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Complete List of Authors:	Nogueira, André; Universidade de Sao Paulo, Zoologia Bragagnolo, Cibele; Universidade Federal de Sao Paulo, Departamento de Ecologia e Biologia Evolutiva daSilva, Marcio ; Universidade Federal da Paraiba Martins, Thais; Universidade Federal da Paraiba Lorenzo, Everton; Universidade Federal da Paraiba Perbiche-Neves, Gilmar; Universidade Federal de Sao Carlos Pinto-da-Rocha, Ricardo; Universidade de Sao Paulo
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Historical signatures in the alpha and beta diversity patterns of Atlantic Forest harvestman communities (Opiliones-Arachnida)

A.A. Nogueira¹, C. Bragagnolo², M.B. DaSilva³, T. K. Martins³, E. P. Lorenzo⁴, G. Perbiche-Neves⁵ and R. Pinto-da-Rocha¹

¹ Instituto de Biociências – Universidade de São Paulo, Departamento de Zoologia. Rua do Matão, travessa 14, 321, 005508-900, São Paulo, SP, Brazil.

² Departamento de Ecologia e Biologia Evolutiva , Universidade Federal de São Paulo, Rua São Nicolau, 210, 09913-030, Diadema, SP, Brazil

³ Departamento de Sistemática e Ecologia, Centro de Ciências Exatas e da Natureza – UFPB, Cidade Universitária, João Pessoa, PB, Brazil

⁴ Centro de Conservação e Manejo de Fauna da Caatinga, Campus Ciências Agrárias - UNIVASF, Projeto de Irrigação Nilo Coelho, Petrolina, PE, Brazil.

⁵ Centro de Ciências da Natureza, Universidade Federal de São Carlos, Rodovia Lauri Simões de Barros, km 12 - SP-189 - Aracaçú, Buri - SP, Brazil.

Corresponding author: andrearanhas@gmail.com

Abstract

The integration of ecological and historical biogeography is fostering the investigation of diversity patterns. We studied alpha and beta diversity patterns of Brazilian Atlantic Forest harvestman (Opiliones, Arachnida) 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, and 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, since every community presents a unique set of species.

Keywords

Richness, biodiversity, biogeography, community ecology, arachnids, Neotropical, harvestmen, Arachnida, Opiliones

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 and identifying the factors responsible for these patterns represents 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.

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 et al. 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 6° to 30° S (SOS Mata Atlântica and INPE 1993), the Atlantic Rain Forest also presents high latitudinal and altitudinal variation, 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 ruptures, Todos os Santos Bay and the São Francisco River.

Such large-scale studies on 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; BirdLife International et al. 2018; Buckley and Jetz 2007; Terribile et al. 2009; Sauer et al. 2014). 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,b*; Rodrigues et al. 2014) although there are exceptions (Dos Santos et al. 2008; Löwenberg-Neto et al. 2008).

Harvestmen (Opiliones, Arachnida) from the Atlantic Rain Forest may represent a good target group for large-scale diversity studies. Tropical harvestmen are nocturnal, hygrophilous animals, with a very poor dispersal capability (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 a very restricted distribution (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 in comparison to 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 to 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 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 areas of endemisms: 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 two Northeast areas of endemism were also recovered for harvestmen, but the topographically complex Southeast and South regions harbor 10 areas of endemism.

This more detailed response of harvestmen is probably due to their poor dispersal capability and heavy dependence on forested, humid habitats (Pinto-da-Rocha et al. 2007). Thus, harvestmen may provide more accurate information for biodiversity conservation, an urgent issue for the Atlantic Rain Forest, as only 12% of its original cover remains, most of it 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 of harvestman communities of the Brazilian Atlantic Rain Forest. More specifically, based on 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, due 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 areas of endemism delimited for Atlantic Rain Forest harvestmen.
- The percentage of protected areas for each area of endemism will be very unbalanced and areas located in the Southeast will be more preserved than areas located in the Northeast Brazilian.

Methods

Study area

Our study area is the Atlantic Rain Forest. We inventoried 63 sites (Supplementary table 1, supplementary material), which were spread across 11 states from three Brazilian regions: Northeast, Southeast and South. The latitudinal range is from 6°43' to 29°40', 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 kilometers towards the interior; semi-deciduous 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* (IBGE 1991).

Most 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 included four sites composed of ombrophilous mixed forest in the state of Paraná, nine sites from Atlantic Rain Forest semi-deciduous formations, and seven sites with dry tropical dense forest (*cerradão*), which represent an ecotone between Atlantic Rain Forest semi-deciduous 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), while 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 the supplementary material (Supplementary table 1).

Harvestman diversity data

Our data bank contains 508 species of Opiliones from 63 sites (Supplementary table 2, supplementary material). We restricted our analysis to the suborder Laniatores, which on average represents more than 90% of the total richness that is typically found in Atlantic Rain Forest harvestmen communities (Bragagnolo and Pinto-da-Rocha 2003; Bragagnolo et al. 2007; Resende et al. 2012*a,b*, Supplementary table 3, supplementary material). 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 (see Supplementary table 4 for information about sampling effort). The sampling method employed was nocturnal hand collecting, in which collectors investigate several microhabitats from the forest floor and the understory, and harvestmen are captured manually. The sampling unit represents one hour of searching by one collector in an area of approximately 300 m² (30 x 10 m), and 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 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 (6 species), which is a well-sampled site (82 samples) with similar geographical and environmental characteristics (sampling effort is presented in Supplementary table 4, supplementary material).

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 an average completeness of 91.6% ($n=28$) (Supplementary table 5, supplementary material).

Environmental variables

Environmental variables were obtained from the CliMond database (Kriticos et al. 2012). We extracted 28 variables, with a 30' resolution (Supplementary table 6, supplementary material). 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 meters).

Harvestman Areas of Endemism

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

Relationships between these areas of endemism 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 areas of endemism: one southern block (SC, PR and SSP – the names of the areas of endemism follow DaSilva et al. 2015) and one southeastern block (SMSP, Boc, LSRJ, Org and Mnt). The two northern areas of endemism, 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 areas of endemism, and 14 sites, which are located primarily in the interior of the country, are outside areas of endemism. Those 49 sites are located in 11 of the 12 areas of endemism, and one site (PARNA do Caparaó-MG) is within the boundaries of two areas of endemism (ES and SEsp) (Supplementary table 1, supplementary material).

Data on Conservation Units

To calculate the protected area of each area of endemism 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), and 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, while 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 area of endemism, 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 shows an advantage to the multiple linear regressions because it avoids the problem of the 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), and further 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, and the relations between compositional dissimilarities and explanatory variables are assessed through I-splines 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 Mikkelsen 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, the interpretation of turnover and boundary

clumping becomes less clear (Leibold and Mikkelsen 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 Mikkelsen 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 (Henrique-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 2016), and EMS was performed with the “metacom” package (Dallas 2016).

Results

Alpha diversity

Alpha diversity ranged from 2 to 57 species per site ($n=63$, mean 16.42 ± 13.4 species), and the average values varied considerably among different regions and forest types. The Northeast region presented smaller values ($n=13$, range 2 to 22, mean 6.9 ± 6 species) than the South ($n=11$, range 5 to 41, mean 16.3 ± 12.3 species) and Southeast regions ($n=39$, range 2 to 57, mean 19.6 ± 14.1 species). 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, mean 4.6 ± 2.5 species). The alpha diversity also decreased drastically in sites with semi-deciduous ($n=9$, range 5 to 14, mean

8.2 ± 3.6 species) and cerrado vegetation ($n=7$, range 2 to 7, mean 3.8 ± 1.6 species) in comparison to localities covered by evergreen forest. Ombrophilous mixed forest ($n=4$, range 6 to 13 mean 10.5 ± 3.1 species) and specially ombrophilous coastal forest ($n=43$, range 2 to 57 mean 20.7 ± 14 species) presented higher number of species, especially in some sites in the Southeast, in the Serra do Mar Mountain chain (Figure 1).

The PLS regressions filtered the effects of environmental variables on harvestman richness, and some trends emerged from these analyses, exhibited in the first four axes, which 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, and 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 (Figure 2) 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, 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, plus geographic distance. The most important variables were isothermality and geographic distance, 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%, by far the largest. Isothermality, a measure of temperature variation (mean diurnal temperature range – temperature annual range), was the most significant environmental variable, and turnover rates were higher between values of 0.6 and 0.65, separating coastal sites from sites inland (Figure 3).

EMS

The species composition of the different sites exhibited strong variation, especially when considering communities from sites in different areas of endemism. 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 three or fewer sites, while only eight species occurred in at least ten sites. Not surprisingly, the species with the largest distribution (25 sites), *Mischonyx squalidus* Bertkau, 1880 (Gonyleptinae, Gonyleptidae), is one of the few widespread harvestmen from the Atlantic Rain Forest. *M. 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 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 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, which have few species in common with other groups of sites. The turnover process is probably occurring between sites within the same areas of endemism, with few species in common between different areas of endemism.

The groups of sites formed are remarkably consistent with the areas of endemism delimited for the Atlantic Rain Forest (Figure 4). Only two exceptions were observed: PET do Alto Ribeira, which belongs to the SSP area of endemism, an area associated with other southern areas of endemism, PR and SC, and which was placed among sites that belong to areas of endemism from the southeastern clade (Figure 4); and the Reserva Natural da Vale, placed with sites from the ES area of endemism, although it belongs to the BA area of endemism.

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 & B. A. Soares, 1946, *Metagonyleptes calcar* [Sundevall](#), 1833 and *Parapucroliia ocellata* [Roewer](#), 1917 (all Gonyleptidae), are shared between these two groups of sites. However, the composition of the sites of central/southern BA 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 an average of 84.2% of the total number of species in southern and southeastern localities. At

sites in central/southern Bahia, gonyleptids accounted for an average of 66.7% of the total species, and 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 concerning the proportion of protected forest for each area of endemism are presented in Table 2. Areas of endemism from the Southeast region were the most protected, including two areas of endemism (SSP and Boc) that were completely protected. Those values are much smaller in the Northeast areas of endemism, and for the ES area of endemism, the proportion of protected forest represents only 1% of the total area.

Discussion

Due to the coverage of our dataset, 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 capability 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 two last, 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 semi-deciduous 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 to be semi-deciduous 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 was higher in the wet summer than in the dry winter, in 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. We consider that it is due to the fact that the species-poor Northeast region has a dry winter, which means that the warmest period coincides with the dry season, in opposition to what is observed in the species-rich South and Southeastern region, 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, although it had a small negative effect, the reason for which is not clear. Places with large altitudinal range, usually mountainous regions, are considered to be the most species-rich places on Earth (Orme et al. 2005; Rahbek 2005). Mountains may increase alpha diversity indirectly, via influences on the regional climate. When located near the coast, mountains generate orographic rainfalls, which help to create and maintain a moist habitat, with optimal climatic conditions for harvestmen. A large altitudinal range may also be related to alpha diversity via another factor, 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, acting as forest refugia (Haffer 1987; Carnaval et al. 2014). Therefore, biological communities from these regions may have lower extinction rates, being 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, as Atlantic Rain Forest harvestman species appear to be much older than Pleistocene refugia (Bragagnolo et al. 2015). Still, due 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 areas of endemism of Bahia and Pernambuco. This study failed to find evidence of refugia in the Southeast, but the authors acknowledged that their models might not be appropriate for areas with steep environmental gradients, as is the case in the South and Southeast regions. Those authors listed evidence from other studies concerning the persistence of forested areas in those regions. Haffer (1987) claimed that orographic rains 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 areas of endemism from the South and Southeast region.

The association between potential refugia and high species richness is observed in our coastal South and Southeastern sites, but not for the species-poor Northeast sites, especially those from the PE area of endemism. 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 to be semi-deciduous 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 semi-deciduous forest (6.9 and 8.2, respectively), although it has a larger average annual

precipitation and moisture (Northeast sites: annual precipitation = 1602.7 ± 286 , mean annual moisture index = 1.01 ± 0.1 ; semi-deciduous forest sites: annual precipitation = 1390.1 ± 224 , mean annual moisture = 0.89 ± 0.9). This suggests the influence of other factors, probably related to the historical aspects.

The large variation in altitudinal range observed in the South and Southeast may be indirectly linked to the large number of species found in these regions. A complex topography indicates a complex geomorphological history, and 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* 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 South and Southeast harvestman fauna. The possible influence of historical factors on the differences between Northeast and South/Southeast fauna also seems to be confirmed by important changes in the 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 semi-deciduous forest, or the Northeast sites, communities would be composed of subsets of species from more diverse sites. However, communities are very different, sharing 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 databank, *Mischonyx squalidus*. The EMS also detected a significant turnover, 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, sorting out sites from the inland semi-deciduous forests, from 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 semi-deciduous forests, as 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 species biology.

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 best models, as 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 about 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 meta-community 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. Figure 4 shows the congruence between groups of sites formed with the areas of endemism, which represents a strong historical effect on Atlantic Rain Forest harvestman patterns of beta diversity. So, the turnover process is probably more gradual between sites from the same area of endemism and steeper when involving sites from different areas of endemism.

The most abrupt changes were observed between areas south and north of the Doce River and between sites in the Bahia and the Pernambuco areas of endemism. Similar ruptures in species distribution are also recognized in other taxa, highlighting the importance of the Doce River region as an effective barrier (Amorin and Pires 1996; Silva et al. 2004; Silva et al. 2012). The separation of the biotas from the Bahia and Pernambuco areas of endemism occurs in the region of the São Francisco River, in which the historic climatic model supported the 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 (Amorin 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, while 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 that 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 area of endemism than to those of the southern/central 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/south 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 those two 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 (Batalha-Filho et al. 2013; Prates et al. 2016; Santos et al. 2007).

As mentioned before, the great reduction in the speciose family Gonyleptidae in the Northeast region impoverishes its communities and may contribute to explaining 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 areas of endemism, ranging from 1 to 100%. The best preserved areas of endemism, including two areas of endemism fully protected (Boc and SSP, Table 2) were located in the Southeast, 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 due to 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.

Inversely, the two areas of endemism with the flattest topography have the smallest proportion of protected area, PE and ES. With only 1% of protected area, ES harbors 55 species, 38 (69%) of which are exclusively from this area of endemism. As the region is already heavily deforested (Figure 1S-g, 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 area of endemism is also very small, corresponding to only 4.5% of the size of this area of endemism. The opilological fauna from the PE area of endemism contains the fewest species, only 11, but also represent a unique fauna, since only two of these species also occur in other area of endemism. As also observed for the ES area of endemism, the region is heavily deforested (Figure 1S-f, supplementary material of Ribeiro et al.

2009). The region received the first Portuguese colonizers, which started large-scale deforestation and agricultural expansion (Dean 1997).

The situation of the PE area of endemism is even worse, if we consider that only 0.4% of its total area is classified as full protection, and the rest is under the more permissive sustainable use regime. In most areas of endemism, the amount of area under full protection is smaller than the sustainable use (47% in average, but if we exclude the two areas with a 100% protection, the average 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, as it may contain much degraded habitat, as rural and agricultural areas. Considering this, increasing the proportion of full protection areas could also be an important recommendation for conservation policies.

Finally, the SC area of endemism was the least protected among the 10 South/Southeast areas of endemism, with only 8% of area located in conservation units. Bergamin et al (2015), 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 semi-deciduous forest, as they are less represented in the Atlantic Rain Forest reserve network than ombrophilous coastal forest.

A final recommendation concerning conservation in a broader way would be the creation of a large number of reserves, spread across large areas and different regions, which would be important due to the restricted distribution of most species. We thus agree with Baselga (2010), which claim that when turnover is the main process observed in compositional changes, conservation efforts should be placed in the creation of a large number of different sites, not necessarily the richest ones.

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. As a consequence, sites from the South/Southeast region, 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 areas of endemism 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/Southeastern sites, are ombrophilous formations, but had a similar number of species to the much drier semi-deciduous 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.

Concerning conservation, our study indicates that the protection of Atlantic Rain Forest harvestman diversity in public reserves varies a lot between the different areas of endemism, which indicates that their communities are not fully protected, as the intense turnover process observed results in a unique set of species for each area of endemism, with few species in

common. The least protected areas are the PE and specially ES areas of endemism. With respectively only 4.5 and 1% of their areas preserved, these localities would be obvious priority choices for the creation of reserves, preferably in the full protection category.

Due to the turnover process observed in our data, the creation of as many reserves as possible, within all the areas of endemism 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 ecological and historical biogeography, a useful and necessary way to understand and protect biodiversity, especially in a very endangered hotspot like the Atlantic Rain Forest.

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Conflict of interest

The authors declare they have no conflict of interest

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Tables

Table 1 – Result of the GDM performed for each geographic division. We present the significant variables for each division, and those selected by the best fitted model, as well as its coefficient sum and the proportional deviance explained by its variables.

Significant environmental variables (coefficient sum > 0)	Significant variables of best fitted models (coefficient sum)	% explained deviance of fitted models with geographic distance and environmental variables (variables of model)
bio0, bio03, bio07, bio35, alt.ran	dist.geo. (25.02)	61.39% (dist.geo+bio01+bio03+bio35)
	bio01(0.942)	60.35% (dist.geo+bio01+bio03)
	bio03(1.89)	58.56% (dist.geo+bio03)
	bio07(0.54)	
	bio35(1.19)	

Variables description: Bio 1- Mean annual temperature; Bio 3 – Isothermality; Bio 7 – Temperature annual range;

Bio 35 – Mean moisture index of coldest quarter; alt.ran. - Altitudinal range of the region (within a 5 km radius)

Table 2 – Area (in hectares) and percentage of protected forests by areas of endemism (AoE) of Atlantic Rain Forest (according to DaSilva et al. 2015). Protected forests were considered federal and state conservation units according National System of Conservation Areas of Brazil (parks, reserves, ecological stations, etc), divided in full protection areas (FP) and sustainable areas (SU) – the former have more preserved forests generally. PE: Pernambuco, BA: Bahia, ES: Espírito Santo, SEsp: Serra do Espinhaço, Mnt: Serra da Mantiqueira, Org: Serra dos Órgãos, Boc: Serra da Bocaina, LSRJ: South litoral of Rio de Janeiro, SMSP: Serra do Mar of São Paulo, SSP: South of São Paulo, PR: Paraná, SC: Santa Catarina.

AoE	Area (Ha)	Forestal area ¹	FP area	SU área	Protected area	% 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 ²	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 ²	137,613	-	137,613	-	137,613	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

¹ Part of PE and BA areas of endemism are covered by Caatinga shrublands.

² Those areas of endemism were delimited according to the limits of full protection conservation unit

Figures captions

Fig 1 – Map of South America, with the study region enlarged. The 63 studied sites are represented by circles, and the color of the circle indicates the number of species by site, increasing from yellow to red. Map from Diva-Gis (Hijmans et al. 2001)

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, B. First (black line) and second component (red line), C. First (black), second (red) and third component (green line), D. First (black), second (red), third (green) and fourth (blue line) components. Variable abbreviations: Isother – isothermally; MtempWetq – mean temperature of the wettest quarter; PrecWetW – precipitation of the wettest week; PrecWarQ – precipitation of the warmest quarter; MoisIS – moisture index seasonality; AltRan – altitudinal range.

Fig 3 – Results of the generalized dissimilarity modeling (GDM) a) Fit of the model. Relationship between compositional dissimilarity between all pair, and the predicted ecological distance of these pairs, estimated by the GDM function; b-e The fitted function of: b) the index of geographic distance, c) annual mean temperature, d) isothermality and e) mean moisture index of coldest quarter

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 of Atlantic Rain Forest harvestmen. Numbers indicate the five major areas

groups (modified from DaSilva, M.B., Pinto-da-Rocha, R., and Morrone, J.J. Historical relationships of areas of endemism of the Brazilian Atlantic rain forest: a cladistic biogeographic analysis of harvestman taxa (Arachnida: Opiliones). *Current Zoology*, 2016, **63**(5): 525-535, by permission of Oxford University Press). c) Legend indicating the Areas of Endemism that belong to each group, and the color by which the groups are represented in the matrix displayed in “a”

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169x66mm (300 x 300 DPI)

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