RAFAELA BASTOS PEREIRA

DIVERSITY PATTERNS OF ONISCIDEA (ISOPODA, CRUSTACEA) ASSOCIATED WITH BRAZILIAN CAVES

LAVRAS – MG
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RESUMO

Compreender os padrões de distribuição das espécies representa um aspecto fundamental não somente aos estudos de Biogeografia fornecendo indícios de condições pretéritas que levaram as linhagens aos locais onde hoje são observadas, mas também para fornecer suporte para a sua conservação. Embora isto seja bem explorado para diversos taxa em todo o mundo, a fauna subterrânea ainda carece de informações a esse respeito. Esta tese foi conduzida com o objetivo de elucidar os padrões de distribuição de Oniscidea associados a cavernas brasileiras, especificamente testando se apresentam um gradiente latitudinal de riqueza e de amplitude de distribuição das espécies. Além disso foram delimitadas áreas de endemismo (AE) com base na interpolação geográfica de endemismos, para as quais foi calculado o índice de distinção taxonômica (Δ^*). Com base nisso foram indicadas áreas prioritárias para a conservação deste grupo e consequentemente da paisagem a que estão associados e toda a biodiversidade nela contida. Observou-se que nem a riqueza nem a amplitude de distribuição de Oniscidea estão relacionados à latitude, mas sim ao número de cavernas presente na mesma faixa latitudinal. Nenhuma relação significativa foi observada quando os troglóbios foram desconsiderados. Quatorze AEs foram identificadas, entre as quais a Província Espeleológica de Arcos-Pains-Doresópolis (PEAPD) e Carste Sul da Bahia destacaram-se como áreas de maior riqueza, enquanto PETAR e Chapada Diamantina apresentaram os maiores valores de Δ^*. A PEAPD foi avaliada mais detalhadamente a fim de comparar os padrões de diversidade taxonômica, filogenética e funcional das assembleias epígea e hipógea de Oniscidea, especialmente testando o efeito dos troglóbios sobre estes padrões, além de verificar que componente da β diversidade predomina na estruturação da comunidade. Desconsiderando os troglóbios, não houve diferenças entre a diversidade taxonômica, filogenética e funcional epígea e hipógea, mas quando estes são considerados as cavernas apresentaram maior diversidade taxonômica. Além disso, a diversidade funcional total foi maior no ambiente hipógeo, mas não houve diferenças entre a β diversidade funcional, ou seja, no quão funcionalmente diferentes as cavernas e os transectos são entre si. Portanto, os troglóbios são os grandes responsáveis pela singularidade taxonômica das cavernas, as quais são mais ricas em espécies filogeneticamente relacionadas e funcionalmente redundantes. Tais resultados reforçam a necessidade de conduzir análises manipulando a presença de algumas espécies para testar seu efeito sobre os padrões observados, bem como de usar abordagens integrativas ao avaliar padrões de diversidade.

Palavras-chave. Biogeografia. Diversidade. Gradiente latitudinal. Regra de Rapoport. Áreas de endemismo. Estruturação de comunidades. Isópodes terrestres.

ABSTRACT

Understanding the patterns of species distribution represents a fundamental aspect not only for Biogeographical studies providing indications of previous conditions that drove the lineages to where we observed them in the present, but also providing support to conservation actions. Although this is largely explored for several taxa worldwide, the subterranean fauna still lacks information on this issue. This thesis was conducted in order to elucidate the distribution patterns of Oniscidea associated with Brazilian caves, specifically testing if they present a latitudinal gradient of richness and range size. Moreover, areas of endemism (AE) were delimited based on the geographical interpolation of endemism, for which the index of taxonomic distinctness (Δ*) was calculated. Posteriorly priority areas of conservation of cave isopods were indicated, consequently of the landscape with which they are associated and all the biodiversity that it contains. Neither richness nor range size are significantly related to the latitude, but rather to the number of caves present in the same latitudinal range. Any significant relationship was observed when troglobites were disregarded. Fourteen AEs were identified, among which the Speleological Province of Arcos-Pains-Doresópolis (SPAPD) and Southern Karst of Bahia stood out as the richest areas, while PETAR and Chapada Diamantina presented the highest values of Δ*. SPAPD was more intensively evaluated in order to compare the patterns of taxonomic, phylogenetic and functional diversity of epigean and hypogean assemblages of Oniscidea, especially testing the effects of troglobites over these patterns, besides verifying which component of β diversity predominates as assembly rule. When disregarding troglobites any significant difference was observed between the taxonomic, phylogenetic and functional diversity of epigean and hypogean habitats, although when they are considered the caves present higher taxonomic diversity. Furthermore, the overall functional diversity was higher in the hypogean habitat, but there were not significant differences between the functional β diversity of the two environments. Therefore, the troglobites are the great responsible by the taxonomic singularity of caves, which are richer in phylogenetically related and functionally redundant species. Such results reinforce the need to conduct analysis manipulating the presence of some species to test their effects over the observed patterns, as well as of using integrative approaches when evaluating the diversity patterns.

Keywords. Biogeography. Latitudinal gradient. Rapoport's Rule. Areas of endemism. Assembly rules. Terrestrial isopods.

SUMÁRIO

PRIMEIRA PARTE

1 INTRODUÇÃO GERAL

Diversas teorias foram propostas em Ecologia de comunidades na tentativa de explicar padrões de diversidade de espécies no espaço e no tempo, tais como as teorias de sucessão ecológica (CLEMENTS, 1916; GLEASON, 1927), biogeografia de ilhas (MACARTHUR & WILSON, 1967) e o gradiente latitudinal, o mais aceito e mais antigo padrão (HAWKINS, 2001). Essas teorias continuam sendo testadas e/ou questionadas, como a teoria neutra de Hubbell (2001). No entanto tem-se percebido que as medidas tradicionais de diversidade até então usadas são pouco informativas com relação à estrutura (WEBB, 2000) e funcionamento (DÍAZ & CABIDO, 2001) das comunidades, já que na maioria das vezes assumem que as espécies são equivalentes (MAGURRAN, 2004).

Uma comunidade composta por espécies pertencentes a diversos gêneros é mais diversa filogeneticamente do que uma composta pelo mesmo número de espécies, porém pertencentes a um mesmo gênero (MAGURRAN, 2004). Nesta segunda comunidade exemplificada, a perda de uma espécie levaria à uma perda muito maior de informação genética do que na segunda, tal como demonstrado por May (1990) and Williams et al (1991). Dessa forma ao definir áreas prioritárias para conservação é preferível estabelecer áreas que contenham a maior diversidade filogenética possível (POLASKY et al, 2001).

Embora a medida mais acurada da relação filogenética de duas espécies quaisquer seja a estimativa da idade do evento de especiação a partir de um ancestral comum mais recente (HARVEY & PAGEL, 1991), muitas vezes esta informação não está disponível, especialmente quando se trata de grandes comunidades. Além disso, o ideal seria sequenciar vários genes já que pode haver diferentes taxas de mudança molecular (WEBB, 2000), o que dificulta ainda mais a execução de trabalhos com comunidades baseados nessa abordagem. Neste sentido, o índice de distinção taxonômica tem se mostrado promissor como indicativo da diversidade dada a facilidade para o calcular e robustez em relação a diferenças na amostragem filogenética (CLARKE & WARWICK 1998, 1999).

Assim como observado para diversidade filogenética, observa-se um crescente interesse por diversidade funcional nos últimos anos e consequentemente uma série de métricas vem sendo propostas para avaliá-la (e. g. PETCHEY & GASTON, 2006; CARDOSO, RIGAL & CARVALHO, 2015). Segundo Tilman (2001), a diversidade funcional representa a diversidade de características das espécies que influenciam o funcionamento das comunidades.

Cianciaruso, Silva & Batalha (2012) supõem que abordagens integrativas envolvendo medidas de diversidade que incorporem informações filogenéticas (WEBB, 2000) e/ou características funcionais das espécies (DIAZ & CABIDO, 2001; PETCHEY & GASTON, 2006) devem ser usadas, as quais podem ser melhores preditoras do que as medidas tradicionais separadamente. Villéger et al (2012), por exemplo, avaliaram comunidades de peixes e observaram um valor extremamente baixo de beta diversidade funcional apesar de uma alta dissimilaridade na composição e dominância de espécies.

Assim, estes autores sugerem que as diversidades taxonômica e funcional devem ser quantificadas simultaneamente já que estas abordagens podem apresentar diferentes padrões e estas diferenças podem contribuir para a compreensão de fatores estruturadores da comunidade.

A estruturação de comunidades vem sendo atribuída à mecanismos relacionados ao nicho e também a mecanismos neutros. Enquanto os modelos baseados em nicho afirmam que diferenças no uso de recursos pelas espécies é que permitem sua coexistência (CHESSON, 2000), modelos neutros atribuem a composição das comunidades a eventos estocásticos (HUBBELL, 2001). No entanto com relação à habitats extremos, como o ambiente subterrâneo, espera-se que as comunidades sejam compostas por espécies morfologicamente semelhantes que evoluíram em convergência, as quais atualmente apresentam equivalência ecológica (HUBBELL, 2006) já que as condições em que se encontram podem atuar como filtros ambientais.

O ambiente subterrâneo apresenta condições restritivas para muitas espécies, como a ausência de luz e oligotrofia (CULVER; PIPAN, 2009). Assim, Gibert & Deharveng (2002) atestam que muitas vezes estes habitats apresentam sub-conjuntos do conjunto regional de espécies. Este ambiente apresenta redes tróficas estruturadas de maneira diferente das externas, sem a presença de produtores primários fotossintetizantes e relativamente poucos predadores. Além disso os organismos em geral apresentam baixa capacidade de dispersão e baixas taxas de recrutamento, o que acaba favorecendo a evolução desta equivalência funcional anteriormente mencionada. No entanto, Fišer, Blejec & Trontelj (2012) avaliaram anfípodes subterrâneos na Europa e observaram que mesmo ambientes pobres em termos energéticos como as cavernas mantém o potencial para diversificação por meio da diferenciação de nichos. No entanto estes aspectos são muito pouco estudados, especialmente em ambientes subterrâneos tropicais.

Embora a América do Sul contenha uma pequena porção das áreas cársticas do mundo, ainda assim existem milhares de cavernas registradas e estudos recentes tem demonstrado quão grande é seu potencial com relação à diversidade de espécies estritamente cavernícolas (e. g. DEHARVENG, 2005; SOUZA-SILVA; FERREIRA, 2015). O Brasil tem quase 17 mil cavernas registradas (Centro Nacional de Pesquisa e Conservação de Cavernas - CECAV, 2017), no entanto informações sobre a fauna subterrânea estão disponíveis para uma ínfima minoria delas. Espécies (e. g. BASTOS-PEREIRA; FERREIRA, 2015; SOUZA; FERREIRA, 2016), gêneros (FIŠER; ZAGMAJSTER; FERREIRA, 2013), famílias (PREVORČNIC; FERREIRA; SKET, 2012) e até sub-ordens novas (SHEAR et al, 2016) vem sendo descobertas nos últimos anos. Isso reforça o quanto ainda há por ser descoberto nas cavernas brasileiras não somente em relação à identidade taxonômica das espécies, mas também as suas relações filogenéticas e funções ecossistêmicas que exercem. Dessa maneira, embora seja de grande importância compreender os padrões de distribuição da fauna cavernícola no Brasil, existe uma lacuna muito grande de informação que acaba por restringir estudos que busquem testar as grandes teorias já propostas para

explicar padrões de distribuição. Além disso, as características peculiares dos ambientes subterrâneos podem fazer dos organismos cavernícolas exceções à regra, ou não, então muito ainda precisa ser estudado neste sentido.

Embora o ambiente subterrâneo possa apresentar condições restritivas para alguns grupos, outros podem se beneficiar deste tipo de ambiente, como por exemplo os crustáceos da ordem Isopoda (TAITI, 2004) dada a sua higrofilia e adaptações morfológicas a diversas condições (SCHMALFUSS, 1984). Os isópodes são frequentemente encontrados em cavernas no Brasil, para as quais atualmente há 39 espécies descritas, sendo 13 delas troglóbias (CAMPOS-FILHO et al, 2014, 2017). Embora muitos trabalhos sejam conhecidos para espécies epígeas deste grupo, os estudos com espécies subterrâneas concentram-se principalmente em abordagens taxonômicas. Além disso há alguns trabalhos de comunidades cavernícolas que contém espécies de isópodes, mas muitas vezes sequer o gênero destas é identificado (e. g. PROUS; FERREIRA; MARTINS, 2004; SIMÕES; SOUZA-SILVA; FERREIRA, 2012). Recentemente Fernandes, Bichuette & Batalha (2016) compararam a diversidade funcional de isópodes epígeos e hipógeos e sugeriram que o ambiente subterrâneo não é tão severo para este grupo, já que uma maior diversidade funcional foi observada para o ambiente subterrâneo. No entanto uma maior discussão sobre este trabalho será feita posteriormente.

Utilizar um grupo específico de organismos associados a cavernas como modelo de estudo pode representar um primeiro passo no avanço da compreensão dos fatores responsáveis pela estruturação de comunidades e consequentemente dos padrões de distribuição das espécies cavernícolas. Isso se reforça ainda mais em um cenário mega-diverso como o Brasil. Dessa forma, dois manuscritos compõem a presente tese que foi conduzida com o objetivo geral de compreender padrões de diversidade de isópodes associados a cavernas no Brasil. O primeiro manuscrito abrange registros de ocorrência de Oniscidea em cavernas de todo o Brasil e objetivou avaliar os padrões de distribuição das espécies, definir áreas de endemismo, bem como áreas prioritárias para conservação destes isópodes. Já o segundo manuscrito abrange uma escala menor, a província espeleológica de Arcos-Pains-Doresópolis, e objetivou comparar a diversidade taxonômica, filogenética e funcional das assembleias de isópodes epígeos e hipógeos desta região.

2 CONCLUSÃO

Os isópodes associados a cavernas brasileiras não se enquadram em padrões clássicos de distribuição de espécies, tais como o gradiente latitudinal e a regra de Rapoport. No entanto uma maior riqueza de espécies em geral está associada a um maior número de cavernas presentes na região.

As cavernas de litologia carbonática compreendem a maior riqueza de espécies, seguida pelas cavernas ferruginosas, o que na verdade é reflexo tanto da predominância destas litologias entre as cavernas no Brasil, quanto ao maior esforço amostral em cavernas inseridas neste tipo de rocha por

interesse econômico. Por outro lado, as maiores amplitudes de distribuição foram observadas para espécies que habitam cavernas inseridas em rochas quartzíticas e graníticas, as quais são mais suscetíveis à colonização por espécies amplamente distribuídas no ambiente epígeo dadas as suas pequenas dimensões. Além disso observou-se que Cerrado e Caatinga compartilham mais gêneros com a Mata Atlântica do que com o bioma Amazônico, desta forma a Mata Atlântica parece ter representado uma importante fonte de espécies para estes biomas hoje menos úmidos.

As cavernas representam ambientes extremamente importantes para a conservação de isópodes terrestres, já que foram identificadas várias áreas de endemismo no presente estudo. A comparação destas áreas considerando as assembleias como um todo ou apenas as espécies troglóbias permite observar que conservar áreas ricas em espécies restritas ao ambiente subterrâneo engloba também uma alta diversidade de espécies troglófilas (ou seja, que podem estabelecer populações viáveis tanto dentro quanto fora das cavernas). Desta forma as espécies troglóbias podem atuar como espécies guarda-chuva para a conservação dos isópodes associados a cavernas no Brasil e certamente junto destes outros grupos taxonômicos e toda a paisagem externa circundante.

Considerando uma escala menor, no entanto utilizando abordagens complementares, observou-se que as assembleias epígeas e hipógeas de Oniscidea apresentam diferentes padrões de diversidade taxonômica, filogenética e funcional, o que ressalta a importância de se aplicar este tipo de metodologia conjunta nos trabalhos que objetivam avaliar padrões de diversidade. Em escalas regionais, mais especificamente na província espeleológica de Arcos-Pains-Doresópolis, fatores históricos podem ser os responsáveis pelos atuais padrões de diversidade observados, visto que os valores de beta diversidade relativos aos componentes de substituição e aninhamento não diferiram dos modelos nulos.

O presente trabalho representa os primeiros passos para a compreensão da Biogeografia de isópodes terrestres associados a cavernas brasileiras. Estudos com base molecular certamente poderão contribuir grandemente para elucidar as relações filogenéticas dos grupos e desta forma fornecer suporte para estudos filogeográficos. No entanto, antes mesmo de prosseguir com estudos moleculares existe uma alta demanda taxonômica no que diz respeito à descrição de inúmeros táxons já coletados. Por outro lado, a morfotipagem feita por especialistas parece ser uma alternativa viável, visto que muitos trabalhos ecológicos não dependem da identidade taxonômica propriamente dita, como por exemplo os estudos de ecologia funcional.

De forma geral, estudar as espécies de isópodes terrestres associados a cavernas no Brasil representa um caminho bastante promissor em diversos aspectos, dada a grande diversidade existente, os poucos estudos ecológicos já publicados e também os poucos pesquisadores que hoje estudam este grupo no Brasil.

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SEGUNDA PARTE

ARTIGO 1 - DO THE SUBTERRANEAN TERRESTRIAL ISOPODS FIT INTO THE CLASSICAL PATTERNS OF SPECIES DISTRIBUTION? ESTABLISHING AREAS OF ENDEMISM AND CONSERVATION PRIORITIES

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Do the subterranean terrestrial isopods fit into the classical patterns of species distribution? Establishing areas of endemism and conservation priorities

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Aim. (i) to evaluate the diversity patterns of of cave terrestrial isopods testing whether there is a latitudinal gradient of richness and range size of such species; (ii) identify and delimit areas of endemism (AE) for Oniscidea associated with caves and (iii) indicate priority areas for the conservation of cave isopods and the associated landscape.

Location. Brazilian caves.

Methods. Records of isopods in caves from the literature and from the largest collection of subterranean invertebrates from Brazil were gathered. A Venn diagram represented the diversity of genera according to the biomes. The Brazilian territory was divided into latitudinal bands of 1° of amplitude. The species richness and their respective range sizes were correlated with the latitude where they occur, as well as with the lithology of caves. The kernel interpolation of centroids of species distribution was used to estimate the overlap among species and posteriorly delimit areas of endemism. The analyses were conducted with and without troglobitic species. The index of taxonomic distinctness (Δ^*) was calculated for each AE.

Results. 1,012 records of Oniscidea species associated with Brazilian caves were listed, which belong to 13 families, 45 genera and 247 species, 107 of them with troglomorphic traits. Caatinga and Brazilian Savannah have more genera in common with Atlantic Forest than with Amazon. No correlations were observed between species richness and latitude, neither between species range size and latitude, in both analysis considering and not considering troglobites, although species richness was weakly correlated with the number of caves in the same latitudinal band. Fourteen AEs were delimited, from which the Speleological Province of Arcos-Pains-Doresópolis and Southern Karst of Bahia stood out as the richest areas, while PETAR, Chapada Diamantina and Serra Leste presented the highest values of Δ^*.

Main conclusions. Atlantic Forest seemed to have worked as source of species for Caatinga and Brazilian Savannah. Instead of following the classic latitudinal pattern, the diversity of isopods associated with Brazilian caves is positively related to the number of caves present in the same latitudinal band. The species range size did not fit in the Rapoport's Rule. Past harsher climate conditions probably were the cause that has led ancient lineages of isopods to colonize the caves as refuges and form such singular centers of diversification of this group in Brazil.

Keywords. Subterranean diversity, isopods, range size, latitudinal gradients

1 INTRODUCTION

The distribution of species richness has been fascinating since the natural historians and pioneers of evolutionary theories like Darwin (1862) and Wallace (1878) until current researches on Ecology and Biogeography. A broad recognition that species richness increased as the latitude decreases occurred in the 1800s and even in 1807 Humboldt proposed the first explanation for the latitudinal gradient of diversity.

Although the majority of studies and the best examples of the gradient for animals have been based on mammals (Simpson, 1964; McCoy & Connor 1980; Kaufman & Willig, 1998; Lyons & Willig 2002), it has already been demonstrated for many taxonomic groups including terrestrial arthropods (Cushman, Lawton & Manly, 1993; Davidowitz & Rosenzweig, 1998; Kocher & Williams, 2000; Lobo, 2000). Willig, Kaufman & Stevens (2003) affirmed the veracity of such pattern regardless taxonomic affiliation, geographic context or time domain, but for all rules there are exceptions and it is not different for the latitudinal gradient of diversity. Sand beach community (Dexter, 1992), Australian butterflies (Dingle, Rochester & Zalucki, 2000), continental benthic copepod species (Reid, 1994), Andian birds (Poulsen & Krabbe, 1997), parasites (Rohde, 1999) are some examples of groups that did not fit on such gradient. These exceptions were primarily attributed to narrow latitudinal extents (gradients quantified over short latitudinal extents, like shorter than 20°), species with parasitic life histories or aquatic floras (Willig et al., 2003).

Schemske (2002) suggested that the gradient depends on historical, geographic, biotic, abiotic and stochastic events. Moreover, latitude represents a surrogate for several other environmental correlated gradients such as temperature, insolation and seasonality which makes difficult the task to find an explanation for the observed patterns. From 1950s on many studies proposed surrogate hypothesis and Pianka (1966) presented the first review of such hypothesis accounting for the latitudinal gradient.

The conditions supporting the gradient may be summarized into six hypotheses: (i) the geographical area hypothesis considers that tropics support more species in function of the larger area and refers to the species-area relationship of the Islands Biogeography Theory (MacArthur & Wilson, 1967); (ii) the productivity hypothesis (Robinson 1966) suggests that the higher input of solar radiation in the tropics determines a higher energy availability, productivity and biomass, what provides support for a higher diversity; (iii) the ambient energy hypothesis is also based on insolation, but in this case the higher richness of tropics is attributed to the solar energy that creates physical conditions that affect the organisms' physiological responses (at higher latitudes the mean conditions are farther from the thermal optimal zones of organisms, what restricts the number of species able to survive in such regions) (Brown, 1988); (iv) the evolutionary speed hypothesis is also related to solar input, however in this case the higher mean temperatures of tropics increase the metabolism and consequently the rates of speciation, therefore enhancing the evolutionary speed (Rohde, 1992); (v) the geometric constraints hypothesis considers that a gradient is produced as a consequence of the random placement of species ranges in a bounded domain, some area limited by physical and/or physiological barriers that restrict the distribution of species (indeed, it may be considered equivalent to a null hypothesis) (Colwell & Hurtt, 1994); finally, (vi) the Rapoport's rule states that the distributional range size of species is directly related to the latitude. The higher seasonal variability at higher latitudes favors organisms with broad climatic tolerances, which usually present large ranges to deal with the great amplitude of conditions. On the other hand, at lower latitudes organisms usually have narrower tolerances and more restrict ranges in function of the lower seasonal variability (Rapoport, 1975; Stevens, 1989). This pattern was already observed for several taxa, although it has never been investigated for subterranean species.

However, subterranean habitats are generally characterized by the permanent absence of light, constant levels of humidity and oligotrophic conditions (Culver & Pipan, 2009). The temperature amplitude decreases exponentially as depth increases below the soil surface (Freeze

& Cherry, 1979) and even considering differences among subterranean systems, the thermal seasonality is lower than at surface, even in shallow subterranean habitats (Culver & Pipan, 2011). Therefore, subterranean environments do not fit in most of the hypothesis proposed to account for the latitudinal gradient of diversity, which are based on insolation and seasonality. However, Culver et al. (2006) supposed that a highly diverse region regarding subterranean species is observed between 42 and 46° in Europe and around 34° in North America, which represents areas of high productivity and density of caves. These authors explained the observed patterns of diversity based on the dependence of cave fauna on epigean food resources carried into the subterranean realm, therefore more productive epigean habitats provide more resources to the hypogean habitats that consequently are richer in species.

Despite of the already proven generality of this gradient, it has been poorly investigated for caves. Trontelj et al. (2009) suggested the potential effect of historic climate oscillations on spatial patterns of range size in groundwaters, since most species present small ranges and have poor dispersal ability. Hugueny, Movellan & Belliard (2011) pointed that range size is negatively related to extinction rates, in this sense many groundwater species probably were extinct in regions of cold Pleistocene climates. Additionally, Zagmajster et al. (2014) studied the geographic variation in range size and beta diversity of groundwater crustaceans in Europe. These authors found that patterns of increasing range size and decreasing species turnover occur at higher latitudes, which were guided by long-term temperature oscillations and not by climatic seasonality.

Although most of the karstic areas of the world are observed in temperate regions and an exceptionally high biodiversity inhabit such systems in function of caves had been used as refuges by ancestors of many current troglobitic species, several troglomorphic species have been discovered in the Neotropics (Deharveng, 2012), especially in Brazil. Events of climatic changes as well as other mechanisms of isolation such as parapatric speciation, oceanic introgressions and regressions may have provided the evolution of many lineages restrict to the caves of such

megadiverse country (e. g. Ferreira, Prous, Bernardi & Souza-Silva, 2010; Souza, Riutort, Ferreira & Leal-Zanchet. *in press*), for which two hotspots of subterranean biodiversity were recently proposed (Souza-Silva & Ferreira, 2016).

Terrestrial isopods are often found inside caves due to their wide variety of morphologies adapted to distinct habits and the need for high humidity to survive (Schmalfuss, 1984). Moreover, they are considered good biogeographic indicators, especially the troglobitic species, given their poor dispersal ability (Taiti, 2004). Currently there are 39 species of Oniscidea recorded for Brazilian caves, 13 of them troglobites (Campos-Filho, Bichuette & Araujo, 2017b), it means, restrict to the subterranean environment. However, as well as for other groups in Brazil, a huge diversity is still waiting for the few expertise taxonomists to be formally described.

Allied to the high biodiversity, Brazilian ecosystems present high rates of endemism (Myers, Mittermeier, Mittermeier, Fonseca & Kent, 2000) and this scenario is even more pronounced for subterranean species, especially the troglobites, which are frequently found in only one or few caves (e. g. Hoch & Ferreira, 2012; 2016). Most of endemic species are not included in areas of permanent protection such as conservation units, moreover caves are frequently inserted in rocks of economic interest and therefore are target of several irreversible impacts (Simões, Souza-Silva & Ferreira, 2014; Ferreira et al., 2015).

The identification of areas of endemism represents a fundamental task not only for biogeographical studies (Nelson & Platnick, 1981) but also for the definition of conservation priorities (Crisci, Katinas & Posadas, 2003). The first definition of such areas emphasized the complete congruence of species distributional range (Nelson & Platnick, 1981), but given the small probability to find it in the nature (Harol & Mooi, 1994), Linder (2001) proposed that areas of endemism are considered the sum of maximally congruent distribution of two or more species.

The distribution of species range size is inherently linked to the way species are distributed across the space. In this sense Weiser et al. (2007) suggested that understanding distributional range sizes may be the key to explain the diversity patterns. In this context, the

present study was conducted in order to evaluate the patterns of diversity of Oniscidea (Isopoda) associated with Brazilian caves testing whether there is a latitudinal gradient of richness and range size of such species. As well as already demonstrated for several taxonomic groups, it is expected that the lower the latitude, the greater the richness and the shorter the range size of species. Moreover, the current study aimed to identify and delimit endemism areas of Oniscidea species associated with Brazilian caves. More species are expected to co-occur in areas with larger number of caves, in this sense it is expected that the areas of endemism coincide with the largest agglomerations of caves in Brazil. Additionally, priority areas for the conservation cave isopods are indicated.

2 METHODS

2.1 Dataset

Data was composed by records of described species of Oniscidea associated with Brazilian caves found in the literature (Campos-Filho, Araujo, Bichuette, Trajano & Taiti,, 2014; Campos-Filho, Taiti & Araujo, 2015; Campos-Filho, Mise, & Sessegolo, 2015; Souza, Ferreira & Senna, 2015; Campos-Filho, Bichuette & Taiti, 2016; Bastos-Pereira, Souza & Ferreira, 2017; Cardoso, Araujo & Bichuette, 2017; Campos-Filho, Bichuette, Montesanto, Araujo, & Taiti, 2017; Campos-Filho, Bichuette & Araujo, 2017), as well as by all specimens of Oniscidea deposited in the Collection of Subterranean Invertebrates (ISLA) of Federal University of Lavras (UFLA), currently the largest biospeleological collection of Latin America. Most of species deposited in the collection are not described yet, therefore individuals were identified until the lowest taxonomic level as possible based on taxonomic papers of the group ensuring that each morphospecies represents a distinct species. Morphospecies were adopted as operational taxonomic units and will be hereafter treated as species. In the case of already described species, the new records present in the collection were added to the dataset. All species were organized in a spreadsheet with the respective longitude and latitude of occurrence.

2.2   Patterns of richness and range size distribution

The Brazilian territory was divided into latitudinal bands with intervals of 1° and all records of Oniscidea were plotted (Fig.1), as well as all caves recorded for Brazil (CECAV, 2017) and the sampled caves containing isopods. A Venn diagram was constructed for the diversity of genera found on each biome by means of the tool provided by Heberle, Meirelles, da Silva, Telles, & Minghim, (2015). The number of recorded caves, sampled caves and species richness was counted for each latitudinal band. The number of sampled caves and those recorded for each latitudinal band were correlated in order to check for sampling bias. A regression analysis was conducted including richness and number of sampled caves of each latitudinal band, which residuals were used in a posterior regression analysis with latitude in order to investigate the existence of a latitudinal pattern of diversity of Oniscidea associated with caves.

The farthest distance between the points of occurrence was used as a proxy of the range size of each species. The mean range size of species of each latitudinal band was related to the respective latitude in a regression analysis in order to check whether the studied species fit into the Rapoport's rule. Moreover, the lithology of each cave was gathered in order to check for a possible influence on the patterns of richness and range size distribution.

The epigean species from which the obligate cave fauna descended were subject to different climate conditions in relation to the current ones, therefore they may bias the observed patterns. In this sense, the analyses were also conducted disregarding the troglobitic species in order to better investigate the patterns. Statistical analyses were conducted in the software R (R Core Team, 2018).
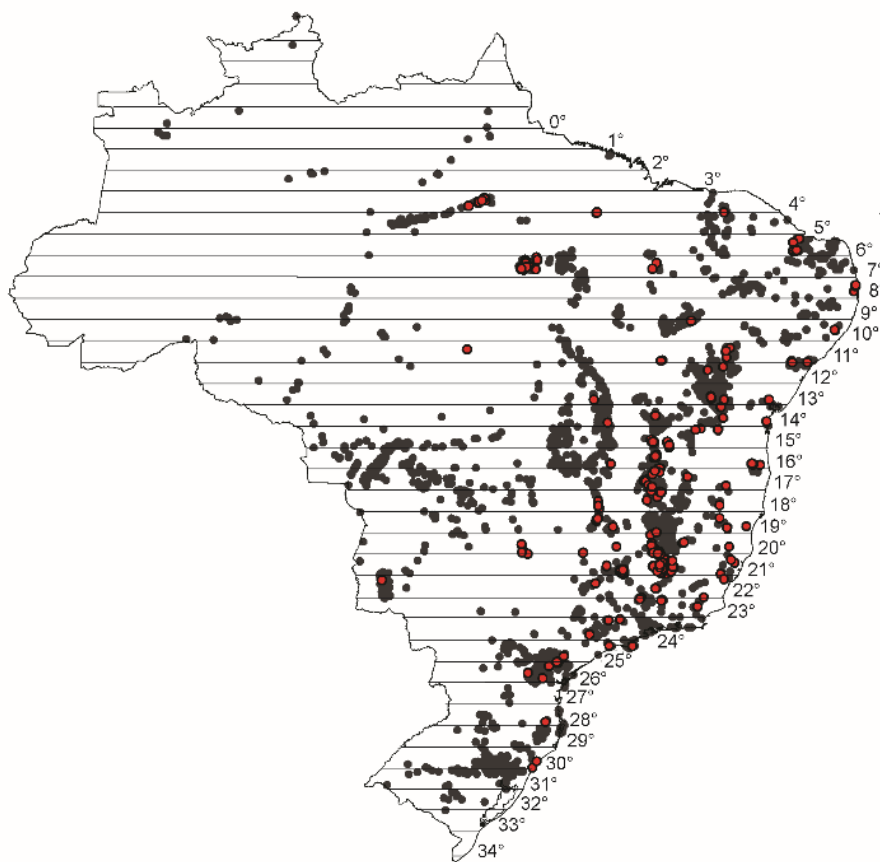
Figure 1. Latitudinal bands used to investigate the diversity patterns of Oniscidea associated with Brazilian caves. Black dots represent all the recorded caves in Brazil. Red dots represent records of Oniscidea in caves.

2.3 Areas of endemism

Oliveira, Brescovit & Santos (2015) proposed a new approach for delimiting areas of endemism based on the quantification of the co-occurrence of species weighed by the distance between the points of distribution records. This new approach does not depend on grid cells, allows the use of occurrence data with gaps and delimits areas of endemism with fuzzy edges. The centroid of longitude and latitude were calculated, as well as the distance between the centroid and the farthest point of occurrence of each species, which was considered the radius of influence. Thereunto, species were sorted into classes established according to their radius of influence (class 1 = from 0 (punctual occurrence) to 2 Km; class 2 = from 2.1 to 10 Km; class 3 = from 10.1 Km to 50 Km; class 4 = from 50.1 Km to 500 Km; class 5 = from 500.1 to 1600 Km).

The amplitude of classes is determined by who is conducting the analysis based on particularities of the studied taxa, but Oliveira et al. (2015) attested that regardless such arbitrariness, there is no significant influence for the results.

The radius of influence is a value required for the kernel index estimation. This index represents a method of interpolation used to delimit areas of endemism in Geographic Information System and is based on circular areas of influence of a given phenomenon. The influence of phenomenon decreases from the centroid to the limits following a Gaussian function (Bailey & Gaterl, 1995), what attributes a fuzzy limit to each area. Overlapping the areas of influence allows estimating the density of occurrence of the phenomenon, in this case, how many species occur in the same area. The more species with overlapping area of occurrence, the higher the kernel index.

A map of density of overlapping areas of occurrence was generated and the kernel index was standardized between 0 and 1 for each class of radius of influence. Posteriorly a consensus map was obtained and isolines were plotted to allow identifying the areas of endemism. The isolines create contours (level curves) within the areas of endemism, thus providing the identification of internal subdivisions. Such procedures were conducted by means of the ArcGIS toolbox GIE (Geographical Interpolation of Endemisms) available at Oliveira et al. (2015). For more details on the method used to delimit and identify the areas of endemism please see Oliveira et al. (2015).

Firstly, the whole dataset was used to delimit areas of endemism, for which the index of taxonomic distinctness (Δ^*) was calculated, which provide cohesive responses to ecological gradients. This index uses one matrix of incidence data and other describing the taxonomic hierarchy of species and attributes distinct weights to different taxonomic levels to calculate the average path length between any two randomly chosen individuals of different species (Clarke & Warwick 1998, 1999). Posteriorly all procedures were repeated considering only troglobitic species of Oniscidea in order to identify strategic areas to preserve species restrict to the subterranean environment.

3 RESULTS

Overall, 1,012 records of Oniscidea species associated with Brazilian caves were gathered belonging to 13 families, 45 genera and 247 species, 107 of them with troglomorphic traits. The records were distributed along the main karstic groups of Brazil (except Paranoá, Araras and Xambioá, which are relatively small speleological units), besides the two largest ferriferous cave systems, the Mineral Province of Carajás and Iron Quadrangle. Single records represented 55% of species, 37.6% of species presented between 2 and 10 records, 7% between 11 and 55 and only one species presented more than 100 records (Armadillidae: *Ctenorillo ferrarai*).

3.1   Patterns of richness and range size distribution

Although Brazilian Savannah presented the highest richness of genera (23), Amazon presented the greatest number of genera exclusively found in this biome (10), followed by Brazilian Savannah (8). The highest richness of genera strictly composed by troglobitic species is found in Brazilian Savannah (*Xangoniscus, Spelunconiscus* and other five potentially new genera of Styloniscidae), among which only *Xangoniscus* is shared with Caatinga. Two genera occurred in the four largest biomes of Brazil, namely Amazon, Atlantic Forest, Brazilian Savannah and Caatinga: *Novamundoniscus* (Dubioniscidae) and *Trichorhina* (Platyarthridae). Caatinga shares more genera with Brazilian Savannah and Atlantic Forest (4) and there are five genera exclusively found in this semi-arid biome, while Brazilian Savannah has eight exclusive genera. Pampa was not included in the Venn diagram (Fig. 2) in order to optimize the interpretability of the figure, since five groups (biomes) would make the diagram more complex. Pampa presented the occurrence of one genera of Porcellionidae. The genus *Circoniscus* is found in Amazon, Brazilian Savannah and Atlantic Forest.
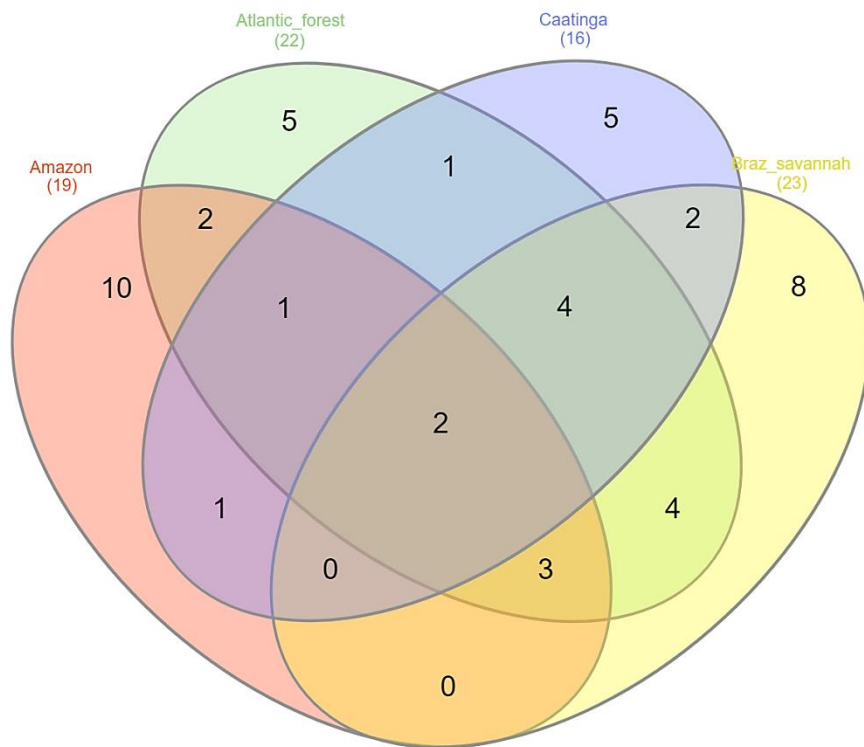
Figure 2: Venn diagram representing the number of genera of cave Oniscidea shared among the largest Brazilian biomes.

The highest richness of species was recorded for limestone and iron ore caves, while the greatest range sizes were observed in caves associated with quartzite and granite rocks (Fig. 3).
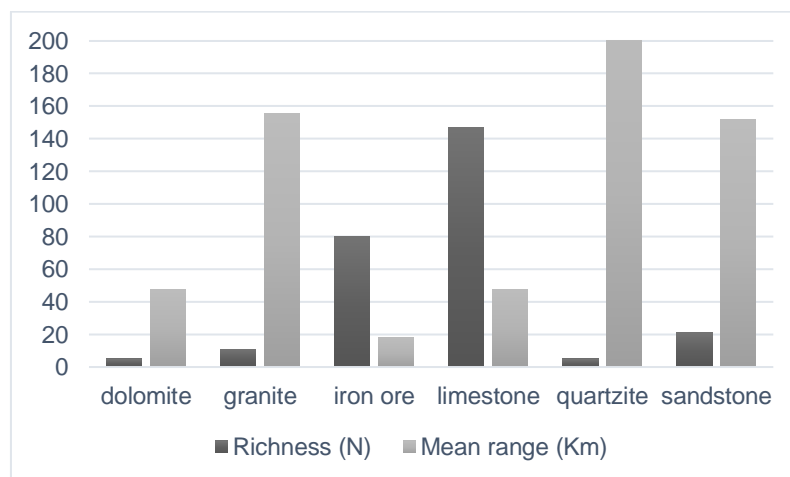
Figure 3. Species richness and range size distribution of terrestrial isopods in caves of different lithologies in Brazil.

The number of sampled caves was correlated with the number of caves recorded for each latitudinal band (correlation coefficient = 0.7216, t = 5.709, p < 0.001). The peak of diversity of

terrestrial isopods was observed between the latitude 20 and 21°, as well as reported when considering only troglobitic species, and the latitudinal band at 7° also presented a remarkable richness (Fig. 4). No significant relationships were observed regarding the latitudinal gradient of richness. Richness was significantly related to the number of caves sampled on each latitudinal band. Additionally, regressions were not significant between the mean range size of species and latitude, neither between range size and number of caves recorded for the same latitudinal band. When troglobitic species were removed from the dataset, any relationship was significant, neither regarding richness nor range size.
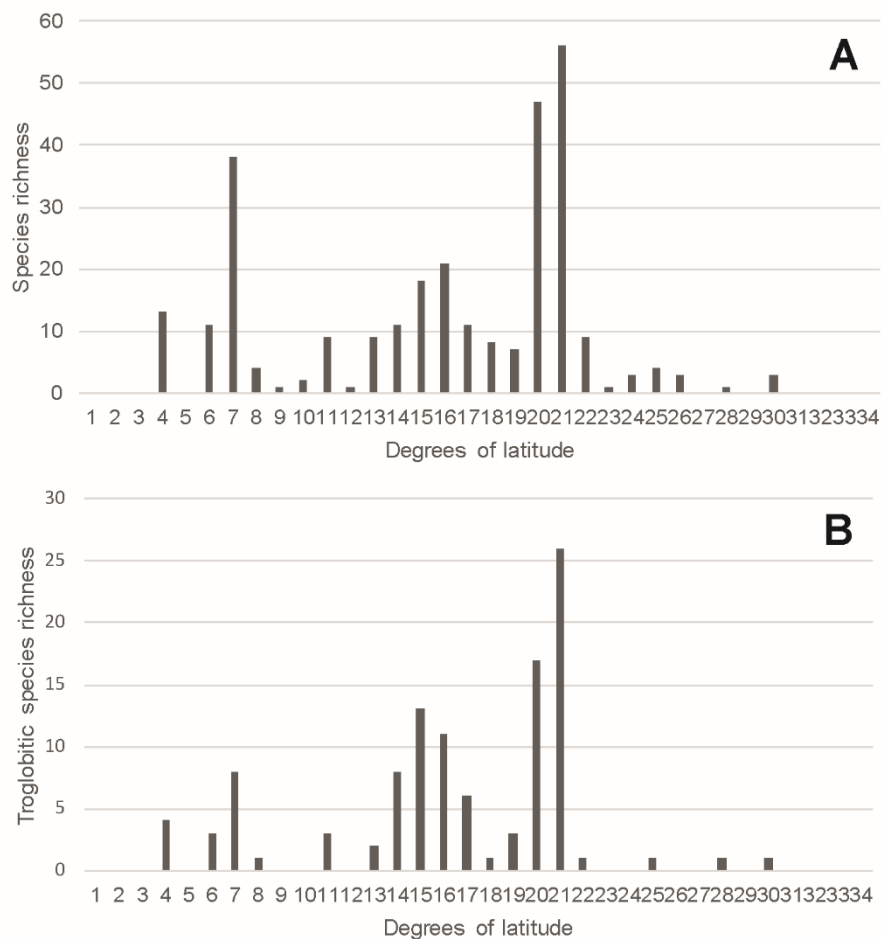
Figure 4. Total richness of terrestrial isopods associated with Brazilian caves per latitudinal bands (A); richness of troglobitic species of terrestrial isopods (B).

3.2   Areas of endemism

Fourteen areas of endemism (AE) were identified for Oniscidea associated with caves in Brazil, all of them geographically separated (Fig. 5). These areas were grouped into four categories based on the biome they belong to, although some of them are situated in transitional regions: Amazon group (AE1 to 4), Caatinga group (AE5 to 8), Brazilian Savannah group (AE9 to 13) and Atlantic Forest (AE14).

Figure 5. Areas of endemism (AE) of Oniscidea associated with caves in Brazil defined based on the Geographical Interpolation of Endemisms.

AE13 is situated in the Iron Quadrangle and supported the highest richness of isopods, with 30 species, although only four of them presented troglomorphic traits. This area presented and intermediate taxonomic distinctness when compared to the others ($\Delta^* = 89.75$). On the other

hand, AE10 is situated in the Karstic Province of Arcos-Pains-Doresópolis and represented the second richest area (S = 26), for which 65% of species (17) are troglobitic. However, this area presented a low taxonomic distinctness ($\Delta^* = 68.98$). AE14 presented the lowest richness (S = 3), but the highest taxonomic distinctness ($\Delta^* = 100.0$). AE10 presented taxonomic distinctness lower to the expected, while the other areas did not present significant differences from the expected value of Δ^* (Fig. 6). More details about the areas of endemism can be observed on Table 1.

Table 1. Location and diversity of areas of endemism delimited for Oniscidea associated with Brazilian caves based on Geographical Interpolation of Endemisms.

Area of endemism (AE)	Region	Species richness (troglobites)	Genera (N)	Families (N)	Recorded caves* (approximately)	Taxonomic distinctness (Δ^*)
AE1	Altamira and Medicilândia	10 (3)	7	5	25	92.13
AE2	Serra Norte	12 (2)	8	6	335	93.74
AE3	Serra Sul	30 (5)	15	8	210	89.32
AE4	Serra Leste	9 (3)	7	6	160	94.15
AE5	Chapada Diamantina	18 (9)	13	9	300	94.40
AE6	Southern Karst of Bahia	14 (10)	9	4	40	82.00
AE7	Vale do Cochá	4 (3)	2	2	60	66.25
AE8	Peruaçu	8 (4)	6	4	205	88.41
AE9	Central-Northern Minas Gerais	14 (9)	7	5	525	89.30
AE10	Karstic Province Arcos-Pains-Doresópolis	26 (17)	5	4	2090	68.98
AE11	Cordisburgo	8 (6)	4	2	60	79.83
AE12	APA Carste Lagoa Santa	14 (3)	7	5	1090	90.74
AE13	Iron Quadrangle	30 (4)	11	6	990	89.75
AE14	PETAR	3 (1)	3	3	430	100.0
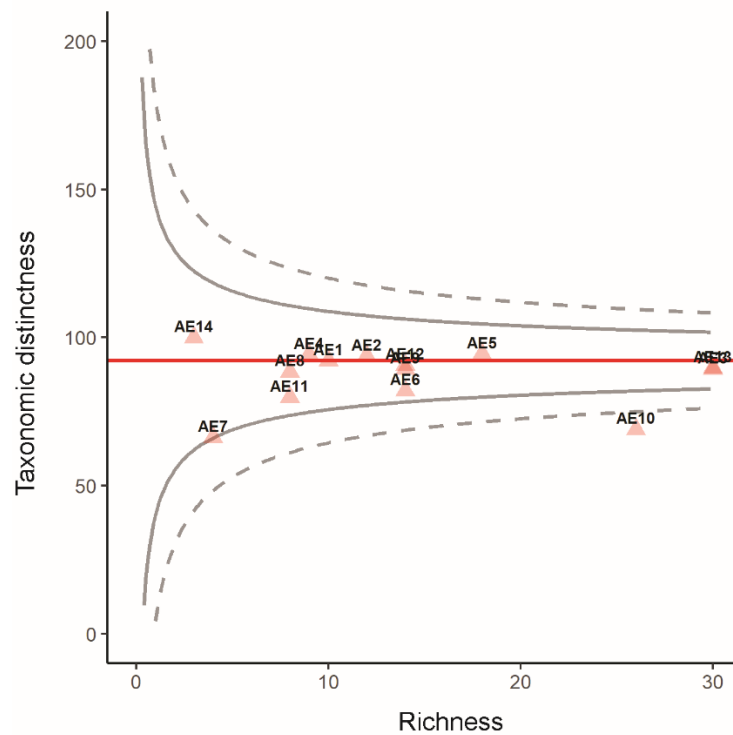
Figure 6. Taxonomic distinctness (Δ^*) of areas of endemism (AE) of Oniscidea associated with Brazilian caves. Red line: expected Δ^* value; grey continuous line: 95% confidence interval; grey dashed line: 99% confidence interval.

Some differences were observed when delimiting areas of endemism considering only troglobitic species of Oniscidea. The Kernel Index was lower for AE2, AE3, AE4 and AE5 since troglobitic species in general present a shorter range of occurrence, what led to a lower overlapping in the species distribution (Fig. 7). On the other hand, the index was higher for AE14 in function of the presence of the troglobitic species *Cylindroniscus flaviae* (Styloniscidae) in ten caves.
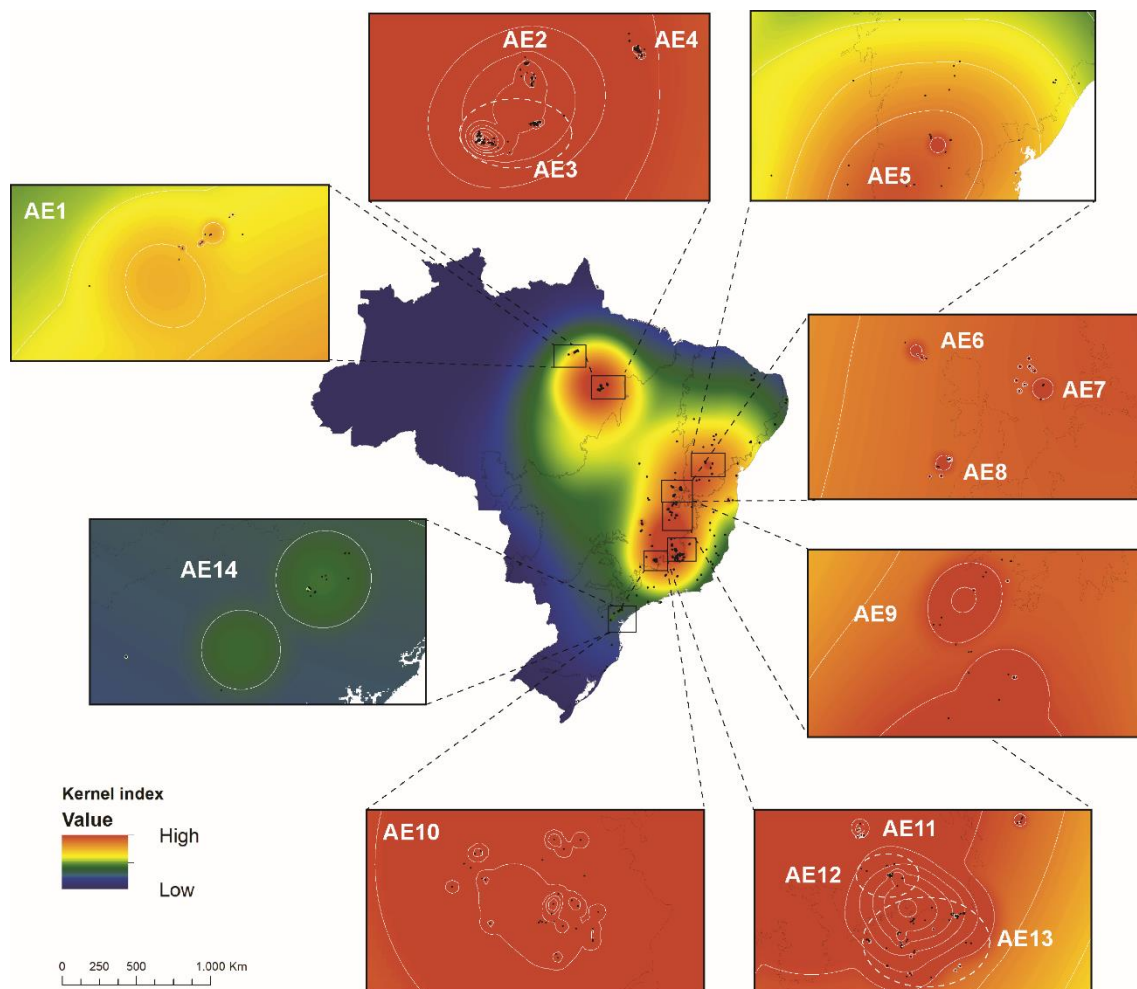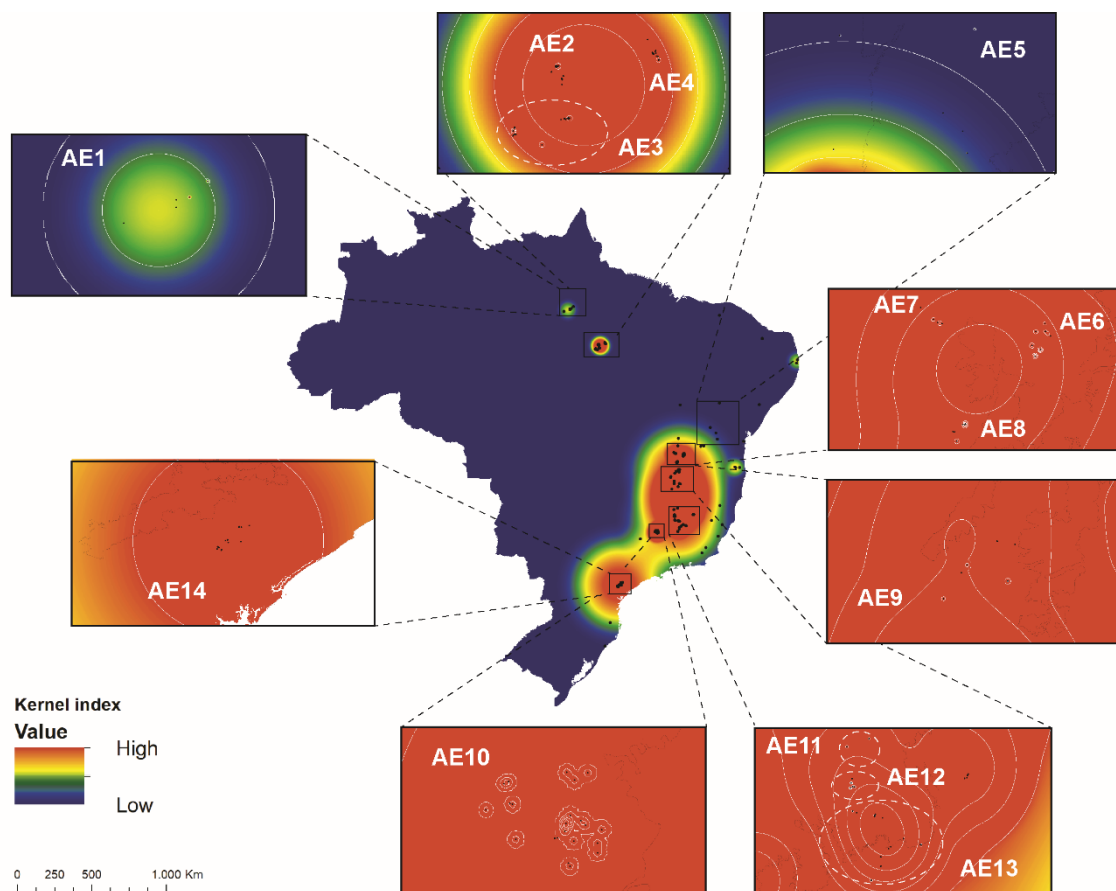
Figure 7. Areas of endemism (AE) of troglobitic Oniscidea associated with caves in Brazil defined based on the Geographical Interpolation of Endemisms.

4 DISCUSSION

Although the Theory of Refugia proposed by Haffer (1969) was contradicted for many reasons, he showed that many taxa present a shared distribution, which may support the proposition of areas of endemism. From then on, several studies have been attempting to elucidate patterns of distribution of species and related historical events that supported the definition of such areas of endemism specially in South America (Cracraft 1985, Amorim & Pires 1996, Silva & Oren 1996, Costa et al., 2000, Silva et al., 2004, Morrone 2006, Sigrist & Carvalho 2008, 2009; Oliveira et al., 2015). However, isopods have been largely neglected on studies regarding biogeography and more specifically areas of endemism.

4.1   Patterns of richness and range size distribution

Differences on the number of coexisting species and their pattern of distribution represent a central issue of ecological research (Gaston & Blackburn, 2000). The highest richness of isopods recorded for limestone and iron ore caves in the present study may have reflected the incomparable greatest sampling effort made in such lithologies. This scenario may be attributed to the noticeable economic interest on the raw material provided by these rocks and to the consequent requirements from environmental agencies to regulate their exploitation (Brasil, 2008). Moreover, limestone and iron ore represent the most common rocks were caves are found in the Brazilian speleological provinces, what also may have been the cause of such greater diversity. On the other hand, the greater range sizes were observed for quartzite and granite caves, which in general represent small cavities and therefore are more susceptible to the colonization by species commonly found in the epigean environment, such as *Atlantoscia floridana* and *Porcellionides pruinosus*, what certainly led to the observed larger range sizes.

Since the number of sampled caves considered in the present study is correlated with the number of caves recorded for each latitudinal band, more caves were sampled where more cavities exist, what softens a possible sampling effect that could have biased the observed patterns of diversity. Contrarily to what was already observed for several taxonomic groups in ecological studies all over the world (Willig et al., 2003), there was no significant relationship between the residuals of the regression between richness and sampled caves and the latitude in which they occur, neither when disregarding the troglobites. In fact, richness was significantly related to the number of caves sampled for each latitudinal band. Similar results were observed by Culver & Pipan (1999), who found a strong relationship between the number of caves in counties and the richness of troglobitic species they contain, although they did not assess latitudinal gradients. These authors explained that large karst areas are expected to have higher diversity, since more caves and greater diversity of habitats are provided for the species, what consequently provides more opportunities for speciation.

Hillebrand (2004) suggested that the decline of diversity with increasing latitude represents a ubiquitous phenomenon, but despite the generality, the gradient is not uniform. There are significant variations in the gradient between scales, geographic regions, realms, habitat types, organism types and body mass. He found that latitudinal gradients were significantly stronger and steeper on regional than on local scales. The weak gradient on local scales indicate that the local diversity is related to the regional one, although local interactions may modify the community structure (Stevens & Willig, 2002). Since the climatic variations are not pronounced in the subterranean realm, even regional scales may work as local scales (with inherent low seasonality), for which is already known that the strength of gradient is lower, what may explain the pattern observed in the present study.

Actually, some characteristics of caves probably hamper the formation of a latitudinal gradient of diversity. As well as in freshwater habitats where both strength and slope of the gradient increase with organism body mass (Hillebrand, 2004), the distribution of body mass is skewed toward small organisms in subterranean habitats. Hillebrand (2004) also observed that the strength of gradient increases with trophic level. However, food webs in subterranean ecosystems presents a truncated nature, usually without primary producers (Gibert & Deharveng, 2002). Rosenzweig (1995) suggested that the biome area presumably contributes to the latitudinal gradient and Dodson (1992) observed a correlation between the richness of crustacean zooplankton and the lake area, but not with latitude, both referring to the species-area relationship. Nonetheless, even considering a regional scale the karstic systems represents a great discontinuity of habitats since considering larger scales the caves and/or systems may also be compared to islands of suitable habitats surrounded by a matrix of rocks non-susceptible to the formation of natural cavities (Christman et al., 2005; Gnaspini, 1997; Holsinger, 2005). In Brazil, the majority of karstic and ferruginous systems are found in inter-tropical regions (CECAV, 2017), therefore the area of suitable habitats by itself may have displaced the gradient.

The relationship between the latitude and distributional range size of species was also investigated in the present study. According to the Rapoport's rule, the area of occurrence of species presents a direct relationship with the latitude where they occur, it means, species from lower latitudes present lower distributional range size and vice-versa (Rapoport, 1975; Stevens, 1989). The hypothesis of seasonal variability (Letcher & Harvey, 1994; Stevens, 1996) suggests that the greater seasonal temperature fluctuations at high latitudes select for more tolerant species, which consequently present greater latitudinal ranges. However, the range size of terrestrial isopods associated with caves was not significantly related to the latitude. In general, there is a low seasonal variability in the subterranean environment, in this sense regardless of considering a large spatial scale in this study (from 0 to 30°), cave species are not broadly tolerant to climate changes. In fact, not all species are capable to colonize extreme environments such as caves in function of the restrictive conditions, therefore caves work as filter for some taxa (Gibert & Deharveng, 2002). On the other hand, those species that colonize such habitat may become restrict to its conditions and consequently do not expand their range sizes, regardless the higher density of caves in the region. Willig et al. (2003) stated that the absence of latitudinal gradient of richness generally coincides with exceptions for the Rapoport's rule.

4.2   Areas of endemism

4.2.1   Amazon group

Amazon areas of endemism are usually reported as past forest refuges that currently have rivers as barriers for the species dispersal (Haffer, 1969; Goldani, Carvalho & Bicca-Marques, 2006). However, Cheng et al. (2013) analyzed speleothems dated by oxygen isotope to characterize the hydroclimate variation and then understand the link between climate change and biodiversity in Amazon. These authors found that the precipitation variability between western and eastern Amazonia exhibited an inverse pattern: during the last glacial period there was a slight increase in precipitation in western Amazonia, but a significant drying in the eastern region of this biome. In this sense, Cheng et al. (2013) proposed an explanation different from Haffer (1969)

and supposed that the higher biodiversity in western Amazonia was maintained under relatively stable climatic conditions, while the glacial–interglacial climatic perturbations may have caused forest fragmentation on eastern Amazonia that consequently led to a loss of biodiversity in this region. However, the richness gradient referred by Cheng et al. (2013) from western to eastern Amazonia is mainly based on trees and mammals' diversity (Hoorn et al., 2010).

Considering the subterranean fauna parallel to what was proposed by the Refugia Hypothesis, since it did not consider caves but forest fragments, this theory represents a plausible explanation for the areas of endemism or centers of diversification situated on eastern Amazonia. During periods of great climatic instability, the isopods as well as other groups of invertebrates previously inhabitants of forests may have colonized the subterranean realm and then give rise to new species in function of the isolation of cave systems allied to the harsh conditions of the external environment in that moment.

AE1 is situated in the left margin of Xingu River, a large tributary of the Amazon River, and at the right margin of Tapajós River. In this sense these rivers may represent a barrier for the dispersal of isopods in this region.

The areas of endemism AE2, AE3 and AE4 correspond to the Serra Norte, Serra Sul and Serra Leste, respectively. Such areas are also situated on eastern Amazonia, although they are at least 600 Km far from AE1. Despite AE2, 3 and 4 compose the called Geological Province of Carajás, Ferreira, Oliveira & Souza-Silva (2015) suggested that each plateau represents a single large cave conformed by macrogalleries interconnected by an intricate system of canaliculi (small voids occurring on the superficial topmost breccia, regionally called "canga formation"). These authors observed a high similarity of troglobitic species among cavities of the same plateau and any troglobitic species was common to the three systems. The similarity among caves of each plateau indicate that species are dispersing probably by means of the interstitial spaces. Considering that troglobitic species are restrict to the hypogean environment, their dispersal is limited to the sub-superficial and subterranean spaces, in this sense the dissimilarity among

plateaus indicate that there is no transit of troglobites among them. The same pattern was observed when considering only species of isopods associated with the caves in the present study. In this sense, distinct areas of endemism were delimited both considering all the isopods recorded for the region and only the troglobites, what reinforces the conformation of Serra Norte, Serra Sul and Serra Leste as distinct centers of diversification regarding the cave fauna.

4.2.2 Caatinga group

In general, when compared to Amazon and Atlantic Forest, Caatinga and Brazilian Savannah are poorly investigated regarding areas of endemism (Oliveira et al. 2015; Simon & Proença, 2000; Santos, Leal, Almeida-Cortez, Fernandes & Tabarelli, 2011; Azevedo, Valdujo & Nogueira, 2016), although such areas have been intensively studied to understand past climate changes and their link with biodiversity patterns. Oliveira et al. (1999) observed alternating periods of increased pollen records of species typical of warm and humid climate, progressive decline in forest taxa and gradual increase of Caatinga taxa in the landscape, which records date in the last 10,990 years. Wang et al. (2004) dated speleothems and travertine deposits using the U/Th method from the Bahia state and present a 210,000 years record of wet periods in northeastern Brazil caused by the displacement of the Intertropical Convergence Zone to the south. The rainforest distribution was affected during these wet periods, which formed a corridor between Amazonian and Atlantic Forests (Por, 1992; Behling, Arz, Pätzold & Wefer, 2000). Posteriorly, Cruz et al. (2009) observed an anti-phased relationship between precipitation in northeastern Brazil and the rest of tropical South America during the Holocene. The authors analyzed oxygen isotopic record from a speleothem from northeastern Brazil from the past 26,000 years and concluded that a predominantly wet climate dominated the currently semi-arid Caatinga during the mid-Holocene in contrast to the climate changes documented in the central Andes (Seltzer, Rodbell & Burns, 2000), western Amazon (van Breukelen, Vonhof, Hellstrom, Wester & Kroon, 2008) and southeastern Brazil (Wang et al., 2007).

Therefore, the semi-arid Caatinga and dry regions of transition between Caatinga and Brazilian Savannah presented previous wetter conditions that provided the diversification of several groups, which are currently confined to smaller areas that encompass high species richness and high degrees of endemism for several taxonomic groups. More than 80 priority areas for conservation were proposed for Caatinga in function of such noticeable diversity (Silva, Souza & Castelleti et al., 2004) and especially the areas 45 (Morro do Chapéu), 46 (Bonito) e 47 (Itaetê/Abaíra) in the Bahia state are congruent with the here proposed AE5 (Region of Chapada Diamantina). Silva et al. (2004) proposed such areas mainly based on the diversity of plants and vertebrates, without considering the subterranean fauna despite of more than 300 cavities recorded for this region. Nevertheless, the congruence of such areas rich in endemic species may indicate that common processes may have limited several lineages associated with these areas, especially the past climate changes (DaSilva et al., 2015; Hoffmeister & Ferrari, 2016). Chapada Diamantina is considered a refuge for birds, reptiles, amphibians, mammals and flora, with a unique faunistic formation since the beginning of Quaternary (Rodrigues-Filho et al., 2002). In this sense, the occurrence of 18 species of isopods associated with caves, especially considering that half of them are troglomorphic and present a high index of taxonomic distinctness, provides support to define it as an area of endemism.

AE6 is situated in the Southern Karst of Bahia in the region of Serra de Iuiú, which is also inserted on the Caatinga biome. It represents a noticeable area of endemism in function of 14 species of isopods associated with caves, from which 10 are restrict to the cave environment, besides other troglobitic taxa already recorded for the region (Ratton et al., 2012; Hoch & Ferreira, 2016). The diversity of isopods in this region is predominated by the family Styloniscidae, which species in general present amphibious habits. This reinforces the possibility of that isopods had colonized subterranean environments as refuges as the external habitat became drier. The surrounding area of caves in Caatinga are predominantly dry in the present, what favors the permanence of the fauna in the subterranean realm (Fernandes, Batalha & Bichuette, 2016), since

isopods are dependent on high levels of moisture, and also the gradual increase of the genetic distance of the populations. Vale do Cochá (AE7) is situated in the region of Montalvânia and Juvenília, state of Minas Gerais. This region was probably subject to similar conditions than those previously mentioned for AE6. The diversity of isopods is also predominated by Styloniscidae in AE7, but represented by other three troglobitic species. It was considered a distinct area of endemism in function of the discontinuity of outcrops between Serra de Iuiú and Vale do Cochá and the singularity of their respective fauna.

4.2.3 Brazilian Savannah group

The region of National Park Cavernas do Peruaçu is situated in a transitional area between Caatinga and Brazilian Savannah and was delimited as other area of endemism for isopods associated with caves (AE8). This region is congruent with area 55 proposed by Silva et al. (2004), which was considered of extreme importance due to the presence of endemic and/or threatened species of birds, mammals, fishes and invertebrates. The cave fauna is noticeable in the region, with high richness and high levels of endemism (e.g. Campos-Filho et al., 2016; Bastos-Pereira et al., 2017). Although AE6, 7 and 8 are part of the same limestone group (Bambuí), the São Francisco river represents a barrier between AE8 and AE6. Despite of the continuity of the outcrops between AE7 and AE8, the singularity of their respective fauna indicate that probably distinct events were responsible by the isolation of the lineages of isopods in such areas.

AE9 is also situated on Northern Minas Gerais like AE8. Strikis (2011) reconstructed the changes in paleo-precipitation and paleoenvironmental features for Northern Minas Gerais during the last 28,000 years based on dating speleothems by U-Th method, high resolution stable isotope (δ_{18}O and δ_{13}C) and trace element ratios. This author observed coinciding climate variations in relation to those from Northeastern Brazil in the same period. The present study recorded a noticeable diversity of isopods associated with caves (14 species, 9 of them with troglomorphic traits). In this sense, as well as for other areas along the Caatinga, as the climate became dryer and external conditions became harsher especially for hygrophilous species like the isopods,

ancient lineages may have colonized the caves and the isolation provided diversification of the group currently dominated by troglomorphic species.

AE10 is located in the Speleological Province of Arcos-Pains-Doresópolis, which region is predominated by semi-deciduous montane seasonal forest (Veloso, Rangel Filho & Lima, 1991). This Speleological Province encompasses more than 15% of all the caves recorded for Brazil (CECAV, 2017), for which dozens of troglobitic species were already collected (Ferreira, R. L., personal communication), although only four of them are formally described (Álvares & Ferreira, 2002; Iniesta & Ferreira, 2013; Souza & Ferreira, 2016; Asenjo, Ferreira, & Zampaulo, 2017). The region shelters an expressive diversity of amphibious species of the family Styloniscidae, which was the cause of the low value of taxonomic distinctness observed in the present study.

According to Köppen classification, the current climate is Cwb type with wet summer and dry winter (Agritempo, 2017). Although the previous climate conditions were not studied in the region, probably there was a long harsh period that led ancestral lineages to colonize and remain in the subterranean realm. Ázara & Ferreira (*in press*) recently found a new species of Opiliones in this region, which epigean relatives inhabit the Atlantic Forest, therefore providing indicatives that this domain had expanded until the region of Arcos-Pains-Doresópolis in the past.

In relation to the isopods, currently it is possible to verify that during the dry season the styloniscideans are not observed in the travertine dams of the caves where they are usually seen during the rainy periods. It is probable that they migrate vertically looking for wetter spaces in the epikarst, since the water of travertine dams in general dries in the winter. Such vertical migration probably led to the isolation of populations on each cave and originated the current extreme levels of endemism, in which each cave shelter one different species of this family.

The region of Cordisburgo (AE11) is also situated in the Brazilian savannah, in the Bambuí group and the climate is also similar to AE10, with dry winter and wet summer. However, there is no continuity of the rock outcrops and the regions present quite different cave faunal

composition. AE11 presented eight species of isopods associated to caves, from which six present troglomorphic traits. This region was considered of biological importance for the conservation of invertebrates what was strongly supported by speleological studies conducted in the region (Drummond et al., 2005).

The Area of Environmental Protection (APA, acronym in Portuguese) Karst of Lagoa Santa is a conservation unit also situated in Bambuí group and is also inserted in the Brazilian savannah. The geomorphological characteristics of the region provided the formation of many natural cavities (Herrmann, Kohler, Duarte & Carvalho, 1998.). Currently there are about 900 recorded caves (CECAV, 2017) for which there are several studies reporting the cave fauna, with at least 30 species of arthropods formally described (e. g. Ferreira and Martins 1999, Mews and Sperber 2008), including the isopods *Spelunconiscus castroi* Campos-Filho, Araujo & Taiti (2014) and *Trichorhina pataxosi* Campos-Filho, Bichuette and Taiti 2016. Overall, fourteen species of isopods were recorded for the caves of AE12, from which three presented troglomorphic traits. AE11 and 12 were considered distinct areas of endemism in function of their geographical isolation and faunal singularity.

Regarding AE13, although it is also part of in a ferriferous geosystem, it presents different patterns of species distribution regarding the cave fauna when compared to AE2, 3 e 4. Caves of the Iron Quadrangle (AE13) do not form distinct groups of species, even there is an apparent geomorphological compartmentalization and there are systems of canaliculi as well as in Serra de Carajás (Ferreira et al., 2015). Although only four troglomorphic species of isopods were recorded for AE13, this area presented the highest richness (30 species). The four troglomorphic species belong to the genus *Trichorhina,* which is mostly composed by endogeous species that generally presents absence or reduction of pigmentation and eyes independently of inhabiting cave environments. In this sense, finding these four troglomorphic species in external collections may be plausible, what is fundamental to affirm the real ecological-evolutionary status of these species.

Nevertheless, it is noticeable the relative low number of troglomorphic species of isopods found in this area.

Most of caves of ferruginous geosystems are inserted in the canga, which consists on wide covers of breccia over the iron formation (Piló, Auler & Martins, 2015). In this sense, although several species of isopods are found in the macrocaves, they probably also inhabit the interstitial and sub-superficial spaces and therefore may access epigean habitats in order to obtain food. Moreover, the Iron Quadrangle is situated in the transition between Brazilian savannah and Atlantic Forest. Especially in areas of canga where the soil is shallow and the vegetation is sparse, the cave environment present milder conditions for the survival of isopods, what may favor their occurrence in such habitats (Ferreira 2005).

4.2.4 Atlantic forest group

AE14 comprises the region of Parque Estadual Turístico do Alto Ribeira (PETAR, acronym in Portuguese), a conservation unit inserted on the Atlantic Forest, which caves are part of the Açungui group. PETAR represents the unique sub-tropical center of endemism of cave isopods and the unique area situated on Atlantic Forest. Only three species of isopods were formally recorded for the caves in this region (*Benthana iporangensis*, *Neotroponiscus iporangaensis* and *Cylindroniscus flaviae*), but there is a huge potential to discover more species as new collections are made, since the 28 recorded troglobitic species were found along more than one century of visits to the Areias system (Souza-Silva & Ferreira, 2016). It is noticeable that AE14 represents an important area of diversification of cave species, what supported its definition as an area of endemism in the present study. Moreover, Ledo & Colli (2017) reaffirmed the importance of the Southeast – Northwestern route as the most ancient connection between the Atlantic and Amazonian forests. Currently the region of PETAR is densely covered by forest vegetation, however previous harsher conditions, for instance during the last glacial maximum, may have led some species to enter the caves as refuge. As well as previously suggested for other

areas, the climatic stability of the subterranean environment may have favored their permanence and consequent diversification.

4.3   Diversity patterns and insights into previous biome connections

In general, the areas of endemism within each biome were delimited in function of the discontinuity of outcrops and the singularity of their respective fauna. However, it is important to highlight that although species presented high levels of endemism, the genera shared among the biomes may shed light into previous connections of the biomes, as well established for other groups like mammals (Costa, 2003).

Although the species of Oniscidea are found since coastal zones to high latitude regions, including desertic and subterranean environments (Schmidt, 2002), the humidity strongly affects both the distribution and abundance of these terrestrial crustaceans (Warburg, Linsenmair, & Bercovitz, 1984). In this sense, Amazon and Atlantic Forest likely have acted as the main sources of species of Oniscidea. Considering that currently Caatinga and Brazilian Savannah have more genera in common with the Atlantic Forest than with Amazon, it is plausible to hypothesize that the former worked as source of species for these currently drier biomes.

Additionally, *Circoniscus intermedius* was recorded in the Amazon (region of Altamira) and Brazilian Savannah (Serra da Bodoquena and APA Carste de Lagoa Santa), which currently belong to two distinct biogeographical domains proposed by Morrone (2006), the Southeastern Amazonian and Chacoan domains. The wide distribution range of this species may corroborate the Southeast-Northwestern route as an important connection between Amazon and Atlantic Forest, as proposed by Ledo & Colli (2017).

4.4   Conservation issues

Although AE1 is surrounded by the Extractive Reserves Verde Para Sempre and Rio Iriri and the National Forests of Tapajós and Caxiuanã, any of the AE1 caves are included in conservation units (CECAV, 2017) and there are no areas of endemism proposed for this region

yet, but the studies are scarce. The landscape in this region is highly fragmented in the present mainly due to wood extraction, what reinforces the need to conduct more studies investigating the diversity patterns of other groups and then provide more support to preserve the caves, forest remnants surrounding them and all the species associated.

Although part of the caves of AE2 to 4 are inserted within the Conservation Unit National Forest of Carajás, the region comprises one of the main sources of iron ore and is target of intense mining activity (Ferreira et a, 2015), besides agricultural practices that generated a highly fragmented landscape around these areas, what is also the scenario observed in the Iron Quadrangle (AE13) and the other AEs. Besides the iron ore, other rocks susceptible to the formation of natural cavities are source of many important raw material for the industry, such as limestone, granite and sandstone. Therefore, there is an increasingly number and magnitude of impacts caused by anthropic activities to natural cavities and the associated biodiversity, and many of them are not included in conservation units that guarantee their protection against such impacts.

It is important to highlight some points when comparing the two maps of areas of endemism supported by all the species of Oniscidea associated with caves and only by troglobites. In the case of troglophilic species, one does not necessarily should preserve the caves to protect their populations since they are probably found in epigean habitats. In this sense, the areas delimited considering all the isopods simply indicate regions rich in species with high degree of endemism. On the other hand, troglobites are restrict to the subterranean environment so that losing the cavities they inhabit may lead to the extinction of such species. The coincidence of areas of endemism defined including all the cave terrestrial isopods with areas defined based only on the occurrence of troglobitic species reveals an important fact: when preserving areas in which troglobites occur other species not-restrict to the subterranean environment but that are coexisting in the same areas will also be preserved, which are parts involved on the maintenance of equilibrium of these ecosystems. In this sense, troglobites may act as umbrella species on

preserving terrestrial isopods associated with Brazilian caves and certainly of many other taxonomic groups inhabiting the same landscape.

In times of permanently increasing demand for natural resources, it is not feasible to protect all the areas, but rather the greatest challenge for ecologists and decision makers is to point priority areas for conservation based on irreplaceable species and their degree of vulnerability (Pressey, 1999; Wilson, Pressey, Newton, Burgman & Possingham, 2005). Considering the results obtained in the present study, priority areas for the conservation of isopods associated with Brazilian caves should be elected based on the richness of troglobites especially due to their restriction to the subterranean environment, while troglophilic species may also be found in epigean habitats. Moreover, it is recommended that the index of taxonomic distinctness should be considered including all the species of isopods associated to the caves. In this sense, if one intends to focus the conservation on the highest richness of troglobitic isopods as umbrella species, the Karstic Province of Arcos-Pains-Doresópolis (AE10), Southern Karst of Bahia (AE6), Chapada Diamantina (AE5) and Central-Northern Minas Gerais (AE9) must be considered the main priority areas for the conservation of Oniscidea associated with caves, in this order of importance. Although AE10 presented the highest richness of isopod species, this area presented a value of Δ^* below the expected by chance certainly in function of the presence of many species of the same genus (Styloniscidae). Regarding the index of taxonomic distinctness, if one intends to focus the conservation efforts on the highest phylogenetic diversity, PETAR (AE14), Chapada Diamantina (AE5), Serra Leste (AE4), Serra Norte (AE2) and Altamira and Medicilândia (AE1) must be prioritized in order of importance, since these AEs stood out with more than 93% of probability of obtaining two distinct species if two specimens are randomly taken from each area.

It is strongly recommended that more studies are conducted with other taxonomic groups associated with Brazilian caves in order to provide more support to define such proposed areas of endemism as centers of diversification. Unfortunately, few studies are available for some of the areas encompassed by the present study, what precluded comparisons of congruent areas of

endemism and posteriorly the elaboration of well supported hypothesis on the causes that led to the current patterns of biodiversity distribution, what reinforces the need to continuing studying such areas as previously mentioned and thus protect them.

5 ACKNOWLEDGMENTS

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ARTIGO 2 - DISTINCT IDENTITIES: TAXONOMIC, PHYLOGENETIC AND FUNCTIONAL PATTERNS OF EPIGEAN AND HYPOGEAN ASSEMBLAGES OF ONISCIDEA IN A NEOTROPICAL LANDSCAPE

Artigo redigido sob as normas do periódico *Journal of Animal Ecology* (versão preliminar)

Distinct identities: taxonomic, phylogenetic and functional patterns of epigean and hypogean assemblages of Oniscidea in a Neotropical landscape

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Abstract

Caves present restrictive conditions for many taxa in function of their environmental filters, what generally led to morphological convergence mainly due to permanent darkness. Some groups, as the isopods, are prone to colonize caves, since they provide amenable conditions for their survival, but the processes guiding the diversity patterns in such environments remain unclear. The present work was conducted to enlighten the patterns of taxonomic, phylogenetic and functional diversity of epigean and hypogean isopods in a Neotropical karstic landscape, especially focusing on testing the effect of troglobites over such patterns. The hypothesis is that considering the entire assemblage the taxonomic, phylogenetic and functional diversity are greater in the hypogean habitat since this environment aggregates an evolutionary historic of the species, what improves the gamma of possibilities of taxa and traits to be found in such habitat. Additionally, the present work aimed to test which component of β diversity predominates on structuring the studied assemblages. It is expected that the turnover component predominates in both habitats due to the fragmented character of the epigean landscape, the natural isolation provided by caves and the poor dispersal ability of isopods. Sampling was conducted in external transects and in caves in a Brazilian karstic province. The taxonomic diversity was represented by the species richness, phylogenetic diversity was calculated by means of the Index of Taxonomic Distinctness and functional diversity was calculated as the mean length of functional dendrograms. Moreover, the taxonomic and functional β diversity components were calculated for epigean and hypogean assemblages. All analyses were conducted with and without troglobites in order to check their effect on the patterns of diversity. When troglobitic species were excluded, there were no significant differences between the taxonomic and functional diversity of epigean and hypogean habitats, but when considering them the hypogean habitat presented the highest taxonomic diversity. There were no differences on the phylogenetic diversity of these environments. Furthermore, the overall functional diversity (FD) was higher in the hypogean environment, but there were no differences between the functional β diversity of the two systems. Therefore, the troglobites are the great responsible by the taxonomic singularity of hypogean habitats, which is richer in phylogenetically related and functionally redundant species. The results reinforce the need to conduct analyses manipulating some species to test their effects over the patterns, as well as the need to use integrative approaches and not only the traditional measurements to explore diversity patterns.

Keywords. Assembly rules, cave species, epigean assemblages, functional redundancy, neutral theory, Oniscidea.

Introduction

The search for patterns and processes responsible by determining species composition and distribution in different communities has been intriguing ecologists for years. The constraints used to predict the community structure, namely the assembly rules (Weiher & Keddy, 1995), have been elucidated by combining niche-based and neutral mechanisms (Tilman, 2004; Cadotte, 2007; Vergnon, Dulvy & Freckleton, 2009). While neutral models assume the functional equivalence of species and dependence of stochastic events to determine the species composition (Hubbell, 2005, 2006), niche-based models assume that the coexistence relies on some differences on the use of shared resources, therefore there should be a limiting similarity between the niches of coexisting species (MacArthur & Levins 1967). On the other hand, environmental factors may act as niche filters and restrict the species composition within local communities (Mouillot, Dumay & Tomasini, 2007).

Traditional measurements of diversity considering only the number of species and their relative abundance have not provided robust predictions regarding the structure and functioning of communities. In this sense, elucidating the processes responsible for the variation in diversity along ecological gradients requires complementary approaches to assess the patterns (Cianciaruso, Silva & Batalha, 2009). Recent studies have incorporated functional and phylogenetic aspects into the previous exclusively taxonomic metrics used to enlighten assembly rules of communities (e.g. Kluge & Kessler, 2011; Cardoso, 2012; Villéger, Miranda, Hernandez, & Mouillot, 2012, Cardoso et al., 2014).

The knowledge regarding functional and phylogenetic relationships of coexisting species may enlighten the underlying processes responsible for the community structure, helping to disentangle the effects of competitive interactions (Stubbs & Bastow Wilson, 2004) from environmental filters (Weiher & Keddy, 1995) and even from random effects (Drake, 1991). Coexisting species increase their probability of persistence as they differ somehow from the other members of community so that it can exploit resources more efficiently and consequently the

pressure of interspecific interactions decreases (MacArthur & Levins 1967, Díaz & Cabido, 1997). In this sense, competition favors the permanence of phenotypically distinct taxa and consequently different lineages, therefore inducing a phenotypic overdispersion, a pattern of greater dispersion than the expected from a randomly selected community (Moulton & Pimm, 1987). Conversely, environmental conditions may limit the occurrence of some taxa in function of constraints to deal with such environmental filters, what leads to a phenotypic clustering, a pattern of lower dispersion than those expected from a randomly assembled community (Weiher & Keddy, 1995). However, a given community may also be subject to neutral processes and then all the observed patterns will not differ from what was expected from random assemblages (Hardy, 2008).

Extremely selective environments are prone to guide evolution to few outcomes, therefore the restrictive conditions act as ecological filters that lead to a convergent evolution even of unrelated organisms (Culver & Pipan, 2009). The permanent darkness in deeper zones as well as scattered and unpredictable food resources commonly observed in subterranean habitats represents harsh conditions for many taxa, therefore caves have been understood as examples of extreme environments (Culver & Pipan, 2009). However, there is an emerging paradigm, which emphasizes the central role of darkness for convergent evolution and assumes the role of habitat size and interspecific competition as drivers of divergent evolution of hypogean species (Trontelj, Blejec & Fišer, 2012; Culver & Pipan, 2015). Nevertheless, caves are subject to strong environmental filters and represent suitable models to elucidate assembly rules (Cardoso, 2012).

Cave communities are expected to shelter filtered subsamples of the regional epigean species pool (Gibert & Deharveng, 2002). However, some species presents "pre-adaptations" that allow them colonizing the subterranean realm, such as nocturnal habit, improvement of mechanoreceptors and chemoreceptors instead of mechanisms for visual guidance, generalist feeding habits, among others (Culver & Pipan, 2009). Crustaceans of the order Isopoda are frequently found in caves all over the world, including Brazil (e.g. Campos-Filho, Araujo,

Bichuette, Trajano, & Taiti, 2014; Reboleira, Gonçalves, Oromí, & Taiti, 2015; Souza et al., 2015; Javidkar et al., 2016). The success of Oniscidea on colonizing terrestrial habitats, the wide variety of morphologies adapted to their habits (Schmalfuss, 1984) and the need for high humidity for survival favored the colonization of subterranean environments. Furthermore, given their poor dispersal ability, isopods are considered good biogeographic indicators, especially the troglobitic species (Taiti, 2004). However, only one study was conducted until the present aiming to elucidate the processes that has been guiding specifically the diversity of isopods within the caves (Fernandes, Batalha, & Bichuette, 2016), which may support further studies on assembly rules of entire subterranean communities.

The present work was conducted with the main aim to enlighten the patterns of taxonomic, phylogenetic and functional diversity of epigean and hypogean isopods in a Neotropical karstic landscape. Podani & Schmera (2006) proposed that the effect of determined species on functional diversity is best evaluated when the functional dendrograms are built with and without such species and posteriorly the results should be contrasted. In this sense, this premise was expanded for taxonomic and phylogenetic approaches and the current work was conducted to test the effect of troglobitic species over the patterns of taxonomic, phylogenetic and functional diversity of epigean and hypogean isopod assemblages in the karstic province of Arcos, Pains and Doresópolis, Brazil. It is expected that, considering the entire assemblage, the three facets of diversity are greater in the hypogean habitat since this environment aggregates an evolutionary historic of the species, either restrict to the subterranean realm or not, what improves the gamma of possibilities of taxa and traits to be found in such habitat. On the other hand, if troglobites are not considered, the expected is no significant differences between the epigean and hypogean diversity, since the species have potential to transit between both habitats. Moreover, the present work aimed to test which component of β diversity predominates on structuring the epigean and hypogean isopod assemblages. Although the assembly rules of cave communities are still unclear (Fišer, Blejec, & Trontelj, 2012; Trontelj et al, 2012; Fernandes et al, 2016), it is

expected that the turnover component predominates in both habitats in function of the fragmented character of the epigean landscape summed to the natural isolation provided by the caves and the poor dispersal ability of isopods.

Material and Methods

Study site

The speleological province of Arcos-Pains-Doresópolis is located in the Southern portion of São Francisco craton and is part of the biggest geological group of carbonate rocks of Brazil (Bambuí formation). The region comprises the watersheds of São Miguel and Ribeirão dos Patos streams, both of them tributaries of São Francisco river (Menegasse, Gonçalves, & Fantinel, 2002). According to Köppen classification, the climate is Cwb with wet summer and dry winter (Agritempo, 2017). The native vegetation corresponds to Brazilian savannah ("Cerrado" biome), with predominance of semi-deciduous montane seasonal forest in the karst region (Veloso, Rangel Filho, & Lima, 1991). However, such vegetation was historically fragmented (especially in the last decades) due to agricultural and mining activities. Forest fragments are limited to altitudes of 500 to 800 m covering the rock outcrops surrounded by pastures (Brasil, 1983).

Currently more than 2500 cavities were already recorded for this speleological province (Cecav, 2017), representing about 15% of all the caves recorded for Brazil. Studies on the subterranean fauna have been continuously conducted in the region in the last 20 years, which harbors 80 troglobitic species distributed in 105 caves (Ferreira, R. L., personal communication). However, only four of them were formally described: the bettles *Coarazuphium pains* Álvares & Ferreira, 2002 and *Metopiellus painensis* Asenjo, Ferreira, & Zampaulo, 2017, the millepede *Pseudonannolene ambuatinga* Iniesta & Ferreira, 2013 and the palpigrade *Eukoenenia cavatica* Souza & Ferreira, 2016.

Sampling methods

A total of 296 caves were inventoried in the speleological province of Arcos-Pains-Doresópolis (Fig. 1). Isopods were recorded in 34 caves, which were sampled by means of active collection conducted by three biologists along the cave extension focusing on potential microhabitats, such as decomposing organic matter, trunks, leaves and guano piles (Fig. 2C). Aquatic habitats such as travertine dams, ponds and streams were also inventoried searching for amphibious isopods with the aid of hand nets. Isopods were collected and preserved in vials containing 70% ethanol.
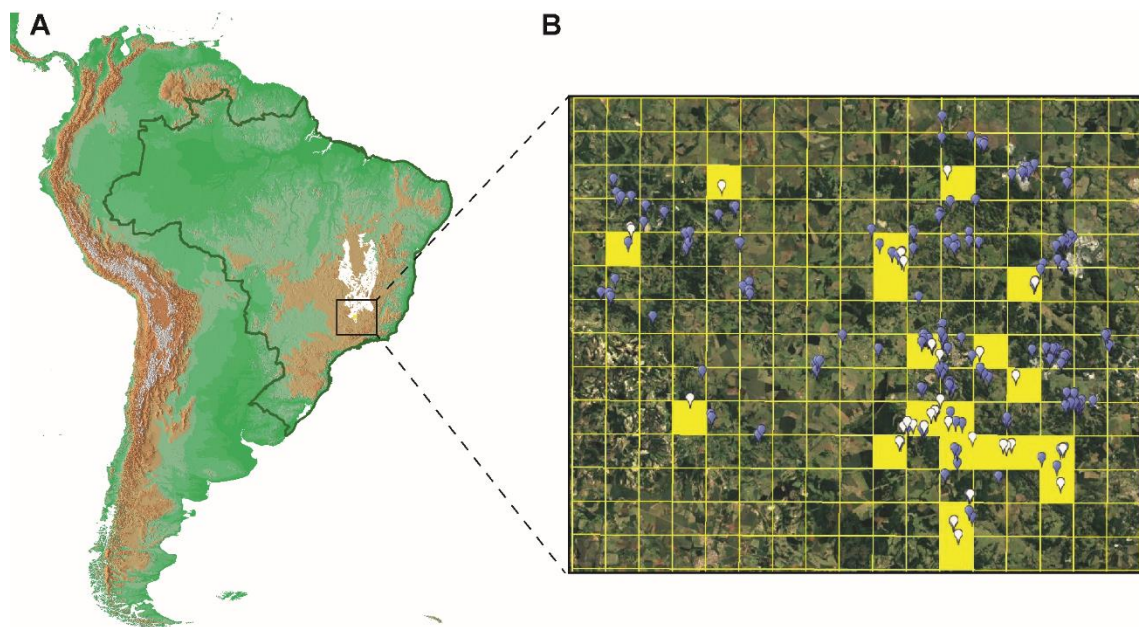
Figure 1. (A) South America with Brazil delimited and the Bambuí Group (in white). (B) Study area divided into a grid (952 Km²) composed by 2 x 2 Km cells. Blue marks represent the 296 caves inventoried and white marks represent caves with records of isopods. Each filled yellow square represents the area where one epigean transect (adjacent to the caves with records of isopods) was sampled.

Caves with records of isopods are distributed along an area of 952 Km². A grid composed by 2x2 Km cells was plotted over this area. Although the inventoried caves occupied 58 cells, only 20 of them contained caves with records of isopods. One transect was demarcated in the largest forest fragment of each cell (Fig. 1 and 2A). Each transect was 100 m long and was divided into 5 equidistant points (25 m). On each of the five points, the leaf litter was removed from an area of 1x1 m, placed in plastic bags and properly identified. Moreover, two sub-samples of soil

were collected on each point by a soil sampler (25 x 25 x 10 cm), which were also placed in plastic bags (Fig. 2B). Active collections were conducted along the 100 m by two biologists with the aid of brushes focusing on trunks and spaces under rocks during one hour, the mean time spent during subterranean collections (Fig. 2BE).

Soil and leaf litter samples were sorted in white plastic trays with the aid of a head lamp and brushes in the same day of collections. Isopods were collected and preserved in vials containing 70% ethanol. Both hypogean and epigean collections were conducted in the rainy season.

Figure 2. (A) One of the fragments of semi-deciduous montane seasonal forest where sampling was conducted in the Speleological Province of Arcos-Pains-Doresópolis (Southeastern Brazil); (B) Soil sampled immediately collected and placed in trays to avoid the escapement of isopods; Active search in the cave (C) and along the transects (D); (E) Isopod found under a decomposing piece of trunk in one transect; (F) Isopod found in a travertine dam in one cave.

Laboratory procedures

Isopods were identified until the lowest taxonomic level as possible based on the literature, but due to taxonomic impediments (many recorded species are still undescribed), morphospecies were defined without commitment of results since the functional diversity is

independent of species identity (Petchey & Gaston, 2002). Functional traits were considered as morphological traits that impact fitness by means of the effects on growth, reproduction and survival, as defined by Violle et al. (2007). For functional analysis, traits were selected based on Fernandes, Batalha, and Bichuette (2016), with some modifications: body length (bl), body width (bw), antenna length (al), volvational capacity (volv), pigmentation (pig), number of ommatidia (omt), number (nme) and type of mechanoreceptors (tme) and habit (hab). Substrate was not considered as a trait in the present study since Fernandes et al (2016) found a low explanatory power for this variable regarding functional diversity of isopods in different habitats. Furthermore, the fact that an isopod was observed in a determined substrate does not necessarily means that it is feeding on it or that is is preferentially associated to it. Traits regarding mechanoreceptors were obtained from scanning electronic microscopy (LEO EVO 40 XVP) images at the Laboratory of Electronic Microscopy of Federal University of Lavras (municipality of Lavras, Minas Gerais state, Brazil). The specimens were mounted on aluminum stubs, placed over a carbon tape, sputter-covered with gold (Baltec SCD 050) and photographed. The number and type of mecanorreceptors contained within an area of 100 mm² of the first pereonite were recorded (Fig. 3).
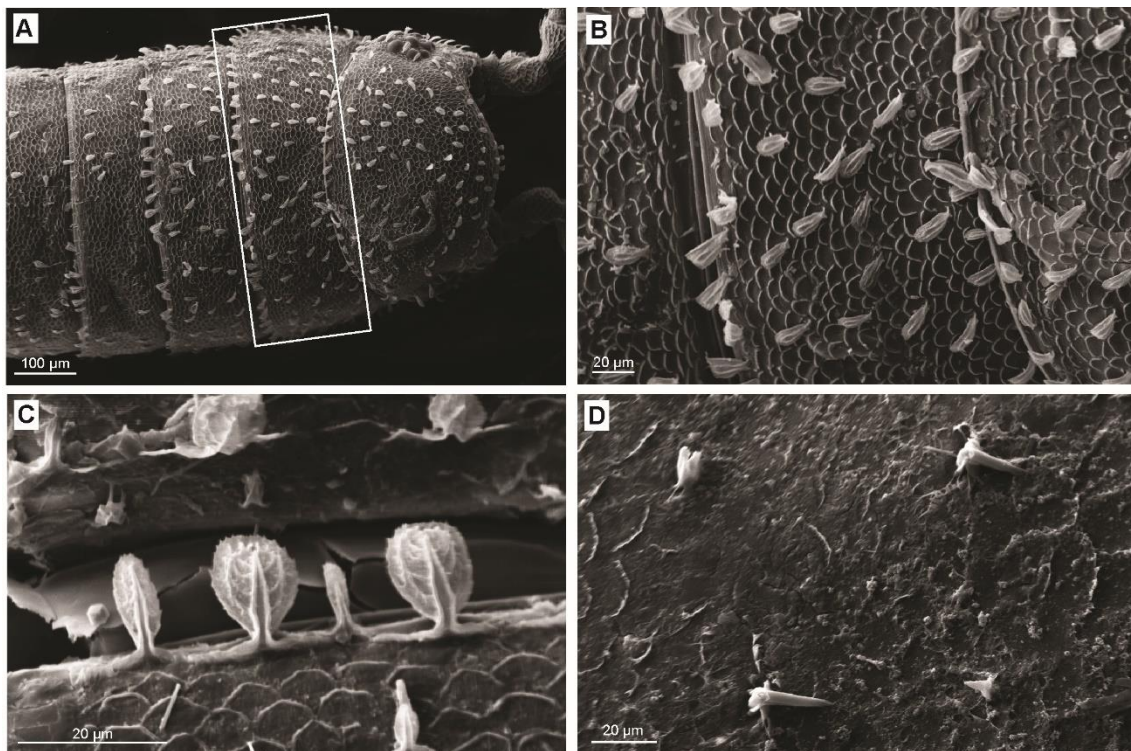
Figure 3. Scanning electronic microscopy images of (A) the selected area (100 mm²) on the first pereonite of each specimen; (B) part of the image used to count the number of mechanoreceptors in a specimen of Dubioniscidae. Images under magnitude superior to 1000 x used to determine the type of mechanoreceptors, such as (C) fan-shaped scale seta and (D) tricorn-like seta.

Data analysis

All analyses were conducted in the software R (R Core Team, 2017). Raw data was composed by two matrices: one assemblage matrix with sites at rows, species at columns and incidence in the cells and a second trait matrix with species at rows, traits at columns and means of attributes in the cells. Two mean values of traits were calculated for species occurring both in epigean and hypogean environments.

Distance matrices were generated for taxonomic and functional data using Euclidean and Gower distances, respectively. A functional dendrogram (*hclust* object) was created based on Petchey & Gaston (2002) using unweighted pair group method with arithmetic mean, as suggested by Podani & Schmera (2006).

Random assemblages with the same number of species than the observed data were generated by shuffling 1000 times the row names of the trait matrix for each environment (epigean, hypogean with and without troglobites (Swenson, 2014). The functional diversity (FD)

was calculated for epigean (FD_{epi}) and hypogean habitats with (FD_{hyp}) and without troglobites (FD_{hypwt}) based on the total branch length of the functional dendrogram (Petchey & Gaston, 2002) for both the randomized and observed data using the function *treeheight* of the package *vegan*. Null distributions of the difference between randomized FD_{epi} and FD_{hyp} (D_{rand1}) and between FD_{epi} and FD_{hypwt} (D_{rand2}) were plotted as histograms and the scores were calculated indicating the position of observed differences ($D_{obs1} = FD_{epi} - FD_{hyp}$; $D_{obs2} = FD_{epi} - FD_{hypwt}$) in the null distribution, what allowed checking the significance of the observed FD difference (Swenson, 2014).

The "effect size" represents the deviation of observed values from the mean of null distribution, with positive values indicating that observed results were higher than the expected and negative values indicating the opposite. Considering that FD may vary in function of species richness, calculating the standardized effect size (SES) is more appropriate to compare the FD of assemblages or communities since it removes the bias associated with differences in species richness (Swenson, 2014). The SES was calculated for data with troglobites by the difference between D_{obs1} and the mean $D_{rand}1$ divided by the standard deviation of $D_{rand}1$. The same was made for assemblages without troglobites calculating the SES by the difference between D_{obs2} and the mean of D_{rand2} divided by the standard deviation of D_{rand2}.

A Principal Component Analysis was conducted based on the trait matrix by means of the function *prcomp* from package *stats* in order to evaluate the relationship between traits and habitat of isopods and consequently assess the efficiency of the chosen traits to distinguish epigean and hypogean taxa. The selection of principal components with higher explanatory power was made based on Broken Stick criterion (MacArthur, 1957) by means of the function available at Zelený (2017). Pairwise correlations were conducted for all the functional traits in order to support interpretations for the functional patterns observed for each habitat.

The average dissimilarity of individual observations to the group centroid in a multivariate space can be used as a measurement of differences in β diversity among distinct areas

by means of an appropriate dissimilarity index, which may have important consequences for interpreting results (Anderson, Ellingsen, & McArdle, 2006). Analyses of multivariate homogeneity of groups' dispersion (variance) were conducted using the function *betadisper* from package *vegan* (Oksanen et al., 2017), which calculates distances between objects and centroids of groups and reduces the original values to principal coordinates. The Euclidean index was used for incidence data, while the Gower distance was used for the functional matrix, which is more appropriate for mixed data (continuous and categorical) (Gower, 1966). Additionally, analyses of variance were carried out to test the significance of differences between the mean dispersion of epigean and hypogean assemblages for taxonomic and functional aspects.

The Taxonomic Distinctness Index (Δ^*) was used as a proxy of phylogenetic diversity of the assemblages, which is robust for variations of sampling effort and provide cohesive response to ecological gradients (Clarke & Warwick 1998, 1999). Based on one matrix of incidence data and other describing the taxonomic hierarchy of each species, the index calculates the average path length between any two randomly chosen individuals of different species by attributing distinct weights to different taxonomic levels. For instance, species of the same genus receive weight 1, while species of the same family but from different genus receive weight 2. Some transects and most of caves had only one species recorded, what would preclude the calculation of this index. In this sense, transects and caves were grouped based on their geographical proximity so that each group contained at least four species maintaining the separation between epigean and hypogean environments. The measures of Δ^* were obtained for each transect or cave groups through the function *taxa2dist* from the package *vegan* and were plotted with confidence intervals (95% and 99%) in relation to the expected average. The Δ^* of epigean and hypogean habitats was compared by t test. The FD was also calculated for each group of transect. Posteriorly, correlation analyses were conducted between richness and taxonomic distinctness and between functional diversity and Δ^*.

The function *beta.multi* from package *BAT* (Cardoso Rigal, & Carvalho, 2015) was used to calculate taxonomic and functional beta diversity (β_{tot}) among multiple sites and its partitioning components (replacement – β_{repl} – and richness differences – β_{rich}) for epigean and hypogean environments. Posteriorly, 1000 random assemblages were generated (for which taxonomic and functional beta diversity and the respective partitioning were calculated) to check if the observed composition differed from those of a randomly assembled community (Gotelli & Graves, 1996). The quantiles of each β diversity component for each habitat were calculated and the observed values were placed in the null distribution, what allowed inferring about the significance of the difference between the observed value and those expected by chance.

Results

The highest total richness (total number of species on each environment) was recorded for the hypogean environment ($S_{hyp} = 26$, $S_{epi} = 11$), although the highest mean number of species of each environment (epigean = mean/transect; hypogean = mean/cave) was recorded for the epigean habitat ($\alpha_{hyp} = 1.47$, $\alpha_{hypwt} = 1.32$ (without troglobites), $\alpha_{epi} = 3.4$). Eight species were exclusively found in the epigean habitat, 23 exclusively in the hypogean (from which, 15 troglobites) and three were shared by the two systems (Fig. 4).
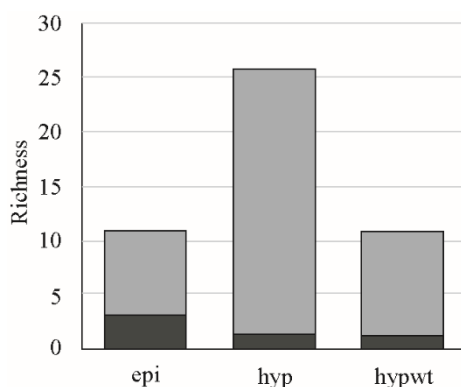

Figure 4. Total richness (light grey) observed for the Oniscidea assemblage in epigean (epi), hypogean (hyp) and hypogean without troglobites (hypwt) environments in the Speleological Province of Arcos-Pains-Doresópolis. The mean richness of each environment is indicated by the dark grey bar.

FD represented the overall functional diversity of each environment. There was a significant difference between FD$_{epi}$ and FD$_{hyp}$, with a higher functional diversity recorded for the hypogean environment (FD$_{epi}$ = 6.21 and FD$_{hyp}$ = 10.54). The SES was negative both for the difference between FD$_{epi}$ and FD$_{hyp}$ (SES = -4.2254) and FD$_{epi}$ and FD$_{hypwt}$ (SES = -1.437186). However, when removing the troglobites from the assemblage, there was no significant difference between the assemblages (FD$_{hypwt}$ = 6.35) (Fig. 5). The mean values of functional traits are presented on Supplementary material.
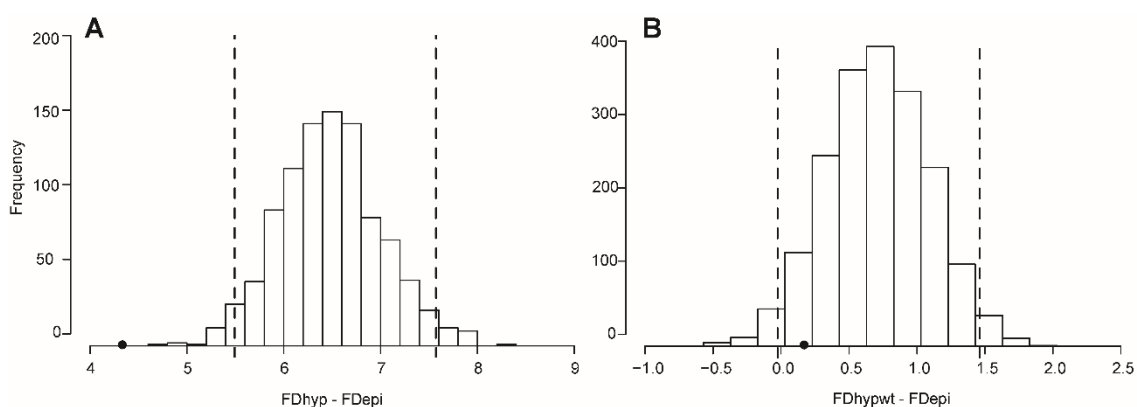
Figure 5. Score (represented by the black dot) of functional diversity difference between hypogean with (A) and without troglobites (B) and epigean assemblages of isopods in the Speleological Province of Arcos, Pains and Doresópolis (Southeastern Brazil).

In the PCA, the first and second principal components were selected based on the Broken Stick criterion, since they explained the greatest part of data variance (PC1 = 45.63% and PC2 = 29.04%, PC1+PC2 = 74.67%) and the others did not differ from randomness. PC1 was mainly related to the subterranean environment, for which the highest values of body length, body width, antenna length and type of mechanoreceptors were recorded for most of the hypogean species, while the lowest values were represented by the subterranean smallest species but with the highest number of mecanoreceptors. On the other hand, PC2 was mainly represented by predominantly epigean species, which were pigmented and presented the highest number of ommatidia (Fig. 6). Furthermore, a strong correlation (higher than 70%) was observed between seven of the 18 possible pairs of traits (Table 1).

Figure 6. Principal Component Analysis of functional traits observed in epigean (black dots) and hypogean (red dots) assemblages of Oniscidea (Isopoda) in the Speleological Province of Arcos, Pains and Doresópolis (Southeastern Brazil). Legend: body length (b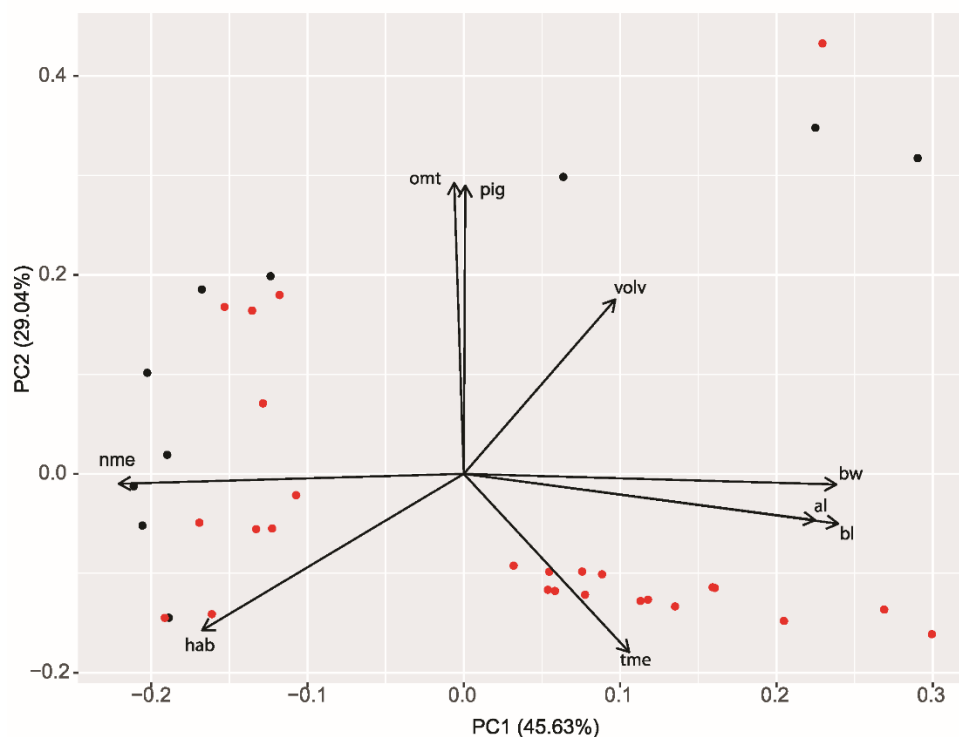l), body width (bw), antenna length (al), volvational capacity (volv), pigmentation (pig), number of ommatidia (omt), number (nme) and type of mechanoreceptors (tme) and habit (hab).

Table 1. Pairwise correlation between functional traits of epigean and hypogean assemblages of Oniscidea in the Speleological Province of Arcos-Pains-Doresópolis.

Traits	t	p	cor
bl x bw	23.102	2.2×10^{-16}	0.9687
bl x al	9.864	1.212×10^{-11}	0.8575
bl x nme	-7.5768	7.036×10^{-9}	0.7881
bw x al	11.094	5.238×10^{-13}	0.8823
bw x nme	-6.6479	1.093×10^{-7}	-0.74
al x nme	-5.9368	9.351×10^{-7}	-0.7083
omt x pig	7.9595	2.309×10^{-9}	0.8025

Legend: body length (bl), body width (bw), antenna length (al), volvational capacity (volv), pigmentation (pig), number of ommatidia (omt), number (nme) and type of mechanoreceptors (tme), habit (hab), cor (correlation coefficient).

Significant differences were observed between the assemblage composition of epigean and hypogean environments (F = 9.1395, p = 0.0039), with higher mean dispersion recorded for the latter (higher taxonomic β diversity in the hypogean habitat) (Fig. 7A and 8A). However,

when troglobites were not included in the analysis, there were no significant differences between the two habitats (F = 0.4263, p = 0.5177) (Fig. 7B and 8B). Regarding the functional traits, there were no significant differences between the variance of epigean and hypogean environments (F = 1.7959, p = 0.1888) (Fig. 7C and 8C). Contrarily, when troglobites were excluded from the assemblage, a higher functional mean dispersion (higher functional β diversity) was recorded for the epigean environment (F = 4.7796, p = 0.0409) (Fig. 7D and 8D).
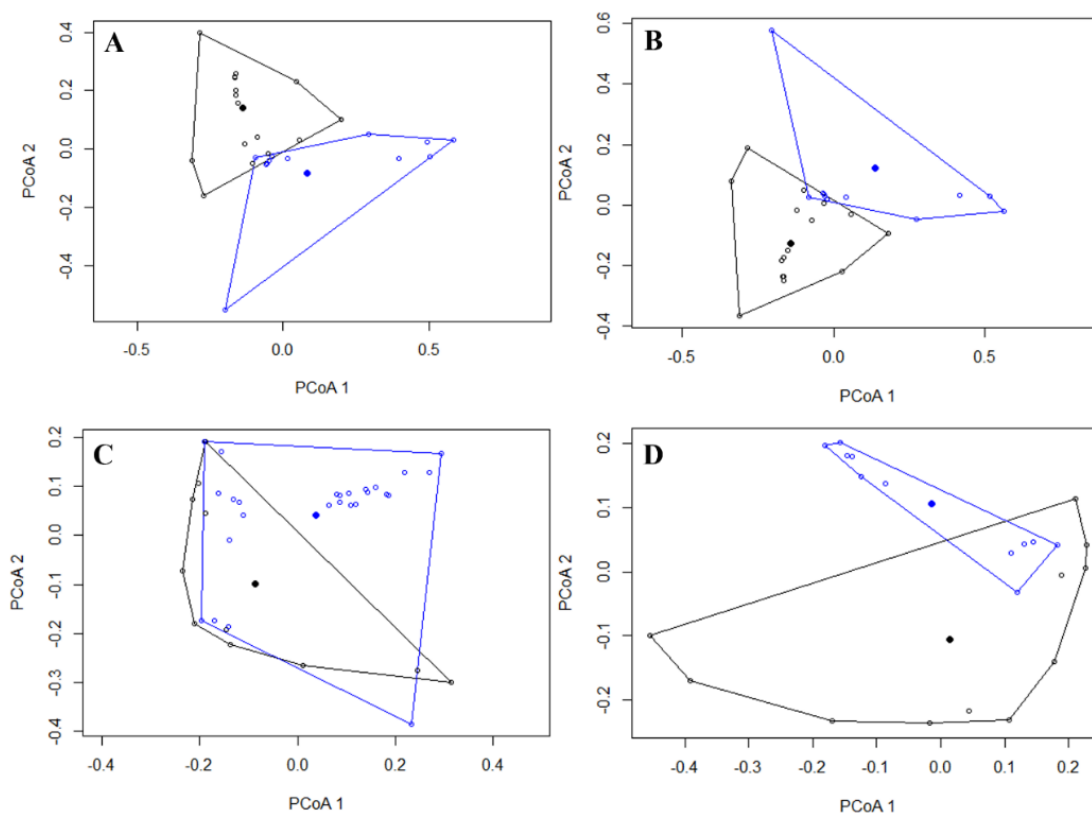
Figure 7. Analyses of multivariate homogeneity of groups dispersion (variance) showing the distances between objects and groups centroids with original values reduced to principal coordinates. (A) Dispersion of incidence data (with troglobites) calculated based on Jaccard distance; (B) Incidence data (without troglobites); (C) Dispersion of functional data (with troglobites) calculated based on the Gower distance; (D) Functional data (without troglobites). Data obtained from Oniscidea assemblages from epigean (black dots and lines) and hypogean (blue dots and lines) systems in the Speleological Province of Arcos-Pains-Doresópolis.
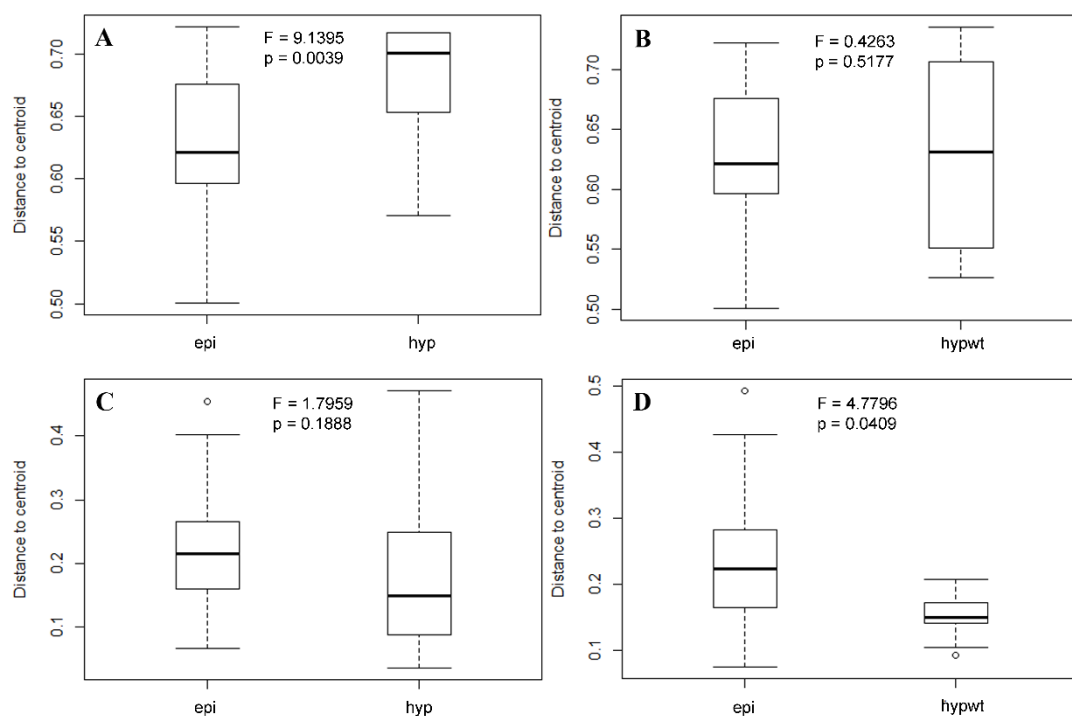
Figure 8. Mean dispersion and variance of (A) incidence data (with troglobites), (B) incidence data (without troglobites), (C) functional data (with troglobites) and (D) functional data (without troglobites) and the respective values obtained through ANOVA. Data obtained from Oniscidea assemblages from epigean (epi) and hypogean (hyp) systems in the Speleological Province of Arcos-Pains-Doresópolis.

The observed values of beta diversity and its components did not differ significantly from the null distribution in any habitat, since all the calculated β values were within the range of values expected by chance, except for epigean taxonomic βrich. However, when the variance of such component (Table 2) is considered, the value is included in the region of null distribution expected to be found by chance.

**Table 2.** Taxonomic and functional β diversity components of epigean and hypogean assemblages of isopods from the speleological province of Arcos-Pains-Doresópolis. βtot: total beta diversity; βrepl: replacement component; βrich: richness differences component.

| | Taxonomic | | | | | |
Environment	βtot	Variance	βrepl	Variance	βrich	Variance
Epigean	0.85	1.4773	0.6	1.0410	0.25	0.4362
Hypogean (with troglobites)	0.95	0.8214	0.8	0.6911	0.15	0.1302
Hypogean (without troglobites)	0.87	1.8379	0.7	1.4848	0.17	0.3530
	Functional					
Environment	βtot	Variance	βrepl	Variance	βrich	Variance
Epigean	0.52	0.9095	0.25	0.4338	0.27	0.4758
Hypogean (with troglobites)	0.62	0.5438	0.49	0.4263	0.13	0.1175
Hypogean (without troglobites)	0.50	1.06167	0.33	0.7006	0.17	0.3610

Regarding the index of taxonomic distinctness, the average value for all transects and caves was 86.427. All the sampling units were placed within the confidence interval of the expected average of Δ* (Fig. 9), except for the group C2. Some groups of sampling units were overlapped since they were composed by the same species. There was no significant difference between the Δ* of transects and caves (t = 1.971, df = 5, p = 0.1041). Moreover, the taxonomic distinctness was not correlated with richness (t = -0.75384, df = 10, p = 0.4683) neither with functional diversity (t = -0.79667, df = 10, p = 0.4441).
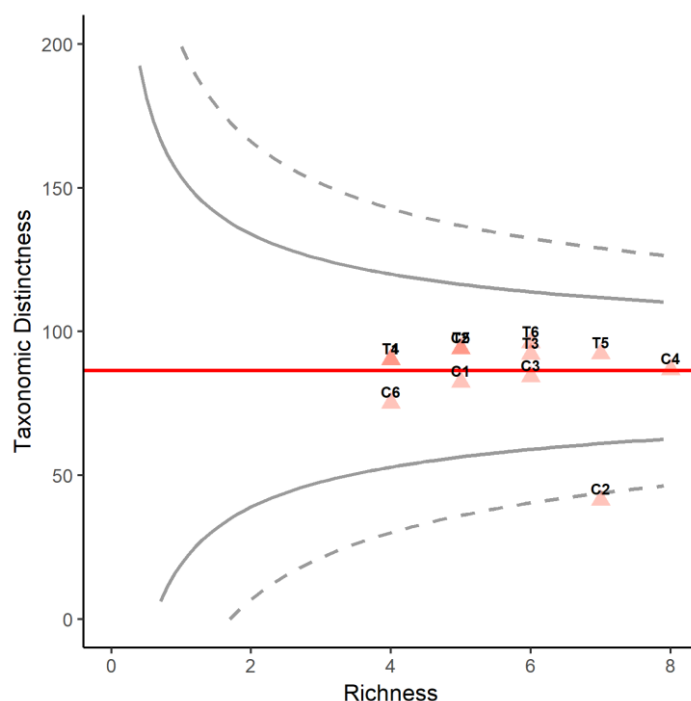
Figure 9. Index of Taxonomic Distinctness (Δ*) calculated for isopod assemblages present in groups of transects (T1 – T6) and caves (C1 to C9) in the Speleological Province of Arcos-Pains-Doresópolis. Some points were overlapped in the graph since the groups were composed by the same species.

Discussion

Analyzing the patterns of taxonomic, phylogenetic and functional diversity of epigean and hypogean isopod assemblages with the inclusion and removal of troglobites led to two distinct scenarios. When troglobitic species are excluded, there were no significant differences between the taxonomic and functional diversity of epigean and hypogean habitats. On the other hand, considering troglobites revealed the highest taxonomic diversity of the hypogean habitat.

Although there are more species in the hypogean environment, there were no differences on the phylogenetic diversity of these environments, since the hypogean species are closely related. Furthermore, although the overall functional diversity (FD) was higher in the hypogean environment, there were no differences when comparing the among-transects (β) and among-caves functional diversity. This means that there is a greater diversity of response functional traits in isopods from the caves environment than from the forest fragments, but there is no difference on how much such functional diversity varies among transects and among caves.

Fernandes et al (2016) compared the functional diversity of surface and subterranean isopods in the biome Caatinga (Brazil) and suggested that despite caves are considered extreme environments for many taxa, for isopods the subterranean conditions are not too harsh since they found a higher FD for this environment. Although there is no information available on the approximate age of lineages yet, when the species (from which many troglobites descended) colonized the caves in the past, the external conditions were distinct from the current ones and represented a less xeric habitat, since some studies have been proving the previous wetter conditions of the currently semi-arid Caatinga (Oliveira et al., 1999; Wang et al., 2004; Cruz et al., 2009). Moreover, these authors conducted the analyses without discriminating the troglobites to verify their effect over the observed pattern, which present exclusive specializations to the subterranean conditions that certainly overdispersed the traits in the functional space. This reinforces the need to conduct analyses with and without troglobites when trying to elucidate assembly rules of subterranean communities (Podani & Schmera, 2006).

Subterranean systems in general provide a lower predation pressure and more amenable environmental conditions, what may favor a higher diversity of functional traits as suggested by Fernandes et al (2016). However, in the present work, the standardized effect size of FD was negative, what indicates that hypogean and epigean habitats were expected to be more functionally distinct than they were in fact. Some authors suggest that environmental filtering may led to negative values of SES, since it constrains the range of traits that coexisting species

exhibit by selecting specific attributes of response traits from the regional pool (Keddy 1992, Díaz et al. 1998; Grime 2006; Garnier et al. 2007). For instance, caves are occupied by species bearing pre-adaptations to the biotic and abiotic peculiarities of the subterranean environment, such as permanent darkness and oligotrophy (Culver & Pipan, 2009). Notwithstanding, even the difference between habitats was lower than expected, FD was higher in the hypogean habitat, what may be related to the higher species richness recorded for this environment. The range of species traits tends to increase with more species present in the community (Janzen, 1985; Sax et al., 2007), thus providing a higher complementarity of functional traits (Williams, 2001).

It is noticeable that troglobites are the great responsible by the taxonomic singularity of caves, which are richer on phylogenetically related and functionally redundant species, but these results do not decrease the need for conservation of all the studied caves. It is important to highlight that the present work was conducted based on response traits, which reflect the influence of the environment over the individual traits. In this sense, affirming that the studied caves are rich in functionally redundant species does not mean that any cave could be destroyed since all the species play the same role, but that the species answered similarly to the evolutionary pressures imposed by the subterranean habitat.

For some groups, like plants (e.g. Kluge & Kessler, 2011, Cardoso et al., 2014), fish (e.g. Logez, Pont, & Ferreira, 2010; Villéger et al., 2012) and dung beetles (e.g. Gagic et al., 2015; Griffiths, Louzada, Bardgett, & Barlow, 2016) there are several works available in the literature using functional traits for ecological analyses of communities. However, for other groups, like the isopods, studies on functional ecology are still incipient (e. g. Zimmer, Pennings, Buck, & Carefoot, 2002; Fernandes et al, 2016). It is well established that fewer dimensions (few traits) in the functional space may increase the redundancy, while more dimensions may decrease this pattern (Petchey & Gaston, 2002). Furthermore, a great number of uncorrelated traits tend to decrease or even cancel this effect (Petchey, Evans, Fishburn, & Gaston, 2007). In the present work one third of the possible pairs of traits were strongly correlated, even though epigean and

hypogean species were not functionally redundant since FD was higher in the hypogean habitat. However, the redundancy is suggested for species of different caves, what will be discussed posteriorly.

Hypogean species presented the highest values of morphological characteristics commonly associated with adaptations to the subterranean environment (body length, body width, antenna length and type of mechanoreceptors) along the PC1, while epigean species presented the highest values of pigmentation and number of ommatidia along the PC2, attributes usually present in surface species (Taiti, 2004). PC1 and PC2 explained together almost 75% of data variance. Fernandes, Batalha, and Bichuette (2016) used the same set of traits (besides the substrate, which was not used in the present study) and PC1 and PC2 explained 64% of variation. In this sense, the analyzed traits seemed to be adequate to distinguish species from the epigean and hypogean habitats.

A higher taxonomic β diversity was observed in the hypogean habitat, what means that the taxonomic composition of caves was more different among themselves than among transects. Differently, when troglobites were removed from the analysis there was no significant difference between the habitats. This pattern may be associated to the disjunction of cave systems and consequent reduced dispersal of organisms so that cave-obligate species usually exhibit narrow distribution (Barr & Holsinger, 1985; Culver, Master, Christman, & Hobbs, 2000; Gibert & Deharveng, 2002; Christman, Culver, Madden, & White, 2005). In general, higher values of beta diversity are expected for assemblages composed by taxa with narrower ranges (Cardoso, 2012). In the present study, each troglobitic species were recorded for only one cave each and successive visits along years led to the observation of the individuals usually associated to travertine dams exclusively in the rainy periods (Ferreira, R. L., personal observations). It may be supposed that the species present a vertical migration looking for wetter portions in the epikarst, since all of them present amphibious habit. As the rainfall increases, the specimens return to the travertine

pools probably to feed on the organic matter carried by the percolation water or other animals (as bats), however this behavior deserves further investigations.

On the other hand, the variance of functional composition did not differ between the epigean and hypogean environments and the removal of troglobites on this analysis attributed a higher variance to the epigean habitat. Even that troglobitic species were expected to be functionally similar given their restriction to the subterranean realm and strong effect of environmental filtering (Pipan & Culver, 2012), the troglobites were the responsible by increasing the variance of functional traits in the studied assemblages. Some troglobitic species presented the highest values of body length and width and antenna length, while one of the lowest attributes of such traits were recorded for one species observed in both habitats (*Pectenoniscus* sp1). In this sense, the presence of troglobites increased the amplitude of the range of hypogean species attributes, thus making their functional variance statistically equal to those observed for the epigean environment. Since FD and taxonomic β diversity were higher in the hypogean, but functional β diversity did not differ between habitats, the hypogean species seem to be functionally redundant. The subterranean conditions are probably similar among caves, then environmental filters selected species with specific traits in order to survive under the peculiarities of this habitat conditions (Weiher & Keddy 1995). In function of the limited dispersion and restriction to the subterranean realm, a strong speciation process has been occurring inside the caves, what originated a remarkable diversity of cave isopods in the Speleological Province of Arcos, Pains and Doresópolis.

Non-random distributions of species and their respective traits may sign that assembly rules of local assemblages have been guided by limiting similarity or environmental filtering (Holdaway & Sparrow, 2006). However, the effects of such processes lead to opposite phenotypic, functional and phylogenetic patterns, what may preclude the detection of the underlying rules (Helmus, Bland, Williams, & Ives, 2007). The observed values of total β diversity and its components did not differ from null models, since all β values (both taxonomic

and functional) were within the range expected by chance. In this sense, random factors seem to be underlying the assembly rules of the studied assemblages. Such randomness uses to be attributed to a primordial importance of historical factors in determining the community composition (Drake, 1991). Independently of the underlying processes guiding the species composition, assessing the β diversity and its components is essential, especially to assist conservation practices (Socolar, Gilroy, Kunin, & Edwards, 2016).

The singular composition of cave communities may accrue from phylogenetic and functional clustering, since not all taxa present pre-adaptations to live under subterranean conditions (Cavender-Bares, Kozak, Fine, & Kembel, 2009; Pausas & Verdú, 2010). However, although the selective pressures may have led to a clustering tendency in relation to the epigean environment, the presence of species that belong to different ecological-evolutionary categories in the subterranean habitat (trogloxene, troglophilic and troglobitic species) attenuates such tendency. In the present study, six families were recorded and any of them were exclusively found in the epigean habitat. However, eight genera were recorded and one new genus was found only in the hypogean environment, which comprised almost half of all the species collected. In this sense, despite the hypogean system presented a substantially higher richness, most of them belong to the same genus, what culminated in a low taxonomic distinctness. Therefore, taxonomic distinctness was not correlated with richness neither with functional diversity, since even species of the same genus (that received the same weight in the analysis) may present different attributes for each functional trait. The lack of congruence between richness, functional diversity and taxonomic distinctness may be related to the fact that the later expresses long-term evolutionary adaptations to the habitat conditions, while richness and functional diversity may respond to short term environmental changes (Gallardo, Gascón, Quintana, & Comín, 2011; Roque et al., 2014).

All groups of transects and caves remained within the confidence interval of the average expected Δ^*, what indicates that caves and transects present a taxonomic distinctness as the expected. The group of caves C2 was positioned beneath the confidence interval, what indicates

that it presented a taxonomic distinctness lower than expected. This group is compounded by five caves that harbor seven species, but all of them belong to the same genus, what was the reason for the low Δ^*observed. If Δ^* was lower for the hypogean habitat, in general, this would indicate that few taxa of the epigean community were capable to colonize the subterranean environment. On the other hand, if Δ^* was higher in the hypogean habitat, the epigean could have suffered long-term impacts that lead to a loss of taxa from different taxonomic levels. On the other hand, higher values of Δ^* in the hypogean habitat may indicate that successive speciation events occurred in the subterranean realm, what improved the richness, and not necessarily that epigean species were lost or locally extinct.

In the present study, there was no significant difference between epigean and hypogean habitat regarding Δ^*. This scenario may represent an effect of species depletion for both epigean and hypogean assemblages in function of changes on the vegetal cover, thus causing a decrease on the species pool, so that only the most tolerant species remained in the small forest fragments.

Hornug, Tóthmérész, Magura, and Vilisics (2007) demonstrated that the distribution of species, spatial and temporal patterns and abundance of isopods depends on the levels of perturbations, food quality and shelter availability. The proportion of dicotyledones in the habitat also may play a regulatory role for isopods (Rushton & Hassall, 1983). Considering a landscape in which great part of the epigean phytophysiognomy was replaced by pastures and mining activity, like the Speleological Province of Arcos, Pains and Doresópolis, the strong modification of the main predictors may have extinguished locally distinct lineages of isopods, with the permanence of the most resistant and tolerants.

Fernandes et al. (2016) suggested that the lower predation pressure and more amenable environmental conditions found inside the caves may have favored a phenotypic overdispersion, with rapid genetic divergence culminating in parapatric speciation. In fact, Howarth (1993) and Howarth and Hoch (2012) had proposed a special case of the parapatric speciation model (Endler, 1977) in which adaptive shifts occurs in function of a reduction in gene flow caused by a steep

environmental gradient even within a contiguous area. It means that populations had invaded the hypogean environment to exploit novel resources and the genetic divergence and speciation occurred in function of the drastic change in habitat conditions (Rivera, Howarth, Taiti, & Roderick, 2002).

Therefore, the first hypothesis that taxonomic, phylogenetic and functional diversity are higher in the hypogean system was partially corroborated. Actually, the taxonomic diversity is higher in the hypogean system, however it is richer in functionally redundant and phylogenetically closely related species. Fernandes et al. (2016) suggested that the milder conditions of subterranean environments may have favored the colonization and functional overdispersion of isopods, however the external environment was substantially different when compared to the present study. Caatinga is a Brazilian biome characterized by predominantly dry conditions, what does not favor the permanence of isopods, which are strongly prone to desiccation. On the other hand, the currently studied region belongs to the Brazilian savannah biome, which despite of the anthropic impacts still maintains some forest fragments that may shelter isopod species. Nevertheless, Gámez-Virués et al (2015) reinforce that the diversity of land covers types is fundamental for maintaining communities even in landscapes subject to high intensity anthropic activities. Even in biomes with milder conditions than the semi-arid, like Brazilian savannah, isopods seem to be best succeeded on colonizing and prevailing in the subterranean environments, especially when the epigean habitats presents a long historic of agricultural and mining activities.

The second hypothesis that the turnover component would predominate as assembly rule in epigean and hypogean assemblages of isopods was refuted, since the observed patterns of beta diversity and its components did not differ from the null model. This indicates that neutral processes are acting over the structure of such assemblages (probably related to historical factors) (Hardy, 2008), or even that the oppose effects of limiting similarity and environmental filtering have been precluding the detection of the assembly rules.

The knowledge on the distribution of diversity along a landscape or between communities supports decision making and definition of priority areas for conservation. In this context, it is greatly important to use an integrative approach to assess biodiversity including taxonomic, functional and phylogenetic aspects, which may behave differently in the same community, as observed. The present work was based on isopod assemblages, but it is strongly recommended to conduct further studies assessing the diversity patterns of communities in their distinct facets, as well as considering different spatial scales.

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Supplementary material

Mean values of functional traits of epigean and hypogean isopods from the Speleological Province of Arcos- Pains-Doresópolis (Southeastern Brazil).

Species/morphospecies	env	N sampled	bl	bw	al	vol v	pi g	omt	nme	tm e	ha b
Dubioniscidae											
***Novamundoniscus* sp1**	hypogean	6	3.51 ± 0.59	1.36 ± 0.21	1.36 ± 0.24	0	1	6.5 ± 0.55	85	1	7
***Novamundoniscus* sp2**	epigean	31	2.45 ± 0.58	0.94 ± 0.22	0.77 ± 0.18	0	1	8.71 ± 1.59	32	1	7
***Novamundoniscus* sp3**	epigean	13	2.09 ± 0.44	0.76 ± 0.08	0.81 ± 0.27	0	1	8.0 ± 0.99	73	1	7
***Novamundoniscus* sp4**	hypogean	3	2.47 ± 0.32	0.82 ± 0.14	0.88 ± 0.25	0	0.5	8.0 ± 0.96	129	1	7
***Novamundoniscus* sp5**	epigean	3	3.07 ± 0.64	1.06 ± 0.12	0.82 ± 0.31	0	1	7.33 ±1.15	88	1	7
***Novamundoniscus* sp6**	hypogean	1	2.83	0.95	1.17	0	1	8.0	51	1	7
Platyrarthridae											
***Trichorhina* sp1**	epigean	18	2.33 ± 0.52	0.84 ± 0.28	0.77 ± 0.17	0	0	0	128	1	7
***Trichorhina* sp2**	epigean	2	1.6 ± 0.4	0.65 ± 0.21	0.54 ± 0.12	0	0	5.0 ± 1.0	74	1	7
***Trichorhina* sp3**	hypogean	1	2.71	0.74	0.61	0	0	0	76	1	7
***Trichorhina* sp4**	epigean	5	1.93 ± 0.97	0.81 ± 0.24	0.77 ± 0.35	0	0	3.0 ± 1.27	126	1	7
***Trichorhina* sp4**	hypogean	2	3.57 ± 0.54	1.49 ± 0.08	1.15 ± 0.13	0	0	3.0 ± 1.11	79	1	7
***Trichorhina* sp5**	hypogean	2	3.42 ± 0.54	1.26 ± 0.31	0.91 ± 0.1	0	0	9.5 ± 0.70	77	1	7
***Trichorhina* sp6**	hypogean	4	3.10 ± 0.20	1.18 ± 0.16	0.99 ± 0.11	0	0	0	67	1	7
***Trichorhina* sp7**	hypogean	10	2.98 ± 0.45	1.24 ± 0.16	1.02 ± 0.15	0	0	0	82	1	7
Philosciidae											
Atlantoscia floridana	epigean	52	3.22 ± 0.48	1.06 ± 0.16	1.29 ± 0.13	0	1	11.0 ± 2.07	3	3	2
Benthana picta	epigean	5	5.61 ± 2.37	2.26 ± 1.09	3.54 ± 2.29	0	1	18.2 ± 4.32	13	3	2
Porcellionidae											
***Porcellio* sp1**	epigean	10	3.41 ± 0.46	1.13 ± 0.27	1.13 ± 0.27	0	1	11.0 ± 1.62	80	1	1
Scleropactidae											
Circoniscus bezzi	epigean	11	9.87 ± 5.85	3.27 ± 2.01	1.81 ± 0.91	1	1	8.0 ± 0.70	6	3	4
Circoniscus bezzi	hypogean	9	9.14 ± 5.07	2.82 ± 1.95	1.77 ± 1.25	1	1	11.0 ± 6.36	0	3	4
Styloniscidae											
***Pectenoniscus* sp1**	epigean	10	2.03 ± 0.19	0.46 ± 0.06	0.51 ± 0.11	0	0	0	126	5	7
***Pectenoniscus* sp1**	hypogean	4	1.81 ± 0.24	0.46 ± 0.06	0.58 ± 0.04	0	0	0	129	5	7
***Pectenoniscus* sp2**	hypogean	5	1.55 ± 0.48	0.32 ± 0.04	0.56 ± 0.05	0	0	0	79	5	7
Styloniscidae sp1	hypogean	6	11.19 ± 1.88	3.76 ± 0.64	3.65 ± 0.85	0	0	0	11	4	6
Styloniscidae sp2	hypogean	6	6.05 ± 0.81	1.89 ± 0.29	1.89 ± 0.33	0	0	0	17	4	6
Styloniscidae sp3	hypogean	4	6.49 ± 0.07	1.83 ± 0.19	1.89 ± 0.15	0	0	0	9	3	6

	env	n	bl	bw	al	volv	pig		omt	nme	tme
Styloniscidae sp4	hypogean	7	6.35 ± 0.60	1.66 ± 0.23	1.92 ± 0.37	0	0	0	25	3	6
Styloniscidae sp5	hypogean	9	6.05 ± 0.02	1.47 ± 0.23	1.5 ± 0.23	0	0	0	18	3	6
Styloniscidae sp6	hypogean	2	5.61 ± 0.14	1.55 ± 0.16	1.78 ± 0.10	0	0	0	10	4	6
Styloniscidae sp7	hypogean	2	7.97 ± 0.58	2.49 ± 0.04	2.8 ± 0.10	0	0	0	9	3	6
Styloniscidae sp8	hypogean	11	11.26 ± 2.03	3.34 ± 0.37	3.67 ± 0.63	0	0	0	14	3	6
Styloniscidae sp9	hypogean	3	8.47 ± 1.08	2.67 ± 0.37	3.48 ± 0.75	0	0	0	17	4	6
Styloniscidae sp10	hypogean	8	8.71 ± 1.13	2.47 ± 0.23	8.61 ± 0.39	0	0	0	9	3	6
Styloniscidae sp11	hypogean	3	5.94 ± 0.54	1.64 ± 0.15	1.51 ± 0.55	0	0	0	13	4	6
Styloniscidae sp12	hypogean	1	7.34	2.14	1.94	0	0	0	4	4	6
Styloniscidae sp13	hypogean	1	6.91	2.05	2.21	0	0	0	11	4	6
Styloniscidae sp14	hypogean	5	7.77 ± 0.47	2.07 ± 0.17	1.64 ± 0.23	0	0	0	15	3	6
Styloniscidae sp15	hypogean	48	8.31 ± 1.35	2.12 ± 0.54	2.25 ± 0.76	0	0	0	12	4	6

Legend. env: environment, n: number of individuals; bl: body length; bw: body width; al: antenna length; volv: volvation capacity; pig: pigmentation; omt: number of ommatidia; nme: number of mechanoreceptors; tme: type of mechanoreceptors; hab: habit; na: non-available data.