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Diversity and distribution of tropical ectomycorrhizal fungi

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ABSTRACT

The tropics were long considered to have few ectomycorrhizal fungi, presumably due to a paucity of ectomycorrhizal host plants relative to higher-latitude ecosystems. However, an increase in research in tropical regions over the past 30 years has greatly expanded knowledge about the occurrence of tropical ectomycorrhizal fungi. To assess their broad biogeographic and diversity patterns, we conducted a comprehensive review and quantitative data analysis of 49 studies with 80 individual data sets along with additional data from GlobalFungi to elucidate tropical diversity patterns and biogeography of ectomycorrhizal fungi across the four main tropical regions: the Afrotropics, the Neotropics, Southeast Asia, and Oceania. Generalized linear models were used to explore biotic and abiotic influences on the relative abundance of the 10 most frequently occurring lineages. We also reviewed the available literature and synthesized current knowledge about responses of fungi to anthropogenic disturbances, and their conservation status and threats. We found that /russula-lactarius and /tomentella-thelephora were the most abundant lineages in the Afrotropics, the Neotropics, and Southeast Asia, whereas /cortinarius was the most abundant lineage in Oceania, and that /russula-lactarius, /inocybe, and /tomentella-thelephora were the most species-rich lineages across all of the tropical regions. Based on these analyses, we highlight knowledge gaps for each tropical region. Increased sampling of tropical regions, collaborative efforts, and use of molecular methodologies are needed for a more comprehensive view of the ecology and diversity of tropical ectomycorrhizal fungi.

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INTRODUCTION

Tropical forests containing ectomycorrhizal (ECM) associations have unique species compositions and ecologies of both plant and fungal symbionts (Corrales et al. 2018). Such ecosystems were long thought to be rare or even absent from most of the tropics (e.g., Pirozynski 1981). Tropical forests are sometimes dominated by ECM plants; these systems may contain a diverse assemblage of ECM fungi, including many undescribed taxa (e.g., Corrales and Ovrebo 2021; Ebenye et al. 2017; Henkel et al. 2012; Watling and Lee 1998). Knowledge about tropical ECM fungal communities has improved over the past three decades due to increased exploration of undersampled regions, environmental sampling from roots and soil, and collection, description, and sequencing of sporocarp specimens (Corrales et al. 2018). Although many recent studies have expanded the available data on tropical ECM fungi, the biogeography and diversity patterns of tropical ECM fungi remain unclear at the global scale (e.g., Cameron et al. 2018).

A previous review about ECM associations in the tropics (Corrales et al. 2018) revealed some biogeographic patterns of tropical ECM host plants across continents and suggested that some ECM fungal lineages could be underrepresented or overrepresented in tropical ecosystems. However, quantitative information about the biogeographic patterns of tropical ECM fungi is still lacking. To fill this knowledge gap, we performed a quantitative data analysis and used available metabarcoding data sets to explore the following questions: (i) What are the most abundant and diverse ECM fungal lineages in the tropics? (ii) Do ECM fungal lineages vary in diversity and abundance across the different tropical regions? and (iii) Do biotic and abiotic

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factors influence regional diversity and abundance of tropical ECM fungi? We also compared long-term sporocarp inventories and root tip sequencing studies to see how the two methods differ in estimating ECM fungal community composition. In addition, we used available literature to review the conservation status and responses to anthropogenic disturbance of tropical ECM fungi.

Responses of tropical ECM fungi to natural and human disturbance.—Deforestation is a significant problem in tropical ectotrophic forests. Research about the effects of land use change on tropical soil fungal communities mostly comes from Southeast Asia, where widespread primary forests dominated by ECM Dipterocarpaceae are heavily logged, due to their high-quality timber, and subsequently converted to oil palm and rubber plantations (e.g., Pang et al. 2021). Recent studies have revealed a strong disturbance-driven change in fungal communities characterized by a decrease in ECM genera such as *Craterellus, Lactarius, Russula, Sebacina*, and *Tomentella* (Brinkman et al. 2019; Kerfahi et al. 2014; McGuire et al. 2015). Anthropogenic disturbance may also have disproportional effects in habitat islands harboring neotropical ECM fungi. Research in lowland arbuscular mycorrhiza (AM)-dominated forests in Panama (Schappe et al. 2020) found that ECM fungi community composition was strongly correlated with host species and basal area of ECM trees, whereas soil variables had a smaller but significant effect. In Guyana, Henkel et al. (2002) mapped ECM fungal sporocarp distribution inside and outside of stands dominated by ECM Fabaceae trees. They found that ECM trees were absent outside the ECM-dominated forest, and that host presence, not soil characteristics, determined the presence and community composition of ECM fungi. In a tropical rainforest on Hainan Island, China, Chen et al. (2019) studied the effects of logging on the ECM fungal community succession over 50 years of regeneration. They found an increase in the relative abundance of the /russula-lactarius lineage in logged forests compared with nearby primary forests. Overall abundance of ECM fungi was also negatively correlated with litter, soil calcium, and water content but was positively correlated with soil pH and bulk density. In contrast, Onguene (2021) reported that loss of host trees led to an almost complete loss of ECM fungi in early successional forests of southern Cameroon. All these studies point to the fact that land use change and successional stage could have strong impacts on tropical ECM fungal communities, including loss of host plants and other significant changes in environmental conditions.

Anthropogenic nitrogen deposition affects ECM fungi and plants in many forests (Lilleskov et al. 2019; Peter et al. 2008). The phenomenon has been less frequently studied in tropical ecosystems, probably because they were not historically believed to be limited by available nitrogen (Brookshire et al. 2012). In Panama, 9 years of nitrogen addition resulted in reduced overall ECM fungal abundance and root colonization in an *Oreomunnea mexicana* (Juglandaceae) forest, with an increase in *Laccaria* and *Lactarius* and a decrease in *Cortinarius* (Corrales et al. 2017). In a Chinese tropical forest, He et al. (2021) found that 2 years of nitrogen addition resulted in a 26% reduction in overall abundance of ECM fungi compared with control plots. However, after 13 years of nitrogen addition, they found no effect in the overall abundance or alpha diversity of ECM fungi. Nevertheless, there was a consistent decline in the relative abundance of *Inocybe* spp. and an increase in Russulaceae spp. Therefore, this apparent resilience of the overall fungal community to long-term nitrogen addition could be associated with comparative changes in abundance of sensitive and resistant species that helped maintain a similar overall relative abundance of ECM fungi. More studies in different systems are necessary to corroborate the generality of this pattern.

Natural changes in soil nitrogen conditions caused by natural disturbances may also alter ECM fungal communities. Alvarez-Manjarrez and Garibay-Orijel (2021) reported a reduction in ECM fungal diversity after hurricane impacts in a Mexican dry forest. They hypothesized that changes in ECM fungal communities were due to a disturbance-driven increase in available soil nitrogen leading to increases in nitrophilic ECM fungi. Tropical ECM fungi seem to show differential responses to nitrogen addition, similarly to what has been observed in temperate forest (Lilleskov et al. 2019). However, at this point, it is difficult to identify patterns due to a scarcity of information and incompatibility among the available studies.

Tropical ECM fungi conservation and IUCN data.—Globally, studies investigating threats to biodiversity rarely consider fungi. This situation is even more pronounced for tropical ecosystems. To date, only 550 species of fungi have been evaluated for the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, a paltry proportion of the 142 500 total red-listed species (IUCN 2022). Although nearly half of these 550 fungal species are ECM, only 33 of them are tropical (FIG. 1). This lack of distribution and population information for tropical ECM fungal species

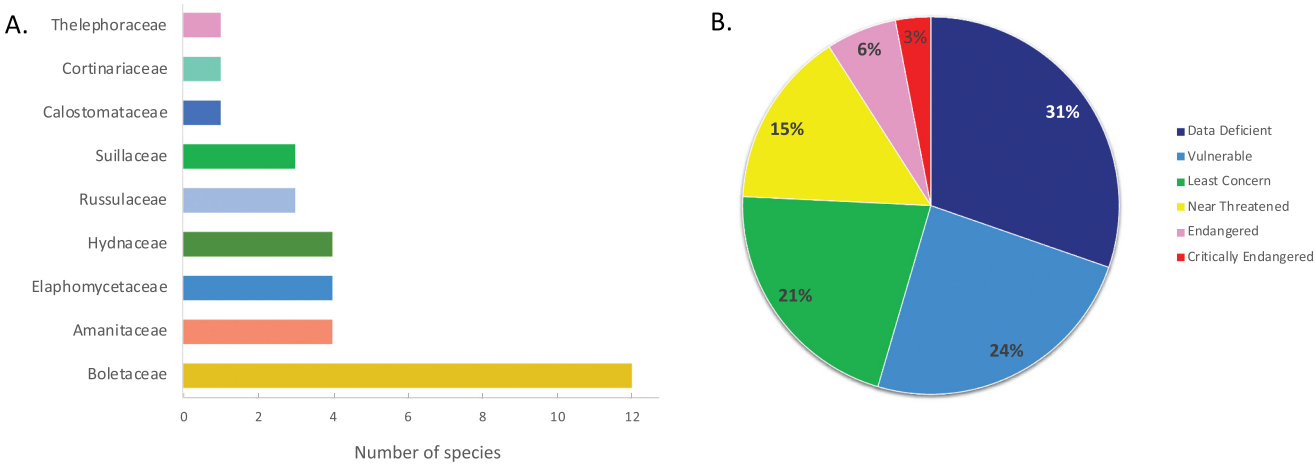

Figure 1. Distribution of the 33 species of tropical ECM fungi thus far evaluated by the IUCN grouped according to (A) Family and (B) conservation status. *Austroboletus amazonicus* is considered Critically Endangered, whereas *Calostoma insigne* and *Spongiforma squarepantsii* are listed as Endangered. According to the IUCN assessment, extremely high rates of habitat loss and small population size are the major threats for these taxa.

hampers conservation efforts (Simijaca et al. 2022). For example, 31% of the evaluated tropical ECM fungal species were categorized as Data Deficient by the IUCN (FIG. 1). In general, the conservation status categorization for tropical fungi has relied on species distribution data and threats to host plants and their ecosystems. ECM fungal species classified as Endangered and Critically Endangered are associated with the family Dipterocarpaceae in Asia or tropical lowland forests in the Amazon (e.g., *Austroboletus amazonicus*; Vasco-Palacios et al. 2020). In contrast, species categorized as Vulnerable are mostly associated with *Quercus* in montane neotropical forests (e.g., *Lactifluus hallingii*; Corrales et al. 2020).

Although causes of deforestation in the tropics vary by region, ectotrophic forests have been highly fragmented and degraded and there have likely been associated population declines for both tree hosts and mycobionts (Grilli et al. 2017; Peay et al. 2007; Simijaca et al. 2022). Tropical Asian dipterocarp forests are highly threatened by logging and conversion to agricultural lands (Mustaffa et al. 2012; Pang et al. 2021). It is noteworthy that 56% of Malaysia's dipterocarp species are Critically Endangered (Mustaffa et al. 2012). In Africa, Madagascar is one of the countries with the highest number of unique plant and animal species. Madagascar is home to many ECM plants, including *Uapaca* spp. (Phyllanthaceae) and the endemic families Sarcolaenaceae and Asteropeiaceae, and has a high diversity of ECM fungi that are widely collected for food (Bâ et al. 2012; Buyck 2002, 2008; Ducousso et al. 2012). Madagascar has nonetheless lost nearly 80% of its original forests, so it seems probable that ECM fungi have also been severely impacted (Carrasco et al. 2020; Horning 2008). A similar situation occurs in neotropical mountains, where deforestation of *Quercus*-dominated forests has been extensive (Clerici et al. 2020; Tellman et al. 2020).

Introduction of exotic ECM tree species and their mycobionts can also negatively impact tropical ECM fungi. For example, the north-temperate *Amanita muscaria* was likely introduced with *Pinus patula* into Colombia sometime between 1950 and 1977 and is now displacing the native ECM fungi of *Q. humboldtii* (Vargas et al. 2019). A similar scenario is playing out in Madagascar where ECM fungi associated with exotic *Eucalyptus* are displacing native ECM fungi (Ducousso et al. 2012).

ECM fungi play fundamental roles in key ecosystem processes such as nutrient cycling, succession, and colonization, so it is critical that they are included in conservation strategies. One major knowledge gap concerns the distribution and population structure of tropical ECM fungi, and such data are necessary to assess threats (e.g., Douhan et al. 2011). Given the lack of information, preserving tropical ectotrophic forests in their primary condition may be the best near-term solution to protect their symbiotic fungi (Suz et al. 2015).

QUANTITATIVE DATA ANALYSIS METHODS

To identify broad distributional patterns of ECM fungi in the tropics, we compiled three independent data sets. First, we conducted a quantitative data analysis to

understand broad-scale patterns of ECM fungal distribution and abundance in the tropics. Our specific goals were to identify the most species-rich and abundant ECM fungal lineages and determine how their occurrences and abundances vary across different regions. To accomplish this, we retrieved the majority of diversity studies published before July 2021 and conducted within the broad tropical latitudes of 23.5°N and 23.5°S (Corrales et al. 2018). From these, a given study was included in the analysis if relative abundance (RA) of ECM fungal lineages could be calculated based on sporocarp and/or ECM root tip sampling. For each of these studies, we manually retrieved the following metadata: geographic province (defined according to Corrales et al. 2018 as Neotropics, Afrotropics, Southeast Asia, or Oceania), latitude, longitude, elevation, mean annual temperature, mean annual precipitation, putative or confirmed ECM host plant(s), and RA of the ECM fungal lineages as defined by Tedersoo and Smith (2013). Each study was also categorized in one of four tropical plant community types: lowland rainforest, dry forest, montane forest, or savanna (Chapin et al. 2012; Corrales et al. 2018). From studies with multiple, geographically discontinuous sampling sites, we retrieved data individually for each site. For studies lacking data for elevation, temperature, and/or precipitation, we used the R packages RGBIF (Chamberlain et al. 2021) and RASTER (Hijams and van Etten 2012) to obtain those data based on geographic coordinates. Then, the 10 most frequently detected ECM lineages across all studies were used in subsequent analyses (SUPPLEMENTARY TABLE 1).

With this data set, we performed one-way analyses of variance (ANOVAs) followed by a post hoc Tukey test to determine whether target ECM fungal lineages varied significantly in abundance in each geographic province and community type. To visualize the patterns of beta diversity across broad tropical regions, we used the RA data (of all the compiled lineages and also the 10 most frequent lineages) to run nonmetric multidimensional scaling (NMDS) analyses using the R package VEGAN (Oksanen et al. 2013) based on Bray-Curtis dissimilarity matrices. Also, environmental data compiled from each study were fitted onto the NMDS ordination using the function *envfit* in the VEGAN package. Finally, we analyzed beta diversity among geographic regions using an ANOVA of multivariate dispersion test using the function *betadisper* in the R package VEGAN (Oksanen et al. 2013).

Generalized linear models (GLMs) were employed to explore biotic and abiotic influences on the RAs of the 10 most frequent tropical ECM lineages. A quasi-family error distribution with an identity link function was used in the models to account for potential overdispersion of the data (Crawley 2007). We also ran a correlation analysis among independent variables so that only uncorrelated variables were included in the final models (correlation <25%). Since altitude was 85.4% correlated with temperature, altitude was excluded. Variables in the final model were temperature (C), latitude, longitude, precipitation (mm), tropical community type (lowland rainforest, dry forest, montane forest, or savanna), host plant family, and geographic province (Neotropics, Afrotropics, Southeast Asia, or Oceania). All statistical analyses were performed in R 4.10 (R Core Team 2021).

The second data set consisted of data from tropical fungal metabarcoding studies available for download from the GlobalFungi Web site (release 3) using the Geosearch tool (Větrovský et al. 2020). These data sets were based primarily on soil or root tip sampling; none were based on sporocarps. Tropical studies were selected by drawing a polygon around the Neotropics (1362 samples), Afrotropics (192 samples), Southeast Asia (1169 samples), and Tropical Oceania (525 samples). The GlobalFungi data set was used to calculate relative richness of species hypotheses (SHs; following 1.5% similarity threshold from the UNITE database) per ECM lineage at the regional scale. Ectomycorrhizal SHs were extracted from the data set using the "primary lifestyle" parameter from the FungalTraits data set (Põlme et al. 2021). Relative richness of species hypotheses were calculated for each of the four tropical regions as the number of species hypotheses belonging to an ECM fungi lineage divided by the total number of species hypotheses.

Finally, we compiled a third data set of long-term inventories of ECM sporocarps and sequencing of ECM root tips from well-studied sites in Cameroon (1 site), Colombia (2 sites), Guyana (1 site), and Panama (2 sites). Then for each site, we calculated the differences between the RA of each ECM lineage as estimated by sporocarp inventories versus root tip inventories. This data set was used to estimate potential sampling-based biases in community composition by exploring differences in ECM lineage RA as estimated by aboveground versus belowground inventories. Since comparisons between the RA of the most frequent ECM lineages above- and belowground ground are useful to identify potential sampling biases, we used one-sample *t*-tests for each ECM fungal lineage to determine whether RA calculated from sporocarp inventories was statistically different from the RA calculated from root tips inventories.

RESULTS

Relative abundance data set.—The final data set included 49 studies with a total of 80 individual data sets (SUPPLEMENTARY TABLE 1). Of these original data sets, 61 were based on ECM root tips or soil, 10 on sporocarps, and 9 on a combination of both of these sampling types. Among the geographic provinces, 39 data sets were from the Neotropics, 11 from the Afrotropics, 26 from Southeast Asia, and 4 from Oceania (SUPPLEMENTARY TABLE 1). Ranges included elevations from 27 to 3500 m, mean annual precipitation from 774 to 7400 mm, and mean annual temperature of 7 to 30 C. The number of data sets by community type were 52 for lowland rainforests, 23 for montane forest, 4 for dry forest, and 1 for savanna.

The 10 most frequently occurring and abundant tropical ECM lineages identified by the quantitative data analysis were /amanita, /boletus, /cantharellus, /clavulina, /cortinarius, /inocybe, /laccaria, /russula-lactarius, /tometella-thelephora, and /sebacina. When studies were clustered by biogeographic province, the /russula-lactarius and /tomentella-thelephora lineages were significantly most abundant in the Afrotropics ($F_{(9,100)} = 13.93$, $p = 2.72 \times 10^{-14}$), the Neotropics ($F_{(9,379)} = 17.07$, $p = 1.11 \times 10^{-16}$), and Southeast Asia ($F_{(9,250)} = 18.28$, $p = 1.11 \times 10^{-16}$) (FIG. 2). These two lineages were least abundant in Oceania, where /cortinarius was the most abundant lineage ($F_{(9,30)} = 13.93$, $p = 5.90 \times 10^{-3}$; FIG. 2).

When clustered by community type, the /russula-lactarius and /tomentella-thelephora lineages were the

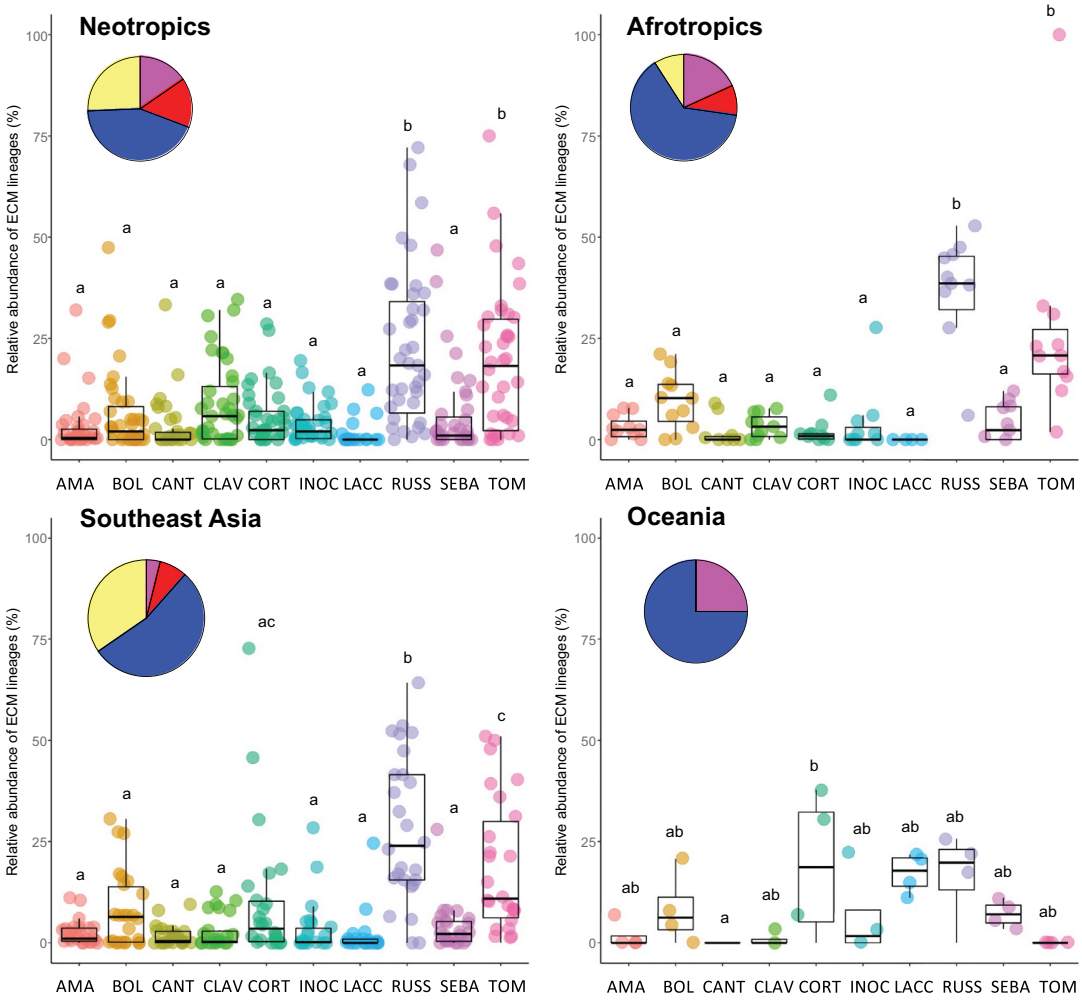

Figure 2. Boxplots of the 10 most frequently found and abundant ECM lineages across the different tropical areas. Means labeled with different letters (a–c) are statistically different based on a post hoc Tukey test ($P < 0.05$). Lineage abbreviations: AMA, /amanita; BOL, /boletus; CANT, /cantharellus; CLAV, /clavulina; CORT, /cortinarius; INOC, /inocybe; LACC, /laccaria; RUSS, /russula-lactarius; SEBA, /sebacina; TOM, /tomentella-thelephora. Pie charts represent the proportion of sample types: root tips (blue), soil (yellow), sporocarps (magenta), and sporocarps and root tips (red).

most abundant in lowland rainforest ($F_{(9,510)}$ = 28.00, $p = 1.11 \times 10^{-16}$; SUPPLEMENTARY FIG. 1). In montane forests, /russula-lactarius was also the most abundant, followed by /tomentella-thelephora and /cortinarius ($F_{(9,219)}$ = 18.70, $p = 1.11 \times 10^{-16}$; SUPPLEMENTARY FIG. 1). In dry forests, /russula-lactarius, /sebacina, and /tomentella-thelephora were the most abundant lineages ($F_{(9,39)} = 4.31$, $p = 1.11 \times 10^{-3}$; SUPPLEMENTARY FIG. 1). Also, the NMDS ordination analysis showed significant differences in the ECM community composition only between the Neotropics and the Afrotropics ($F = 3.803$, $p = 0.013$; FIG. 3).

Generalized linear models also showed trends among lineages (TABLE 1). For example, the RA of /russula-lactarius showed a positive association with six different host plant families and tropical montane forest, whereas /inocybe showed a negative association with seven of the plant host families and with tropical montane forests but had a positive association with tropical savannas. For the /boletus lineage, the only significant effect was a strong positive association with *Pakaraimaea dipterocarpacea* (Cistaceae). The RA of /laccaria showed a negative association with temperature, whereas /clavulina was positively associated with the Neotropics and negatively associated with Juglandaceae. Whereas /cortinarius was positively associated with montane forests and the Nothofagaceae and Myrtaceae, /sebacina was positively associated only with dry forest. None of the variables had a significant impact on the RA of /amanita, /cantharellus, or /tomentella-thelephora (TABLE 1).

GlobalFungi data set.—We identified 3248 metabarcoding samples from tropical areas in the GlobalFungi database (1362 in Neotropics, 192 in Afrotropics, 1169 in Southeast Asia, 525 tropical Oceania), mostly studies from soil, rhizosphere soil, or roots. The total number of ECM SH varied among the regions, with 406 in the Neotropics, 344 in the Afrotropics, 713 in Southeast Asia, and 621 in tropical Oceania. Data from GlobalFungi showed similar patterns of SH richness among fungal ECM lineages across tropical geographic provinces. When comparing the relative richness per ECM lineage (defined as the total number of SH in an ECM lineage/total number of ECM SH), /russula-lactarius, /inocybe, and /tomentella-thelephora were the three most species-rich lineages in all of the tropical provinces (FIG. 4). We also found that /cortinarius, /sebacina, /amanita, and /pisolithus-scleroderma were always among the most species-rich lineages throughout the tropics. The /cortinarius and the Atheliales ECM lineages were particularly species-rich in tropical Oceania and Southeast Asia (FIG. 4). Oceania and

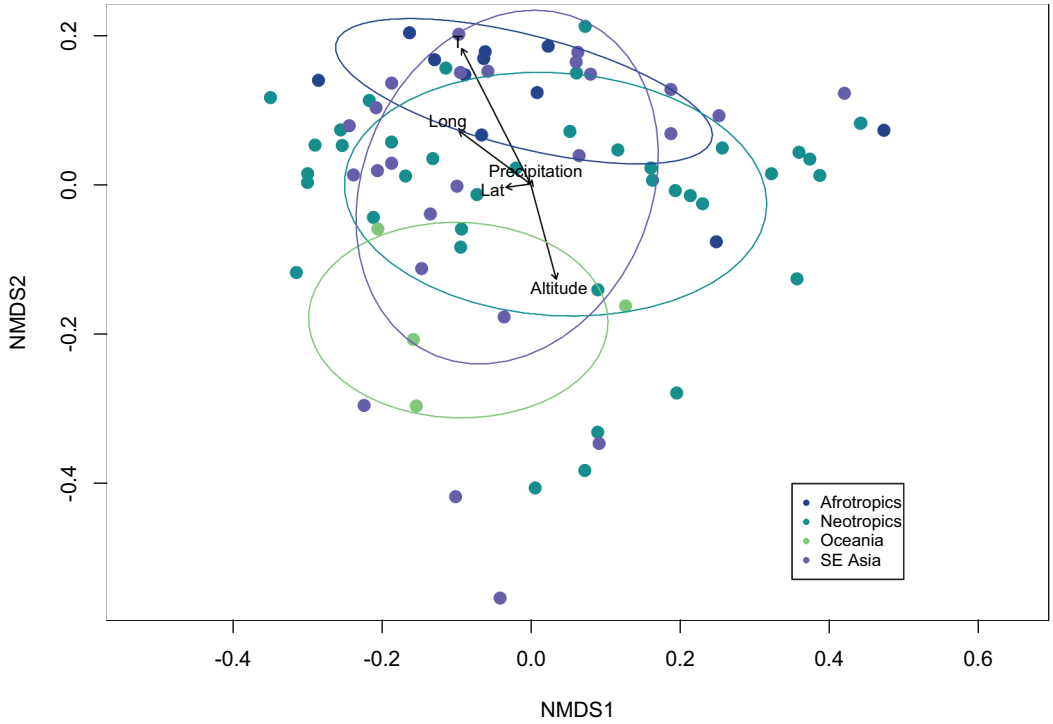

Figure 3. Nonmetric multidimensional scaling (NMDS) plot showing differences in the ECM fungal community composition among tropical areas (*betadisper*: ANOVA *F*-value = 3.8, $p = 0.013$). Two spatial (latitude and longitude) and three environmental (precipitation, temperature, and altitude) variables are plotted (temperature: $p < 0.049$; see text for further explanation).

Table 1. Final Generalized Linear Models (GLMs) for the 10 most frequently found and abundant ECM lineages in tropical areas.

Lineage	Variable	Coefficient estimate	*t*-value	*Pr*(>|*t*|)
/amanita	No significant associations found			
/boletus	Host family: Cistaceae	43.51	3.936	0.0002
/cantharellus	No significant associations found			
/clavulina	Continent: Neotropics	10.23	2.28	0.030
	Host family: Juglandaceae	−12.32	−2.09	0.040
/cortinarius	Ecosystem type: tropical montane forest	14.14	2.15	0.036
	Host family: Nothofagaceae	44.52	3.12	0.003
	Myrtaceae	19.52	2.17	0.034
/inocybe	Ecosystem type: tropical montane forest	−11.63	−3.68	0.0006
	tropical savannas	27.43	5.62	0.000001
	Host family: Cistaceae	−18.64	−3.02	0.004
	Codominance	−18.64	−3.02	0.004
	Dipterocarpaceae	−15.06	−3.62	0.0007
	Fabaceae	−16.69	−3.87	0.0003
	Myrtaceae	−11.69	−2.71	0.009
	Nothofagaceae	−14.93	−2.18	0.034
	Nyctaginaceae	−13.98	−3.12	0.003
/laccaria	Temperature	−0.49	−2.8	0.007
/russula-lactarius	Ecosystem type: tropical montane forest	34.43	3.38	0.0014
	Host family: Cistaceae	51.10	2.57	0.013
	Dipterocarpaceae	34.06	2.55	0.014
	Fabaceae	52.74	3.8	0.0004
	Fagaceae	29.55	2.85	0.006
	Juglandaceae	41.2	3.23	0.002
	Nyctaginaceae	32.05	2.22	0.031
/tomentella-thelephora	No significant associations found			
/sebacina	Ecosystem type: tropical dry forest	11.73	2.21	0.031

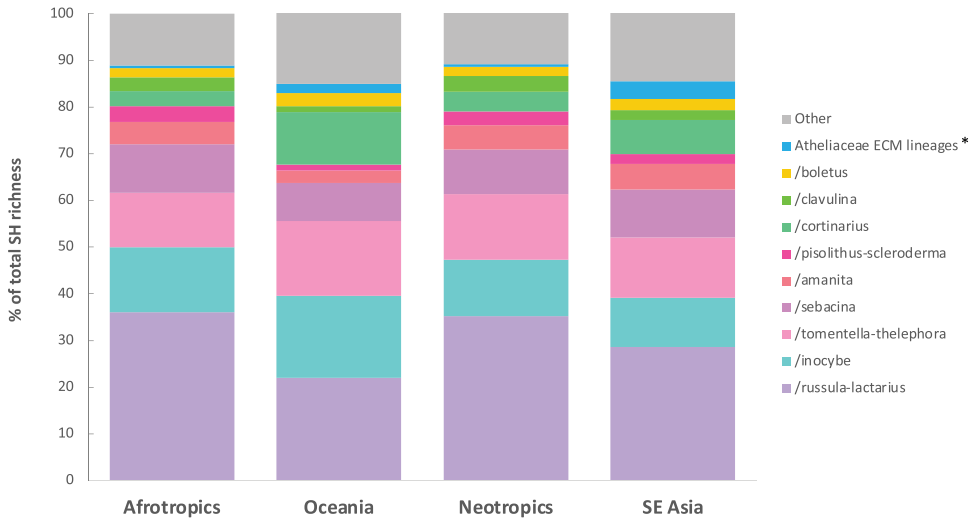

Figure 4. Relative richness of species hypothesis (SH) of ectomycorrhizal fungi among continents based on GlobalFungi data. *Atheliaceae may include several different ECM lineages (represented by species of *Amphinema, Byssocorticium, Piloderma*, and *Tylospora*) (Tedersoo & Smith 2013).

Southeast Asia also had a higher diversity of "other ECM lineages" and less dominance by /russula-lactarius.

Aboveground and belowground data set.—The aboveground versus belowground comparison showed that /amanita and /laccaria were usually underrepresented belowground, whereas /russula-lactarius, /tomentella-thelephora, and /sebacina were usually overrepresented. Only /amanita was statistically overrepresented aboveground (FIG. 5).

DISCUSSION

Our quantitative data analysis found high RA and species richness of the /russula-lactarius and /tomentella-thelephora lineages in all of the tropical biogeographic provinces (FIG. 2). This result is in line with the most

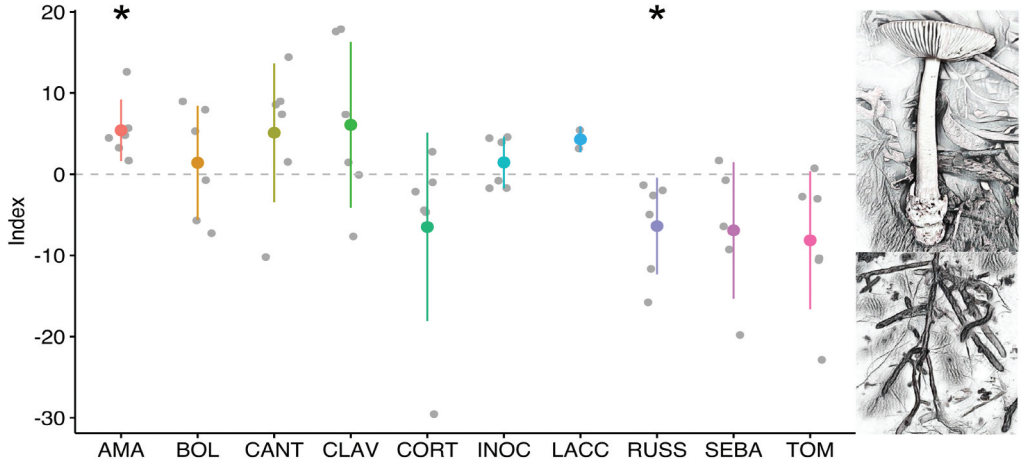

Figure 5. Comparison of relative abundance (RA) between aboveground and belowground sampling from six experiments done at the same study sites in Panama, Colombia, Guyana, and Cameroon. The zero line represents the case where a lineage has equal RA in belowground and aboveground samples. Asterisks indicate lineages that are significantly different from 0. Lineage abbreviations: AMA, /amanita; BOL, /boletus; CANT, /cantharellus; CLAV, /clavulina; CORT, /cortinarius; INOC, /inocybe; LACC, /laccaria; RUSS, /russula-lactarius; SEBA, /sebacina; TOM, /tomentella-thelephora.

recent analysis of global soil fungal diversity that places *Tomentella* as the most species-rich and abundant soil fungal genus worldwide, with *Russula, Cortinarius, Sebacina*, and *Inocybe* also in the top ten (Tedersoo et al. 2022).

The /russula-lactarius lineage has previously been suggested to be most diverse in tropical ecosystems (e.g., Buyck 1990; De Crop et al. 2017; Hackel et al. 2022; Tedersoo and Nara 2010). Although global patterns of diversity for the /russula-lactarius lineage remain controversial, Buyck (1990) also suggested that /russula-lactarius (as Russulaceae) may have a center of origin in the Afrotropics based on the high number of species known from the region. Buyck et al. (2018) also noted that many African *Russula* species are nested in the earliest diverging clades of the lineage. These patterns are strongly supported by recent phylogeographic studies (Hackel et al. 2022). In contrast, Looney et al. (2016) suggested a temperate origin for *Russula* with subsequent radiations into the tropics. Our results unequivocally show /russula-lactarius as one of the most abundant and species-rich lineage in the tropics, but additional surveys and phylogenetic assessment are needed to clarify the biogeographic history of the lineage (Buyck et al. 2018).

Although /inocybe was not particularly abundant in our RA analysis, Inocybaceae was nonetheless the second-most species-rich family based on the GlobalFungi analysis that included all tropical regions (FIG. 4). Matheny et al. (2009) suggested that the /inocybe lineage evolved with angiosperm hosts in the Paleotropics. In our analysis, /inocybe showed a strong positive association with the tropical savanna community type, as suggested previously by Buyck and Eyssartier (1999), Matheny et al. (2009), and Meidl et al. (2021). This strong savanna association of /inocybe may help explain the relatively low diversity of the group reported from lowland tropical rainforests (e.g., Henkel et al. 2012; Horak et al. 2015; Tedersoo et al. 2011). A strong positive association was found between /cortinarius and the host plant families Nothofagaceae and Myrtaceae in our GLM analysis, similar to results from south-temperate *Nothofagus* forests (Truong et al. 2019, 2017). Our ANOVA per biogeographic province also found a particularly high abundance of /cortinarius in tropical forests of Oceania (TABLE 1; FIG. 2). These results are consistent with the Southern Hemisphere origin of Nothofagaceae and the ECM lineages within Myrtaceae (Sanmartín and Ronquist 2004; Thornhill et al. 2015).

The /sebacina lineage was also abundant and highly diverse in all of the tropical geographic regions despite the fact that this lineage is assumed to be of temperate origin (Tedersoo et al. 2014). However, Tedersoo et al. (2014) demonstrated that the internal transcribed spacer (ITS) region of /sebacina has evolved faster in the tropics and the highest known phylogenetic diversity within the lineage is in Central America. Our GLM analysis and ANOVA indicated that /sebacina was positively associated with tropical dry forest (TABLE 1; SUPPLEMENTARY FIG. 1). The /clavulina lineage was positively associated with the Neotropics, which is not surprising since this lineage may have evolved in the tropics (Kennedy et al. 2012) and hot spots of /clavulina

diversity have been identified in Guyana (Uehling et al. 2012) and southern Mexico (Pérez-Pazos et al. 2019).

A number of studies in tropical and temperate sites have found discrepancies between ECM fungal diversity estimated from sporocarp surveys versus those based on belowground molecular sampling. These disjuncts were most likely due to methodological limitations such as polymerase chain reaction (PCR) bias (for belowground inventories based on metabarcoding), or time of sampling and/or inconspicuous sporocarps being missed (for aboveground sporocarp inventories). Carriconde et al. (2019) studied ECM fungi in forests dominated by ECM *Nothofagus* and *Arillastrum* (Myrtaceae) in New Caledonia and found only a 16% overlap between species recovered as sporocarps and on root tips during 1 year of continuous sampling. However, the dominant /cortinarius lineage had a similar RA from both root tips and sporocarps. Similarly, taxa in the /sebacina and /tomentella-thelephora lineages were abundant on ECM root tips in *Dicymbe*-dominated forests in Guyana and in *Pseudomonotes tropenbosii* (Dipterocarpaceae) in Colombian Amazon but were recovered much less frequently in sporocarp surveys (e.g., Smith et al. 2011, 2017; Vasco-Palacios and Boekhout In press). Smith et al. (2011) suggested that this might be due to the cryptic resupinate basidiomata in these lineages that are difficult to find and taxonomically categorize in the field. A recent study from temperate forests in Denmark demonstrated that soil sequencing and long-term sporocarp surveys generated similar metrics for species richness and species composition for Agaricomycetes (Frøslev et al. 2019). Frøslev et al. (2019) also showed that sporocarp-based species richness in Russulaceae was higher than that of the belowground molecular surveys, a result also noted in ongoing studies in *Gilbertiodendron dewevrei* forests of Cameroon where the /russula-lactarius sporocarp species to belowground operational taxonomic unit (OTU) ratio was approximately 150:37 (T. W. Henkel and R. A. Koch, unpubl. data). Overall, however, our comparative analysis showed the opposite trend, with higher belowground richness of /russula-lactarius (FIG. 5). This may be due to the difficulty in identifying the high number of undescribed tropical species of the lineage (Adamčík et al. 2019).

Tropical ECM fungi: Future directions and regional knowledge gaps.—

Oceania

There are still only a few studies of ECM fungal communities from Oceania (e.g., Adams et al. 2006; Tedersoo and Põlme 2012; Waseem et al. 2017). Islands with forests rich in ECM trees, such as New Caledonia and Papua New Guinea, have barely been sampled (Tedersoo and Põlme 2012; Waseem et al. 2017). Carriconde et al. (2019) studied both aboveground and belowground ECM fungi in New Caledonia and recovered only a portion of the ECM fungi estimated to be present. Another major knowledge gap is the lack of sampling of several lineages of ECM host plants known to occur in Oceania, including species of *Pomaderris* (Rhamnaceae) (Nge et al. 2021), *Casaurina* and *Allocausurina* (Casaurinaceae), and *Gastrolobium, Oxylobium, Mirbelia*, and *Jacksonia* in the Fabaceae subfamily Faboideae tribe Mirbelieae (Brundrett 2009). Warcup (1980) suggested that many Australian plants not traditionally considered ECM have the ability to form ECM associations. However, Warcup (1980) applied a very broad interpretation of ectomycorrhizal associations that has been disputed (e.g., Brundrett 2009; Tedersoo et al. 2010a); therefore, many Australian ECM plants still need to be examined in order to determine their mycorrhizal status. It is important to emphasize that many of the confirmed ECM plants from Oceania are endemic and therefore are likely to host unique ECM fungi. Known lineages of ECM fungi specific to Oceania also deserve further study, including endemic Mesophelliaceae and other unique members of the Hysterangiales as well as the /aleurina and /austropaxillus lineages (Davoodian et al. 2021; Hosaka et al. 2008; Perry et al. 2007; Skrede et al. 2011).

Neotropics

Our analyses suggest that the Neotropics may have relatively low overall ECM fungal diversity, but many of the region's potentially ectotrophic systems remain understudied. Although the greater Amazon Basin is the largest expanse of lowland tropical forest in the world, little is known about ECM associations over vast areas. It is possible that ECM associations are relatively rare in Amazonia, as a recent meta-analysis of >2000 tree inventory plots across greater Amazonia revealed few ectotrophic monodominant forests outside of the Guiana Shield (ter Steege et al. 2019). Nonetheless, the discovery of forests dominated by ECM trees and highly diverse in ECM fungi in Guyana and Colombia (e.g., Henkel et al. 2002; Vasco-Palacios and Boekhout In press; Vasco-Palacios et al. 2018) and widespread lowland communities with low densities of ECM plants in Brazil, French Guiana, and Ecuador (Jaouen et al. 2019; Roy et al. 2016; Tedersoo et al. 2010b) implicate the South American lowland tropics as a critical region for future discoveries.

This is exemplified by the country of Venezuela, in which few modern studies of ECM fungi and plants have

been undertaken. Lying between the known ECM hot spots in Guyana and Colombia, Venezuela contains a wide array of putatively ECM host plants, including at least 15 species of *Dicymbe*, several species of *Aldina*, and one of *Pakaraimaea* (Hokche et al. 2008; Moyersoen 1993, 2006; Ramos et al. 2016; Stergios and Aymard C 2008). Even outside of closed canopy rainforests dominated by ECM trees, there is ample evidence that species of *Neea, Gaupira, Pisonia* (Nyctaginaceae), and *Coccoloba* (Polygonaceae) are regularly ECM and may host diverse and/or unique ECM fungi (Alvarez-Manjarrez et al. 2018; Hackel et al. 2022; Haug et al. 2005; Magnago et al. 2022; Tedersoo et al. 2010b). The tropical montane regions of Mexico and Central America are also understudied. More work is needed to fully document the ECM fungal diversity within the forests of *Quercus, Pinus*, and Juglandaceae that change rapidly across strong elevation gradients in this region (Corrales and Ovrebo 2021; Garibay-Orijel et al. 2020).

Afrotropics

In the African tropics, there are vast areas with diverse assemblages of ECM plants, but ECM fungi have only been studied in a fraction of these forests. There are currently 119 known ECM host plant species from tropical Africa in Fabaceae subfam. Detarioideae, Phyllanthaceae, and Dipterocarpaceae as well as in Sarcolaenaceae and Asteropeiaceae (Bâ et al. 2012; Corrales et al. 2018). Many studies of African ECM plants have investigated their mycorrhizal status or ecophysiology (e.g., Alexander and Högber 1986; Bâ et al. 2012; Ducousso et al. 2008; Högberg and Piearce 1986; Newbery et al. 1988; Onguene and Kuyper 2001), and there are also ECM fungal sporocarp inventories for several equatorial and subtropical regions (e.g., Buyck et al. 1996; Heinemann 1958; Kamalebo et al. 2018; Riviere et al. 2007). Some of these sporocarp inventories were from forests with confirmed ECM host trees (e.g., *G. dewevrei* in Congo [Verbeken and Buyck 2002]; *Microberlinia* and *Tetraberlinia* in Cameroon [Buyck et al. 1996]), but in many studies the ECM host plants were unidentified. As noted by Tedersoo (2017), efforts to document the belowground diversity of ECM fungal communities in tropical Africa would do well to focus on the fungi associated with *Monotes* and *Marquesia* (Dipterocarpaceae), unstudied detarioid species in the genera *Cryptosepalum, Didelotia, Monopetalanthus, Paraberlinia, Pelligriniodendron*, and *Toubaouate*, the gymnosperm genus *Gnetum* (Gnetaceae), and species in the endemic Malagasy genera of the Sarcolaenaceae and Asteropeiaceae (e.g., *Leptolaena, Sarcolaena, Schizolaena, Xyloolaena*, and *Asteropeia*). In addition, most of the environmental sequencing studies from Africa were based on a small number of individual host plants and/or sites, so ECM fungal diversity may thus far have been underestimated.

Southeast Asia

Tropical Asia has also been underexplored, particularly given the fact that this region has the highest number of reported tropical ECM host plants, including species of Dipterocarpaceae, Fagaceae, and Juglandaceae (Brearley 2012; Corrales et al. 2018). Tropical Asia also had the highest ECM fungal diversity of all the tropical regions based on our analysis of GlobalFungi data (FIG. 3). We suspect, however, that many ECM fungal lineages still remain unknown in Asia.

A recent study comparing root-associated fungal communities from roots of two related ECM Juglandaceae species with disjunct distributions in Southeast Asia and Central America found that 70% of the OTUs for Southeast Asia and 56% for Central America could not be identified to genus (Corrales et al. 2021). Despite a similar sampling effort, the diversity of all root-associated fungi, including saprotrophic, endophytic, and mycorrhizal species, on ECM Juglandaceae in Southeast Asia was 3506 OTUs compared with Central America's 1603 OTUs, although ECM fungi were less well represented in Southeast Asia. Corrales et al. (2021) concluded that the apparent difference in ECM diversity was likely due to a low proportion of ECM fungi that were accurately identified from Asia versus the better-sampled fungi of Central America.

Tropical China is known as a hot spot of fungal diversity, with an estimated 5056 macrofungal species reported from 1192 genera (Zhuang 2001). However, many taxa in the region have not been sampled using molecular techniques, so some groups remain underrepresented in global databases (Corrales et al. 2021). Dipterocarpaceae is an important ECM family in Southeast Asia, but out of the 16 genera only 10 have been confirmed as ECM based on empirical studies and the associated ECM fungi have never been sampled from many genera, such as *Marquesia, Monotes, Neobalanocarpus, Parashorea, Stemonoporus*, and *Upuna* (Corrales et al. 2018). Indeed, although there are evolutionary connections with taxa from other regions, fungi in East Asia have a high rate of endemism and more work is needed to improve understanding of fungal diversity and evolution in this region (Ge et al. 2020; Han et al. 2020).

Other open questions about tropical ECM symbiosis and future perspectives.—An intriguing question regarding tropical ECM fungi involves identifying the factors driving the striking differences in abundance of ECM host plants between the Neotropics and Southeast

Asia. These patterns have likely been influenced by biogeographic patterns and the evolutionary histories of the dominant ECM plant families Dipterocarpaceae and Fagaceae (Ashton 1988; Deng et al. 2018; Manos and Stanford 2001). However, it has also been hypothesized that differences in soil fertility and the dominant soil types between Asia and the Neotropics might have favored ECM symbiosis in Southeast Asia (Fujii et al. 2018).

More research is also needed to understand putatively ECM fungal lineages that are common in the tropics but whose biology is not well understood. These include members of the Trechisporales, in particular taxa with macroscopic fruiting bodies that belong to the *Trechispora terrestris* species complex. Taxa in this group may compose a distinct ECM lineage, as they are consistently associated with healthy roots and sporocarps are frequently found in spatial proximity to host plants (Rosenthal et al. 2017; Vanegas-León et al. 2019). Similarly, members of the /xenasmatella lineage were discussed as ECM in Tedersoo and Smith (2013) and have been documented on roots in several tropical sites on different continents (Carriconde et al. 2019; Peay et al. 2010; Smith et al. 2011; Vasco-Palacios and Boekhout In press). However, the taxa in this group have not been carefully studied and require further attention to confirm a functional ECM status.

Despite the immense progress in elucidating tropical ECM plants and fungi over the past century, much remains unknown about these associations. Future studies could fruitfully focus on the following: (i) investigations implementing molecular methodologies and long-term sporocarp sampling to extensively recover more ECM fungal diversity from additional tropical regions; (ii) collaborations among international networks and scientists in studying the evolution, ecology, biogeography, and systematics of tropical ECM fungi; (iii) collaborative efforts toward determining how different ecological factors affect the functioning and diversity of ECM fungi in tropical systems; and (iv) engaging local citizen scientists to learn more about tropical ECM fungi and expand sampling in tropical regions using large collaborative and outreach approaches.

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