

Diversity and community composition of ectomycorrhizal fungi in a dry deciduous dipterocarp forest in Thailand

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Abstract Large forest areas of South-East Asia, are dominated by the Dipterocarpaceae tree family, which contains many important timber species. Unlike many other tropical trees, Dipterocarpaceae rely on ectomycorrhizal (ECM) root symbiosis for their mineral nutrition. This study aims to document the richness and community composition of ECM fungi in a dry deciduous forest in Thailand. Combining morphological and molecular identification methods revealed 69 species of ECM fungi that belong to 17 phylogenetic lineages. The */russula-lactarius*, */tomentella-thelephora*, */sordariales*, */sebacina* and */cantharellus* lineages were the most species-rich. The fungal richness is comparable to other tropical rain forest sites, but the phylogenetic community structure has elements of both tropical and temperate ecosystems. Unlike tropical rain forests, the *Cenococcum geophilum* complex was one of the most frequent fungal taxa that had a relatively high ITS genetic diversity over the small sampling area. This study provides the first snapshot insight into the fungal community of dry dipterocarp forests. However, it is necessary to broaden the

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spatial and temporal scales of sampling to improve our understanding of the below-ground relations of dry and humid tropical forests.

Keywords Community structure · Dipterocarpaceae · Dry tropical forest · Ectomycorrhizal symbiosis · Southeast Asia

Introduction

Nearly 90% of terrestrial plants establish mycorrhizal interactions with soil fungi that provide mineral nutrients to their host plants in exchange for carbon (Brundrett 2009). Ectomycorrhizal (ECM) associations are formed by a restricted group of higher plant families such as Pinaceae, Betulaceae, Fabaceae, Dipterocarpaceae, Fagaceae and Myrtaceae (Brundrett 2009). These trees are ecologically and economically important components of boreal and temperate forest communities in the Northern Hemisphere and Australia, and patches of rain forest habitats in Africa, South America and Southeast Asia (Taylor and Alexander 2005).

Ectomycorrhizal fungi are estimated to comprise 20,000–25,000 species, most of which belong to the Basidiomycota and Ascomycota (Rinaldi et al. 2008). These species belong to >60 phylogenetic lineages that have independently evolved from saprotrophic ancestors (Tedersoo et al. 2010a). Most ECM fungi are able to establish symbioses with a broad range of hosts in both temperate and tropical ecosystems (Bruns et al. 2002; Ishida et al. 2007; Diédhiou et al. 2010; Smith et al. 2011; Tedersoo et al. 2011).

Knowledge of ECM fungal diversity has traditionally relied on fruit-body surveys. Such 'above-ground' surveys of fungal diversity in tropical forests have revealed diverse communities of ECM fungi (e.g. Chalermpongse 1993; Watling and Lee 1995; Buyck et al. 1996; May and Simpson 1997; Sims et al. 1997; Watling et al. 2002; Ramanankierana et al. 2006; Riviere et al. 2007; Henkel et al. this issue). However, fruit-bodies are ephemeral sexual structures that often require specific detection methods such as raking of soil and turning over dead wood. Moreover, many ECM fungal lineages have never been found producing fruit-bodies (Tedersoo et al. 2010a). The absence of fruit-bodies and short-term superficial search efforts have resulted in the discrepant view of above- and below-ground fungal diversity and community structure (Gardes and Bruns 1996; but see Smith et al. 2007).

Molecular identification studies on ECM fungi on root tips have greatly benefited our understanding about the ECM fungal communities and revealed many novel plant-fungal associations (Taylor 2008; Tedersoo et al. 2010a). As most of the below-ground studies are performed in the temperate Northern Hemisphere, information about ECM fungal communities is sparse in tropical ecosystems (Tedersoo and Nara 2010). Only recently, tropical rain forests in SE Asia (Sirikantaramas et al. 2003; Yuwa-Amornpitak et al. 2006; Peay et al. 2010), Africa (Tedersoo et al. 2007, 2010b, 2011; Diédhiou et al. 2010; Suvi et al. 2010) and South America (Tedersoo et al. 2010c; Smith et al. 2011) have been studied for below-ground ECM fungal richness. However, to the best of our knowledge, no such studies are available from tropical dry forests that cover relatively large areas in North India and SE Asia, but also in South Africa and South America.

Communities of ECM fungi are usually dominated by members of the */tomentella*-*thelephora* and */russula*-*lactarius* lineages in both temperate and tropical rain forest ecosystems, but temperate forests are more rich in terms of species and phylogenetic lineages (Tedersoo and Nara 2010). In temperate forests, the *Cenococcium geophilum* complex is

one of the characteristic ECM fungal taxa. These asexual ascomycetes form short black ECM on root tips of multiple hosts in various habitats (Trappe 1962; LoBuglio 1999). Due to the lack of fruit-bodies, their life cycle, taxonomy and biogeography remains poorly understood (Douhan et al. 2007; Boehm et al. 2009). The reports of *Cenococcum* in tropical ecosystems are restricted to SE Asia and Australia (Chen and Cairney 2002; Brearley et al. 2003).

In this study, we examined the ECM fungal community in a 4-ha dry tropical dipterocarp forest in Phitsanulok province, Thailand. Our primary goals were to characterize the below-ground ECM fungal diversity and to provide insights into their phylogenetic community structure.

Materials and methods

Site description and sampling

The study was performed in a 200 m × 200 m square plot at the Wildlife Conservation, Development and Extension station in Phitsanulok province, Thailand (100°34'48"N, 16°51'15"E, 160 m above sea level). A single site was selected to provide comparable data to most previous studies on ECM fungal communities. The annual rainfall averages ca. 1,250 mm and mean annual temperature is around 27°C in the study area. The rainy season usually lasts from May to October. The soils are ultisols and have a loamy texture. The vegetation is dominated by species of Dipterocarpaceae including *Shorea obtusa*, *S. siamensis*, *Dipterocarpus obtusifolius* and *Dipterocarpus tuberculatus* that account for >90% of basal area (Panwittayakul and Srikampol 2006). The site is usually subjected to annual burning that consumes most of the litter and understorey vegetation, but other anthropogenic disturbance is minimal. The age of oldest trees is estimated to be around 100 years (Sawarng pers. comm.).

A total of 194 soil samples (15 cm × 15 cm to 10 cm depth) were randomly collected within a few meters of the Dipterocarpaceae hosts in March 2009 (early dry season) with no attempt to distinguish among host species. Individual samples were taken at least 4 m apart. Within 48 h after collection, roots were carefully separated from soil and cleaned by rinsing in tap water. Roots were placed under an Olympus ZS40 stereomicroscope in large Petri dishes filled with water and examined for the presence of colonized ECM roots. Root tips were identified as ECM when they possessed a rounded apex and fungal mantle. Only living ECM roots were analyzed further. Different ECM morphotypes were distinguished based on mantle colour, surface roughness, the presence of emanating hyphae and rhizomorphs (Agerer 1987–2002). If available, at least two representative ECM root tips per morphotype per sample were stored in CTAB buffer (1% cetyltrimethylammonium-bromide, 100 mM Tris-HCl (pH 8.0), 1.4 M NaCl, and 20 mM EDTA) for molecular analyses.

Molecular analyses

DNA was extracted from ECM root tips by using a Qiagen DNeasy 96 Plant Kit (Qiagen, Crawley, UK), following the manufacturer's protocol. For identification of ECM fungi, the rDNA Internal Transcribed Spacer (ITS) region was selected, because it has been most widely used in fungal identification studies and provides sufficient resolution at the species

level (Taylor 2008; Begerow et al. 2010). The primer pair itsOF-T (5' acttggtcatttagaggaagt 3') combined with LB-W (5' cttttcatctttccctcacgg 3') was used to amplify all fungi, except black ascomycetes, for which the primer LA-W (5' cttttcatctttcgatcactc 3') was used instead (Tedersoo et al. 2008). Unsuccessfully amplified DNA extracts were re-amplified using primers itsOF-T in combination with universal primers its4 (5' tcctccgcttattgatatgc 3') or its2 (5' gctgcgtttcttcacgatgc 3') or specific primers targeting each fungal lineage (see Tedersoo et al. 2008, 2011; Bahram et al. 2011). The PCR conditions followed Tedersoo et al. (2006). PCR products were examined on 1% agarose gels under UV-light and purified using Exo-Sap enzymes (Sigma, St. Louis, MO, USA). Sequencing was performed with the primer its5 (5' ggaagtaaagtcgtaacaagg 3') and/or its4 at Macrogen Inc., Seoul, South Korea. Sequences were assembled into contigs, check, and, if necessary, manually corrected using Sequencher 4.9 software (GeneCodes Corp., Ann Arbor, MI, USA). Species were delimited based on 97.0% ITS sequence similarity based on global pairwise sequence alignments, except the asexual *C. geophilum* that was conservatively treated as a single species. Fungal taxa were identified by running MEGABLAST and BLASTn queries against the International Sequence Database (INSD) and UNITE database (Abarenkov et al. 2010a) as implemented in the PlutoF workbench (Abarenkov et al. 2010b). All unique sequences were submitted to both INSD and UNITE.

We conducted a phylogenetic analysis to address phylogenetic placement of members of the *C. geophilum* complex in Thailand. First, we downloaded all 313 full-length ITS sequences from the INSD and UNITE databases (as of November 2010). The alignment of ITS sequences was constructed by use of Mafft ver. 6 (Kato and Toh 2008) and corrected manually. Introns in the rRNA 18S gene were trimmed off. Most redundant (i.e. >99% similar and from the same region) and all low-quality sequences were removed and the remaining sequences were re-aligned. The final alignment comprised 71 sequences and 492 nucleotide characters. Maximum Likelihood phylograms were constructed by use of RAxML with 200 fast bootstrap replicates and the Gamma model of rate heterogeneity (Stamatakis et al. 2008). Because the only ITS sequence of *Glonium*, the closest known relative of *Cenococcum* (Boehm et al. 2009), actually represents *Epicoccum* sp., we selected a sequence (INSD accession AF373056; Girlanda et al. 2002) of a cultured isolate from non-ectomycorrhizal root tissue as an outgroup. This sequence has 86.3% similarity to the closest *Cenococcum* isolates.

Results

In total, 99 out of 194 soil samples (51.0%) contained living ECM roots. In these samples, 283 root tips were subjected to molecular analyses. ECM fungi were successfully identified from 194 root tips (68.5% success), but many root tips yielded putatively endophytic fungi. By using 97% sequence similarity threshold over the entire ITS region, we identified 69 fungal species that belong to 17 phylogenetic lineages of ECM fungi (Table 1). Except for the *C. geophilum* complex, infraspecific ITS sequence similarity always exceeded 99%. The *C. geophilum* complex comprised an additional seven ITS types at 97% sequence similarity level (Fig. 1), but these were treated as a single species following most previous studies. The phylogram revealed several moderately supported groups of putatively non-mycorrhizal (mostly originating from plant tissues and soil) isolates basal to the *C. geophilum* complex, although sharing high ITS sequence similarity (92–94% to *Cenococcum*). Both the rarefied species accumulation curve and Jackknife2 minimal species richness estimate continued rising with increasing sampling effort, whereas Chao2 estimate started

Table 1 Frequency and identification of ectomycorrhizal fungal species in a dry deciduous forest

Species	UNITE code		Identity %	Frequency
/russula-lactarius Thai01	UDB004700	<i>Russula</i> cf. <i>pectinata</i> HQ604835	92.5	32
/russula-lactarius Thai02	UDB004701	Russulaceae sp. DQ061886	91.3	7
/russula-lactarius Thai03	UDB004702	<i>Russula</i> sp. FJ196952	87.2	9
/russula-lactarius Thai04	UDB004703	<i>Gymnomyces redolens</i> DQ403803	87.3	6
/russula-lactarius Thai05	UDB004704	<i>Russula</i> sp. FJ196952	87.3	3
/russula-lactarius Thai06	UDB004705	<i>Lactarius</i> cf. <i>gerardii</i> GU258272	87.8	5
/russula-lactarius Thai07	UDB004706	Russulaceae sp. FJ946953	93.5	3
/russula-lactarius Thai08	UDB004707	<i>Russula</i> cf. <i>viscida</i> AB458684	98.2	2
/russula-lactarius Thai09	UDB004708	<i>Russula</i> cf. <i>foetens</i> DQ422023	95.1	2
/russula-lactarius Thai10	UDB004709	<i>Russula</i> sp. AF345248	98.7	1
/russula-lactarius Thai11	UDB004710	<i>Gymnomyces redolens</i> DQ403803	90.9	1
/russula-lactarius Thai12	UDB004711	<i>Lactarius</i> aff. <i>uyedae</i> GU258296	98.9	1
/russula-lactarius Thai13	UDB004712	<i>Russula</i> sp. AF350059	99.0	1
/russula-lactarius Thai14	UDB004713	<i>Russula lepida</i> DQ422013	87.9	1
/russula-lactarius Thai15	UDB004714	<i>Russula atrovirens</i> GU222260	92.9	2
/russula-lactarius Thai16	UDB004715	<i>Russula laurocerasi</i> EU598184	96.8	1
/russula-lactarius Thai17	UDB004716	<i>Lactarius pseudoluteopus</i> FM999659	90.0	1
/russula-lactarius Thai18	UDB004717	<i>Russula densifolia</i> AB291763	96.7	1
/russula-lactarius Thai19	UDB004718	<i>Lactarius</i> aff. <i>gerardii</i> GU258222	91.4	1
/russula-lactarius Thai20	UDB004719	n.a.		1
/russula-lactarius Thai21	UDB004720	<i>Russula crustosa</i> EU598193	86.6	1
/russula-lactarius Thai22	UDB004764	<i>Lactarius</i> cf. <i>piperatus</i> AB459515	99.1	1
/tomentella-thelephora Thai01	UDB004721	<i>Tomentella sublilacina</i> UDB002972	92.2	2
/tomentella-thelephora Thai02	UDB004722	Thelephoraceae sp. FN669279	91.6	5
/tomentella-thelephora Thai03	UDB004723	<i>Tomentella sublilacina</i> UDB002972	92.5	4
/tomentella-thelephora Thai04	UDB004724	<i>Tomentella sublilacina</i> UDB002972	91.7	2
/tomentella-thelephora Thai05	UDB004725	Thelephoraceae sp. GQ268671	92.1	2
/tomentella-thelephora Thai06	UDB004726	Thelephoraceae sp. DQ146371	98.9	1
/tomentella-thelephora Thai07	UDB004727	Thelephoraceae sp. FM955848	96.4	2
/tomentella-thelephora Thai08	UDB004728	Thelephoraceae sp. FM955848	93.6	1
/tomentella-thelephora Thai09	UDB004729	<i>Tomentella sublilacina</i> UDB002972	92.8	1
/tomentella-thelephora Thai10	UDB004730	<i>Tomentella sublilacina</i> UDB002972	92.4	1
/tomentella-thelephora Thai11	UDB004731	<i>Tomentella sublilacina</i> UDB002972	92.6	1

Table 1 continued

Species	UNITE code		Identity %	Frequency
/tomentella-thelephora Thai12	UDB004732	Thelephoraceae sp. GQ268669	91.3	1
/tomentella-thelephora Thai13	UDB004733	Thelephoraceae sp. AB453036	97.8	1
/tomentella-thelephora Thai14	UDB004734	Thelephoraceae sp. FJ455005	94.2	1
/tomentella-thelephora Thai15	UDB004735	Thelephoraceae sp. AY874385	94.2	2
/tomentella-thelephora Thai16	UDB004736	Thelephoraceae sp. GU553375	90.7	2
/tomentella-thelephora Thai17	UDB004746	Thelephoraceae sp. AJ893308	91.6	1
<i>C. geophilum</i> s. lato	UDB004739-45	<i>Cenococcum geophilum</i> GU998677	95.2	28
/sordariales Thai01	UDB004747	<i>Phialemonium curvatum</i> GU205097	85.4	9
/sordariales Thai02	UDB004748	<i>Rhodoveronaea varioseptata</i> FJ617560	93.0	3
/sordariales Thai03	UDB004749	<i>Rhodoveronaea varioseptata</i> FJ617560	Partial	2
/sordariales Thai04	UDB004750	Sordariales sp. GQ268561	88.0	3
/amanita_Thai01	UDB004751	<i>Amanita</i> sp. GQ268548	Partial	1
/amanita_Thai02	UDB004755	<i>Amanita</i> sp. GQ268548	88.9	1
/laccaria_Thai01	UDB004752	<i>Laccaria</i> sp. FJ168597	93.7	2
/marcelleina-peziza gerardii Thai01	UDB004753	<i>Hydnobolites cerebriformis</i> EU784271	Partial	3
/marcelleina-peziza gerardii Thai02	UDB004754	<i>Hydnobolites</i> sp. EF417805	94.7	1
/sebacina Thai02	UDB004756	<i>Sebacina</i> sp. EU326168	88.2	5
/sebacina Thai03	UDB004757	<i>Sebacina</i> sp. EF417803	94.3	3
/sebacina Thai05	UDB004758	<i>Sebacina</i> sp. HQ022221	89.1	1
/sebacina Thai06	UDB004759	<i>Sebacina</i> sp. EU910925	95.1	1
/ceratobasidium1 Thai01	UDB004760	<i>Ceratobasidium</i> sp. GQ268601	96.9	2
/ceratobasidium1 Thai02	UDB004761	<i>Ceratobasidium</i> sp. GQ175300	90.7	1
/clavulina Thai01	UDB004762	<i>Clavulina</i> cf. <i>cristata</i> AB459513	97.8	1
/clavulina Thai02	UDB004763	<i>Clavulina</i> sp. FJ454922	93.8	1
/cantharellus Thai01	UDB004765	<i>Craterellus tubaeformis</i> HM468495	80.5	4
/cantharellus Thai02	UDB004766	<i>Pseudocraterellus sinuosus</i> GU590932	81.8	1
/cantharellus Thai03	UDB004767	<i>Craterellus tubaeformis</i> HM468495.1	74.0	1
<i>Scleroderma columnare</i>	UDB004768	<i>Scleroderma columnare</i> AB459512	99.6	2
<i>Astraeus odoratus</i>	UDB004769	<i>Astraeus odoratus</i> AJ629878	99.6	2
/inocybe Thai01	UDB004770	<i>Inocybe rimosa</i> HQ604624	85.7	1

Table 1 continued

Species	UNITE code		Identity %	Frequency
/inocybe Thai02	UDB004771	<i>Inocybe</i> sp. GQ893000	94.1	1
/inocybe Thai03	UDB004772	<i>Inocybe rimosa</i> EU523562	89.7	2
/elaphomyces Thai01	UDB004773	<i>Elaphomyces guangdongensis</i> HM357250	87.6	2
/elaphomyces Thai02	UDB004774	<i>Elaphomyces guangdongensis</i> HM357250	88.1	1
Atheliales Thai01	UDB004775	Atheliaceae sp. HM488526	85.9	1
/boletus Thai01	UDB004776	Boletales sp. GQ268584	93.8	1

to level off (Fig. 2). Jackknife2 and Chao2 respectively estimated the minimum richness to be 124 and 105 species at the study site.

In terms of species richness, the /*russula-lactarius*, /*tomentella-thelephora*, /*sordariales*, /*sebacina* and /*cantharellus* lineages dominated, comprising 22, 17, 4, 4 and 3 species, respectively (Table 1). Four lineages—/amanita, /boletus, /elaphomyces and an unassigned Atheliales group—were represented by a single species. Except for the species of Atheliales, all sequences were confidently assigned to ECM fungal lineages. Only 9 of the 69 species matched with sequences from public databases at the 97% sequence similarity cut-off (*Russula* cf. *viscida*, *Lactarius* aff. *uyedae*, *Clavulina* cf. *cristata*, *Lactarius* cf. *piperatus*, *Scleroderma columnare*, *Astraeus odoratus*, *Russula* sp. AF345248, *Russula* sp. AF350059, *Thelephoraceae* sp. DQ146371). Four of these taxa were identified to species based on the available reference sequences and identifications (Table 1). Among all species, /*russula-lactarius* Thai01 (92% similarity to *Russula* cf. *pectinata*) and the *C. geophilum* complex were the most frequent species that were found in 32 and 28 samples, respectively. All other species occurred in <10 samples and included 37 singletons.

Discussion

Richness of species and phylogenetic lineages of ECM fungi in the dry dipterocarp forest site are comparable to previous studies in tropical rain forests, matching the lower limits of tropical ecosystems (compare Tedersoo and Nara 2010; Tedersoo et al. 2011). The rising species accumulation curve and Jackknife minimum richness estimator curve suggest that many ECM fungal species remained undetected. This is consistent with the moderate sequencing success and a single sampling event in the dry season.

The ECM fungal phylogenetic community has similar features to both tropical and temperate forests. Substantial dominance of members of the /*russula-lactarius* and /*tomentella-thelephora* lineages, and the lack of many temperate lineages are characteristic of tropical ecosystems. Furthermore, an unidentified species of ECM Atheliales was found. This species displayed close affinities to previously obtained sequences from tropical rain forests of Borneo (Peay et al. 2010), Cameroon (Tedersoo et al. 2010b), Gabon (Tedersoo et al. 2011) and Guyana (Smith et al. 2011), substantiating the tropical cross-continental connection and indicating a wide distribution of this undescribed, potentially tropical ECM fungal lineage. By contrast, the low richness of the /*boletus* lineage and the presence of /*cenococcum* and /*laccaria* lineages in the dry dipterocarp forest site are indicative of temperate affinities (Tedersoo and Nara 2010; Tedersoo et al. 2010a).

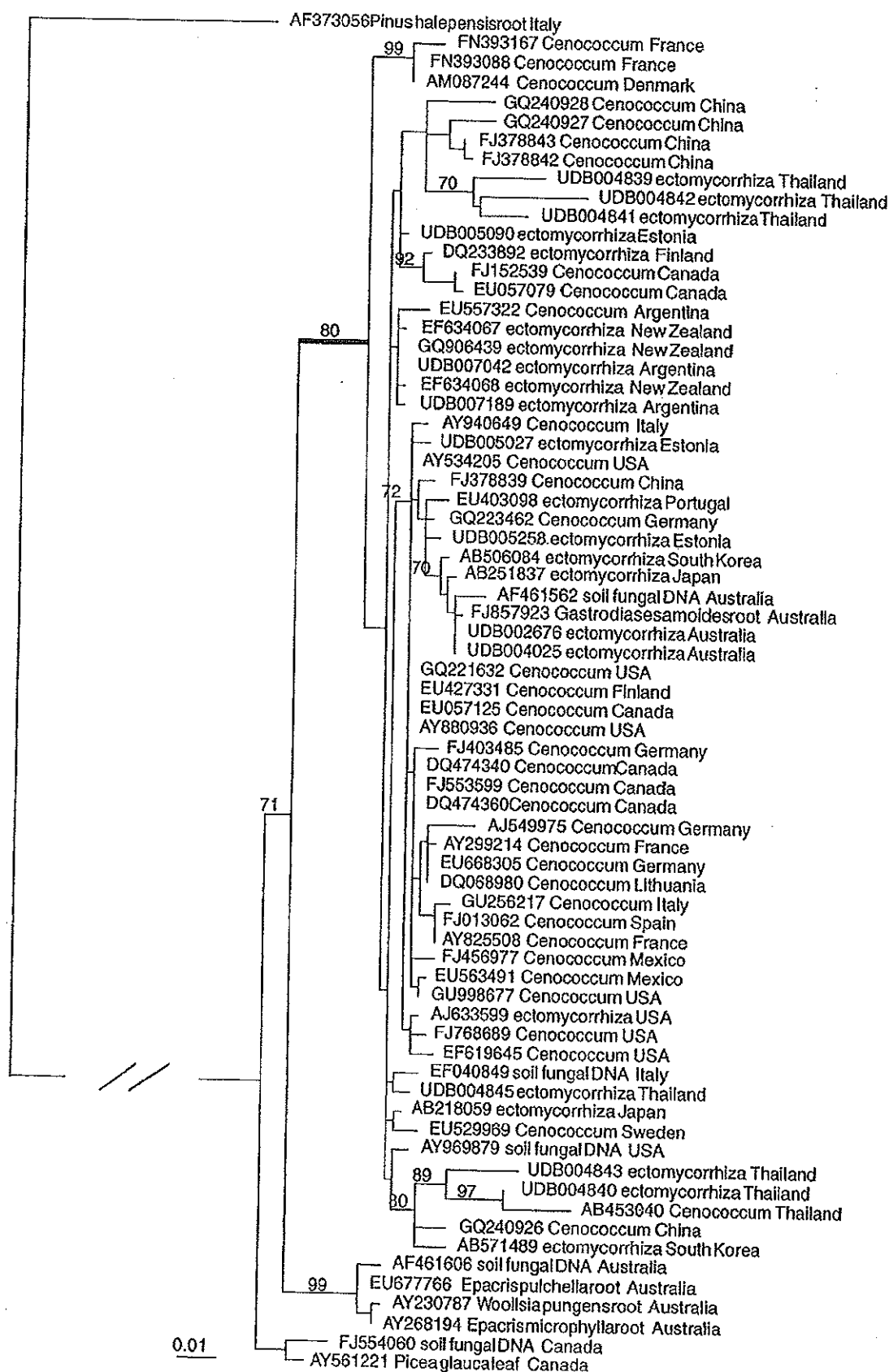


Fig. 1 Maximum likelihood phylogram of the *Cenococcum geophilum* complex (=the */cenococcum* lineage; thick branch) as based on ITS sequences. Phylogenetic placement of isolates from Thailand is indicated in bold. Fast bootstrap support values >70 are shown above branches

Watling and Lee (2007) suggested that there are probably around 60 undescribed species of *Russula* and *Lactarius* in Thailand and Malaysia. A large proportion of our sequences in the /*russula-lactarius* lineage displayed low similarity to publicly available DNA sequences of the ITS region due to paucity of molecular studies on taxonomy and soil ecology of tropical fungi (Tedersoo et al. 2011, but see Smith et al. 2011). Therefore, many additional taxa are expected to be found if sampling is extended both spatially and temporally.

The /*tomentella-thelephora* lineage was the second most species-rich group in this study, which corroborates previous findings in SE Asian rain forests dominated by Dipterocarpaceae and other tropical forests (Sirikantaramas et al. 2003; Peay et al. 2010; Tedersoo and Nara 2010). Lee and Patahayah (2003) and Lee et al. (2002) isolated a *Tomentella* spp. from roots of *Shorea parvifolia* and observed growth promotion of tree seedlings when inoculated onto the Dipterocarpaceae and Fabaceae hosts. Although Corner (1968) monographed the Thelephoraceae family in SE Asia and recognized 30 species, further work on the taxonomy of this important group is clearly required.

Members of the *C. geophilum* complex were among of the most frequent colonizers on Dipterocarpaceae root tips in this study. Although previous molecular identification studies reported no *Cenococcum* on root tips of Dipterocarpaceae (Sirikantaramas et al. 2003; Yuwa-Amornpitak et al. 2006; Peay et al. 2010; Tedersoo et al. 2011), its conspicuous ECM morphotypes have been described in forest nurseries (Brearley et al. 2003). As revealed from long branches in the phylogram (Fig. 1), genetic variation of the ITS region is relatively high among isolates of the *C. geophilum* complex in this single forest site. Sequences from Thailand tended to cluster into two poorly supported groups. Interestingly, all *Cenococcum* sequences from Australia grouped together and all sequences from Argentina and New Zealand formed another cluster, raising a hypothesis that *Cenococcum*

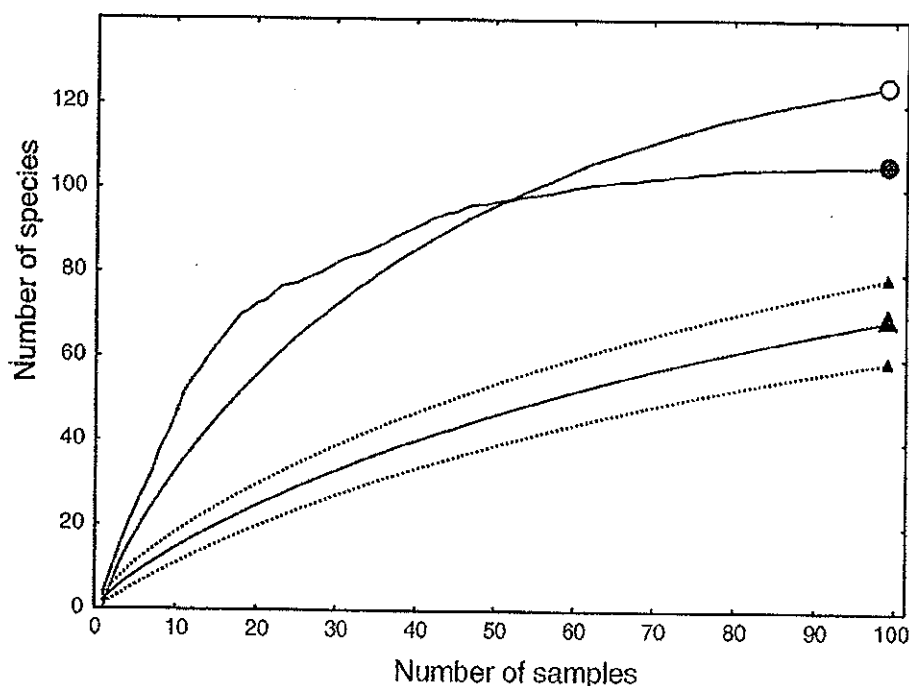


Fig. 2 Rarefied species accumulation curve (indicated with a large triangle) from ECM samples taken from a dry deciduous dipterocarp forest in Thailand, its 95% confidence intervals (dotted line, small triangles), Chao2 (closed circle) and Jackknife2 (open circle) minimum species richness estimates as based on species distribution of ECM fungi

may have only recently arrived to these regions. Close phylogenetic relationships with putative endophytes are suggestive of relatively recent evolution of this ECM lineage from biotrophic rather than saprotrophic ancestors. Clearly, sequence analysis of additional genes is required to address biogeographic patterns and evolutionary origin of the *C. geophilum* complex (Douhan et al. 2007). The great frequency of *Cenococcum* in our study site can be explained by annual burning and high summer temperatures, because *Cenococcum* is regarded as highly tolerant of heat (LoBuglio 1999; Buscardo et al. 2010).

In conclusion, the dry dipterocarp forest site has comparable ECM fungal richness with other tropical rain forest sites, but the fungal community has some temperate affinities. Spatial and temporal extension in sampling is necessary to further generalize about the ECM fungal community ecology in these habitats. The *C. geophilum* complex, characteristic of temperate ecosystems appears to be genetically highly diverse in SE Asia.

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References

- Abarenkov K, Nilsson RH, Larsson K-H, Alexander IJ, Eberhardt U, Erland S, Høiland K, Kjølter R, Larsson E, Pennanen T, Sen R, Taylor AFS, Tedersoo L, Ursing B, Vrålstad T, Liimatainen K, Peintner U, Kõljalg U (2010a) The UNITE database for molecular identification of fungi—recent updates and future perspectives. *New Phytol* 186:281–285
- Abarenkov K, Tedersoo L, Nilsson RH, Vellak K, Saar I, Veldre V, Parmasto E, Proust M, Aan A, Ots M, Kurina O, Ostonen I, Jõgeva J, Halapuu S, Põldmaa K, Toots M, Truu J, Larsson K-H, Kõljalg U (2010b) PlutoF—a web based workbench for ecological and taxonomic research with an online implementation for fungal ITS sequences. *Evol Bioinform* 6:189–196
- Agerer R (1987–2002) Colour atlas of ectomycorrhizae. Einhorn-Verlag, Schwäbisch Gmünd, Germany
- Bahram M, Põlme S, Kõljalg U, Tedersoo L (2011) A single European aspen (*Populus tremula*) tree individual may potentially harbour dozens of *Cenococcum geophilum* ITS genotypes and hundreds of species of ectomycorrhizal fungi. *FEMS Microbiol Ecol* 75:313–320
- Begerow D, Nilsson RH, Unterseher M, Maier W (2010) Current state and perspectives of fungal DNA barcoding and rapid identification procedures. *Appl Microbiol Biotechnol* 87:99–108
- Boehm EWA, Mugambi GK, Miller AN, Huhndorf SM, Marinowitz S, Spatafora JW, Schoch CL (2009) A molecular phylogenetic reappraisal of the Hysteriaceae, Mytiliniaceae and Gloniaceae (Pleosporomycetidae, Dothideomycetes) with key to world species. *Stud Mycol* 64:49–83
- Brearley FQ, Press MC, Scholes JD (2003) Nutrients obtained from leaf litter can improve the growth of dipterocarp seedlings. *New Phytol* 160:101–110
- Brundrett MC (2009) Mycorrhizal associations and other means of nutrition of vascular plants: understanding global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. *Plant Soil* 320:37–77
- Bruns TD, Bidartondo MI, Taylor DL (2002) Host specificity in ectomycorrhizal communities: what do the exceptions tell us? *Integr Comp Biol* 42:352–359
- Buscardo E, Rodríguez-Echeverría S, Martín MP, De Angelis P, Pereirra JS, Freitas H (2010) Impact of wildfire return interval on the ectomycorrhizal resistant propagules communities of a mediterranean open forest. *Fungal Biol* 114:628–636
- Buyck B, Thoen D, Watling R (1996) Ectomycorrhizal fungi in the Congo-Guinea region. *Proc R Soc Edinb* 104B:313–333
- Chalermpongse A (1993) Biodiversity of mycorrhizal fungi in the dipterocarp forests of Thailand. In: Anon. (eds) BIO-REFOR: proceedings of Tsukuba-Workshop, pp 143–153. BIO-REFOR, IUFRO-SPDC, Tsukuba Science City, Japan
- Chen DM, Cairney JW (2002) Investigation of the influence of prescribed burning on ITS profiles of ectomycorrhizal and other soil fungi at three Australian sclerophyll forest sites. *Mycol Res* 106: 532–540
- Corner EJJ (1968) A monograph of *Thelephora*. *Nova Hedw* 27:1–110

- Diédhiou AG, Selosse MA, Galiana A, Diabaté M, Dreyfus B, Bâ AM, De Faria SM, Béna G (2010) Multi-host ectomycorrhizal fungi are predominant in a Guinean tropical rainforest and shared between canopy trees and seedlings. *Environ Microbiol* 12:2219–2232
- Douhan GW, Martin DP, Rizzo DM (2007) Using the putative asexual fungus *Cenococcum geophilum* as a model to test how species concepts influence recombination analyses using sequence data from multiple loci. *Curr Genet* 52:191–201
- Gardes M, Bruns TD (1996) Community structure of ectomycorrhizal fungi in a *Pinus muricata* forest: above-and below-ground views. *Can J Bot* 74:1572–1583
- Girlanda M, Ghignone S, Luppi AM (2002) Diversity of sterile root-associated fungi of two Mediterranean plants. *New Phytol* 155:481–498
- Ishida TA, Nara K, Hogetsu T (2007) Host effects on ectomycorrhizal fungal communities: insight from eight host species in mixed conifer-broadleaf forests. *New Phytol* 174:430–440
- Katoh K, Toh H (2008) Recent developments in the MAFFT multiple sequence alignment program. *Brief Bioinform* 9:286–298
- Lee SS, Patahayah M (2003) Host specificity of dipterocarp ectomycorrhizal fungi. In: Aminah H, Ani S, Sim HC, Krishnapillay B (eds) *Proceedings of the Seventh Round-Table Conference on Dipterocarps*. Asia Pacific Association of Forestry Research Institutions, Kuala Lumpur, Malaysia, 7–10 October 2002, pp 214–217
- Lee SS, Patahayah M, Lapeyrie F (2002) Exotic vs. indigenous ectomycorrhizal fungi for inoculation of dipterocarps. In: Ishii K, Masumori M, Suzuki K (eds) *BIO-REFOR: Proceedings of Tokyo-Workshop*, BIO-REFOR, IUFRO-SPDC, pp 84–87
- LoBuglio KF (1999) *Cenococcum*. In: Cairney JW, Chambers SM (eds) *Ectomycorrhizal fungi: key genera in profile*. Springer, Berlin, pp 187–309
- May TW, Simpson JA (1997) Fungal diversity and ecology in eucalypt ecosystems. In: Williams J, Woinarski J (eds) *Eucalypt ecology: individuals to ecosystems*. Cambridge University Press, Cambridge, pp 246–277
- Panwittayakul C, Srikampol Y (2006) Taxonomy study of family Rubiaceae at Phitsanulok wildlife development and extensive conservation station. Dissertation, Naresuan University (in Thai)
- Peay KG, Kennedy PG, Davies SJ, Tan S, Bruns TD (2010) Potential link between plant and fungal distributions in a dipterocarp rainforest: community and phylogenetic structure of tropical ectomycorrhizal fungi across a plant and soil ecotone. *New Phytol* 185:529–542
- Ramanankierana N, Ducousso M, Rakotoarimanga N, Prin Y, Thioulouse J (2006) Arbuscular mycorrhizas and ectomycorrhizas of *Uapaca bojeri* L (Euphorbiaceae): sporophore diversity, patterns of root colonization, and effects on seedling growth and soil microbial catabolic diversity. *Mycorrhiza* 17: 195–208
- Rinaldi AC, Comadini-O, Kuyper TW (2008) Ectomycorrhizal fungal diversity: separating the wheat from the chaff. *Fung Div* 33:1–45
- Riviere T, Diédhiou AG, Diabate M, Senthilarasu G, Natarajan K, Verbeken A, Buyck B, Dreyfus B, Bena G, Ba AM (2007) Genetic diversity of ectomycorrhizal basidiomycetes from African and Indian tropical forests. *Mycorrhiza* 17:415–428
- Sims K, Watling R, de la Cruz R, Jeffries P (1997) Ectomycorrhizal fungi of the Philippines: a preliminary survey and notes on the geographic biodiversity of the Sclerodermatales. *Biodivers Conserv* 6:45–58
- Sirikantaramas S, Sugioka N, Lee SS, Mohamed LA, Lee HS, Szmidt AE, Yamazaki T (2003) Molecular identification of ectomycorrhizal fungi associated with Dipterocarpaceae. *Tropics* 13:69–77
- Smith ME, Douhan GW, Rizzo DM (2007) Ectomycorrhizal community structure in a xeric *Quercus* woodland based on rDNA sequence analysis of sporocarps and pooled roots. *New Phytol* 174:847–863
- Smith ME, Henkel TW, Aime MC, Fremier AK, Vilgalys R (2011) Ectomycorrhizal fungal diversity and community structure on three co-occurring leguminous canopy tree species in a Neotropical rainforest. *New Phytol* 192:699–712
- Stamatakis A, Hoover P, Rougemont J (2008) A rapid bootstrap algorithm for the RAxML web-servers. *Syst Biol* 57:755–759
- Suvi T, Tedersoo L, Abarenkov K, Gerlach J, Beaver K, Kõljalg U (2010) Mycorrhizal symbionts of *Pisonia grandis* and *P. sechellarum* in Seychelles: identification of mycorrhizal fungi and description of new *Tomentella* species. *Mycologia* 102:522–533
- Taylor AFS (2008) Recent advances in our understanding of fungal ecology. *Coolia* 51:197–212
- Taylor AFS, Alexander IJ (2005) The ectomycorrhizal symbiosis: life in the real world. *Mycologist* 19:102–112
- Tedersoo L, Nara K (2010) General latitudinal gradient of biodiversity is reversed in ectomycorrhizal fungi. *New Phytol* 185:351–354

- Tedersoo L, Suvi T, Larsson E, Kõljalg U (2006) Diversity and community structure of ectomycorrhizal fungi in a wooded meadow. *Mycol Res* 110:734–748
- Tedersoo L, Suvi T, Beaver K, Kõljalg U (2007) Ectomycorrhizal fungi of the Seychelles: diversity patterns and host shifts from the native *Vateriopsis seychellarum* (Dipterocarpaceae) and *Intsia bijuga* (Caesalpiniaceae) to the introduced *Eucalyptus robusta* (Myrtaceae), but not *Pinus caribea* (Pinaceae). *New Phytol* 175:321–333
- Tedersoo L, Jairus T, Horton BM, Abarenkov K, Suvi T, Saar I, Kõljalg U (2008) Strong host preference of ectomycorrhizal fungi in a Tasmanian wet sclerophyll forest as revealed by DNA barcoding and taxon-specific primers. *New Phytol* 180:479–490
- Tedersoo L, May TW, Smith ME (2010a) Ectomycorrhizal lifestyle in fungi: global diversity, distribution, and evolution of phylogenetic lineages. *Mycorrhiza* 20:217–263
- Tedersoo L, Nilsson RH, Abarenkov K, Jairus T, Sadam A, Saar I, Bahram M, Bechem E, Chuyong G, Kõljalg U (2010b) 454 Pyrosequencing and Sanger sequencing of tropical mycorrhizal fungi provide similar results but reveal substantial methodological biases. *New Phytol* 188:291–301
- Tedersoo L, Sadam A, Zambrano M, Valencia R, Bahram M (2010c) Low diversity and high host preference of ectomycorrhizal fungi in Western Amazonia, a neotropical biodiversity hotspot. *ISME J* 4:465–471
- Tedersoo L, Bahram M, Jairus T, Bechem E, Chinoya S, Mpumba R, Leal M, Randrianjohany E, Razafimandimbison S, Sadam A, Naadel T, Kõljalg U (2011) Spatial structure and the effects of host and soil environments on communities of ectomycorrhizal fungi in wooded savannas and rain forests of Continental Africa and Madagascar. *Mol Ecol* 20:3071–3080
- Trappe JM (1962) *Cenococcum graniforme*—its distribution, ecology, mycorrhiza and inherent variation. PhD thesis, University of Washington, Seattle, Washington
- Watling R, Lee SS (1995) Ectomycorrhizal fungi associated with members of the Dipterocarpaceae in Peninsular Malaysia. *J Trop For Sci* 7:657–669
- Watling R, Lee SS (2007) Mycorrhizal mycodiversity in Malaysia. In: Jones EBG, Hyde KD, Vikineswary S (eds) Malaysian fungal diversity. Mushroom Research Centre, University of Malaya and Ministry of Natural Resources and Environment, Malaysia, pp 201–219
- Watling R, Lee SS, Turnbull E (2002) The occurrence and distribution of putative ectomycorrhizal basidiomycetes in a regenerating south-east Asian rainforest. In: Watling R, Frankland JC, Ainsworth AM, Isaac S, Robinson CH (eds) Tropical mycology vol. 1. Macromycetes, CAB International, pp 25–43
- Yuwa-Amornpitak T, Vichitsoonthonkul T, Tanticharoen M, Cheevadhanarak S, Ratchadawong S (2006) Diversity of ectomycorrhizal fungi on Dipterocarpaceae in Thailand. *J Biol Sci* 6:1059–1064



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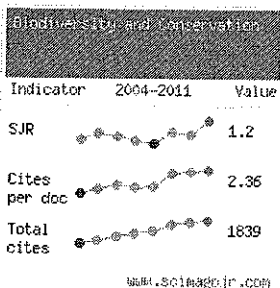
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