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Fungal perspective on neotropical biogeography: poroid fungi (Agaricomycetes: Hymenochaetales and Polyporales) and the Brazilian moist forests

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ABSTRACT

Biogeographical analyses using species lists of wood-inhabiting, poroid Hymenochaetales and Polyporales were performed to infer the relationship of major Neotropical morphoclimatic domains: Amazon, Atlantic and Caatinga moist forests. Parsimony analysis of endemicity, UPGMA clustering and NMDS ordination were computed with data of 18 localities and 245 species, all indicating that the northern Atlantic Forest is more related to the Amazon than to its southern portion. Also the results agree with the hypothesis that the Brejos Nordestinos is a distinct biota from both the Amazon and Atlantic Forest. Annual temperature and rainfall are strongly related with the resulting NDMS site scores. A distance similarity decay of similarity analysis suggests a moderate to low, but statistically significant, influence of the geographic distance on assemblages' composition. The limited distribution of many poroid fungal taxa also emphasizes the fragility of these organisms to habitat loss.

1. Introduction

In Brazil lie major areas of the two largest American tropical forests: the Atlantic and Amazonian forests (Fig. 1). The Atlantic Forest occurs on the east coast of Brazil, stretching towards Argentina and Paraguay in the southern region. The Atlantic Forest is separated from the Amazon by seasonally dry vegetation, the Cerrado in central and the Caatinga in northeast Brazil (Veloso et al., 1991). Based on a compilation of distribution data of several taxa, Silva and Castaleti (2003) divided the Atlantic Forest morphoclimatic domain into eight ecoregions: Araucaria Forests, Bahia, Diamantina, Interior Forests, Pernambuco, Brejos Nordestinos, São Francisco and Serra do Mar. The Brejos Nordestinos are moist forest patches inside the Caatinga domain, but still thought to be part of the Atlantic Forest biota. Similarly, the Amazon (Cracraft, 1985; Silva et al., 2005) is also divided in eight ecoregions (Belém, Guiana, Imeri, Inambari, Napo, Rondônia, Tapajós and Xingu), all of them, at least partially, in Brazil.

Several hypotheses concerning the biogeographic and historical relationship of these forests have been postulated and tested based on the occurrence of various organisms (e.g., Andrade-Lima, 1982; Costa et al., 2000; Costa, 2003; Silva and Castaleti, 2003; Quijada-Mascareñas et al., 2007; Santos et al., 2007; Fouquet et al., 2012). Each taxon responded differently to the climate change since the end of Pleistocene, when these forests were a continuum, due to

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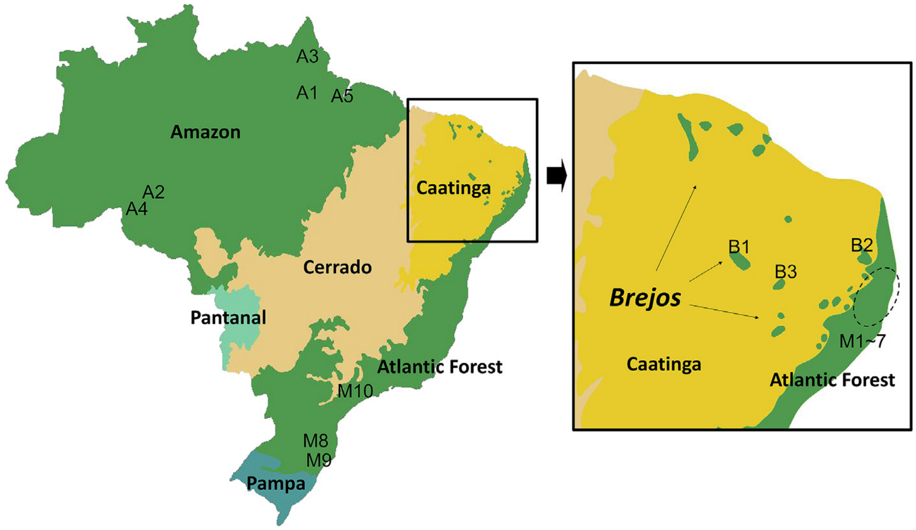

Fig. 1. Map of Brazil showing the six morphoclimatic domains. Codes show the location of the study sites included in the analyses (see Table 1).

physiological properties and dispersion limitations. However, most results confirmed the previous connection between the Atlantic and Amazon forests and the heterogeneity of the Atlantic Forest, and also that the Brejos Nordestinos is a single biogeographic unity. Nevertheless, little to nothing is known about the biogeographic relationship of microrganisms and fungi and how they responded to climate properties and historical events that shaped these neotropical ecosystems.

Inventories of poroid fungi are being successfully used to address issues such as conservation biology, and the ecological and biogeographical relationship of ecosystems in temperate regions (e.g., Heilmann-Clausen et al., 2014; Runnel and Lõhmus, 2017; Ordynets et al., 2018). Poroid fungi are a morphological group of Agaricomycetes that produce macroscopic structures for sexual reproduction (basidiomata), most of them known as bracket fungi, in which fertile elements are arranged in tubes whose openings in the underside give a porous appearance. Around 80–90% of the poroid fungi are classified in Polyporales and Hymenochaetales, representing around 2300 species of the about 21,000 species of Agaricomycetes (Kirk et al., 2008). They are decomposers of cellulose and hemicellulose, and the only organisms capable of decomposing lignin efficiently, thus have a key role in nutrient cycling (Deacon, 2006).

Bio- and phylogeography of fungal taxa have been accessed previously (e.g. Wu et al., 2000; Hibbet, 2001; Jeandroz et al., 2008; Moncalvo and Buchanan, 2008; Matheny et al., 2009; O'Donnell et al., 2011; Heilmann-Clausen et al., 2014; Tedersoo et al., 2014), but still little is known in the neotropical region. Gibertoni et al. (2015) compared the distribution of poroid fungi between the Northeast Atlantic Forest and Caatinga (Brejos Nordestinos) and among endemism centres in the Brazilian Amazon (Gibertoni et al., 2016). Both papers showed little or no difference among the ecoregions, and low similarities among sampling units. Salvador-Montoya et al. (2015) reported the disjunct distribution of a mostly parasitic poroid Hymenochaetaceae species in South American seasonal dry forests (Caatinga, semideciduous and semidecidous Atlantic Forest and and lowland seasonally dry Peruvian forests). In our study we test if the distribution of free-living wood-inhabiting poroid fungi occurring in major neotropical moist forests is related to morphoclimatic domains and also to their subregions, previously proposed based on the occurrence of other organisms. Additionally we infer which are the primary constraints for neotropical poroid fungi occurring in moist forests, correlating climatic and geographical factors to their observed distribution.

2. Materials and methods

The study areas are listed in Table 1. The specimen sampling and identification followed the usual methodologies for the group (Lindblad, 2001; Gibertoni et al., 2007; Gibertoni, 2008): excursions were undertaken in the Amazon (5 fragments), Atlantic (7) and Caatinga (3) moist forests (Fig. 1; Table 1) (for more details see Gibertoni et al., 2015, 2016). The fragments were visited several times during the dry and rainy seasons, and all resupinate and pileate wood-inhabiting poroid fungi were collected in at least one transect delimited in each area. Also, data from poroid fungi in the southern portion of the Atlantic Forest were added to the study: one fragment of Araucaria Forest ecoregion (Westphalen and Silveira, 2012, 2013) and two of Interior Forest ecoregion (Westphalen et al., 2010; Motato-Vásquez and Gugliotta, 2014; Motato-Vásquez et al., 2015). All fungal names were consulted in the on-line databases Index Fungorum (http://www.indexfungorum.org) and MycoBank (http://www.mycobank.org) to avoid taxonomic inconsistencies which may affect the statistical analyses. Only species of Polyporales and Hymenochaetales occurring in dead wood were included in the analyses, resulting in 245 species (supporting data). For the sake of simplicity, any subdivision within a morphoclimatic domain is named ecoregion.

Climatic variables (minimum temperature, maximum temperature, average temperature and rainfall) were acquired from the 2.5 min resolution WorldClim version 2 data (Fick and Hijmans, 2017). Latitude, longitude and elevation values were recorded using a GPS device or acquired in the literature (supplementary data).

A data matrix of presence (1) and absence (0) of the species in each study area was constructed. All statistical analyses were performed in the statistics platform R (R Core Team, 2016), using the *phangorn* (Schliep, 2011), *pvclust* (Suzuki and Shimodara, 2015) and *vegan* (Oksanen et al., 2016) packages functions. The functions settings were default unless stated otherwise.

An UPGMA clustering (function *pvclust,* package *pvclust*) was performed with a dissimilarity matrix (Jaccard's index) of the raw data. The *pvclust* function also provides an approximately unbiased *p*-value (AU) computed by a multiscale bootstrap re-sampling. Values closer to 100 indicate a strongly supported clade. Bootstrapping was performed with 10,000 re-samplings.