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Phylogenetic diversity and affiliation of tropical African ectomycorrhizal fungi

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Abstract

Ectomycorrhizal fungi form a mutualistic symbiosis with plant roots, and are key for nutrient cycling in many ecosystems. Here we study the ectomycorrhizal fungal communities in the Ouémé Supérieur reserve forest in Benin (West Africa). We use phylogenetic methods to test if the species from the study site are closer to other tropical African species than to species from other regions. The Ouémé Supérieur community was represented by nine Operational Taxonomic Units in *Amanitaceae*, one in *Boletaceae*, one in *Cantharellaceae*, one in *Cortinariaceae*, two in *Inocybaceae*, fourteen in *Russulaceae* and three in *Sclerodermataceae*. Of these thirty-one Operational Taxonomic Units, twenty had no record in other areas, and unique Operational Taxonomic Units were found in all families except *Boletaceae* and *Sclerodermataceae*. The added phylogenetic diversity from these unique Operational Taxonomic Units tended to be higher than expected by chance in all families but *Cantharellaceae*. The Operational Taxonomic Units are generally fairly distinct and contribute proportionally to the phylogenetic diversity, reflecting that they do not only represent recently diverging species, but also more divergent lineages. Our analyses of the different families show that the communities of *Amanitaceae*, *Inocybaceae*, and *Russulaceae* are more closely related to the general Afrotropic community than expected by chance, at least measured as the nearest taxon distance. The lack of significant patterns in the other families may be due to lack of power, but the wide distribution of many Operational Taxonomic Units suggests that there are not likely to be strong patterns. It is only for *Russulaceae* that there is a significant pattern in the Ouémé Supérieur ectomycorrhizal fungal communities at a regional scale, with the Operational Taxonomic Units being less closely related than expected. At a global scale the patterns seem to reflect the overall distribution of the Afrotropic ectomycorrhizal fungal community. The phylogenetic patterns in the Afrotropic communities differ between families, from clustered to no clear pattern to over-dispersed measured as mean average phylogenetic distance. Each family seems to have its own biogeographic history, and there is no clear pattern for the ectomycorrhizal fungal community at large. Despite the lack of comprehensive taxonomic work to identify fungi in a region, it is still possible to draw some conclusions on their diversity using molecular phylogenetic methods. However, limited success in getting good sequence data from

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specimens, probably due to preservation issues in the field, and the lack of well annotated molecular data from many regions limit the power of these inferences.

Key words – community assemblage – mycorrhizal fungi – Operational Taxonomic Units – phylogeny – west Africa

Introduction

Fungal diversity is unevenly studied across the globe, with much focus given to the northern temperate and boreal regions of Europe and North America, while tropical regions have received less attention (McGuire et al. 2013). This bias largely reflects where most mycologists reside (Gryzenhout et al. 2012, Piepenbring & Yorou 2017). The lack of comprehensive taxonomic work in the tropics is a great impediment to diversity studies in the region, and many studies have applied names based on north temperate taxa for lack of better alternatives. However, such names are likely to be misapplied (Hawksworth 2012).

Studies of global fungal diversity (Kõljalg et al. 2013, Tedersoo et al. 2014a) have demonstrated that different continents share very few species but that similar biomes display similar assemblages of lineages. Thus, at a larger spatial scale, it seems that species distributions have been conditioned by isolation due to geographical barriers (e.g., mountains and oceans), and *in situ* speciation processes in their new environments. This would presumably lead to regional communities with closely related species. However, the observation that most genera have a cosmopolitan distribution (Tedersoo et al. 2010) suggests that fungal lineages do get around and that the image may be more complex.

Ectomycorrhizal (EcM) fungi are a diverse group of mutualistic root symbionts that receive carbon from their plant partners and in return enhance nutrient uptake and resistance to stress and disease in the plant partner (Smith & Read 2010, Smith & Bonito 2012). Ectomycorrhizal fungal communities have been studied to a great extent in north temperate regions, but to a much lesser extent in tropical regions (Corrales et al. 2018). Existing studies show that the diversity of EcM fungi in the tropics is generally low in forests with few EcM trees (Diédhiou et al. 2010, Tedersoo et al. 2011, Michaëlla Ebenye et al. 2017), but in monodominant EcM forests rivals the diversity of temperate and boreal sites (Morris et al. 2008, Peay et al. 2010). Although EcM fungal communities in the tropics generally have lower phylogenetic diversity than temperate systems (Tedersoo et al. 2014b), with some of the EcM lineages present in temperate areas lacking in the tropics (e.g., /suillus-rhizopogon; Tedersoo et al. 2010), many lineages appear to have a tropical origin and are highly diverse there (Matheny et al. 2009, Kennedy et al. 2012, Looney et al. 2016).

While studies on fruiting-bodies in the tropics often are hampered by lack of reference work, most community studies based on environmental samples use highly variable internal transcribed spacer (ITS) region of the rDNA (Schoch et al. 2012), and lack precise phylogenetic placement of the species. Thus, they have limited resolution to put the detected species in a broad taxonomic context in order to provide large-scale perspectives on the diversity (Vanie-Leabo et al. 2017, Furneaux et al. 2021). Furthermore, while many species do not produce fruiting bodies at any given time, and thus will be missed in fruiting body inventories, environmental samples are usually limited in the area that they cover (a few square cm per sample). By sampling at many time points and using molecular methods the downsides of fruiting body inventories can be limited. Access to fruiting bodies also makes it possible to generate sequences from different genomic regions that are known to be from the same species, something that is difficult in studies from environmental samples. Highly variable barcoding regions can thus be used for near species identification (Lücking et al. 2014, Kõljalg et al. 2019), and more conserved regions for phylogenetic placement. It is therefore possible to move beyond comparisons of Operational Taxonomic Units (OTU) composition, and get insights into larger scale patterns in the diversity of an area, and how it relates to global diversity.

In tropical West Africa, not only is the regional species pool diversity of EcM fungi poorly known (Piepenbring et al. 2020), but community assemblages are even less well studied. Here we

investigate the species composition of the EcM fungal community in the Ouémé Supérieur Reserve Forest (OSRF) in Benin, West Africa and put it in an African and global perspective. Based on an exhaustive fruiting-body sampling of a total area of 2.25 ha over three years we use morphological and barcoding methods to identify OTUs, and we use phylogenetic methods based on trees inferred from partial sequences of the large subunit of the nuclear ribosomal DNA (LSU) and the second largest subunit of the RNA polymerase II gene (RPB2) to draw perspectives on the community assembly.

Materials & Methods

Study site

The present study was conducted in the *Forêt Classée de l'Ouémé Supérieur* (Ouémé Supérieur Reserve Forest; OSRF), located between 9°11'-9°47' N and 1°58'-2°28' E in north central Benin. The study area has a rainy season from May to October, which strongly contrasts with a long and severe dry season from October to April. The OSRF is situated in the Guineo-Sudanian Zone (GSZ; Adomou 2005), and harbors a mosaic of vegetation types including *Fabaceae*-dominated woodlands, wooded savanna, shrub savanna and gallery forests (Schnell 1976, White 1983).

Three permanent plots of 50m x 50m were installed at each of three sites identified in the OSRF. The three plots at each site were chosen to be dominated by one of three EcM trees: *Isoberlinia doka* Craib & Stapf., *Isoberlinia tomentosa* (Harms) Craib & Stapf or *Uapaca togoensis* Pax.

Specimen sampling, preservation and preliminary identification

Mycological surveys were conducted at a frequency of two visits/week/plot from June to October, which is the fruiting period for mushrooms in the region (Yorou et al. 2001), during two years (2015–2016) resulting in a total of 234 surveys. Sampling consisted of harvesting all EcM specimens in the plots and selecting a representative specimen of each putative morphospecies. After a preliminary identification in the field, each representative specimen was dried using a field dryer (De Kesel 2001). To secure good quality samples for DNA extraction and PCR, small samples of the fresh specimen were also dried in plastic bags with silica gel in 2016. Additional specimens were collected opportunistically during 2017 as part of an ethnomycological study (Furneaux et al. in prep.). These specimens were dried with an electric dryer (Stöckli) at 40–60°, with a small subsample extracted prior to drying and preserved in cetyl-trimethyl-ammonium bromide buffer (CTAB). All voucher specimens are deposited at the herbarium of the University of Parakou (UNIPAR; abbreviations according to Index Herbariorum; Thiers, continuously updated), with sample splits stored at the Systematic Biology department at Uppsala University.

Preliminary field identification of harvested species was made from a large collection of more than 1500 color pictures of known macromycetes in the region and with the help of numerous monographs (De Kesel et al. 2002, Härkönen et al. 2003, De Kesel & Malaisse 2010, Ndong et al. 2011). Specimens were then subjected to a detailed anatomical description by mean of a light microscope (Leica DM2700) equipped with a drawing tube and scaled ocular.

For each morphospecies, a subset of specimens was selected for ITS barcoding. One specimen per person that had collected the morphospecies (max 7 specimens) were selected, to account for possible differences in the concept of the species between people. Even when collected by fewer than 4 people, at least 4 specimens were selected per morphospecies, if available, to account for possible cryptic diversity.

DNA isolation, amplification and sequencing

DNA was extracted from specimens using either the DNeasy Plant Mini kit (Quiagen) or CTAB extraction (Zolan & Pukkila 1986) including cleaning with chloroform:isoamyl alcohol and alcohol precipitation. The ITS region was amplified by PCR using primer pairs ITS1-F (Gardes &

Bruns 1993) and ITS4-B1 (Tedersoo et al. 2007), ITS1 and ITS4 (White et al. 1990), or ITS1 and LB-W (Tedersoo et al. 2008). ITS sequences generated by Furneaux et al. (in prep) from the 2017 specimens were also included. After clustering of specimens into OTUs (see below), LSU and RPB2 were amplified from one specimen per OTU, using primer pairs LR0R (Hopple Jr & Vilgalys 1994) and LR5 (Vilgalys & Hester 1990) and fRPB2-5f (Liu et al. 1999) and bRPB2-7R (Liu et al. 1999), respectively. The reaction conditions for ITS region were 2 min at 95°C, followed by 35 cycles of 15 s at 95°C, 30 s at 55°C and 60 s at 72°C, and finally 10 min at 72°C. Concerning LSU region, the reaction conditions were 3 min at 95°C, followed by 35 cycles of 15 s at 95°C, 30 s at 52°C and 60 s at 72°C, and finally 10 min at 72°C. For RPB2 region, the reaction conditions were 2 min at 94°C, followed by 9 cycles of 10 s at 96°C, 45 s at 61°C and 60 s at 72°C, and by 37 cycles of 10 s at 96°C, 45 s at 53°C, 60 s at 72°C and finally by 10 min at 72°C. PCR products were then purified enzymatically using the ExoSAP-IT® PCR Products Purification Kit for ABI and sequenced using the Sanger method at Macrogen Labs, Europe. The PCR primers were also used for sequencing, except for ITS, where in some cases ITS1 and ITS4 (the innermost primer pair) were used for sequencing when other primers were used for PCR, and for RPB2, where the internal primers bRPB2-6F and bRPB2-6R2 (Matheny 2005) were used in addition to the PCR primers.

Forward and reverse reads were assembled and edited using the Staden package v.1.7.0 (Staden 1996).

Barcoding

To distinguish species that had been lumped together based on morphology, the ITS sequences were clustered into single-linkage OTUs based on pairwise alignments using BLASTCLUST (version 2.2.26; Altschul et al. 1990, Dondoshansky & Wolf 2000) with a 97% cut-off (Nilsson et al. 2019). A multiple sequence alignment was also performed with MUSCLE 3.6 (Edgar 2004) in AliView (Larsson 2014), sorting the sequences according to the guide tree. The multiple sequence alignment was inspected to see how distinct the clusters were, and if they had any obvious structure within them. One specimen per cluster was selected to sequence the LSU and RPB2 regions for phylogenetic reconstruction.

Phylogenetic analyses

For those families where we produced at least one high quality LSU sequence of sufficient length (at least >300 bp), reference sequences were downloaded from GenBank (Benson et al. 2018). If we only had specimens from one genus of the family, based on morphological identification and BLAST searches of our sequences, we only downloaded sequences from that genus. LSU and RPB2 sequences were extracted from the GenBank data using PifCoSm (Sánchez-García et al. 2020) and linked into species based on GenBank annotations. Only species with LSU were kept, and each family and gene region was aligned separately using mafft V7.464 (Katoh et al. 2019) with maxiterate set to 1000, and the local pair option (l-ins-i strategy). Long sequences which included regions that were only homologous with a few other sequences were trimmed to reduce the proportion of missing data in the alignment. Outgroup taxa were added if no internal rooting point could be identified. The data matrix was iteratively cleaned by manual inspection of the alignment in AliView version 1.18 (Larsson 2014) and trees generated by FastTree (GTR model; Price et al. 2010). After each iteration of cleaning the alignment, the sequences were realigned using mafft as described above. Once cleaning was complete our sequences were added and the data was realigned again. OTUs represented by only a short part of LSU were removed, as were sequences with many ambiguity symbols, or that were suspected to be chimeric. OTUs that were misidentified and did not belong to the target family, based on the results of BLAST searches, were also excluded. A phylogeny was created with RAxML 8.2.11 (Stamatakis 2014), making 10 searches for the maximum likelihood (ML) tree with the default algorithm, and 1000 bootstrap replicates. The branches of the ML tree were re-estimated to reduce long branch lengths due to missing data (-f k option). All analyses were done with a separate partition for each gene region,

and implementing the GTR model with the gamma distribution to model rate differences between sites for each partition.

Outgroups were chosen as follows: *Limacella* as outgroup for *Amanita* (Moncalvo et al. 2000); *Hydnomerulius* (*Paxillaceae*) as outgroup for *Boletaceae* (Wu et al. 2014); *Craterellus* as outgroup for *Cantharellus* (Buyck et al. 2014); *Crepidotus* as outgroup for *Inocybaceae* (Matheny 2005); and *Tremellogaster* as outgroup for *Scleroderma* (Louzan et al. 2007). *Cortinarius* was rooted with sect. *Austroduracini* (*Cortinarius viscincisus*, *Cortinarius austroduracinus*, and *Cortinarius viridibasalis*) (Stensrud et al. 2014, Soop et al. 2019); and *Russulaceae* was rooted on the branch between *Russula* plus *Lactifluus*, and *Lactarius* plus *Multifurca* (De Crop et al. 2017).

Evolutionary ecological analysis

Tips of the phylogenetic tree belonging to clades with internal branches shorter than 0.002, roughly equivalent to 99.8% similarity, as suggested for LSU by Vu et al. (2018), were clustered together. In addition, tips corresponding to the same UNITE 3% species hypothesis (USH; Kõljalg et al. 2013, Nilsson et al. 2019) were identified based on ITS sequences assigned to the tip by PifCoSm, and all tips belonging to the clade stemming from the most recent common ancestor of each USH were clustered together, as long as there was no conflict with other USHs. Conflicts between USHs were resolved manually, with consideration for the phylogenetic relations between the involved tips, the strength of the link between LSU, RPB2, and ITS sequences (e.g., from the same specimen or not), and with the goal to remove as few tips as possible from each USH. These clusters were used as OTUs, and one random tip per OTU was kept for subsequent analyses.

Although national borders do not always correspond to ecologically relevant borders between biogeographic regions, country is the most commonly available locality information in global sequence databases. Therefore, for the Picante analysis, we divided the countries of the world into nine different regions according to continental divisions and climatic resemblance: Afrotropic, Palearctic, Nearctic, Mesoamerica, Neotropic, East-Asia, Indomalaya, Oceania and Australasia (Fig. 1). Each region was treated as a single community of EcM fungi, with species marked as present/absent in each community on the basis of their collection locality, as indicated in NCBI for the sequences of the tips in the OTU, or in Unite for the USH that the OTU was based on. If no annotation was available from either of these two sources, articles that included any of the sequences of the tips that the OTU was based on were searched for location information. For two OTUs in *Cantharellaceae*, the annotations from NCBI were corrected based on the original publication (Ariyawansa et al. 2015). Despite the literature review; for some OTUs, there was no geographical annotation.

Taxonomic annotation of OTUs is based on GenBank, UNITE or OSRF collection annotation. Little effort was made to correct taxonomic annotations, as our analyses are based on OTUs delimited by phylogeny and sequence similarity, and not on taxonomically defined species. However, specifically for Inocybaceae, we replaced the old names with the current names from Index Fungorum (https://www.indexfungorum.org) as of February 2022, in order to include the new generic classification of Inocybaceae from Matheny et al. (2020).

Mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) were calculated using the Picante package in R (Kembel et al. 2010) for each family based on their respective ML trees. The expected values for MPD (ses.mpd) and MNTD (ses.mntd) under a random distribution were calculated from 10 000 random shuffles of the tip labels across the respective tree (Kembel et al. 2010, Heckenhauer et al. 2017). For both standardized metrics, a negative standardized metric reflects a clustering of species while a positive standardized metric reflects a relative over-dispersion of species (Mazel et al. 2016). MPD is generally taken to be more sensitive to tree-wide patterns of phylogenetic clustering and evenness, while MNTD is more sensitive to patterns of evenness and clustering closer to the tips of the phylogeny (Kembel et al. 2010). Analogously, low P values indicate low probability of the observed clustering by chance, while high P values indicate low probability of the observed over-dispersed pattern by chance.

For each family three sets of analyses were done for each of MPD and MNTD: 1) for OTUs present in OSRF and elsewhere in the Afrotropics; 2) for OTUs from all regions, with OSRF counted as a distinct region separate from the rest of the Afrotropics; and 3) for OTUs from all the regions, with OSRF included with the rest of the Afrotropics. The MPD and MNTD separating the taxa of the different communities was calculated for OSRF and all the regions. Additionally, phylogenetic diversity (PD) was calculated as total branch length (Faith 1992) for OSRF and all regions, with values for the Afrotropics calculated both including and excluding OSRF. The unique PD added by OSRF and each region was calculated as the total branch length that was only present when the OTUs unique to the area were included in the phylogeny. The observed unique PD was compared to 1 000 random draws of as many excluded OTUs to test if the added diversity was higher than expected by chance, i.e., a low P value indicates a low chance of observing such high added PD, while a high P value indicates low chance of observing such low added PD.

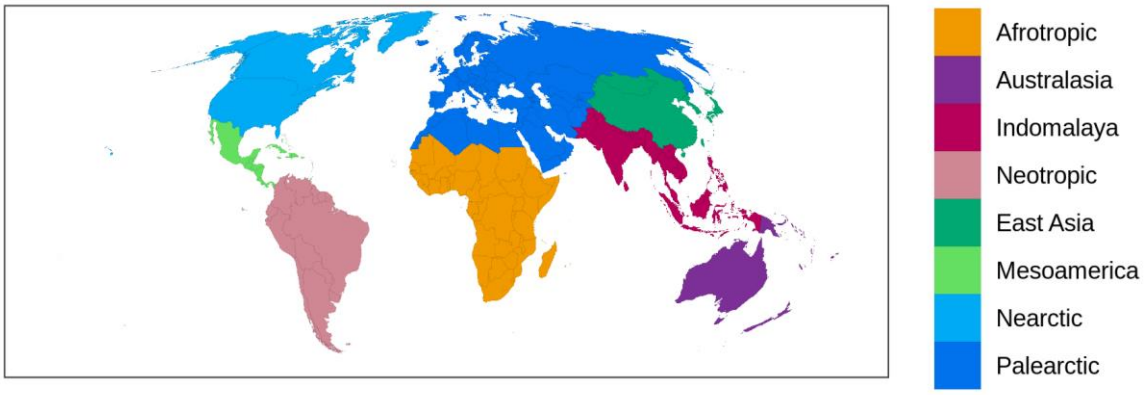


Figure 1 – Map of biogeographical regions. Oceania not visible due to the small size of its constituent countries.

Results

Identification of species

The study made 3325 collections that were sorted into 179 taxonomic units based on morphology. We successfully generated ITS sequences from 111 specimens of these 179 units. Clustering the ITS sequences resulted in 62 clusters, of which 8 were identified as non-EcM lineages after blasting (Supplementary Table 1). Of the 54 remaining clusters, LSU was successfully sequenced from 37 with sufficient length and quality to be included in the phylogenetic analyses. The EcM clusters belonged to eight families, but no LSU sequence was successfully generated for the specimen belonging to *Clavulinaceae*, leaving seven families for phylogenetic analyses. For five of the seven families, we had representatives of only one genus: *Amanita* (*Amanitaceae*), *Xerocomus* s.l. (*Boletaceae*), *Cantharellus* (*Cantharellaceae*), *Cortinarius* (*Cortinariaceae*), and *Scleroderma* (*Sclerodermataceae*). For *Boletaceae* sequences from the whole family was still used due to the taxonomic uncertainties in genus delimitation and annotation in GenBank.

OTUs

Our datasets comprised 3064 OTUs with geographic annotation, of which 31 were found in OSRF, and 232 were found in the Afrotropics (Table 1). 324 OTUs were found in two regions, and an additional 181 in more than two regions. The OTU with the widest distribution was *Russula cyanoxantha*, which was found in all regions except the Afrotropics and Oceania. All the included EcM families had at least one OTU distributed in five or more regions, except *Cantharellaceae* for which only two OTUs were found in two regions, and none were found in more than two (Fig. 4).

The Afrotropics shared OTUs with all other regions except Oceania. The largest number of Afrotropic OTUs were shared with the Palearctic (12 OTUs), East Asia (11 OTUs), and the Nearctic (10 OTUs). However, 91% of the Afrotropic OTUs were unique to the Afrotropics. Only Australasia had as large a proportion of unique OTUs, while most other regions had considerably lower proportions. All regions shared at least one OTU with every other region except for Oceania, which only had two OTUs: *Lactifluus leoninus*, also found in East Asia, Indomalaya, and Australasia; and *Inocybe tauensis* which was unique to the region.

OSRF

Specimens from OSRF included nine OTUs belonging to *Amanitaceae*, of which six were only sequenced from OSRF, two had been sequenced from the Afrotropics before, and one had previously only been sequenced from Indomalaya and East Asia. One of the OTUs that had previously been found in the Afrotropics, which included specimens annotated as the well-known temperate species *Amanita phalloides*, was also well-represented from the Pale- and Nearctic. There was one OTU including specimens from OSRF belonging to *Boletaceae*, which also included sequences from Mesoamerica. We found one OTU of *Cantharellaceae* from OSRF, that was not found in any other areas, but was morphologically identified as *Cantharellus addaiensis*, a known Afrotropic species, and was phylogenetically close (but not sister) to another OTU identified with that name. The OSRF specimens also included one OTU of *Cortinariaceae*, which did not include any sequences from other areas, or group close to any other sequences from African collections. There were two OTUs of *Inocybaceae* from OSRF, neither of which included sequences from other regions. The most OTU rich group in OSRF was *Russulaceae* with 14 OTUs, of which one included two of the initial ITS sequence clusters. Seven of the OTUs included sequences from other studies, of which three had been found in the Afrotropics and one had been found also in the Nearctic, Palearctic, and East Asia. For the remaining three no additional geographic annotation was included. There were three OTUs of *Sclerodermataceae* found in OSRF. None of them had previously been sequenced from the Afrotropics, but all had been sequenced from other regions.

Phylogenetic diversity

OSRF

The *Amanitaceae* OTUs from OSRF (Fig. 2) show no significant clustering at a regional level (P_{mpd} = 0.34; P_{mntd} = 0.20). On a global scale they tended to be clustered at shallow phylogenetic depths (P_{mntd} = 0.084), but there was no clear signal at deeper phylogenetic levels (P_{mpd} 0.42). The unique PD of *Amanitaceae* was not significantly longer than the mean from the randomizations (P = 0.38). As the OSRF sequences included only one OTU each for *Boletaceae* (Fig. 3), *Cantharellaceae* (Fig. 4), and *Cortinariaceae* (Fig. 5), it was not possible to calculate MPD or MNTD. The *Cantharellaceae* OTUs (Fig. 4) added significantly lower unique PD (P > 0.999) while the *Cortinariaceae* OTUs added significantly higher unique PD (P < 0.001). For the OSRF OTUs of Inocybaceae (Fig. 6), there were no clear signal at either regional (P_{mntd} = 0.63; P_{mpd} = 0.62), or global scales (P_{mntd} = 0.89; P_{mpd} = 0.89). The unique PD of *Inocybaceae* was not significantly different from expected (P = 0.19). The OSRF OTUs of *Russulaceae* (Fig. 7) were significantly over-dispersed on deep phylogenetic levels, both at regional (P_{mpd} = 0.99), and global (P_{mpd} = 0.99) scales. At a shallow phylogenetic level, there was no clear signal (regional: P_{mntd} = 0.82; global: P_{mntd} = 0.83). The unique PD of *Russulaceae* was not higher than expected by chance (P = 0.07). For *Sclerodermataceae* (Fig. 8), there was no clear signal at either regional or global scales (regional: P_{mpd} = 0.74; P_{mntd} = 0.85; global: P_{mpd} = 0.77; P_{mntd} = 0.86). Although it was only in *Cortinariaceae* that the added unique PD was significantly higher than expected by chance and it was only in *Cantharellaceae* that the added unique PD was significantly lower than expected (Table 2), there was nevertheless a tendency for the added unique PD to be higher than expected by chance for the number of OTUs (i.e., P < 0.5).

At a community level it was only *Inocybaceae* and *Russulaceae* that had a shorter distance

between OSRF and the Afrotropics on both scales, while *Amanitaceae* had closer distance between OSRF and the Afrotropics on a shallow phylogenetic scale (Supplementary Tables 2–8).

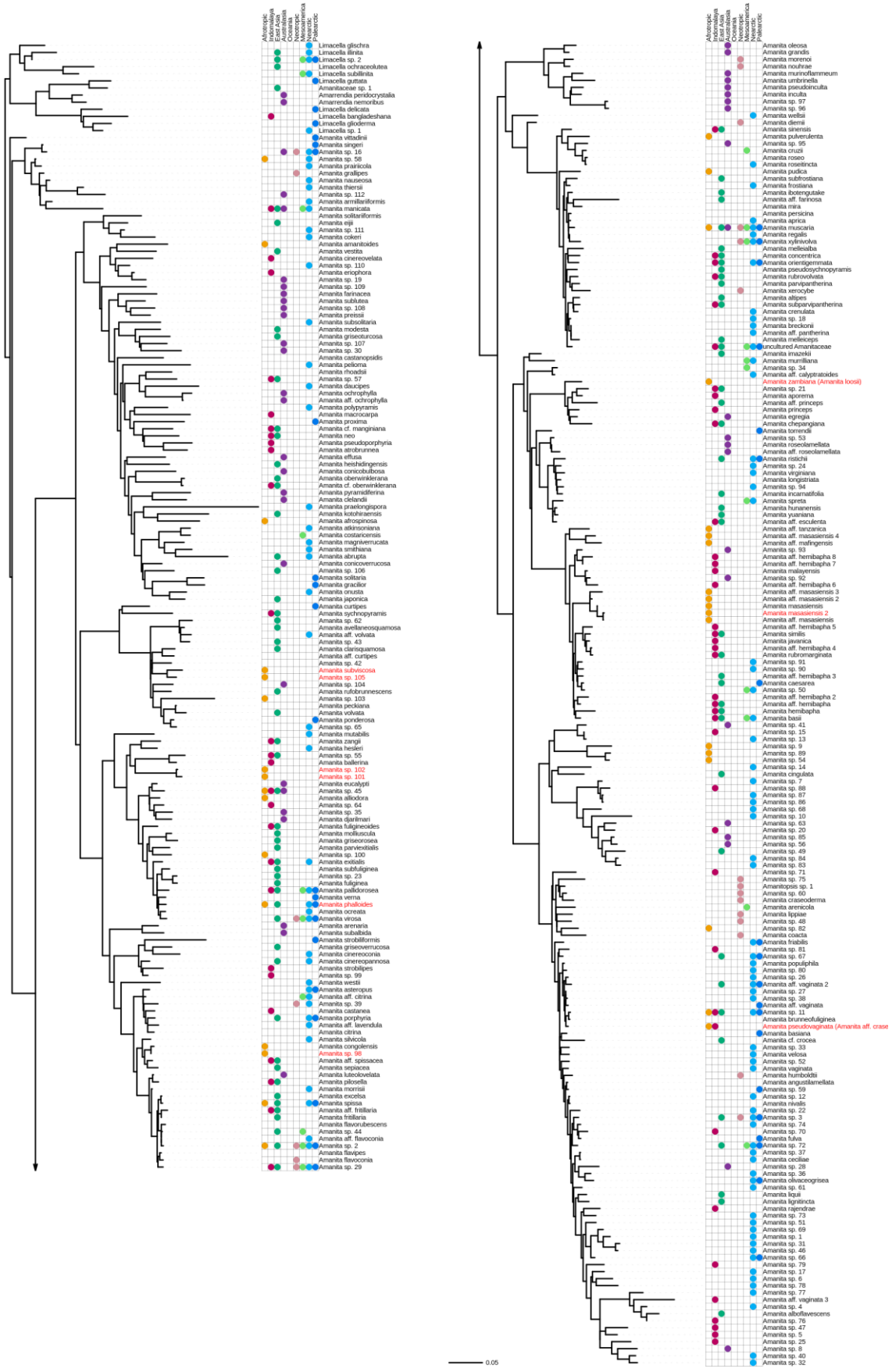


Figure 2 – ML tree and biogeographic occurrence matrix for Amanitaceae OTUs.

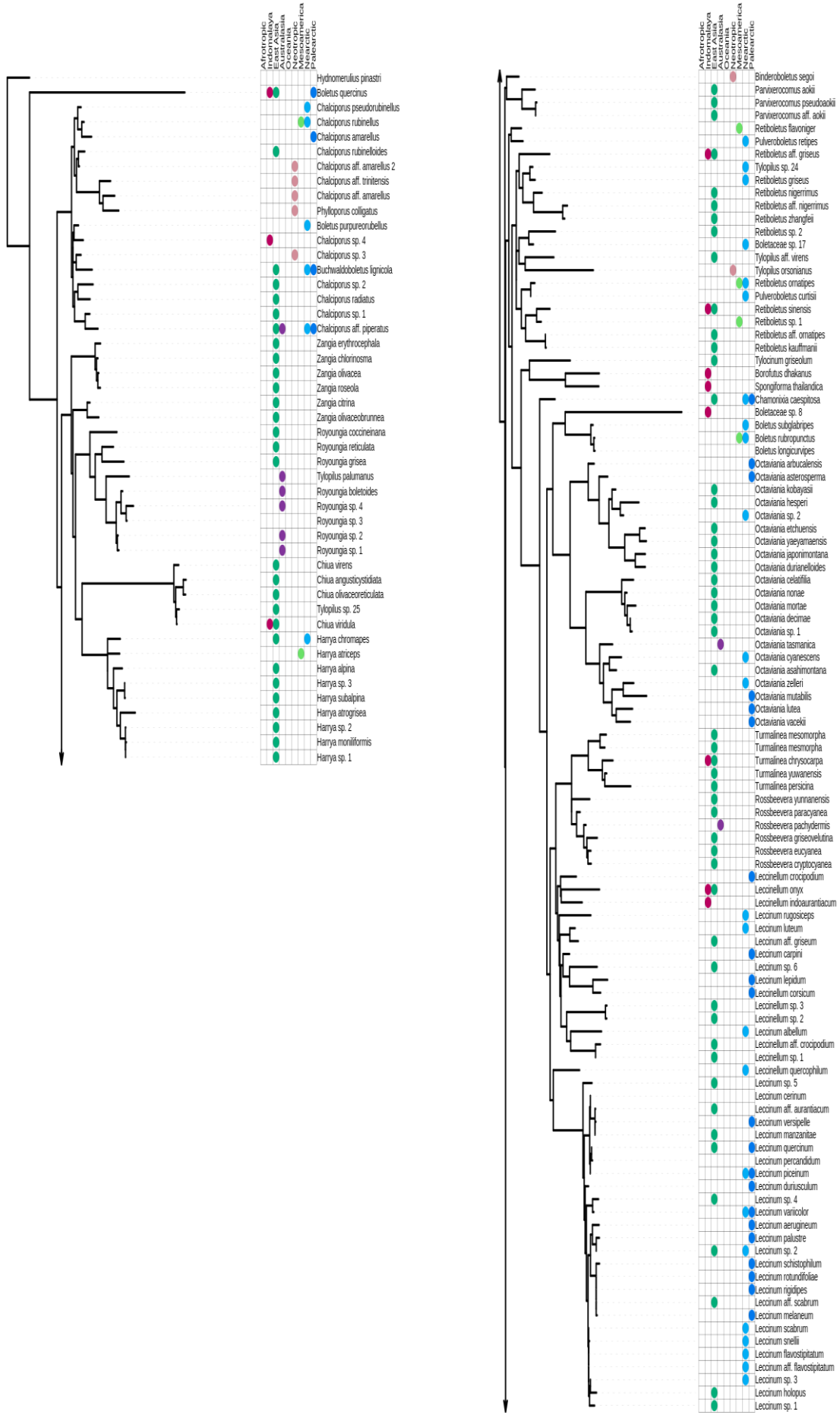
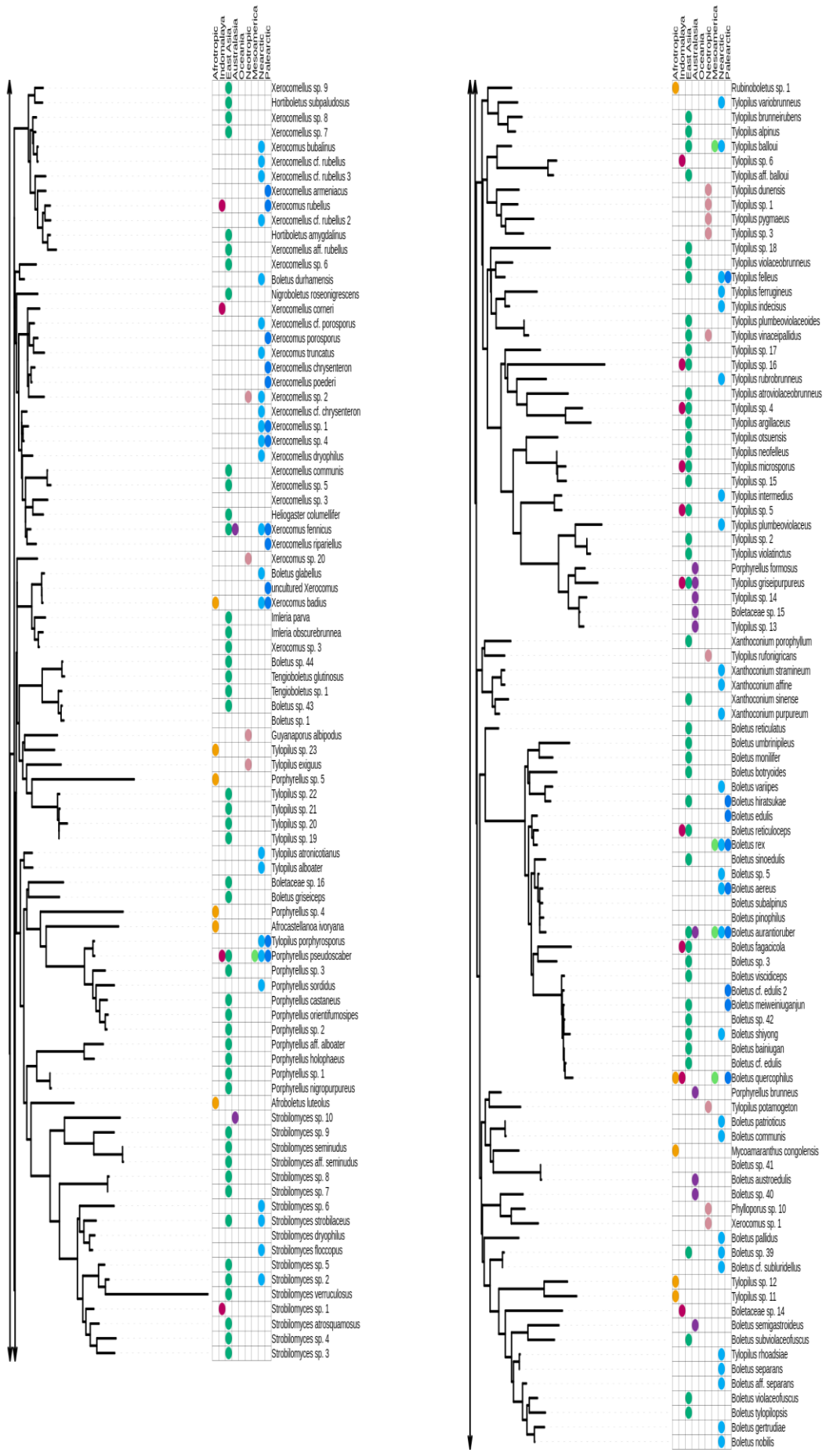


Figure 3 – ML tree and biogeographic occurrence matrix for Boletaceae OTUs.



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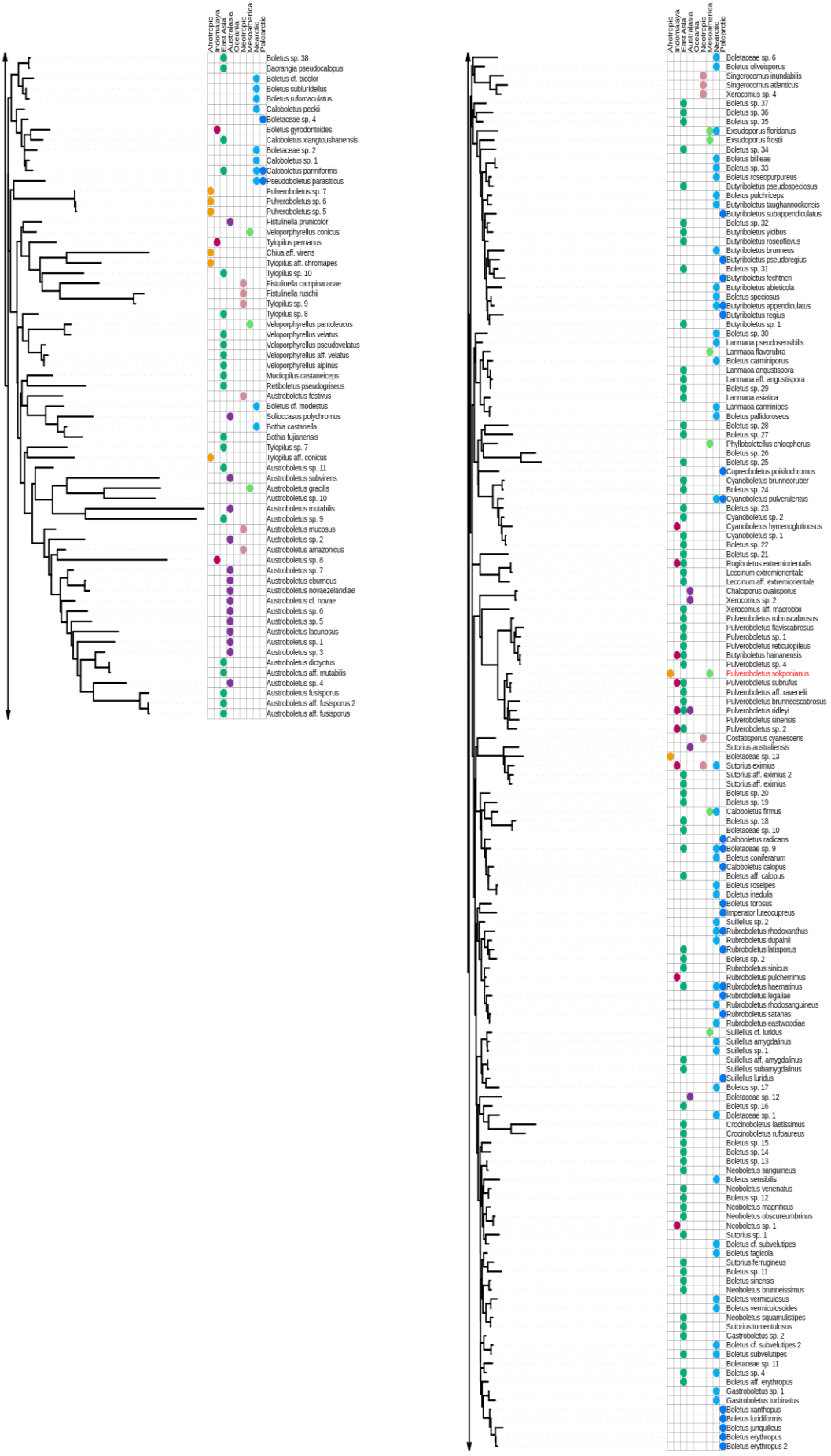

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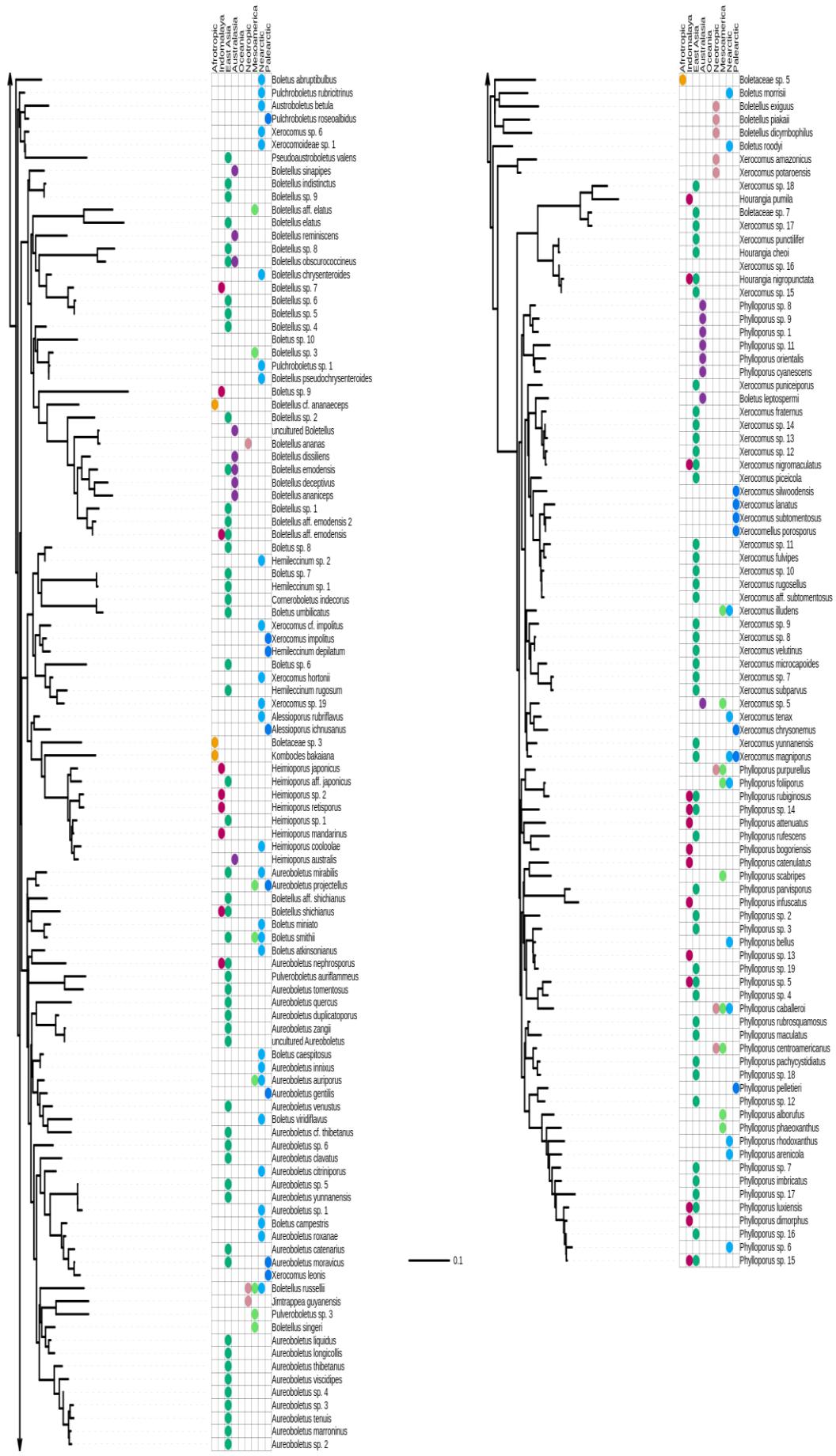

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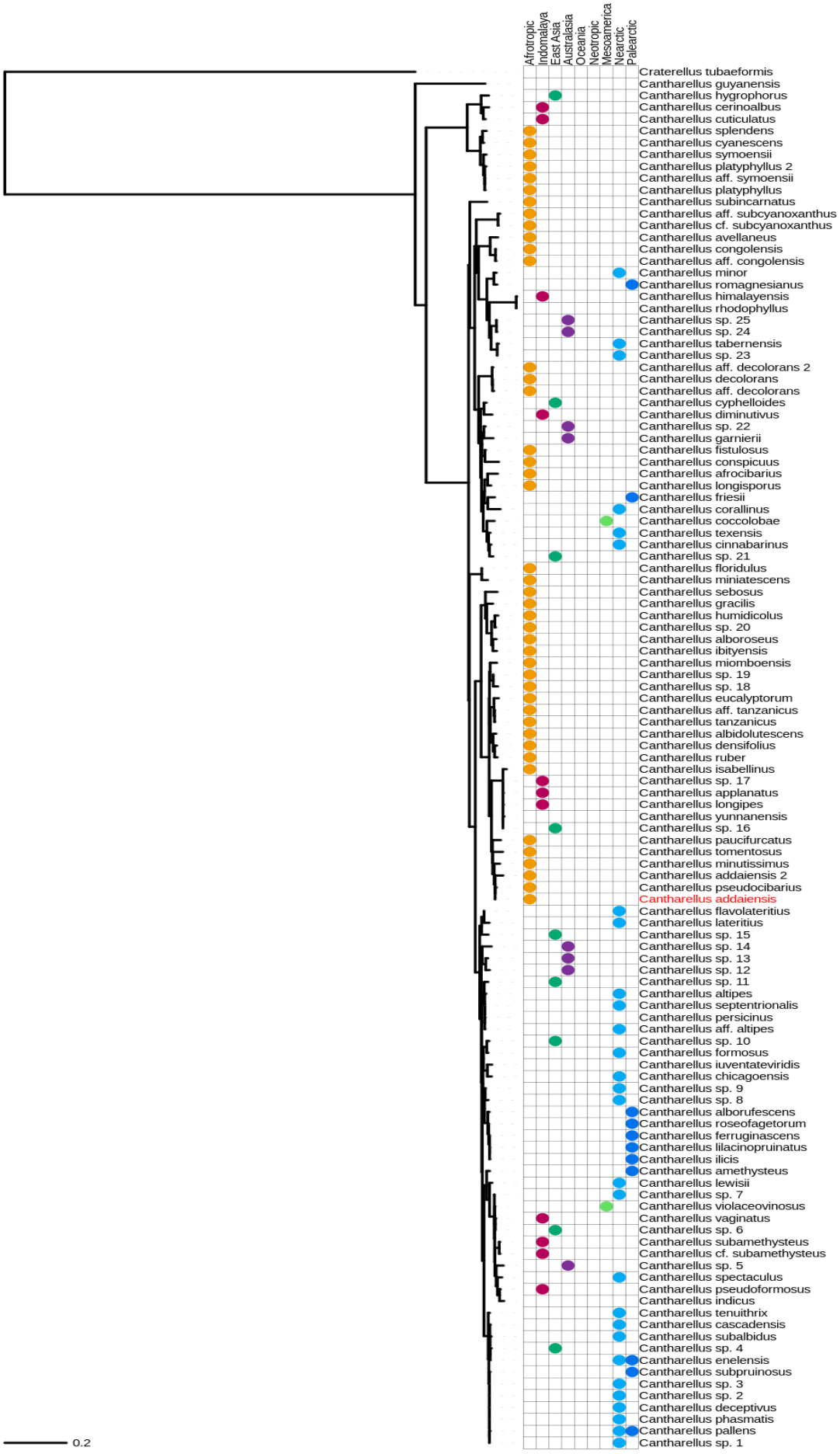

Figure 4 – ML tree and biogeographic occurrence matrix for Cantharellaceae OTUs.

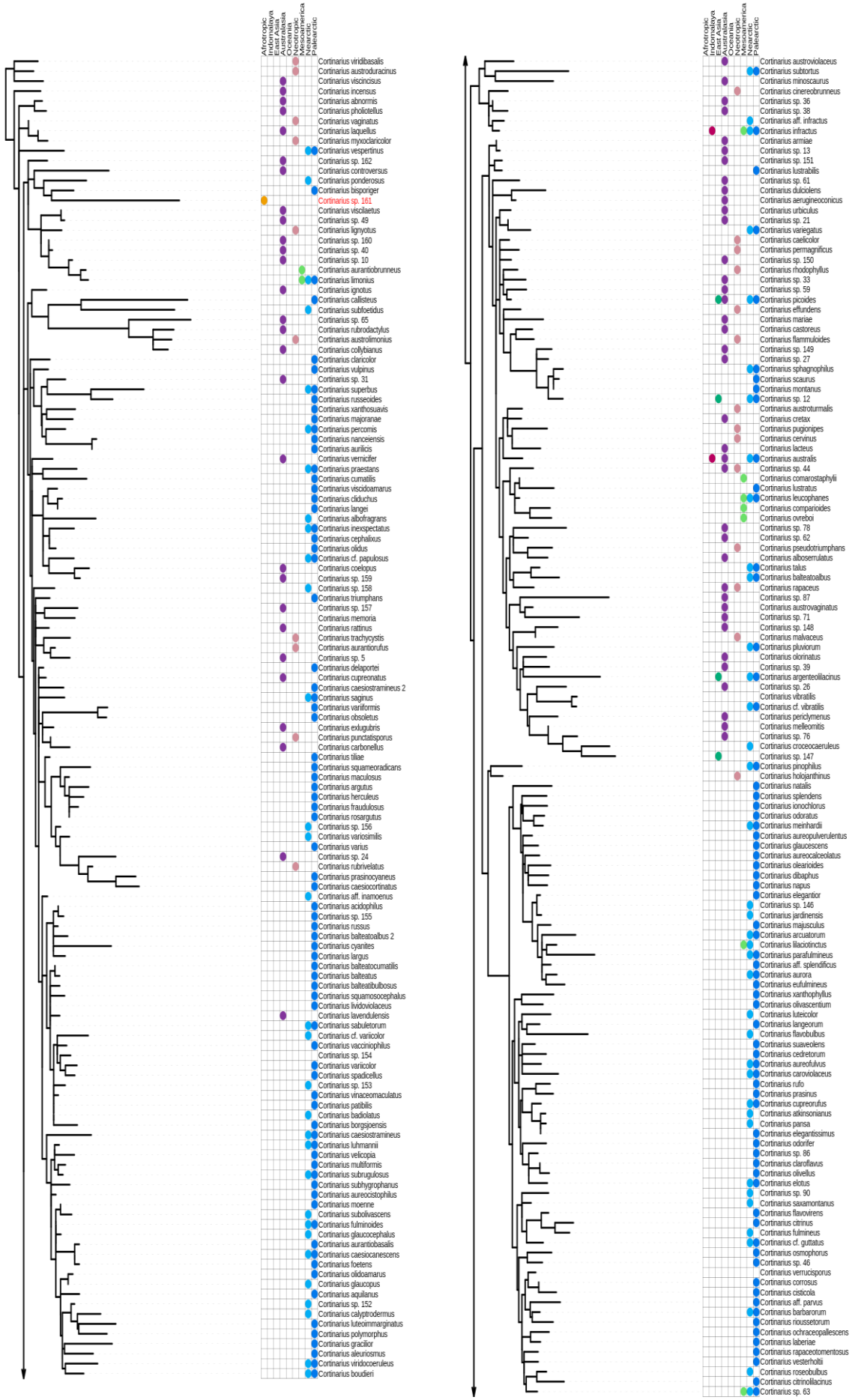

Figure 5 – ML tree and biogeographic occurrence matrix for Cortinariaceae OTUs.

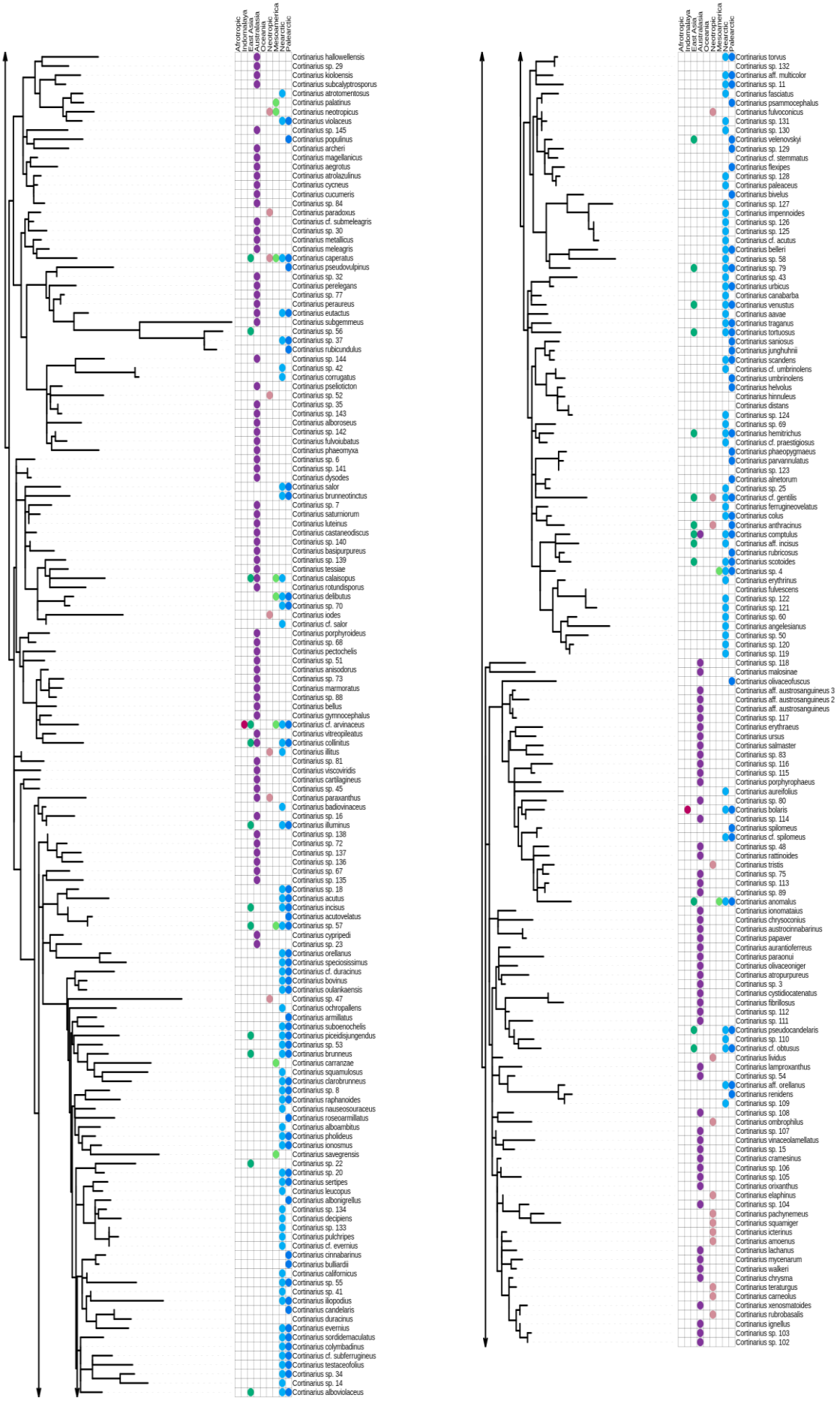

Figure 5 – Continued.

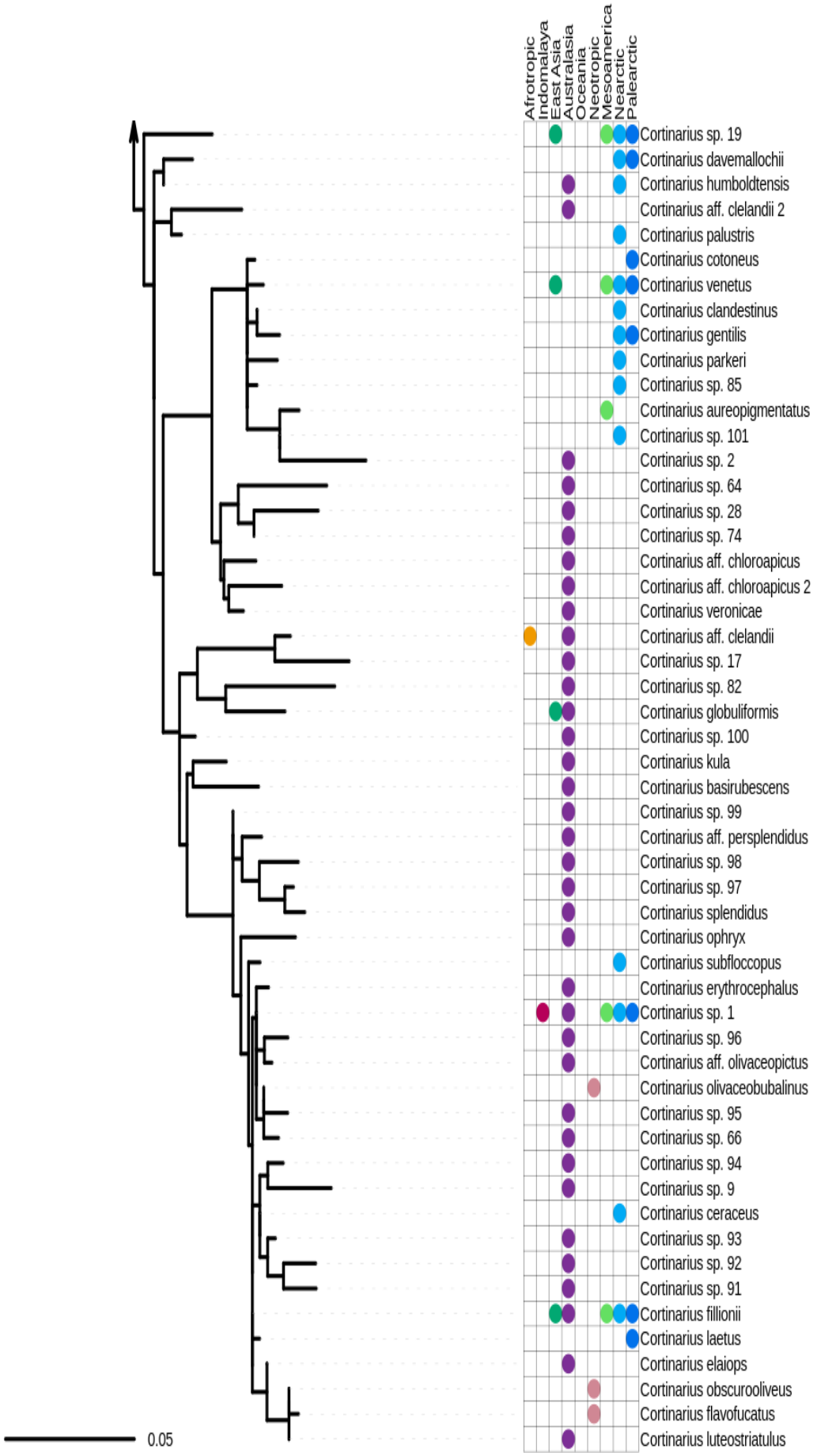

Figure 5 – Continued.

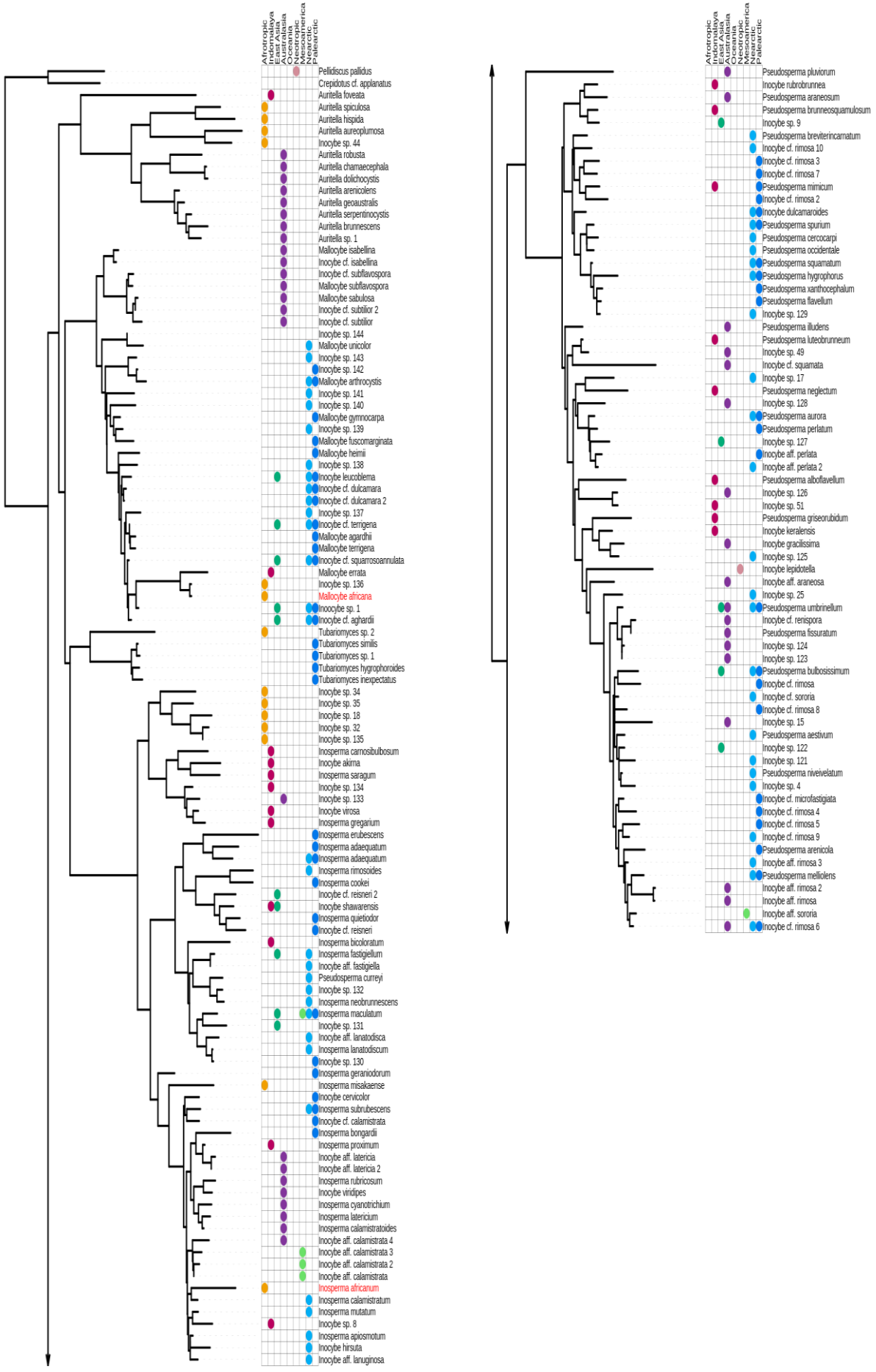

Figure 6 – ML tree and biogeographic occurrence matrix for Inocybaceae OTUs.

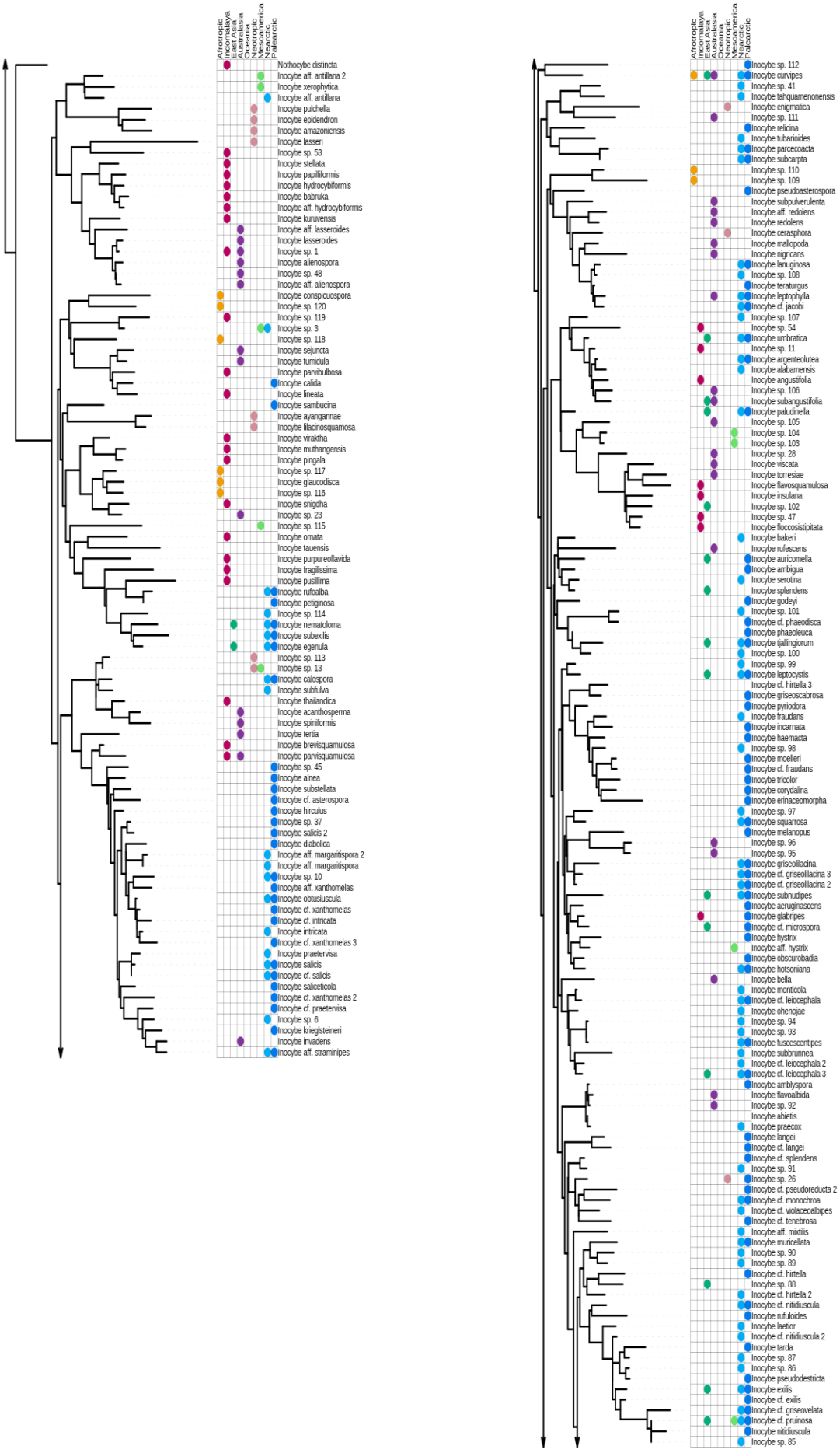

Figure 6 – Continued.

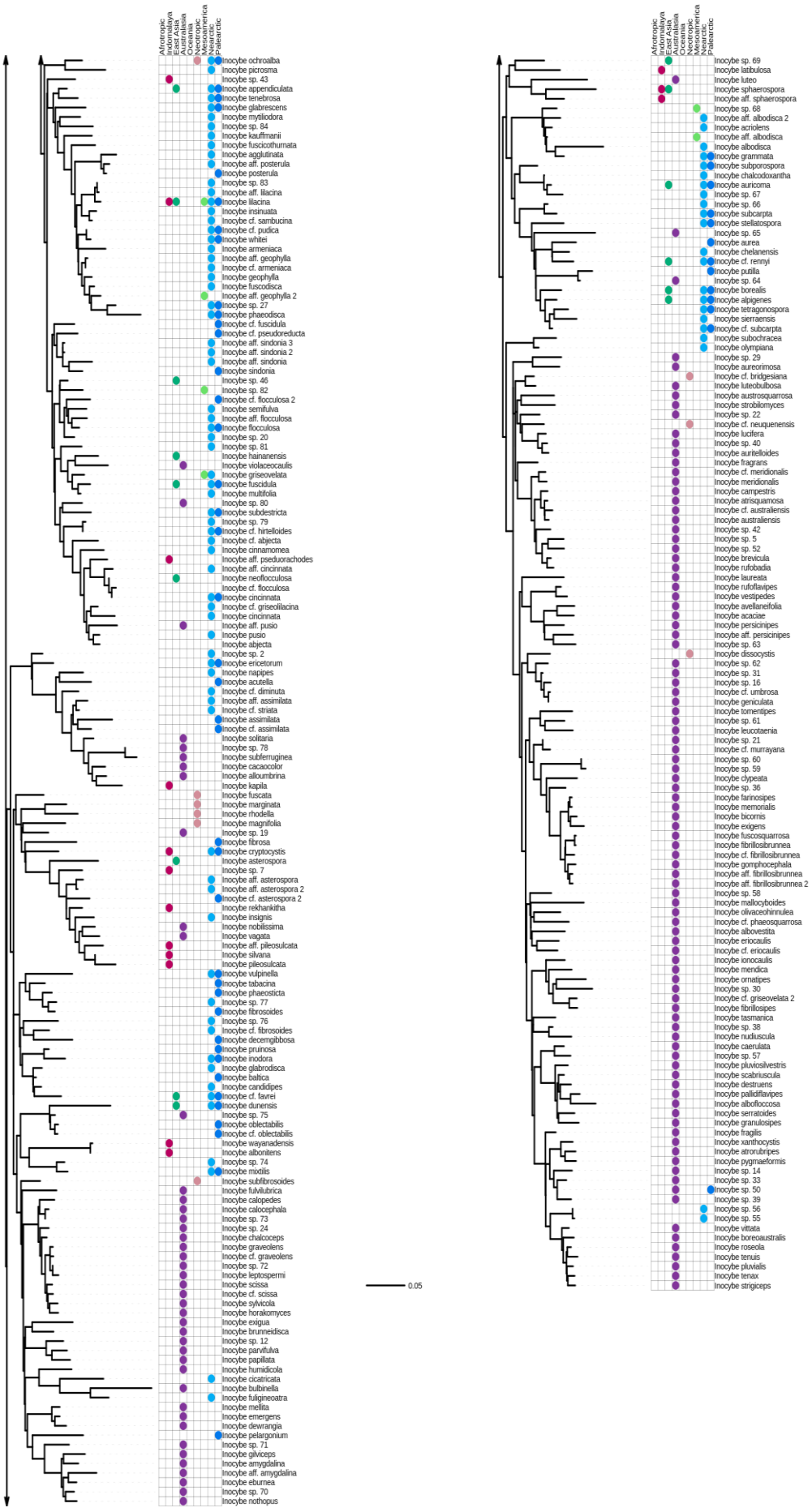

Figure 6 – Continued.

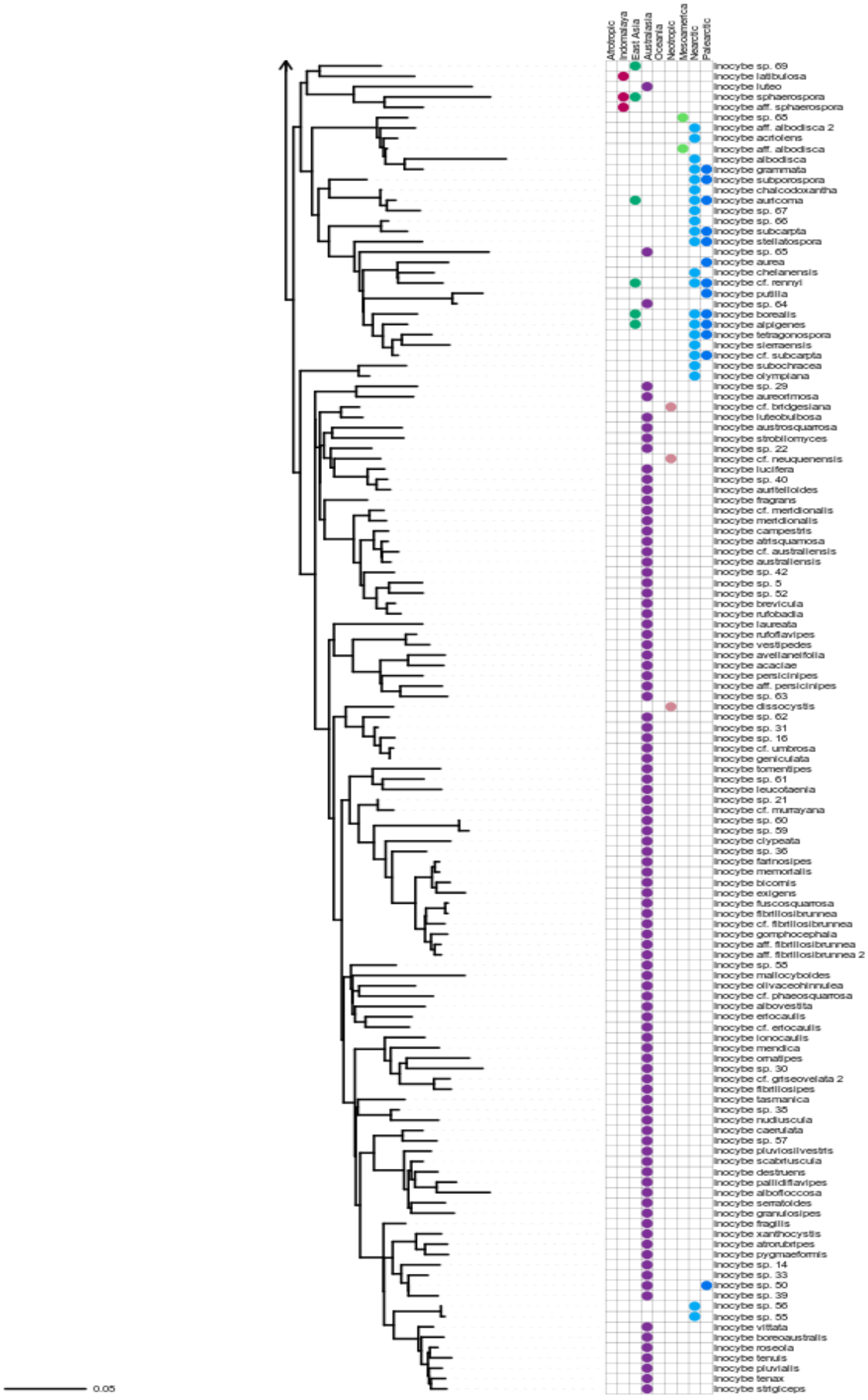

Figure 6 – Continued.

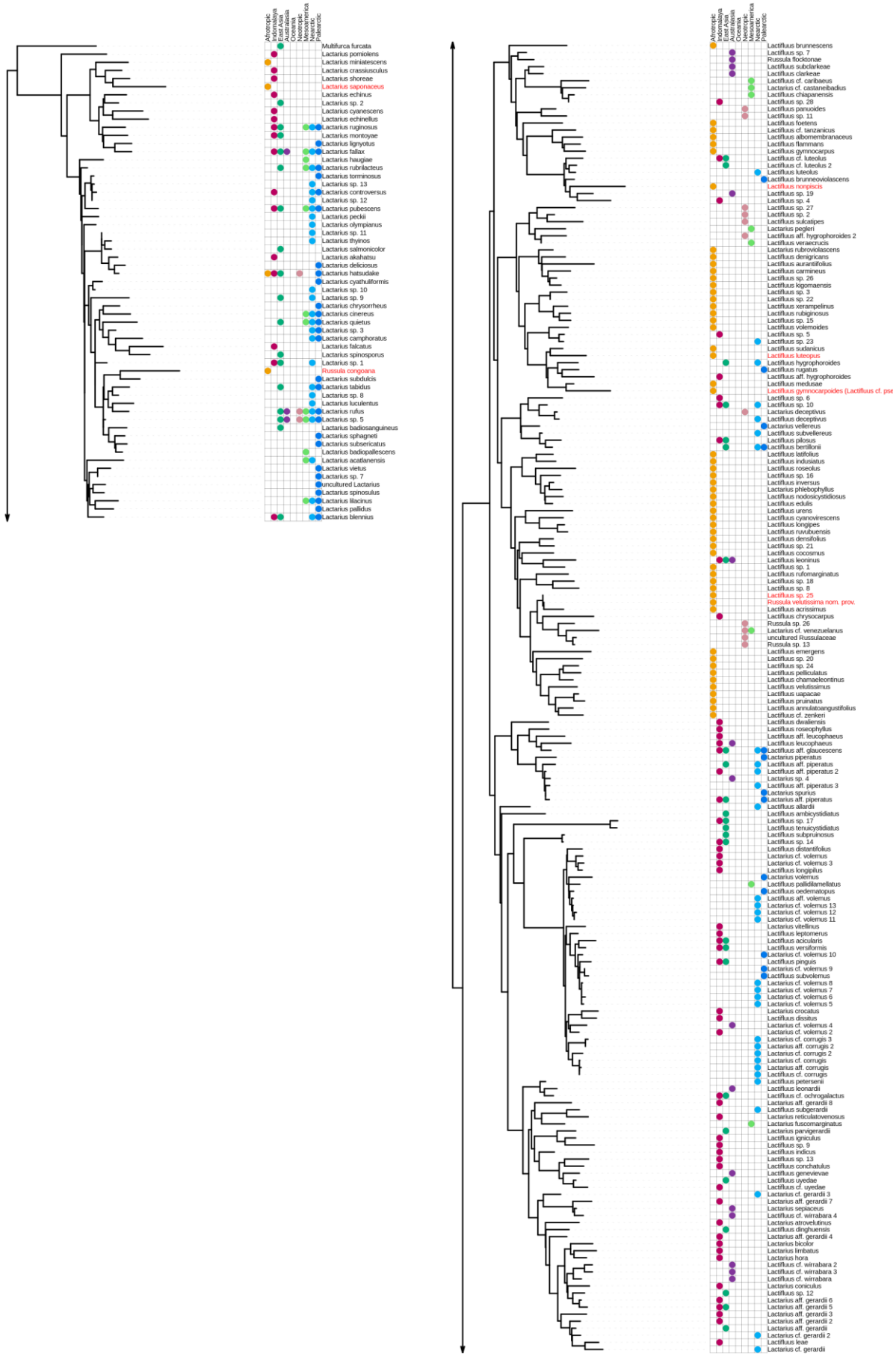

Figure 7 – ML tree and biogeographic occurrence matrix for Russulaceae OTUs.

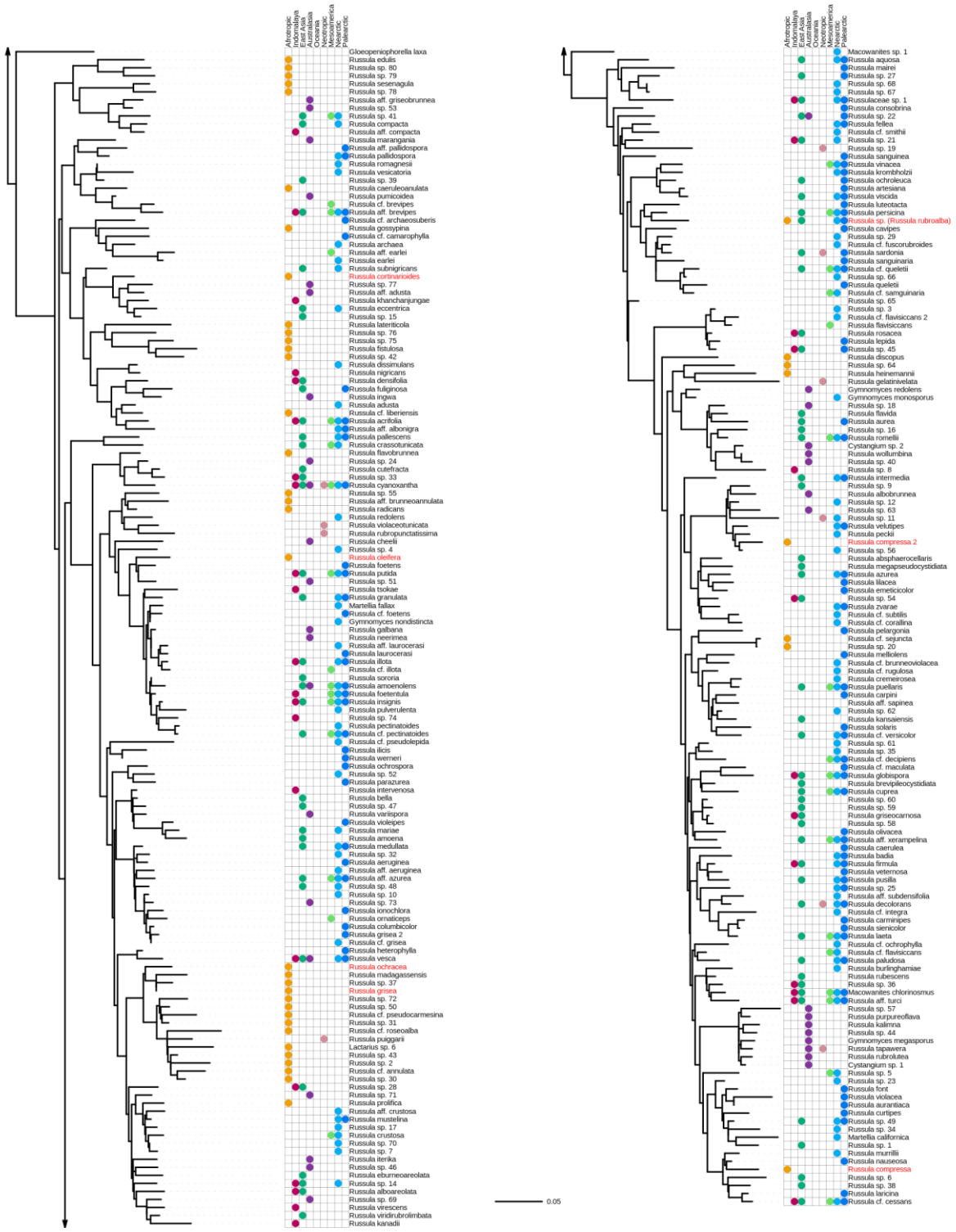

Figure 7 – Continued.

Biogeographic regions

The Afrotropic OTUs of *Amanitaceae* were significantly clustered on shallow phylogenetic scales (P_{mntd} = 0.00), but not on deeper scales (P_{mpd} = 0.60). This pattern was also observed for the other regions, although many tended to be clustered also at deeper scales. The Afrotropic *Boletaceae* OTUs were significantly over-dispersed at both on deep and shallow scales (P_{mntd} = 0.97; P_{mpd} = 0.98). *Boletaceae* in most other regions, except Indomalaya, were clustered at shallow scales, but there is no general pattern for deeper scales. The Afrotropic *Cantharellus* OTUs were clustered at shallow phylogenetic depths (P_{mntd} = 0.00), but with no clear pattern at deeper depths (P_{mpd} = 0.91). *Cantharellus* OTUs in most other regions were also clustered on shallow scales,

except for East Asia and Mesoamerica, where there was no clear pattern, but there is no general pattern for *Cantharellus* at deeper scales. The two Afrotropic *Cortinarius* OTUs were over-dispersed at both deep and shallow phylogenetic scales (P_{mntd} = 0.98; P_{mpd} = 0.98). There was no easily discerned general pattern for *Cortinarius* among the other regions. The Afrotropic *Inocybaceae* OTUs seemed to be clustered at shallow scales (P_{mntd} = 0.028) but over-dispersed on deeper scales (P_{mpd} = 1.00). *Inocybaceae* of most regions were clearly clustered at shallow scales. Indomalayan *Inocybaceae* were also over-dispersed at deeper scales, but most regions are, or tend to be, clustered also at deeper scales or to have no clear pattern. The Afrotropic *Russulaceae* OTUs were clustered at deeper phylogenetic scales (P_{mpd} = 0.00), but have no clear pattern at shallow scales (P_{mntd} = 0.38). Other regions also tended to be clustered at deep phylogenetic scales, or to have no clear pattern, and may also be clustered at more shallow scales. The Afrotropic *Sclerodermataceae* OTUs showed no clear pattern at either shallow (P_{mntd} = 0.80) or deep phylogenetic scales (P_{mpd} = 0.74). The same goes for all the other regions where *Sclerodermataceae* were found, but Australasia tended to be clustered at deep scales (Supplementary materials).

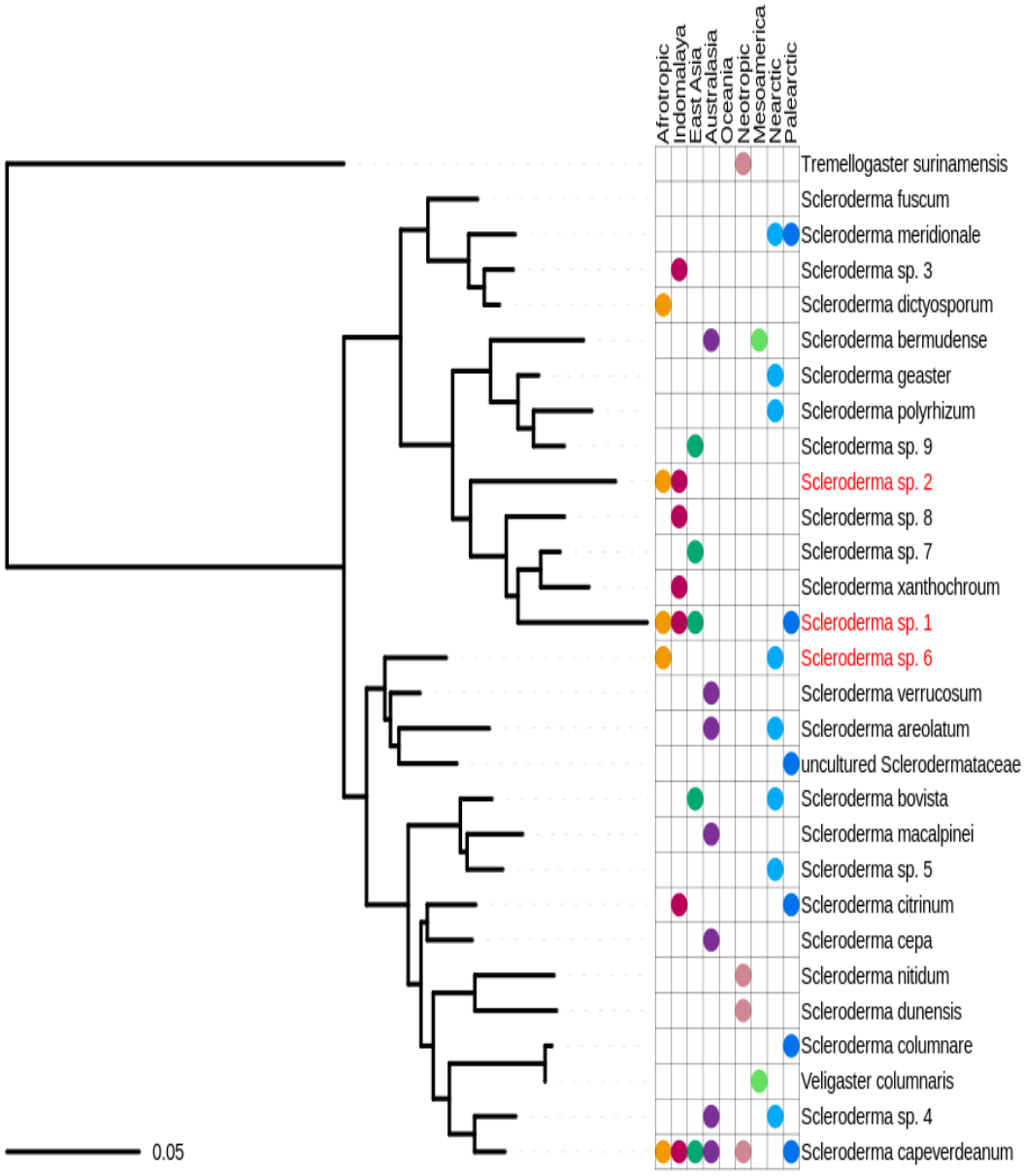

Figure 8 – ML tree and biogeographic occurrence matrix for Sclerodermataceae OTUs.

Table 1 Variation in total OTU richness (SR) and phylogenetic diversity (PD) of EcM families between different regional communities.

	Amanitaceae		Boletaceae		Cantharellaceae		Cortinariaceae		Inocybaceae		Russulaceae		Sclerodermataceae	
	SR	**PD**	**SR**	**PD**	**SR**	**PD**	**SR**	**PD**	**SR**	**PD**	**SR**	**PD**	**SR**	**PD**
Global total	332	10.67	728	35.06	111	2.67	598	11.11	677	22.73	533	15.83	28	1.06
OSRF	9	0.92	1	0.22	1	0.26	1	0.14	2	0.52	14	1.48	3	0.34
Afrotropic (incl. OSRF)	34	1.99	23	3.46	43	1.43	2	0.23	23	2.10	101	4.93	5	0.42
Afrotropic (excl. OSRF)	27	1.84	22	3.37	42	1.43	1	0.11	21	2.00	90	4.35	2	0.25
Indomalaya	66	3.34	60	7.72	11	0.82	5	0.25	67	4.63	102	4.80	7	0.47
East-Asia	95	4.31	365	19.94	9	0.74	33	1.36	47	2.97	126	5.23	5	0.39
Australasia	50	3.20	57	5.69	8	0.50	224	4.59	215	8.23	56	2.74	7	0.41
Oceania	0	0.00	0	0.00	0	0.00	0	0.00	1	0.29	1	0.15	0	0.00
Neotropic	22	1.10	42	3.87	1	0.22	49	1.45	22	1.86	24	1.73	4	0.39
Mesoamerica	21	1.44	38	3.60	2	0.34	25	0.99	20	1.61	53	2.99	2	0.29
Nearctic	118	4.43	173	8.48	28	0.68	197	4.69	224	7.78	171	5.79	8	0.45
Palearctic	41	2.13	88	4.53	11	0.46	241	5.32	199	7.93	139	5.08	6	0.44

Table 2 Variation in unique OTUs (SR) and unique phylogenetic diversity (PD) of EcM families between different regional communities with values for the Afrotropics calculated excluding OSRF communities.

	Amanitaceae			Boletaceae			Cantharellaceae			Cortinariaceae			Inocybaceae			Russulaceae			Sclerodermataceae		
	SR	**PD**	**P**	**SR**	**PD**	**P**	**SR**	**PD**	**P**	**SR**	**PD**	**P**	**SR**	**PD**	**P**	**SR**	**PD**	**P**	**SR**	**PD**	**P**
Global total	332	10.67	-	728	35.06	-	111	2.67	-	598	11.11	-	677	22.73	-	533	15.83	-	28	1.06	-
OSRF	6	0.13	0.383	0	0	-	1	1e-6	>0.999	1	0.10	0.001	2	0.07	0.194	10	0.28	0.065	0	0	-
Afrotropic (incl. OSRF)	26	0.81	0.012	20	2.31	<0.001	43	0.95	0.006	1	0.10	0.002	22	1.26	<0.001	99	3.58	<0.001	1	0.01	0.936
Afrotropic (excl. OSRF)	19	0.60	0.021	20	2.31	<0.001	42	0.94	0.006	0	0	-	20	1.19	<0.001	86	3.08	<0.001	1	0.01	0.939
Indomalaya	34	0.80	0.278	28	1.83	<0.001	11	0.19	0.175	0	0	-	59	2.13	<0.001	54	1.40	0.008	3	0.05	0.643
East-Asia	47	1.17	0.126	307	10.49	0.489	9	0.09	0.558	3	0.07	0.083	13	0.34	0.258	37	0.69	0.816	2	0.02	0.896
Australasia	46	1.49	<0.001	49	2.67	0.002	8	0.15	0.137	210	3.23	0.156	207	5.56	0.030	46	0.84	0.881	3	0.05	0.687
Oceania	0	0.00	-	0	0.00	-	0	0.00	-	0	0	-	1	0.10	0.006	0	0	-	0	0.00	-
Neotropic	14	0.28	0.537	35	2.26	<0.001	1	0.26	0.008	41	0.55	0.564	19	1.20	<0.001	15	0.53	0.002	3	0.33	0.007
Mesoamerica	4	0.06	0.697	17	0.77	0.101	2	0.03	0.310	8	0.16	0.085	14	0.31	0.508	14	0.25	0.762	1	1e-6	>0.999
Nearctic	82	1.64	0.804	127	2.76	>0.999	26	0.20	0.951	83	1.04	0.846	134	2.55	0.999	86	1.22	>0.999	3	0.04	0.786
Palearctic	17	0.49	0.081	56	1.18	0.980	9	0.07	0.751	130	1.81	0.608	106	2.67	0.197	66	1.30	0.787	2	0.02	0.813

Discussion

With 26 OTUs that had not previously been recorded from the Afrotropics, this study represents a significant addition of molecular sampling of African EcM fungal diversity. Further, 20 OTUs are not linked with previous sequences that have geographic annotation, so it also represents a valuable contribution to the global sampling. In most EcM lineages, the proportion of PD added to the tree by these unique OSRF OTUs was higher than the expected average for that number of OTUs. This means that these are not only shallow tips in the tree, but represent fairly distinct lineages. Of the 31 OTUs that were found in this study, 20 were linked to a taxon name based on clustering with named sequences (in UNITE or GenBank) or by morphological identification. However, these were very unevenly distributed among the EcM lineages. All the OTUs from *Boletaceae* (1 OTU), *Inocybaceae* (2 OTUs), and *Cantharellaceae* (1 OTU), and 12 of the 13 OTUs in *Russulaceae* from OSRF were linked to a name, but only 5 of 9 OTUs of *Amanitaceae* and 1 of 3 OTUs of *Sclerodermataceae*, and the single OTU of *Cortinariaceae*, were not linked to a name. However, the *Inocybaceae* species were only recently described based partially on materials from this study (Aïgnon et al. 2021a, b), and it would not have been possible to link them to a name at the time of their collection. It is, further, uncertain if all the name assignments are correct, as some names are attached to more than one OTU, even if they are far apart in the phylogenies. One of the *Amanita* specimens from OSRF clusters with *Amanita phalloides* into an OTU that also includes *Amanita subjunquillea*. This specimen in fact represents a separate species that was recently described as *Amanita albolimbata* (Codjia et al. 2020), the first lethally poisonous *Amanita* reported from Benin.

Although we did add considerable molecular sampling to what was previously available, our sampling was greatly reduced by problems getting good quality PCR products and sequences. This could be due to many factors of which poorly controlled temperatures in the field dryers may be one (De Kesel 2001). This could result in problems both if the temperature was too high, resulting in degraded DNA, or too low, resulting in contamination by saprotrophic molds and yeasts. There were also problems with heterozygous or inter-copy indels, giving polymorphic sequence reads.

Although the majority of OTUs were confined to one biogeographical region, many were distributed in several regions. This was true for all the lineages except *Cantharellus*, where only *C. pallens* and *C. enelensis* were found in two regions (Nearctic and Palearctic). The limited distribution of *Cantharellus* species may be a consequence of their under-representation in environmental samples, due to primer mismatches and ITS length variation (Buyck et al. 2014), and therefore their distribution was not as well captured by UNITE records. Indeed, a recent eDNA-based study reported poor representation of *Cantharellus* in gallery forest where fruit bodies of this genus are frequently observed (Meidl et al. 2021). The increased rate of molecular evolution may have also led to more narrowly defined OTUs within *Cantharellus*, as USH were part of our clustering. However, the very clear signal of clustering at shallow depths in the phylogeny for most regions speaks against this being the only explanation, and previous studies based on other OTU and area annotation criteria have also found obvious geographic signal (Buyck et al. 2014).

Our OTUs were defined to be reasonable estimates of species level taxa, but may include cases of splitting species and, as shown above for *Amanita phalloides*, do include cases of lumping species. The many widespread OTUs should therefore not necessarily be taken as an indication that species often are widespread, but rather that lineages do move around on a relatively short time scale (but perhaps still millions of years; Ryberg 2015). Given estimates of molecular clock rates and ages of the entire clades (Wang et al. 2010, Ryberg & Matheny 2012) it seems unlikely that plate tectonics are a major explanation of this pattern, which is probably instead largely due to occasional long-distance dispersal events. Since sequence records of a species in a region are limited by sampling and easily available annotations, it is very likely that the number of OTUs that are widely dispersed is underestimated, and that at least some OTUs that were only found in one region in reality exist in more. The exact frequency and range of long-distance dispersal events are therefore difficult to determine. More detailed biogeographic studies of each clade, and phylogeographic studies are needed to address that question.

Our phylogenies generally had many branches without strong support, and should therefore not be taken as a basis for taxonomic revisions and similar work, but should be sufficient for reasonable estimates of phylogenetic distances, as used here. The OSRF OTUs do not show any common, and most often no clear, phylogenetic pattern in either a regional or global context. This may be partially due to the limited number of OTUs from OSRF. There is also no clear pattern for Afrotropic species, but it seems that clustering at some phylogenetic scale is more common than over-dispersion. This could possibly be a result of speciation within biogeographic regions. If this is common, it is possible that the pattern is blurred by relatively frequent long-distance dispersals. Patterns of over-dispersal at shallow phylogenetic scales could be a consequence of frequent speciation after long-distance dispersal to another region. At deeper scales, it may be due to ecological divergence, resulting in more distantly related taxa having small niche overlap, so that they more easily establish and coexist in the regional communities. Both geographical contexts for speciation may have happened within each EcM lineage, and there may be different levels of niche differentiation. The differences in patterns between the different EcM clades may be explained by which process is most prominent in that clade, and the lack of clear pattern may be due to the simultaneous action of both processes canceling each other out. The pattern observed in any given clade may also depend on the age of the clade and the length of time the processes have had to act. That the *Russulaceae* in OSRF are over-dispersed at deeper phylogenetic scales probably reflects that we have species from three of the four genera in the family. There may of course also be other processes involved, such as key similarities/differences between specific geographic regions or interactions with parasites, and not least, sampling and annotation biases between regions.

Although it seems to be the case that EcM lineages do get around, there are still observable geographic patterns. In three of the families, the OSRF community is phylogenetically closer to the rest of the Afrotropics than to the other regions. This was, however, difficult to discern based on taxonomic annotations alone. Although the phylogenetic context adds some insights, it still lacks power due to the paucity of GenBank annotations and uneven distribution of taxon sampling around the globe.

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Supplementary Table 1 Different clusters identified.

OTU	**Species**	**Voucher**	**Accession number (ITS)**
1	*Agaricus* sp.	HLA-0227	MZ027741
		HLA-0175	MZ027742
2	*Agaricus* sp.	HLA-0193	MZ027743
3	*Agaricus* sp.	BADOU-0262-A	MZ027745
		SB-0272-B	MZ027749
		BADOU-0251-B	MZ027751
		SB-0180	MZ027754
		SB-0216	MZ027755
4	*Leucocoprinus* sp.	SB-0353-A	MZ027757
5	*Crepidotus* sp.	HLA-0067	MZ027761
6	*Amanita* sp.	BADOU-0225.1	MZ027765
7	*Amanita* sp.	BADOU-0259	MW835231
8		JEIC-0114-A	MZ027766
		KIT-0081-B	MZ027770
		HLA-0225	MZ027772
		HLA-0281	MZ027773
9	*Amanita* sp.	HLA-0298	MZ027775
		JEIC-0009	MZ027776
		KIT-0366	MZ027777
		KIT-0065-B	MZ027779
		HLA-0334	MZ027780
		SB-0199	MZ027781

Supplementary Table 1 Continued.

OTU	Species	Voucher	Accession number (ITS)
		SB-0416	MZ027782
		HLA-0094	MZ027783
		HLA-0152	MZ027784
10	*Amanita* sp.	HLA-0024-A	MZ027787
		HLA-0188	MZ027790
11	*Amanita* sp.	HLA-0118	MZ027791
		SB-0438	MZ027792
12	*Amanita* sp.	LAG-0183	MZ027794
		BADOU-0157	MZ027795
		BADOU-0252	MZ027796
		BADOU-0006	MZ027797
		BADOU-0017	MZ027798
		BADOU-0248-B	MZ027800
		BADOU-0046	MZ027801
13	*Amanita* sp.	KIT-0050	MW829790
14	*Amanita* sp.	JEIC-0147	MW829797
15	*Amanita* sp.	LAG-0096	MW829789
16	*Amanita* sp.	BRF-4071	MW829796
17	*Amanita* sp.	HLA-0173	MW829794
18	*Amanita* sp.	BADOU-0205	MW829795
19	*Amanita* sp.	HLA-0153	MW829793
20	*Amanita* sp.	KIT-0131	MW835233
21	*Amanita* sp.	HLA-0100	MW835232
22	*Termitomyces* sp.	LAG-0081	MZ027803
23	*Termitomyces* sp.	BADOU-0029	MZ027804
24	*Termitomyces* sp.	SB-0432	MZ027805
25	*Porphyrellus* sp.	HLA-0243	MZ027807
		HLA-0006	MZ027808
		LAG-0124-A	MZ027809
26	*Pulveroboletus* sp.	HLA-0341	MZ027814
		KIT-0086	MW829791
27	*Boletus* sp.	LAG-0101	MW829792
28	*Tylopilus* sp.	KIT-0345	MW829807
29	*Scleroderma* sp.	LAG-0015-B	MZ027818
		BADOU-0213	MZ027820
		SB-0352	MZ027821
		HLA-0021	MZ027823
		HLA-0237	MZ027824
30	*Scleroderma* sp.	JEIC-0041	MZ027826
		SB-0090	MW826270
31	*Scleroderma* sp.	KIT-0315	MW826268
32	*Cantharellus addaiensis*	LAG-0148	MW829787
33	*Cortinarius* sp.	HDR-0032	MW829788
34	*Scleroderma* sp.	BADOU-0240	MW826269
35	*Clavulina* sp.	HLA-0063	MZ027829

Supplementary Table 1 Continued.

OTU	Species	Voucher	Accession number (ITS)
36	*Lactarius* sp.	KIT-0221	MZ027830
		KIT-0068-B	MZ027832
37	*Lactifluus* sp.	LAG-0006	MZ027838
38		LAG-0200	MW856422
39		HLA-0003	MZ027840
40		HLA-0181	MZ027842
41	*Lactifluus* sp.	SB-0442	MW829801
42	*Lactifluus* sp.	KIT-0151	MW829800
43	*Lactifluus* sp.	HLA-0183	MZ027845
		LAG-0199	MZ027846
44	*Russula* sp.	KIT-0215	MZ027849
		BADOU-0192	MW829804
45	*Russula* sp.	JEIC-0022	MZ027850
		KIT-0238	MW829798
46	*Russula* sp.	KIT-0222	MW856420
47	*Russula* sp.	SB-0162-B	MZ027854
		HLA-0087	MZ027856
48	*Russula* sp.	HLA-0241	MW829812
49	*Russula* sp.	BADOU-0128	MZ027858
		KIT-0209	MZ027859
		HLA-0245	MZ027861
		BADOU-0170	MZ027862
50	*Russula* sp.	HDR-0036	MZ027864
		LAG-0130-A	MZ027867
		HLA-0213	MZ027869
51	*Russula* sp.	BRF-4151	MW829806
52	*Russula* sp.	BADOU-0258-B	MZ027876
		SB-0096	MW829810
53	*Russulaceae* sp.	SB-0436	MW856421
54	*Russula* sp.	HLA-0331	MZ027878
55	*Russula* sp.	LAG-0142	MW829811
56	*Russula* sp.	BRF-4104	MW829809
57	*Russula* sp.	BADOU-0203	MZ027881
58	*Russula* sp.	SB-0070	MZ027883
		BADOU-0230	MW829805
		HLA-0102	MZ027884
		HLA-0036	MZ027887
		HLA-0125	MZ027888
59	*Russula* sp.	BRF-4144	MW829803
60	*Russula* sp.	KIT-0035	MW835234
61	*Russula* sp.	SB-0115	MW880709
62	*Russula* sp.	LAG-0147	MZ027890
		JEIC-0001	MW856423

Supplementary Table 2 Variation of standardized effect size (SES) of mean nearest taxon distances (mntd) and mean pairwise distances (mpd) of Amanitaceae.

Supplementary Table 2.1 Variation of standardized effect size (SES) of mean nearest taxon distances (mntd) of Amanitaceae between communities with Afrotropic including OSRF communities.

	ntaxa	mntd.obs	mntd.rand.mean	mntd.rand.sd	mntd.obs.rank	mntd.obs.z	mntd.obs.p	runs
Afrotropic	34	0.056	0.0860	0.010	17	-2.900	0.001	10000
Indomalaya	66	0.062	0.067	0.005	1855.5	-0.904	0.185	10000
East Asia	95	0.053	0.060	0.004	685	-1.495	0.068	10000
Australasia	50	0.072	0.074	0.007	3812	-0.313	0.381	10000
Oceania	0	NA	NA	NA	NA	NA	NA	10000
Neotropic	22	0.044	0.102	0.014	1	-3.850	0.000	10000
Mesoamerica	21	0.068	0.104	0.015	113	-2.270	0.011	10000
Nearctic	118	0.044	0.055	0.003	3	-3.386	0.000	10000
Palearctic	41	0.051	0.080	0.008	4	-3.284	0.000	10000

Supplementary Table 2.2 Variation of standardized effect size (SES) of mean pairwise distances (mpd) of Amanitaceae between communities with Afrotropic including OSRF communities.

	ntaxa	mpd.obs	mpd.rand.mean	mpd.rand.sd	mpd.obs.rank	mpd.obs.z	mpd.obs.p	runs
Afrotropic	34	0.292	0.287	0.012	6342	0.366	0.634	10000
Indomalaya	66	0.290	0.287	0.008	6197	0.320	0.619	10000
East Asia	95	0.289	0.287	0.006	5733	0.201	0.573	10000
Australasia	50	0.297	0.287	0.010	8339	0.983	0.833	10000
Oceania	0	NA	NA	NA	NA	NA	NA	10000
Neotropic	22	0.224	0.288	0.016	8	-3.884	0.000	10000
Mesoamerica	21	0.266	0.287	0.016	1035	-1.267	0.103	10000
Nearctic	118	0.265	0.288	0.005	1	-3.935	0.000	10000
Palearctic	41	0.269	0.287	0.011	580	-1.596	0.057	10000

Supplementary Table 2.3 Variation of standardized effect size (SES) of mean nearest taxon distances (mntd) of Amanitaceae between communities with OSRF communities out of Afrotropic.

	ntaxa	mntd.obs	mntd.rand.mean	mntd.rand.sd	mntd.obs.rank	mntd.obs.z	mntd.obs.p	runs
Afrotropic	27	0.077	0.094	0.012	932	-1.298	0.093	10000
Indomalaya	66	0.062	0.067	0.005	1843	-0.899	0.184	10000
East Asia	95	0.053	0.060	0.004	738	-1.460	0.073	10000
Australasia	50	0.07242196	0.074	0.007	3802	-0.308	0.380	10000
Oceania	0	NA	NA	NA	NA	NA	NA	10000
Neotropic	22	0.044	0.101	0.015	1	-3.806	0.000	10000
Mesoamerica	21	0.068	0.103	0.015	100	-2.255	0.000	10000
Nearctic	118	0.044	0.055	0.003	5	-3.357	0.000	10000
Palearctic	41	0.051	0.080	0.008	2	-3.333	0.000	10000
OSRF	9	0.106	0.148	0.031	867	-1.357	0.086	10000

Supplementary Table 2.4 Variation of standardized effect size (SES) of mean pairwise distances (mpd) of Amanitaceae between communities with OSRF communities out of Afrotropic.

	ntaxa	mpd.obs	mpd.rand.mean	mpd.rand.sd	mpd.obs.rank	mpd.obs.z	mpd.obs.p	runs
Afrotropic	27	0.289	0.288	0.014	5237	0.099	0.523	10000
Indomalaya	66	0.290	0.287	0.008	6237	0.336	0.623	10000
East Asia	95	0.289	0.287	0.006	5702	0.204	0.570	10000
Australasia	50	0.297	0.288	0.010	8364	0.977	0.836	10000
Oceania	0	NA	NA	NA	NA	NA	NA	10000
Neotropic	22	0.224	0.287	0.016	10	-3.821	0.000	10000
Mesoamerica	21	0.266	0.287	0.017	995	-1.259	0.099	10000
Nearctic	118	0.265	0.288	0.005	2	-3.984	0.000	10000
Palearctic	41	0.269	0.288	0.011	597	-1.607	0.059	10000
OSRF	9	0.285	0.288	0.028	4434	-0.077	0.443	10000

Supplementary Table 3 Variation of standardized effect size (SES) of mean nearest taxon distances (mntd) and mean pairwise distances (mpd) of Boletaceae.

Supplementary Table 3.1 Variation of standardized effect size (SES) of mean nearest taxon distances (mntd) of Boletaceae between communities with Afrotropic including OSRF communities.

	ntaxa	mntd.obs	mntd.rand.mean	mntd.rand.sd	mntd.obs.rank	mntd.obs.z	mntd.obs.p	runs
Afrotropic	23	0.206	0.161	0.021	9774	2.068	0.977	10000
Indomalaya	60	0.170	0.129	0.012	9992	3.377	0.999	10000
East Asia	365	0.054	0.070	0.002	1	-5.349	0.000	10000
Australasia	57	0.122	0.131	0.012	2397	-0.728	0.239	10000
Oceania	0	NA	NA	NA	NA	NA	NA	10000
Neotropic	42	0.119	0.141	0.015	714	-1.430	0.071	10000
Mesoamerica	38	0.124	0.144	0.016	981	-1.270	0.098	10000
Nearctic	173	0.053	0.093	0.005	1	-6.946	0.000	10000
Palearctic	88	0.051	0.116	0.009	1	-6.845	0.000	10000

Supplementary Table 3.2 Variation of standardized effect size (SES) of mean pairwise distances (mpd) of Boletaceae between communities with Afrotropic including OSRF communities.

	ntaxa	mpd.obs	mpd.rand.mean	mpd.rand.sd	mpd.obs.rank	mpd.obs.z	mpd.obs.p	runs
Afrotropic	23	0.375	0.306	0.033	9767	2.069	0.976	10000
Indomalaya	60	0.382	0.307	0.020	9997	3.747	0.999	10000
East Asia	365	0.324	0.307	0.006	9984	2.818	0.998	10000
Australasia	57	0.375	0.306	0.020	9991	3.330	0.999	10000
Oceania	0	NA	NA	NA	NA	NA	NA	10000
Neotropic	42	0.282	0.307	0.024	1495	-1.039	0.149	10000
Mesoamerica	38	0.266	0.307	0.025	556	-1.572	0.055	10000
Nearctic	173	0.227	0.307	0.010	1	-7.427	0.000	10000
Palearctic	88	0.270	0.307	0.016	111	-2.262	0.011	10000

Supplementary Table 4 Variation of standardized effect size (SES) of mean nearest taxon distances (mntd) and mean pairwise distances (mpd) of Cantharellaceae.

Supplementary Table 4.1 Variation of standardized effect size (SES) of mean nearest taxon distances (mntd) of Cantharellaceae between communities with Afrotropic including OSRF communities.

	ntaxa	mntd.obs	mntd.rand.mean	mntd.rand.sd	mntd.obs.rank	mntd.obs.z	mntd.obs.p	runs
Afrotropic	43	0.023	0.060	0.033	57	-1.140	0.005	10000
Indomalaya	11	0.043	0.098	0.077	598	-0.706	0.059	10000
East Asia	9	0.100	0.107	0.090	6835	-0.075	0.683	10000
Australasia	8	0.032	0.109	0.092	104	-0.831	0.010	10000
Oceania	0	NA	NA	NA	NA	NA	NA	10000
Neotropic	1	NA	NA	NA	NA	NA	NA	10000
Mesoamerica	2	0.170	0.220	0.371	6628	-0.135	0.662	10000
Nearctic	28	0.014	0.070	0.044	1	-1.243	0.000	10000
Palearctic	11	0.031	0.099	0.078	88	-0.852	0.008	10000

Supplementary Table 4.2 Variation of standardized effect size (SES) of mean pairwise distances (mpd) of Cantharellaceae between communities with Afrotropic including OSRF communities.

	ntaxa	mpd.obs	mpd.rand.mean	mpd.rand.sd	mpd.obs.rank	mpd.obs.z	mpd.obs.p	runs
Afrotropic	43	0.199	0.220	0.063	5804	-0.330	0.580	10000
Indomalaya	11	0.245	0.224	0.155	8473	0.132	0.847	10000
East Asia	9	0.179	0.221	0.170	4709	-0.246	0.470	10000
Australasia	8	0.124	0.221	0.180	1871	-0.535	0.187	10000
Oceania	0	NA	NA	NA	NA	NA	NA	10000
Neotropic	1	NA	NA	NA	NA	NA	NA	10000
Mesoamerica	2	0.170	0.222	0.382	6643	-0.135	0.664	10000
Nearctic	28	0.083	0.220	0.087	1	-1.578	0.000	10000
Palearctic	11	0.075	0.220	0.150	8	-0.960	0.000	10000

Supplementary Table 5 Variation of standardized effect size (SES) of mean nearest taxon distances (mntd) and mean pairwise distances (mpd) of Cortinariaceae.

Supplementary Table 5.1 Variation of standardized effect size (SES) of mean nearest taxon distances (mntd) of Cortinariaceae between communities with Afrotropic including OSRF communities.

	ntaxa	mntd.obs	mntd.rand.mean	mntd.rand.sd	mntd.obs.rank	mntd.obs.z	mntd.obs.p	runs
Afrotropic	2	0.219	0.110	0.038	9897	2.829	0.989	10000
Indomalaya	5	0.079	0.078	0.018	5388	0.030	0.538	10000
East Asia	33	0.056	0.047	0.005	9506	1.687	0.950	10000
Australasia	224	0.024	0.029	0.001	2	-3.486	0.000	10000
Oceania	0	NA	NA	NA	NA	NA	NA	10000
Neotropic	49	0.036	0.043	0.004	453	-1.632	0.045	10000
Mesoamerica	25	0.050	0.050	0.006	4895	-0.053	0.489	10000
Nearctic	197	0.028	0.030	0.001	594	-1.559	0.059	10000
Palearctic	241	0.026	0.028	0.001	727	-1.453	0.072	10000

Supplementary Table 5.2 Variation of standardized effect size (SES) of mean pairwise distances (mpd) of Cortinariaceae between communities with Afrotropic including OSRF communities.

	ntaxa	mpd.obs	mpd.rand.mean	mpd.rand.sd	mpd.obs.rank	mpd.obs.z	mpd.obs.p	runs
Afrotropic	2	0.219	0.110	0.038	9893	2.857	0.989	10000
Indomalaya	5	0.100	0.110	0.020	3230	-0.483	0.322	10000
East Asia	33	0.119	0.110	0.007	8844	1.218	0.884	10000
Australasia	224	0.095	0.110	0.002	1	-6.283	0.000	10000
Oceania	0	NA	NA	NA	NA	NA	NA	10000
Neotropic	49	0.098	0.110	0.005	217	-1.928	0.021	10000
Mesoamerica	25	0.120	0.110	0.008	8710	1.146	0.870	10000
Nearctic	197	0.114	0.110	0.002	9598	1.769	0.959	10000
Palearctic	241	0.111	0.110	0.002	7307	0.625	0.730	10000

Supplementary Table 6 Variation of standardized effect size (SES) of mean nearest taxon distances (mntd) and mean pairwise distances (mpd) of Inocybaceae.

Supplementary Table 6.1 Variation of standardized effect size (SES) of mean nearest taxon distances (mntd) of Inocybaceae between communities with Afrotropic including OSRF communities.

	ntaxa	mntd.obs	mntd.rand.mean	mntd.rand.sd	mntd.obs.rank	mntd.obs.z	mntd.obs.p	runs
Afrotropic	23	0.094	0.122	0.014	258	-1.931	0.025	10000
Indomalaya	67	0.086	0.088	0.006	3961	-0.250	0.396	10000
East Asia	47	0.071	0.098	0.008	5	-3.056	0.000	10000
Australasia	215	0.044	0.061	0.002	1	-6.188	0.000	10000
Oceania	1	NA	NA	NA	NA	NA	NA	10000
Neotropic	22	0.108	0.123	0.015	1559	-1.021	0.155	10000
Mesoamerica	20	0.087	0.127	0.016	59	-2.466	0.005	10000
Nearctic	224	0.038	0.060	0.002	1	-8.389	0.000	10000
Palearctic	199	0.048	0.062	0.002	1	-4.984	0.000	10000

Supplementary Table 6.2 Variation of standardized effect size (SES) of mean pairwise distances (mpd) of Inocybaceae between communities with Afrotropic including OSRF communities.

	ntaxa	mpd.obs	mpd.rand.mean	mpd.rand.sd	mpd.obs.rank	mpd.obs.z	mpd.obs.p	runs
Afrotropic	23	0.361	0.266	0.027	10000	3.480	0.999	10000
Indomalaya	67	0.302	0.266	0.015	9929	2.350	0.992	10000
East Asia	47	0.271	0.266	0.019	5952	0.264	0.595	10000
Australasia	215	0.234	0.266	0.007	1	-4.17	0.000	10000
Oceania	1	NA	NA	NA	NA	NA	NA	10000
Neotropic	22	0.226	0.265	0.027	858	-1.417	0.085	10000
Mesoamerica	20	0.272	0.266	0.029	5745	0.204	0.574	10000
Nearctic	224	0.246	0.266	0.007	47	-2.633	0.004	10000
Palearctic	199	0.254	0.266	0.007	632	-1.541	0.063	10000

Supplementary Table 6.3 Variation of standardized effect size (SES) of mean nearest taxon distances (mntd) of Inocybaceae between communities with OSRF communities out of Afrotropic.

	ntaxa	mntd.obs	mntd.rand.mean	mntd.rand.sd	mntd.obs.rank	mntd.obs.z	mntd.obs.p	runs
Afrotropic	21	0.111	0.125	0.015	1816	-0.909	0.181	10000
Indomalaya	67	0.086	0.088	0.006	4061	-0.247	0.406	10000
East Asia	47	0.071	0.098	0.008	8	-3.032	0.000	10000
Australasia	215	0.044	0.061	0.002	1	-6.119	0.000	10000
Oceania	1	NA	NA	NA	NA	NA	NA	10000
Neotropic	22	0.108	0.123	0.015	1561	-1.028	0.156	10000
Mesoamerica	20	0.087	0.127	0.016	51	-2.471	0.005	10000
Nearctic	224	0.038	0.060	0.002	1	-8.388	0.000	10000
Palearctic	199	0.048	0.062	0.002	1	-5.037	0.000	10000
OSRF	2	0.433	0.266	0.113	8970	1.4706	0.896	10000

Supplementary Table 6.4 Variation of standardized effect size (SES) of mean pairwise distances (mpd) of Inocybaceae between communities with OSRF communities out of Afrotropic.

	ntaxa	mpd.obs	mpd.rand.mean	mpd.rand.sd	mpd.obs.rank	mpd.obs.z	mpd.obs.p	runs
Afrotropic	21	0.355	0.266	0.028	9999	3.083	0.999	10000
Indomalaya	67	0.302	0.266	0.015	9925	2.340	0.992	10000
East Asia	47	0.271	0.266	0.018	5939	0.261	0.593	10000
Australasia	215	0.234	0.266	0.007	1	-4.142	0.000	10000
Oceania	1	NA	NA	NA	NA	NA	NA	10000
Neotropic	22	0.226	0.266	0.028	846	-1.408	0.084	10000
Mesoamerica	20	0.272	0.265	0.029	5730	0.207	0.572	10000
Nearctic	224	0.246	0.266	0.007	55	-2.641	0.005	10000
Palearctic	199	0.254	0.266	0.007	615	-1.540	0.061	10000
OSRF	2	0.433	0.266	0.113	8971	1.474	0.897	10000

Supplementary Table 7 Variation of standardized effect size (SES) of mean nearest taxon distances (mntd) and mean pairwise distances (mpd) of Russulaceae.

Supplementary Table 7.1 Variation of standardized effect size (SES) of mean nearest taxon distances (mntd) of Russulaceae between communities with Afrotropic including OSRF communities.

	ntaxa	mntd.obs	mntd.rand.mean	mntd.rand.sd	mntd.obs.rank	mntd.obs.z	mntd.obs.p	runs
Afrotropic	101	0.062	0.064	0.003	3702	-0.337	0.370	10000
Indomalaya	102	0.063	0.063	0.003	4162	-0.224	0.416	10000
East Asia	126	0.049	0.059	0.003	3	-3.317	0.000	10000
Australasia	56	0.054	0.077	0.005	2	-3.796	0.000	10000
Oceania	1	NA	NA	NA	NA	NA	NA	10000
Neotropic	24	0.081	0.100	0.011	427	-1.717	0.042	10000
Mesoamerica	53	0.070	0.078	0.006	903	-1.344	0.090	10000
Nearctic	171	0.040	0.053	0.002	1	-5.574	0.000	10000
Palearctic	139	0.045	0.057	0.002	1	-4.334	0.000	10000

Supplementary Table 7.2 Variation of standardized effect size (SES) of mean pairwise distances (mpd) of Russulaceae between communities with Afrotropic including OSRF communities.

	ntaxa	mpd.obs	mpd.rand.mean	mpd.rand.sd	mpd.obs.rank	mpd.obs.z	mpd.obs.p	runs
Afrotropic	101	0.253	0.270	0.004	5	-3.592	0.000	10000
Indomalaya	102	0.264	0.270	0.004	768	-1.440	0.076	10000
East Asia	126	0.262	0.270	0.004	239	-2.013	0.023	10000
Australasia	56	0.263	0.270	0.006	1318	-1.109	0.131	10000
Oceania	1	NA	NA	NA	NA	NA	NA	10000
Neotropic	24	0.280	0.270	0.011	8023	0.839	0.802	10000
Mesoamerica	53	0.271	0.270	0.006	5434	0.131	0.543	10000
Nearctic	171	0.255	0.270	0.003	1	-4.630	0.000	10000
Palearctic	139	0.251	0.270	0.003	1	-5.059	0.000	10000

Supplementary Table 7.3 Variation of standardized effect size (SES) of mean nearest taxon distances (mntd) of Russulaceae between communities with OSRF communities out of Afrotropic.

	ntaxa	mntd.obs	mntd.rand.mean	mntd.rand.sd	mntd.obs.rank	mntd.obs.z	mntd.obs.p	runs
Afrotropic	90	0.061	0.066	0.004	1075	-1.244	0.107	10000
Indomalaya	102	0.063	0.063	0.003	4059	-0.250	0.405	10000
East Asia	126	0.049	0.059	0.003	2	-3.287	0.000	10000
Australasia	56	0.054	0.077	0.005	2	-3.866	0.000	10000
Oceania	1	NA	NA	NA	NA	NA	NA	10000
Neotropic	24	0.081	0.100	0.011	420	-1.701	0.041	10000
Mesoamerica	53	0.070	0.078	0.006	828	-1.375	0.082	10000
Nearctic	171	0.040	0.053	0.002	1	-5.632	0.00	10000
Palearctic	139	0.045	0.057	0.002	1	-4.273	0.00	10000
OSRF	14	0.137	0.121	0.016	8327	0.963	0.832	10000

Supplementary Table 7.4 Variation of standardized effect size (SES) of mean pairwise distances (mpd) of Russulaceae between communities with OSRF communities out of Afrotropic.

	ntaxa	mpd.obs	mpd.rand.mean	mpd.rand.sd	mpd.obs.rank	mpd.obs.z	mpd.obs.p	runs
Afrotropic	90	0.246	0.270	0.004	1	-5.018	0.000	10000
Indomalaya	102	0.264	0.270	0.004	819	-1.410	0.081	10000
East Asia	126	0.262	0.270	0.004	220	-2.027	0.021	10000
Australasia	56	0.263	0.270	0.006	1293	-1.132	0.129	10000
Oceania	1	NA	NA	NA	NA	NA	NA	10000
Neotropic	24	0.280	0.270	0.011	8028	0.843	0.802	10000
Mesoamerica	53	0.271	0.270	0.006	5489	0.142	0.548	10000
Nearctic	171	0.255	0.270	0.003	1	-4.621	0.000	10000
Palearctic	139	0.251	0.270	0.003	1	-5.037	0.000	10000
OSRF	14	0.310	0.270	0.015	9973	2.516	0.997	10000

Supplementary Table 8 Variation of standardized effect size (SES) of mean nearest taxon distances (mntd) and mean pairwise distances (mpd) of Sclerodermataceae.

Supplementary Table 8.1 Variation of standardized effect size (SES) of mean nearest taxon distances (mntd) of Sclerodermataceae between communities with Afrotropic including OSRF communities.

	ntaxa	mntd.obs	mntd.rand.mean	mntd.rand.sd	mntd.obs.rank	mntd.obs.z	mntd.obs.p	runs
Afrotropic	5	0.100	0.083	0.024	8133	0.725	0.813	10000
Indomalaya	7	0.068	0.074	0.019	4807	-0.268	0.480	10000
East Asia	5	0.069	0.082	0.023	3165	-0.532	0.316	10000
Australasia	7	0.055	0.074	0.019	1484	-0.959	0.148	10000
Oceania	0	NA	NA	NA	NA	NA	NA	10000
Neotropic	4	0.127	0.090	0.028	8865.5	1.334	0.886	10000
Mesoamerica	2	0.166	0.128	0.065	8599	0.583	0.859	10000
Nearctic	8	0.052	0.070	0.017	1341	-1.016	0.134	10000
Palearctic	6	0.080	0.077	0.021	6575	0.137	0.657	10000

Supplementary Table 8.2 Variation of standardized effect size (SES) of mean pairwise distances (mpd) of Sclerodermataceae between communities with Afrotropic including OSRF communities.

	ntaxa	mpd.obs	mpd.rand.mean	mpd.rand.sd	mpd.obs.rank	mpd.obs.z	mpd.obs.p	runs
Afrotropic	5	0.130	0.126	0.034	7541	0.105	0.754	10000
Indomalaya	7	0.119	0.127	0.027	5667	-0.267	0.566	10000
East Asia	5	0.124	0.126	0.034	6614	-0.066	0.661	10000
Australasia	7	0.093	0.127	0.027	338	-1.202	0.033	10000
Oceania	0	NA	NA	NA	NA	NA	NA	10000
Neotropic	4	0.199	0.127	0.040	8768	1.744	0.876	10000
Mesoamerica	2	0.166	0.127	0.065	8637	0.605	0.863	10000
Nearctic	8	0.107	0.127	0.025	2073	-0.758	0.207	10000
Palearctic	6	0.118	0.127	0.031	5196	-0.303	0.519	10000

Supplementary Table 8.3 Variation of standardized effect size (SES) of mean nearest taxon distances (mntd) of Sclerodermataceae between communities with OSRF communities out of Afrotropic.

	ntaxa	mpd.obs	mpd.rand.mean	mpd.rand.sd	mpd.obs.rank	mpd.obs.z	mpd.obs.p	runs
Afrotropic	2	0.119	0.126	0.064	5244	-0.104	0.524	10000
Indomalaya	7	0.119	0.127	0.027	5663	-0.257	0.566	10000
East Asia	5	0.124	0.126	0.034	6596.5	-0.071	0.659	10000
Australasia	7	0.093	0.126	0.027	343	-1.206	0.034	10000
Oceania	0	NA	NA	NA	NA	NA	NA	10000
Neotropic	4	0.199	0.127	0.040	8787	1.762	0.878	10000
Mesoamerica	2	0.166	0.127	0.065	8608.5	0.603	0.860	10000
Nearctic	8	0.107	0.127	0.025	2122	-0.762	0.212	10000
Palearctic	6	0.118	0.127	0.031	5192	-0.301	0.519	10000
OSRF	3	0.138	0.127	0.048	7851	0.231	0.785	10000

Supplementary Table 8.4 Variation of standardized effect size (SES) of mean pairwise distances (mpd) of Sclerodermataceae between communities with OSRF communities out of Afrotropic.

	ntaxa	mpd.obs	mpd.rand.mean	mpd.rand.sd	mpd.obs.rank	mpd.obs.z	mpd.obs.p	runs
Afrotropic	2	0.119	0.126	0.064	5244	-0.104	0.524	10000
Indomalaya	7	0.119	0.127	0.027	5663	-0.257	0.566	10000
East Asia	5	0.124	0.126	0.034	6596.5	-0.071	0.659	10000
Australasia	7	0.093	0.126	0.027	343	-1.206	0.034	10000
Oceania	0	NA	NA	NA	NA	NA	NA	10000
Neotropic	4	0.199	0.127	0.040	8787	1.762	0.878	10000
Mesoamerica	2	0.166	0.127	0.065	8608.5	0.603	0.860	10000
Nearctic	8	0.107	0.127	0.025	2122	-0.762	0.212	10000
Palearctic	6	0.118	0.127	0.031	5192	-0.301	0.519	10000
OSRF	3	0.138	0.127	0.048	7851	0.231	0.785	10000