Relatório de atividades de campo

Projeto: Diversidade de opiliões (Arachnida – Araneae) da Mata Atlântica. Padrões e relações com fatores ambientais e históricos.

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Descrição das atividades

Essa expedição teve como objetivo a procura de uma espécie em particular de opilião, *Cobania picea*, que ocorre no PARNA. No entanto, não encontramos nenhum exemplar. Nós também realizamos algumas amostras noturnas ao redor do alojamento.

Utilizamos dados obtidos na literatura e em outras expedições e coleta para compilar uma lista de espécies de opiliões registrados no PNI, apresentada abaixo.

Tabela 1. Lista de espécies de opiliões (Arachnida-Araneae) do PARNA de Itatiaia.

Família	**Subfamília**	**Espécie**
Cryptogeobiidae	s.c.s.	Cryptogeobiidae sp.2
Cryptogeobiidae	s.c.s.	Cryptogeobiidae sp.3
Cryptogeobiidae	s.c.s	*Cryptogeobius hirsutus*
Cryptogeobiidae	s.c.s.	*Heteromeloleptes fasciatus*
Cryptogeobiidae	s.c.s.	*Heteromeloleptes padbergi*
Gonyleptidae	Bourguyiinae	*Asarcus longipes*
Gonyleptidae	Caelopoyginae	*Ampheres luteus*
Gonyleptidae	Caelopoyginae	*Arthodes xantopygus*
Gonyleptidae	Caelopyginae	*Pristocnemis perlatus*
Gonyleptidae	Caelopyginae	*Pristocnemis pustulatus*
Gonyleptidae	Cobaniinae	*Cobania picea*
Gonyleptidae	Goniosomatinae	*Acutisoma hamatum*
Gonyleptidae	Goniosomatinae	*Acutisoma longipes*
Gonyleptidae	Goniosomatinae	*Goniosoma macracanthum*
Gonyleptidae	Goniosomatinae	*Goniosoma unicolor*
Gonyleptidae	Goniosomatinae	*Mitogoniella taquara*
Gonyleptidae	Gonyleptinae	*Acanthogonyleptes fulvigranulatus*
Gonyleptidae	Gonyleptinae	*Gonyleptellus bimaculatus*
Gonyleptidae	Gonyleptinae	*Gonyleptes pseudoguttatus*
Gonyleptidae	Gonyleptinae	*Gonyleptes saprophilus*
Gonyleptidae	Gonyleptinae	*Gonyleptes* sp.2
Gonyleptidae	Gonyleptinae	*Mischonyx squalidus*
Gonyleptidae	Gonyleptinae	*Mischonyx processigerus*

Gonyleptidae	Gonyleptinae	*Neosadocus bufo*
Gonyleptidae	Gonyleptinae	*Uracantholeptes anomalus*
Gonyleptidae	Mitobatinae	*Mitobates* sp.3
Gonyleptidae	Pachylinae	*Bunoplus pachypalpis*
Gonyleptidae	Pachylinae	*Discocyrtus granulatus*
Gonyleptidae	Pachylinae	*Discocyrtus melanacanthus*
Gonyleptidae	Pachylinae	*Discocyrtus pizai*
Gonyleptidae	Pachylinae	*Discocyrtus wygodzinskyi*
Gonyleptidae	Pachylinae	*Discocyrtus* sp.1
Gonyleptidae	Pachylinae	*Discocyrtus* sp.5
Gonyleptidae	Pachylinae	*Eusarcus armatus*
Gonyleptidae	Pachylinae	*Itatiaincola nanus*
Gonyleptidae	Pachylinae	*Maromba dandrettai*
Gonyleptidae	Pachylinae	*Metagyndoides granulatus*
Gonyleptidae	Pachylinae	*Meteusarcoides caudatus*
Gonyleptidae	Pachylinae	*Meteusarcoides mutilatus*
Gonyleptidae	Pachylinae	Pachylinae sp.3
Gonyleptidae	Pachylinae	*Paraluederwaldtia bituberculata*
Gonyleptidae	Pachylinae	*Singram* sp.3
Gonyleptidae	Pachylinae	*Triglochinura indicta*
Gonyleptidae	Pachylinae	*Uropachylus itatiaia*
Gonyleptidae	Progonyleptoidellinae	*Moreiranula moreirae*
Gonyleptidae	Progonyleptoidellinae	*Moreiranula picta*

s.c.s – sem classificação em subfamílias

Esses dados nos permitiram incluir o PNI em um estudo sobre a diversidade de opiliões na Mata Atlântica. Apresentamos em anexo duas publicações resultantes dessa pesquisa.

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ARTICLE

Historical signatures in the alpha and beta diversity patterns of Atlantic Forest harvestman communities (Arachnida: Opiliones)

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Abstract: The integration of ecology and historical biogeography is fostering the investigation of diversity patterns. We studied alpha and beta diversity patterns of Brazilian Atlantic Forest harvestman (Arachnida: Opiliones) communities and related them to environmental and historical factors. Our data bank contains 508 species from 63 sites, encompassing almost the entire latitudinal range of Atlantic Forest. Alpha diversity was higher in coastal sites in the south and southeast regions and decreased in sites inland, as well as in sites in the coastal northeast region, especially in northern Bahia state. Alpha diversity was positively influenced by precipitation and altitudinal range, but the low number of species in northeastern coastal sites seems to be more related to the historical distribution of Neotropical harvestman lineages than to recent environmental factors. Geographic distance was the most influential factor for beta diversity. Compositional changes were also remarkably congruent with areas of endemism delimited for Atlantic Forest harvestmen. The percentage of protected areas for each area of endemism was very unbalanced, and Espírito Santo and Pernambuco states were the least protected areas. The turnover process observed in the compositional changes indicates that conservation strategies should include as many reserves as possible because every community presents a unique set of species.

Key words: richness, biodiversity, biogeography, community ecology, arachnids, Neotropical harvestmen, Arachnida, Opiliones.

Résumé : L'intégration de l'écologie et de la biogéographie historique produit des avancées dans l'étude des motifs de diversité. Nous avons étudié les motifs de diversité alpha et bêta de communautés de faucheurs (arachnides : opilions) de la forêt atlantique brésilienne et les avons reliés à des facteurs environnementaux et historiques. Notre banque de données renferme 508 espèces de 63 sites, couvrant presque toute l'étendue latitudinale de la forêt atlantique. La diversité alpha est plus élevée dans les sites côtiers des régions du Sud et du Sud-Est et diminue dans les sites de l'intérieur, ainsi que dans les sites de la région côtière du Nord-Est, particulièrement dans le nord de l'État de Bahia. Si les précipitations et l'étendue altitudinale exercent une influence positive sur la diversité alpha, le faible nombre d'espèces dans les sites côtiers du Nord-Est semble quant à lui être davantage associé à la répartition historique de lignées de faucheurs néotropicaux qu'à des facteurs environnementaux récents. La distance géographique est le facteur exerçant la plus grande influence sur la diversité bêta. Les variations de la composition concordent aussi remarquablement bien avec les zones d'endémisme délimitées pour les faucheurs de la forêt atlantique. Le pourcentage d'aires protégées dans chaque région d'endémisme est très déséquilibré, et les États d'Espírito Santo et de Pernambuco sont les régions les moins protégées. Le processus de renouvellement observé dans les variations de la composition indique que les stratégies de conservation devraient comprendre le plus de réserves possible, puisque chaque communauté présente un ensemble d'espèces unique. [Traduit par la Rédaction]

Mots-clés : richesse, biodiversité, biogéographie, écologie des communautés, arachnides, faucheurs néotropicaux, arachnides, opilions.

Introduction

Alpha diversity or local species richness represents the most basic information about biodiversity. Beta diversity indicates the variation in species from one place to another (Whittaker 1960). Combined, these parameters represent key data for establishing conservation priorities and designing conservation strategies (Socolar et al. 2016). Studying alpha and beta diversity patterns and identifying the factors responsible for these patterns represent one of the central goals of biological subdisciplines such as community ecology, biogeography, and macroecology (Brown 1995; Gaston 2000); it is also vital information for conservation.

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Current patterns of biodiversity distribution result from a combination of historical and contemporary processes. So, an increasing number of studies have been trying to integrate these factors in the analysis of biodiversity by exploring patterns and processes of species richness (Buckley and Jetz 2007; Terribile and Diniz-Filho 2009) or exploring patterns and processes of changes in composition between places (Leprieur et al. 2011; DaSilva et al. 2014).

The Brazilian Atlantic Rain Forest is one of the most endangered biodiversity hotspots (Myers et al. 2000). This biome has all of the required characteristics for this title: high species richness and a high endemism level, with ancient and continued human pressure and extensive habitat loss (Ribeiro et al. 2009). Spanning from 06°S to 30°S (SOS Mata Atlântica and INPE 1993), the Atlantic Rain Forest also presents high latitudinal and altitudinal variations, and this variety of environments and habitats has been used to explain its impressive biodiversity (Oliveira-Filho and Fontes 2000; Durães and Loiselle 2004; Werneck et al. 2011; Vasconcelos et al. 2014).

More recently, an increasing number of studies have attempted to assess the influence of historical events on biodiversity in the Atlantic Rain Forest (e.g., Weir 2006; Martins 2011; Carnaval et al. 2014). For example, paleoclimate model reconstruction revealed that regions where forest formations persisted over time were coincident with current patterns of endemism and diversity (Carnaval and Moritz 2008), which suggests that those areas represent forest refugia. The role of geographic barriers in those patterns is also investigated (DaSilva et al. 2017), and the biome has some well-known spots that are believed to have had a major influence on limiting species distribution and thus shaping diversity patterns, such as the Doce River, in the state of Espírito Santo, and the region in the north of Bahia state, with two geographic barriers, Todos os Santos Bay and the São Francisco River.

Such large-scale studies of Atlantic Rain Forest are usually focused on vertebrates, as the foundations for this kind of study are much more established for those groups, with a better known taxonomy and geographic distribution (Morante-Filho et al. 2016; Melchior et al. 2017). Indeed, for several vertebrate groups, large databases, sometimes of global extension, are available (Stotz et al. 1996; Ceballos et al. 2005; Patterson et al. 2005; Buckley and Jetz 2007; Terribile and Diniz-Filho 2009; Sauer et al. 2014; BirdLife International and Handbook of the Birds of the World 2018). In contrast, for diverse tropical invertebrate groups, even basic alpha and beta diversity patterns remain poorly understood, with available knowledge typically restricted to inventories at the local or landscape scale (Bragagnolo et al. 2007; Proud et al. 2011, 2012; Resende et al. 2012*a*, 2012*b*; Rodrigues et al. 2014), although there are exceptions (Dos Santos et al. 2008; Löwenberg-Neto et al. 2008).

Harvestmen (Arachnida: Opiliones) from the Atlantic Rain Forest may represent a good target group for large-scale diversity studies. Tropical harvestmen are nocturnal, hygrophilous animals with very poor dispersal capabilities (Mestre and Pinto-da-Rocha 2004; Pinto-da-Rocha et al. 2007). The low vagility leads to very high endemism levels, with several species exhibiting very restricted distributions (e.g., DaSilva and Gnaspini 2009; Bragagnolo and Pinto-da-Rocha 2012). Therefore, 97.5% of harvestmen species from the Atlantic Rain Forest are endemic to this biome (Pinto-da-Rocha et al. 2005). The diversity of harvestman communities from the Atlantic Rain Forest has been studied previously (Pinto-da-Rocha et al. 2005), and the main findings were that richness increases in sites near the coast compared with sites inland. However, that study was restricted to the south and southeast Brazilian regions and the patterns were not related to any explicative variables.

In this study, we analyze alpha and beta diversity patterns of Atlantic Rain Forest harvestmen, including areas from the northeast region, and relate them to environmental variables and historical factors. The influence of historical factors will be analyzed considering the proposal of delimitation of 12 areas of endemism (AoE) for Atlantic Rain Forest harvestmen (DaSilva et al. 2015). This number is much higher than those reported in similar studies of different animal and plant taxa, which usually recover three main AoE: two in the northeast region (one with its center in Pernambuco state and the other in Bahia state) and one associated with the Serra do Mar mountain chain in the southeast region (see revision in DaSilva et al. 2015). The 2 northeast AoE were also recovered for harvestmen, but the topographically complex southeast and south regions harbor 10 AoE.

This more detailed response of harvestmen is probably due to their poor dispersal capabilities and heavy dependence on forested, humid habitats (Pinto-da-Rocha et al. 2007). Thus, harvestmen may provide more accurate information for biodiversity conservation, which is an urgent issue for the Atlantic Rain Forest because only 12% of its original cover remain and most of it is scattered in small fragments (Ribeiro et al. 2009).

The aim of the present study is to test the role of current environmental conditions versus historical factors in determining the main patterns of alpha and beta diversity patterns of harvestman communities of the Brazilian Atlantic Rain Forest. More specifically, based on the literature, we want to test the following hypothesis:

- Alpha diversity will be positively related with precipitation and (or) humidity.
- Changes in species composition will be more related to a turnover than to a nestedness process, owing to the small distribution of most species (every site is likely to have its own set of species).
- The beta diversity patterns found can explain and are correlated with the AoE delimited for Atlantic Rain Forest harvestmen.
- The percentage of protected areas for each AoE will be very unbalanced and areas located in the southeast will be more preserved than areas located in the northeast region of Brazil.

Materials and methods

Study area

Our study area is the Atlantic Rain Forest. We inventoried 63 sites (Supplementary Table S1),[1] which were spread across 11 states from three Brazilian regions: northeast, southeast, and south. The latitudinal range is from 06°43′S to 29°40′S, which encompasses nearly all of the latitudinal variation of the biome. Although the Atlantic Rain Forest harbors a large diversity of environments and ecosystems, it can be roughly separated into three major components: evergreen ombrophilous forest, which is located on the coast or up to a few hundred kilometres towards the interior; semideciduous forest formations, which are situated in more inland areas, primarily in the states of São Paulo and Paraná, and characterized by a seasonal climate with a marked dry season (Oliveira-Filho and Fontes 2000); and ombrophilous mixed forest, which is situated in the interior of the southern states of Rio Grande do Sul, Santa Catarina, and Paraná. This formation is characterized by a subtropical climate and by the dominant presence of the Neotropical pine (*Araucaria angustifolia* (Bertol.) Kuntze) (IBGE 1991).

The majority of our sampled sites (43) are composed of ombrophilous coastal forests, with many of the sites located in the southeast region, followed by the northeast and south regions. We also

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[1] Supplementary tables are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2018-0032.

included four sites composed of ombrophilous mixed forest in the state of Paraná, nine sites from Atlantic Rain Forest semideciduous formations, and seven sites with dry tropical dense forest (cerradão), which represent an ecotone between Atlantic Rain Forest semideciduous forest and savanna-like cerrado vegetation.

Two main climatic regimes can be distinguished for the Atlantic Rain Forest: in the northeast region, the climate is characterized by a dry summer (from December to March) and a rainy winter (from May to August), whereas in the southeast and south regions, we observe the opposite pattern (Andrade-Lima 1981). Moreover, in the Atlantic Rain Forest, climate also varies according to several factors, primarily latitude, longitude, and altitude. Temperatures are much higher in the northeast states than in the southeast and south subtropical localities. With respect to longitude, a seasonality gradient of decreasing humidity and increasing precipitation can be observed from coastal to inland areas, while altitude usually increases precipitation and humidity, especially in mountainous regions (Câmara 2003).

Basic information about the sites, such as geographic coordinates, protection status, and forest type, are presented in Supplementary Table S1.[1]

Harvestman diversity data

Our data bank contains 508 species of Opiliones from 63 sites (Supplementary Table S2).[1] We restricted our analysis to the suborder Laniatores, which, on average, represents more than 90% of the total richness that is typically found in communities of Atlantic Rain Forest harvestmen (Bragagnolo and Pinto-da-Rocha 2003; Bragagnolo et al. 2007; Resende et al. 2012*a*, 2012*b*; Supplementary Table S3[1]). The remaining species belong to the suborder Eupnoi, while the suborders Dyspnoi and Cyphophthalmi are absent.

Diversity data were obtained from two main sources: standardized sampling and information from museum collections (for information about sampling effort see Supplementary Table S4).[1] The sampling method employed was nocturnal hand collecting, in which collectors investigate several microhabitats from the forest floor and the understory and the harvestmen are captured manually. The sampling unit represents 1 h of searching by one collector in an area of approximately 300 m^2 (30 m × 10 m); sampling campaigns were performed by four collectors. This method is commonly employed in Neotropical arachnid inventories (Bragagnolo et al. 2007; Bonaldo et al. 2009; Azevedo et al. 2013) and represents the most effective method for assessing tropical harvestman diversity (Tourinho et al. 2014).

The other source of data involved reviewing material in museum collections and compiling species recorded in some of our studied localities. We included data from the main arachnological collections in the Atlantic Rain Forest: Museu Nacional do Rio de Janeiro (MNRJ), Museu de Zoologia da Universidade de São Paulo (MZSP), and Instituto Butantan (IBSP), and a regional collection from northeastern sites (UFPB Arachnological Collection). This approach allowed us to greatly improve the size and coverage of our data bank and to offer a much more complete view of the diversity patterns of Atlantic Rain Forest harvestman communities. But it also poses a challenge due to the use of different data sources and variations in sampling efforts.

We are, however, confident that all the sites that we included in the analysis meet basic-quality standards. For some areas with low sampling effort or number of vials stored in museums, comparisons with similar, well-sampled sites suggest that most of the community is recorded. For example, for Porto Cabral and ESEC Caetetus, we recorded five species in each locality, a number of species very close to that obtained in the PE do Morro do Diabo (six species), which is a well-sampled site (82 samples) with similar geographical and environmental characteristics (sampling effort is presented in Supplementary Table S4).[1]

For the sites whose data was based only on standardized sampling, we compared the observed richness with the number of species calculated by the richness estimator Chao 1 (Chao 1984). We calculated the inventory completeness, which is the proportion between the observed and the estimated richness. We used 70% of completeness as a minimum proportion, based on a study with Neotropical spider communities that showed that above that threshold, raising the percentage of sampled species becomes increasingly difficult in terms of costs and time spent in the field (Azevedo et al 2013). Our sampled sites had a mean completeness of 91.6% (n = 28) (Supplementary Table S5).[1]

Environmental variables

Environmental variables were obtained from the CliMond database (Kriticos et al. 2012). We extracted 28 variables, with a 30 s spatial resolution (Supplementary Table S6).[1] This database offers information about the main climatic factors, such as temperature, precipitation, moisture, and radiation, as well as variables obtained from the PCA axis, which combines the values of all climatic data. We excluded variables related to radiation because we believe that radiation does not directly influence harvestmen, as they have cryptic and nocturnal habits.

We also calculated the altitudinal range of the region surrounding each locality. To obtain this range, we used the coordinates to determine the location of the site of interest on GoogleMaps, in the "Terrain" mode, which displays a topographic map, with level contours with a 20 m resolution. The next step was to determine a 5 km radius around each locality and to identify the lowest and the highest altitudes within this radius (altitudinal range (alt.ran), in metres).

Harvestman AoE

The influence of evolutionary history on diversity patterns will be assessed based on the proposed 12 AoE for Atlantic Rain Forest harvestmen (Fig. 4 and Table 1 from DaSilva et al. 2015; Fig. 4*b* of our study). These AoE were established with a parsimony analysis of endemicity based on the distributional data for 123 harvestman species.

Relationships between these AoE have also been proposed based on cladistic biogeographic analysis (DaSilva et al. 2017), which provides a hypothesis concerning how the evolutionary history of those areas can be related to historical events. Results showed the formation of two large blocks of AoE: one southern block (SC, PR, and SSP; the names of the AoE follow DaSilva et al. 2015) and one southeastern block (SMSP, Boc, LSRJ, Org, and Mnt). The two northern AoE (PE and BA) and SEsp were associated, while the relationship of the more central ES was more uncertain (DaSilva et al. 2017).

Among our 63 sites, 49 are distributed within AoE and 14 sites, which are located primarily in the interior of the country, are outside AoE. Those 49 sites are located in 11 of the 12 AoE, and 1 site (PARNA do Caparaó-MG) is within the boundaries of 2 AoE (ES and SEsp) (Supplementary Table S1).[1]

Data on conservation units

To calculate the protected area of each AoE for Atlantic Rain Forest harvestmen, we compiled all federal and state conservation units from the Conservation Units National Register of the Ministry of Environment of Brazil (http://www.mma.gov.br/areas-protegidas/cadastro-nacional-de-ucs). They are divided in two categories: full protection units and sustainable use units — the former have the objective of preserving nature, permitting only indirect use of their natural resources (e.g., parks, reserves, ecological stations), whereas the latter have the goal of sustainable use of resources, reconciling human presence in protected areas (e.g., environmental protection areas, extractive reserves; MMA/Brasil 2011). Thus, it is expected that full protection units have more preserved forests, whereas sustainable use units can incorporate human affected sites, such as agricultural crops and even towns. We calculated the percentage of protected area, comparing the area of each category and the total protected for each AoE, in hectares. Private and municipal conservation units were not compiled because they are little represented in total area.

Data analysis

Alpha diversity

We used the number of species (richness) recorded in each site as a simple and robust measure of alpha diversity. To correlate harvestman richness with environmental variables, we used partial least squares (PLS) regressions. PLS has an advantage over multiple linear regressions because it avoids the problem of collinearity of environmental variables. PLS decomposes variables into orthogonal scores and loadings (Mevik and Wehrens 2007). The "classical orthogonal score" algorithm fit method was employed. To select more important variables acting on the richness dependent variable, we calculated the variable importance in the projection (VIP). Furthermore, we plotted the regression coefficients of the four most important components.

Beta diversity

To assess the patterns of beta diversity, we carried out a generalized dissimilarity modeling (GDM) analysis. GDM is a nonlinear matrix regression technique that is used to analyze spatial patterns in the compositional dissimilarity between pairs of locations as a function of environmental variables and geographical distance (Ferrier et al. 2007; Fitzpatrick et al. 2013). GDM is a community-level modeling analysis, which means that this technique focuses on the collective — or emergent — property of biodiversity, such as beta diversity, by investigating the community as a whole. This approach is more adequate for data sets that contain several rare species with few records (Fitzpatrick et al. 2011), as in our case. This analysis has been increasingly used in studies of large-scale diversity patterns (Fitzpatrick et al. 2011, 2013; Jewitt et al. 2016) due to its ability to incorporate the curvilinear relationship between compositional dissimilarity and ecological (or geographical) distance and to identify variations in turnover rates across environmental gradients (Ferrier et al. 2007).

GDM is based on matrix regressions; the relations between compositional dissimilarities and explanatory variables are assessed through I-spline basis functions. The importance of each variable is estimated via maximum likelihood, by using the sum of the coefficient of the I-spline functions (three were calculated for each response variable). These functions can be plotted and they represent a partial regression fit, showing the importance of each variable when the others are held constant. The importance of the variables can be assessed based on the height and the slope of the function, which also indicates whether the turnover rate varies across the gradients represented by the variables (Fitzpatrick et al. 2013). For a more detailed explanation of GDM see Ferrier et al. (2007).

The first analysis included all of the variables that did not present collinearity ($p > 0.7$) between them. Variables with zero-sum coefficients were excluded and the analysis was rerun. The most important variables and the best-fitted model were selected via step selection (backward elimination), with variables being ordered according to the sums of their coefficients and the least significant variable discarded. The best model was the model that explained the greatest amount of variance in the data and had a smaller number of variables. To assess their significance, the models were compared with null models (100 matrix permutations).

We also used elements of meta-community structure (EMS) analysis (Leibold and Mikkelson 2002), which assessed three metrics of the community in a presence–absence matrix ordered by reciprocal averaging. This technique associates sites based on the similarity of their fauna and species by focusing on their distribution among the sites.

The first metric analyzed is coherence, which evaluates the consistency of the distribution of species along the sites ordered by similarity. The analysis of coherence is a preliminary step; if the coherence is not significant, then the interpretation of turnover and boundary clumping becomes less clear (Leibold and Mikkelson 2002). The second metric is turnover and the analysis performs calculations to determine if the pattern of species substitution across the sites represents a gradual replacement of species across the sites or corresponds to the loss of species in certain sites, which would represent a nested pattern. The third metric is boundary clumping, which is defined as "…the degree to which the boundaries of different species range are clustered together" (Leibold and Mikkelson 2002). This approach is considered to be a promising framework because it allows the characterization of metacommunity patterns over large regions. In addition, by associating community patterns with turnover or nestedness, the analysis offers insights about the underlying structuring mechanisms that are responsible for the observed patterns (Henriques-Silva et al. 2013).

All analyses were performed in the R software (R Core Team 2016). We used the "pls" package version 2.4 for R (Mevik et al. 2013), GDM was performed with the "gdm" package (Manion et al. 2016), and EMS was performed with the "metacom" package (Dallas 2016).

Results

Alpha diversity

Alpha diversity ranged from 2 to 57 species per site (n = 63, 16.42 ± 13.4 species per site (mean ± SD)) and the mean values varied considerably among different regions and forest types. The northeast region presented smaller values (n = 13, range 2 to 22 species per site, 6.9 ± 6 species per site) than the south region (n = 11, range 5 to 41 species per site, 16.3 ± 12.3 species per site) and the southeast region (n = 39, range 2 to 57 species per site, 19.6 ± 14.1 species per site). The number of species decreased more sharply north of Todos os Santos Bay, in the north of the state of Bahia (n = 11, range 2 to 9 species per site, 4.6 ± 2.5 species per site). The alpha diversity also decreased drastically in sites with semideciduous (n = 9, range 5 to 14 species per site, 8.2 ± 3.6 species per site) and cerrado (n = 7, range 2 to 7 species per site, 3.8 ± 1.6 species per site) vegetation compared with localities covered by evergreen forest. Ombrophilous mixed forest (n = 4, range 6 to 13 species per site, 10.5 ± 3.1 species per site) and specially ombrophilous coastal forest (n = 43, range 2 to 57 species per site, 20.7 ± 14 species per site) presented higher number of species, especially in some sites in the southeast region, in the Serra do Mar Mountain chain (Fig. 1).

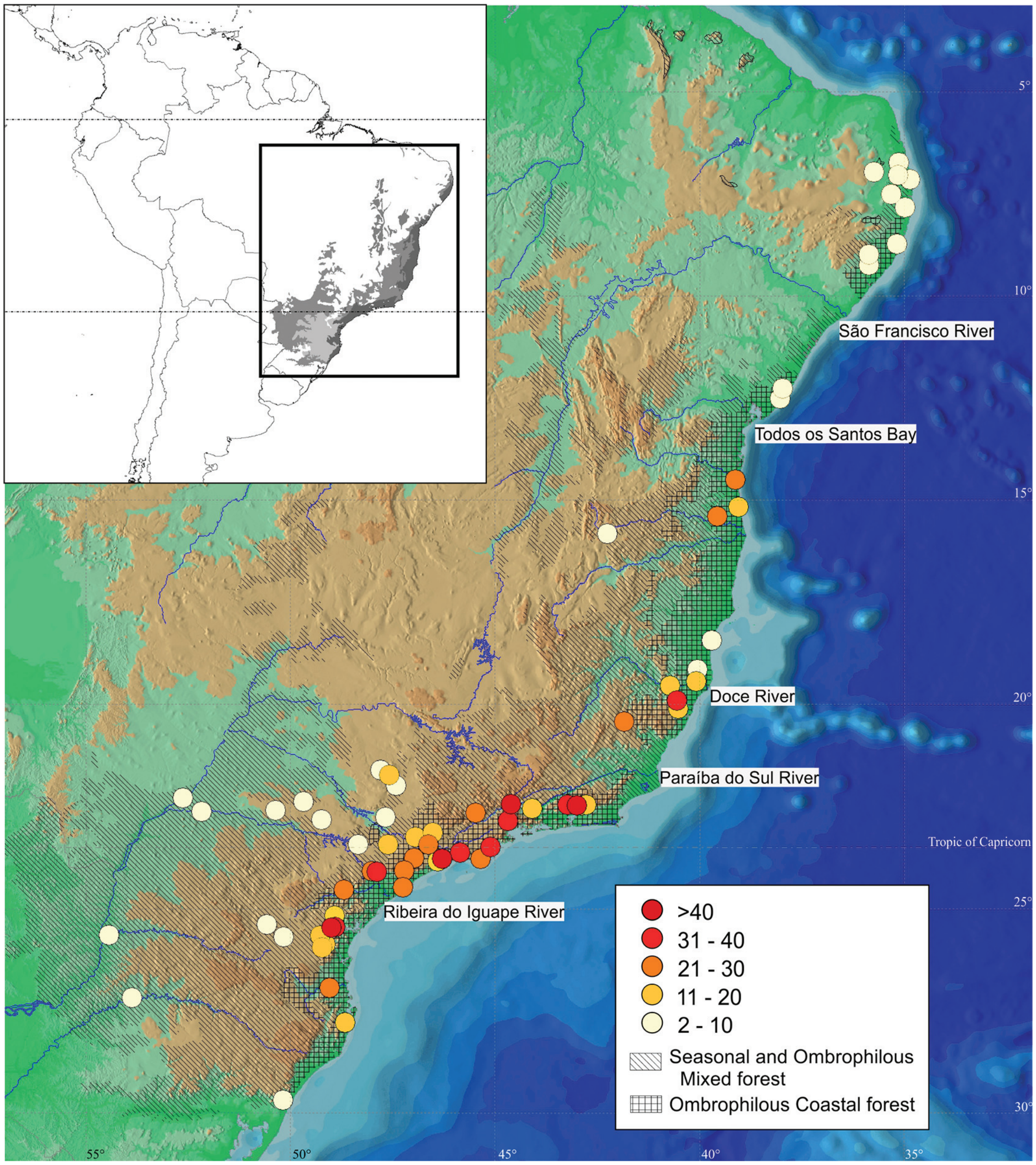
The PLS regressions filtered the effects of environmental variables on harvestman richness; some trends emerged from these analyses, exhibited in the first four axes that together explained 62% of species richness and 99.6% of environmental data correlation. These results were consistent in the first four axes. On species richness, there were positive effects (increases of species) of precipitation of wettest week and warmest quarter, as well as altitudinal range, in the region of the sampled locality. However, the same precipitation of warmest quarter and altitudinal range also had a minor negative effect on richness (Figs. 2*a*–2*d*) in other components. Results of VIP showed higher contribution of precipitation in warm months and altitude range for most harvestman species.

Beta diversity

GDM

This analysis was performed with nine environmental variables and geographic distances. Four of them, however, did not have any effect on the data, with a coefficient sum of zero: annual precipitation, precipitation seasonality, precipitation of the wettest quarter, and lowest weekly moisture index. The remaining five were significant: annual mean temperature, isothermality,

Fig. 1. Map of South America, with the study region enlarged. The 63 studied sites are represented by circles. The color of the circle indicates the number of species by site, increasing from yellow to red (in the online color version; white to dark gray in the print version). Map from DIVA-GIS (from Hijmans et al. 2001, reproduced with permission © 2018 R.J. Hijmans).



temperature annual range, mean moisture index of the coldest quarter, and altitudinal range. Geographic distance was also selected (Table 1).

The best-fitted model explained 61.39% of the deviance in the dissimilarity of harvestman communities and contained four variables: annual mean temperature, isothermality, mean moisture index of the coldest quarter, and geographic distance. The most important variables were isothermality and geographic distance, which were present in all models. Moreover, the model containing only those two variables had an explanatory power only slightly smaller than the best model with four variables.

Geographic distance was the single most important predictor, with a coefficient sum of 25.2%, which by far was the largest. Isothermality, a measure of temperature variation (mean diurnal temperature range – temperature annual range), was the most significant environmental variable; turnover rates were higher between values of 0.6 and 0.65, separating coastal sites from sites inland (Fig. 3).

EMS

The species composition of the different sites exhibited strong variation, especially when considering communities from sites in different AoE. Most species have a restricted distribution and are present in a few of the sampled areas. In fact, 87.2% of the species are present in 3 or fewer sites, while only eight species occurred in at least 10 sites. Not surprisingly, the species with the largest distribution (25 sites), *Mischonyx squalidus* Bertkau, 1880 (Gonyleptidae, Gonyleptinae), is one of the few widespread harvestmen from the Atlantic Rain Forest. *Mischonyx squalidus* is a very abundant species and is also capable of occupying disturbed and urban environments.

Nonetheless, even with this patchy and sparse distribution of species, it was possible to detect significant patterns related to the

Fig. 2. Coefficient plots of four most important components (*a*–*d*) generated by partial least squares (PLS) regressions explaining correlations between harvestman alpha diversity and the six most influential environmental variables filtered by this analysis, pointing explicability values of *X* (dependent variable, alpha diversity) and *S* (environmental variables). The explicative proportion is accumulative along the four components: (*a*) first component (black, solid line); (*b*) first (black, solid line) and second (red, long-dashed line) components; (*c*) first (black, solid line), second (red, long-dashed line), and third (green, short-dashed line) components; (*d*) first (black, solid line), second (red, long-dashed line), third (green, short-dashed line), and fourth (blue, dash-dotted line) components. Variables are isothermality (Isother), mean temperature of the wettest quarter (MtempWetq), precipitation of the wettest week (PrecWetW), precipitation of the warmest quarter (PrecWarQ), moisture index seasonality (MoisIS), and altitudinal range (AltRan). Color version online.

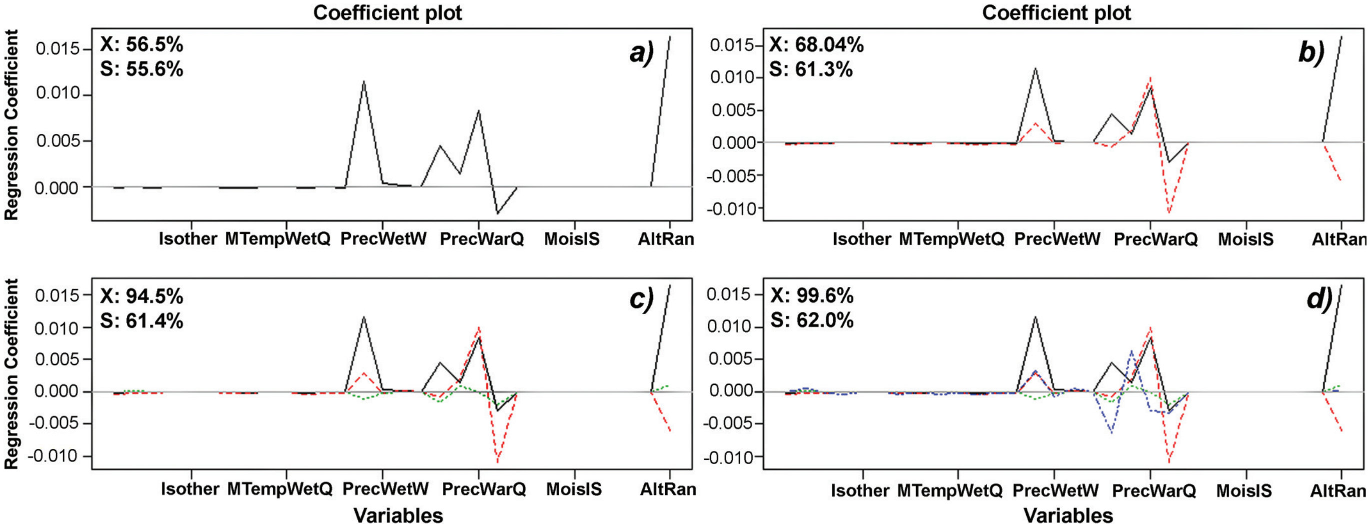


Table 1. Result of the generalized dissimilarity modeling performed for each geographic division.

Significant environmental variables (coefficient sum > 0)	Significant variables of best-fitted models (coefficient sum)	Percent explained deviance of fitted models with geographic distance and environmental variables (model variables)
bio01, bio03, bio07, bio35, alt.ran	dist.geo. (25.02) bio01 (0.942) bio03 (1.89) bio07 (0.54) bio35 (1.19)	61.39 (dist.geo + bio01 + bio03 + bio35) 60.35 (dist.geo + bio01 + bio03) 58.56 (dist.geo + bio03)

Note: Variables are mean annual temperature (bio01), isothermality (bio03), temperature annual range (bio07), mean moisture index of coldest quarter (bio35), and altitudinal range of the region (within a 5 km radius; alt.ran). We present the significant variables for each division and those selected by the best-fitted model, as well as the coefficient sum and the proportional deviance explained by the variables.

Fig. 3. Results of the generalized dissimilarity modeling (GDM) analysis. (*a*) Fit of the modelshowing the relationship between compositional dissimilarity between all pairs, as well as the predicted ecological distance of these pairs, estimated by the GDM function. The fitted functions of (*b*) the index of geographic distance, (*c*) annual mean temperature, (*d*) isothermality, and (*e*) mean moisture index of coldest quarter are shown. Color version online.

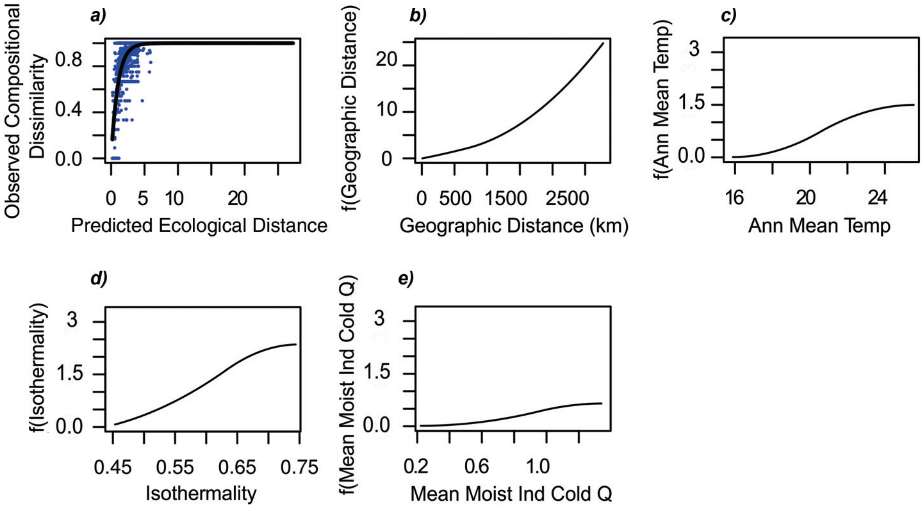
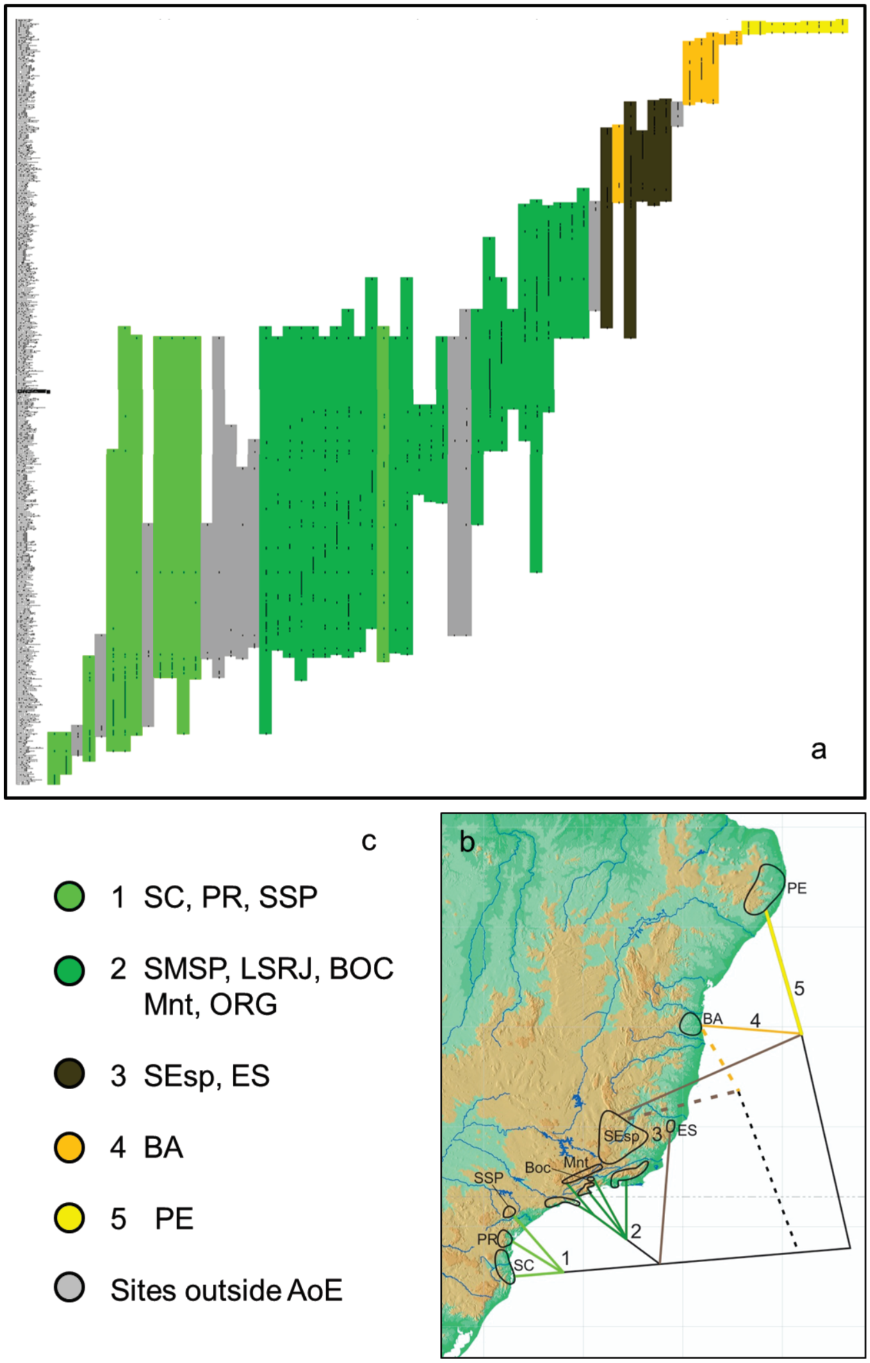


Fig. 4. (*a*) Matrix of sites (columns) by species (rows) interpolated and ordered by reciprocal averaging. (*b*) Area cladogram showing the relationships of the areas of endemism (AoE) of Atlantic Rain Forest harvestmen. Numbers indicate the five major AoE groups (modified from DaSilva et al. 2017, reproduced with permission of Curr. Zool., vol. 63, issue 5, p. 531, ©2017 Oxford University Press). (*c*) Legend indicating the AoE that belong to each group. The colors of the groups correspond to the colors in the matrix displayed in *a*. For definitions of the AoE refer to DaSilva et al. 2015.



observed changes in the composition of communities. Our EMS analysis indicated significant coherence (z = 11.86, p < 0.01), a significant turnover (z = –15.91, p < 0.01), and significant boundary clumping (Morisita index = 4.68, p < 0.01) indicating a clustered pattern of species distribution. The significant turnover and non-significant nestedness is in agreement with the results of the GDM and indicates a gradual transfer of species from one site to another. However, the significant boundary clumping indicates abrupt transitions in the composition, which means that groups of species have similar distributions and that it is possible to observe in the ordinate matrix large "blocks" of sites that have few species in common with other groups of sites. The turnover process is probably occurring between sites within the same AoE, with few species in common between different AoE.

The groups of sites formed are remarkably consistent with the AoE delimited for the Atlantic Rain Forest (Figs. 4*a*–4*c*). Only two exceptions were observed: (1) PET do Alto Ribeira, which belongs to the SSP AoE, an area associated with other southern AoE (PR

Table 2. Area and percentage of protected forests by areas of endemism (AoE) of Atlantic Rain Forest (according to DaSilva et al. 2015).

AoE	Area (ha)	Forestal area* (ha)	FP area (ha)	SU area (ha)	Protected area (ha)	% FP	% SU	% Protected
PE	14 032 000	7 016.00	36 413.9	285 421.2	313 947.2	0.5	4.1	4.5
BA	15 092 000	10 061.33	264 310.0	651 498.4	952 532.7	2.6	6.5	9.5
ES	1 148 000	—	7 202.3	4 189.4	11 391.8	0.6	0.4	1.0
SEsp	5 125 000	—	150 571.4	363 064.1	473 510.1	2.9	7.1	9.2
Mnt	1 610 000	—	59 847.3	588 692.2	588 692.2	3.7	36.6	36.6
Org	1 384 000	—	91 706.1	399 084.4	490 790.6	6.6	28.8	35.5
Boc†	25 000	—	25 000.0	—	25 000.0	100	—	100
LSRJ	533 000	—	177 575.9	57 107.6	210 186.7	33.3	10.7	39.4
SMSP	3 217 000	—	315 634.7	916 258.9	1 231 893.7	9.8	28.5	38.3
SSP†	137 613	—	137 613.0	—	137 613.0	100	—	100
PR	5 011 000	—	354 403.1	1 430 096.1	1 667 862.4	7.1	28.5	33.3
SC	3 759 000	—	240 187.2	59 855.0	300 042.1	6.4	1.6	8.0

Note: Protected forests were considered federal and state conservation units according the National System of Conservation Areas of Brazil (parks, reserves, ecological stations, etc.), divided into full protection areas (FP) and sustainable areas (SU); FP has more preserved forests generally. AoE are Pernambuco (PE), Bahia (BA), Espírito Santo (ES), Serra do Espinhaço (SEsp), Serra da Mantiqueira (Mnt), Serra dos Órgãos (Org), Serra da Bocaina (Boc), South litoral of Rio de Janeiro (LSRJ), Serra do Mar of São Paulo (SMSP), South of São Paulo (SSP), Paraná (PR), and Santa Catarina (SC).

*Part of the PE and BA AoE are covered by Caatinga shrublands.

†AoE delimited according to the limits of the FP unit.

and SC), and which was placed among sites that belong to AoE from the southeastern clade (Fig. 4*b*); (2) Reserva Natural da Vale, placed with sites from the ES AoE, although it belongs to the BA AoE.

The largest compositional difference observed in our data set involves comparisons of sites from northeastern Brazil to the remaining areas studied. Only three species (*Eusarcus incus* H.E.M. Soares and B.A. Soares, 1946, *Metagonyleptes calcar* Roewer, 1913, and *Parapucrolia ocellata* Roewer, 1917; all Gonyleptidae) are shared between these two groups of sites. However, the composition of the sites of central–southern Bahia is considerably different from that of the sites north of Todos os Santos Bay.

Gonyleptids are dominant in most parts of the Atlantic Rain Forest and represent a mean of 84.2% of the total number of species in southern and southeastern localities. At sites in central–southern Bahia, gonyleptids accounted for a mean of 66.7% of the total species; at sites located farther north (north of Todos os Santos Bay), the relative importance of gonyleptids decreased sharply (33.3%) and the relative importance of the Cosmetidae and Stygnidae families increased.

Conservation

Results regarding the proportion of protected forest for each AoE are presented in Table 2. AoE from the southeast region were the most protected, including two AoE (SSP and Boc) that were completely protected. Those values are much smaller in the northeast AoE; for the ES AoE, the proportion of protected forest represents only 1% of the total area.

Discussion

Due to the coverage of our data set, our study offers the most complete picture of the alpha and beta diversity patterns of Atlantic Rain Forest harvestman communities and is the first study to relate these patterns to explicative factors. Our study is also one of the few analyses of beta diversity to include nearly the whole extent of the Atlantic Rain Forest. The results reflect well-known aspects of the biology of Opiliones, such as their poor dispersal capabilities and their dependence on humidity, but it is possible to perceive an influence of historical factors on alpha and especially beta diversity patterns.

Alpha diversity

Alpha diversity was positively related to the precipitation of the wettest week, of the warmest quarter, and to altitudinal range, but also had a minor negative relationship with these last two, as expected by our first hypothesis. Our results also confirmed the main findings reported by Pinto-da-Rocha et al. (2005), with alpha diversity peaking in south and southeast coastal sites and decreasing in semideciduous forest sites and in cerrado sites in the interior. However, this pattern varies regionally, as the sites in the northeast were species-poor even though they were composed of coastal forest, which will be discussed later. In this region, the Atlantic Rain Forest is a narrow strip, especially in its northern limits in the states of Paraíba and Pernambuco (>50 km; Oliveira-Filho and Fontes 2000). These forests have a more seasonal climate and receive less rain and experience higher temperatures than forests in the south and southeast regions. Consequently, some of these coastal sites are considered semideciduous and open ombrophilous forest formations (IBGE 1991).

The general pattern is consistent with the strong dependence of harvestmen on humidity (Santos 2007), which has already been shown to influence diversity. Harvestman richness and abundance were higher in the wet summer than in the dry winter in the southeastern mountains (Almeida-Neto et al. 2006). Thus, the positive effect of the two variables related to precipitation was expected.

However, the precipitation of the warmest quarter also presented a minor negative effect. This minor negative effect can be explained by the species-poor northeast region having a dry winter, such that the warmest period coincides with the dry season, which is opposite to what is observed in the species-rich south and southeast regions with a wet summer. Precipitation of the wettest week, in contrast, combines the maximum values of precipitation for all sites, regardless of the season, which is the reason why it had a stronger positive effect on alpha diversity without negative influences.

The altitudinal range of the study region was also an important positive factor for alpha diversity, but it also had a small negative effect, the reason for which is not clear. Places with large altitudinal range, usually mountainous regions, are considered the most species-rich places on Earth (Orme et al. 2005; Rahbek 2005). Mountains may increase alpha diversity indirectly, through influences on the regional climate. When located near the coast, mountains generate orographic rainfalls that help to create and to maintain a moist habitat, which is optimal climatic conditions for harvestmen. A large altitudinal range may also be related to alpha diversity through another factor that is more closely related to historical aspects. The slopes of mountainous regions exhibit greater climatic stability over time, allowing the maintenance of forest formations during periods of climatic variation and acting as forest refugia (Haffer 1987; Carnaval et al. 2014). Therefore, biological communities from these regions may have lower extinction rates because they are able to conserve a large regional species pool. In contrast, in localities that experience environmental instability, the species pool may be reduced.

It is important to mention that refugia probably did not play a role in increasing richness by promoting speciation because Atlantic Rain Forest harvestman species appear to be much older than Pleistocene refugia (Bragagnolo et al. 2015). Still, towing to the optimal environmental conditions, communities from refugia may experience lower extinction rates than communities located in more unstable areas. Thus, refugia probably played an important role in conserving local alpha diversity. There is a record in the literature of refugia presenting a larger number of species than the surrounding areas (Keppel et al. 2012), and a study of the diversity of mite harvestmen from the humid Australian tropics (Boyer et al. 2016) found that the past (during the last glacial maximum) climatic suitability was a better predictor of present-day diversity than present-day climatic suitability. Thus, the role of refugia in maintaining a large number of species appears to be unequivocal.

Carnaval and Moritz (2008) modeled the past climatic conditions in the Atlantic Rain Forest and found evidence of forest refugia in the northeast, in the regions corresponding to the AoE of Bahia and Pernambuco. However, they found no evidence of refugia in the southeast region, but they acknowledged that their models might not be appropriate for areas with steep environmental gradients, which is the case in the south and southeast regions. Carnaval and Moritz (2008) also listed evidence from other studies concerning the persistence of forested areas in those regions. Haffer (1987) claimed that orographic rainfalls probably maintained forested and humid areas on the slopes of the Serra do Mar mountain chains, supporting several small refugia, which probably correspond to the numerous AoE from the south and southeast regions.

The association between potential refugia and high species richness is observed in our coastal south and southeast sites, but not for the species-poor northeast sites, especially those from the PE AoE. One possible explanation for this result could be the environmental differences between northeast and southeast–south coastal sites. In the northeast region, the Atlantic Rain Forest is a narrow strip, especially in its northern limits in the states of Paraíba and Pernambuco (>50 km; Oliveira-Filho and Fontes 2000). These forests have a more seasonal climate, receive less rain, and experience higher temperatures than forests in the south and southeast regions. Consequently, some of these coastal sites are considered semideciduous and open ombrophilous forest formations (IBGE 1991). However, the observed differences in climatic conditions appear to be of a smaller magnitude than the differences in the number of species. On average, northeast sites have a smaller number of species than sites with semideciduous forest (6.9 and 8.2 species, respectively), although northeast sites have a larger mean annual precipitation and moisture (northeast sites: annual precipitation = 1602.7 ± 286 (mean ± SD), annual moisture index = 1.01 ± 0.1 (mean ± SD); semideciduous forest sites: annual precipitation = 1390.1 ± 224, annual moisture = 0.89 ± 0.9).This suggests the influence of other factors that are probably related to historical aspects.

The large variation in altitudinal range observed in the south and southeast regions may be indirectly linked to the large number of species found in those regions. A complex topography indicates a complex geomorphological history; the emergence of mountain chains, river valleys, and other geological features probably promoted the speciation of local groups and led to an increase in the regional species pool (Thomé et al. 2014; Bragagnolo et al. 2015; DaSilva et al. 2015). DaSilva et al. (2016) provided a theoretical example of how recurrent vicariant events at reiterative barriers could have increased the number of species in the narrow endemic *Heteromitobates* Roewer, 1913 genus of harvestmen in the southeast Atlantic Rain Forest.

In contrast, the thin strip of forest in the northeast Atlantic Rain Forest has a less complex topography, indicating that their biota had not been subjected to the vicariance events faced by the harvestman fauna of the south and southeast regions. The possible influence of historical factors on the fauna differences between the northeast and the south–southeast regions also seems to be confirmed by important changes in the species composition as is discussed below.

Beta diversity

Harvestman communities of the Atlantic Rain Forest were characterized by intense changes in composition, even over short distances, as a consequence of the restricted distribution of most species. All of the analyses employed indicated a strong effect of historical events on current beta diversity patterns. Also, the first hypothesis was supported by our results, as turnover was the prevalent process responsible for compositional differences between sites.

A nestedness pattern would imply that in localities with fewer species, such as the sites from the inland semideciduous forest or the northeast sites, communities would be composed of subsets of species from more diverse sites. However, communities are very different and share few species. This indicates that most species did not expand their range, either because of their narrow climatic tolerance (Santos 2007) or because of dispersal limitations. Species-poor communities from the inland sites have a particular set of species, most of them not present in the species-rich sites covered by ombrophilous forest, with a few exceptions, such as the most widespread species in our data bank, *M. squalidus*. The EMS also detected a significant turnover that was observed in the ordered matrix.

Results of the GDM showed the contribution of geographic distance and three environmental variables on the observed pattern of beta diversity. The most important was isothermality, which sorted out sites from the inland semideciduous forests from the more humid, coastal sites with ombrophilous forests. The values where faunal substitution peaked correspond mainly to sites somewhat inland but relatively near the coast, representing a transition between coastal and semideciduous forests, like PE Serra da Cantareira, Atibaia, PE Serra do Japi, and FLONA de Ipanema. A recent study showed a strong seasonal effect on the life cycle of a species of Atlantic Rain Forest harvestman (Pagoti and Willemart 2015), offering more evidence of the influence of temperature variation on the biology of the species.

Annual mean temperature and mean moisture index of the coldest quarter were also significant, but geographic distance was the variable that contributed the most to the observed pattern of beta diversity, being present in all the best models, and was considered the single most important variable. This result is certainly linked to the low vagility of harvestmen. Taxa with poor dispersal capabilities are believed to show stronger signs of historical effects on distribution (Graham et al. 2006; Cavender-Bares et al. 2009), as such taxa are less likely to colonize new environments and expand their areas of occurrence. Geographical barriers, such as mountains, rivers, and valleys, may be overcome by vagile taxa, which can expand their distribution and confound their biogeographic history. However, for dispersal-limited taxa, such as harvestmen, those barriers often limit distribution, offering clues and insights regarding the events that shaped the present distribution of the group.

The EMS offers additional evidence for the importance of historical factors for beta diversity. This analytical technique is considered to provide a promising framework by allowing the characterization of metacommunity patterns over large regions. Although this analysis detected a significant turnover, it also showed significant boundary clumping, indicating that several species have common distributional limits. Figures 4*a*–4*c* show the congruence between groups of sites formed with the AoE, which represents a strong historical effect on Atlantic Rain Forest harvestman patterns of beta diversity. Thus, the turnover process is probably more gradual between sites from the same AoE and steeper when involving sites from different AoE.

The most abrupt changes were observed between areas south and north of the Doce River and between sites in the Bahia and the Pernambuco AoE. Similar breaks in species distribution are also recognized in other taxa, highlighting the importance of the Doce River region as an effective barrier (Amorim and Pires 1996; Silva et al. 2004, 2012). The separation of the biotas from the Bahia and Pernambuco AoE occurs in the region of the São Francisco River in which the historic climatic model supported two large refugia (Carnaval and Moritz 2008). However, other authors claim that the slightly southern Todos os Santos Bay region could represent a more effective barrier (Amorim and Pires 1996; Silva et al. 2012; DaSilva et al. 2017).

The region between the bay and the São Francisco River includes a narrow strip of humid Atlantic Rain Forest that extends near the coast, whereas the rest of the region is covered by cerrado vegetation (IBGE 1991), which probably denotes an unstable region, with Todos os Santos Bay located in a huge and ancient sedimentary basin (Blaich et al. 2008). Our data appear to support the above hypothesis based on the fauna recorded at Fazenda Camurujipe and RPPN Fazenda Lontra Saudade. Both sites are situated between these two barriers (north of Todos os Santos Bay and south of the São Francisco River). Richness and family composition of these sites are much more similar to those of the northern sites of the Pernambuco AoE than to those of the central–southern Bahia sites, suggesting that the Todos os Santos Bay region does indeed represent a much more important historical event for harvestmen than the São Francisco River.

Changes in composition at the family level are also important. Gonyleptidae dominate communities south of the Rio Doce, representing the clear majority of species in all sites. The relative importance of this family decreases in sites located in central–southern Bahia and decreases even further in sites located north of Todos os Santos Bay, where the Cosmetidae and Stygnidae families become dominant. This family composition is similar to that of Amazonian harvestman communities for which the Cosmetidae and Stygnidae families are central components (Pinto-da-Rocha and Bonaldo 2006; Tourinho et al. 2014). Thus, as observed for other groups, the northeast Atlantic Rain Forest harvestman fauna contains a mixture of Atlantic Rain Forest and Amazonian components, highlighting ancient connections between these two forest formations (Santos et al. 2007; Batalha-Filho et al. 2013; Prates et al. 2016).

As mentioned before, the great reduction in the speciose family Gonyleptidae in the northeast region impoverishes its communities and may explain the observed differences in alpha diversity between the northeast region and the south–southeast regions. The smaller presence of Gonyleptidae species at lower latitudes may reflect the southern origins and biogeographic history of this family.

Conservation

The proportion of protected areas varied wildly between different AoE, ranging from 1% to 100%. The best-preserved AoE, including two AoE fully protected (Boc and SSP; Table 2), were located in the southeast region, most of them from the Serra do Mar mountain chain. It is noteworthy that several of those reserves correspond to mountainous regions where the original vegetation tends to be preserved because of the unsuitability of the land for human activities such as agriculture and livestock. Mountain slopes are also usually under legal protection, even outside of conservation units.

Conversely, the two AoE with the flattest topography (PE and ES) have the smallest proportion of protected area. With only 1% of protected area, ES harbors 55 species, 38 (69%) of which are exclusively from this AoE. As the region is already heavily deforested (Fig. 1S-g in the supplementary material of Ribeiro et al. 2009), increasing the protection of this region would be a conservation priority for harvestman diversity.

The protected area of the PE AoE is also very small, corresponding to only 4.5% of the size of this AoE. The opiliological fauna from the PE AoE contains the fewest species, only 11, but also represent a unique fauna because only two of the species occur in other AoE. Like the ES AoE, the PE region is heavily deforested (Fig. 1S-f in the supplementary material of Ribeiro et al. 2009). The region received the first Portuguese colonizers, who started large-scale deforestation and agricultural expansion (Dean 1997).

The situation of the PE AoE is even worse if we consider that only 0.4% of its total area is under full protection; the rest is under the more permissive sustainable use regime. In most AoE, the amount of area under full protection is smaller than the sustainable use (47%, on average, but if we exclude the two areas with a 100% protection, then the mean proportion decreases to 37% under full protection). As harvestmen are very sensitive to environmental disturbances (Bragagnolo et al. 2007), sustainable use areas may be unsuitable for several species because they may contain much degraded habitat such as rural and agricultural areas. Thus, increasing the proportion of full protection areas could also be an important recommendation for conservation policies.

Finally, the SC AoE was the least protected among the 10 south–southeast AoE, with only 8% of area located in conservation units. Bergamin et al. (2017), studying beta diversity based on floristic surveys, concluded that Araucaria, or ombrophilous mixed forest, should receive priority attention for the creation of protected areas, along with semideciduous forest, because they are less represented in the Atlantic Rain Forest reserve network than ombrophilous coastal forest.

A final conservation recommendation in a broader context would be the creation of a large number of reserves spread across large areas and across different regions. This final recommendation is important because of the restricted distribution of most harvestman species. We agree with Baselga (2010), who stated that when turnover is the main process observed in compositional changes, then conservation efforts should be placed in the creation of a large number of different sites, not necessarily focusing on the richest sites.

Conclusion

Our study presented the most complete picture of alpha and beta diversity patterns of Atlantic Rain Forest harvestmen, with a data bank covering almost all the latitudinal range of the biome.

We tested and confirmed the positive relationship between alpha diversity and precipitation. Large altitudinal ranges also had a positive effect on the number of species, although the mechanisms behind this relationship are not clear. Consequently, sites from the south–southeast regions, several of them combining these characteristics, were the most species-rich.

However, for both alpha and beta diversity patterns, there was evidence of a strong historical effect, such as the determinant influence of geographic distance on beta diversity patterns, as well as the congruence between the compositional changes and the AoE for Atlantic Rain Forest harvestmen. The low alpha diversity observed in the northeastern coastal sites is probably more related to the historical distribution of Neotropical harvestman lineages than to environmental factors. Northeastern forests, although not as humid as coastal south–southeast sites, are ombrophilous formations, but had a similar number of species to the much drier semideciduous forest sites. The low vagility and dependence on forested habitats of the vast majority of harvestman species certainly magnified the historical footprint in its diversity patterns.

Regarding conservation, our study indicates that the protection of Atlantic Rain Forest harvestman diversity in public reserves varies a lot between the different AoE, which indicates that their communities are not fully protected because the intense turnover process observed resulted in a unique set of species for each AoE, with few species in common. The least-protected areas are the PE and ES AoE. With only 4.5% and 1%, respectively, of their areas preserved, PE and ES would be obvious priority choices for the creation of reserves under the full protection category.

Due to the turnover process observed in our data, the creation of as many reserves as possible within all the AoE would be the most appropriate strategy to protect Atlantic Rain Forest harvestman communities, as well as other groups with similar requirements (DaSilva et al. 2015). Finally, our study represents another example of a more integrated approach between ecology and historical biogeography, a useful and necessary direction to understand and protect biodiversity, especially in a very endangered hotspot like the Atlantic Rain Forest.

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Spatial variation in phylogenetic diversity of communities of Atlantic Forest harvestmen (Opiliones, Arachnida)

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Abstract. 1. The study of diversity has become increasingly sophisticated, including the use of measures of phylogenetic diversity.

2. We calculate the spatial variation in species richness, taxonomic beta diversity, and alpha and beta phylogenetic diversity (PDα and PDβ, respectively) of Atlantic Forest harvestman communities using a data set containing 556 species from 68 sites, distributed in 12 Brazilian states.

3. We compare the congruence of phylogenetic and taxonomic diversity patterns, and also compare PDα with null model expectations, to check for phylogenetic clustering or overdispersion in communities.

4. Species richness and PDα are correlated, peaking in southern and south-eastern coastal sites and decreasing towards the interior and towards the north-east. PDα in north-eastern sites was higher than expected, while a clustered phylogenetic pattern characterised most other sites.

5. Communities in the southern and south-eastern regions were dominated by species from the large family Gonyleptidae, presenting a high richness and a low PDα. As the dominance of Gonyleptidae decreased towards the north, where local communities have fewer species, but a higher PDα, they contain representatives of other families. The beta diversity was more sensitive to the compositional changes involving closely related Gonyleptidae species, while PDβ is more influenced by deeper phylogenetic compositional changes, between more distant lineages.

6. Phylogenetic diversity may be of special importance to assess the conservation value of distantly related lineages. These species-poor groups are less likely to influence taxonomic-based diversity analyses, but their importance for conservation arises from their phylogenetic distinctiveness, captured by PDα and PDβ measures.

Key words. Arachnids, beta diversity, neotropical, nestedness, turnover.

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Introduction

The study of diversity, which used to include only basic alpha and beta diversity measures, developed decades ago (Whittaker, 1960), has become increasingly sophisticated in the past 10 years (Petchey & Gaston, 2006; Vamosi *et al*., 2009). One measure of biodiversity, in particular, phylogenetic diversity (PD; Faith, 1992), has generated a lot of interest (e.g. Cadotte *et al*., 2010; Morlon *et al*., 2011; Weinstein *et al*., 2014; Honorio Coronado *et al*., 2015; Nunes *et al*., 2015; da Silva *et al*., 2016; Moura *et al*., 2017; Almeida *et al*., 2018). PD measures the phylogenetic distance among all species present in a community and compares this distance against the total phylogenetic diversity of the taxa in a particular region. In other words, local PD reflects how much of the total PD of a taxon, or how many lineages (i.e. clades from a phylogenetic tree), is represented in a community. Thus, PD unveils a historical aspect of diversity, which may also offer insights into the processes involved in structuring the community (Webb, 2000; Cavender-Bares *et al*., 2009).

The comparison of observed PD patterns with those expected by chance can also be very useful. This is usually done with the aid of null models, which randomise the placement of species in the phylogenetic trees used for the calculation of PD. When all or most species in the same community are more related to one another than expected by chance, it is said that the community presents a clustered PD pattern. In this scenario, the main process structuring the community may be an environmental filtering allowing only species that share ecological/biological characteristics (and also most likely related) to persist in the environment. Conversely, when species in a community are less related than expected by chance, phylogenetic overdispersion is suspected. In this case, exclusive competition among similar (and also most likely related) species would be the most important driving force structuring the community (see Webb *et al*., 2002 for a comprehensive review).

Not surprisingly, historical factors, such as the diversification and dispersal history of lineages, also influence PD measures (Lessard *et al*., 2012). For example, a recent increase in the speciation rate of a particular lineage would result in several closely related species. This would be reflected in high local species richness with relatively low PD. On the other hand, the PD of a community that mostly includes species that originated a long time ago would be higher (Zupan *et al*., 2014), even if richness is low.

Finally, PD can be compared with other measures of taxonomic diversity, for instance species richness. Until recently, taxonomic diversity was the most common diversity parameter used in ecological and macroecological studies (Gaston, 2000; Whittaker *et al*., 2001), also providing the main source of information for conservation strategies (Cardoso *et al*., 2004; Diniz-Filho *et al*., 2010). For this reason, it is important to ascertain whether PD and species richness are congruent (Zupan *et al*., 2014; Fournier *et al*., 2017).

More recently, a phylogenetic approach has also been adopted by community ecologists to investigate beta diversity patterns (Cavender-Bares *et al*., 2009). By considering the phylogenetic position of a species and its relationship with other co-occurring species, phylogenetic beta diversity (PDβ) reflects a high amount of evolutionary information of the studied taxa in a given area (Cardoso *et al*., 2013; Winter *et al*., 2013). This cannot be ascertained when using traditional beta diversity indices, which only take into account changes in taxonomic composition (Tuomisto, 2010).

For the most part, PD patterns have been established in studies involving plants and vertebrates (Webb, 2000; Vamosi *et al*., 2009; Devictor *et al*., 2010; Zupan *et al*., 2014; Moura *et al*., 2017), since the taxonomy and phylogeny of these groups have been more thoroughly studied (Patterson *et al*., 2005; Ridgely *et al*., 2005; Bininda-Emonds *et al*., 2007). The PD patterns of invertebrate communities have been less studied, especially in tropical forests, the most species-rich environments on Earth. There are a few exceptions though (e.g. Cardoso *et al*., 2014; Arnan *et al*., 2017), including a study on Australian mite harvestman (Boyer *et al*., 2016), performed in Queensland. It looked for a correlation between the PD in past and current environmental conditions, showing that the PD was positively related to present day and especially to past (last glacial maxima, about 18 ka) environmental suitability.

Harvestmen (Opiliones, Arachnida) from the Atlantic Forest (AF) may also be good candidates for such studies. The basic aspects of their biology are known, for instance their nocturnal and cryptic habits, and their dependence on humidity (Pinto-da-Rocha *et al*., 2007). Most tropical harvestman species have very poor dispersal capability (Mestre & Pinto-da-Rocha, 2004; Bragagnolo *et al*., 2015), which results in a high degree of endemism (97.5% of the AF's harvestman are endemic; Pinto-da-Rocha *et al*., 2005). The latter can be very informative in biogeographic studies, since the distribution of species that are poor dispersers carries a strong historical signal (Graham *et al*., 2006; Cavender-Bares *et al*., 2009).

Most importantly, the taxonomy of AF harvestmen is reasonably well resolved, and several recent revisions and phylogenetic analyses are available (e.g. DaSilva & Gnaspini, 2009; Yamaguti & Pinto-da-Rocha, 2009; Bragagnolo & Pinto-da-Rocha, 2012; Pinto-da-Rocha *et al*., 2014; Bragagnolo *et al*., 2015). Even though species richness patterns and beta diversity of AF harvestmen have already been addressed in a previous publication (Pinto-da-Rocha *et al*., 2005), that study was restricted to the south and south-east regions, excluding the north-east, which is the place where the AF is the least studied and the most threatened.

The Brazilian Atlantic Forest is a biodiversity hot spot (Myers *et al*., 2000; Laurance, 2009). There, one can find great biological diversity and high levels of endemism, combined with ancient and intense anthropogenic pressure. We believe that the study of the phylogenetic diversity patterns of the AF's harvestmen, a group particularly sensitive to environmental disturbances (Bragagnolo *et al.*, 2007) and historical factors (DaSilva *et al.*, 2017), will: (i) improve the current state of knowledge about the local biodiversity; (ii) provide insights into the processes responsible for the current diversity patterns; and (iii) provide information that might be helpful for conservation. Besides, to our knowledge, this is the first time that the phylogenetic diversity of any invertebrate group from the Atlantic Forest is quantified and analysed.

In this study, we assess the phylogenetic diversity of the harvestman communities of the AF. Our main goals are to:

1. Calculate the alpha (PDα) and beta (PDβ) phylogenetic diversities for these communities.
2. Compare PDα and PDβ with taxonomic alpha and beta diversities, to check if they are congruent. This has important implications for conservation issues, as they are usually based solely on taxonomic diversity.
3. The observed patterns of PDα will be compared with those generated by null models, to investigate whether Atlantic Forest harvestman communities present patterns of phylogenetic clustering or overdispersion, or not.

Methods

Study area

We inventoried 68 sites (Fig. 1) throughout the Atlantic Forest biome, spread across eleven states from north-eastern, south-eastern and southern Brazil. The latitudinal range varied from 6°43′ to 29°40′, encompassing most of the biome. The AF harbours a great diversity of environments and ecosystems, such as restingas (coastal white-sand woodlands), high altitude forests and rock outcrop dwarf forests (Neves *et al.*, 2017), which can be classified into three major components: (i) evergreen ombrophilous forest, on the coast or a few hundred kilometres towards the interior; (ii) semi-deciduous forests, in more inland areas, mainly in the south-eastern and southern states of São Paulo and Paraná; and (iii) ombrophilous mixed forest, in the interior of the southern states of Rio Grande do Sul, Santa Catarina, and Paraná (Oliveira-Filho & Fontes, 2000). In the south-east and northern south regions, the climate is seasonal with a marked dry season. In the south, the climate is subtropical and the vegetation is dominated by the Neotropical pine *Araucaria angustifolia* (Bertol.) Kuntze 1898 (IBGE 1991).

Most AF sampling sites (n = 45) encompass ombrophilous coastal forests and are scattered in the south, south-east, and north-east. There are also six sites composed of ombrophilous mixed forest in the state of Paraná, nine sites encompassing semi-deciduous formations, and eight sites in dry tropical dense forest (*cerradão*), which represents an ecotone between semi-deciduous forest and savannah-like *cerrado* vegetation.

The climate of the AF changes with latitude. The north-eastern region is characterised by dry summers (from December to March) and rainy winters (from May to August), while in the south-eastern and southern regions, the summer is wet and the winter is dry (Andrade-Lima, 1981). Basic information about the sites, such as geographic coordinates, preservation status, and forest type, is presented in the supporting information (Appendix S1).

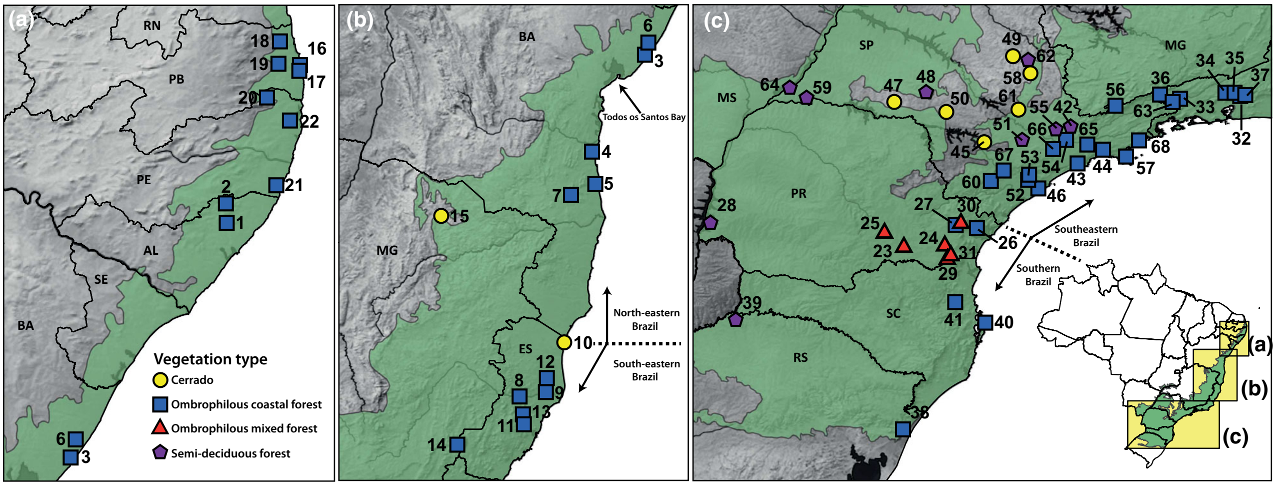

Fig. 1. Study area and sampling sites. (a) north-east region; (b) Bahia (north-east) and Minas Gerais and Espírito Santo (south-east) states; (c) south-east and south states. State abbreviations, from north to south: RN, Rio Grande do Norte; PB, Paraíba; PE, Pernambuco; AL, Alagoas; SE, Sergipe; BA, Bahia; MG, Minas Gerais; ES, Espírito Santo; RJ, Rio de Janeiro; SP, São Paulo; MS, Mato Grosso do Sul, PR, Paraná; SC, Santa Catarina; RS, Rio Grande do Sul. Legend of the sites is presented in Appendix S1. [Colour figure can be viewed at wileyonlinelibrary.com]

Harvestman species occurrence data

A database containing data on 556 species of Opiliones from the 68 sampling sites (Appendix S2, supporting information) was analysed. The main collecting method employed was nocturnal hand collecting, a method usually employed in arachnological inventories (Bragagnolo *et al.*, 2007; Tourinho *et al.*, 2014). A more detailed description of this database can be found in Nogueira *et al.* (in press). We restricted our analysis to the suborder Laniatores, which represents approximately 90% of the total species richness that is typically found in AF harvestman communities (Bragagnolo *et al.*, 2007; Resende *et al.*, 2012a,b). The suborder Dyspnoi is represented by only one described species, and there are several unresolved issues in the taxonomy of Eupnoi. No phylogenetic analysis including AF species of these two suborders has ever been conducted. Additionally, no Cyphophthalmi species has ever been recorded in the Brazilian Atlantic Forest (Benavides & Giribet, 2007; Dasilva *et al.*, 2010).

Harvestman phylogeny

Harvestman phylogeny is presented as supporting information, in Appendix S3.

Data analysis

Spatialisation of diversity components. We assessed the spatial variation in species richness, beta diversity, alpha (PDα) and beta (PDβ) phylogenetic diversity, and the nestedness and turnover partitions of the beta diversity and phylogenetic beta diversity. Each parameter was calculated for each sampling site throughout the Atlantic Forest and interpolated through an empirical Bayesian kriging (EBK) model (Krivoruchko, 2012). The resultant surface map shows the spatial variation in the diversity component analysed. EBK considers that if the data distribution is Gaussian, then intermediate values between observed values can be predicted by the linear combination of the nearby observed values, proportionally to their distances (Krivoruchko, 2012). The EBK analysis was implemented in ArcGIS 10.3 (ESRI, 2014), using the 'smooth circular' search neighbourhood with 'smoothing factor' 0.01. All surface maps (i.e. raster data sets) are displayed with Stretched renderer, which displays continuous raster cell values across a gradual ramp of colours, with a 2.5 standard deviation stretch type, in ArcGIS.

Species richness and beta diversity. The species richness was calculated as the number of species recorded at each locality. To calculate the beta diversity (βsor, *sensu* Baselga, 2010), we build an absence–presence matrix of harvestman species per locality transformed into linear values through non-metric multidimensional scaling (NMDS), using the Bray–Curtis dissimilarity coefficient. This was carried out using the metaMDS function of the R package vegan (Oksanen *et al.*, 2017). The values of each axis of the NMDS were subjected to EBK and then assembled into a single RGB map, a routine described in detail by Oliveira *et al.* (2017). By contrast, unlike Oliveira *et al.* (2017), who excluded the areas with less than ten records from their analysis, which could represent poorly sampled areas, we used the information from all sampling sites. We consider that the harvestman species richness is truly low at some sampling sites (i.e. northeastern Brazil drier areas, DeSouza *et al.*, 2017a,b), and does not result from sampling bias, as some localities have been surveyed with high sampling effort (i.e. Dias *et al.* 2006; Podgaiski *et al.*, 2007). This issue is discussed in Nogueira *et al.* (in press). A categorical map was produced to visualise the spatial clustering of areas throughout the AF, through an Iso Cluster Unsupervised Classification, performed in ArcGIS, with an *a priori* input for 12 classes. This number of classes is based on the number of known areas of endemism proposed for Atlantic Forest harvestmen (see DaSilva *et al.*, 2015).

Beta diversity partition. To evaluate the contribution of each beta diversity component to the overall beta diversity, we calculated a dissimilarity matrix accounting for spatial turnover (replacement; βsim, *sensu* Baselga, 2010), measured as Simpson pairwise dissimilarity, and a dissimilarity matrix accounting for nestedness-resultant dissimilarity (βnes, *sensu* Baselga, 2010), measured as the nestedness fraction of Sorensen pairwise dissimilarity, using the R package betapart (Baselga & Orme, 2012). These matrices were subjected to NMDS and the same procedures described for the total beta diversity. The NMDS however did not reach a solution after 50 000 interactions for the nestedness fraction. Thus, a site-by-site nestedness fraction was calculated as $\beta\text{nes} = \beta\text{sor} - \beta\text{sim}$ (Baselga, 2010). The similarity of the beta diversity maps for each of the three NMDS axes and the respective maps for the nestedness and turnover partitions was accessed through the correlation of maps, calculated in ArcGIS 10.3 (ESRI, 2014).

Phylogenetic alpha diversity (PDα). A strict consensus tree of the most parsimonious trees obtained from the molecular and morphological analyses was used to calculate the alpha and beta phylogenetic diversities. For mathematical purposes, all branch lengths of the consensus tree were set to 1. The observed alpha phylogenetic diversity was calculated as Faith (1992)'s phylogenetic alpha diversity (PDα) on the phylogenetic consensus cladogram. This index represents the sum of the total length of the phylogenetic branch for a given site. Additionally, the expected phylogenetic diversity was calculated for all subsets of the phylogeny, based on an analytic solution for expected PDα. In other words, the expected phylogenetic diversity calculates PDα based on multiple simulations of random combinations of species in a hypothetical site, with species richness in this hypothetical site varying from one to the maximum number of species present in the phylogeny. These analyses were carried out with the R package picante (Kembel *et al*., 2010). The PDα values were subjected to EBK to spatialise its variation.

Phylogenetic beta diversity (PDβ) and its components. Three distance matrices were calculated with the consensus phylogenetic tree. The first two accounted for the phylogenetic turnover (dissimilarity matrix accounting for phylogenetic turnover, measured as Simpson derived pairwise phylogenetic dissimilarity) and nestedness (dissimilarity matrix accounting for nestedness-resultant phylogenetic dissimilarity, measured as the nestedness fraction of Sorensen derived pairwise phylogenetic dissimilarity) components of the phylogenetic beta diversity. The third represented the sum of both values (dissimilarity matrix accounting for phylogenetic beta diversity, measured as Sorensen derived pairwise phylogenetic dissimilarity). This analysis was carried out using the 'phylo.beta.pair' function of the package betapart (Baselga & Orme, 2012), using the Sorensen dissimilarity index, then computing the PhyloSor index (Bryant *et al*., 2008). The values were subjected to NMDS and the same procedures described for the total beta diversity.

Results

Phylogenetic analysis

The total evidence phylogenetic analysis of the implied alignment generated by the re-diagnosis via IP in TNT found eight trees with 64 269 steps (0.25% shorter than DO/IP). The analysis exclusively based on molecular data found one tree with 63 477 steps. The best IQ-TREE's maximum log-likelihood score was −27 904.383 for the molecular data set and −32 787.921 for the total evidence data set.

The consensus cladogram of eight most parsimonious trees of the total evidence analysis is presented in Fig. 2. Our results revealed the following main family relationships within Gonyleptoidea: Agoristenidae and Stygnopsidae were the first groups to diverge in Gonyleptoidea. Stygnidae is the sister group of all other Gonyleptoidea. Cryptogeobiidae is sister to Gerdesiidae, and Metasarcidae + Cosmetidae, as previously suggested by Pinto-da-Rocha *et al*. (2014). Nomoclastidae is sister to Gonyleptidae, *sensu* Pinto-da-Rocha *et al*. (2014). Cranaidae, Ampycidae, and Manaosbiidae should be considered as separate families, and they form a clade that is sister to Gonyleptidae.

The phylogenetic hypotheses with different optimality criterion and data sets (trees presented in Appendix S4, Figures S1-S5 as supporting information) do not present the same relationships between the Gonyleptoidea families mentioned previously. The following are the most outstanding differences. Cosmetidae is paraphyletic in molecular parsimony analysis only: *Ferckeria* and *Metalibitia* are sisters to Metasarcidae + others Cosmetidae clade. Maximum likelihood and Bayesian inference analyses resulted in the south-east Brazilian genus *Gonycranaus* being more closely related to Cryptogeobiidae than the Amazonian *Gerdesius*, which results in a paraphyletic Gerdesiidae. *Zamora* and *Cutervolus* form a clade only after total evidence analyses using parsimony and Bayesian inference. Finally, the position and composition of the clades containing the Peruvian genera *Acrographinotus*, *Hyperpachylus*, *Junicus*, *Palcapachylus*, and *Pichitus* are highly variable in all hypotheses.

Species richness and phylogenetic alpha diversity

The number of harvestman species ranged from 2 to 57 per site ($n = 68$, mean 16.6 ± 13 species), and the average values varied considerably among different regions and forest types. Species richness was higher in south-eastern coastal sites, especially in the states of São Paulo and Rio de Janeiro (Fig. 3a), where local communities reached more than 40 or even 50 species (Appendix S1). The number of species decreased inland and northwards, especially north of Todos os Santos Bay (Fig. 1b).

The observed pattern of alpha phylogenetic diversity (PDα) was similar to that of species richness, with greater values in south-eastern Brazil, especially in the region of the Coastal Chain Serra do Mar, in the state of Rio de Janeiro and eastern portion of the state of São Paulo (Fig. 3b). The main difference was that the PDα observed in the north-eastern region was higher than expected, especially north of Todos os Santos Bay (Fig. 3c), and also in the westernmost interior areas of the AF, while the PDα obtained for most of the coastal ombrophilous forest sites was lower than expected (Fig. 4). In all cases, the variation in PD however was within the IC limits, which indicates that the phylogenetic structure of the communities under study was not significant and therefore our results do not deviate from a random pattern. Since the calculation of PD based on the other optimality criteria, such as Bayesian inference and maximum likelihood analysis (presented in Appendix S4, Figures S6–S11), did not reveal important differences from the results obtained with parsimony analysis of total evidence, all of our results are based on the latter. As supporting information, we present the relationship between the distance between phylogenetic trees and the spatial correlation between the observed and the expected phylogenetic diversity (Appendix S4, Figure S12).

Beta diversity and phylogenetic beta diversity

The beta diversity pattern of the AF harvestman communities was characterised by high taxonomic variation through the sampled localities. The resulting classification divided the AF in 12 classes, including two in the north-east, five in the south-east, and five in the south (Fig. 5a).

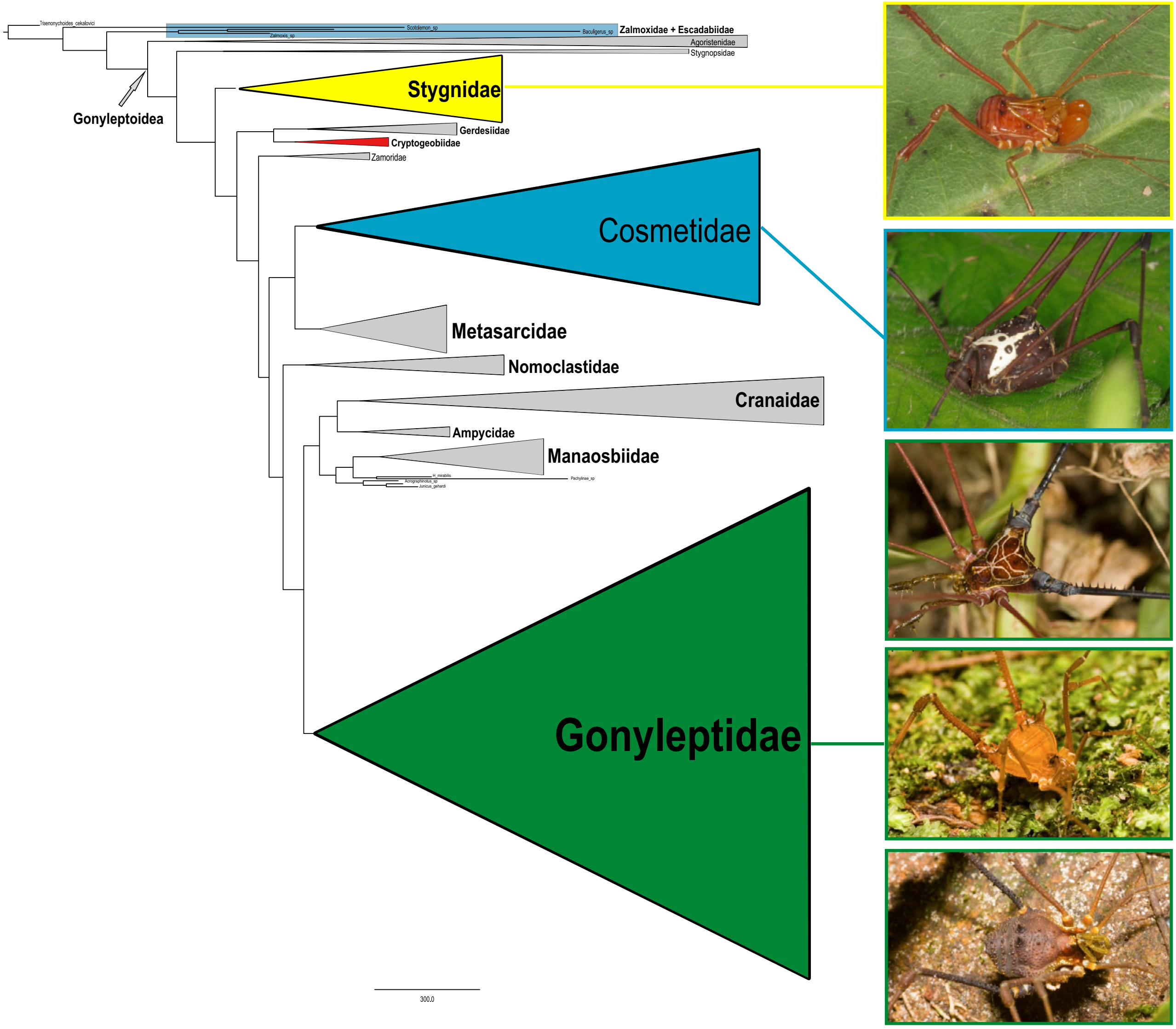

Fig. 2. Phylogenetic tree used in the phylogenetic diversity analysis. Clades width is proportional to the number of species in the family. Pictures show representatives of the families Stygnidae, Cosmetidae, and Gonyleptidae, from top to bottom. [Colour figure can be viewed at wileyonlinelibrary.com].

Turnover was by far the most important process driving the changes in species composition, being strongly positively correlated (0.94) with the total beta diversity pattern (Fig. 5b), while the site-by-site beta diversity was negatively correlated with its nestedness fraction (−0.37).

Additionally, differences in the number of species per family at each region were detected. Gonyleptidae represents the vast majority of harvestman species in the localities south of Todos os Santos Bay (Fig. 5c). This family accounts for 88% of the total species in southern/south-eastern (without ES) Brazil and for 70% in the region from the south-eastern state of Espírito Santo to central/south Bahia. But this proportion decreases sharply north of Todos os Santos Bay (graphics in Fig 5c), dropping to 33% of total species richness, while the relative importance of other families, such as Cosmetidae and Stygnidae, increases.

The phylogenetic beta diversity and beta diversity (Fig. 6b) differed somewhat, with the first harbouring a smaller number of categories (six). While the south and the southern portion of the south-east region are roughly divided into five different classes by beta diversity, the PDβ reunites them into a single class, including coastal and interior regions. The PDβ also suggests a smaller number of categories for the gradual changes observed from the north-east to the south-east. As observed for the partition of beta diversity, phylogenetic turnover was the predominant process accounting for the PDβ (Fig. 6a and b).

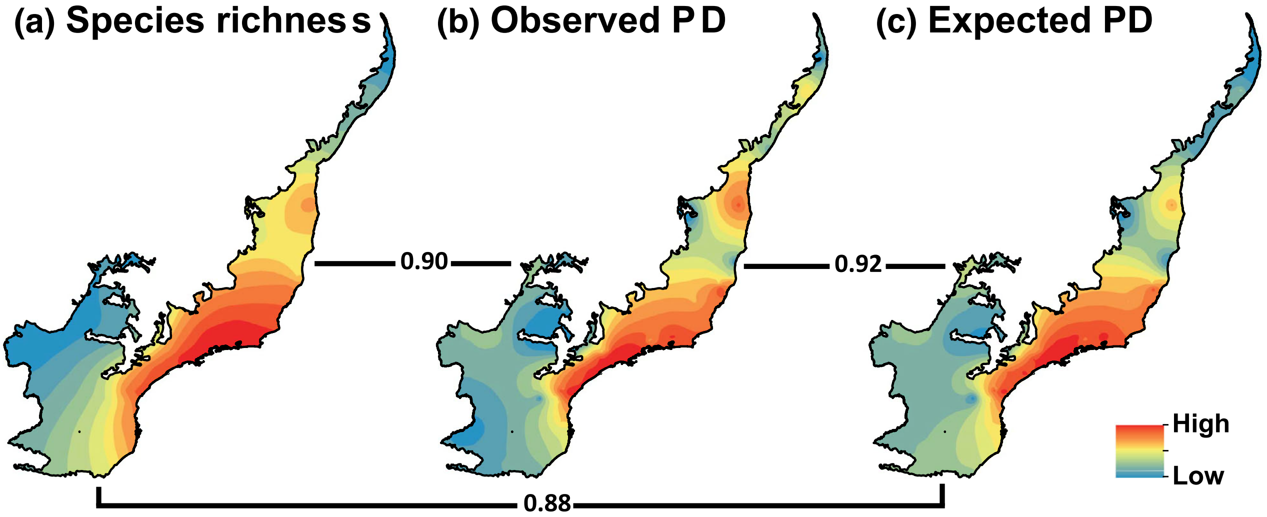

Fig. 3. Richness and phylogenetic alpha diversity (PDα) of Atlantic Forest harvestmen. (a) Richness pattern. Colours indicate the number of species, increasing from blue to red. (b) Observed PDα, values increasing from blue to red. (c) Expected PDα, values increasing from blue to red. Lines linking the maps show the correlation (value in the middle of the line) between them. [Colour figure can be viewed at wileyonlinelibrary.com].

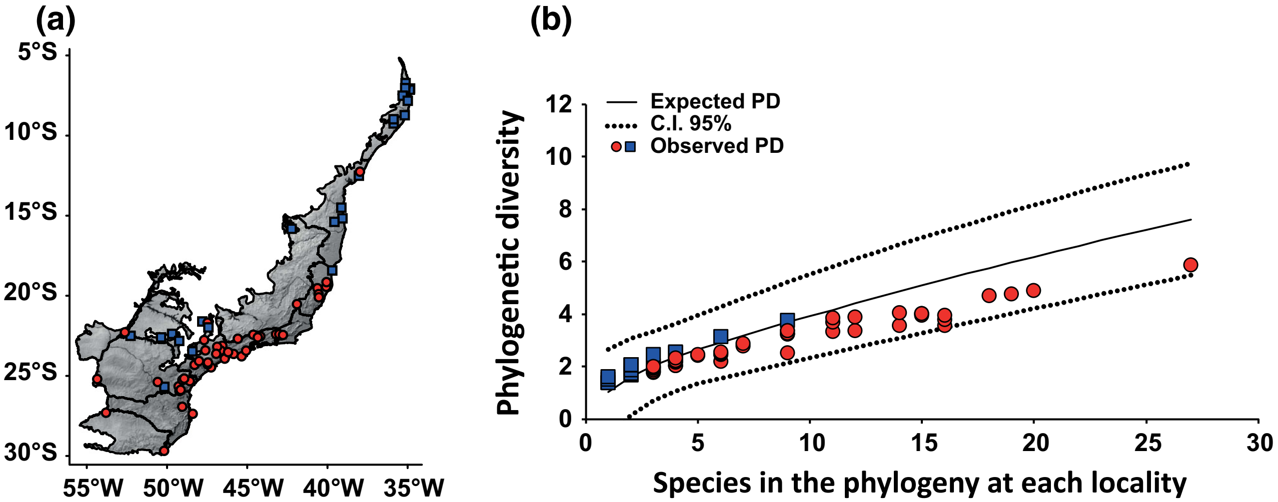

Fig. 4. Relationship between observed and expected phylogenetic alpha diversity (PDα), for each site. (a) Map showing the location of the sampled sites; (b) correlation between observed PDα and number of species present in the phylogeny for each site. Black line indicates the values for the expected PD, and dashed lines represent the 95% confidence interval. Sites represented by blue squares are those whose observed PDα values are above the average expected PD, while those represented by red circles have observed PDα values below this average. [Colour figure can be viewed at wileyonlinelibrary.com].

By contrast, the overall observed PDβ patterns were weakly explained by the phylogenetic nestedness, exhibiting a negative correlation between two out of the three NMDS axes subjected to EBK (Fig. 6c).

Discussion

To our knowledge, our study is the first to investigate the large-scale spatial diversity pattern, including phylogenetic diversity metrics, of an invertebrate group from the Atlantic Forest. In our data, phylogenetic diversity was informative, revealing patterns that cannot be uncovered by traditional (taxonomic) diversity measures alone.

The PDα of the species-poor north-eastern sites (north of Todos os Santos Bay) was relatively large. Those sites are among the few that have a PDα similar or slightly larger than the expected average, while the PDα values of all remaining sampled sites, especially the species-rich south-

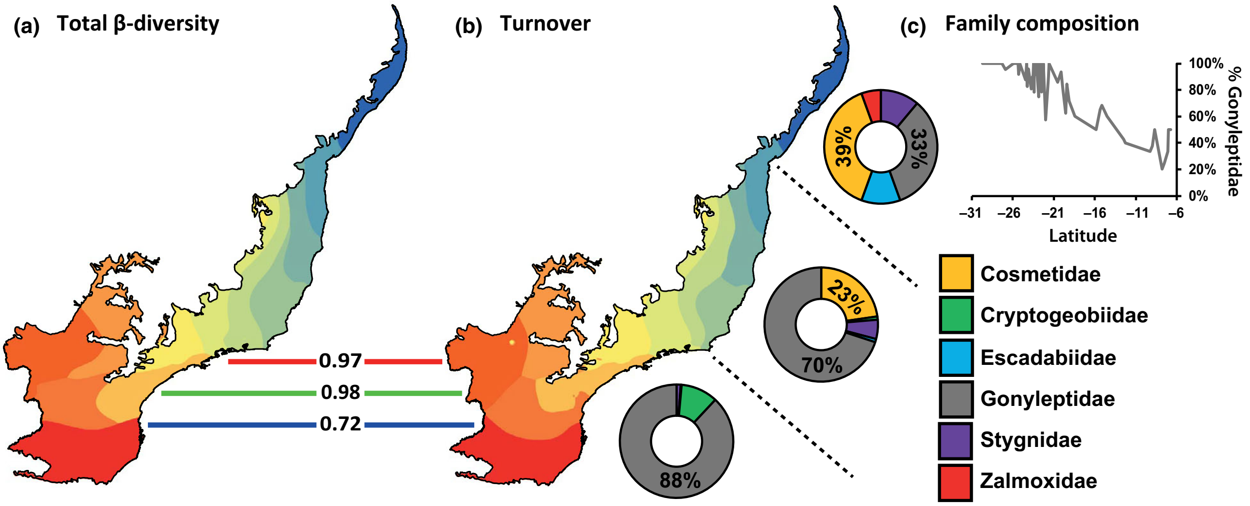

Fig. 5. Beta diversity pattern of Atlantic Forest harvestman communities. (a) total beta diversity; (b) beta diversity due to turnover; (c) relative importance of harvestman families in three different regions of the Atlantic Forest (south and south-east (except ES state); ES, north of MG and BA states; north-east region above the Todos os Santos Bay) and the percentage of Gonyleptidae species at each latitude. Different colours indicate differences in composition of the communities, for each map. The lines indicate the correlation between the three-first NMDS axis between total beta diversity and turnover (1 – red, 2 – green, and 3 – blue). [Colour figure can be viewed at wileyonlinelibrary.com].

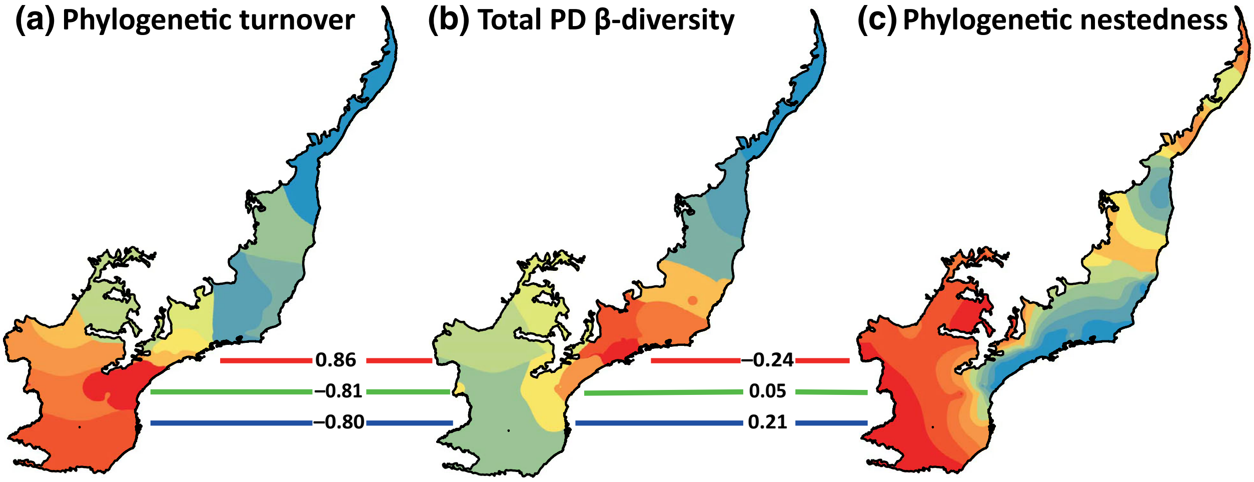

Fig. 6. Phylogenetic beta diversity (PDβ) pattern of Atlantic Forest harvestman communities. (a) PDβ variation due to turnover; (b) total PDβ; (c) PDβ variation due to nestedness. Different colours indicate different communities, in terms of phylogenetic variation. The lines indicate the correlation between the three-first NMDS axis between total PDβ in relation to turnover and nestedness partitions (1 – red, 2 – green, and 3 – blue). [Colour figure can be viewed at wileyonlinelibrary.com].

eastern coastal sites, were below the expected average. These results can be explained by the profound differences observed in the distribution of the main families of AF harvestmen, outlined below, which affected all diversity measures.

The species-rich family Gonyleptidae encompasses most, if not all harvestman species observed in the south and south-east regions. Towards the north-east, the number of gonyleptid species decreases sharply, and other, less speciose families increase in numbers of species

(Stygnidae, Escadabiidae, Kimulidae, and Zalmoxidae), especially north of Todos os Santos Bay, in northern Bahia. The region ranging from central Bahia to the state of Espírito Santo seems to represent a transition zone, where Gonyleptidae is still the dominant family, but with a lower relative importance.

Cosmetidae and Stygnidae, usually dominant families in Amazon harvestman communities (Pinto-da-Rocha & Bonaldo, 2006; Tourinho *et al*., 2014), were also important components of north-east sites, especially north of Todos os Santos Bay. Stygnidae occurs mainly in central America and northern South America (Pinto-da-Rocha, 1997), suggesting that its components need warmer conditions than those observed in the south, and south-east, where only two species are found, in its northern part. Thus, the larger-than-expected PDα, observed in the north-east, results from the composition of its species-poor communities, which include species in four or five families, some distantly related (i.e. the non-Gonyleptoidea families Zalmoxidae and Escadabiidae). In the coastal south-east, by contrast, communities include a greater number of species, but from only one or two families.

Species that belong to ancient and distant lineages tend to have a large impact on the PDα (Redding *et al*., 2008; Winter *et al*., 2013). In the case of north-east sites under investigation, the presence of these lineages may be related to the past historical connection between the northern AF and the Amazon forest, a pattern previously observed in other groups of organisms (Santos *et al*., 2007; Batalha-Filho *et al*., 2013; Prates *et al*., 2016). Besides, Cosmetidae, Zalmoxidae, and Escadabiidae species occur in areas that are drier and harsher (i.e. semiarid Caatinga biome) than those occupied by gonyleptids (see Kury (2003) for Gonyleptidae records). Some Cosmetidae species were also present in some of the dry, semi-deciduous forests sites from the interior of the state of São Paulo. Their presence there was responsible for the relatively higher PDα values than those observed for the south/south-eastern coastal sites.

Environmental conditions are certainly important in shaping the diversity patterns of harvestman species. As mentioned before, most harvestmen, and especially gonyleptids, are highly dependent on humidity (Santos, 2007). This is reflected on the species richness map: richness is highest in the wet southern and south-eastern coastal sites, a pattern consistent with previous observations by Pinto-da-Rocha *et al.* (2005).

The importance of climate may suggest that environmental filtering, a process usually associated with phylogenetic clustering, had an effect on the predominant pattern observed in our data. Environmental filtering would select species with certain physiological and/or ecological attributes, necessary to survive in their environment (Webb, 2000; Webb *et al*., 2002; Cavender-Bares *et al*., 2009). As those traits are often shared by closely related species, analyses would detect a clustering effect.

Our results however also offer evidence that environmental conditions may not be the preponderant factor acting on the observed diversity patterns. Sites from the north-east, north of Todos os Santos Bay, were characterised by a small number of species, similar to that observed in the drier interior, westernmost sites. It is important to note that the forests from those north-east sites are not as humid as the southern/south-eastern coastal forests (IBGE 1991); however, we believe that the differences observed in species richness far exceed the climatic differences between the regions being compared (Nogueira *et al.* in press), since the coastal north-eastern AF is still much more humid than the interior semi-deciduous AF.

In a study of the PDβ patterns of snake communities from the AF, Moura *et al.* (2017) found that the snake communities from the southern and south-eastern regions are more closely related than those from north-eastern Brazil, as observed for the AF harvestmen in our study. The authors suggested that the phylogenetic structure of AF snake assemblages may be constrained by the distribution of major snake lineages. Therefore, the differences in the 'biogeographic species pool' might explain why the snake assemblages in the southern AF are phylogenetically clustered, whereas those in the northern AF are overdispersed (Moura *et al*., 2017).

This phylogenetic diversity difference between northern and southern AF areas described for snakes also seems to apply to AF harvestmen. Even though our results were not significant, the PDα values obtained for communities from lower latitudes were higher than expected, while those from the south and south-east showed lower PDα values. This reflects the fact that the regional species pool changes according to the region (Fig. 5c). The northern AF has lineages that seem to be more distantly related from one another than those in the southern and south-eastern AF, where almost all compositional changes occur within one single family.

Northern snake communities however presented large taxonomic richness, unlike what was observed in our study. The higher temperatures and drier climate of the north-east are more suitable to cold-blooded reptiles (e.g. snakes) than to harvestmen, which are much more prone to water loss (Santos, 2007) and, as a consequence, present a smaller regional species pool.

Thus, this smaller biogeographic species pool in the north-east was most likely the factor limiting the total richness metrics. One explanation is that the AF covers a much larger area in the south and south-east regions than in the north-east, where it is but a narrow strip of about 50 km inlands, especially north of Todos os Santos Bay (Oliveira-Filho & Fontes, 2000). Moreover, the speciose family Gonyleptidae is not well represented in lower latitudes, as its members are more adapted to cold climates (Fig. 5c). In other places in South America, this family also has a large number of species in higher latitudes, for instance the Chilean humid temperate forests (Hara *et al*., 2012; Silva *et al*., 2013).

Our result differs from Boyer *et al.* (2016) for Australian mite harvestmen. PDα and taxonomic alpha diversity patterns were congruent, and both were positively associated with climate suitability during the last glacial maxima. We consider that this congruence between PDα and taxonomic alpha diversity may reflect the fact that Boyer *et al.* (2016) worked with a much smaller number of species (n = 24), all from a single genus, *Austropurcellia* (Pettalidae, Cyphophtalmi). Therefore, the species pool used in their study is much more homogeneous than the one in our study. Moreover, our study area is also much larger (approximately 3000 km N–S range) and heterogeneous than the Australian Wet Tropics (approximately 500 km N–S range), investigated by Boyer and collaborators, which probably also contributed to the larger variation in diversity measures observed in our results. Concerning beta diversity, the sharp differences observed in community composition were expected, owing to the extreme low vagility of Opiliones (Mestre & Pinto-da-Rocha, 2004). Most species have a very restricted distribution, which is reflected in the distributional record maps of taxonomic revisions (e.g. DaSilva & Gnaspini, 2009; Yamaguti & Pinto-da-Rocha, 2009; Bragagnolo & Pinto-da-Rocha, 2012 – also see Figure S13, Appendix S4), and their high degree of endemism. Indeed, 97% of the AF harvestmen are exclusive to this ecosystem (Pinto-da-Rocha *et al.*, 2005). As a consequence of this great replacement of species from site to site, total beta diversity was highly related to its turnover component, while nestedness was negligible.

The comparison between the beta diversity and PDβ in our data revealed some important and complementary results. While several works showed important similarities between those two metrics (Devictor *et al.*, 2010; Leprieur *et al.*, 2012; Arnan *et al.*, 2017), our results presented considerable differences. The location of the three northern categories is similar, especially in their coastal portion, where most of our data was collected. In the central south-east and in the south regions, however, there are marked differences, as categories in the different maps present different shapes and limits. Another interesting result can be observed in the southern portion of the AF, as this region is considered as one category by PDβ and as two by taxonomic beta. In this region, Gonyleptidae species represent the vast majority of species. Even though the region has several species-rich sites, there are few phylogenetic differences among them, since there are several related species in the species pool, some of which belong to the same clade. In other words, the compositional changes observed from one community to another, in this region, are enough to be reflected in the beta diversity measures, but they are not phylogenetically deep enough to produce important changes in PDβ.

In summary, our results indicate that the diversity measures of AF harvestmen were considerably influenced by the peculiar biogeography of this group. The impressive dominance of Gonyleptidae species in southern and most of south-eastern AF resulted in communities with species that are phylogenetically closer than those in the northern portion of the AF, on average. The comparison of species richness and PDα also revealed that some areas, despite having low richness, presented relatively large PDα values, which were due to the presence of distant lineages. PDβ results were also not very congruent with those from beta diversity, indicating that measures of taxonomic diversity may not be a good indicator of phylogenetic diversity and that this must be taken it account when planning conservation strategies (Rodrigues & Gaston, 2002).

This highlights the importance of comprehensive approaches to the study of biodiversity, including many and complementary measures of diversity. The phylogenetic diversity component may be of special importance in assessing the conservation value of distantly related lineages. These species-poor groups are less likely to influence taxonomic-based diversity analyses, and as such, their value to the ecosystems in which they reside may be overlooked if taxonomy alone is used.

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Authors' contribution

Data were collected by A.A.N., C.B., M.B.D., and R.P.R. L.S.C. did the analysis and made the figures, and also described these procedures in Methods section. A.A.N. wrote the manuscript. All the authors discussed the results. The work was conceived by R.P.R., C.B., and A.A.N.

Conflict of interest

The authors declare they have no conflict of interest.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Information on the study areas: location, number of harvestmen species and type of vegetation.

Appendix S2. Sites × species matrix.

Appendix S3. Harvestmen phylogeny and supplementary tables.

Appendix S4. Supplementary figures.

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