Doctoral Thesis (Abridged)

博士論文 (要約)

Ectomycorrhizal fungal communities of secondary *Tristaniopsis* forests in Indonesia

(インドネシアにおけるトリスタニオプシスの優占する二次林の外生菌根菌群集)

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Acronyms and abbreviations

BLAST	basic local alignment search tool
C	carbon
CIMTROP	center for international cooperation in the sustainable management of tropical peatlands
CTAB	cetyltrimethylammonium bromide
DBH	diameter at breast height
db-RDA	distance-based redundancy analysis
DDBJ	DNA databank of Japan
DNA	deoxyribonucleic acid
ECM	ectomycorrhiza
GPS	global positioning system
INSD	international nucleotide sequence databases
ITS	internal transcribed spacer
LGM	last glacial maximum
ML	maximum likelihood
N	nitrogen
NCBI	national center for biotechnology information
nMDS	non-metric multidimensional scaling
MOTU	molecular operational taxonomic unit
PCR	polymerase chain reaction
SD	standard deviation

Abstract

Introduction

Dominant trees in many forest ecosystems are associated with ectomycorrhizal (ECM) fungi and depend on them for growth and survival. In fact, the availability of ECM fungi and their species composition could be the most significant determinant of host seedling establishment in disturbed areas, within boreal, temperate, and subtropical regions. However, there is no previous study documenting ECM fungal communities in heavily disturbed tropical areas. Available data of ECM fungi in Southeast Asia are mostly from undisturbed Dipterocarpaceae forests, largely because this dominant ECM host is often replaced by fast growing arbuscular mycorrhizal host trees after disturbance. However, in some parts of Southeast Asia, potentially ECM trees belonging to Myrtaceae become dominant in disturbed sites, although the information about their ECM colonization and ECM fungal communities is scarce.

Myrtaceae includes both arbuscular mycorrhizal and ECM host lineages. The latter includes *Eucalyptus*, on which many ECM fungi have been documented. *Tristaniopsis* is another ECM host lineage in Myrtaceae, as a recent study showed that some *Tristaniopsis* species endemic to New Caledonia are associated with diverse ECM fungi. In Indonesia, other *Tristaniopsis* species are found in very different settings, such as heavily disturbed areas, but their ECM associations were unknown. ECM fungi on such pioneer trees are important because they may help the regeneration of late-successional ECM hosts like Dipterocarpaceae. The objectives of this study are (1) to confirm the ECM colonization of *Tristaniopsis* under secondary tropical forest settings, (2) to characterize ECM fungal diversity and species composition, (3) to clarify how many ECM fungal species are shared with other tree species, especially with Dipterocarpaceae, (4) to quantify the effects of

environmental and biogeographical factors on ECM fungal communities, (5) to infer evolutional origin of individual ECM fungi found in secondary *Tristaniopsis* forests, and (6) to clarify how the observed ECM fungal communities are related to those of the surrounding areas, including Southeast Asia, Oceania, and New Caledonia.

Materials and Methods

Soil samples were collected from nine secondary *Tristaniopsis* forests located in Bangka (four sites) and Palangka Raya (five sites). We randomly collected 25 soil samples (5cm x 5cm to 10cm depth) per site in Bangka and 30 soil samples per site in Palangka Raya. Each sampling point was selected within a few meters from a *Tristaniopsis* tree to have a better chance of collecting its ECM roots. The interval between samples was at least 5 m apart to avoid collecting the same ECM fungal clones. ECM roots contained in each soil sample were carefully separated from soil aggregate, cleaned in tap water, and classified into morphotypes under a stereomicroscope.

Three ECM tips per morphotype were subjected to DNA extraction separately. PCR and sequencing were performed targeting ITS regions in ribosomal DNA. Obtained sequences were grouped into molecular operational taxonomic units (MOTUs) based on ≥97% similarity threshold. The identify of each MOTU (species hereafter) was assigned based on BLAST results in INSD (International Nucleotide Sequence Database). Host species of each ECM tip was identified by chloroplast DNA. The relative importance of soil parameters, successional stage, hosts and geographical distance in structuring ECM fungal communities were analyzed by NMDS, perMANOVA and db-RDA. The distribution of ECM fungi detected in this study and their evolutional origin were explored beyond the research areas using INSD. Phylogenetic similarities of ECM fungal

communities were compared with those of other forests in Southeast Asia, Oceania, and New Caledonia, by UniFrac.

Results and Discussion

Of 250 soil samples collected from the nine sites, 186 (74.4%) contained ECM tips from which 1465 ECM root tips were used for molecular identification. Sequences were successfully obtained from 853 root tips (58.2%). In total, 127 ECM fungal species (18 families) were identified with the ITS similarity threshold of 97%: 56 and 79 ECM fungal species from Bangka and Palangka Raya, respectively. Only 18 ECM fungal species were represented by five or more soil samples, while 81 species were singletons (i.e., found in a single soil) and 12 species were doubletons. The most species-rich ECM fungal families were Thelephoraceae (26 species), Russulaceae (25 species), and Boletaceae (13 species). The most frequently observed species was Thelephoraceae sp.1, which was found in 39 of 250 soil samples, followed by *Russula* sp.1 (29 soils) and Thelephoraceae sp.12 (19 soils). The jackknife2 richness estimator indicated that there would be at least 145 species within the research sites.

In total, 11 host families were identified from ECM tips examined. Myrtaceae (57.3%) represented by *Tristaniopsis* was the most dominant host group, followed by Dipterocarpaceae (19.4%), Fagaceae (7.3%), Fabaceae (7.3%) and Gnetaceae (2.4%). The existence and dominance of Dipterocarpaceae indicate that this late-successional host group can regenerate after disturbance under the presence of *Tristaniopsis* and its ECM fungi.

ECM fungal communities of co-exiting host families (Myrtaceae and Dipterocarpaceae) were not significantly different (pseudo-F=1.09, R^2=0.07, P=0.32). In

fact, all the ECM fungal species that appeared five or more soil samples were shared between Myrtaceae and Dipterocarpaceae, suggesting no host specificity in these tropical ECM fungi. Disturbance type (pseudo-F=1.08, R^2=0.22, P=0.35) also did not significantly affect ECM fungal communities. However, ECM fungal communities were affected by sampling locations (pseudo-F =2.51, R^2=0.17, P=0.03).

Most of ECM fungal species detected in this study had no previous records in INSD. Only 10 of 127 ECM fungi matched with previous records at >97% ITS similarities. Eight of them were from Lambir Hill National Park, Sarawak (Peay *et al.*, 2010). The other two species were recorded from Seychelles (Tedersoo *et al.*, 2007) and *Heimioporus* sporocarps in Bangka. None of ECM fungal species in this study matched with those associated with *Tristaniopsis* in New Caledonia (Waseem *et al.*, 2017), *Eucalyptus*, and numerous ECM host trees in temperate regions.

Due to the lack of host diversity in Bangka, relative importance of host, succession stage and soil factors in structuring ECM fungal communities were analyzed only in Palangka Raya. Although all soil properties (total C, total N, C/N ratio, and pH) were significantly different among sampling locations, only pH (pseudo-F=3.74, P=0.001), total nitrogen (pseudo-F=6.74, P=0.0001) and total carbon (pseudo-F=5.25, P=0.0001) had significant effects on the ECM fungal communities. Successional stage (inferred from DBH) was also a significant determinant of ECM fungal communities (pseudo-F=2.69, P=0.014).

Palangka Raya shared eight ECM fungal species with Bangka Island, five species each with Lambir Hill or Bukit Bangkirai, both of which are mixed dipterocarp forests. Bangka shared four ECM fungal species with Lambir Hill and three species with

Bangkirai. All these regions belonged to Sunda land, which formed a continuous land mass in the last ice age. No species sharing was confirmed with New Caledonia, where four of the *Tristaniopsis* ECM fungi were shared with Australian *Eucalyptus*. These results indicate that Wallace line could function as a biogeographical boundary for ECM fungi as for plants and animals, although further research across the line is necessary.

In phylogenetic analyses, many ECM fungi confirmed in this study formed monophyletic clades with species from Africa, South America, Australia (including New Zealand), all of which belonged to Gondwana, the southern super continent existed until the Jurassic. Some other ECM fungi formed endemic clades that were composed of Indomalaya sequences including ours, suggesting long history of local diversification. These results suggest that ECM fungi in Indonesian *Tristaniopsis* forests are of Gondwana origin, corresponding well with host Myrtaceae biogeography.

Conclusion

Secondary tropical forests dominated by *Tristaniopsis* trees in Bangka and Palangka Raya were found to harbor diverse ECM fungi, many of which were highly likely to be new species that had no records in previous studies. All dominant ECM fungi were shared between *Tristaniopsis* and Dipterocarpaceae, which was confirmed to be regenerating naturally at the research sites. In addition, some ECM fungi confirmed in this study were also shared with primary dipterocarp forests. While primary dipterocarp rainforests often become arbuscular mycorrhizal ecosystems after disturbance, our results suggest that secondary forests dominated by *Tristaniopsis* trees remain ECM ecosystems and could function as ECM fungal refugia during the era of escalating human induced disturbance. We may be able to apply pioneer tropical ECM trees like *Tristaniopsis* to the

recovery of dipterocarp forests in Southeast Asia, providing compatible ECM fungi to late-successional dipterocarps.

Chapter 1 General introduction

1.1 Biodiversity loss and restoration attempts in tropical rainforests areas

The tropical rainforest is a hot and moist biome, typically occurring in a band within 15–20° on both sites of the equator. Tropical rainforests receive a monthly average precipitation of at least 60 mm, with no prolonged dry season. The combination of constant warmth and abundant moisture makes the tropical rainforest a suitable environment for many plants and animals. The latitudinal diversity gradient, in which biodiversity increases from the poles to the equator, is well documented for various plant and animal groups (Sechrest *et al.*, 2002) are endemic to 25 global biodiversity hotspots (Myers *et al.*, 2000), more than half of which are located in tropical forests.

Southeast Asia harbors four biodiversity hotspots (Sundaland, Indo-Burma, the Philippines, and Wallacea). More than 5,000 species of vascular plants, including many endemic species, are distributed within a 10,000 km^2 area (Dirzo & Raven, 2003). However, forest degradation and deforestation have impacted the region over the last few decades. The main drive of this destruction is industrial agriculture (i.e., oil palm plantations) (FAO, 2016). Unmanaged slash-and-burn for the opening of new agriculture areas is also responsible for the loss of tropical rainforests. These practices have released large amounts of carbon dioxide into the atmosphere, approximately 1.5 PgC per year from 2000 through 2006 alone (Canadell *et al.*, 2007). Within the past two decades, Southeast Asia has lost more than 33 million ha of forest, with an annual deforestation rate of 0.72% (Figure 1.1). Such tremendous forest loss is becoming a severe threat to biodiversity (Fitzherbert *et al.*, 2008).

Forest restoration has become a global issue (Chazdon, 2008; Normile, 2010). However, attempts at reforestation are affected by many factors. Adequate stocks of seedlings of native tree species and proper understanding of their ecological traits are the most critical factors (Koh *et al.*, 2013). In Southeast Asia, the Dipterocarpaceae family is the focal tree group for reforestation because of its economic and ecological importance. Dipterocarpaceae make up 10% of all tree species and 80% of canopy species in primary forests on Borneo Island (Ashton, 1988), supporting the forestry-based economy and numerous wildlife in the area. Dipterocarp species produce seeds at irregular intervals, often once in several years, in regional synchrony with other plants of the same species, a phenomenon known as mast seeding or masting (Curran & Webb, 2000). Their seeds start to germinate immediately after landing, and do not survive drying or freezing (Bonner, 1990) which makes their preservation difficult. These biological traits present a significant challenge to providing enough seeds and seedlings for the restoration of dipterocarp forests (Kettle *et al.*, 2011). Seedling production from cuttings is applicable to some dipterocarp species (Kenzo *et al.*, 2019), yet genetically uniform seedlings could be a concern.

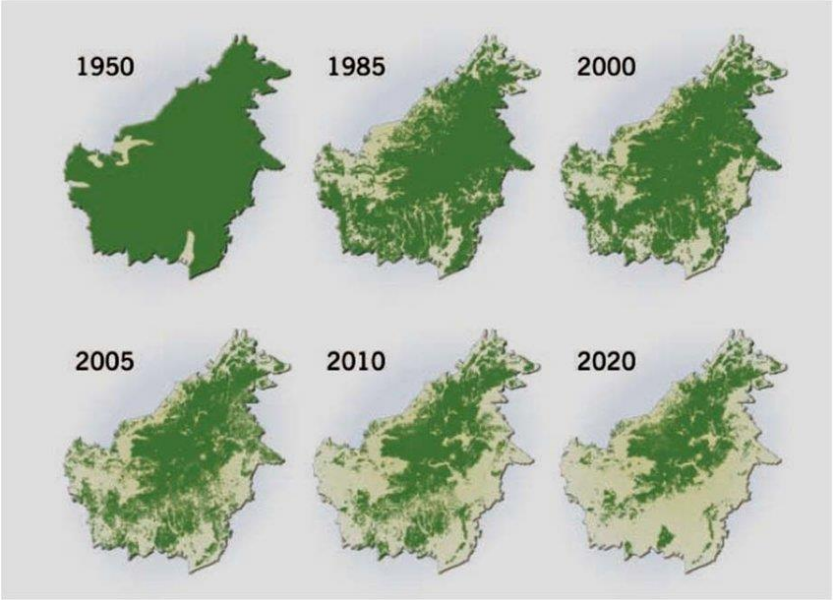

Figure 1.1 Forest coverage loss in Borneo and projection toward 2020 (GRID-Arendal, 2008).

1.2 Mycorrhiza symbiosis

Most land plants develop mutually beneficial relationships with soil fungi on their fine roots. In this symbiosis, called mycorrhiza, soil fungi effectively absorb and transfer soil nutrients to the host in exchange for photosynthesis products (Smith & Read, 2008). There are two major types of mycorrhizal symbiosis: arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) (Figure 1.2). AM is the most primitive and widespread type, observed in more than 85% of terrestrial plant families. ECM associations are found in about 10% of terrestrial plant families, which are mostly woody plants

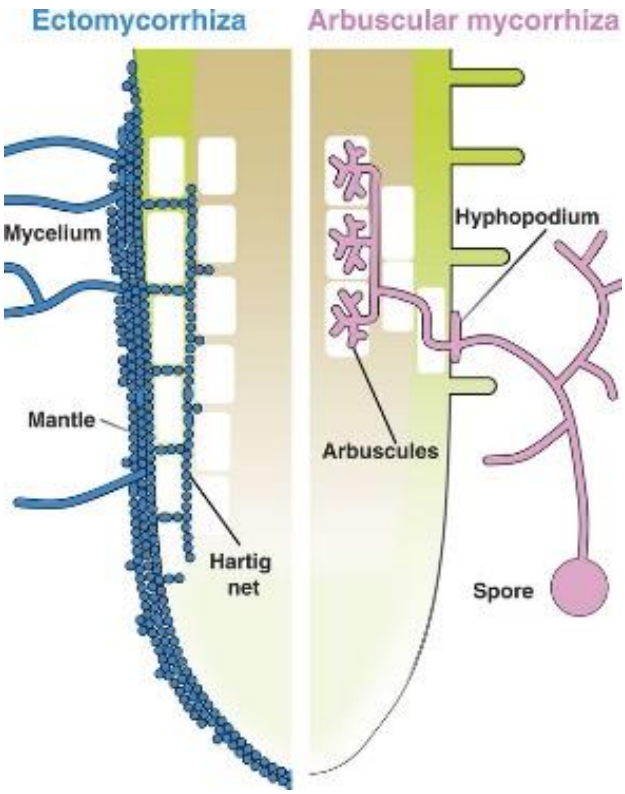

Figure 1.2 Two major types of mycorrhizal symbiosis (Bonfante & Genre, 2010).

Dominant trees in many forest ecosystems form ECM symbioses (Figure 1.3). The dominance of ECM trees is generally lower in the tropics than in temperate regions, yet the most dominant tree group in tropical primary forests, namely, Dipterocarpaceae in Southeast Asia, forms ECM associations (Figure 1.4).

Most ECM fungi belong to the highly evolved fungal group Basidiomycota, which often produce mushrooms on the soil. ECM fungi are very species-rich, and hundreds of species inhabit a single 1 ha forest (Miyamoto *et al.*, 2018). By associating with various ECM fungi, host trees can utilize various organic nutrient forms and adapt to broader habitat conditions (Baxter & Dighton, 2001), as well as increase their tolerance to drought (Parke *et al.*, 1983) and disease (Sylvia, 1983). The availability and composition of ECM fungi might be the most significant determinant of seedling establishment in heavily disturbed areas (Nara, 2006a). ECM fungi also have essential roles in nutrient cycling in

forest ecosystems (Courty *et al.*, 2010; Dickie *et al.*, 2013; Finlay, 2004). Therefore, they are considered critical components of forest ecosystems, although they have been long overlooked, simply due to the difficulty observing them.

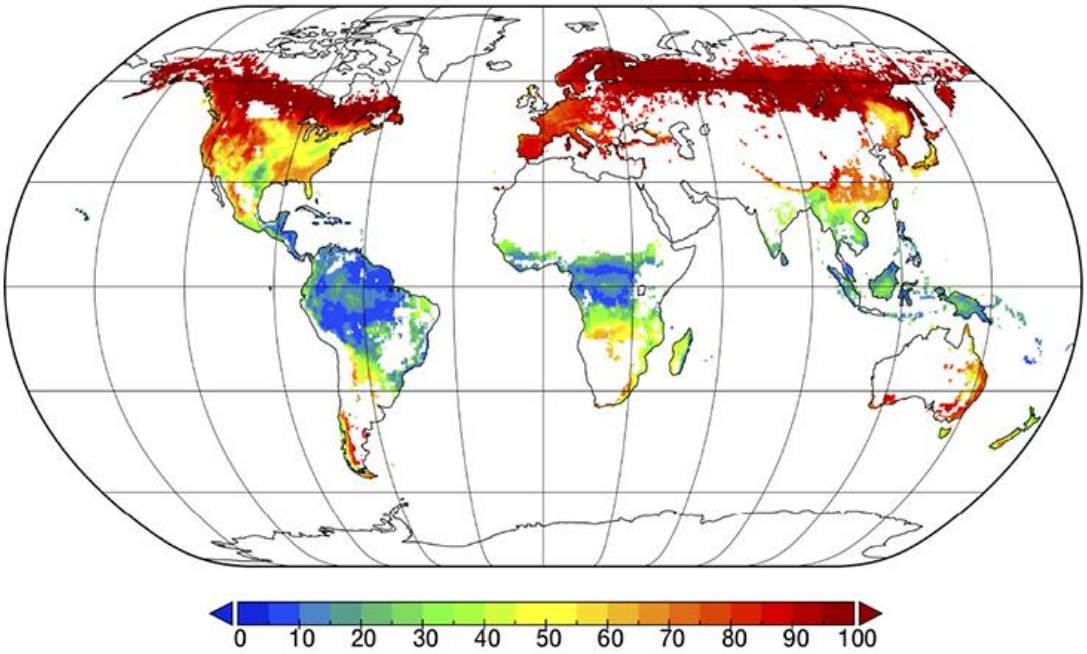

Figure 1.3 Percent biomass of trees associated with ectomycorrhizal fungi (Steidinger *et al.*, 2019).

Available data of ECM symbioses in Southeast Asia are mostly from undisturbed Dipterocarpaceae forests (Henkel *et al.*, 2002; Peay *et al.*, 2010; Phosri *et al.*, 2012; Sirikantaramas *et al.*, 2003). These dominant ECM host trees are often replaced by fast-growing AM trees (e.g., *Macaranga* and *Mallotus*) after disturbance (Brearley *et al.*, 2004; Slik *et al.*, 2003). However, in some parts of Southeast Asia, potential ECM trees belonging to the Myrtaceae become dominant in disturbed forests (Sancayaningsih & Bait, 2015). Although their ECM colonization and ECM fungal communities are unknown, they may have critical roles in maintaining ECM ecosystems and facilitating the establishment of late-successional ECM trees.

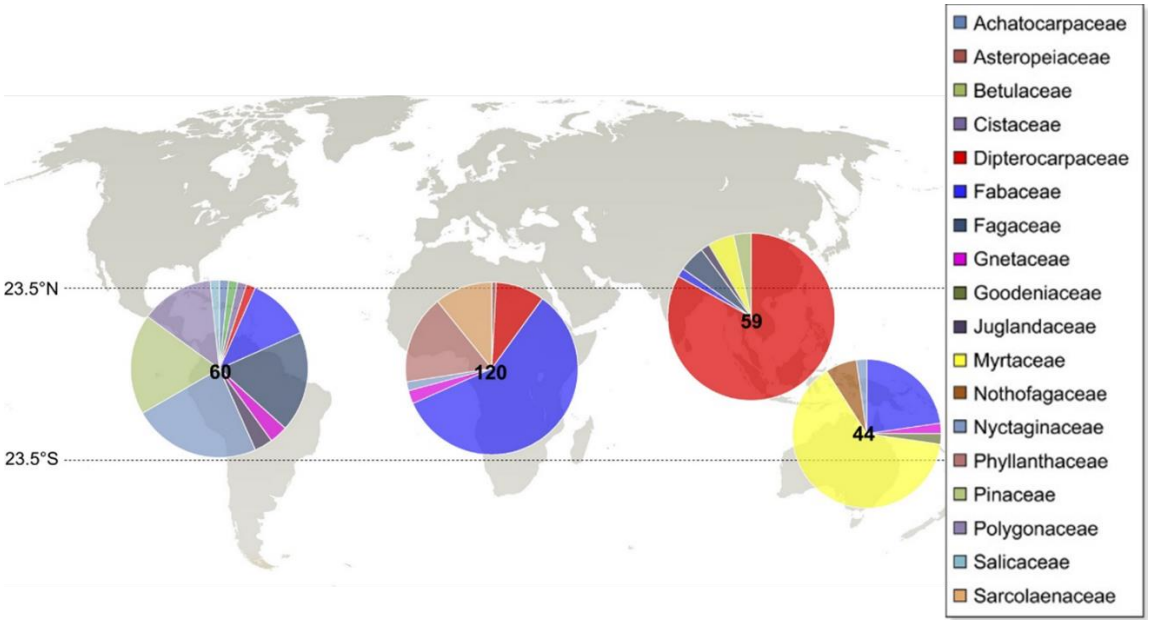

Figure 1.4 Total numbers of confirmed ECM plant species in tropical regions: Neotropic, Afrotropic, Indomalaya, and Australasia. Colors correspond to the number of species from individual plant families (Corrales *et al.*, 2018).

1.3 *Tristaniopsis* in Indonesian secondary forests

The Myrtaceae family are evergreen dicotyledonous plants. All species in this group are woody plants (tall trees and shrubs), usually with numerous showy stamens, often with peeling bark, and always containing essential oils. Recent estimations suggest that the Myrtaceae family includes more than 5000 species in more than 130 genera. This family has a wide distribution in tropical and temperate regions and is commonly found in the world's biodiversity hotspots (Christenhusz & Byng, 2016; Govaerts *et al.*, 2019).

Myrtaceae includes both arbuscular and ECM lineages. The latter includes *Eucalyptus*, on which ECM fungi have been documented in native areas such as Australia (Adams *et al.*, 2006) and some introduced areas such as Seychelles (Tedersoo *et al.*, 2007) and Africa (Ducousso *et al.*, 2012). *Tristaniopsis* is another ECM host lineage in the Myrtaceae (Figure 1.5), distributed widely in Southeast Asia (Cambodia, Myanmar,

Malaysia, Indonesia), New Guinea, New Caledonia, and Australia (Wilson & Waterhouse, 1982).

Tristaniopsis is one of 8 members of the tribe Kanieae, in the subfamily Myrtoide (Wilson & Waterhouse, 1982). *Tristaniopsis* can be canopy trees with heights reaching 30 m and diameters of up to 40 cm. Many *Tristaniopsis* species have red to brown bark, which is irregularly cracked and coarsely flaky in scroll-like pieces. Flowers are yellow-brown, hairy, inflorescence rachis, calyx lobes 1 × 1 mm, petal 1.5 mm long, filament stamen 1–2 mm long, 3–10 per cluster, anther 0.1 mm. Elliptic seeds are up to 1 × 0.8 cm. Leaves are elliptic to obovate, 6–17 × 2–7 cm; auriculate leaves are found in the juvenile stage, and are less distinct at maturity (Ashton, 2005). *Tristaniopsis* is common at higher elevations of 1000–2000 m, but seldom at lower altitudes. Many species can re-sprout from the trunk and branches (Benson & McDougall, 1998), having high fire resistance (Burrows, 2008).

Waseem *et al.* (2017) recently described ECM fungi associated with *Tristaniopsis* endemic to New Caledonia. In their study, *Tristaniopsis* forests were located in ultramafic and volcano-sedimentary soils. In Indonesia, other *Tristaniopsis* species are found in secondary forests, usually in podzol and latosol soils, and rarely in peat soil. The types of ECM fungal communities present on such pioneer *Tristaniopsis* trees in Indonesia remain unknown. Because ECM fungi that colonize pioneer trees play important roles in facilitating late-successional ECM tree species (Nara, 2006b), *Tristaniopsis* ECM fungi may be key to the regeneration of dipterocarp trees.

Figure 1.5 Leaves and trunk of a *Tristaniopsis* sp. (a) and its flowers and immature fruits (b).

1.4 Objectives and the outline of the thesis

The main objective of this study was to obtain scientific knowledge about pioneer ECM trees and ECM fungal communities that can be potentially applicable to the regeneration of dipterocarp forests. To achieve this goal, we investigated ECM fungal communities of secondary tropical forests in Indonesia, specifically in Bangka and Central Kalimantan (Figure 1.6). In Chapter 2, we describe how we confirmed ECM colonization of *Tristaniopsis* under secondary tropical forest settings and give descriptions of ECM fungal communities. The relative importance of host, environmental, and geographical factors in structuring ECM fungal communities is also quantified. As described in Chapter 3, to infer the evolutional origin of ECM fungi in secondary *Tristaniopsis* forests, we performed phylogenetic analyses of individual ECM fungal components with closely related sequences in the International Nucleotide Sequence

Database Collaboration (INSDC) databases. We also compared the ECM fungal communities with those of surrounding regions (Southeast Asia, Oceania, and New Caledonia) based on the number of shared species and phylogenetic distance. Chapter 4 summarizes the key findings of this study and provides overall discussions including the potential application to forestry and conservation in the tropics. The knowledge obtained from this study will broaden our understanding of tropical ECM fungal ecology and biogeography.

Figure 1.6 Location of the study sites: Bangka Island (black) and Central Kalimantan (red).

Chapter 2 (pp. 20 to 42) and **Chapter 3** (pp. 43 to 55) of my doctoral thesis cannot be made public on the Internet for 5 years from the date of doctoral degree conferral because that part is scheduled to be published as part of journal.

Chapter 4. General discussion

4.1 Key findings

Late-successional host trees such as Dipterocarpaceae cannot grow well in disturbed sites because of the intense sunlight that induces photoinhibition (Kenzo *et al.*, 2011; Turner, 1990) and the lack ECM fungi. Therefore, pioneer ECM trees that can survive the disturbance might be the key to the recovery of dipterocarp forests. The key findings of this study are as follows:

1) *Tristaniopsi*s species in secondary forests in Indonesia were associated with diverse ECM fungi, many of which did not have previous records and are potentially new species.

2) Dipterocarp tree regeneration was confirmed in secondary *Tristaniopsis* forests in Palangka Raya, where all dominant ECM fungi were shared between *Tristaniopsis* and Dipterocarpaceae.

3) ECM fungal communities in Indonesian *Tristaniopsis* forests were structured by environmental factors, particularly pH, soil nutrients, and successional stage, but not by host identity.

4) Bangka and Kalimantan Islands shared many common ECM fungal species, irrespective of forest type, namely, secondary *Tristaniopsis* forests and primary dipterocarp forests. Nevertheless, no species were shared between Indonesian and New Caledonian *Tristaniopsis* forests.

5) Many ECM fungi inhabiting Indonesian *Tristaniopsis* forests were phylogenetically close to species from Gondwana components. Some other ECM fungi were included in endemic clades.

4.2 Barriers to ECM fungal migration

Potential barriers to ECM fungal migration include host specificity, different environmental conditions, and geographical isolation. As we found no sign of host specificity in tropical ECM fungi, host differences could not be the limiting factor for tropical ECM fungal migrations. In fact, *Tristaniopsis* forests and primary dipterocarp forests shared substantial numbers of common ECM fungi even across different islands. As for the environmental factors, succession stage, pH, and soil nutrients (N and C) were the most significant in shaping ECM fungal communities. Environmental factors would affect ECM fungal establishment. Moreover, the absence of shared ECM fungal species between Indonesia and Thailand (Phosri *et al.*, 2012), which were connected in the last ice age, may be the result of these environmental factors and not from the limitation of spore dispersal.

The absence of shared ECM fungal species between Indonesian and New Caledonian *Tristaniopsis* forests could be explained by distance decay effect and geographic isolation. Moreover, Indonesian *Tristaniopsis* forests shared no common ECM fungi with tropical Africa, South America, or Australia. This is in sharp contrast to temperate ECM fungi, most of which are shared among Asia, Europe, and North America (Miyamoto *et al.*, 2018), probably due to the land bridges in recent ice ages. Because biogeographical boundaries in the tropics (e.g., the Wallace Line) have remained disconnected even during ice ages (Bird *et al.*, 2005; Cannon & Manos, 2003), the period of isolation would be much longer in the tropics. Interestingly, these patterns correspond well with the floristic regions, where Africa, Southeast Asia, and South American tropics are separated into different realms while temperate Asia, North America, and Europe are all grouped into the Holarctic realm (Gentry, 1982; Olson *et al.*, 2001). Therefore,

geographic isolation mechanisms for land plants (e.g., the sea) may have equally affected ECM fungal migration. We may be able to distinguish relevant biogeographic realms for ECM fungi by further studies in the tropics.

4.3 Potential applications of *Tristaniopsis* trees

The absence of compatible ECM fungi could be the most critical factor preventing the establishment of ECM host trees (Nara, 2006a). After the clearcutting of primary dipterocarp forests, pioneer species *Macaranga* or *Mallotus* become dominant (Slik *et al.*, 2003), changing ECM ecosystems into AM environments. This can inhibit the re-establishment of dipterocarp trees, which depend on ECM fungi.

In this study, we found that pioneer *Tristaniopsis* trees can harbor ECM fungi that are compatible with Dipterocarpaceae. Moreover, in belowground roots, we detected many dipterocarp ECM tips in secondary *Tristaniopsis* forests after clearcutting, indicating the natural regeneration of Dipterocarpaceae at the sites. Thus, it is very likely that *Tristaniopsis* trees and their ECM fungi are promoting the establishment of Dipterocarpaceae. We may be able to develop effective application methods from these findings. Direct planting of dipterocarp trees in disturbed sites often results in failure because of intense sunlight. Instead, pioneer trees such as *Acacia mangium*, *Acacia auriculiformis*, and *Falcataria moluccana* are often used for initial planting (Nibbering, 1999; Otsamo *et al.*, 1997). However, all of these trees are AM species, and thus would not help dipterocarp re-establishment in terms of mycorrhizal associations. If we use *Tristaniopsis* trees for initial planting after clearcutting or forest fires, they can provide adequate shade and compatible ECM fungi, and thus may be able to facilitate the establishment of Dipterocarpaceae.

We may also be able to apply *Tristaniopsis* trees for the conservation of regional ECM fungal resources. As shown in Chapter 3, most ECM fungi in the studied region are endemic. Thus, escalating deforestation in this region would increase the risk of extinction of these endemic ECM fungi, as well as local plants and animals. When we consider the essential roles of ECM fungi in forest ecosystems, we should develop effective conservation methods to conserve such endemic ECM fungi. Unfortunately, many ECM fungi are difficult to cultivate on nutrient media, and require substantial costs and efforts when possible. Instead, ECM fungal strains can be maintained in association with host seedlings in greenhouses or nurseries. Natural *Tristaniopsis* forests could also function as conservation areas for ECM fungi, but we do not know where or to what extent *Tristaniopsis* forests are distributed in Indonesia. Apparently, further research is needed before considering the applications.

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Supplementary material

Table S1 ECM fungal species and their frequencies in secondary *Tristaniopsis* forests in Indonesia.

Lineage*	**Frequency**									
	B1	**B2**	**B3**	**B4**	**P1**	**P2**	**P3**	**P4**	**P5**	**Host**
/amanita										
Amanita sp. 1	1	0	0	0	1	0	1	1	0	M, D
Amanita sp. 2	0	1	0	0	0	0	0	0	0	M
Amanita sp. 3	0	1	0	0	0	0	0	0	0	-
Amanita sp. 4	0	0	1	0	0	0	0	0	0	-
/atheliales2										
Atheliaceae sp. 1	4	0	1	0	0	0	1	0	2	M
Atheliacea*e* sp. 2	0	0	1	0	0	0	0	0	0	M
Atheliacea*e* sp. 3	0	0	1	0	0	0	0	0	0	-
Atheliacea*e* sp. 4	0	0	0	0	0	0	2	0	1	M, D
Atheliacea*e* sp. 5	0	0	0	0	0	0	0	0	1	-
/boletus										
Austroboletus sp. 1	1	0	0	0	0	0	0	0	0	-
Austroboletus sp. 2	0	1	0	0	0	0	0	0	0	M
Austroboletus sp. 3	0	0	0	0	0	0	0	0	1	M
Boletaceae sp. 1	0	1	0	0	0	0	0	0	0	-
Boletaceae sp. 2	0	0	0	0	3	0	0	0	0	D, Fb, Gn
Boletales sp. 1	2	0	0	0	2	1	0	2	1	M, D
Boletellus sp. 1	0	0	0	1	0	0	0	0	0	M
Boletellus sp. 2	0	0	0	0	1	0	0	0	0	-
Boletus sp. 3	0	0	0	0	0	0	1	0	0	M
Borofutus sp.	0	0	0	0	0	3	0	0	0	M
Heimioporus sp.	0	1	0	0	0	0	0	0	0	M

/cenococcum										
Cenococcum geophilum 1	5	1	8	0	0	0	0	0	0	M
Cenococcum geophilum 2	0	1	0	0	0	0	0	0	0	M
Cenococcum geophilum 3	0	0	0	0	1	15	0	0	0	M, D
Cenococcum geophilum 4	0	0	0	0	0	0	0	0	4	M, D
/clavulina										
Clavulina sp. 1	0	1	0	0	0	0	0	0	0	
Clavulina sp. 2	0	0	0	0	3	3	0	0	0	M, Fb
Clavulina sp. 3	0	0	0	0	2	0	0	0	0	D
Clavulina sp. 4	0	0	0	0	1	0	0	0	0	-
Clavulina sp. 5	0	0	0	0	1	0	0	0	0	-
Sistotrema sp. 1	0	0	0	0	2	0	0	0	0	D
Sistotrema sp. 2	0	0	0	0	0	0	0	0	1	-
Sistotrema sp. 3	0	0	0	0	1	0	0	0	0	-
/coltricia										
Coltricia sp. 1	0	1	0	0	0	0	0	0	0	-
Coltricia sp. 2	0	0	0	0	0	0	0	1	0	-
Coltricia sp. 3	0	0	0	0	0	0	0	1	0	D
Coltriciella sp. 1	0	1	0	0	0	0	0	0	0	M
Coltriciella sp. 2	0	1	0	1	0	0	0	0	0	-
Coltriciella sp. 3	0	1	0	0	0	0	0	0	0	M
Coltriciella sp. 4	0	0	0	1	0	0	0	0	0	M
Coltriciella sp. 5	0	0	0	0	1	0	0	0	0	Fb

/cortinarius										
Cortinarius sp. 1	0	0	0	1	0	0	0	0	0	-
Cortinarius sp. 2	0	1	0	0	0	0	0	0	0	-
Cortinarius sp. 3	1	0	0	0	0	0	0	0	0	M
Cortinarius sp. 4	0	0	0	0	0	0	1	0	0	M
Cortinarius sp. 5	0	0	0	0	0	0	0	0	1	-
Cortinarius sp. 6	0	0	0	0	0	0	1	0	0	-
Cortinarius sp. 7	0	0	0	0	0	0	0	0	1	Fg
Cortinarius sp. 8	0	0	0	0	0	0	0	0	1	-
/elaphomyces										
Elaphomyces sp. 1	1	1	0	0	1	0	0	1	0	M
Elaphomyces sp. 2	0	0	0	0	0	0	2	0	0	-
Elaphomyces sp. 3	0	0	0	0	0	0	0	0	1	D
Elaphomyces sp. 4	0	0	0	0	1	0	0	0	0	M
/inocybe										
Inocybe sp. 1	0	0	0	0	4	0	0	0	0	M, D
Inocybe sp. 2	0	0	0	0	0	0	0	2	0	D
Inocybe sp. 3	0	0	0	0	0	1	0	0	0	-
Inocybe sp. 4	0	0	0	0	0	0	1	0	0	M
/laccaria										
Laccaria sp. 1	1	0	0	0	0	0	0	0	0	M
Laccaria sp. 2	0	0	0	0	0	0	0	0	1	M, Fg
/pisolithus-scleroderma										
Scleroderma sp. 1	0	0	0	0	0	0	4	0	3	M, D, Fg
Scleroderma sp. 2	0	0	0	0	0	1	0	0	0	Gn
/russula-lactarius										

Lactarius sp. 1	0	1	0	0	0	0	0	0	0	-
Lactarius sp. 2	0	0	0	0	0	0	3	0	7	M, D, Fb, Fg
Lactarius sp. 3	0	0	0	0	0	0	0	0	3	D, Fg
Russula sp. 1	4	0	1	0	9	3	7	4	1	M, D, Fb, Fg
Russula sp. 2	4	0	0	0	5	0	2	4	1	M, D, Fb, Fg
Russula sp. 3	1	1	1	0	0	0	0	0	0	M
Russula sp. 4	0	1	0	0	0	0	0	0	0	-
Russula sp. 5	0	1	0	0	0	0	0	0	0	-
Russula sp. 6	0	0	0	1	0	0	0	0	0	-
Russula sp. 7	0	0	0	0	4	0	3	1	2	M, D, Fb
Russula sp. 8	0	0	0	0	0	2	0	0	0	D
Russula sp. 9	0	0	0	0	4	0	0	0	2	D
Russula sp. 10	0	0	0	0	0	0	4	0	0	M, D, Fg
Russula sp. 11	0	0	0	0	0	3	0	0	0	M, D, Fb
Russula sp. 12	0	0	0	0	0	0	0	0	2	M, Fg
Russula sp. 13	0	0	0	0	0	0	0	1	0	-
Russula sp. 14	0	0	0	0	0	0	0	0	1	M
Russula sp. 15	0	0	0	0	0	1	0	0	0	D
Russula sp. 16	0	0	0	0	1	0	1	0	1	-
Russula sp. 17	0	0	0	0	1	0	0	0	0	D
Russula sp. 18	0	0	0	0	0	0	1	0	0	-
Russula sp. 19	0	0	0	0	0	0	0	1	0	M
Russula sp. 20	0	0	0	0	0	0	0	0	1	-
Russula sp. 21	0	0	0	0	0	0	0	0	1	Fg
Russula sp. 22	0	0	0	0	0	0	0	0	1	M

/tomentella-thelephora

Thelephoraceae sp. 1	6	0	1	0	1	0	7	13	11	M, D, Fb, Fg, Gn
Thelephoraceae sp. 2	4	0	2	0	3	2	6	1	0	M, D, Gn
Thelephoraceae sp. 3	1	0	0	0	0	0	0	0	0	-
Thelephoraceae sp. 4	1	0	0	0	0	0	0	0	0	M
Thelephoraceae sp. 5	1	0	0	0	0	0	0	0	0	M
Thelephoraceae sp. 6	1	0	0	0	0	0	0	0	0	-
Thelephoraceae sp. 7	1	0	0	0	0	0	0	0	0	-
Thelephoraceae sp. 8	0	0	1	0	0	0	0	0	0	-
Thelephoraceae sp. 9	0	0	1	0	0	0	0	0	0	-
Thelephoraceae sp. 10	0	0	1	0	0	0	0	0	0	-
Thelephoraceae sp. 11	0	0	1	0	0	0	0	0	0	-
Thelephoraceae sp. 12	0	0	0	0	0	0	4	7	8	M, D, Fg
Thelephoraceae sp. 13	0	0	0	0	0	2	2	1	0	Fg
Thelephoraceae sp. 14	0	0	0	0	0	1	1	1	1	M
Thelephoraceae sp. 15	0	0	0	0	0	0	0	1	3	M, D
Thelephoraceae sp. 16	0	0	0	0	0	0	0	1	0	M, D
Thelephoraceae sp. 17	0	0	0	0	0	0	1	0	0	M
Thelephoraceae sp. 18	0	0	0	0	0	0	0	0	2	M
Thelephoraceae sp. 19	0	0	0	0	1	0	0	1	0	M
Thelephoraceae sp. 20	0	0	0	0	0	0	0	0	3	Fg
Thelephoraceae sp. 21	0	0	0	0	2	0	0	2	1	D
Thelephoraceae sp. 22	0	0	0	0	0	0	0	0	1	-
Thelephoraceae sp. 23	0	0	0	0	1	0	0	0	0	-
Thelephoraceae sp. 24	0	0	0	0	0	0	2	1	1	M, D
Thelephoraceae sp. 25	0	0	0	0	0	0	1	0	0	M
Thelephoraceae sp. 26	0	0	0	0	0	0	0	1	0	D
Not assigned to lineages										

Agaricomycetes	0	1	0	0	0	0	0	0	0
Clavariaceae sp. 1	1	0	1	0	0	0	0	0	0
Clavariacae sp. 2	0	0	0	0	0	1	0	0	0
Clavulinaceae sp. 1	0	2	0	3	0	0	0	0	0
Clavulinaceae sp. 2	0	0	0	1	0	0	0	0	0
Clavulinaceae sp. 3	0	0	0	1	0	0	0	0	0
Clavulinaceae sp. 4	0	0	0	1	0	0	0	0	0
Corticiales	0	0	0	0	0	0	0	1	0
Cortinariaceae sp. 1	0	2	0	0	0	0	0	0	0
Craterellus sp. 1	0	1	0	0	0	0	0	0	0
Craterellus sp. 2	0	1	0	0	0	0	0	0	0
Craterellus sp. 3	0	1	0	0	0	0	0	0	0
Sebacina sp. 1	0	0	2	0	0	0	0	0	0
Xenasmatella sp.1	0	0	0	0	0	0	2	2	1
Xenasmatella sp.2	0	0	0	0	0	0	1	0	0
Xerocomus sp. 1	0	1	0	0	0	0	0	0	0

*Based on UNITE information

Abbreviations for hosts are as follows, M (Myrtaceae), D (Dipterocarpaceae), Fg (Fagaceae), Fb (Fabaceae), Gn (Gnetaceae).

Table S2 ECM fungal host species identified in this study.

Host	Frequency		Total	ECM associated	Closest BLAST match		Query Cover	%Ident
	Bangka	Palangka Raya			Acc. No.	Organism		
Myrtaceae sp.1	-	108	108	36	KU564752.1	*Actephila sessilifolia*	99	99.28
Dipterocarpaceae sp.1	1	52	53	29	NC_040966.1	*Shorea pachyphylla*	100	98.22
Myrtaceae sp.2	45	3	48	27	KM895945.1	*Tristaniopsis laurina*	99	99.42
Fagaceae sp.1	1	20	21	14	KX163021.1	*Quercus robur*	99	99.46
Fabaceae sp.1	-	18	18	9	KM510309.1	*Dalbergia velutina*	99	99.63
Dipterocarpaceae sp.2	-	9	9	4	KY973108.1	*Cotylelobium burkii*	100	99.64
Gnetaceae	-	7	7	2	AP014923.1	*Gnetum ula*	99	99.46
Chyrsobalanaceae	-	6	6	1	JQ898702.1	*Magnistipula glaberrima*	99	99.46
Moraceae	-	4	4	-	MH332390.1	*Ficus deltoidea*	99	99.81
Santalaceae	-	3	3	2	EF464520.1	*Dendrotrophe varians*	100	99.82
Dipterocarpaceae sp.3	-	3	3	2	MH791329.1	*Hopea dryobalanoides*	100	99.81
Calophyllaceae	-	2	2	1	MF435428.1	*Calophyllum sp.*	99	100
Anacardiaceae	-	2	2	1	MN126106.1	*Magnifera indica*	100	99.79
Fabaceae sp.2	-	1	1	-	MH549715.1	*Acacia auriculiformis*	100	100
Fabaceae sp.3	-	1	1	-	MN591110.1	*Dialium guineense*	99	99.62
Nepenthaceae	-	1	1	2	NC_041271.1	*Nepenthes mirabilis*	100	99.44

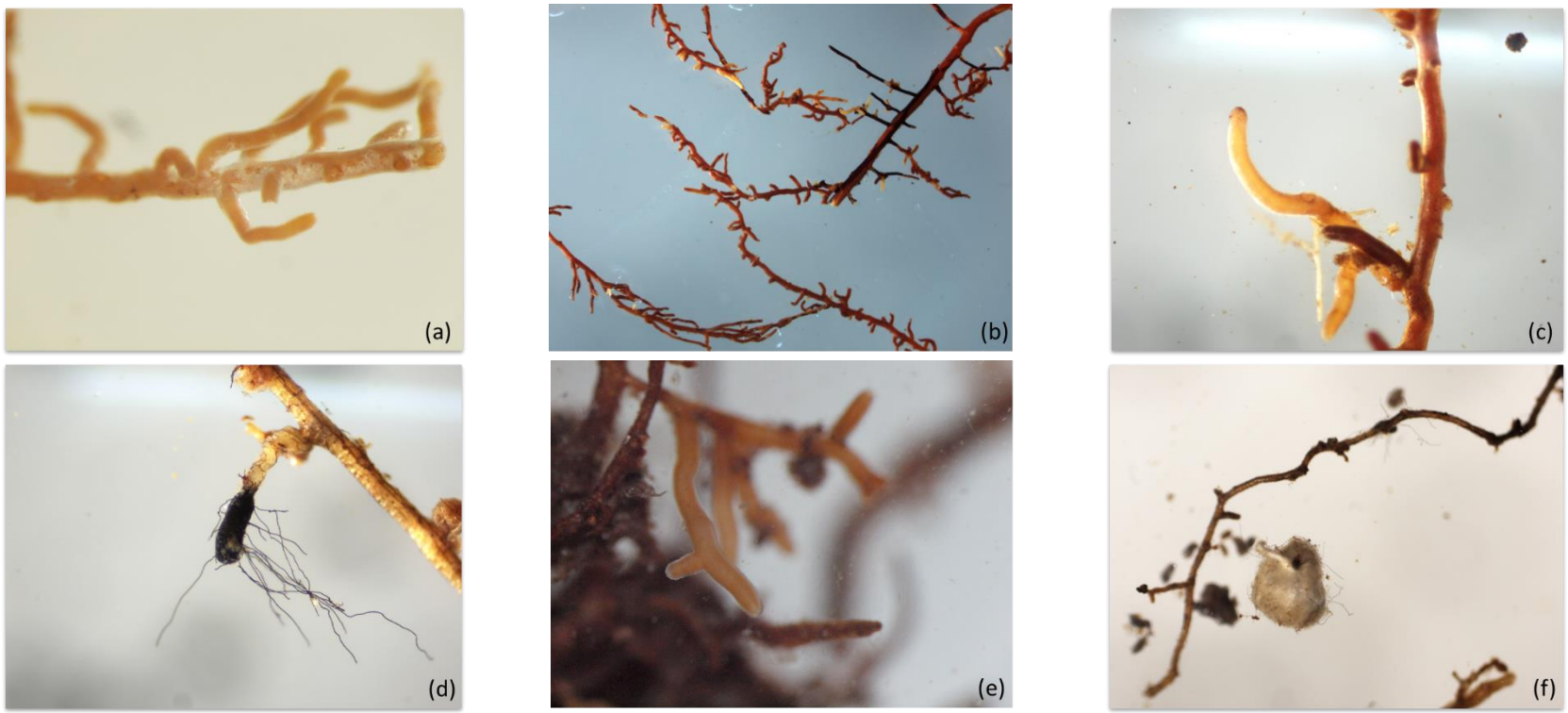

Figure S1 Photographs of ECM fungi found in the study sites. (a) Thelephoraceae sp. 1; (b) Thelephoraceae sp. 12; (c) *Russula* sp. 1; (d) *Cenococcum geophilum*; (e) *Heimioporus* sp.; and (f) *Borofutus* sp.

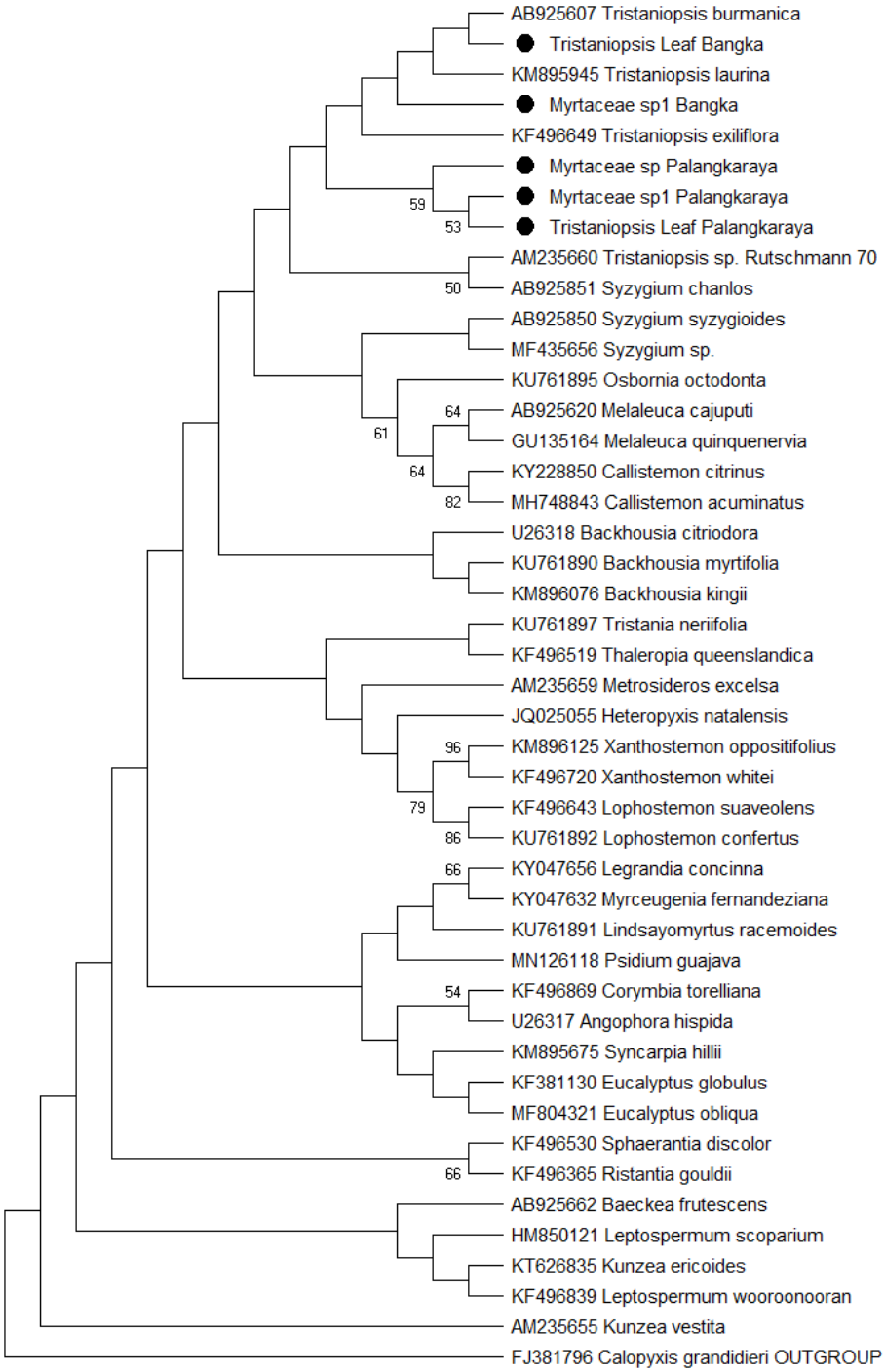

Figure S2 Phylogenetic tree topography of Myrtaceae including *Tristaniopsis* in Bangka and Palangka Raya (bullets) based on ML using *rbcL* gene sequences. Bootstrap values are indicated along the branches; support values > 50% are shown.

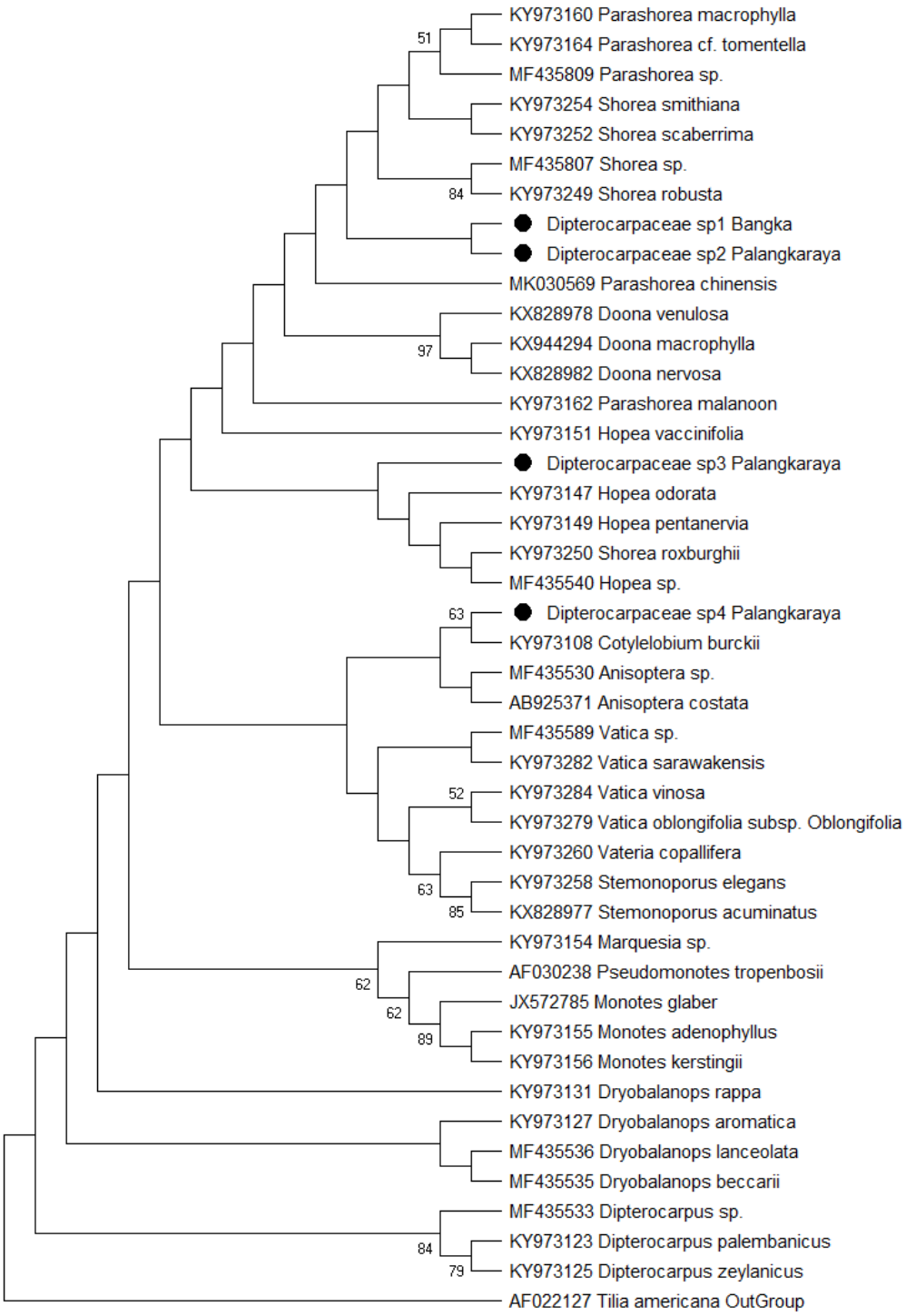

Figure S3 Phylogenetic tree topography of Dipterocarpaceae including ECM tips from Bangka and Palangka Raya (bullets) based on ML using *rbcL* gene sequences. Bootstrap values are indicated along the branches; support values > 50% are shown.

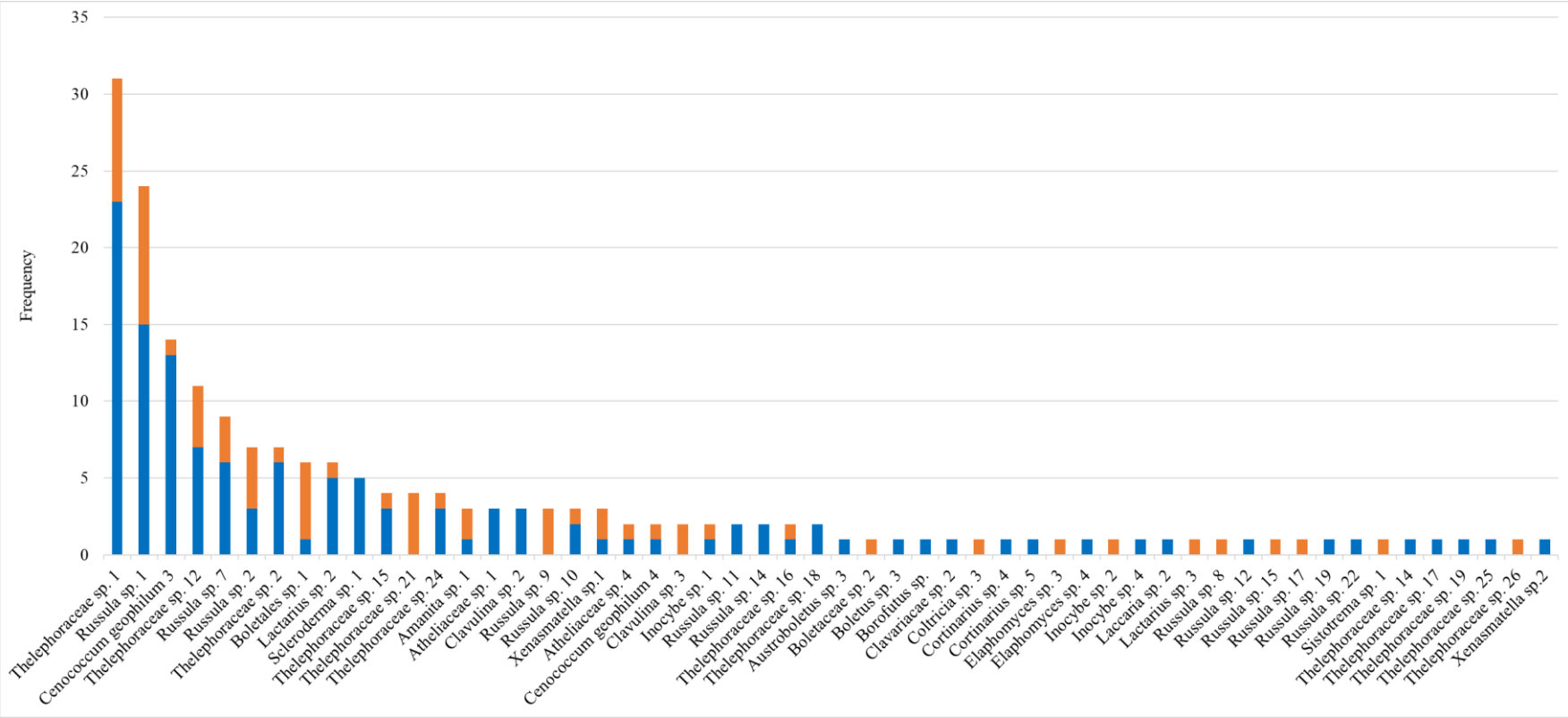

Figure S4 Species compositions and frequencies of ECM fungi found on Myrtaceae (*blue*) and Dipterocarpaceae (*orange*) in Palangka Raya, Indonesia

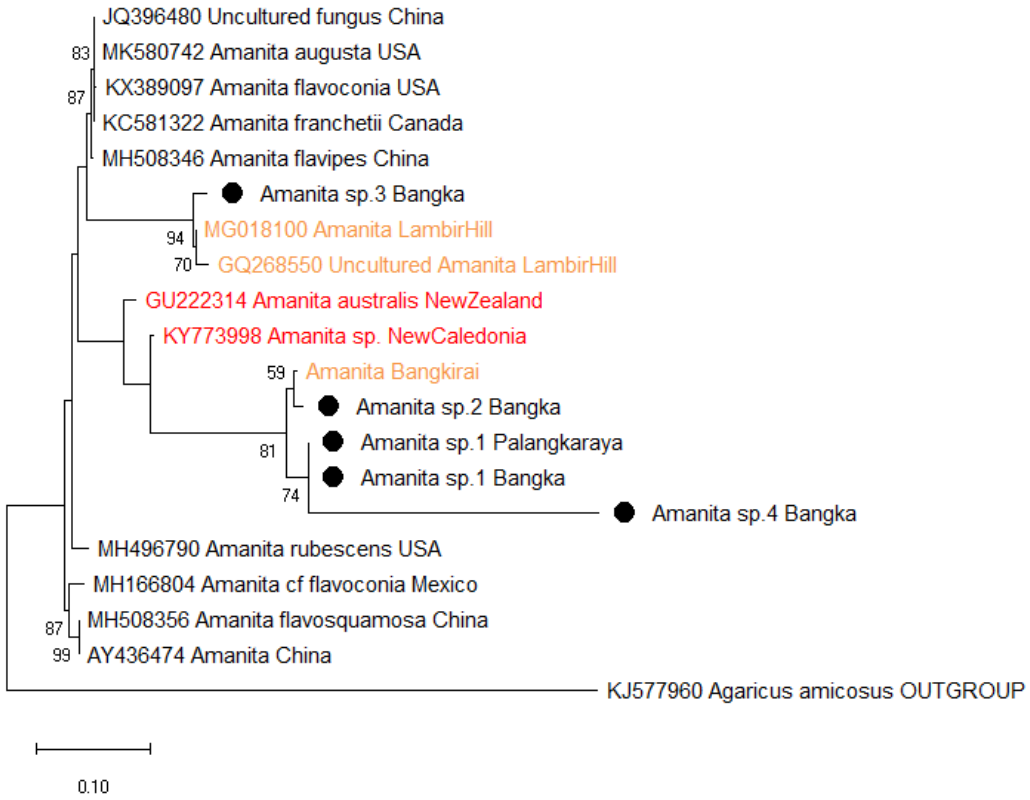

Figure S5 Phylogenetic tree of the ECM fungal lineage /amanita based on ML using ITS region sequences. Bootstrap values are indicated along the branches; support values > 50% are shown. Sequences obtained from Bangka and Palangka Raya are marked with bullet points. Species from Gondwana components (Africa, South America, and Australia) are shown in red; species from Southeast Asia are in orange.

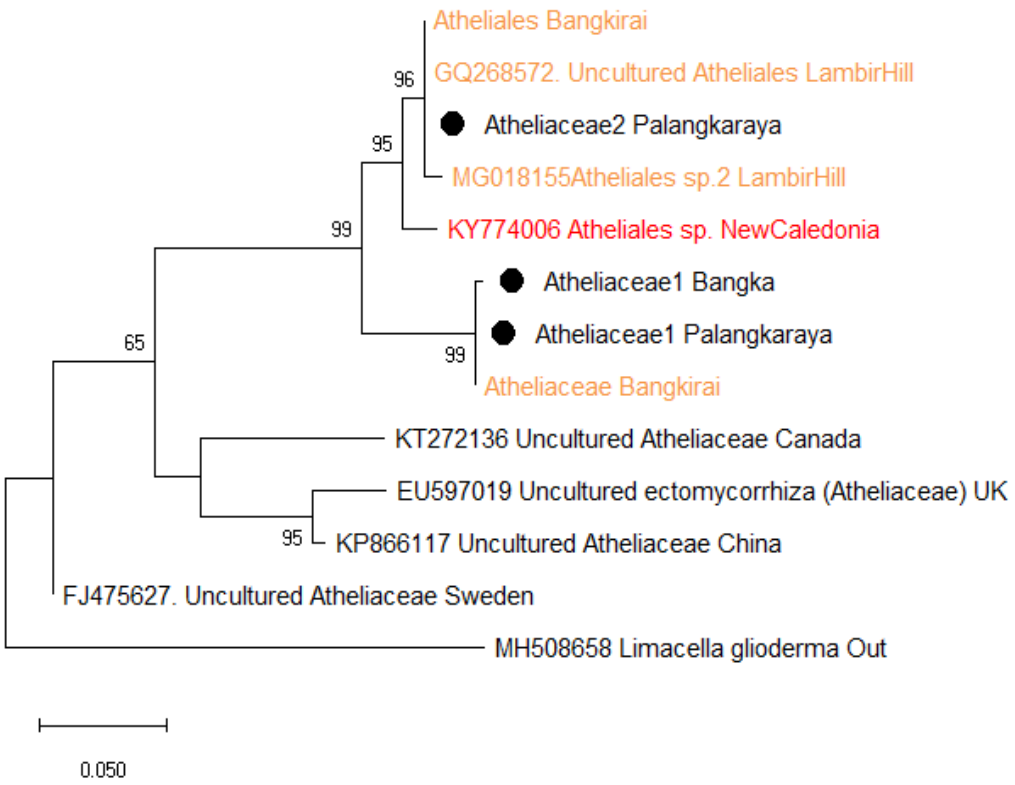

Figure S6 Phylogenetic tree of the ECM fungal lineage /atheliacea based on ML using ITS region sequences. Bootstrap values are indicated along the branches; support values > 50% are shown. Sequences obtained from Bangka and Palangka Raya are marked with bullet points. Species from Gondwana components (Africa, South America, and Australia) are shown in red; species from Southeast Asia are in orange.

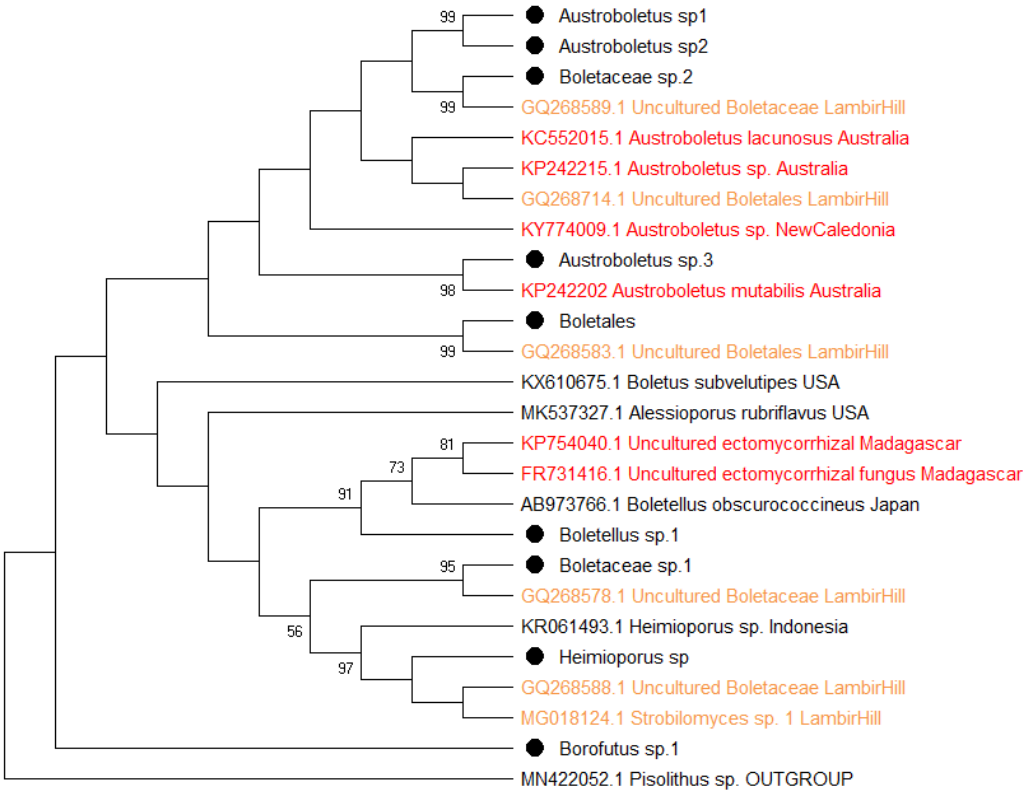

Figure S7 Phylogenetic tree topography of ECM fungal lineage */boletus* based on ML using ITS region sequences. Bootstrap values are indicated along the branches; support values > 50% are shown. Sequences obtained from Bangka and Palangka Raya are marked with bullet points. Species from Gondwana components (Africa, South America, and Australia) are shown in red; species from Southeast Asia are in orange.

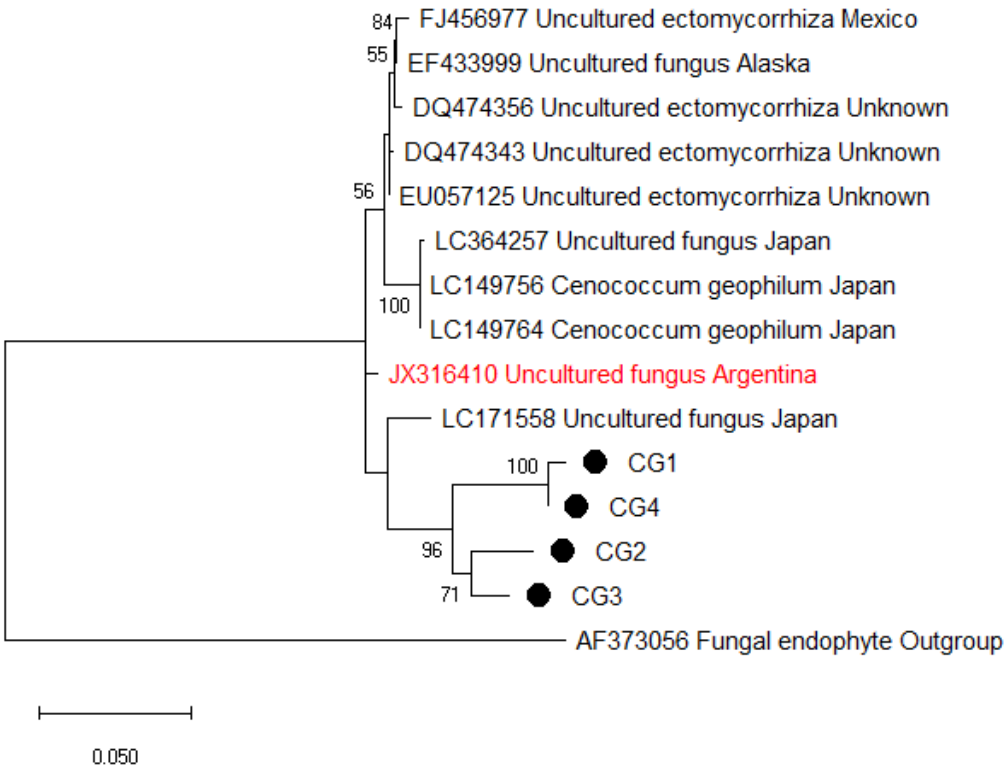

Figure S8 Phylogenetic tree of ECM fungal lineage */cenococcum* based on ML using ITS region sequences. Bootstrap values are indicated along the branches; support values > 50% are shown. Sequences obtained from Bangka and Palangka Raya are marked with bullet points. Species from Gondwana components (Africa, South America, and Australia) are shown in red; species from Southeast Asia are in orange.

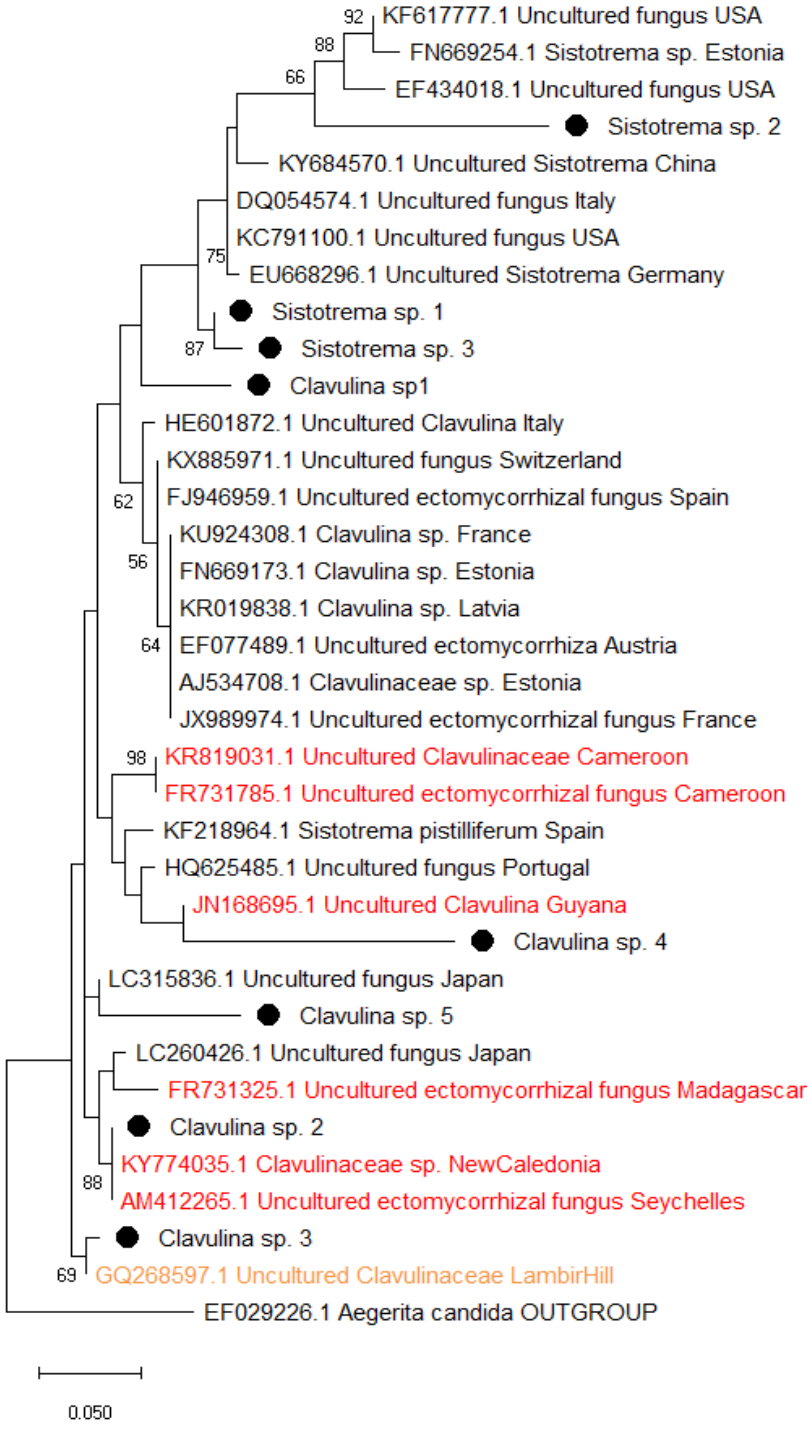

Figure S9 Phylogenetic tree of ECM fungal lineage */clavulina* based on ML using ITS region sequences. Bootstrap values are indicated along the branches; support values > 50% are shown. Sequences obtained from Bangka and Palangka Raya are marked with bullet points. Species from Gondwana components (Africa, South America, and Australia) are shown in red; species from Southeast Asia are in orange.

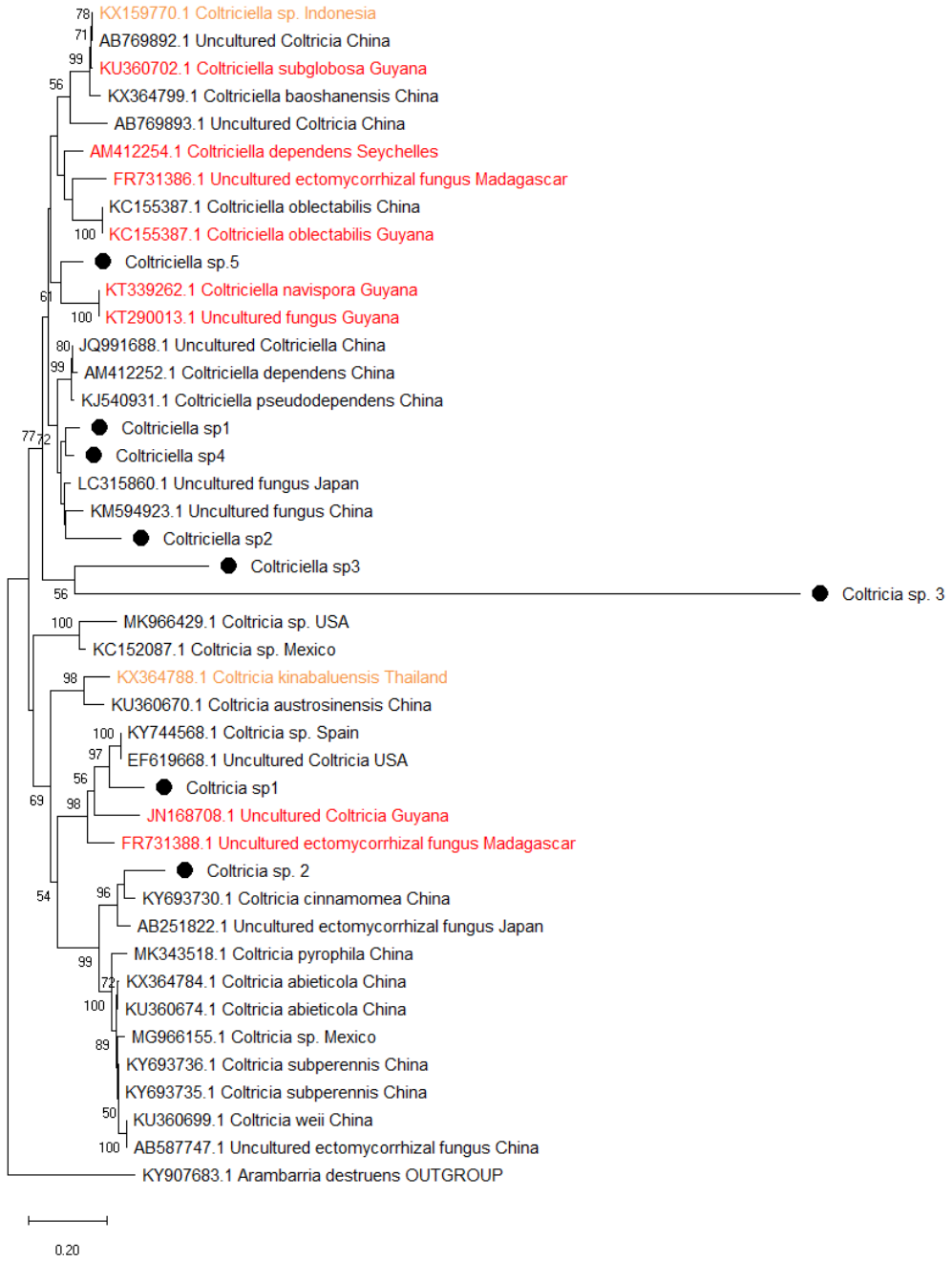

Figure S10 Phylogenetic tree of ECM fungal lineage */coltricia* based on ML using ITS region sequences. Bootstrap values are indicated along the branches; support values > 50% are shown. Sequences obtained from Bangka and Palangka Raya are marked with bullet points. Species from Gondwana components (Africa, South America, and Australia) are shown in red; species from Southeast Asia are in orange.

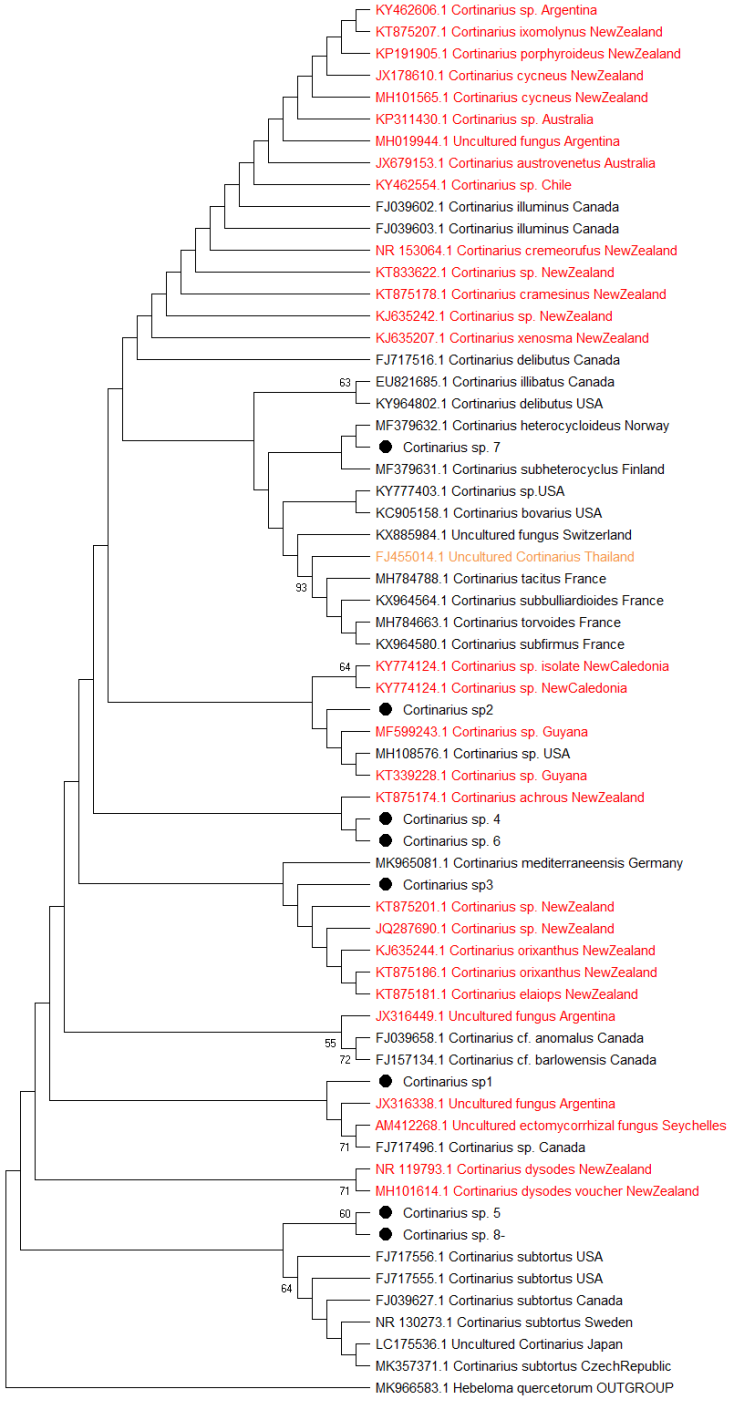

Figure S11 Phylogenetic tree topography of ECM fungal lineage */cortinarius* based on ML using ITS region sequences. Bootstrap values are indicated along the branches; support values > 50% are shown. Sequences obtained from Bangka and Palangka Raya are marked with bullet points. Species from Gondwana components (Africa, South America, and Australia) are shown in red; species from Southeast Asia are in orange.

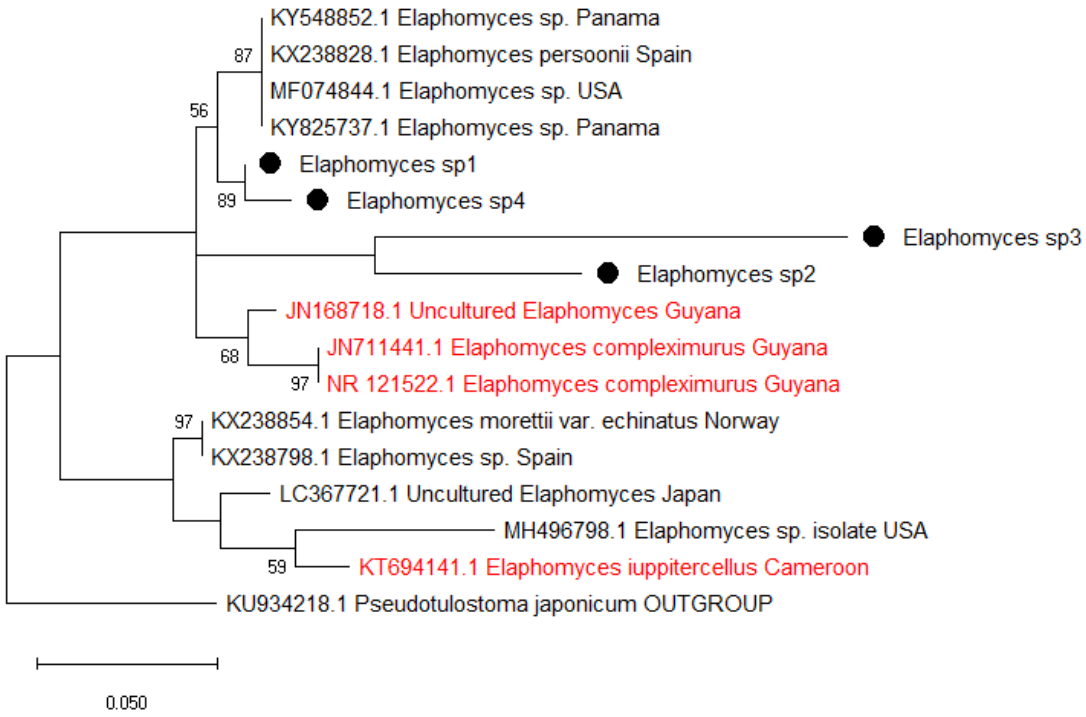

Figure S12 Phylogenetic tree of ECM fungal lineage */elaphomyces* based on ML using ITS region sequences. Bootstrap values are indicated along the branches; support values > 50% are shown. Sequences obtained from Bangka and Palangka Raya are marked with bullet points. Species from Gondwana components (Africa, South America, and Australia) are shown in red; species from Southeast Asia are in orange.

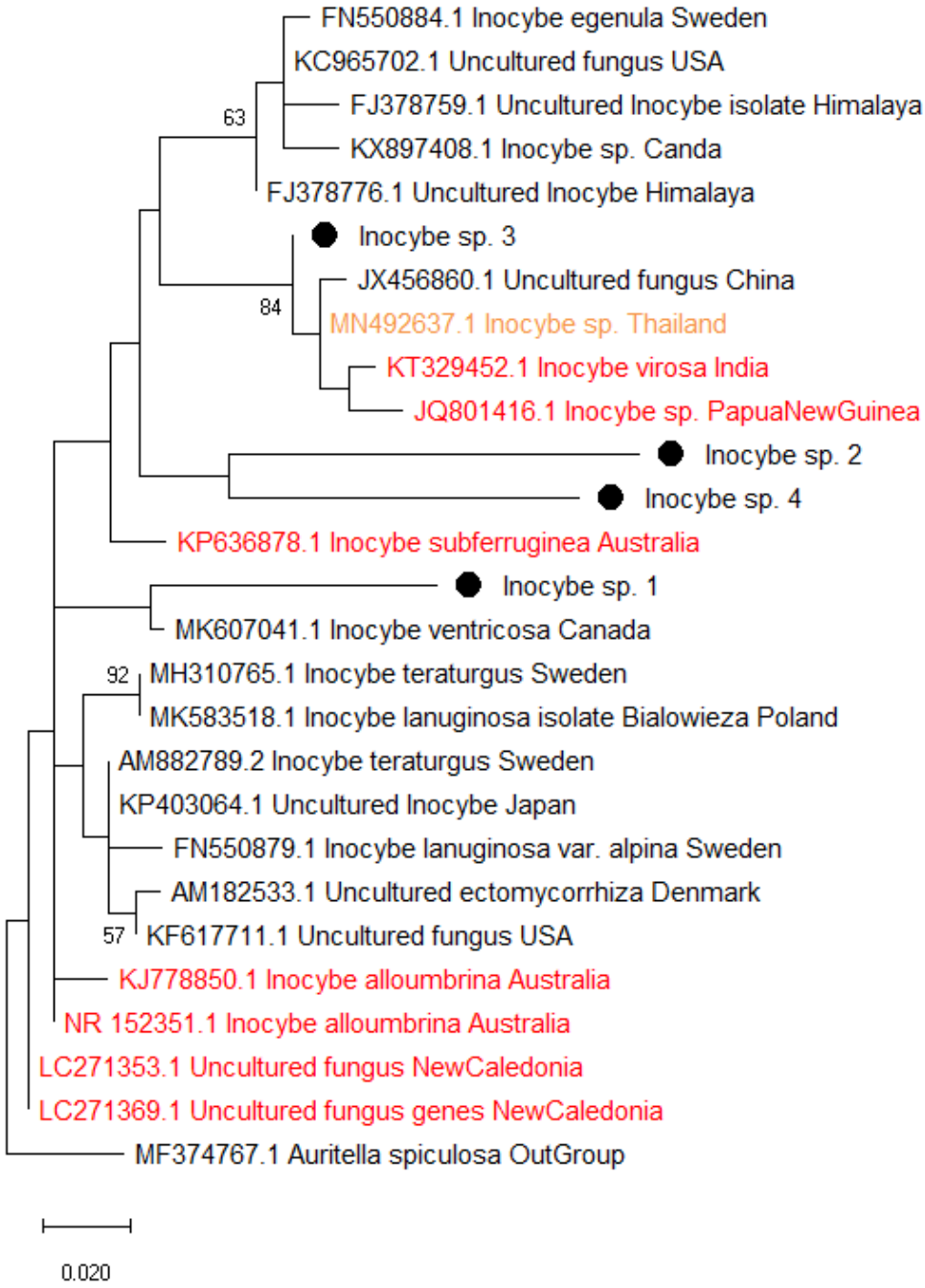

Figure S13 Phylogenetic tree of ECM fungal lineage */Inocybe* based on ML using ITS region sequences. Bootstrap values are indicated along the branches; support values > 50% are shown. Sequences obtained from Bangka and Palangka Raya are marked with bullet points. Species from Gondwana components (Africa, South America, and Australia) are shown in red; species from Southeast Asia are in orange.

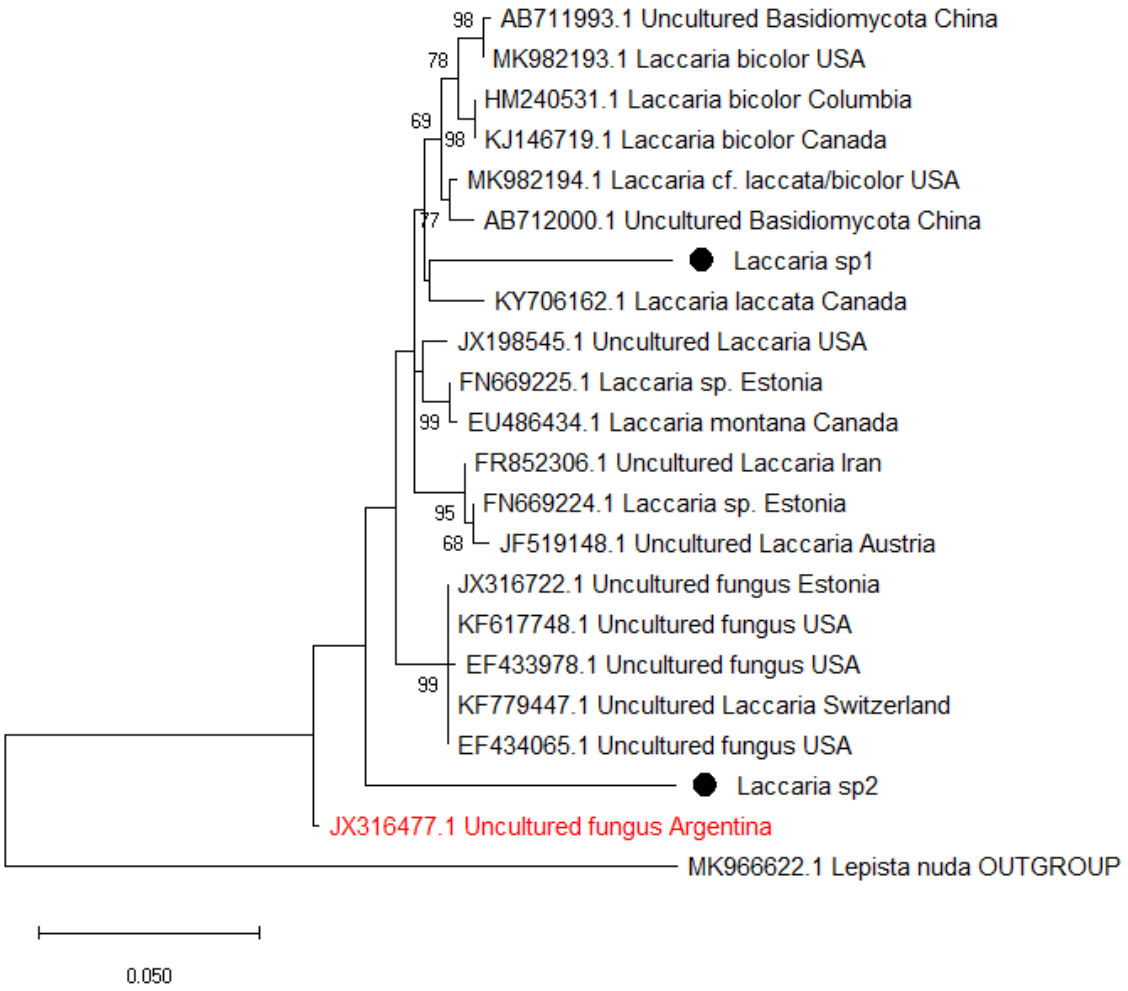

Figure S14 Phylogenetic tree of ECM fungal lineage */laccaria* based on ML using ITS region sequences. Bootstrap values are indicated along the branches; support values > 50% are shown. Sequences obtained from Bangka and Palangka Raya are marked with bullet points. Species from Gondwana components (Africa, South America, and Australia) are shown in red; species from Southeast Asia are in orange.

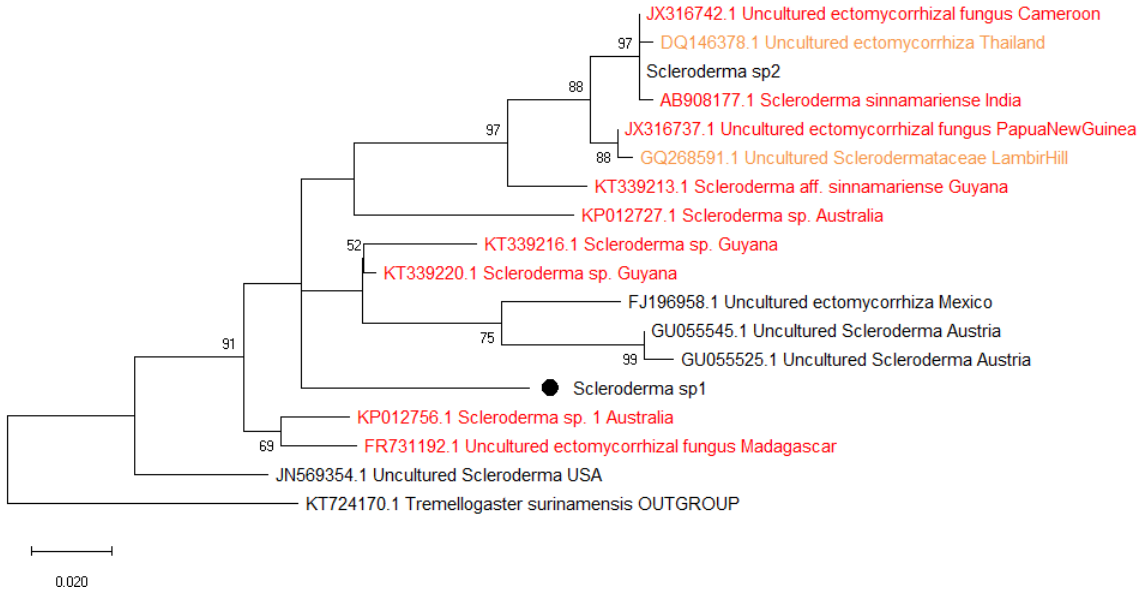

Figure S15 Phylogenetic tree of ECM fungal lineage */scleroderma* based on ML using ITS region sequences. Bootstrap values are indicated along the branches; support values > 50% are shown. Sequences obtained from Bangka and Palangka Raya are marked with bullet points. Species from Gondwana components (Africa, South America, and Australia) are shown in red; species from Southeast Asia are in orange.

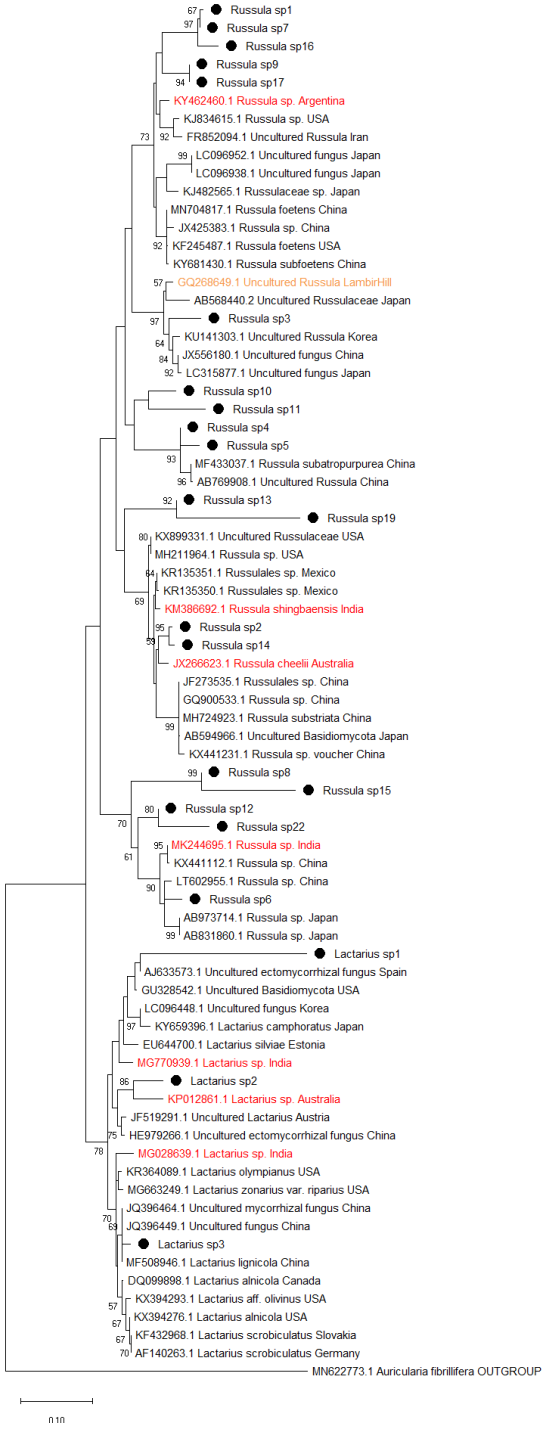

Figure S16 Phylogenetic tree of ECM fungal lineage */russula-lactarius* based on ML using ITS region sequences. Bootstrap values are indicated along the branches; support values > 50% are shown. Sequences obtained from Bangka and Palangka Raya are marked with bullet points. Species from Gondwana components (Africa, South America, and Australia) are shown in red; species from Southeast Asia are in orange.

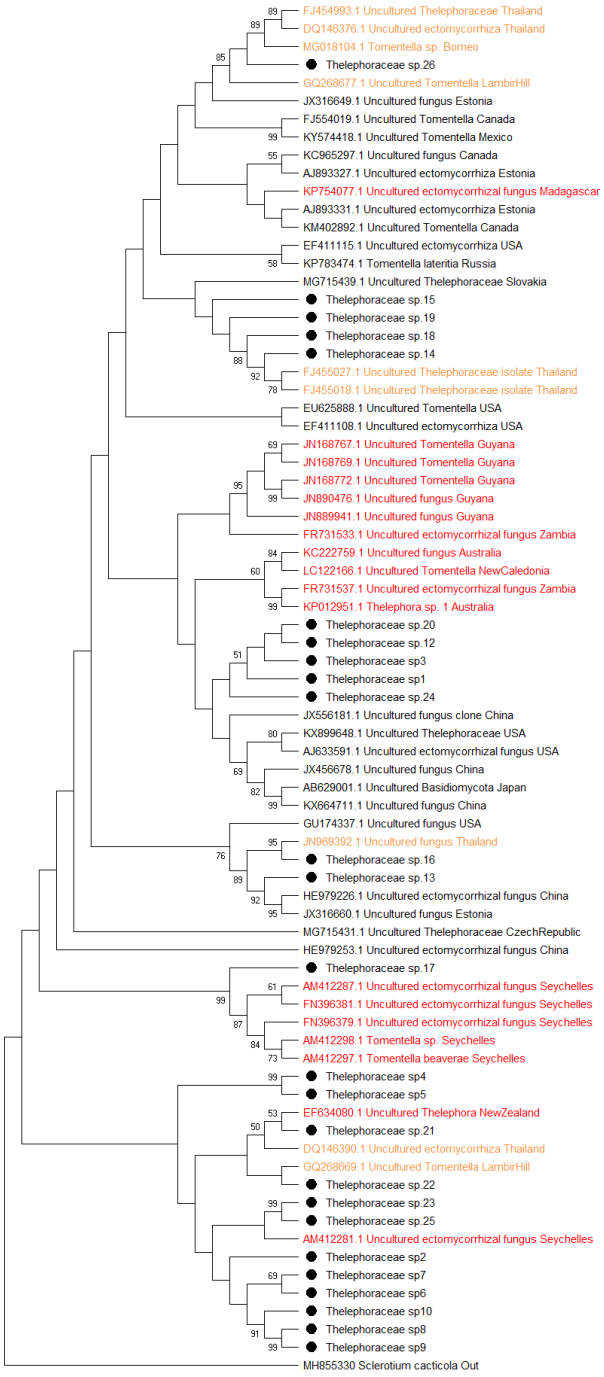

Figure S17 Phylogenetic tree topography of ECM fungal lineage */tomentella-thelephora* based on ML using ITS region sequences. Bootstrap values are indicated along the branches; support values > 50% are shown. Sequences obtained from Bangka and Palangka Raya are marked with bullet points. Species from Gondwana components (Africa, South America, and Australia) are shown in red; species from Southeast Asia are in orange.