

Ectomycorrhizal fungal sporocarp diversity and discovery of new taxa in *Dicymbe* monodominant forests of the Guiana Shield

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Abstract Ectomycorrhizal (ECM) fungi historically were considered poorly represented in Neotropical forests but in the central Guiana Shield substantial areas are dominated by leguminous ECM trees. In the Upper Potaro Basin of Western Guyana, ECM fungi were sampled for 7 years during the rainy seasons of 2000–2008 in three 1-ha plots in primary monodominant forests of the ECM canopy tree *Dicymbe corymbosa* (*Fabaceae* subfam. *Caesalpinioideae*). Over the plot sampling period sporocarps of 126 species of putative or confirmed ECM fungi were recovered. These taxa represented 13 families and 25 genera of primarily *Agaricomycetes*, but also *Ascomycota* (*Elaphomycetaceae*), the majority of which are new to science. *Russulaceae* contained the most species (20 *Russula*; 9 *Lactarius*), followed by *Boletaceae* (8 genera, 25 spp.), *Clavulinaceae* (17 *Clavulina*), and *Amanitaceae* (16 *Amanita*). An additional 46 species of ECM fungi were collected in forests of the Upper Potaro Basin outside the study plots between 2000 and 2010, bringing the regional number of ECM species known from sporocarps to 172. This is the first long-term ECM macrofungal dataset from an ECM-dominated Neotropical forest, and sporocarp diversity is comparable to that recorded for ECM-diverse temperate and boreal forests. While a species accumulation curve indicated that ECM sporocarp diversity was not fully recovered inside of the plots, ~80% of the total species were recovered in the first year. Sequence data from ECM roots have confirmed the ECM status of 56 taxa represented by corresponding sporocarp data. However, >50% of ECM fungal species from roots remain undiscovered as sporocarps, leading to a conservative estimate of > 250 ECM species at

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the Potaro site. *Dicymbe* forests in Guyana are a hotspot for ECM fungal diversity in the Neotropics.

Keywords *Ascomycota* · *Basidiomycota* · Biodiversity · *Dicymbe* · Guyana · Macrofungi · Mycorrhizas · Neotropics

Introduction

In contrast to temperate and boreal forests rich in ectomycorrhizal (ECM) plants and fungi, lowland tropical rainforests had in the past been presumed to be impoverished in ECM associations (Dennis 1970; Pirozynski 1981). This impression was reinforced by root surveys demonstrating the prevalence of arbuscular-mycorrhizal (AM) trees in a number of lowland rainforests with high woody plant diversity (e.g., Redhead 1968; Thomazini 1974; St. John 1980; Bereau et al. 1997; McGuire et al. 2008). Hypotheses were proposed for the apparent dominance of AM associations in many lowland tropical forests which centered on the lack of host specificity in AM fungi and the resulting competitive equivalence of AM trees (Janos 1987).

Early mycofloristic studies in the Paleotropics, however, indicated that ECM associations must exist in some lowland rainforests because families and genera of obligate ECM fungi (e.g., *Amanita*, *Russulaceae*, *Boletaceae*) were found in association with caesalpinoid legumes in Africa, and with *Dipterocarpaceae* and *Fagaceae* in Asia (e.g., Beeli 1935; Heim 1955; Heinemann 1954; Corner and Bas 1962; Corner 1972; Watling and Lee 1995; Buyck et al. 1996). Studies eventually confirmed, via root excavations, the presence of ectomycorrhizas on several tropical tree lineages, including numerous species of *Dipterocarpaceae* (e.g., Singh 1966; Becker 1983; Alexander and Högberg 1986), members of the African *Caesalpinioideae*, tribe Amherstieae (Alexander and Högberg 1986; Newbery et al. 1988), and the genus *Uapaca* (Thoen and Ba 1989). Subsequently, the role of ectomycorrhizas in facilitating forest dominance by ECM trees in the Paleotropics has been investigated (e.g., Curran 1994; Moyersoen et al. 1998; Torti and Coley 1999).

Until recently the ECM associations of Neotropical rainforests have not been studied. Evidence for ECM symbioses in the lowland Neotropics was initially limited to collections of ECM fungi with *Quercus oleoides* in Costa Rica (Singer et al. 1991), leguminous or *Nyctaginaceae* hosts in central Amazonia and Southern Venezuela (Bas 1978; Singer and Araujo 1979; Singer et al. 1983; Moyersoen 1993), or with undetermined hosts in Venezuela and the Lesser Antilles (Dennis 1970; Pegler 1983). In Singer's Amazonian studies, ECM roots were confirmed on the papilionoid leguminous host genus *Aldina* and the gymnosperm liana *Gnetum*, and a variety of ECM basidiomycetes were found exclusively in forest types dominated by *Aldina* (e.g., Singer and Araujo 1979). Moyersoen (2006) also confirmed the ECM status of the endemic *Pakaraimaea dipterocarpacea* (*Dipterocarpaceae*) in Venezuela. Studies using root anatomical diagnosis or direct sequencing have confirmed the occurrence of ectomycorrhizas on trees and lianas of *Coccoloba* (*Polygonoaceae*) across the Neotropics, and sporocarp species have been documented in association with the confirmed ECM seaside host *Coccoloba uvifera* (L.) L. (Kreisel 1971; Miller et al. 2000; Guzman et al. 2004; Tedersoo et al. 2010b; Henkel and Smith unpublished data).

Since the pioneering study of Singer and Moyersoen in Amazonia, the discovery of forests rich in leguminous ECM trees of the genus *Dicymbe* and associated fungi in the central Guiana Shield region of Guyana has driven new studies on tropical

ectomycorrhizas (Henkel et al. 2002). Over the last 12 years numerous new species and genera of ECM fungi have been described from Guyana (e.g., Henkel 1999; Miller et al. 2001; Aime et al. 2003; Largent et al. 2008; Fulgenzi et al. 2010; Uehling et al. 2011). The ecology of tropical monodominant forests has also been studied in these Guyanese *Dicymbe* systems (e.g., Henkel 2003; McGuire 2007; Woolley et al. 2008).

The framework for many of these studies has been an array of 1-ha study plots established in 2000 in *Dicymbe corymbosa* monodominant forests of Guyana's Upper Potaro Basin. The purpose of the current study is to summarize systematic ECM sporocarp sampling in three of these plots over 7 years between 2000 and 2008. The sporocarp-based ECM fungal diversity reported here will complement an ongoing belowground molecular-based diversity study. Comparisons of Guyana's ECM fungal diversity to those of other regions, the impact of new taxon discovery, and the unusual sporocarp production habits and macromorphologies of Guyanese ECM fungi will also be discussed.

Methods

Study site

The study was conducted during 2000–2008 in the Upper Potaro River Basin in the central Pakaraima Mountains of Guyana (Fig. 1). The site is situated in an intermountain valley at 700–800 m elevation on hilly terrain adjacent to the main river course. This area is densely forested with a mosaic of mature *Dicymbe*-dominated and mixed forest stands. Obvious signs of prior anthropogenic disturbance were absent from the area. Upland soils are either of grey or brown sands derived from sandstone parent materials, or ridges of lateritic red clays and loams derived from igneous intrusions (Henkel 2003). Precipitation is estimated at 3,500–4,000 mm annually, with peaks during May–July and December–January; no months experience less than 100 mm precipitation (Fanshawe 1952; Henkel 2003). Further

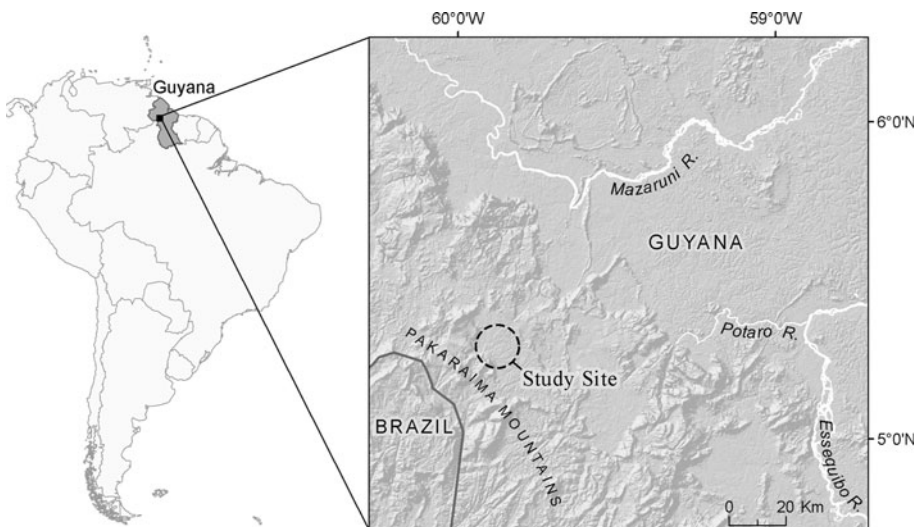


Fig. 1 Location of the study site in the Pakaraima Mountains, Upper Potaro River Basin of Guyana (from Degagne et al. 2009)

details of the geology, soils, climate, and vegetation of the Potaro site can be found in Henkel (2003), Henkel et al. (2005b), and Degagne et al. (2009).

Study plots

Three 1-ha plots were established in *D. corymbosa*-dominated forest during May 2000 in the vicinity of a base camp along the Upper Potaro River. Plot boundary positions were randomly chosen within larger areas (>3 ha) perceived as having homogeneous coverage of *Dicymbe*-dominated forest, away from sharp transitional edges to other forests (Henkel 2003). *Dicymbe* plot 1 (P1) was located on a ridge top (800 m elevation) 2 km south-east of the base camp at 5° 16' 33.1" N; 59° 54' 58.6" W, and was delimited as a rectangle 250 × 40 m. P1 had red clay-loam soils with exposures of small sandstone boulders and ironstone concretions. *Dicymbe* plot 2 (P2) was located ~1 km east of P1 at 5° 16' 27.7" N; 59° 54' 42.5" W on a gentle W–E slope, and was delimited as a 200 × 50-m rectangle. Soils at P2 were red clay-loams with no rock exposures. *Dicymbe* plot 3 (P3) was at an outlying position across the west bank of the Potaro River ~5 km W–SW of the base camp at 5° 18' 15.0" N; 59° 55' 52.4" W, delimited at 200 × 50 m on a gentle W–SW slope with frequent lateritic exposures and ironstone gravel present in the otherwise red silty-loam soils. All plots were divided and marked into 10 × 10 m (100 m²) quadrats. Percent of stand basal area for *D. corymbosa* on these plots was P1: 83%, P2: 75%, and P3: 63%, with the other occasional co-occurring canopy tree species belonging primarily to the *Caesalpinioideae*, *Lecythidaceae*, and *Chrysobalanaceae* (Henkel 2003).

Macrofungal sampling

Fungi were sampled in the plots over a 4–6 week period spanning the main May–July rainy seasons of 2000–2004, 2006, and 2008. No sampling was performed during 2005 and 2007. The onset and decline of heavy rainy seasons are considered optimal periods for macrofungal production in tropical forests (Corner 1972; Singer and Araujo 1979). While studies in temperate forests have indicated that at least 3 years of repeated sporocarp sampling may be needed to recover >75% of the species occurring at a site (Fogel 1976; Arnolds 1992; Vogt et al. 1992; Schmit et al. 1999), other studies have indicated that longer sampling periods inevitably lead to more macrofungal species being recovered (e.g., Straatsma et al. 2001). All plots were sampled at least once a week during each sampling season. A given plot sampling event consisted of randomly selecting five of the 100 m² quadrats and using 4–6 persons to collect all epigeous macrofungal fruiting bodies present in each of these quadrats. Macrofungi belonging to ECM genera were sorted into morphologically distinct species (“morphospecies”) and their presence recorded in each quadrat of occurrence. For 2000–2004 and 2006, sporocarps of each morphospecies were counted and the number recorded per quadrat. Sequestrate fungi were collected if evident at the soil surface. In addition, fruiting substratum was recorded for each morphospecies. On average one or two *Dicymbe* plots were sampled per day; one round of sampling for the three *Dicymbe* plots was usually completed in 5–6 days. During a particular year, a given quadrat was only sampled once, but was potentially sampled in following years. A total of 4–10 complete sampling rounds were performed per year (range of 20–50 quadrats/plot). A total of 630 quadrats (210/plot) were sampled over the 7 year period. Morphospecies of saprotrophic macrofungi were also recorded but will be reported elsewhere (Aime et al. unpublished data). Additional species of putatively ECM fungi only found in *Dicymbe*

forests outside of the study plots were collected with 3–6 general forays during May–August of every year from 2000 to 2010 in the Upper Potaro area. Numbers of off-plot taxa were not included in within-plot calculations, but were considered in estimating the known regional ECM fungal diversity. Voucher specimens made for ECM fungi are housed at the University of Guyana (holotypes), Humboldt State University, Louisiana State University, the University of Wyoming, and Duke University.

Determinations

Macrofungal species were categorized as ECM if they were in genera or lineages for which the ECM symbiosis has been reported or demonstrated (Miller 1983; Singer 1986; Tedersoo et al. 2010a). These included species within genera of the *Basidiomycota* families *Amanitaceae*, *Bankeraceae*, *Boletaceae*, *Cantharellaceae*, *Clavulinaceae*, *Coltriciaceae*, *Cortinariaceae*, *Hysterangiaceae*, *Inocybaceae*, *Russulaceae*, *Sebacinaceae* sensu lato, *Thelephoraceae* sensu lato, *Tricholomataceae* sensu lato, and the *Ascomycota* family *Elaphomycetaceae*. Generic level taxonomy for agaricoid and boletoid fungi followed that of Singer (1986), for cantharelloid and clavarioid fungi Corner (1950, 1966, 1970), for *Bankeraceae* Coker and Beers (1951), for *Coltriciaceae* Gilbertson and Ryvarden (1986), for *Hysterangiaceae* Castellano et al. (1989), for *Thelephoraceae* sensu lato Corner (1968) and Larsen (1968), for *Sebacinaceae* sensu lato Oberwinkler (1964) and Wells and Bandoni (2001), and for *Elaphomycetaceae* Trappe (1979) and Miller et al. (2001). Determinations of previously described species were made in consultation with Bas (1978), Corner (1950, 1966, 1970, 1972), Dennis (1970), Pegler (1983), Singer et al. (1983), Singer et al. (1991), and other primary sources (see citations in Henkel et al. publications cited here). Fungi were identified at several levels of certainty: (1) at the species level for taxa formally described between 1999 and 2011 by TWH and colleagues; (2) at the species level as previously described taxa; (3) at the species level for species new to science but not yet formally published (designated here with proposed binomial followed by “ined”.); (4) at the morphospecies level (i.e., morphologically distinct at the species level but not yet determined; designated here with genus name followed by “sp. 1”, “sp. 2” etc.); and (5) as species complexes; these taxa were identified at the species or morphospecies level, and were morphologically identical among different collections, but molecular data indicated that cryptic sympatric species exist within the taxon. For the plot sporocarp data a species complex is treated as a single taxon.

Data analyses

Frequency (i.e., the number of 100 m² quadrats in which a species was recovered during the total sampling period/total number of quadrats sampled over the three plots × 100) was calculated for each ECM fungal species (Pielou 1977). A species accumulation curve was calculated for the three combined plots by graphing the total number of macrofungal species recovered against increasing numbers of 100 m² quadrats sampled over the study period (Colwell 2006). A dominance–diversity curve for ECM fungal species based on individual frequencies for all taxa was drawn for the three plots combined (Whittaker 1972; Bills et al. 1986). Number of ECM fungal species was calculated for combined and individual plots. Jaccard’s index of similarity of the ECM assemblage was calculated for each interplot comparison among the three plots (Colwell 2006).

Results

Taxa sampled within the three forest plots

A total of 126 distinct morphospecies of ECM fungi were recovered from the combined plots over the course of the study (Table 1). These taxa represented 13 families and 25 determined genera of primarily *Agaricomycetes*, but also *Ascomycota* (*Elaphomycetaceae*). Among these families, *Russulaceae* contributed the most species (20 *Russula*; 9 *Lactarius*), followed by *Boletaceae* (8 genera, 25 spp.), *Clavulinaceae* (17 *Clavulina*), and *Amanitaceae* (16 *Amanita*). Additional taxa were found in the *Inocybaceae* (8 *Inocybe*), *Coltriciaceae* (3 *Coltricia*, 2 *Coltriciella*), *Cantharellaceae* (3 *Cantharellus*, 3 *Craterellus*), *Cortinariaceae* (4 *Cortinarius*), *Thelephoraceae* (4 *Tomentella*, 1 *Thelephora*), *Hysterangiaceae* (2 *Hysterangium*), *Sebacinaceae* (2 *Sebacina*, 1 *Tremellodendron*), *Elaphomycetaceae* (1 *Elaphomyces*, 1 *Pseudotulostoma*), *Tricholomataceae* sensu lato (two spp. of uncertain generic affinities), and one *Boletaceae* sequestrate species of undetermined generic affinity. The last three taxa were considered ECM because they fruit exclusively in *Dicymbe* forests and because two have been found on *Dicymbe* ECM roots with molecular methods (Smith and Henkel unpublished data).

The species accumulation curve indicated that within-plot ECM fungal diversity was not fully recovered over the total sampling period (Fig. 2). Nonetheless, nearly 80% of species were recovered in the first year when 150 out of 630 quadrats were sampled. The relatively flat slope of the curve after 150 quadrats is due to the fact that only ~30 spp. of new ECM fungi were detected over the additional six sampling seasons.

The frequency-based dominance-diversity curve for the 126 ECM species recovered across plots exhibits the negative exponential curve characteristic of macrofungal multi-year plot studies (i.e., a small number of species strongly dominate, an intermediate group is moderately frequent, with a long tail of rare species—Fig. 3). Only 30 species occurred at > 10% frequency and only six of these occurred at > 50% frequency (Table 2; Fig. 4). The most frequently encountered taxon was *Clavulina sprucei* (78.4%), a white coralloid fungus fruiting in troops on organic matter accumulations at the base of large *D. corymbosa* trees (Henkel et al. 2011). The taxonomic distributions of these dominant species reflect the overall relative distribution of families and genera in the total taxa list, with *Clavulinaceae* contributing ten species, *Russulaceae* five, *Boletaceae* four, and *Inocybaceae* three. Also of interest among the most frequent taxa is the presence of multiple species in families that were otherwise not speciose (Table 2). These included the *Sebacinaceae*, with the coralloid *Tremellodendron ocreatum* occurring as the third most frequent taxon at 67%, and the resupinate *Sebacina incrustans* at 10.8%. For *Elaphomycetaceae*, the two known plot species were both frequent, with *Pseudotulostoma volvata* and *Elaphomyces squamatus* ined. occurring at frequencies of 27.9 and 16.3%, respectively.

Comparison of the ECM fungal assemblages for the three individual plots revealed a near-uniform composition with 100 species recorded in P1, 98 species in P2, and 107 species in P3. The number of shared ECM fungal species and Jaccard's percent similarity for plot pairs was P1–P2: 89/73.5, P1–P3: 96/76.4, and P2–P3: 90/75.6.

Taxa sampled off of the study plots

Forty-six species of putatively ECM fungi not occurring in the study plots have been recorded in *Dicymbe* forests of the Upper Potaro region (Table 3). Most off-plot species occur in genera also represented on the plots, but exceptions include species of *Entoloma*

Table 1 Ectomycorrhizal fungal taxa, frequency of occurrence, and representative voucher specimens recorded over 7 years of annual sampling between 2000 and 2008 in three 1-ha plots of *D. corymbosa*-dominated forest in the Upper Potaro River Basin, Guyana

Family	Species ^{1,2}	Frequency ³	Representative vouchers ⁴
<i>Boletaceae</i>	<i>Xeroconus luteus</i> ined.	11.6	TH 7421, 8802, 9177
	<i>Xeroconus exiguus</i> ined.	3.3	TH 8252, 8850
	<i>Xeroconus edmundii</i> ined.	1.0	TH 8035, 8385, 8109
	<i>Xeroconus amazonicus</i> Singer complex	0.2	TH 8087, 8176, 8839
	<i>Xeroconus</i> sp. 1	0.2	TH 8091, 8846, 8848
	<i>Xeroconus subliminus</i> ined.	0.2	TH 8459, 8865
	<i>Xeroconus</i> sp. 2	0.2	TH 9173
	<i>Tylophilus potamogeton</i> var. <i>irengensis</i> T.W. Henkel	22.2	TH 6266 , 8153, 8801
	<i>Tylophilus exiguus</i> T.W. Henkel	18.7	TH 6283 , 8482, 8929
	<i>Tylophilus</i> aff. <i>ballouii</i> #2	9.2	TH 8218, MCA 4288
	<i>Tylophilus ballouii</i> (Peck) Singer	8.9	TH 8185, 8226, 8916
	<i>Tylophilus orsonianus</i> Fulgenzi & T.W. Henkel	3.2	TH 8106 , 8480, 8926
	<i>Tylophilus cyanostipitatus</i> ined.	3.3	TH 8107, 8086, 8805
	<i>Tylophilus rufonigricans</i> T.W. Henkel	2.7	TH 6376 , 8486, 8925
	<i>Tylophilus eximius</i> (Peck) Singer	1.3	TH 8017, 8600, 8988
	<i>Tylophilus vinaceipallidus</i> (Corner) T.W. Henkel	0.8	TH 8060, 8466, 8859
	<i>Gyroporus</i> aff. <i>castaneus</i> (Bull.) Quel.	9.2	TH 8206, 8915
	<i>Pulveroboletus viridisquamulosus</i> ined.	0.2	TH 8371, 9154b, MCA 1840
	<i>Phylloporus colligatus</i> Neves & T.W. Henkel	0.6	TH 8026 , 9107, MCA 4352
	<i>Chalciporus</i> aff. <i>trinitensis</i> Singer	0.2	TH 8012, MCA 3949
	<i>Austroboletus rostrupii</i> (Syd. & P. Syd.) Horak	0.2	TH 8189, 9120
	<i>Boletellus exiguus</i> T.W. Henkel & Fulgenzi	11.0	TH 7436, 8696 , 9189
	<i>Boletellus ananas</i> var. <i>ananas</i> (M.A. Curtis) Murrill	2.2	TH 8168, 9188, MCA 984
	<i>Boletellus dicymbophilus</i> Fulgenzi & T.W. Henkel	0.6	TH 8011, 8152, 8616
	<i>Boletellus piakaii</i> T.W. Henkel & Fulgenzi	0.3	TH 8728 , 8878, MCA 1902
	<i>Amanitaceae</i>	<i>Amanita craseoderma</i> Bas	10.0
<i>Amanita</i> sp.1		6.2	TH 8342, 8507
<i>Amanita</i> sp. 2		4.3	TH 8083, MCA 3155, 3991
<i>Amanita xerocybe</i> Bas		4.0	TH 8198, 8485, 8930
<i>Amanita</i> sp. 3		2.4	TH 8034, 8931
<i>Amanita</i> sp. 4		2.2	TH 8257, 8461, 8955
<i>Amanita</i> sp. 5		2.1	TH 7664
<i>Amanita</i> sp. 6		1.7	TH 8195
<i>Amanita aurantiobrunnea</i> Simmons, T.W. Henkel & Bas		1.6	TH 6431 , 8040, 8937
<i>Amanita perphaea</i> Simmons, T.W. Henkel & Bas		1.4	TH 6229 , 7471, 8942

Table 1 continued

Family	Species ^{1,2}	Frequency ³	Representative vouchers ⁴
	<i>Amanita lanivolvula</i> Bas	1.4	TH 7514, 8123, 9151
	<i>Amanita</i> sp. 7	1.1	TH 8201
	<i>Amanita</i> sp. 8	0.6	TH 8043, 8183, 8986
	<i>Amanita</i> sp. 9	0.5	TH 8056, 8455, 9043
	<i>Amanita</i> sp. 10	0.5	TH 8224
	<i>Amanita</i> sp. 11	0.2	TH 8165, 8920
<i>Cantharellaceae</i>	<i>Craterellus excelsus</i> T.W. Henkel & Aime	42.4	TH 7515, 8235 , MCA 3107
	<i>Craterellus olivaceoluteum</i> ined.	0.5	TH 7411, 8913, MCA 1358
	<i>Craterellus potaroensis</i> ined.	0.3	TH 8137, 8999, 9075
	<i>Cantharellus atratus</i> Corner complex	66.2	TH 8243, 9203, MCA 990
	<i>Cantharellus pleurotoides</i> T.W. Henkel, Aime & S.L. Mill.	1.6	TH 8528 , 8877, MCA 1908
	<i>Cantharellus guyanensis</i> Mont.	0.8	TH 8242, MCA 3948, 981
<i>Clavulinaceae</i>	<i>Clavulina sprucei</i> (Berk.) Corner complex	78.4	TH 8221, 9122, MCA 3989
	<i>Clavulina amazonensis</i> Corner	71.4	TH 8463, 8742, 9191
	<i>Clavulina caespitosa</i> T.W. Henkel, Meszaros & Aime	52.9	TH 8225, 8496, 8709
	<i>Clavulina tepurumenga</i> T.W. Henkel & Aime	38.7	TH 8217 , 8498, MCA 3116
	<i>Clavulina humicola</i> T.W. Henkel, Meszaros & Aime	36.8	TH 8245, 8737
	<i>Clavulina monodiminutiva</i> T.W. Henkel, Meszaros & Aime	26.5	TH 8246, 8191, 8738
	<i>Clavulina dicymbetorum</i> T.W. Henkel, Meszaros & Aime	17.5	TH 8326, 8478, 8730
	<i>Clavulina nigricans</i> Thacker & T.W. Henkel	15.1	TH 7440, 8284 , MCA 1115
	<i>Clavulina pakaraimensis</i> ined.	12.4	TH 8254, 9194, MCA 3118
	<i>Clavulina griseohumicola</i> T.W. Henkel, Meszaros & Aime	10.8	TH 8259, 8729 , 9243
	<i>Clavulina alba</i> ined.	6.8	TH 8286, 8940, MCA 3184
	<i>Clavulina effusa</i> Uehling, T.W. Henkel & Aime	4.9	TH 8386, 8511, 9193
	<i>Clavulina rosiramea</i> ined.	2.5	TH 8954
	<i>Clavulina kunnudlutsa</i> T.W. Henkel & Aime	2.4	TH 8460, 8932 , MCA 3916
	<i>Clavulina guyanensis</i> ined.	2.2	TH 9245, MCA 3141, 1154
	<i>Clavulina cinereoglebosa</i> Uehling, T.W. Henkel & Aime	1.1	TH 8561, MCA 4023
	<i>Clavulina craterelloides</i> Thacker & T.W. Henkel	0.2	TH 7493, 8234 , MCA 983
<i>Coltriciaeae</i>	<i>Coltriciella oblectabilis</i> (Lloyd) Kotl., Pouzar & Ryvar den	7.3	TH 8560, MCA 1759, 2157
	<i>Coltriciella navispora</i> T.W. Henkel, Aime & Ryvar den	0.5	TH 7576 , MCA 2156, 3927
	<i>Coltricia montagnei</i> (Fr.) Murrill	2.9	TH 8344, 8558, 9108
	<i>Coltricia fibrosa</i> Aime & Ryvar den	1.9	MCA 2054 , 1040, 2266

Table 1 continued

Family	Species ^{1,2}	Frequency ³	Representative vouchers ⁴
	<i>Coltricia verrucata</i> Aime, T.W. Henkel & Ryvarden	0.2	MCA 962 , 2160
<i>Cortinariaceae</i>	<i>Cortinarius</i> aff. <i>galeriniformis</i> Singer complex	15.9	TH 8546, MCA 2318, 3973
	<i>Cortinarius</i> aff. <i>kerrii</i> Singer	5.2	TH 8211, 8539
	<i>Cortinarius</i> aff. <i>amazonicus</i> Singer & Araujo complex	4.3	TH 8193, 8166, MCA 3928
	<i>Cortinarius</i> sp. 1	1.7	TH 8219, 9178, MCA 3969
<i>Elaphomycetaceae</i>	<i>Pseudotulostoma volvata</i> O.K. Mill. & T.W. Henkel	27.9	TH 7022 , 8481, 8975
	<i>Elaphomyces digitatus</i> Castellano, T.W. Henkel & S.L. Mill	16.3	TH 8493, 8887 , MCA 995
<i>Hysterangiaceae</i>	<i>Hysterangium</i> sp. 1	8.1	TH 8361, 8517, MCA 1087
	<i>Hysterangium</i> sp. 2	1.4	TH 8359, 8901, MCA 3933
<i>Inocybaceae</i>	<i>Inocybe ayangananae</i> Matheny, Aime & T.W. Henkel	22.7	TH 7451, 8160, MCA 1232
	<i>Inocybe pulchella</i> Matheny, Aime & T.W. Henkel	21.3	TH 8103, 9185, MCA 1879
	<i>Inocybe epidendron</i> Matheny, Aime & T.W. Henkel	12.1	TH 9186, MCA 1473 , 1880
	<i>Inocybe marginata</i> ined.	1.9	TH 8921, MCA 1882, 3190
	<i>Inocybe lasseri</i> Dennis	0.6	MCA 1971
	<i>Inocybe enigmata</i> ined.	0.5	MCA 1490, 1868, 2353
	<i>Inocybe lilacinosquamosa</i> Matheny, Aime & T.W. Henkel	0.2	TH 8394, 8004, MCA 976
	<i>Inocybe lepidotella</i> ined.	0.2	MCA 1881
<i>Russulaceae</i>	<i>Russula campinensis</i> (Singer) T.W. Henkel, Aime & S.L. Mill.	47.5	TH 7403, 8305, MCA 982
	<i>Russula metachromatica</i> ssp. <i>tarumaensis</i> Singer	19.7	TH 7439, 8300, MCA 3907
	<i>Russula</i> aff. <i>puiggarii</i> (Speg.) Singer complex #1	12.7	TH 8310, MCA 1835, 3994
	<i>Russula venezuelana</i> Singer	7.3	TH 7874, 7534, SLM 10014
	<i>Russula</i> cf. <i>leguminosarum</i> Singer	7.0	TH 7425, MCA 3958
	<i>Russula</i> aff. <i>pluvialis</i> Singer	5.1	TH 7940, 8212, 9230
	<i>Russula obtusopunctata</i> Buyck	4.6	TH 7916, SLM 10113
	<i>Russula glutinovelata</i> ined.	4.3	TH 8233, 8699, MCA 1692
	<i>Russula formicarius</i> ined.	1.4	TH 8258, 9145, MCA 3935
	<i>Russula</i> cf. <i>ammicola</i> Singer	1.3	TH 7446, 8228
	<i>Russula</i> sp. 1	1.1	TH 7658, 8339, 8468
	<i>Russula paxilliformis</i> ined.	1.0	TH 7657, 8270
	<i>Russula</i> sp. 2	1.0	MCA 4008
	<i>Russula rubroglutinata</i> ined.	0.8	TH 7949, 8307, MCA 2096
	<i>Russula caulofructus</i> ined.	0.8	TH 8299, MCA 1834
	<i>Russula</i> sp. 3	0.6	MCA 1646, 4010
	<i>Russula</i> sp. 4	0.5	TH 7880, 8320

Table 1 continued

Family	Species ^{1,2}	Frequency ³	Representative vouchers ⁴
	<i>Russula metachromatica</i> ssp. <i>metachromatica</i> Singer	0.5	TH 7678, 8215, MCA 3944
	<i>Russula batistae</i> Singer	0.2	TH 8236, 8227, MCA 4007
	<i>Russula</i> aff. <i>puiggarii</i> (Speg.) Singer complex #2	0.2	TH 8308, MCA 1784, 3954
	<i>Lactarius humicola</i> ined.	54.0	TH 9224, SLM 10023
	<i>Lactarius panuoides</i> Singer	11.3	TH 7460, 8306, MCA 1653
	<i>Lactarius subiculatus</i> ined.	8.3	TH 7922, 8210, MCA 3938
	<i>Lactarius brunellus</i> S.L. Mill., Aime & T.W. Henkel	3.7	TH 7641 , 9130, SLM 10168
	<i>Lactarius multiceps</i> S.L. Mill., Aime & T.W. Henkel	3.2	TH 7656 , 9154a, SLM 10146
	<i>Lactarius</i> sp. 1	1.6	TH 7481, 8273, 9240
	<i>Lactarius</i> sp. 2	0.8	TH 8338, 9234, MCA 3979
	<i>Lactarius</i> aff. <i>brasiliensis</i> Singer	0.5	TH 7677, 8237, 9217
	<i>Lactarius lignyophilus</i> ined.	0.5	TH 8251, 9239
<i>Sebacinaceae</i>	<i>Tremellodendron ocreatum</i> (Berk.) P. Roberts	67.0	TH 7426, 8577, MCA 2069
	<i>Sebacina incrustans</i> (Pers.) Tul. & C. Tul.	10.8	TH 8484, 8974, MCA 1975
	<i>Sebacina</i> sp. 1	3.2	TH 8996
<i>Thelephoraceae</i>	<i>Tomentella</i> sp. 1	2.9	TH 8544, 8568, MES 348
	<i>Tomentella</i> sp. 2	1.1	TH 8483
	<i>Tomentella</i> sp. 3	1.0	TH 8977, 8973a
	<i>Tomentella</i> sp. 4	0.2	TH 8622, 9167
	<i>Thelephora</i> sp. 1	7.1	TH 8105, MCA 1888, 3131
<i>Tricholomataceae</i>	" <i>Tricholoma</i> " <i>Agaricales</i> sp. 1	7.5	TH 8115, 9050, MCA 1677
	" <i>Tricholoma</i> " <i>Agaricales</i> sp. 2	0.3	TH 8269, 8512, 8941
Indet	<i>Boletaceae</i> sequestrate incertae sedis #1	0.2	TH 9163, MCA 1513, 1684

¹ Author citations of scientific names are included here, as an exception to journal policy, in view of the additional information this brings with regard to undescribed taxa and period where others were described.

² Taxa lacking epithets are morphologically distinct species level taxa as yet unidentified to species; taxa with epithets followed by "ined." have been tentatively determined as new to science but are not yet formally described

³ Percentage of 630,100 m² subplots in three 1-ha plots in which taxon occurred over 7 years of sampling. Taxa within genera were listed in descending order of frequency of occurrence

⁴ TH numbers are in Terry Henkel's collection series (housed at Humboldt State University); MCA numbers are in M. Catherine Aime's collection series (Louisiana State University); SLM numbers are in Steven L. Miller's collection series (University of Wyoming); MES numbers are in Matthew E. Smith's collection series (Duke University); numbers in bold are type collections

Total number of species is 126

sensu stricto (*Entolomataceae*; Largent et al. 2008), *Phyllobolites* (*Paxillaceae* sensu lato), *Scleroderma* and *Tremellogaster* (*Sclerodermatineae*), *Sarcodon* (*Bankeraceae*), and an additional sequestrate *Boletaceae* species of undetermined generic affinity. Addition of

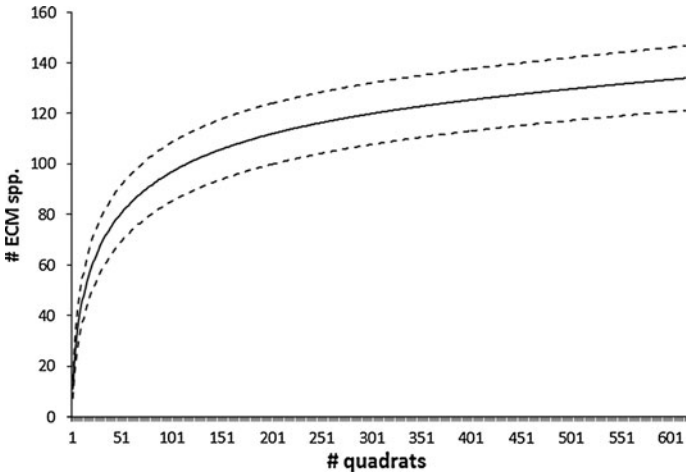


Fig. 2 Combined plots species accumulation curve for ECM fungi sampled in 100 m² quadrats in three 1-ha plots of *D. corymbosa*-dominated forest in the Upper Potaro Basin of Guyana, over 7 years between 2000 and 2008; 630 quadrats were sampled. *Upper* and *lower* lines represent 95% confidence intervals

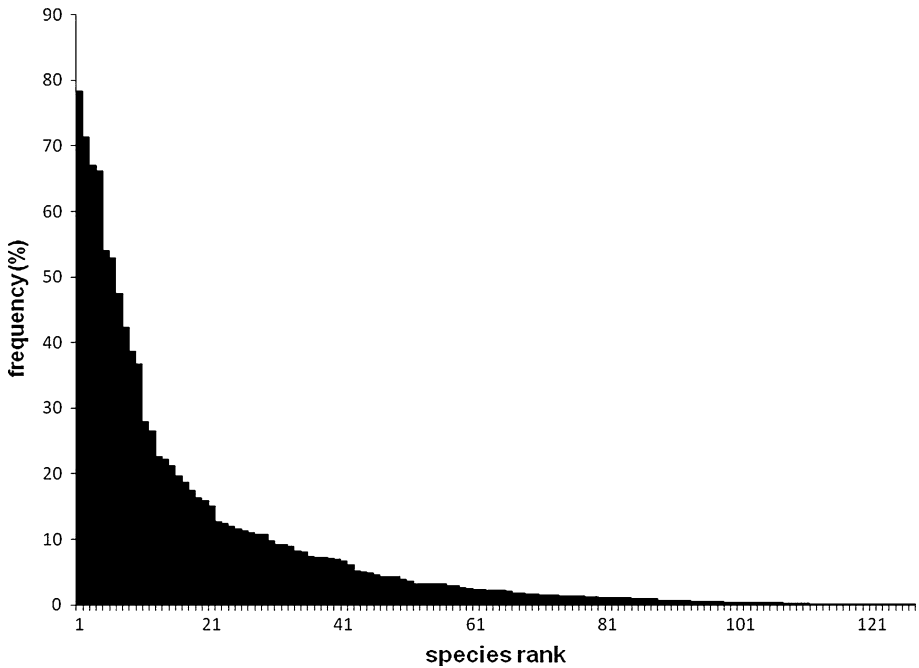


Fig. 3 Dominance-diversity curve for 126 ECM fungal species occurring in three 1-ha study plots of *D. corymbosa*-dominated forest over 7 years from 2000 to 2008 in the Upper Potaro Basin, Guyana. Frequency-based on species occurrence in 630,100 m² quadrats

off-plot taxa yields a currently known regional ECM fungal sporocarp diversity of 172 species. Fifty-six of these have been confirmed via molecular methods as ECM symbionts (Table 4; Smith et al. 2011; unpublished data).

Table 2 Frequency, number of sporocarps, and fruiting substratum of ECM fungi occurring at $\geq 10\%$ frequency on three 1-ha study plots of *D. corymbosa*-dominated forest over 7 years between 2000 and 2008 in the Upper Potaro Basin, Guyana

Species	Frequency (%) ¹	# Sporocarps ²	Fruiting substratum ³
<i>Clavulina sprucei</i>	78.4	34973	ETR, EH
<i>Clavulina amazonensis</i>	71.4	7876	E
<i>Tremellodendron ocreatum</i>	67.0	5038	E
<i>Cantharellus atratus</i>	66.2	3700	ETR
<i>Lactarius humicola</i> ined.	54.0	1174	EH
<i>Clavulina caespitosa</i>	52.9	2579	E
<i>Russula campinensis</i> .	47.5	18606	ETR
<i>Craterellus excelsus</i>	42.4	1824	E
<i>Clavulina tepurumenga</i>	38.7	1946	E
<i>Clavulina humicola</i>	36.8	10277	ETR, EH
<i>Pseudotulostoma volvata</i>	27.9	477	E
<i>Clavulina monodiminutiva</i>	26.5	19972	ETR
<i>Inocybe ayangannae</i>	22.7	291	E
<i>Tylopilus potamogeton</i> var. <i>irengensis</i>	22.2	307	E
<i>Inocybe pulchella</i>	21.3	330	ETR
<i>Russula metachromatica</i> ssp. <i>tarumaensis</i>	19.7	240	EH
<i>Tylopilus exiguus</i>	18.7	228	ETR
<i>Clavulina dicymbetorum</i>	17.5	726	E
<i>Elaphomyces squamatus</i> ined.	16.3	426	E
<i>Cortinarius</i> aff. <i>galeriniformis</i> complex	15.9	146	E
<i>Clavulina nigricans</i>	15.1	209	E
<i>Russula</i> aff. <i>puiggarii</i> complex #1	12.7	108	E
<i>Clavulina pakaraimensis</i> ined.	12.4	1491	E
<i>Inocybe epidendron</i>	12.1	136	ETR
<i>Xerocomus luteus</i> ined.	11.6	142	E
<i>Lactarius panuoides</i>	11.3	2413	ESUB
<i>Boletellus exiguus</i>	11.0	143	ETR
<i>Clavulina griseohumicola</i>	10.8	6664	ETR, EH
<i>Sebacina incrustans</i>	10.8	117	EH
<i>Amanita craseoderma</i>	10.0	63	E

¹ Percentage of 630,100 m² subplots in three 1-ha plots in which taxon occurred over 7 years of sampling

² Individual sporocarps were counted in each quadrat of occurrence for 2000–2004 and 2006

³ Fruiting substratum is point of origin or attachment of sporocarps during development; *E*, mineral soil/organic layer interface; *EH*, on well defined, partially decomposed organic materials in upper litter horizons on forest floor; *ETR*, on organic matter deposits on elevated positions above the ground line on trunks of *D. corymbosa*; *ESUB*, developing from a pre-established hyphal subiculum on surfaces above groundline

Discussion

Plot-based macrofungal studies in the Neotropical lowlands

There have been very few plot-based studies of macrofungal diversity in the Neotropical lowlands and most included <1 year of sampling and focused on non-ECM fungi. Litter



Fig. 4 Five frequently occurring ECM fungi among prominent families in the *Dicymbe* plots. **a** *Tylopilus potamogeton* var. *irengensis* (Boletaceae). Note the blue ammonia stains on pileus characteristic of *Tylopilus* sect. *Potamogetones*. **b** *Russula campinensis* (Russulaceae). Note tiny pleurotooid basidiomata and exposed subtending ectomycorrhizas. **c** *Cantharellus atratus* (Cantharellaceae). **d** *Amanita craseoderma* (Amanitaceae). **e** *Tremellodendron ocreatum* (Sebacinaceae sensu lato). Bars = 10 mm

saprotrophs have been systematically sampled in Ecuador (Hedger 1985; Lodge and Cantrell 1995), Puerto Rico (Lodge and Cantrell 1995) and Brazil (Braga-Neto et al. 2008) but only two Brazilian studies have sampled ECM sporocarps in plots (Singer and Araujo 1979; Singer and Araujo-Aguiar 1986). The diversity and host preferences among polypores and other wood saprotrophs have also been studied with repeated sampling in Costa Rica (Lindblad 2001), Panama (Gilbert et al. 2002a, b), and Puerto Rico (Schmit

Table 3 Ectomycorrhizal fungal taxa recorded outside of the 1-ha study plots in *Dicymbe*-dominated forests from 2000 to 2010 in the Upper Potaro River Basin, Guyana

Family	Species ^{1,2}	Representative vouchers ³
<i>Boletaceae</i>	<i>Austroboletus festivus</i> (Singer) Wolfe	TH 8164, 8732
	<i>Fistulinella cinereoalba</i> Fulgenzi & T.W. Henkel	TH 8471 , 9233, MCA 964
	<i>Pulveroboletus</i> cf. <i>rosaemariae</i> Singer	TH 8232
	<i>Tylophilus pakaraimensis</i> T.W. Henkel	TH 6610 , 8965, MCA 1024
	<i>Xerocomus</i> sp. 3	TH 9585, MCA 4004
<i>Amanitaceae</i>	<i>Amanita calochroa</i> C.M. Simmons, T.W. Henkel & Bas	TH 6426 , MCA 1075, 3927
	<i>Amanita campinaranae</i> Bas	TH 8453, 9552, MCA 3940
	<i>Amanita cyanopus</i> C.M. Simmons, T.W. Henkel & Bas	TH 7083 , 8912
	<i>Amanita cyanochlorinosma</i> ined.	TH 8375, 9172, MCA 3962
	<i>Amanita floccosus</i> ined.	TH 8247, 9110, MCA 4423
	<i>Amanita</i> sp. 12	TH 9128
	<i>Amanita</i> sp. 13	TH 9251
<i>Bankeraceae</i>	<i>Sarcodon pakaraimensis</i> ined.	TH 9513
	<i>Cantharellaceae</i>	<i>Cantharellus</i> cf. <i>hystrix</i> Corner
<i>Clavulinaceae</i>	<i>Craterellus atratoides</i> ined.	TH 9232, MCA 1313
	<i>Clavulina cerebriformis</i> Uehling, T.W. Henkel & Aime	MCA 4022
<i>Coltriciaeae</i>	<i>Clavulina albofragilis</i> ined.	TH 8987
	<i>Coltricia cinnamomea</i> (Jacq.) Murrill	MCA 1601
<i>Cortinariaceae</i>	<i>Cortinarius</i> sp. 2	TH 9115, MCA 3899
	<i>Cortinarius</i> sp. 3	TH 8613, MCA 1838, 4033
	<i>Cortinarius</i> sp. 4	TH9 124, MCA 2412
<i>Elaphomycetaceae</i>	<i>Elaphomyces compleximurus</i> Castellano, T.W. Henkel & S.L. Mill	TH 8880
<i>Entolomataceae</i>	<i>Entoloma fragilum</i> Largent & Aime	MCA 2415
	<i>Entoloma illinitum</i> Largent & Aime	MCA 2488
	<i>Entoloma olivaceocoloratum</i> Largent & T.W. Henkel	TH 8855 , 9136
	<i>Entoloma rugosostriatum</i> Largent & T.W. Henkel	TH 6766
	<i>Entoloma</i> sp. 1	TH 9118
	<i>Entoloma</i> sp. 2	TH 9137
<i>Inocybaceae</i>	<i>Inocybe amazoniensis</i> Singer	MCA 3142
	<i>Inocybe</i> cf. <i>matrisdei</i> Singer	MCA 3917
	<i>Inocybe megalocarpa</i> ined.	MCA 1822, 2441, TH 9132
<i>Paxillaceae</i>	<i>Phyllobolites miniatus</i> (Rick) Singer	TH 8525
<i>Russulaceae</i>	<i>Russula</i> sp. 5	MCA 3957
	<i>Russula</i> sp. 6	MCA 1856
	<i>Russula</i> sp. 7	TH 9568

Table 3 continued

Family	Species ^{1,2}	Representative vouchers ³
	<i>Russula</i> sp. 8	TH 9157
	<i>Russula</i> sp. 9	TH 9140
	<i>Lactarius</i> cf. <i>annulifer</i> Singer	TH 9014
<i>Sclerodermataceae</i>	<i>Scleroderma sinnamariense</i> Mont.	TH 8281, MCA 2168
	<i>Scleroderma</i> sp. 1	MES 350
	<i>Tremellogaster surinamensis</i> E. Fisch.	MCA 1164, 1985, SLM 10112
<i>Sebacinaceae</i>	<i>Sebacina</i> sp. 2	TH 8622
<i>Thelephoraceae</i>	<i>Tomentella</i> sp. 5	TH 9569
Indet.	<i>Boletaceae</i> sequestrate incertae sedis #2	TH 9514
	<i>Boletaceae</i> sequestrate incertae sedis #3	TH 9061, 9067

¹ Author citations of scientific names are included here, as an exception to journal policy, in view of the additional information this brings with regard to undescribed taxa and period where others were described.

² Taxa lacking epithets are morphologically distinct species level taxa as yet unidentified to species; taxa with epithets followed by “ined.” have been tentatively determined as new to science but are yet to be formally described

³ *TH* numbers are in Terry Henkel’s collection series (housed at Humboldt State University); *MCA* numbers are in M. Catherine Aime’s collection series (Louisiana State University); *SLM* numbers are in Steven L. Miller’s collection series (University of Wyoming); *MES* numbers are in Matthew E. Smith’s collection series (Duke University); numbers in bold are type collections

Total number of species is 46

2005). Non-plot-based lists of macrofungi including a few taxa in ECM families or genera have recently appeared for lowland Colombia (Vasco-Palacios et al. 2005) and Ecuador (Petersen and Læssøe 2008). In Mexico, recent plot studies have enumerated macrofungal richness but focused primarily on montane sites dominated by *Quercus*, *Fagus*, or *Pinus* and recovered ECM fungi with north-temperate rather than tropical affinities (Munguia et al. 2003, 2005; Gomez-Hernandez and Lilliams-Linera 2011). Moyersoen (1993) listed several ECM fungal species associated with *Aldina* and *Nyctaginaceae* hosts in Venezuela.

Singer and Araujo (1979) studied ECM fungi on plots in white sand campinarana forest near Manaus, Brazil, and replicated the study in seasonally flooded igapo forest on the Rio Negro (Singer and Araujo-Aguiar 1986). Each study suffered from short sampling periods (6 months to 1 year) and non-replicated plot designs. Nonetheless, their results were consistent with those from Guyanese forests (Henkel et al. 2002) in showing that both ECM host plants and ECM sporocarps were restricted to specific forest types (e.g., upland white sand campinarana and periodically inundated igapo). Furthermore, ECM sporocarps were reliably absent from adjacent forests without ECM plants. The Brazilian and Guyanese forests were similar in having high diversity and frequency of *Boletaceae* and *Russulaceae*. These forests also shared some ECM species (e.g., *Amanita xerocybe*, *Amanita craseoderma*, *Tylopilus potamogeton*, *Cantharellus guyanensis*) that are endemic to the greater Guiana Shield region (Henkel 1999; Simmons et al. 2001; Henkel et al. 2004a).

The great discrepancy in ECM fungal species richness between the Guyanese *Dicymbe* plots reported here (126 spp.) and Singer’s campinarana (36 spp.) and igapo (18 spp.) sites must in large part be due to disproportionate sampling effort, making comparisons tenuous.

Table 4 Fifty six ECM fungal sporocarp species or species complexes recorded within the three 1-ha *Dicymbe* plots and off-plot in this study that have been confirmed as ECM symbionts by ITS sequence-matching with ECM roots in a study of Smith et al. (2011)¹ and unpublished data² of Henkel, Smith, Aime and Matheny in the Upper Potaro Basin of Guyana

Family	Species	Sequenced sporocarp voucher
<i>Amanitaceae</i>	<i>Amanita</i> sp. 3	TH 9128
	<i>Amanita</i> sp. 12	TH 8931
<i>Boletaceae</i>	<i>Austroboletus rostrupii</i>	TH 8189
	<i>Boletellus ananas</i> var. <i>ananas</i>	TH 9188
	<i>Boletellus exiguus</i>	TH 9189
	Boletaceae sequestrate incertae sedis #1	TH 9163
	<i>Gyroporus</i> aff. <i>castaneus</i>	TH 8915
	<i>Pulveroboletus</i> cf. <i>rosaemariae</i>	TH 8232
	<i>Pulveroboletus viridisquamulosus</i> ined.	TH 9154b
	<i>Tylopilus ballouii</i>	TH 8916
	<i>Tylopilus cyanostipitatus</i> ined.	TH 8805
	<i>Tylopilus exiguus</i>	TH 8929
	<i>Tylopilus orsonianus</i>	TH 8926
	<i>Tylopilus pakaraimensis</i>	TH 8965
	<i>Tylopilus potamogeton</i> var. <i>irengensis</i>	TH 8801
	<i>Tylopilus vinaceipallidus</i>	TH 8859
	<i>Xerocomus amazonicus</i> complex	TH 8839
	<i>Xerocomus luteus</i> ined.	TH 8802
<i>Xerocomus exiguus</i> ined.	TH 8850	
<i>Cantharellaceae</i>	<i>Cantharellus atratus</i> complex	TH 9203
	<i>Cantharellus</i> cf. <i>hystrix</i>	TH 9204
	<i>Craterellus olivaceoluteum</i> ined.	TH 8913
<i>Clavulinaceae</i>	<i>Clavulina cerebriformis</i>	MCA 4022
	<i>Clavulina humicola</i>	TH 8737
	<i>Clavulina monodiminutiva</i>	TH 8738
	<i>Clavulina sprucei</i> complex #1	MCA 3989
	<i>Clavulina sprucei</i> complex #2	TH 9122
	<i>Clavulina sprucei</i> complex #3	TH 8221
<i>Cortinariaceae</i>	<i>Cortinarius</i> aff. <i>amazonicus</i> complex #1	MCA 3928
	<i>Cortinarius</i> aff. <i>amazonicus</i> complex #2	TH 9113
	<i>Cortinarius</i> aff. <i>galeriniformis</i> complex #1	MCA 2318
	<i>Cortinarius</i> aff. <i>galeriniformis</i> complex #2	TH 8546
	<i>Cortinarius</i> sp. 1	MCA 3969
<i>Elaphomycetaceae</i>	<i>Pseudotulostoma volvata</i>	TH 8975
<i>Inocybaceae</i>	<i>Inocybe ayangannae</i>	TH 8160
	<i>Inocybe epidendron</i>	TH 9186
	<i>Inocybe marginata</i> ined.	MCA 3917
	<i>Inocybe pulchella</i>	TH 9185
	<i>Inocybe lepidotella</i> ined.	MCA 1881
<i>Russulaceae</i>	<i>Lactarius brunellus</i>	TH 9130
	<i>Lactarius lignyophilus</i> ined.	TH 9239

Table 4 continued

Family	Species	Sequenced sporocarp voucher
	<i>Lactarius multiceps</i>	TH 9154a
	<i>Lactarius panuoides</i>	TH 7460
	<i>Lactarius subiculata</i> ined.	TH 7922
	<i>Lactarius humicola</i> ined.	TH 7578
	<i>Russula</i> aff. <i>pluvialis</i>	TH 7940
	<i>Russula</i> aff. <i>puiggarii</i> complex #2	MCA 3954
	<i>Russula campinensis</i>	TH 7403
	<i>Russula</i> cf. <i>ammicola</i>	TH 7446
	<i>Russula formicarius</i> ined.	TH 9145
	<i>Russula metachromatica</i> ssp. <i>metachromatica</i>	TH 7698
	<i>Russula rubroglutinata</i> ined.	TH 7949
	<i>Russula</i> sp. 2	MCA 4008
	<i>Russula</i> sp. 4	TH 7880
	<i>Russula</i> sp. 6	MCA 1856
<i>Thelephoraceae</i>	<i>Tomentella</i> sp. 1	MES 348
	<i>Tomentella</i> sp. 3	TH 8977

¹ ITS sequences available on GenBank; obtained from ectomycorrhizas of *D. corymbosa*, *Dicymbe altonii*, or *Aldina insignis*; see Smith et al. (2011) ECM fungal diversity and community structure on three co-occurring leguminous canopy tree species in a Neotropical rainforest. New Phytol doi:10.1111/j.1469-8137.2011.03844.x

² Taxa in bold have been recovered on ECM roots of *D. corymbosa* within a study plot reported here

Additionally, certain taxa now known to be ECM (e.g., *Tomentella*, *Sebacina*) may have been overlooked or ignored by Singer. Nonetheless, the Guyanese *Dicymbe* forests appear to have a higher alpha-diversity. A contributing factor may be that *D. corymbosa* maintains stand basal area proportions of 60–90% and has enormous numbers of seedlings and saplings in the Guyana plots, which results in complete dominance of fine roots available for ECM fungi (Henkel 2003). The ample resources available to ECM fungi should allow for greater “species packing” over time and result in higher alpha-diversity (Schmit 2005). At Singer’s Brazilian sites, no data were given on relative proportions of confirmed ECM trees, although species of the main ECM-forming papilionoid host genus *Aldina* are common in the region (Mardegan et al. 2009).

Although the proportion of *Aldina* spp. at Singer’s campinarana or igapo sites is unknown, the densities of these hosts are unlikely to reach the extreme conspecific density and biomass levels found for *D. corymbosa* in Guyana (Henkel 2003). If this is the case, resources available for ECM fungi would be reduced in *Aldina* stands and overall symbiotic activity and mycobiont diversity more modest (Schmit 2005). Conversely, the capacity of *Aldina* spp. to host a diverse assemblage of ECM fungi cannot be discounted. Smith et al. (2011) found that the Guyanese canopy tree *Aldina insignis* hosted a similar level of belowground ECM fungal diversity as two sympatric *Dicymbe* spp., even though *A. insignis* occurred as scattered mature individuals in stands otherwise heavily dominated by *Dicymbe*. While site-specific studies of ECM fungi in the lowland Neotropics are extremely limited, Guyanese *Dicymbe* forests appear to be the most ECM-diverse sites currently known.

Diversity of Guyana ECM fungi relative to the greater Neotropics

Singer et al. (1983) composed the only existing monographic study on Neotropical ECM fungi. All known ECM fungal taxa from lowland tropical sites of South America, Central America, and the Caribbean were included, along with taxa from *Quercus*- or *Pinus*-dominated sites of Central America. The monograph was based on taxa listed or described by Singer and colleagues, Dennis (1970), Pegler (1983), and in other primary literature including Bas (1978) for *Amanita*. Among the Brazilian lowland sites, a total of 80 ECM fungal species were reported from 19 genera in 11 families. An additional 63 species are noted for Central America and the Caribbean, totaling 143 known ECM fungal species for the lowland Neotropics in 1983. Since then, collecting and taxonomic study have added a number of new species or distribution records for ECM fungi from *Quercus* forests of Costa Rica (e.g., Singer et al. 1991; Halling and Mueller 2001, 2002; Buyck and Halling 2004), Panamanian lowland rainforest (e.g., Buyck and Ovrebo 2002), Northern Caribbean islands (e.g., Miller et al. 2000), and Eastern Brazil (Wartchow et al. 2010).

Collectively these efforts yield a conservative and rough estimate of the total ECM fungal sporocarp species known from the lowland Neotropics (not including Guyana) of 150–200 described species. The Upper Potaro site in Guyana thus has a similar level of ECM fungal diversity as that known from the entire remainder of the lowland Neotropics, with 172 species currently known from a single local collecting area. The majority of the Guyana taxa have been or will be described as new to science and this will continue to drastically increase the number of ECM fungi known from the Neotropics.

Comparison with ECM fungal diversity of north temperate and boreal sites

Plot-based ECM fungal sporocarp diversity studies in the north temperate and boreal zones vary markedly in the area sampled, frequency of sampling, study duration, relative proportion of ECM trees, stand age, and overall vegetative composition. Variation in these factors makes it difficult to compare ECM fungal alpha-diversity between sites. Leacock (1997) summarized modern plot-based results but several important studies have been published since that time (e.g., O'Dell et al. 1999; Straatsma et al. 2001; Straatsma and Krisai-Greilhuber 2003; Richard et al. 2004).

Several temperate studies that focused on late-seral or old growth forests found ECM fungal diversity comparable to our study. Salo (1993) found 125 ECM fungal species in late-seral coniferous and mixed forests of Finland over 1 year of repeated sampling in 5.96 ha. These results are remarkably similar to the 126 spp. found at the Potaro site over 7 years with a cumulative sampling area of 6.3 ha. Similarly, ECM sporocarp richness of 100–200 spp. has been found in forests as diverse as nutrient poor spruce in Norway (Gulden et al. 1992), Northern hardwood-conifer forests of Quebec (Nantel and Neumann 1992), mixed *Pseudotsuga-Tsuga* forests of Washington (O'Dell et al. 1999), old growth stands of red pine in Minnesota (Leacock 1997), and old growth *Quercus ilex* forests of Corsica (Richard et al. 2004). Total sampling area and sampling periods for these studies ranged from 0.25 to 10.2 ha and 2 to 4 years. Other studies with smaller sampling areas may have found high species richness per sampling unit (e.g., Bills et al. 1986; Villeneuve et al. 1989). While numerous caveats influence the interpretation of sporocarp-based diversity studies, it nonetheless seems safe to conclude that the ECM fungal alpha-diversity recorded in Guyana's *Dicymbe* forests is comparable to that of ECM-diverse Holarctic forests. These results conflict with the hypothesis of Tedersoo and Nara (2010) that ECM

fungi follow a “reversed” latitudinal gradient whereby temperate sites host higher levels of ECM fungal diversity than those of the tropics.

New taxon discovery

It is clear from ongoing taxonomic study that many Guyanese ECM fungi are new to science. Of the 126 ECM species found in the study plots, 23.0% (29) were previously described from other regions, 53.2% (67) have been described or determined as new species or varieties from Guyana, and 23.8% (30) require further study (Table 1). Of the additional 46 “off-plot” species, 23.9% (11) were previously described, 34.8% (16) have been described or determined as new, and 19 require further study (Table 3). Thus, of the 172 recognized morphospecies, 48.2% (83/172) have been described or determined as new from Guyana to date. Preliminary determinations indicate that many indet. taxa are new to science and await formal description (Henkel et al. unpublished data).

In the speciose *Agaricomycetes* families from Guyana that have been well studied, new species discovery rates are extremely high. For *Clavulinaceae*, 17/19 (89.5%) of known species have been or are likely to be described as new (Thacker and Henkel 2004; Henkel et al. 2005a, 2011; Uehling et al. 2011). A similar situation holds for *Inocybaceae*, where 8/11 (72.7%) of known species have been or will be described as new (Matheny et al. 2003, 2011). For *Amanita*, 4/6 taxa included by Simmons et al. (2001) were described as new, and the remaining two species (*Amanita lanivolva* and *A. xerocybe*) were previously described from Singer’s Brazilian sites (Table 1; Bas 1978). Additional Brazilian *Amanita* (e.g., *A. campinaranae*) occur in Guyana, but many of the remaining undetermined *Amanita* spp. appear new to science. The situation is different for the genus *Russula*, which has been more thoroughly characterized in the Neotropics (Dennis 1970; Singer et al. 1983; Pegler 1983; Buyck and Ovrebo 2002). In *Russula* 68.8% (11/16) of species that have been determined from Guyana were previously described, although some determinations remain tentative. Overall, with ~44% of the ECM taxa remaining to be formally described or requiring further study, new taxon discovery rates will likely remain between 60 and 70%.

Alternative sporocarp production strategies of ECM fungi in *D. corymbosa* forests

Many ECM fungi recovered in this study are typically terrestrial and produce their sporocarps on the forest floor at the interface between the mineral soil and the organic layer. However, numerous ECM fungi regularly produce sporocarps above the forest floor in *D. corymbosa* forests. Due to the complex reiterative morphology of mature *D. corymbosa* trees, large amounts of litter and humus accumulate aboveground on root mounds and tree pseudotrunks, and are permeated by adventitious *Dicymbe* roots and ectomycorrhizas (Henkel 2003; Woolley et al. 2008). The sporocarps of many of the typically terrestrial taxa can occasionally be found on these elevated organic soils but a number of species appear to exclusively produce sporocarps at elevated positions. For most of these species the basidiomata arise directly from humic deposits on trees up to 2+ m above the forest floor. Within the ECM assemblage on the plots, basidiomata of 20 species among the *Boletaceae*, *Cantharellaceae*, *Coltriciaceae*, *Inocybaceae*, and *Russulaceae* were found only in elevated positions (Henkel 1999; Henkel et al. 2000, 2006a; Aime et al. 2003, 2007; Matheny et al. 2003; Mayor et al. 2008; Fulgenzi et al. 2008; Neves et al. 2010). An additional group of six species were usually found in elevated positions, but were also sometimes found at ground level arising from deep litter (e.g., *Boletellus ananas*, *Clavulina sprucei*, *C. humicola*) (Mayor et al. 2008; Henkel et al. 2005a, 2011). It was also

notable that many of the “obligately elevated” taxa were among the most frequent and prolific sporocarp producers (Table 2).

Lactarius panuoides, *L. brunellus*, *L. multiceps*, and *L. subiculatus* form perennial subicula from which multiple flushes of tiny pleurotoid or centrally-stipitate basidiomata arise (Henkel et al. 2000; Miller et al. 2002; Miller and Henkel 2004). Additionally, subiculate and resupinate ECM taxa “climb” living seedlings via apogeotropic rhizomorph extension, forming subicula and/or basidiomata 20–30 cm above the ground on stems, leaves, branches, and fallen logs (e.g., *Clavulina effusa*, pleurotoid *Lactarius*, *Tomentella* and *Sebacina* spp.) (Miller and Henkel 2004; Henkel et al. 2004b; Uehling et al. 2011).

Pseudotulostoma volvata (*Elaphomycetaceae*) forms epigeous ascomata with a powdery, spore-bearing gleba elevated on a stalk >5 cm above the ground. The ascospores are dispersed via rain splash during the rainy season (Miller et al. 2001; Henkel et al. 2006b). The closest relatives of *Pseudotulostoma* are *Elaphomyces* spp., vertebrate-dispersed false truffles that develop belowground. A number of other agarics that arise directly from the forest floor have grossly accentuated stipe lengths, such as *Cortinarius* aff. *kerrii* which reaches heights of 20–30 cm or more. Overall, the propensity for elevated sporocarp production, whether on humic deposits on tree trunks, by subiculum development, or via enhanced stipe lengths, may be an adaptive syndrome for effective rainy season spore dispersal (Miller and Henkel 2004). Given the highly saturated conditions of the forest floor in Guyana *Dicymbe* forests, it is not surprising that these features have evolved in numerous unrelated fungal lineages. A study is in progress in the plots reported here to determine whether mycorrhizas of these species are restricted to elevated organic soils (Smith and Henkel, unpublished data).

Unusual morphologies of ECM fungi

Many ECM fungi from Guyanese *Dicymbe* forests have unusual features that deviate from the “typical” morphologies of their temperate relatives (Fig. 5). Some species of the typically clavarioid *Clavulina* have basidiomata that are infundibuliform and *Craterellus*-like (*C. craterelloides*; Thacker and Henkel 2004) or resupinate to effusor-coralloid (*C. cinereoglebosa*, *C. cerebriformis*, and *C. effusa*; Uehling et al. 2011). Species in numerous genera have extremely small basidiomata atypical of their respective genera (e.g., *Inocybe epidendron*, *I. pulchella*, *Cantharellus pleurotoides*, *L. panuoides*, *L. brunellus*, *L. multiceps*, *Tylopilus exiguus*, *Boletellus exiguus*, *Amanita* sp. 4, *Clavulina monodiminutiva*, *Russula campinensis*, *Coltriciella navispora*) (Matheny et al. 2003; Aime et al. 2003; Henkel et al. 2005a). Also, numerous species combine diagnostic features of multiple genera (e.g., *T. exiguus*, *T. cyanostipitatus*, *C. pleurotoides*) (Henkel 1999; Henkel et al. 2006a). The evolutionary significance of these morphological syndromes is unclear but such morphological divergence often requires reassessment of generic concepts (e.g., Henkel 1999; Thacker and Henkel 2004; Uehling et al. 2011).

Insights into belowground diversity of ECM fungi in *Dicymbe* forests

It has been well-established since Gardes and Bruns (1996) and Horton and Bruns (2001) that site-specific ECM fungal sporocarp diversity may not correspond to the ECM community found on ECM roots. Sporocarp enumerations often underestimate total ECM fungal diversity because molecular root surveys regularly yield additional unknown species



Fig. 5 Four ECM species from Guyana with unusual macromorphologies for the genus or family in which they occur. **a** *Clavulina craterelloides* (*Clavulinaceae*). **b** *Clavulina cerebriformis* (*Clavulinaceae*) (from Uehling et al. 2011). **c** *Pseudotulostoma volvata* (*Elaphomycetaceae*). **d** *Lactarius panuoides* (*Russulaceae*). Bars 10 mm

(reviewed in Smith and Read 2008). Assigning molecular barcode data to identifiable, nameable sporocarp species is especially important for tropical ECM fungal studies as local sporocarp species are likely to be new and not previously represented on sequence databases such as GenBank. In recent molecular studies of tropical ECM systems, this disjunct has been compounded because few, if any, efforts were made to collect or quantify sporocarps. Instead researchers have relied on sequence databases to identify DNA sequences from tropical ECM roots to lineage and species level operational taxonomic units (OTUs) rather than compare them with site-specific databases of ECM sporocarps to identify some, at least, directly to species (e.g., Diédhiou et al. 2010; Peay et al. 2010; Tedersoo et al. 2010b). Such root-based studies have recovered between 39 and 111 ECM fungal ITS-OTUs. Tropical studies integrating sporocarp and ECM root data are limited to

Riviere et al. (2007) where a combined 199 ECM fungal species were found in association with African caesalpinoid and *Phyllanthaceae* hosts (but see Tedersoo et al. 2007 for the Seychelles). In Guyanese *Dicymbe* forests the large ECM sporocarp diversity is well-documented and the ITS rDNA barcode region has been sequenced for nearly all of the 172 ECM fungal sporocarp species (Smith et al. 2011, Smith and Henkel, unpublished data). While 56 out of 172 ECM Guyanese sporocarp species have been unequivocally confirmed as ECM symbionts of leguminous hosts based on molecular matches with ECM roots (Table 4), the potential for “missing” ECM fungal diversity in these systems is becoming evident.

Smith et al. (2011) examined the diversity of ECM fungi on the roots of three sympatric ECM leguminous canopy tree species, *Dicymbe altsonii*, *D. corymbosa*, and *Aldina insignis*. Nineteen individuals of each host species were sampled over ~ 1 km² of primary forest located ~ 10 km east of the Potaro site reported here. Of the 118 spp. of ECM fungi recovered from roots across the three hosts, 71 (60.2%) were not represented in the regional sporocarp database and probably represent unique, unsampled species. Recently, Henkel and Smith (unpublished data) sampled ECM roots from large, reiterated *D. corymbosa* trees in each of the three sporocarp sampling plots reported here. Preliminary analysis of the resulting root fungal ITS data indicated that $\sim 50\%$ of the sequences did not correspond with sporocarp species found in the same plots. Therefore, with 172 regional ECM fungal species known from sporocarps, simple extrapolation gives a conservative estimate of at least 258 total ECM fungal species in the Upper Potaro region. Clearly, a full assessment of aboveground and belowground diversity will reinforce the recognition that *Dicymbe* forests are a hotspot for Neotropical ECM fungal diversity.

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