overlapped and more specialized. In mammals, diet is a very important characteristic for evolutionary history (Price *et al*., 2012). Trophic specialization might be related to diversification rates, being highest in herbivores than in carnivores and omnivores that have the lowest rate (Price *et al*., 2012). On the other hand, such pattern might be related to the formation of the Isthmus of Panama, an

important gateway for the cricetids to enter into the South American continent. With the input of new rodents, marsupials might have suffered a strong pressure to evolve their niches. Since marsupials are currently more arboreal than cricetid rodents (Paglia *et al.*, 2012), we could hypothesize that they became more arboreal with the presence of cricetid rodents that would have occupied other environments. Nevertheless, the arboreality is a primitive characteristic considering all marsupials in the world (Shattuck & Willians, 2010; Rasmussen, 1990) and this is why the relationship between arboreality and greater longevity is not present in this group, despite being present in other mammals in which arboreal characteristic is derived (Shattuck & Willians, 2010). Following this situation, marsupials may not have changed their niche, but conserved it, presenting current niche conservatism. Evolutionary age of marsupials was important in determining the divergence relationship between themselves and the cricetid rodents. In other words, the basal group was more relevant than the derived clade. If marsupials maintained their functional characteristics, the functional divergence among groups might be mediated by the marsupials, as it is the more conservative group. On the other hand, we can think that part of non-arboreal marsupials may have been extinct with the colonization of cricetid rodents because the old fauna was replaced by a new one as we do not expect that there were non-occupied environments waiting for a new fauna.

Cricetid rodents suffered rapid evolutionary and ecological diversification since they colonized the South American continent (Smith & Patton, 1999; D'Elia, 2003). Thus, cricetid rodents likely evolved their niche since they began exploring new habitats in the South American continent. There are indications that they had a rapid radiation in the new continent (Smith & Patton, 1999), showing that they could have had high dispersal abilities. This effective radiation may be related to the origin of the group because taxa that originated in North America were more easily adapted in other regions

(Smith *et al.,* 2012; Morales-Castilla *et al*., 2012; Romdal *et al.,* 2013). In the Great American Biotic Interchange, more mammalian genera dispersed southward than northward (Woodburne, 2010) and the fauna from North America had more success in South America than the biota that migrated from south to north (Smith *et al*., 2012). Even niche conservatism is asymmetric among lineages that have distinct origins and this ultimately determines the biodiversity gradients (Smith *et al.,* 2012). Rodents also had an important role in the functional relationship with marsupials although their evolutionary age had only an indirect association. This may indicate that cricetid rodents are still exploring the continent and there was not enough time to find this pattern in the large scale.

Environmental pressures are very important in determining whether an individual is able to settle in a certain place. On a broad scale, the climatic variables are always the most compatible to express the environment as a whole. Temperature generally determines patterns of distribution of different organisms (Stevens, 2011; Morales-Castilla *et al.,* 2012). Here, it was not different. Temperature also explained the pattern of functional divergence among groups. Beyond this, precipitation is even more important than temperature and presented a negative association which means that the groups are more similar where precipitation is higher. This may be related to the increase in food availability (Ernest *et al.,* 2000). Limiting resources may influence the consumer dynamics (Ernest *et al.,* 2000) and Hawkins *et al*. (2003) found that annual rainfall was the best predictor of terrestrial birds richness in low latitudes. Stevens *et al.* (2012) demonstrated that desert small mammal communities in North America present a degree of phylogenetic structure which depends on the environmental heterogeneity related to ecological similarities among rodent species. A wide variety of resources allows more similar species to coexist (Stevens *et al.,* 2012). Dramatic fluctuations in

rainfall led changes in small mammal population in central-north Chile (Meserve *et al.*, 2011). We used land cover variables in an attempt to describe local environmental processes that would not be expressed only by climatic variables. These local environmental variables did not determine the functional pattern among groups probably because this pattern is on large scale.

In conclusion, the interplay between different kinds of explanatory factors drives community assembly and ecosystem functionality. The Isthmus of Panama changed the biota that occurred in South America and is still affecting the assembly of biological communities and ecological processes among taxa, even when they have distinct evolutionary history and ecological characteristics.

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Supplementary Material

The following supplementary material is related to this article:

Appendix S1 Reference, country, latitude, longitude, sampling effort, trap type of 103 communities considered in this study. References appear right after the table.

Appendix S2 Head-body length (in millimeter), tail length (in millimeter), weight (in grams), diet and form of locomotion of 46 marsupials and 129 cricetid rodent species. Numbers with asterisks represent missing values, which were extrapolated by the mean of the genus. After the table, we show all the references used to build this matrix.

BIOSKETCH

Larissa Oliveira Gonçalves is a graduate student. Her master thesis aimed to answer which are the main macroecological factors determining functional divergence between marsupials and cricetid rodents in South American continent.

Nilton Carlos Cáceres has broad research interests in ecology and evolution, including community ecology, and behavioural ecology, besides evolution of form and function, working on a variety of taxa both globally and regionally.

Leandro Da Silva Duarte is a community ecologist. His research aims to investigate the ways the phylogenetic structure of communities interacts with environmental and spatial factors, as well as with ecological traits of species assembled in communities.

FIGURE LEGENDS

Figure 1 Steps to obtaining the mean functional distance between marsupials and cricetids within each community. We obtain the Gower's distance matrix from the trait matrix and, then, the functional dendrogram. C1 represents community 1 containing four species (two marsupials and two cricetids). 1 e 2 represent sum of branch lengths that connect one cricetid to marsupials; 3 e 4 represent sum of branch lengths that connect the other cricetid to marsupials. The mean of these sums will be the MFD observed.

Figure 2 Phylogenetic tree of marsupials and cricetid rodents that occur in 103 communities in South America. Black lines represent the cricetid rodent clade and grey lines represent marsupial clade. The scale is displayed in 20 million years (20my).

Figure 3 A) Hypothetical model of Path analysis. B) Steps used for the model selection (in I, we selected the best variables for the functional divergence; in II the previous predictors became response variables and a new selection was performed for each of them and so on in III); H = historical factors, LC = land cover variables, C = Climatic variables, FR= Functional Redundancy.

Figure 4 Pattern of functional divergence between marsupials and cricetid rodents along the South American continent. Circle sizes represent functional divergence values. These values vary from -2.5 to 4.8.

Figure 5 Latitudinal patterns of evolutionary age of cricetid rodents. Basal clades were more represented in the northern portion of the continent.

Figure 6 Final model of path analysis showing the causal relationships between historical (hexagon), environmental (ellipse) and functional (rectangle) variables. The path coefficients in the arrows are the standardized regression coefficients. Dashed lines represent non-significant relationships between variables. Continuous lines represent

significant relationship between variables. Thicker lines represent direct relationships with functional divergence and other relationship with coefficients greater than 0.4.

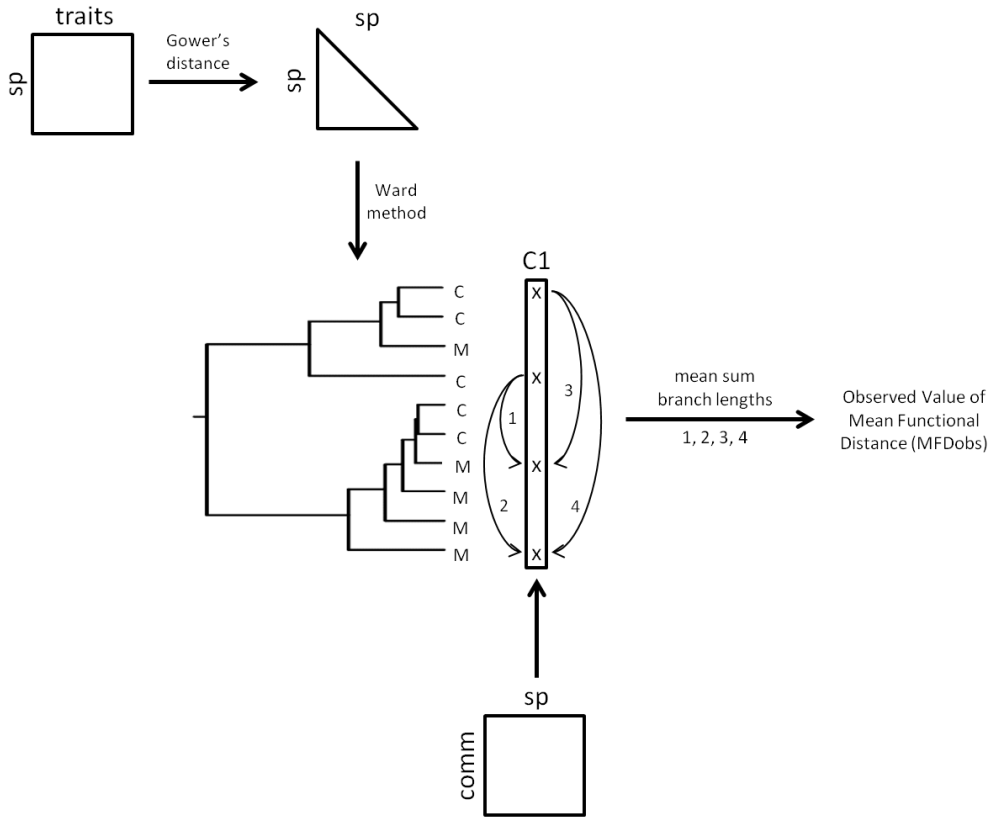
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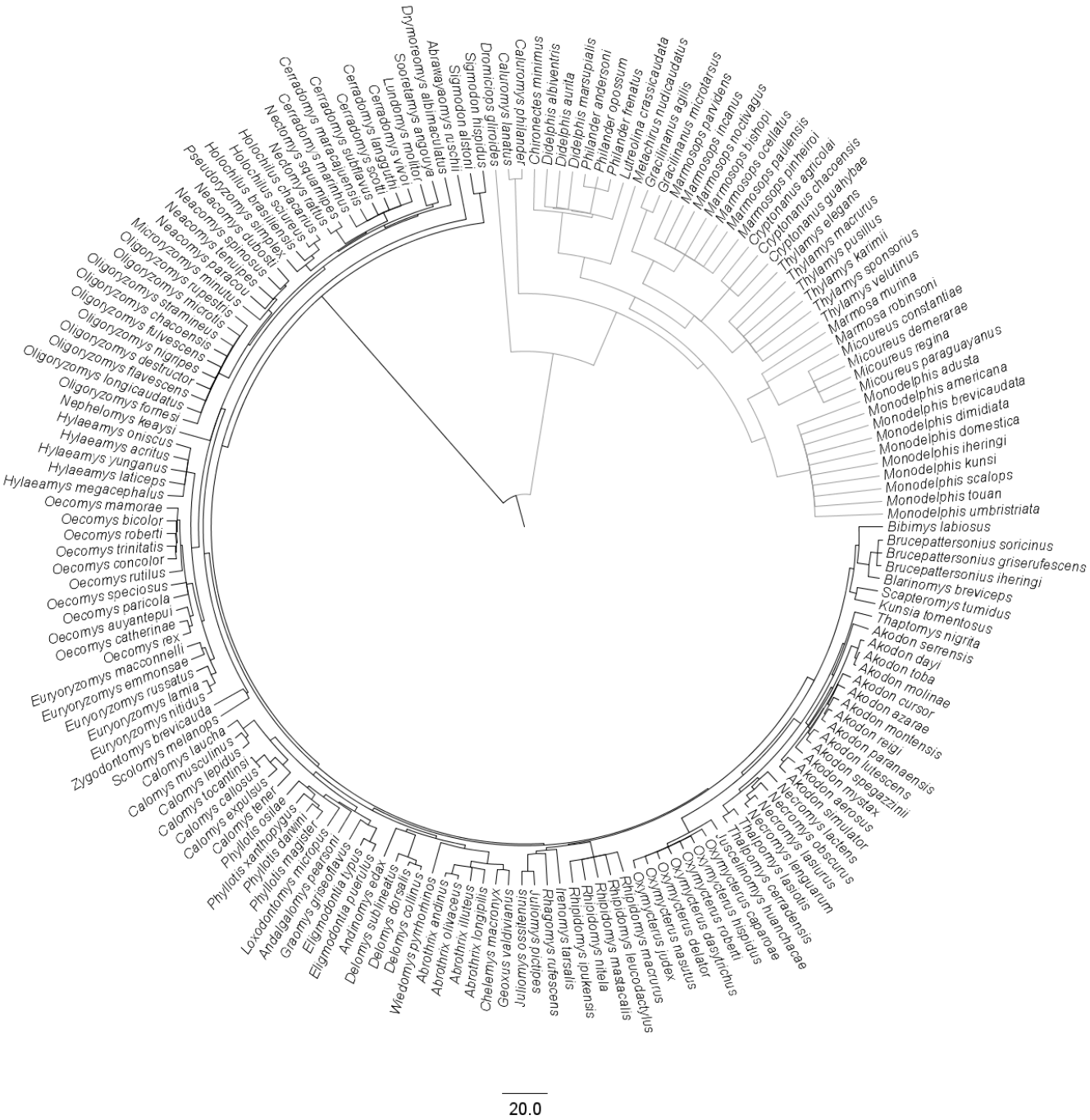
Fig 1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Sigmodon alstoni
Sigmodon ruschii
Abrawayaomys albimaculatus
Drymoreomys albimaculatus
Sooretamys angouya
Lundomys molitor
Cerradomys vivoi
Cerradomys langguthi
Cerradomys subflavus
Cerradomys scotti
Cerradomys marcajuensis
Cerradomys marinhus
Nectomys squamipes
Nectomys rattus
Holochilus chacarius
Holochilus sciureus
Holochilus brasiliensis
Pseudoryzomys simplex
Neacomys dubosti
Neacomys spinosus
Neacomys tenuipes
Neacomys paracou
Microryzomys minutus
Oligoryzomys rupestris
Oligoryzomys microtis
Oligoryzomys stramineus
Oligoryzomys chacoensis
Oligoryzomys fulvescens
Oligoryzomys nigripes
Oligoryzomys destructor
Oligoryzomys flavescens
Oligoryzomys longicaudatus
Oligoryzomys fornesi
Nephelomys keaysi
Hylaeamys oniscus
Hylaeamys acritus
Hylaeamys yunganus
Hylaeamys laticeps
Hylaeamys megacephalus
Oecomys mamorae
Oecomys bicolor
Oecomys roberti
Oecomys trinitatis
Oecomys concolor
Oecomys rutilus
Oecomys speciosus
Oecomys paricola
Oecomys auyantepui
Oecomys catherinae
Oecomys rex
Euryoryzomys macconnelli
Euryoryzomys emmonsae
Euryoryzomys russatus
Euryoryzomys lamia
Euryoryzomys nitidus
Zygodontomys brevicauda
Scolomys melanops
Calomys laucha
Calomys musculinus
Calomys lepidus
Calomys tocantinsi
Calomys callosus
Calomys expulsus
Calomys tener
Phyllotis osilae
Phyllotis xanthopygus
Phyllotis darwini
Phyllotis magister
Loxodontomys micropus
Andalgalomys pearsoni
Graomys griseoflavus
Eligmodontia typus
Eligmodontia puerulus
Andinomys edax
Delomys sublineatus
Delomys dorsalis
Delomys collinus
Wiedomys pyrrhorhinos
Abrothrix andinus
Abrothrix olivaceus
Abrothrix illuteus
Abrothrix longipilis
Chelemys macronyx
Geoxus valdivianus
Juliomys ossitensis
Juliomys pictipes
Rhagomys rufescens
Irenomys tarsalis
Rhipidomys ipukensis
Rhipidomys nitela
Rhipidomys mastacalis
Rhipidomys leucodactylus
Oxymycterus judex
Oxymycterus nasutus
Oxymycterus delator
Oxymycterus roberti
Oxymycterus hispidus
Juscelinomys huanchacae
Thalpomys cerradensis
Thalpomys lasiotis
Necromys lasiurus
Necromys lactens
Necromys obscurus
Akodon simulator
Akodon aerosus
Akodon mystax
Akodon spegazzinii
Akodon lutescens
Akodon paranaensis
Akodon reigi
Akodon montensis
Akodon azarae
Akodon cursor
Akodon molinae
Akodon toba
Akodon dayi
Akodon serrensis
Thaptomys nigrita
Kunsia tomentosus
Scapteromys tumidus
Blarinomys breviceps
Brucepattersonius iheringi
Brucepattersonius griserufescens
Brucepattersonius soricinus
Bibimys labiosus
Monodelphis umbristriata
Monodelphis touan
Monodelphis scalops
Monodelphis kunsi
Monodelphis iheringi
Monodelphis domestica
Monodelphis dimidiata
Monodelphis brevicaudata
Monodelphis americana
Monodelphis adusta
Micoureus paraguayanus
Micoureus regina
Micoureus demerarae
Micoureus constantiae
Marmosa robinsoni
Marmosa murina
Thylamys velutinus
Thylamys sponsorius
Thylamys karimii
Thylamys pusillus
Thylamys macrurus
Thylamys elegans
Cryptonanus guahybae
Cryptonanus chacoensis
Cryptonanus agricolai
Marmosops pinheiroi
Marmosops ocellatus
Marmosops bishopi
Marmosops noctivagus
Marmosops incanus
Marmosops parvidens
Marmosops microtarsus
Gracilinanus agilis
Gracilinanus nudicaudatus
Metachirus crassicaudata
Lutreolina crassicaudata
Philander frenatus
Philander opossum
Philander andersoni
Philander marsupialis
Didelphis aurita
Didelphis albiventris
Didelphis marsupialis
Chironectes minimus
20.0

Fig 2

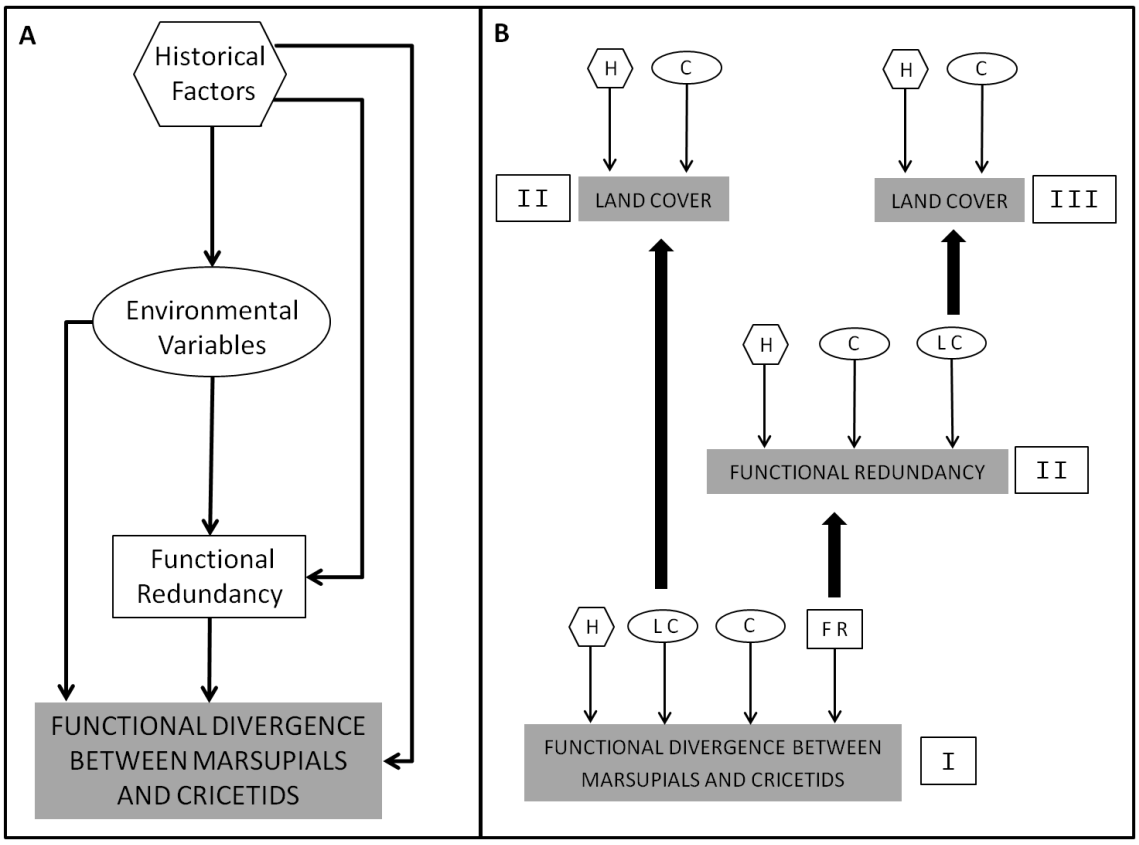
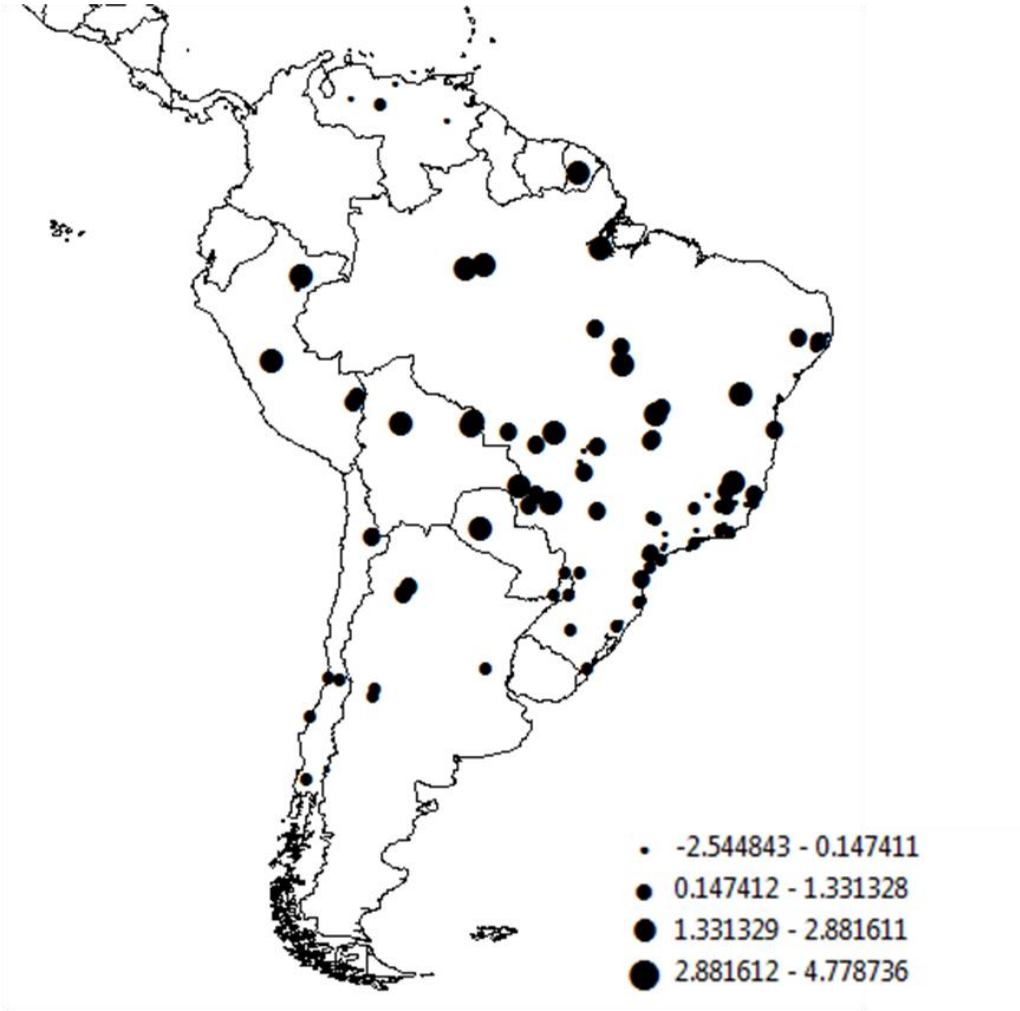

A
Historical Factors
Environmental Variables
Functional Redundancy
FUNCTIONAL DIVERGENCE BETWEEN MARSUPIALS AND CRICETIDS
B
H
C
II
LAND COVER
H
C
LAND COVER
III
H
C
LC
FUNCTIONAL REDUNDANCY
II
H
LC
C
FR
FUNCTIONAL DIVERGENCE BETWEEN MARSUPIALS AND CRICETIDS
I

Fig 3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0.147412 - 1.331328
1.331329 - 2.881611
2.881612 - 4.778736

Fig 4

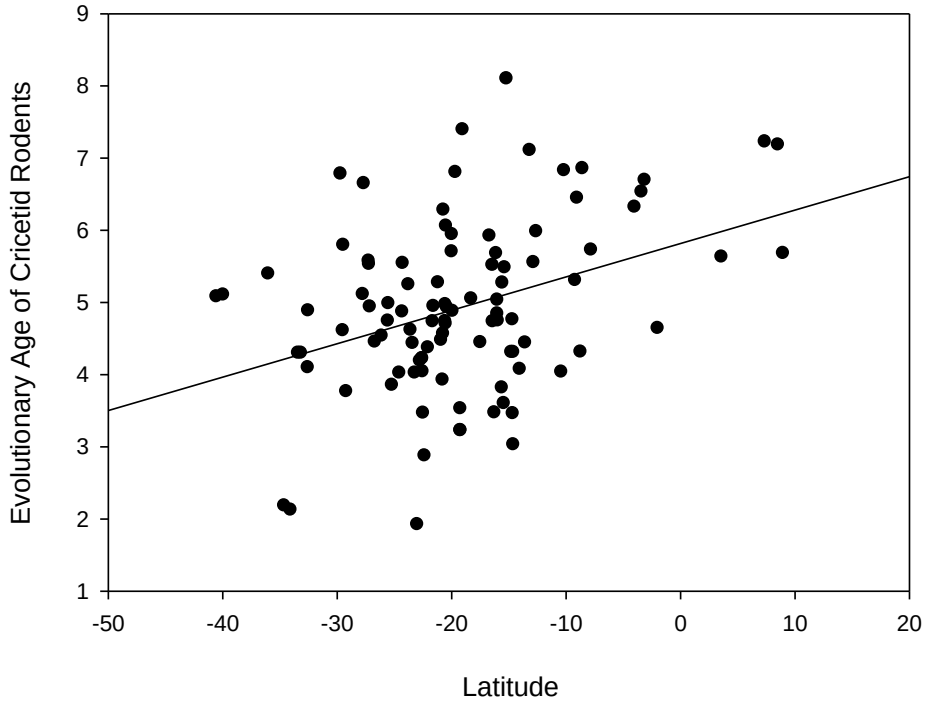
Evolutionary Age of Cricetid Rodents
9
8
7
6
5
4
3
2
1
-50
-40
-30
-20
-10
0
10
20
Latitude

Fig 5

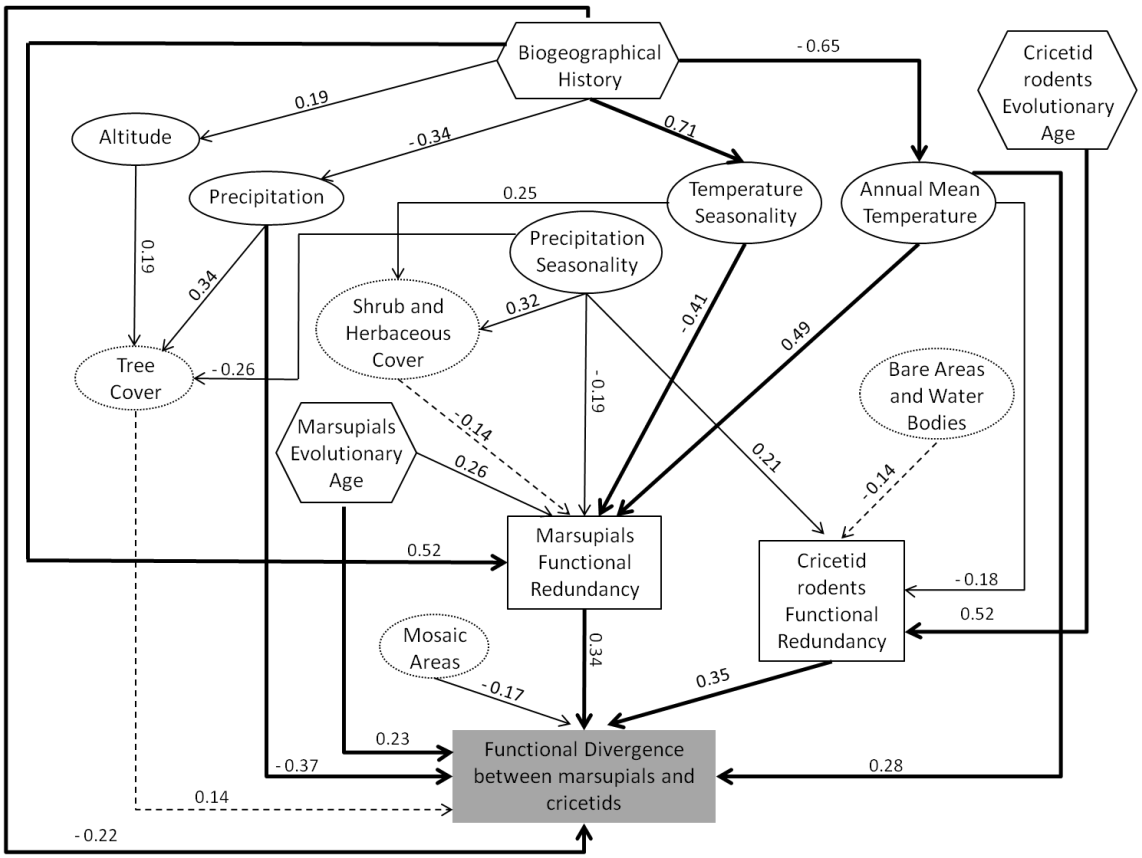
Biogeographical History
Cricetid rodents Evolutionary Age
Altitude
Precipitation
Temperature Seasonality
Annual Mean Temperature
Precipitation Seasonality
Shrub and Herbaceous Cover
Tree Cover
Bare Areas and Water Bodies
Marsupials Evolutionary Age
Marsupials Functional Redundancy
Cricetid rodents Functional Redundancy
Mosaic Areas
Functional Divergence between marsupials and cricetids
0.19
-0.34
0.71
-0.65
0.25
0.19
0.34
0.32
-0.41
0.49
-0.26
-0.14
-0.19
0.26
0.21
-0.14
0.52
-0.18
0.52
0.34
-0.17
0.35
0.23
-0.37
0.28
0.14
-0.22

Fig 6

Appendix S1

	Reference	Latitude	Longitude	Country	Trap type	Trap-nights
1	Kelt (2000)	-40.5	-73	Chile	live traps	2894
2	Thibault *et al. (*2011)	-39.92	-71.42	Argentina	live traps	3416
3	Saavedra & Simonetti (2004)	-35.98	-72.68	Chile	live traps	8747
4	Thibault *et al*. (2011)	-34.59	-68.14	Argentina	live traps	1600
5	Corbálan & Ojeda (2004)	-34.03	-67.97	Argentina	live traps	4410
6	Thibault *et al*. (2011)	-33.38	-70.52	Chile	live traps	5528
7	Munoz-Pedrero *et al. (*2010)	-33.12	-71.4	Chile	live traps	1476
8	Sponchiado *et al.* (2012)	-32.53	-52.53	Brazil	live traps	4320
9	Thibault *et al*. (2011)	-32.5	-60	Argentina	live traps	36060
10	Lima *et al.* (2010)	-29.67	-53.72	Brazil	live and pitfall traps	2240
11	Marques *et al.* (2011) Pedó *et al.* (2010)	-29.47	-50.22	Brazil	live and pitfall traps	5754
12	Marques *et al.* (2011)	-29.42	-50.4	Brazil	live traps	11596
13	Dalmagro & Vieira (2005)	-29.17	-50.08	Brazil	live traps	5178
14	Graipel *et al.* (2006)	-27.72	-48.53	Brazil	live traps	12132
15	Cherem *et al.* (2011)	-27.63	-48.83	Brazil	live and pitfall traps	50097
16	Ferro & Barquez (2009)	-27.2	-65.93	Argentina	live traps	3440
17	Melo *et al.* (2011)	-27.17	-53.92	Brazil	live and pitfall traps	6932
18	Cirignoli *et al.* (2011)	-27.1	-54.97	Argentina	live and pitfall traps	5310
19	Ferro & Barquez (2009)	-26.67	-65.63	Argentina	live traps	4181
20	Quadros & Cáceres (2001)	-26.07	-48.63	Brazil	live traps	1920
21	Crespo (1982)	-25.52	-54.13	Argentina	live traps	>1000
22	Quadros *et al. (*2000)	-25.48	-53.12	Brazil	live traps	4380
23	Bergallo *et al.* (1998)	-25.17	-47.98	Brazil	live traps	5040
24	Bergallo *et al.* (1998)	-24.53	-47.25	Brazil	live traps	5040
25	Vieira & Monteiro-Filho (2003)	-24.28	-48.35	Brazil	live traps	3547
26	Vieira & Monteiro-Filho (2003)	-24.23	-48.06	Brazil	live traps	15227
27	Pardini & Umetsu (2006) Umestu & Pardini (2007)	-23.73	-47.07	Brazil	live and pitfall traps	9168
28	Barros-Battesti *et al*. (2000)	-23.55	-46.93	Brazil	live traps	2888
29	Pinheiro & Geise (2008)	-23.37	-44.83	Brazil	live and pitfall traps	1680
30	Bittencourt & Rocha (2003)	-23.18	-44.2	Brazil	live traps	7474
31	Jaksic *et al.* (1999)	-22.97	-68.22	Argentina	live traps	2736
32	Bonvicino *et al*. (2002)	-22.72	-46.92	Brazil	live traps	1830
33	Viveiros de Castro & Fernandez (2004)	-22.54	-42.28	Brazil	live traps	51122

34	Pires *et al.* (2002)	-22.52	-42.28	Brazil	live traps	1618
35	Vieira *et al.* (2009)	-22.5	-42.86	Brazil	live traps	1200
36	Geise *et al.* (2004)	-22.45	-44.58	Brazil	live traps	1500
37	Yahnke (2006)	-22.33	-60.33	Paraguay	live traps	23296
38	Gentile *et al.* (2000)	-22.03	-42.68	Brazil	live traps	12250
39	Lyra-Jorge *et al.* (2001)	-21.62	-47.62	Brazil	live and pitfall traps	3672
40	Talamoni & Dias (1999)	-21.55	-47.85	Brazil	live traps	2400
41	Cáceres *et al.* (2008)	-21.15	-51.87	Brazil	live and pitfall traps	1426
42	Rocha *et al.* (2011b)	-20.88	-44.83	Brazil	live traps	10080
43	Paglia *et al.* (1995)	-20.75	-42.85	Brazil	live traps	5760
44	Cáceres *et al.* (2007)	-20.7	-56.85	Brazil	live traps	430
45	Moreira *et al.* (2009)	-20.67	-42.43	Brazil	live traps	3168
46	Thibault *et al. (*2011)	-20.52	-41	Brazil	live traps	7264
47	Cáceres *et al.* (2011a)	-20.5	-55.3	Brazil	live and pitfall traps	11865
48	Bonvicino *et al.* (2002)	-20.47	-41.8	Brazil	live traps	3231
49	Cáceres *et al.* (2010) Hannibal & Cáceres (2010)	-20.45	-55.53	Brazil	live traps	2950
50	Pinto *et al.* (2009)	-20.37	-40.47	Brazil	live traps	2160
51	Passamani & Ribeiro (2009) Passamani & Fernandez (2011)	-19.95	-40.52	Brazil	live traps	23285
52	Oliveira *et al.* (2007)	-19.93	-43.88	Brazil	live traps	7115
53	Andreazzi *et al.* (2011)	-19.88	-56.38	Brazil	live traps	21560
54	Grelle (2003) Stallings *et al.* (1991)	-19.63	-42.55	Brazil	live traps	68220
55	Godoi *et al.* (2010)	-19.2	-57.57	Brazil	pitfall traps	4032
56	Cáceres *et al.* (2011b)	-19.2	-57.55	Brazil	pitfall traps	16992
57	Cáceres *et al.* (2011b)	-19.18	-57.62	Brazil	live and pitfall traps	4620
58	Fonseca & Robinson (1990)	-19	-42	Brazil	live traps	57120
59	Rodrigues *et al. (*2002)	-18.25	-52.88	Brazil	live and pitfall traps	13562
60	Cáceres *et al.* (2008)	-17.45	-53.1	Brazil	live and pitfall traps	1248
61	Bonvicino *et al.* (1996)	-16.65	-52.78	Brazil	live traps	1050
62	Bonvicino *et al.* (1996)	-16.4	-52.45	Brazil	live traps	2100
63	Cáceres *et al.* (2008)	-16.37	-51.95	Brazil	live and pitfall traps	1350
64	Aragona & Marinho-Filho (2009)	-16.23	-56.37	Brazil	live traps	38635
65	Thibault *et al.* (2011)	-16.07	-47.92	Brazil	live traps	49810
66	Santos & Henriques (2010) Henriques *et al.* (2006)	-15.97	-47.93	Brazil	live traps	2380
67	Nitikman & Mares (1987)	-15.97	-47.95	Brazil	live traps	12170
68	Mares *et al.* (1986)	-15.93	-47.88	Brazil	live traps	85101

69	Santos & Henriques (2010)	-15.57	-48.12	Brazil	live traps	3040
70	Ribeiro e Marino-Filho (2005)	-15.53	-47.6	Brazil	live traps	6600
71	Santos-Filho *et al.* (2008)	-15.4	-58.35	Brazil	live and pitfall traps	17600
72	Lacher Jr. & Alho(2001)	-15.33	-55	Brazil	live traps	4821
73	Pardini (2004)	-15.17	-39.02	Brazil	live traps	7776
74	Emmons (2009)	-14.75	-61.03	Bolivia	live traps	13118
75	Vargas & Simonetti (2004)	-14.65	-66.07	Bolivia	live traps	4240
76	Emmons (2009)	-14.61	-60.86	Bolivia	live traps	6962
77	Emmons (2009)	-14.58	-60.92	Bolivia	live traps	7540
78	Emmons (2009)	-14.58	-60.91	Bolivia	live traps	4700
79	Bonvicino et al. (2002)	-14.01	-47.55	Brazil	live traps	2665
80	Bonvicino et al. (2002)	-13.53	-47.17	Brazil	live traps	1440
81	Thibault et al. (2011)	-13.14	-69.61	Peru	live traps	5600
82	Thibault et al. (2011)	-12.81	-69.35	Peru	live traps	1600
83	Pereira & Geise *et al.* (2009)	-12.57	-41.37	Brazil	live traps	10216
84	Stevens & Husband (1998)	-11.18	-37.42	Brazil	live traps	6144
85	Bezerra *et al.* (2009)	-10.38	-50	Brazil	live and pitfall traps	5459
86	Mena & Medellin (2010)	-10.13	-75.55	Peru	live traps	5515
87	Rocha *et al.* (2011a)	-9.17	-50.17	Brazil	live and pitfall traps	32074
88	Asfora & Pontes (2009)	-9	-35.87	Brazil	live traps	1600
89	Asfora & Pontes (2009)	-8.7	-35.83	Brazil	live traps	1600
90	Geise et al. (2010)	-8.53	-37.25	Brazil	live traps	1391
91	Asfora & Pontes (2009)	-8.25	-35.08	Brazil	live traps	1600
92	Thibault *et al*. (2011)	-7.77	-51.96	Brazil	live traps	22800
93	Thibault *et al.* (2011)	-4.92	-73.67	Peru	live traps	5820
94	Thibault *et al*. (2011)	-4.5	-73.42	Peru	live traps	2888
95	Hice & Schmidly (2002)	-3.97	-73.42	Peru	pitfall traps	2530
96	Barnett & Cunha (1994)	-3.37	-61.43	Brazil	live traps	3578
97	Malcolm (1991)	-3.1	-60.02	Brazil	live traps	25920
98	Ribeiro Junior *et al. (*2011)	-1.95	-51.6	Brazil	pitfall traps	1206
99	Thibault *et al*. (2011)	3.62	-53.2	French Guiana	live traps	4701
100	Thibault *et al*. (2011)	7.4	-62.82	Venezuela	live traps	2225
101	Thibault *et al*. (2011)	8.55	-67.6	Venezuela	live traps	38329
102	Utrera *et al.* (2000)	9	-69.75	Venezuela	live traps	34455
103	Thibault *et al*. (2011)	10.07	-66.45	Venezuela	live traps	1920

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Appendix S2

Species	Head-Body Length	Tail Length	Weight	Diet	Locomotion
Marsupials					
Caluromys lanatus	273.3	393.5	350.3	Frugivore/Omnivore	Arboreal
Caluromys philander	224.3	303.5	246.5	Frugivore/Omnivore	Arboreal
Chironectes minimus	297.5	370.0	670.0	Piscivore	Semiaquatic
Cryptonanus agricolai	85.5	104.5	18.0	Insectivore/Omnivore	Arboreal
Cryptonanus chacoensis	91.0	110.5	15.0	Insectivore/Omnivore	Arboreal
Cryptonanus guahybae	92.0	113.0	18.0	Insectivore/Omnivore	Arboreal
Didelphis albiventris	360.7	360.0	1030.5	Frugivore/Omnivore	Scansorial
Didelphis aurita	402.5	384.0	1105.9	Frugivore/Omnivore	Scansorial
Didelphis marsupialis	452.5	431.5	1362.5	Frugivore/Omnivore	Scansorial
Dromiciops gliroides	190.0	100.0	20.0	Insectivore	Arboreal
Gracilianus agilis	95.3	134.0	22.0	Insectivore/Omnivore	Arboreal
Gracilinanus microtarsus	91.7	149.0	29.3	Insectivore/Omnivore	Arboreal
Lutreolina crassicaudata	325.0	273.0	554.8	Piscivore	Terrestrial
Marmosa murina	120.6	183.5	36.3	Insectivore/Omnivore	Scansorial
Marmosa robinsoni	149.0	179.0	71.0	Frugivore/Omnivore	Scansorial
Marmosops bishopi	103.5	126.5	19.5	Insectivore/Omnivore	Scansorial
Marmosops incanus	131.5	204.0	59.9	Insectivore/Omnivore	Scansorial
Marmosops noctivagus	135.0	172.5	47.5	Insectivore/Omnivore	Scansorial
Marmosops ocellatus	122.0	166.0	30.0	Insectivore/Omnivore	Scansorial
Marmosops parvidens	100.0	149.0	26.0	Insectivore/Omnivore	Scansorial
Marmosops paulensis	125.5	178.5	43.0	Insectivore/Omnivore	Scansorial
Marmosops pinheiroi	107.5	145.5	26.0	Insectivore/Omnivore	Scansorial
Metachirus nudicaudatus	355.0	284.0	345.5	Insectivore/Omnivore	Terrestrial
Micoureus constantiae	142.0	193.5	70.5	Insectivore/Omnivore	Arboreal
Micoureus demerarae	175.0	257.0	119.0	Insectivore/Omnivore	Arboreal
Micoureus paraguayanus	196.0	195.5	95.0	Insectivore/Omnivore	Scansorial
Micoureus regina	230.0	266.0	118.6	Insectivore/Omnivore	Scansorial
Monodelphis adusta	110.1	53.0	36.0	Insectivore/Omnivore	Terrestrial
Monodelphis americana	103.0	50.0	29.0	Insectivore/Omnivore	Terrestrial
Monodelphis brevicaudata	140.5	79.0	78.8	Insectivore/Omnivore	Terrestrial
Monodelphis dimidiata	99.6	58.5	44.6	Insectivore/Omnivore	Terrestrial
Monodelphis domestica	151.0	68.5	115.0	Insectivore/Omnivore	Terrestrial
Monodelphis scalops	139.1	61.0	61.0	Insectivore/Omnivore	Terrestrial
Monodelphis iheringi	87.0	47.0	11.0	Insectivore/Omnivore	Terrestrial
Monodelphis kunsi	82.5	41.0	19.0	Insectivore/Omnivore	Terrestrial
Monodelphis touan	159.0	88.0	82.0	Insectivore/Omnivore	Terrestrial
Monodelphis umbristriata	123.0	53.0	90.0	Insectivore/Omnivore	Terrestrial
Philander andersoni	265.0	293.5	325.0	Insectivore/Omnivore	Scansorial
Philander frenatus	260.0	279.5	450.0	Insectivore/Omnivore	Scansorial
Philander opossum	300.5	294.0	487.5	Insectivore/Omnivore	Scansorial
Thylamys elegans	120.7	110.6	28.9	Insectivore/Omnivore	Scansorial

Thylamys karimii	103.5	87.5	59.0	Insectivore/Omnivore	Scansorial
Thylamys macrurus	127.3	144.5	34.4	Insectivore/Omnivore	Scansorial
Thylamys pusillus	100.1	117.0	22.0	Insectivore/Omnivore	Arboreal
Thylamys sponsorius	100.0	138.0	34.0*	Insectivore/Omnivore	Arboreal
Thylamys velutinus	50.0	78.0	20.7	Insectivore/Omnivore	Scansorial
Cricetid Rodents					
Abrawayaomys ruschi	125.5	100.5	55.0	Frugivore/Granivore	Semifossorial
Abrothrix andinus	146.8	80.7*	27.5	Omnivore/Herbivore/Folivore	Terrestrial
Abrothrix illuteus	111.0	84.5	47.8	Omnivore	Terrestrial
Abrothrix longipilis	107.2	82.7	38.9	Insectivore/Omnivore	Terrestrial
Abrothrix olivaceus	164.0	75.0	23.0	Granivore/Omnivore	Terrestrial
Akodon aerosus	110.5	78.0	60.0	Insectivore/Omnivore	Terrestrial
Akodon azarae	94.0	67.0	22.0	Insectivore/Omnivore	Terrestrial
Akodon cursor	104.0	93.0	45.5	Insectivore/Omnivore	Terrestrial
Akodon dayi	121.0	83.0	32.5	Insectivore/Omnivore	Terrestrial
Akodon lutescens	79.5	57.0	20.7	Insectivore/Omnivore	Terrestrial
Akodon molinae	101.5	79.0	31.0	Insectivore/Omnivore	Terrestrial
Akodon montensis	107.0	89.5	44.1	Insectivore/Omnivore	Terrestrial
Akodon mystax	85.0	68.0	19.0	Insectivore/Omnivore	Terrestrial
Akodon paranaensis	109.8	83.1	32.4	Insectivore/Omnivore	Terrestrial
Akodon reigi	107.5	88.0	30.1	Insectivore/Omnivore	Terrestrial
Akodon serrensis	97.6	84.8	26.3	Insectivore/Omnivore	Terrestrial
Akodon simulator	111.0	80.0	42.5	Insectivore/Omnivore	Terrestrial
Akodon spegazzinii	91.5	68.0	28.6	Insectivore/Omnivore	Terrestrial
Akodon toba	118.6	85.1	51.2	Insectivore/Omnivore	Terrestrial
Andalgalomys pearsoni	109.0	127.0	45.0	Herbivore	Terrestrial
Andinomys edax	163.0	137.0	69.8	Herbivore	Scansorial
Bibimys labiosus	85.0	76.0	30.0	Insectivore/Omnivore	Semifossorial
Blarinomys breviceps	105.0	42.5	36.0	Insectivore/Omnivore	Semifossorial
Brucepattersonius griserufescens	103.0	103.0	23.7	Insectivore/Omnivore	Semifossorial
Brucepattersonius iheringi	100.0	94.0	28.0	Insectivore/Omnivore	Semifossorial
Brucepattersonius soricinus	103.0	83.0	25.0	Insectivore/Omnivore	Semifossorial
Calomys callosus	98.0	72.3	29.9	Frugivore/Granivore	Terrestrial
Calomys expulsus	99.7	2.1	28.2	Frugivore/Granivore	Terrestrial
Calomys laucha	65.0	48.0	19.0	Frugivore/Granivore	Terrestrial
Calomys lepidus	69.5	44.5	20.6	Frugivore/Granivore	Terrestrial
Calomys musculinus	96.0	91.0	21.0	Frugivore/Granivore	Terrestrial
Calomys tener	77.5	60.6	14.5	Frugivore/Granivore	Terrestrial
Calomys tocantinsi	90.1	66.6	25.3	Frugivore/Granivore	Terrestrial
Cerradomys langguthi	136.3	169.6	62.6	Frugivore/Granivore	Terrestrial
Cerradomys maracajuensis	167.0	189.5	114.0	Frugivore/Granivore	Terrestrial
Cerradomys marinhus	168.0	191.0	108.4	Frugivore/Granivore	Terrestrial
Cerradomys scotti	134.0	149.5	90.0	Frugivore/Granivore	Terrestrial
Cerradomys subflavus	160.0	177.5	73.0	Frugivore/Granivore	Terrestrial
Cerradomys vivoi	143.3	177.4	77.6	Frugivore/Granivore	Terrestrial
Chelemys macronyx	129.0	56.7	71.0	Insectivore/Omnivore	fossorial

Delomys collinus	253.0	126.0	47.0	Frugivore/Granivore	Terrestrial
Delomys dorsalis	127.0	132.0	60.0	Frugivore/Granivore	Terrestrial
Delomys sublineatus	125.0	105.0	60.0	Frugivore/Granivore	Terrestrial
Drymoreomys albimaculatus	136.3	170.3	55.0	Insectivore/Omnivore	Terrestrial
Eligmodontia puerulus	84.8	80.4	28.5	Seed predator/Herbivore	Terrestrial
Eligmodontia typus	83.5	94.0	28.5	Seed predator/Herbivore	Terrestrial
Euryoryzomys emmonsae	137.7	152.0	72.0	Frugivore/Granivore	Terrestrial
Euryoryzomys lamia	141.0	145.5	65.0	Frugivore/Granivore	Terrestrial
Euryoryzomys macconnelli	290.8	149.5	66.5	Frugivore/Granivore	Terrestrial
Euryoryzomys russatus	135.0	139.0	85.0	Frugivore/Granivore	Terrestrial
Euryoryzomys nitidus	259.8	130.5	55.2	Frugivore/Granivore	Terrestrial
Geoxus valdivianus	96.0	45.6	30.8	Insectivore/Omnivore	Semifossorial
Graomys griseoflavus	85.5	105.0	90.0	Seed predator/Herbivore	Terrestrial
Holochilus brasiliensis	193.0	198.0	210.0	Frugivore/Herbivore	Semiaquatic
Holochilus chacarius	164.0	167.0	150.0	Frugivore/Herbivore	Semiaquatic
Holochilus sciureus	164.0	150.0	139.7	Frugivore/Herbivore	Semiaquatic
Hylaeamys acritus	145.0	119.6	57.0	Frugivore/Granivore	Terrestrial
Hylaeamys laticeps	275.8	130.0	49.1	Frugivore/Granivore	Terrestrial
Hylaeamys megacephalus	236.0	112.0	45.4	Frugivore/Granivore	Terrestrial
Hylaeamys oniscus	221.1*	116.5*	59.0	Frugivore/Granivore	Terrestrial
Hylaeamys yunganus	227.8	104.4	39.0	Frugivore/Granivore	Terrestrial
Irenomys tarsalis	109.2	160.2	43.2	Herbivore/Frugivore/Granivore	Arboreal
Juliomys ossitenuis	201.5	111.0	23.0	Frugivore/Seed predator	Arboreal
Juliomys pictipes	94.0	108.8	23.5	Frugivore/Seed predator	Arboreal
Juscelinomys huanchacae	172.0	98.0	99.0	Insectivore/Omnivore	Terrestrial
Kunsia tomentosus	235.3	169.0	426.0	Herbivore	Semifossorial
Loxodontomys micropus	129.0	95.6	70.8	Herbivore/Omnivore	Terrestrial
Lundomys molitor	193.0	235.0	358.5	Frugivore/Omnivore	Semiaquatic
Microryzomys minutus	76.0	122.0	13.5	Herbivore/Seed predator/Omnivore	Scansorial
Neacomys dubosti	76.0	79.0	14.0	Frugivore/Granivore	Terrestrial
Neacomys paracou	73.0	73.0	14.0	Frugivore/Granivore	Terrestrial
Neacomys spinosus	182.0	96.7	31.0	Frugivore/Granivore	Terrestrial
Neacomys tenuipes	83.0	96.0	19.0	Frugivore/Granivore	Terrestrial
Necromys lactens	145.5*	71.0*	32.9	Omnivore	Terrestrial
Necromys lasiurus	123.0	69.0	42.2	Frugivore/Omnivore	Terrestrial
Necromys lenguarum	123.0*	69.0*	42.2*	Frugivore/Omnivore	Terrestrial
Necromys obscurus	190.5	75.0	43.5	Frugivore/Omnivore	Terrestrial
Nectomys rattus	210.8	214.5	239.8	Frugivore/Omnivore	Semiaquatic
Nectomys squamipes	200.7	208.4	229.0	Frugivore/Omnivore	Semiaquatic
Nephelomys keaysi	159.47*	185.5*	58.3	Omnivore	Terrestrial
Oecomys auyantepui	110.0	116.0	42.0	Frugivore/Seed predator	Arboreal
Oecomys bicolor	94.0	112.0	28.0	Frugivore/Seed predator	Arboreal
Oecomys catherinae	141.0	166.0	70.0	Frugivore/Seed predator	Arboreal
Oecomys concolor	128.0	141.0	32.8	Frugivore/Seed predator	Arboreal
Oecomys mamorae	136.0	166.0	79.0	Frugivore/Seed predator	Arboreal

Oecomys paricola	100.0	100.0	37.0	Frugivore/Seed predator	Arboreal
Oecomys rex	152.0	158.0	60.0	Frugivore/Seed predator	Arboreal
Oecomys roberti	286.7	160.9	233.2	Frugivore/Seed predator	Arboreal
Oecomys rutilus	84.0	98.0	20.0	Frugivore/Seed predator	Arboreal
Oecomys speciosus	152.52*	137.97*	73.4	Herbivore/Seed predator/Omnivore	Arboreal
Oecomys trinitatis	293.5	161.8	61.0	Frugivore/Seed predator	Arboreal
Oligoryzomys chacoensis	223.4	129.0	23.0	Frugivore/Granivore	Scansorial
Oligoryzomys destructor	92.0	121.5	25.2	Frugivore/Granivore	Scansorial
Oligoryzomys flavescens	87.0	109.7	18.8	Frugivore/Granivore	Scansorial
Oligoryzomys fornesi	72.3	100.1	14.0	Frugivore/Granivore	Scansorial
Oligoryzomys fulvencens	80.5	101.0	16.3	Frugivore/Granivore	Scansorial
Oligoryzomys longicaudatus	99.0	124.0	29.7	Granivore	Scansorial
Oligoryzomys microtis	89.0	91.0	19.5	Frugivore/Granivore	Scansorial
Oligoryzomys nigripes	92.0	116.0	25.4	Frugivore/Granivore	Scansorial
Oligoryzomys rupestris	82.9	121.1	13.8	Frugivore/Granivore	Scansorial
Oligoryzomys stramineus	94.3	118.6	27.1	Frugivore/Granivore	Scansorial
Oxymycterus caparaoe	128.9	90.4	46.4	Insectivore/Omnivore	Semifossorial
Oxymycterus dasytrichus	148.8	125.2	94.9	Insectivore/Omnivore	Semifossorial
Oxymycterus delator	144.5	91.3	78.3	Insectivore/Omnivore	Semifossorial
Oxymycterus hispidus	165.3	111.5	90.8	Insectivore/Omnivore	Semifossorial
Oxymycterus judex	150.2	115.5	92.5	Insectivore/Omnivore	Semifossorial
Oxymycterus nasutus	123.3	86.7	50.0	Insectivore/Omnivore	Semifossorial
Oxymycterus roberti	127.0	110.0	83.7	Insectivore	Terrestrial
Phyllotis darwini	124.0	135.5	50.8	Granivore/Omnivore	Terrestrial
Phyllotis magister	132.0	138.0*	68.5	Omnivore/Herbivore	Terrestrial
Phyllotis osilae	126.0	131.0	43.6	Omnivore/Herbivore	Terrestrial
Phyllotis xanthopygus	127.5	147.5	52.4	Herbivore/Folivore	Terrestrial
Pseudoryzomys simplex	115.0	116.0	50.0	Frugivore/Omnivore	Terrestrial
Rhagomys rufecens	85.5	99.6	22.0	Insectivore/Omnivore	Scansorial
Rhipidomys ipukensis	121.0	140.0	66.0	Frugivore/Seed predator	Arboreal
Rhipidomys leucodactylus	349.0	194.3	80.0	Frugivore/Seed predator	Arboreal
Rhipidomys macrurus	133.4	169.3	80.3	Frugivore/Seed predator	Arboreal
Rhipidomys mastacalis	136.7	168.9	86.9	Frugivore/Seed predator	Arboreal
Rhipidomys nitela	115.5	148.8	41.0	Frugivore/Seed predator	Arboreal
Scapteromys tumidus	172.0	153.0	124.0	Insectivore/Omnivore	Semiaquatic
Scolomys melanops	94.5	67.0	26.5	Herbivore	Terrestrial
Sigmodon alstoni	137.0	91.0	55.7	Herbivore	Terrestrial
Sigmodon hispidus	167.5	91.0*	110.7	Herbivore	Terrestrial
Sooretamys angouya	161.0	192.0	116.0	Frugivore/Granivore	Terrestrial
Thalpomys cerradensis	101.0	73.0	24.0	Frugivore/Granivore	Terrestrial
Thalpomys lasiotis	80.7	50.1	17.2	Frugivore/Granivore	Terrestrial
Thaptomys nigrita	90.6	44.5	21.3	Insectivore/Omnivore	Terrestrial
Wiedomys pyrrhorhinos	100.0	173.0	34.0	Frugivore/Omnivore	Scansorial
Zygodontomys brevicauda	121.5	98.5	47.5	Frugivore/Granivore	Terrestrial

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Considerações finais

Diferentes fatores podem determinar a estrutura de comunidades biológicas (Wu *et al.,* 2012). Além disso, esses fatores podem ser de naturezas muito distintas, tais como fatores ecológicos e funcionais (relacionados a interações com o ambiente e com outras espécies) e fatores históricos e evolutivos (Webb *et al*., 2002). Os pequenos mamíferos sul-americanos (marsupiais e roedores cricetídeos) apresentam um padrão de dispersão no continente sul-americano bastante distinto e intrigante. Os roedores cricetídeos apresentam uma colonização muito mais recente no continente do que os marsupiais, apenas durante a formação do Istmo do Panamá (Eisenberg & Redford, 1989). Com a sua chegada, modificações na estrutura das comunidades podem ter acontecido já que atualmente esses grupos ocupam nichos bastante diversos e também específicos. O embasamento desta ideia está em algumas evidências de substituição de fauna descritas para o período do Grande Intercâmbio entre as Américas - *GABI*, em inglês, *Great American Biota Interchange* (Morales-Castilla et al., 2012; Woodburne 2010; Webb, 1978). Desta forma, esses dois grupos são bastante interessantes não só do ponto de vista funcional, mas também das questões geográficas relacionadas a suas histórias evolutivas.

Encontramos um padrão de partição de nicho entre marsupiais e roedores cricetídeos ao longo do continente sul-americano, havendo uma tendência latitudinal nesse padrão, com maior diferenciação de nicho em direção ao norte do continente – que foi a grande porta de entrada dos cricetídeos. Essa abordagem pôde ser utilizada através de uma nova métrica de divergência funcional proposta no capítulo 1 desta dissertação. Essa métrica avalia a variação dos atributos funcionais entre dois clados coocorrentes na mesma comunidade através da comparação de pares de clados

filogenéticos que coocorrem na mesma comunidade, distinguindo o quanto similiar ou diferente funcionalmente esses clados são.

No capítulo 2, verificamos que tanto fatores climáticos e funcionais quanto fatores evolutivos e históricos determinam o padrão latitudinal de divergência funcional entre esses clados. Essa sobreposição de tipos distintos de determinantes pode acontecer justamente porque eles podem ocorrer em escalas distintas (Ghaham & Fine, 2008; Cardillo, 2011). Os processos ecológicos estão mais diretamente relacionados a efeitos locais e processos histórios e geográficos estão mais associados a escalas regionais (Webb *et al*., 2002; Wiens & Donoghue, 2004).

Em nossa análise, fatores ecológicos relacionam-se a quanto cada grupo é funcionamente redundante e mostraram-se bastante importantes na estruturação das comunidades de pequenos mamíferos aqui representadas. Fatores evolutivos estão relacionados à idade evolutiva média de cada um dos clados em cada comunidade. O grupo mais basal (os marsupiais) se mostrou diretamente mais importante em determinar a relação de divergência funcional. Fatores históricos estão relacionados ao processo de formação do Istmo do Panamá e demostram que comunidades mais distantes desse ponto apresentam padrões um pouco distintos das que estão mais próximas geograficamente. O Istmo do Panamá permitiu a invasão de uma biota totalmente diferente no continente (Webb, 1978; Woodburne 2010) e, ainda hoje, continua determinando padrões funcionais entre os grupos que aqui já estavam e os que chegaram neste período.

Acreditamos, considerando alguns atributos funcionais, que os marsupiais apresentam uma conservação de nicho mais intensa que os roedores cricetídeos e que, esses últimos, por apresentarem uma irradiação e diversificação bastante intensa no continente sul-americano ainda podem estar sofrendo uma evolução nos seus nichos.

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