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Diversity and Distribution of Ectomycorrhizal Fungi from Amazonian Lowland White-sand Forests in Brazil and French Guiana

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ABSTRACT

White-sand forests are thought to host many ectomycorrhizal fungi, as demonstrated by the numerous fruiting body collections made by Rolf Singer in the lower Rio Negro in the late 1970s. Despite recognition of the importance of ectomycorrhizal fungi in white-sand forests, there has not yet been a systematic examination of diversity and taxonomic composition across white-sand forests, or more widely across lowland Amazonian forests. In an effort to broaden our view of ectomycorrhizal fungal diversity and distribution on white-sand forests, we collected ectomycorrhizal fruiting bodies in 10 plots of white-sand forests in Brazil and French Guiana between 2012 and 2014. We collected 221 specimens and 62 morphospecies, from the 10 plots, confirming that all studied white-sand forests host ectomycorrhizal fungi. Additionally, we searched for taxa associated with white sands among specimens deposited in Brazilian herbaria. We report 1006 unique ectomycorrhizal specimen records in 18 Brazilian herbaria, of which 137 specimens and 64 species are reported from white-sand forests, mainly in the state of Amazonas, Brazil. Russulaceae and Amanitaceae were frequent in all habitats, and *Cortinarius* were more frequent on white sands. Our results highlight the high diversity and heterogeneity of ectomycorrhizal communities on white-sand forests, and the wide distribution of ectomycorrhizal fungi throughout Brazil, irrespective of soil type.

Abstract in Portuguese is available with online material.

Key words: Amanitaceae; Boletaceae; *campina*; *campinarana*; Herbarium; Russulaceae.

WHITE-SAND AREAS FROM THE AMAZON BASIN HAVE BEEN EXTENSIVELY INVESTIGATED TO UNDERSTAND THEIR FORMATION, isolation, and the peculiar flora they host. Compared to plant communities growing on *terra firme* soil, a typical clay-rich soil from the Amazon, white-sand forests are often less productive (they have two-third less biomass than *terra firme* forests; Baraloto *et al.* 2011) and less diverse (Damasco *et al.* 2013), but this is off-set by their high endemicity related to adaptations to drought and to their peculiar substrate (Fine *et al.* 2010). Indeed, white-sand soils are nutrient-poor, the result of high drainage and high acidity, and are mentioned as among the poorest soils in the world (Janzen 1974). As a consequence, much research devoted to them has focused on root morphology, for example, thickness of root mats in white sands (Stark & Jordan 1978), or plant mineral nutrition, for example, the importance of root symbioses in this environment (Luizão *et al.* 2007, Mardegan *et al.* 2009).

It is known that in tropical forests, trees can form an association with several mycorrhizal fungi, and obtain water and nutrients in exchange for some of their photosynthates (Smith & Read 2008). This association can be either with members of Glomeromycota, leading to vesicular-arbuscular mycorrhiza (VAM), or with Ascomycota and Basidiomycota, leading to ectomycorrhiza (Smith & Read 2008). According to our present understanding, ectomycorrhizal (EM) diversity shows a unimodal distribution centered in the temperate zone (Tedersoo & Nara 2010, Tedersoo *et al.* 2012), and EM symbioses are relatively rare in the Neotropics, or at least detected in only a few habitats (Becerra & Zak 2011, Bâ *et al.* 2014). According to the numerous observations of EM fungi reported from the Rio Negro by Singer and Araújo (1979), white-sand forests may constitute an exception to this pattern (Singer *et al.* 1983). Based on Singer and Araújo's (1979) pioneering survey, Singer (1988) hypothesized that on white sands, EM fungi conferred to their host the ability

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to acquire more nutrients and water than plants involved in other symbioses, and, hence, EM symbioses were more prevalent on white sands than elsewhere in the lowland Amazon.

Although several plant-related studies refer to Singer and Araújo's results (1979), recent studies investigating global patterns of EM fungi diversity (treated as species richness) omitted Amazonian white-sand ecosystems, and only included data from EM sampling of highly specialized monodominant *Dicymbe* (Fabaceae: Caesalpinioideae) forest in Guyana (Janzen 1974, Henkel *et al.* 2002, 2012, Henkel 2003, Smith *et al.* 2011, 2013) and *Nothofagus* forests in Argentina as representative of the Neotropics (Tedersoo *et al.* 2012). That said, Tedersoo and Smith (2013) recognized that EM associations in the tropics remain understudied, and numerous observations on roots have revealed puzzling plant-fungi associations in the Neotropics, such as 'cicatrizing' ectomycorrhiza described by Singer and Aguiar (1986), the occurrence of Basidiomycota mycelium on roots in the Mata Atlântica (Andrade *et al.* 2000), or unidentified structures on tree roots in French Guiana (Béreau & Garbaye 1994, Béreau *et al.* 1997). A recent review from Becerra and Zak (2011) provides a list of all known EM host plants for the Neotropics, although there exist many more host plant observations scattered in the literature. A case in point is the checklist of EM fungi from southern Brazil (Sulzbacher *et al.* 2013b), which reports only potential hosts, but does not confirm any of the associations.

Although studies of EM associations in Neotropical lowlands have been comparatively meager, they provide evidence that EM communities exhibit low diversity (Haug *et al.* 2005, Tedersoo *et al.* 2010b), and that EM fruiting bodies are not restricted to Amazonian white sands. In the Guyana sandstone highlands, ongoing long-term surveys have unraveled the diversity of EM fruiting bodies associated with *Dicymbe corymbosa*, *D. altsonii*, and *D. jenmanii* (Fabaceae: Caesalpinioideae), *Aldina insignis* (Fabaceae: Papilionoideae), and *Pakaraimaea dipterocarpacea* (Dipterocarpaceae), which locally dominate the forest (Janzen 1974, Henkel *et al.* 2002, 2012, Henkel 2003, Smith *et al.* 2011, 2013). To date, researchers have found 174 EM species across 17 families and 31 genera (Henkel *et al.* 2012; list available at http://tropicalfungi.org/wp-content/uploads/UPDATED-Total-Taxa-List-4-11-13.pdf). In Brazil, since Singer and Araújo's inventories (1979), and besides the recent description of *Sarcodon atroviridis* (Komura *et al.* 2015) and *Amanita tenacipulvis* from white-sand forests (Wartchow 2015), EM fungi have been reported mainly outside of white sands. Up to 144 EM species have been recorded from sand dunes and plantations in the South (Trierveiler-Pereira & Baseia 2009, Sulzbacher *et al.* 2013b) and nine species were described from Mata Atlântica and arid habitats in the Northeast (Menolli *et al.* 2009a,b, Wartchow *et al.* 2009, 2012, 2013, Wartchow & Cavalcanti 2010, Coimbra *et al.* 2012, Sá *et al.* 2013a). It is of interest that most studies on EM fungi in the Neotropics continue to uncover species new to science, especially in dry ecosystems.

Given the aforementioned numerous recent publications, of mostly individually described species on various forms of white sands, we consider it times for a reassessment of the hypothesis that white-sand forests host more EM symbioses and species than other ecosystems in the Amazon. As Peay *et al.* (2010) point out, EM fungi are "not everywhere" and EM communities are shaped by isolation and distance (Peay *et al.* 2007). Prance (1996) hypothesized that high levels of endemicity of angiosperms found in white-sand forests may be explained by allopatric speciation between islands of these forests scattered in the Amazon. In an analogous manner to plants, allopatric speciation between white-sand forests may contribute to a high level of EM endemicity.

Until now, morphological and molecular comparisons of Singer's original collection of fungi with recently described species from Brazil and Guyana were limited by poor conservation conditions in herbaria. Moreover, few sequences are available on public databases for Brazilian EM fungi: 278 sequences can be found on Genbank, representative of only a few genera, that is, *Cantharellus* (2), *Suillus* (2), *Boletinellus* (3), *Tulasnella* (25), *Sebacina* (97), and *Ceratobasidium* (149), the latter three genera were isolated from orchid roots (search on GenBank on 28/02/2015, http://www.ncbi.nlm.nih.gov). Morphological observations are essential given the lack of sequences available for barcoding comparison of specimens. Comparison of Singer's original descriptions with more recently described specimens will allow us to test if taxa are specifically associated with white sands, or rather generalist, possibly endemic or rather widespread in the lowland Amazon.

One method to assess if EM fungi are more diverse on and specifically associated with white sands is to compare not only specimens but communities, described by standardized inventories, between distant white-sand forests. Remote sensing methods that estimate biomass and map land cover types (Saatchi *et al.* 2000, Saatchi *et al.* 2011) have facilitated location of forests on white sands (representing only 3% of the Amazon lowland - Ter Steege *et al.* 2000), identifiable because they have lower canopy height than forests on *terra firme* soils. Another method is to draw a synthesis from the recent published literature on EM species from Brazil, an approach previously applied in Southern Brazil (Sulzbacher *et al.* 2013b). Although the wealth of specimens deposited in collections are an excellent and underexploited data source (Brock *et al.* 2009), only a small subset of specimens housed in herbaria forms the basis of publications. For Brazil, the Virtual Herbarium of Plants and Fungi presently integrates about 178,000 records for fungal specimens through the *specie-s*Link network (http://www.splink.org.br/), provided by 19 biological collections; 17 from Brazil and two from North America. Although the data need to be carefully reviewed and there are few geographical coordinates, they can serve, among other uses, as the basis for checklists and species distribution maps, as emphasized by Braga-Neto *et al.* (2013).

In this age of molecular barcoding, studying species distribution from specimen descriptions might be objected to as lacking scientific rigor in terms of data quality or quantity. However, this seems to be less problematic for EM fungi, because most EM fungi produce visible fruiting bodies (Tedersoo *et al.* 2010a) and their morphology is rather conserved, at least at the genus level (Singer 1986). As several genera show a worldwide distribution, mycologists have readily observed and recognized EM genera, and deposited specimens in Brazilian herbaria, awaiting more precise determination by specialist taxonomists. Additionally, as the ability to form ectomycorrhiza is rather conserved at the genus level (Tedersoo *et al.* 2010a, Tedersoo & Smith 2013), even specimens deposited and identified as "*Cantharellus* sp.", for instance, can provide information about the distribution, diversity and potential hosts of EM fungi.

Our objective in writing this paper is: (1) to re-evaluate the hypothesis that EM fungi are more diverse on and specifically associated to white sands; and (2) to provide an update on the diversity and distribution of EM fungi in Brazil based on field inventories along the Rio Negro and in French Guiana, and on records of specimens deposited in herbaria. We draw a first sketch of EM fungi distribution in Brazil, and more specifically on white sands in the Amazonian lowlands, and illustrate how treasure troves provided by recent on-line herbaria databases may be usefully exploited.

METHODS

DIVERSITY OF EM FUNGI ON WHITE-SAND FORESTS BASED ON FIELD INVENTORIES.—*Site location and description.*—All white-sand forest sites were located on hydromorphic spodosols, characterized by fast drainage and high acidity. We investigated four sites of white-sand forests close to Manaus, along the Rio Cuieiras, Amazonas, Brazil. We visited these sites either in April 2012 or August 2014 (Table S1), and selected them based on Landsat maps, which delimited areas having low canopy trees close to *terra firme* plateaus. Our sites were 10–20 km distant from Singer's original collecting site described on herbarium specimen labels as "road Manaus-Caracaraí" (Fig. S1). We collected fruiting bodies along transects from *Igapó* forest limits (flooded at the time) to the edge of *terra firme* plateaus. In the field, we identified *campinarana* and *campina* by their sandy soil, and the presence of characteristic plants, such as *Attalea* spp. (Arecaceae; Jirka *et al.* 2007), *Pagamea duckei* (Rubiaceae; Anderson 1981), *Protium heptaphyllum* (Burseraceae; Anderson 1981), and dominant trees, such as *Aldina heterophylla* (Fabaceae: Papilionoideae; Anderson 1981). We characterized *Campina* by a lower canopy compared to *campinarana* (<15 m). Additionally, we visited six sites from March to July 2014 in French Guiana (Table S1). The study forests are well delineated and were previously studied by Baraloto *et al.* (2011). In contrast to Brazilian sites, French Guianan white-sand forests do not occur close to *igapó* forests. All studied French Guianan sites were located along the coast, from Kourou to the border of Suriname, and unlike white-sand forests in Northeast Brazil, they do not grow on sand dunes. White-sand forests in French Guiana may have a different origin from the *campinaranas* around Manaus; whatever the origin, they share at least several features: low diversity (richness), are often dominated by Fabaceae, have a low canopy, and many plants are sclerophyllous (De Granville 1988).

Field inventories and specimen identification.—In Brazil, we collected fruiting bodies from 200 m × 100 m (2 ha) plots on white-sand forest. Eleven collectors carefully inspected each plot during 1 d, and collected all fruiting bodies. In French Guiana, we collected fruiting bodies along a trail 2-km long at three sites: Awala-Yalimapo, Amana PK181 and Mana. Three collectors followed each trail during 1 d. We collected fruiting bodies 5 m from the trail on each side (resulting in 2000 m *10 m = 2 ha plots). As in Brazil, three collectors investigated 200 m × 100 m plots during 1 d in Kourou, Laussat, and Paracou. For each plot, we recorded the occurrence of putative Neotropical EM hosts, as described in the literature (synthesized in Becerra & Zak 2011, Table S1), and herbarium vouchers were deposited in CAY and INPA for French Guianan and Brazilian sites, respectively. Morphological characters allowed identification of fruiting bodies to genus and the EM condition was assumed if the genus was previously recorded as such (Singer 1986, Tedersoo *et al.* 2010a, Tedersoo & Smith 2013). We distinguished morphospecies in the field, and compared them between plots. Specimens were dried slowly in a fruit dehydrator, and later preserved in silica gel. Brazilian specimens were deposited at INPA and duplicates sent to FLOR. All herbarium acronyms follow the Index Herbariorum (Thiers, [continuously updated]). French Guianan specimens are stored at the EcoFoG lab, Kourou, and will later be deposited at PC. Whenever possible, we identified fungi to species based on morphology and published descriptions (*e.g.,* Pegler & Fiard 1983, Singer 1986, Henkel *et al.* 2012, 2014, Sá *et al.* 2013b).

Diversity and similarity of EM communities on white sand.—In their published studies, Singer and Araújo (1979) and Singer and Aguiar (1986) do not provide complete datasets from which their results are drawn, and only a list of species (species richness data) is available. All the following statistical tests were performed on R 1.65 (http://www.R-project.org/). To measure EM community diversity, distinct morphospecies were listed per plot (*e.g., Lactifluus* sp. 1, *Lactifluus* sp. 2). Species accumulation curves were drawn for collections from the Rio Cuieiras region and French Guiana using the specaccum function in vegan (Oksanen *et al.* 2013). The differences in species richness and Chao estimates between French Guianan and Rio Cuieiras plots, and between *campina* and *campinarana,* were compared using Mann–Whitney tests. The effect of geographical distance on community similarity (estimated by Bray-Curtis distances) was tested by a Mantel test (999 permutations). The similarity between communities was visualized by non-metric multidimensional scaling (NMDS), and the effect of forest type (*campina*/*campinarana*) and region (French Guiana/Rio Cuieiras) was tested using an Adonis test in R.

DIVERSITY OF EM FUNGI ON WHITE SANDS BASED ON HERBARIUM RECORDS.—*EM specimens deposited in Brazilian herbaria.*—We searched in herbarium databases for putative EM genera that may have been collected in Amazonian lowlands and for which the EM condition is phylogenetically conserved; that is, all or nearly all, species known are EM (Tedersoo *et al.* 2010a, Tedersoo & Smith 2013). We included genera treated as EM in Brazil according to the recent review of Sulzbacher *et al.* (2013a). In our study we queried only Basidiomycota, as these are more readily observable and, hence, sampled than Ascomycota. In our survey of herbarium specimens, we targeted 63 genera: *Albatrellus, Amanita, Amphinema, Austroboletus, Austropaxillus, Bankera, Boletellus, Boletinellus, Boletus, Byssocorticium, Calostoma, Cantharellus, Ceratobasidium, Clavariadelphus, Clavulina, Coltricia, Coltriciella, Cortinarius, Craterellus, Durosaccum* (a synonym of *Pisolithus*), *Fistulinella, Gautieria, Gloeocantharellus, Gyrodon, Gyroporus, Hebeloma, Hydnellum, Hydnum, Hysterangium, Inocybe, Laccaria, Lactarius, Lactifluus, Leccinum, Octaviana, Paxillus, Phaeocollybia*, *Phellodon, Phlebopus, Phyllobolетellus, Phyllobolites, Phylloporus, Piloderma, Pisolithus, Porphyrellus, Pseudotomentella, Pulveroboletus, Rhizopogon, Russula, Sarcodon, Scleranglum, Sebacina, Strobilomyces, Suillus, Thelephora, Tomentella, Tomentellopsis, Tricholoma, Tulasnella, Tylopilus, Tylospora, Xanthoconium*, and *Xerocomus.* Using the *species*Link network (http://splink.cria.org.br), a Brazilian biodiversity data base, which integrates data from over 100 mostly Brazilian herbaria, we searched for records of the aforementioned genera (query date: 10/02/2015). Names were checked and replaced by valid synonyms. Doubtful identifications were removed by taxonomic specialists. Following the Checklist of Plants and Fungi of Brazil (http://reflora.jbrj.gov.br/downloads/vol1.pdf), we classified records into native and introduced species. On this basis and considering ecological data, non-native EM fungi from obviously cultivated sites were removed from our list.

Distribution of EM fungi and detection of white-sand-associated taxa.—When available, ecological data were retrieved from record descriptions. The records were placed into one of the following classes: (1) Amazonian white-sand forests (*campina*, *campinarana*); (2) other Brazilian sandy habitats (dunes/*restinga,* coastal forest growing on sandy soils and geographically distant from Amazonian white sands)*;* (3) Mata Atlântica and Amazonian terra firme forests that both grow on clay-rich soils; and (4) unknown soil type. The distribution of species cannot be used for a χ^2 test due to the low number of observations per species. Therefore, instead, we used the distribution of genera among these habitats for comparison by a χ^2 test in R 1.65 (http://www.R-project.org/). Geographical coordinates, either reported in the specimen description or derived from locality names, were used to produce EM genera distribution maps using QGIS 2.2 (http://www.qgis.org). Information on substrate (white sands or sand) is reported in our maps, but was not extrapolated from geographical position. To detect taxa strictly associated with white sands in Brazil, fungi determined to species and associated with white sands, sandy soils, and clay-rich soils were compared. Moreover, to detect putative endemics among fungi determined to species and associated with white sands, EM fungi known from sandstone sites of the highlands of Guyana (Henkel *et al.* 2012; list available on http://tropicalfungi.org/wp-content/uploads/UPDATED-Total-Taxa-List-4-11-13.pdf), white sands in French Guiana, and white sands in Brazil were compared and the result was schematized by Venn diagrams.

RESULTS

DIVERSITY OF EM FUNGI ON WHITE-SAND FORESTS BASED ON FIELD INVENTORIES.—*Field inventories and specimen identification.*—We observed EM fruiting bodies on all white-sand forests in Brazil

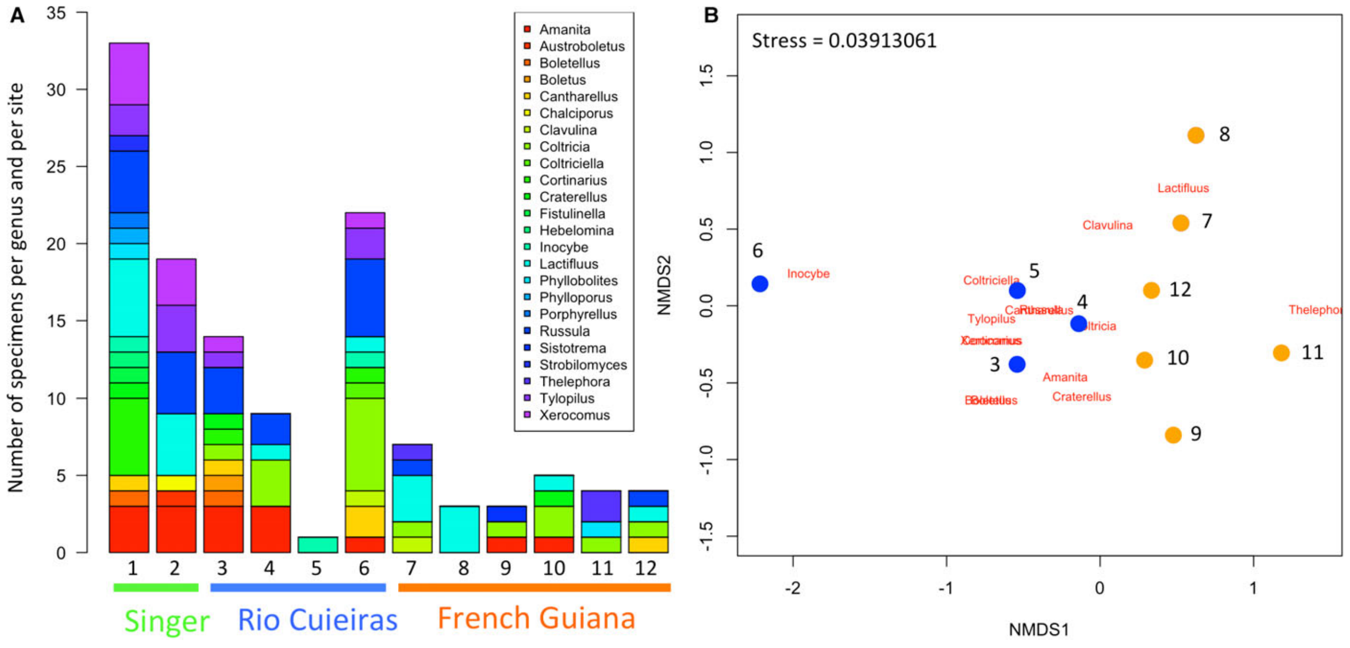

FIGURE 1. (A) Number of distinct morphotypes per genus and per plot, reported from Singer & Araújo (1979) and Singer & Aguiar (1986) (green), from sampling in Rio Cuieiras (blue) and in French Guiana (orange). (B) Non-Metric Multidimensional scaling (NMDS) ordering Rio Cuieiras (blue) and French Guianan plots (orange).

and French Guiana (Fig. S2; Table S2). In all, 221 fruiting bodies were observed, belonging to 62 morphospecies and 23 genera (Table S2). In Rio Cuieiras, we identified to species *Boletellus ananas*, *Cantharellus guyanensis, Lactifluus annulifer, Russula puiggarii, Tylopilus potamogeton,* and *Xerocomus amazonicus*, species originally recorded by Singer (Table S2). With respect to morphospecies, we cannot unequivocally equate our collections to those described by Singer (1988). A specimen similar to *Tylopilus rufonigricans* described from Guyana was observed in Rio Cuieiras. In French Guiana, *Amanita xerocybe* and *A. lanivolva* were observed, two species described from Brazil and frequently recorded in Guyana.

Diversity and similarity of EM communities on white sand.—In our inventories, *Cantharellus guyanensis* and *Coltricia* spp. made up a large proportion of observed EM fungi, however, with the exception of *C. guyanensis*, we did not find any other shared species or morphospecies between Brazil and French Guiana. On each plot, from one to 22 morphospecies were observed. Based on morphospecies occurrence, plots in Rio Cuieiras were often richer than French Guianan sites (Fig. 1A), but still, this difference was not highly significant (Mann–Whitney test, $P = 0.0529$) and the difference between *campina* and *campinarana* was not significant at all ($P = 0.330$). Species accumulation curves pointed to lower diversity of EM communities in French Guiana (Fig. S3), and in fact, Chao estimates predicted up to 243 species in Rio Cuieiras and only 196 in French Guiana. With respect to site, Chao estimates were not significantly different between French Guiana and Rio Cuieiras (Mann–Whitney tests, $P = 0.2395$). The similarity between communities was not explained by geographic distance (Mantel test, $P = 0.26$), nor by the difference between *campina* and *campinarana* (Adonis test, $P = 0.401$), but communities were statistically different between Brazilian and French Guianan sites (Adonis test, $P = 0.013$).

Diversity of EM fungi on white sand based on herbarium records.—*EM genera deposited in Brazilian herbaria.*—Our queries for the 63 target genera resulted in 1681 unique specimens records (2642 including duplicates), deposited in 18 herbaria: CMCEPEC, FLOR, FURB, HFSL-FUNGOS, HUEFS, ICN, INPA, IPA, IRAI, JPB, MBM, MPUC, NYBG_BR, R, RB, SP-FUNGI, UFRN-FUNGOS, and URM. Hereafter, when we use the term "record", we mean a single collector number not including duplicates. *Lactarius* sp. should probably be renamed as *Lactifluus* sp. but this would require direct specimen observation, therefore records were not renamed for Russulaceae, except for *Russula obtusopunctata,* which is a synonym of *Lactarius venezuelanus* (Buyck & de Meijer 1999). Two species are mentioned but were never described in the literature, *Durosaccum brunneum*, which could be a *Pisolithus* sp., and *Craterellus horridus*. In both cases, the record of the genus was kept in the dataset. Most records of *Tricholoma* (22 records) were removed, as they probably refer to *Macrocybe* sp., especially *Macrocybe titans*, a common saprobic fun-

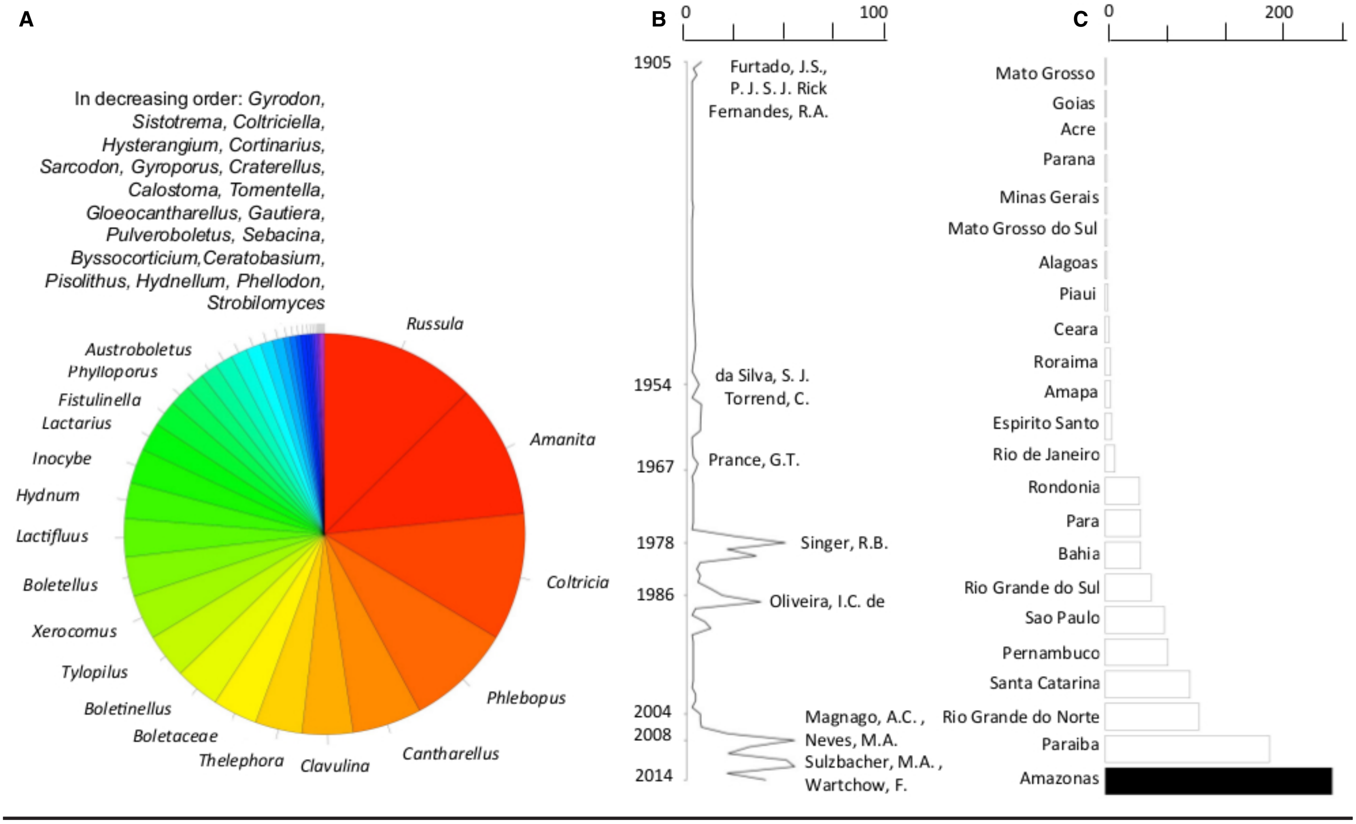

FIGURE 2. Number of specimens deposited in Brazilian herbaria per fungal genus (A), per year (B) and per state (C). Remarkable collectors that began and enriched EM specimen collections are indicated over the time scale.

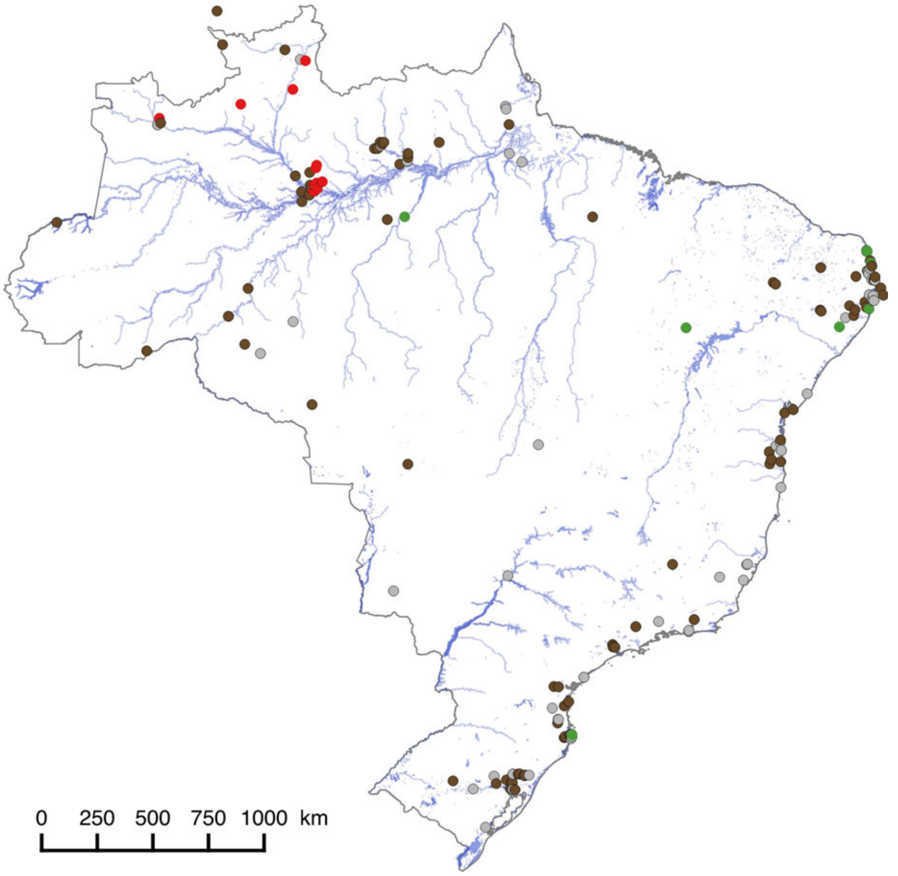

FIGURE 3. Map of collection sites drawn from herbarium specimens, highlighting specimens collected on white-sand areas (red), sandy soil (green), or on non-flooded clay rich soils (black). Gray dots indicate records without any information on the habitat.

gus. As the EM habit of *Phylloporia* is doubtful, we chose to be conservative and excluded this genus (represented by 383 records) although it is accepted by Sulzbacher *et al.* (2013a). The genus *Boletus* is not recorded from Brazil (except from plantations) but several *Tylopilus*, *Xerocomus* and *Phlebopus* spp. were originally deposited under the name *Boletus* sp. For this reason, we kept records of *Boletus* sp. from native habitats and report them as "Boletaceae" (36 records). Thirty-six EM records from *Eucalyptus* and 53 from *Pinus* plantations were removed, along with other 356 EM records, belonging to 49 introduced species. Additionally, all records of *Inocybe* sp., *Laccaria* sp., and *Hebeloma* sp., from University campuses and from botanical gardens, were removed (29 records).

The remaining dataset comprises 1006 records, that is, 62.3 percent of our initial search, and represents 40 genera and 175 species. Members of *Russula*, *Amanita*, *Coltricia*, *Phlebopus*, and *Cantharellus* were particularly numerous (Fig. 2A). Specimens were collected from 1905 (by J. Rick, a pioneer of Brazilian mycology) to 2014. Over this period, 164 collectors contributed to deposit specimens, of which 548 were later identified by 86 taxonomists. Almost all of the collections of ectomycorrhizal fruiting bodies were collected during just a few years: 1954, 1978, and 2008–2015 (Fig. 2B), in part due to notable contributions by R. Singer. Most EM records are located in the state of Amazonas (257), followed by Paraíba (186), and Rio Grande do Norte (107; Fig. 2C); overall, EM fungi were reported in 23 out of the 27 Brazilian states (Fig. 2C), and were especially frequent along the coast (Fig. 3).

Distribution of EM fungi and detection of white-sand-associated taxa.— According to notes associated to records, 137 specimens were collected on white-sand forests. The first mention of EM fungi on white sands was made by Prance in 1967 close to Manaus, and R.B. Singer deposited 72 records from white sand between 1977 and 1980 (136 EM specimens from all substrates). Ecological data were available for 559 records, of which 114 were collected on sandy soil, and 364 on non-flooded clay-rich soil and the remaining records (81) had no soil data. The distribution of genera was statistically different on white sand as compared to sandy soil ($\chi^2 = 101.15$, $P < 0.0001$) and other habitats ($\chi^2 = 303.03$, $P < 0.0001$). Certain EM genera were totally absent from white sands, that is, *Albatrellus, Boletinellus, Byssocorticium, Calostoma, Ceratobasidium, Gautieria, Gloeocantharellus, Gyrodon, Gyroporus, Hydnellum, Hydnum, Hysterangium, Phellodon, Phylloporus, Pulveroboletus, Sebacina, Strobilomyces, Thelephora*, and *Tomentella*; although we did sample Tomentella on the white sands in French Guiana. In contrast, the proportion of *Amanita, Cantharellus, Cla-*

TABLE 1. *List of species mentioning white-sand forests in herbarium records, ordered per fungal family. Some species that were not detected from herbarium but described from campinarana by Singer and Araújo (1979) and Wartchow (2015) were added (*). WS: taxa recorded only from white sands.*

Province	Family	Species	Habitat
Amazonas	Amanitaceae	*Amanita* sp. (several species)	
		*Amanita xerocybe**	WS
		*Amanita sulcatissima**	WS
		Amanita campirananae	WS
		*Amanita tenacipulvis**	WS
	Bankeraceae	*Sarcodon atroviridis*	
		Sarcodon sp. (several species)	
	Boletaceae	*Austroboletus olivaceus*	WS
		Boletellus ananas	
		Boletellus fallax	WS
		Boletellus minor	WS
		Fistulinella campinaranae	WS
		Phlebopus braziliensis	WS
		*Phyllobolites miniatus**	
		Phylloporus gymnocystis	WS
		*Porphyrellus olivaceus**	WS
		*Strobilomyces pauper**	WS
		Tylopilus aculeatus	WS
		Tylopilus arenarius	WS
		*Tylopilus potamogeton (and var. aquarius)**	WS
		Xerocomus amazonicus	WS
		Xerocomus brasiliensis	
		Xerocomus campinaranae	WS
		Xerocomus globulifer	WS
		Xerocomus scrobiculatus	WS
		Xerocomus sp. (several species)	
	Cantharellaceae	*Cantharellus guyanensis*	WS
		Cantharellus sp.	
		Craterellus '*horridus*' ined.	WS
		*Craterellus orinocenis**	
		Craterellus sp.	
	Clavulinaceae	*Clavulina amazonensis*	
		Clavulina panurensis	
		Clavulina sp. (several species)	
	Cortinariaceae	*Cortinarius amazonicus*	WS
		Cortinarius campinaranae	WS
		Cortinarius galeriniformis	WS
		Cortinarius kerrii	WS
		Cortinarius umbilicatus	WS
		*Hebelomina amazonensis**	WS
		Inocybe amazonensis	
	Hymenochaetaceae	*Coltricia cinnamomea*	
		Coltricia sp. (several species)	
		Coltriciella oblectabilis	
	Russulaceae	*Lactifluus amazonensis*	
		Lactifluus annulifer	
		Lactifluus brasiliensis	WS
		Lactifluus campinensis	WS
		Lactifluus subreticulatus	WS
		*Lactarius reticulatus**	
		*Lactarius venezuelanus**	
		Russula batistae	
		Russula campinicola	WS
		Russula leguminosarum	WS
		Russula melanoptamica	WS
		Russula nanella	WS
		Russula obtusopunctata (synonym of Lactarius venezuelanus)	WS
		*Russula orinocensis**	
		Russula pachycystis	WS
		Russula puiggarii	
		Russula sp. (several species)	
		Russula verna	WS

vulina, Cortinarius, Lactifluus, Russula, and *Xerocomus* was higher on white sand than on other soil type or substrates (χ^2 tests, all P-values < 0.001; Fig. S2A, B and C). With respect to species, at least 64 were observed on white sands and 37 were apparently restricted to this substrate, for example, *Cortinarius* and many Boletaceae (Table 1). Finally, based on identified species only, 17 were shared between white sands in Brazil and Guyana, three occurred both on the white sands of French Guiana and Guyana, and only one was recorded on the white sands both in French Guiana and Brazil (Fig. S5B).

DISCUSSION

A FIRST SKETCH OF EM FUNGI DISTRIBUTION.—Tapping the enormous genetic and morphological resources housed in herbaria has become a trend among molecular ecologists seeking reference material for barcoding (Särkinen *et al.* 2012, Peay 2014) or data for species distribution modeling (Wollan *et al.* 2008). As yet, data-mining of mycological collections held in herbaria are isolated cases (Wollan *et al.* 2008), and more often used for producing checklists (*e.g.,* use of the Myxomycota collection deposited at URM; Agra *et al.* 2014) than for making distribution maps. Metadata are sometimes hard to summarize, and need to be carefully filtered and assessed (see Agerer *et al.* 2000). We have illustrated all the correction steps necessary to obtain such metadata: removing duplicates, checking names and synonyms, searching for doubtful identification, and even correcting family names. In our case, we also tried to exclude recently introduced species, growing in botanical gardens or plantations, which considerably reduced our dataset while greatly increasing its significance.

Despite the need to filter and correct, herbarium records remain a fruitful information source and are replete with notes on habitats, on putative hosts, which have been rarely analyzed.

Although single observations may be doubtful, when taken together, numerous records allow us to discern EM fungi distribution patterns in Brazil. Indeed, we retrieved 1006 records representing 40 genera and 175 species, from all over Brazil (Fig. 3). The resultant pattern from this first distribution map of EM fungi in Brazil (Fig. 3) is strongly suggestive of a sampling bias, probably explained by the fact that most mycological collecting in the Neotropics is relatively recent, handled by few taxonomists (Fig. 2). One thousand records accumulated over a century is far less than what was collected on a single 1-ha plot in Guyana over the past 20 yr (Henkel *et al.* 2012), but at least, the number of sites investigated can provide information on species distribution, not only over the Amazonian lowlands but also among the diverse forest types of Brazil.

WHITE-SAND FORESTS: GOOD HUNTING GROUNDS FOR MUSHROOMS?.—Finding and exploring white-sand forests is challenging in the Amazonian lowlands because of their scattered distribution. Since Singer's studies in the late 1970s, few mycologists have paid attention to EM fungi in these ecosystems. As EM fungi are thought to be rare in the Neotropics outside of monodominant forests (Smith & Read 2008, Kropp 2009), their absence from Amazonia was never perceived as a gap in our understanding of EM distribution (Tedersoo *et al.* 2012). In only 3 d of sampling, we observed as many morphospecies in Rio Cuieiras as Singer did, from 1979 to 1986, and we recorded 64 white-sand-associated species from herbaria. We can conclude that white-sand forests are good hunting grounds for EM fungi, but they are not the only sites: dunes and semi-arid ecosystems also have many EM fungi (Fig. 3 and Fig. S5A; Sulzbacher *et al.* 2013b). Interestingly, we also recorded EM fungi from clay-rich soils (Fig. S5A), more specifically *Cantharellus* sp. and *Amanita* sp. Indeed, *Scleroderma minutisporum* was previously described from a terra firme forest (Alfredo *et al.* 2012). The scattered distribution of EM fungi determined from records lacking ecological data in Brazil (309 sites; Fig. 3) and the numerous specimens collected on 'soil' require further investigation, but support the idea that EM fungi colonize a variety of habitats in Brazil.

ENDEMISM VERSUS (WHITE-) SAND ASSOCIATED TAXA.—White-sand forests are known to host many endemic plants, that are white-sand specialists (Anderson 1981, Damasco *et al.* 2013). Based on our sampling, we detected many site-specific morphospecies, but without species identification and more sampling we cannot comment on whether they are endemic. Moreover, the high variation in our sampling as shown by the lack of a plateau in our rarefaction curves suggests that with more sampling effort more species should be collected, especially along the Rio Negro. Geographical distances did not explain the low similarity between plots, but again, the low species richness of some plots limits any conclusion on isolation and endemicity. Taken together, these data support the proposition that white-sand forests are quite heterogeneous, this is reinforced by the multiplicity of names this habitat has received depending on soil organic matter content, tree height and dominant tree species (Anderson 1981). This heterogeneity remains difficult to interpret (Anderson 1981), and indeed, we did not find any significant difference between EM communities from *campina* and *campinarana*.

Based on herbarium records, we detected 37 EM taxa specifically associated with white sands (Table 1; Fig. S5A), mostly *Cortinarius* and Boletaceae (Table 1). Again, as many morphospecies in herbaria and in our recent collections were only determined to genus, we can expect to increase the number of species associated with white sands, for example among Amanitaceae. On the other hand, a few wide-spread species were recorded, such as *Cantharellus guyanensis, Russula puiggarii*, and *Amanita xerocybe*. These species can be found in very diverse habitats, even on *terra firme* (Singer & Araújo 1979, this study). *Cantharellus guyanensis,* which is widely distributed across Brazil to Venezuela and Colombia (Henkel *et al.* 2014), is particularly noteworthy in that it is a fragrant, delectable species.

Based on species descriptions, we know that only 15 species described by Singer in the Amazon were detected in *Dicymbe* forest in the Guiana Highlands (Henkel *et al.* 2012, Fig. S5B). Parallels are often drawn between the Guiana Highlands and the Amazonian lowlands, especially the Amazonian white sands (Prance 1996). First, white sands may partly result from Guiana shield weathering (Kubitzki 1989), and second, phylogeography of some plant families, for example, Gentianaceae, have confirmed that both regions have undergone a common history (Frasier *et al.* 2008). On the other hand, dispersion and isolation is mentioned as a key driver of speciation for EM taxa that have colonized the Roraima region and especially the Guiana Highlands (Moyersoen 2012). The same pattern of endemism is expected on white-sand areas that are often isolated (Prance 1996), and specimens from these places need to be compared not only between such sites but also with specimens from the Guiana Highlands and dunes in Brazil. Such a comparison would likely help us trace the history of EM families in the Neotropics and disentangle the role of history and edaphic factors in determining EM communities, as has been shown for plants (Fine & Kembel 2011, Fine *et al.* 2013).

EM SYMBIOSIS: BELOW THE SURFACE OF WHITE SANDS.—Our data are in agreement with the observation that EM symbioses are generally rare in the Amazon, and that species richness is extremely low compared to the paleotropics or monodominant forests in Guyana. However, we show that EM fungi persist in hyperdiverse forests, probably in association with a few host trees or lianas, such as species of Polygonaceae, Nyctaginaceae, and Gnetaceae observed on white sands. In general, tree dominance is a trait often associated with EM symbioses (Torti *et al.* 2001, McGuire 2007, Bâ *et al.* 2014), we can assume that the occurrence of EM fungi may deeply influence tree community structure and diversity, especially on white sands. Interestingly, while most studies undertaken on EM communities conclude that the phylogeny of host trees has a major effect on EM fungi diversity, the reverse is not true, and EM fungi remain forgotten by plant ecologists when considering determinants of plant diversity patterns. Investigating tree roots in the Neotropics, in both white-sand and other forests, would contribute to better understanding of the distribution of symbiotic fungi and their associated host trees, and perhaps the factors promoting edaphic specialization notable among white-sand plants (Fine & Kembel 2011, Fine *et al.* 2013).

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SUPPORTING INFORMATION

Additional Supporting Information may be found with online material:

TABLE S1. *Description of white-sand forests sites investigated close to Rio Cuieiras, mentioning EM host trees.*

TABLE S2. *Inventories of EM fruiting bodies.*

FIGURE S1. Maps reporting Singer study site and sites investigated in this study around Manaus in Brazil and sampling sites in French Guiana.

FIGURE S2. Ectomycorrhizal specimens from the Rio Cuieiras site.

FIGURE S3. Species accumulation curves for Rio Cuieiras and French Guiana showing the accumulation of morphospecies per plot.

FIGURE S4: Distribution maps of Amanitaceae and Russulaceae, Boletaceae, and *Cortinarius* collection sites in Brazil, gathered from herbarium data.

FIGURE S5. Venn Diagram representing the shared species among habitats in Brazil and between white sands in French Guiana, in Brazil, and as a comparison, recorded in the Guyana highlands.

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