Agr. Nat. Resour. 58 (2024) 653–664

AGRICULTURE AND NATURAL RESOURCES

Journal homepage: http://anres.kasetsart.org

Review article

Yeast communities and other microbial components in tropical peat swamp forests

Pannida Khunnamwong[a,b], Savitree Limtong[a,b,c,*]

[a] *Department of Microbiology, Faculty of Science, Kasetsart University, Bangkok 10900, Thailand*

[b] *Biodiversity Center Kasetsart University (BDCKU), Bangkok 10900, Thailand*

[c] *Academy of Science, Royal Society of Thailand, Bangkok 10300, Thailand*

Article Info

Article history:
Received 24 April 2024
Revised 18 August 2024
Accepted 22 August 2024
Available online 30 September 2024

Keywords:
Climate change,
Peatlands,
Peat swamp forest,
Tropic,
Yeast communities

Abstract

Tropical peat swamp forests (PSFs), also known as peatlands, coexist with swamp forests, and form a unique ecosystem that serves as an important global carbon reservoir. Climate change can have major effects on microbial communities in this ecosystem. To understand these effects, it is necessary to know the composition of their microbial diversity. Therefore, this study reviewed many articles related to PSFs and their microbial communities and then analyzed and summarized microbial communities and, specifically, yeast communities. This review article has provided a current list of yeasts found in PSFs. In addition, differences in yeast composition were found in these communities, not among the different types of PSF, but also in PSFs of the same type. These differences could arise, not only from using different investigation techniques, but also from differences in various environmental factors in the PSFs that were studied. This review article should be useful for not only researchers working specifically on climate change effects on microbial communities in the PSFs, but also for researchers working generally on microbial communities in other ecosystems.

* Corresponding author.
E-mail address: fscistl@ku.ac.th (S. Limtong)

https://doi.org/10.34044/j.anres.2024.58.5.12

Introduction

Peatlands are areas with a unique ecosystem characterized by the natural accumulation of partially decayed organic matter from plant biomass under waterlogged, anoxic and acidic conditions (Wieder et al., 2006; Too et al., 2018, 2021). The accumulation of this partially degraded organic matter over long periods leads to the build-up of a thick layer of peat in waterlogged ground (Chimner and Ewel, 2005; Dobrovol'skaya et al., 2014). This ecosystem covers 3% (approximately 4 million km^2) of the earth's surface area in the boreal, temperate, Arctic and tropical zones across many countries (Blodau, 2002; Rezanezhad et al., 2016; Wieder et al., 2016). Most peatlands are in Russia, Canada and the USA (Alaska), accounting for approximately 75% of global peatlands. The remaining peatlands are in Southeast Asia, in other areas of northern Europe and in South America (Rydin and Jeglum, 2006). Tropical peat swamp forests (PSFs), known as peatlands, coexist with swamp forests and are distributed across the tropical zone (United Nations Development Programme (UNDP), 2006). Of the world's PSFs, more than 60% are in South-East Asia, including Indonesia, Malaysia, Papua New Guinea, Brunei, Vietnam, the Philippines and Thailand (Rieley et al., 1996; Page et al., 2006). In Thailand, PSFs are mainly located in the southern region (approximately 63,982 ha), such as in Surat Thani province, Nakhon Si Thammarat province, Narathiwat and Trang province, with the remaining ones in the eastern region, for example, Rayong province (Nuyim, 2003; Jaiboon et al., 2016; Boonmak et al., 2020; Nasanit et al., 2020; Satianpakiranakorn et al., 2020). Peat in PSFs is formed from the incomplete decomposition of the branches, stems, roots and leaves of woody plants under high rainfall and high temperature conditions, whereas peat in temperate and boreal peatlands originates mainly from *Sphagnum* mosses, grasses, sedges and shrubs (Cameron et al., 1989; Nuyim, 2003; Posa et al., 2011; Rieley et al., 2016). Peat domes in PSFs can accumulate to depths of 0.5–20 m (Whitmore, 1975).

Peatlands are important reservoirs of global carbon, storing a considerable amount of carbon (500–1,000 gt) below ground due to the low rate of organic matter degradation; consequently, they play an important role in the global carbon cycle (Nichols and Peteet, 2019; Yu et al., 2021; Le Geay et al., 2024). Despite the climate change situation, this ecosystem is considered the largest natural terrestrial carbon storage repository (Wang et al., 2021; Le Geay et al., 2024). Degradation of this ecosystem has the potential to change greenhouse gas (GHG) emissions (Swails et al., 2024).

It has been claimed that climate change has significant effects on microbial diversity and its function, with this often related to the reduction of carbon storage and the changing GHG level in peatlands (Zhou et al., 2020; Robinson et al., 2023; Zhao et al., 2024). However, as found in various studies, climate change not always leads to a reduction in microbial diversity, as it can also increase microbial diversity (Skogen et al., 2018; Zhou et al., 2020; Nottingham et al., 2022). Therefore, more studies need to be carried out to gain a better understanding of climate change effects on microbial diversity and its function in each ecosystem. Information is required on microbial diversity in the communities of each ecosystem to understand the changing microbial diversity. Therefore, this review article has summarized the diversity in PSFs of microbial communities, especially yeast communities.

Physical and chemical characteristics of peat

Peat usually has an organic matter content of more than 30% and an organic carbon content of more than 18% (Hankaew, 2000; Agus et al., 2011). The physical and chemical characteristics of peat depend on various natural factors, including: vegetation composition and its degree of decomposition; nutrient availability; net primary productivity; accumulation of time; climatic factors, such as water availability and temperature; water table depth; pH; oxygen concentration; and other anthropogenic disturbances (Whitmore, 1975; Nuyim, 2003; Firdaus et al., 2011; Stivrins et al., 2017). Most PSFs are ombrotrophic peatlands, deriving nutrients and water from rainfall and dust (Yule and Gomez, 2009; Ong et al., 2015). In PSFs, plant leaf litter releases tannic acid, resulting in dark brown, acidic water (Yule and Gomez, 2009). This dark brown water reduces light penetration, preventing photosynthesis of organisms in the water which, combined with a slow flow rate and high temperature, results in an anoxic environment. The anoxic environment and toxic compounds released from plant leaf litter inhibit microbial activities, resulting in a reduced rate of decomposition; therefore, the outcome is a high carbon concentration (Yule, 2010; Yule et al., 2016). Consequently, with the combination of the low rate of organic matter decomposition and the low nutrient input leads to PSFs becoming a low nutrient environment (Yule and Gomez, 2009). The amounts of mineral nutrients, especially phosphorous and potassium,

are richer at the outer PSF margins but decrease towards their centers (Whitmore, 1975). The pH values of peat in PSFs are acidic in the range 2.9–4.9 (Yule and Gomez, 2009; Jaiboon et al., 2016; Boonmak et al., 2020; Nasanit et al., 2020).

Plant communities in tropical peat swamp forests

The diverse plant species accommodated in PSFs are different to those in temperate and boreal peatlands that are rich in mosses and herbs (Nuyim, 2003; Posa et al., 2011; Rieley et al., 2016). More than 470 plant species were reported in PSFs in Thailand (Phengkhlai et al., 1991). In Kalimantan, Indonesia, 310 species of plants were recorded (Simbolon and Mirmanto, 1999), while 260 plant species were reported in PSF in Peninsular Malaysia (Latiff, 2005). PSFs can be classified into two types based on their plant communities (Murdiyarso et al., 2019): primary or fertile PSF and secondary PSF (originally a primary PSF but transformed through drought, wildfires or land use conversion). Fires within secondary PSFs are common while fewer such events occur within primary PSFs (Cole et al., 2019). Primary PSFs have a greater diversity of plant species than secondary PSFs (Phengkhlai et al., 1991; Murdiyarso et al., 2019). Plant species in primary PSFs commonly have a well-defined root system (*Aglaonema marantifolium*, *Artocarpus elasticus*, *Bhesa indica*, *Campnosperma coriaceum, Calophyllym sclerophyllum, Dillenia indica*, *Baccaurea bracteata*, *Eugenia claviflora Eugenia longiflora*, *Eleiodoxa conferta*, *Endiandra macrophylla*, *Eugenia kunstleri, Eugenia oblata, Eugenia muelleri*, *Ganua motleyana, Flagellaria indica*, *Korthalsia grandis*, *Licuala paludosa Macaranga pruinosa, Neesia malayana, Sterculia gilva* and *Stemonurus secundiflorus* climbing plants). In contrast, plant communities in secondary PSFs are dominated by *Melaleuca* spp. and grass species (Phengkhlai et al., 1991; Hankaew, 2000; Nuyim, 2003).

The predominant plants reported in the Kuankreng (KK) secondary PSF in Cha-uat district, Nakhon Si Thammarat province, Thailand, were: *Melaleuca cajuputi*, *Cyperus imbricatus*, *Lepironia articulata* and *Typha angustifolia*, while the plant community in the Rayong Botanical Garden (RBG) secondary PSF, Klaeng district, Rayong province, Thailand, is dominated by *Melaleuca quinquenervia*, *Garcinia cowa*, *Calamus deerratus* and *Shorea bracteolata* (Santisuk and Niyomtham, 1985; Kanitjinda et al., 2016).

Microbial communities in tropical peat swamp forests

Microbial communities in peatlands are important, not only because they determine the transformation of organic matter, but also as they affect mineralization and nutrient absorption of plants that consequently affect the productivity and functioning of peatlands (Andersen et al., 2013). However, the knowledge base of microbial communities in peatlands, including PSFs is relatively limited, with the microbial communities in boreal and temperate peatlands having received greater attention (Thormann et al., 2007; Preston et al., 2012; Andersen et al., 2013; Kiheri et al., 2020; Kitson and Bell, 2020; Lamit et al., 2021). A few articles have reported bacterial diversity in PSFs in Malaysia (Jackson et al., 2009; Jackson and Raub, 2010; Roslan et al., 2015), in Thailand (Kanokratana et al., 2011) and in Brunei (Tripathi et al., 2016).

In PSFs in Malaysia, it has been reported that greatest diversity was in the microbial communities dominated by bacterial members of the phyla *Proteobacteria* and *Acidobacteria*; however, no methanogens were detected (Jackson et al., 2009; Jackson and Raub, 2010). In addition, the bacterial diversity and activity decreased in deeper sediments. Archaea, particularly the phylum *Crenarchaeota*, were present below the peat surface and played a role in methane emissions (Jackson et al., 2009; Jackson and Raub, 2010). Bacteria in the genera *Dyella*, *Klebsiella* and *Paraburkholderia* of the phylum *Proteobacteria* were isolated from the North Selangor PSF, Malaysia. The dominant phylum of bacteria in the PSF in Selangor, Malaysia, was the *Proteobacteria* and the most abundant genus was *Rhodoplanes*, which may be involved in nitrogen fixation. The families *Methanomassiliicoccaceae* and *Methylocystaceae* were the most abundant methanogens and methanotrophs, respectively (Too et al., 2018). The prokaryotic community in peat soil samples from three types of forest in Sarawak, Malaysia was recently determined through a meta-16S rRNA gene amplicon analysis using Illumina Miseq. The results revealed that bacteria in the phyla *Acidobacteria*, *Proteobacteria*, *Actinobacteria* and *Firmicutes* covered 80–90% of the total prokaryotic abundance (Dom et al., 2021). *Burkholderia*, which has the ability to produce ligninase, was found in a PSF in the Pekan forest reserve, Malaysia (Roslan et al., 2015). Furthermore, *Paenibacillus tyrfis* and *Burkholderia paludis*, isolated from soil in two PSFs in Malaysia, were proposed as two novel bacterial species with antimicrobial-producing capabilities (Aw et al., 2016; Ong et al., 2016).

In Thailand, bacterial communities in the Sirindhorn (SD) or To Daeng PSF (a primary PSF located in various districts in Narathiwat province, southern Thailand) were dominated by aerobic, facultative and anaerobic microorganisms. *Actinobacteria* and *Protobacteria* (mainly *Alphaproteobacteria*) were the major groups, with minor groups comprising archaea in the order *Methanomicrobiales* and eukaryotic microorganisms (Kanokratana et al., 2011). The acid-resistant purple non-sulfur bacteria *Rhodopseudomonas palustris* and two *Serratia* species were detected in both primary and secondary areas of Kantulee (KT) PSF in Surat Thani province and the KK secondary PSF in Thailand; however, they each had a low population (Nookongbut et al., 2019).

In Indonesia, the effects of drainage and forest fires on the methanotrophic activity and community structure of peat soils in a PSF were studied, with the results revealing that the population of methanotrophs (*Methylomonas* spp.) was not affected (Arai et al., 2014).

Although only one report has been identified regarding actinobacterial diversity in a PSF in Thailand (Kanokratana et al., 2011), namely, the KT PSF, various novel species of actinobacteria have been proposed from strains isolated from peat soil samples, including: *Amycolatopsis acidicola* (Teo et al., 2020); *Amycolatopsis acididurans* (Teo et al., 2021); *Pseudonocardia acidicola* (Klaysubun et al., 2020); *Streptomyces acidicola* (Lipun et al., 2020); and *Streptomyces acididurans* (Chantavorakit et al., 2021). Furthermore, the species identified in the RBG PSF were: *Kitasatospora humi* (Klaysubun et al., 2022a); *Streptomyces humicola* (Klaysubun et al., 2022b); and *Streptomyces silvisoli* and *Streptomyces tropicalis* (Klaysubun et al., 2023).

Only a few articles on PSFs have reported on their fungal diversity. Fungi, including filamentous fungi and yeasts, have been discovered to depths of 2.5 m (Jackson and Raub, 2010; Jaiboon et al., 2016). In the PSF in Central Kalimantan, Indonesia, most fungi were isolated from the upper part (10–20 cm) of the peat; however, at a depth of 2.5 m, some fungi were still detected (Artiningsih et al., 2000). Most were basidiomycetes, such as white-rot fungi in the genera *Coriolopsis*, *Fomes*, *Polyporus* and *Amauroderma* along with brown-rot fungi in the genera *Poria*, *Lentinus* and *Serpula*. Kanti and Sudiana (2019) assessed fungal diversity in four types of tropical peatland land use: early pristine peat swamp forest; un-drained deforested peatlands; drained deforested peatlands; and degraded peatlands under agriculture in Central Kalimantan, Indonesia. They reported observations of 11 genera: *Acremonium*, *Aspergillus*, *Chaetomium*, *Cladosporium*, *Fusarium*, *Paecilomyces*, *Penicillium*, *Pythium*, *Trichoderma*, *Verticellum* and *Verticillium*. Pinnoi et al. (2006) reported finding saprobic fungi isolated from decaying palm material of *Eleiodoxa conferta* in the SD PSF, Thailand. They identified 251 fungal isolates to species level and 176 isolates to the generic level, while 35 isolates could not be identified. The identified taxa were divided into ascomycetes (38%), basidiomycetes (2%) and anamorphic fungi (60%). The most common taxa (higher than 5% of total isolates) were: *Cancellidium applanatum*, *Xylomyces aquaticus*, *Astrosphaeriella* sp. and *Stilbohypoxylon moelleri*. *Phruensis brunneispora*, isolated from the decaying trunk of a palm tree (*Licuala longecalycata*) in the SD PSF, Thailand, was proposed as a novel genus and species (Pinruan et al., 2004). Various strains of fungi in the genera *Aspergillus, Penicillium, Trichoderma* and *Gongronella* were isolated from organic soil in a secondary PSF in Thailand, with some strains showing a high level of ability to inhibit tyrosinase (Dej-adisai et al., 2021). Among the strains with high-level anti-tyrosinase activity, *Aspergillus flavus* SPSF318 demonstrated a high level of activity against tyrosinase, as well as moderate antioxidant and antibacterial activities. *Polyancora globosa* obtained from a PSF in Malaysia was proposed as a novel genus and species of an aeroaquatic fungus (Voglmayr and Yule, 2006).

Methodology for assessment of yeasts in peat and peat soil

Currently, the assessment of yeasts in natural habitats is carried out using both culture-dependent and culture-independent techniques. The culture-dependent technique is based on the isolation of yeasts using an appropriate culture medium and appropriate conditions. Subsequently, pure cultures are identified based on their molecular and phenotypic characteristics. On the other hand, in the culture-independent technique, total genomic deoxyribonucleic acid (DNA) is extracted directly from the samples and, using various techniques, is subjected to polymerase chain reaction (PCR) amplification and separation to identify a single microorganism. These techniques include denaturing gradient gel electrophoresis, temperature gradient gel electrophoresis, automated ribosomal DNA restriction analysis, restriction fragment length polymorphism, ribosomal intergenic spacer analysis and automated ribosomal intergenic spacer analysis, which may be combined with DNA sequence-based identification (Limtong and Nasanit, 2017; Mašínová et al., 2017; Yurkov, 2017). However, yeast identification from environmental sequences is not yet accurate due to incomplete reference databases, insufficient taxonomic resolution of the

DNA markers that are used and computational errors that occur in the classification of sequences (Yurkov, 2017).

Thormann et al. (2007) used a culture-dependent technique to assess the diversity of yeast in peat from peatlands. Peat samples were aseptically collected from peatlands in Saskatchewan, Canada (at depths of 5 cm and 25 cm), and West Siberia, Russia (at depths of 0–20 cm). Yeast isolation was carried out based on direct-plating techniques (Table 1) using agar medium from the peat sample after surface sterilization in hydrogen peroxide, with the sample washed with sterilized, distilled water three times to eliminate surface contaminants. Yeast strains were identified using the Yeast Identification Test Panel (YT Microplate) of Biolog (Biolog; CA, USA), based on biochemical characteristics (oxidation and assimilation tests of carbon sources). Yeast identities were confirmed with published information on the morphological and physiological characteristics for each species. Yeast taxonomy followed the 2007 Index Fungorum (http://www.indexfungorum.org/).

The culture-dependent approach, with an enrichment technique for yeast isolation and a molecular technique for yeast identification, was used to investigate yeasts in the SD PSF, southern Thailand (Jaiboon et al., 2016), as shown in Fig. 1. Yeasts were isolated based on the enrichment technique using two enrichment media comprising yeast extract malt extract broth for all yeast isolation and xylose-yeast nitrogen base broth for xylose-assimilating yeast isolation (Table 1). Yeasts were identified based on molecular taxonomy using analysis of the sequence similarity of the D1/D2 domains of the large subunit (LSU) rRNA gene.

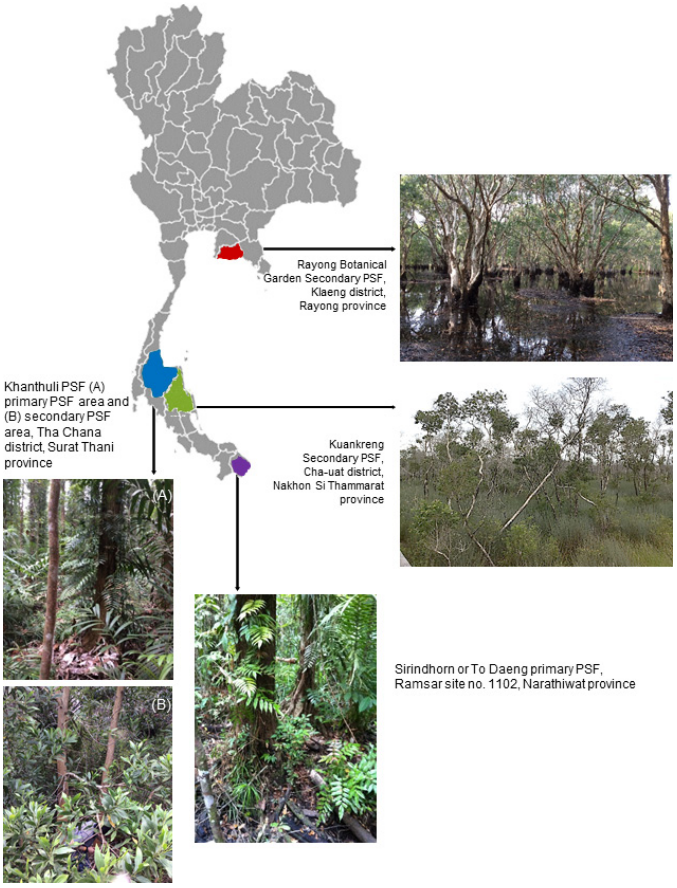

Fig. 1 Tropical peat swamp forests (PSFs) in Thailand in which yeast communities were investigated and summarized in this review

Table 1 Techniques used for isolation of yeasts from peat and peat soil

Technique	Culture medium	Incubation conditions	Yeast colony purification	References
Direct-plating technique	1) Potato dextrose agar (PDA) supplemented with oxytetracycline 2) PDA supplemented with oxytetracycline and additive* (50% benomyl) 3) PDA supplemented with oxytetracycline and additive* [solution containing 50% benomyl, dichloran (2,6-dichloro-4-nitroaniline), phenol in ethanol] *For selectively isolated basidiomycetes	22°C in the dark, examined daily for the first week, every other day for the following 4 wk, and every 5 d for the following 3 mth	Cross-streaking on malt extract agar	Thormann et al. (2007)
Enrichment technique	1) Yeast extract-malt extract (YM) broth 2) Xylose-yeast nitrogen base broth Both media supplemented with 0.025% sodium propionate (to inhibit filamentous fungal growth) and 0.02% chloramphenicol (to inhibit bacterial growth)	30°C on a rotary shaker for 2 d	Cross-streaking on YM agar	Jaiboon et al. (2016); Boonmak et al. (2020); Satianpakiranakorn et al. (2020)
Dilution plate technique	YM agar supplemented with 0.025% sodium propionate and 0.02% chloramphenicol	25°C, 3–7 d	Cross-streaking on a YM agar	Boonmak et al. (2020); Satianpakiranakorn et al. (2020)

The criteria described by Kurtzman and Robnett (1998) were used to identify ascomycetous yeasts, in which strains with 0–3 nucleotide differences were conspecific or sister species, and strains showing >6 nucleotide substitutions were different species. The criteria described by Fell et al. (2000) were used for basidiomycetous yeasts, in which strains differing by ≥2 nucleotide substitutions in the D1/D2 domains represented different taxa. The phylogenetic analysis of the D1/D2 domains of the LSU rRNA gene was used to confirm the identification of yeast species. The enrichment technique using YM broth, supplemented with chloramphenicol and sodium propionate, was also applied to isolate yeasts from peat samples collected from the KT PSF in both the primary and secondary areas, as shown in Fig. 1 (Boonmak et al., 2020), and from the KK and RBG secondary PSFs, also shown in Fig. 1 (Satianpakiranakorn et al., 2020). The enrichment technique appeared to support the growth of ascomycetous yeasts better than was the case with basidiomycetous yeasts (Limtong et al., 2014). Yeasts from peat or peat soil samples collected from these three PSFs were assessed beginning with yeast isolation undertaken using a dilution plate technique, as shown in Table 1 (Boonmak et al., 2020; Satianpakiranakorn et al., 2020). Yeast identification was based on sequence similarity and phylogenetic analysis of the D1/D2 domains of the LSU rRNA gene sequence.

The culture-independent technique was used to assess yeasts in peat and peat soil samples collected from both the primary and secondary PSF areas in the KT PSF and from the KK secondary PSF by Nasanit et al. (2020), based on isolating DNA from the peat or peat soil samples. The D1/D2 domains of the LSU rRNA gene were amplified based on PCR using the primers NL1 and NL4 (Kurtzman and Robnett, 1998) and subsequently were purified. Cloning vectors were used to construct the recombinant plasmids of the purified PCR products obtained from each sample and transformed into *E. coli* competent cells. The recombinant clones of each clone library were screened based on colony PCR, with the PCR products then being restriction analyzed using digestion with three restriction enzymes: *Hae*III, *Hin*fI and *Cfo*I. The restriction fragment patterns were visualized using an agarose gel and clustered. Next, representatives of the PCR products from each pattern of each clone library were purified and sequenced using the NL1 and NL4 primers. Yeasts were identified based on their sequence similarity in the D1/D2 domains of the LSU rRNA gene using the criteria described by Kurtzman and Robnett (1998) and Fell et al. (2000). In addition, the phylogenetic tree was considered for yeast identification as the LSUs in some yeast taxa were variable (Fell et al., 2000).

Yeast communities in tropical peat swamp forests

Only a few of the articles on yeast diversity in peat or peat soil from peatlands have reported on yeast communities in peatlands in Canada and Russia, and in PSFs in Thailand. Our research group is only the group that report on the diversity of yeasts in PSFs in Thailand. Jaiboon et al. (2016) carried out an assessment of yeasts in peat in the SD PSF, the largest primary PSF in southern Thailand. A culture-dependent approach was used, based on an enrichment technique and molecular identification, based on analysis of the D1/D2 domains of the LSU rRNA gene sequence similarity and phylogenetic analysis. In total, 65 yeast strains were isolated from 15 peat samples and identified as 10 known yeast species comprising five species each in the phyla *Ascomycota* and *Basidiomycota*, and one unidentified basidiomycetous yeast species (Table 2). The dominant species was *Rhodotorula mucilaginosa*, followed by *Schwanniomyces polymorphus* var. *africanus*, *Cyberlindnera subsufficiens* and *Debaryomyces fabryi*. In addition, one novel yeast species, *Nakazawaea todaengensis*, was discovered and proposed (Polburee et al., 2017).

Boonmak et al. (2020) used culture-dependent techniques to evaluate yeast diversity in peat and peat soils from the primary and secondary PSF areas of the KT PSF. They used the dilution plate and enrichment techniques for yeast isolation, with identification conducted by analyzing the sequence similarity of the D1/D2 domains of the LSU rRNA gene alone or combined with internal transcribed spacer regions and subsequently confirmed based on phylogenetic analysis of the D1/D2 domains' sequence. Yeast strains from the primary PSF area of the KT PSF consisted of nine known species and two novel species *Candida kantuleensis* (Nitiyon et al., 2018) and *Saturnispora kantuleensis* (Khunnamwong and Limtong, 2018) in the phylum *Ascomycota* and six species in the phylum *Basidiomycota* (Table 2). The secondary PSF area of the KT PSF produced seven known yeast species in the phylum *Ascomycota*, and four known species and one novel species (*Cryptotrichosporon siamense*) in the phylum *Basidiomycota* (Kaewwichian et al., 2018). The most prevalent yeasts in the primary PSF area were *C. kantuleensis*, *Cyb. subsufficiens* and *Geotrichum candidus*, while the common yeast species were in the phylum *Ascomycota*, with a lower member in the phylum *Basidiomycota*. *Saitozyma podzolica* and *Papiliotrema laurentii* were the most frequently found yeast species in the secondary PSF area. The following species were detected in both primary and secondary PSF areas: *Cyb. subsufficiens*, *G. candidus* and *R. mucilaginosa*.

Table 2 Summary of known and novel yeast species in peats or peat soils from tropical peat swamp forests (PSFs) in Thailand assessed using culture-dependent and culture-independent methods

Yeast taxon	SD primary PSF[1]	KT primary PSF[2,3]	KT secondary PSF[2,3]	KK secondary PSF[2,4]	RBG secondary PSF[4]
Phylum *Ascomycota*					
Candida albicans			E		
Candida kantuleensis[5]		E	E		
Candida maltose			E		
Candida tropicalis			E		
Candida xiaguanensis					D
Cyberlindnera subsufficiens	E	D, E	E	E	
Debaryomyces fabryi	E				
Geotrichum candidum		D, E, I	D, E, I		
Hannaella phetchabunensis					D
Hanseniaspora lindneri				E	
Hanseniaspora thailandica (invalid)		E			
Kurtzmaniella natalensis		D			
Kurtzmaniella quercitrusa		D, E			
Metschnikowia chrysomelidarum		D			
Metschnikowia koreensis		E			E
Meyerozyma guilliermondii	E				
Nakazawaea todaengensis[6]	E				
Pichia kudriavzevii			E		
Pichia pseudolambica			E	E	
Saccharomyces cerevisiae		I	I	I	
Saturnispora diversa	E				
Saturnispora kantuleensis[7]		D, E			
Scheffersomyces spartinae				D, E	
Schwanniomyces polymorphus var. africanus	E				
Schwanniomyces vanrijiae var. vanrijiae		E			
Schwanniomyces polymorphus var. polymorphus				D	D, E
Schwanniomyces vanrijiae var. yarrowii					E
Starmerella kuoi					D
Wickerhamiella azyma					E
Wickerhamomyces anomalus				D	
Yamadazyma jaroonii		D			
Phylum *Basidiomycota*					
Apiotrichum mycotoxinivorans				D	
Cryptotrichosporon siamense[8]			D		
Curvibasidium pallidicorallinum		E			
Cutaneotrichosporon mucoides	E				
Hannaella pagnoccae					D
Hannaella taiwanensis	E				
Hanseniaspora lindneri				E	
Malassezia restricta				I	
Papiliotrema flavescens	E	E			
Papiliotrema laurentii	E		ED	ED	ED
Papiliotrema ruineniae		D			
Piskurozyma taiwanensis					E, D
Rhodosporidiobolus poonsookiae					D
Rhodosporidiobolus ruineniae		D			E
Rhodosporidiobolus nylandii				E	
Rhodotorula mucilaginosa	E	ED	D		
Rhodotorula taiwanensis				D, E	
Rhodotorula toruloides				E	
Saitozyma flava		D			
Saitozyma podzolica			D	D	D
Solicoccozyma keelungensis				I	
Sporobolomyces blumeae				E	
Sterigmatomyces halophilus			I	I	

[1]Jaiboon et al. (2016); [2]Nasanit et al. (2020); [3]Boonmak et al. (2020); [4]Satianpakiranakorn et al. (2020); [5]Nitiyon et al. (2018); [6]Polburee et al. (2017); [7]Khunnamwong and Limtong (2018); [8]Kaewwichian et al. (2018)

SD = Sirindhorn; KT = Khanthuli; KK = Kuankreng; RBG = Rayong Botanical Garden;

D = dilution plate technique; E = enrichment technique; I: culture-independent technique

Yeast communities in the peat and peat soils collected from the KK secondary PSF were investigated using a culture-dependent approach and two isolation techniques (dilution plate and enrichment). Identification of the studied yeast strains was based on similarity analysis of the D1/D2 domains of the LSU rRNA gene sequence (Satianpakiranakorn et al., 2020). Of the yeast strains obtained, 63% were derived from the enrichment isolation technique and 37% from the dilution plate technique. They were identified as five species in the phylum *Ascomycota* and nine species in the phylum *Basidiomycota* (Table 2). Based on these results, some species could be detected only using the dilution plate technique or the enrichment technique, whereas other species (*Sch. spartinae*, *P. laurentii* and *R. taiwanensis*) were detected using both techniques. In the same study (Satianpakiranakorn et al., 2020), yeast strains isolated from the peat or peat soil samples collected from the RBG secondary PSF were assessed using the same two isolation techniques (dilution plate and enrichment). Nearly the same number of yeasts were obtained using the dilution plate technique (17 strains) as for the enrichment technique (15 strains) and were linked to seven species in the phylum *Ascomycota* and six species in the phylum *Basidiomycota*. The number of basidiomycetous yeast strains (56%) was slightly higher than that of ascomycetous yeasts (44%).

Nasanit et al. (2020) used a culture-independent technique or environmental DNA (e-DNA) technique to assess yeast communities in PSFs in Thailand the KT PSF in both the primary and secondary PSF areas and the KK secondary peat swamp forest (PSF). Their study extracted DNA from peat or peat soil samples, with the clone libraries of each sample separately constructed using PCR products of the D1/D2 domains of the LSU rRNA gene. About 53% of yeast-related operational taxonomic units (OTUs) were obtained. The yeast-related OTUs obtained from the primary PSF area of the KT PSF were identified as only two yeast species in the phylum *Ascomycota* and one species in the phylum *Basidiomycota* (Table 2), while four yeast species in the phylum *Ascomycota* and one species in the phylum *Basidiomycota* were detected in the KT PSF's secondary PSF area. In both the primary and secondary PSF areas, most of the yeast-related OTUs detected were in the phylum *Ascomycota*, with the dominant species being *G. candidus*. In the KK primary PSF area, one species in the phylum *Ascomycota* and three species in the phylum *Basidiomycota* were reported, whereas most yeast-related OTUs found in the KK secondary PSF area belonged to the phylum *Basidiomycota*, with *Solicoccozyma keelungensis* the dominant species. *Saccharomyces cerevisiae* was the only species common to all areas.

The results of these investigations, as shown in Table 2, indicated that some yeast species in the PSFs appeared to occur frequently: *Cys. subsufficiens*, *S. cerevisiae*, *P. laurentii* and *R. mucilaginosa*. In contrast, it was only in the secondary PSFs that *Sai. podzolica* was detected. Some yeast species (*S. cerevisiae* and *Ste. halophilus*) could be detected only using the culture-independent technique. In addition, both yeast strains in the phyla *Ascomycota* and *Basidiomycota* were found similar proportions. However, this finding was drawn from only a few investigations, with more studies needed to reach a reliable conclusion.

These investigations of yeast communities in four PSFs in Thailand revealed that the yeast communities differed both in the same and different types of PSF (Table 2). Differences in yeast communities between the two primary PSFs and among the secondary PSFs could have resulted from using different investigation techniques (Jaiboon et al., 2016; Boonmak et al., 2020; Nasanit et al., 2020; Satianpakiranakorn et al., 2020; Thormann et al., 2007). In addition, differences in yeast communities could be found when comparing the same type of PSF, even when using the same isolation technique from the culture-dependent approach. This was apparent in the comparison of the yeast communities of the three secondary PSFs, namely, KT, KK, and BRG PSFs that were in different locations, with 12, 10 and 12 yeast species, respectively being detected. Of these species, only two (*P. laurentii* and *Sai. podzolica*) were identified in all three secondary PSFs, whereas the other 28 species were detected only in one PSF (Kaewwichian et al., 2018; Boonmak et al., 2020; Satianpakiranakorn et al., 2020). These differences could have resulted from variations in environmental factors as reported in other microbial communities and plant communities (Lamit et al., 2021); physical and chemical characteristics of the investigated peat or peat soil (Preston et al., 2012); depth of the sample (Thormann et al., 2007); and depth of the water table (Kitson and Bell, 2020; Lamit et al., 2021). However, further in-depth studies should be conducted on the factors affecting yeast communities.

Conclusion

Currently, relatively little is known about microbial communities in PSFs, especially on yeast, as most of the research has been focused on bacteria, actinobacteria and fungi. Yeast communities in PSFs have been studied mainly in Thailand. These studies were carried out in four PSFs in southern and eastern Thailand. Each PSF contained a primary PSF type or a secondary PSF type or both primary and secondary PSF types. Different yeast communities were revealed in all the investigated PSFs. These differences could have resulted from using different investigation techniques or from differences in the various environmental factors in the investigated PSFs, or from both. Therefore, further studies on yeast communities in any ecosystem in one period of time should apply multiple investigation techniques to determine the composition of these communities. As yeast communities in the PSF ecosystem have received less attention, more investigations should be conducted on yeast communities in these ecosystems. In addition, the role of yeasts and climate change effects on yeast communities in PSFs should be determined.

Conflict of Interest

The authors declare that there are no conflicts of interest.

References

Agus, F., Hairiah, K., Mulyani, A. 2011. Measuring Carbon Stock in Peat Soils: Practical Guidelines. World Agroforestry Centre (ICRAF). Bogor, Indonesia.

Andersen, R., Chapman, S.J., Artz, R.R.E. 2013. Microbial communities in natural and disturbed peatlands: A review. Soil Biol. Biochem. 57: 979–994. doi.org/10.1016/j.soilbio.2012.10.003

Arai, H., Hadi, A., Darung, U., Limin, S.H., Hatano, R., Inubushi, K. 2014. A methanotrophic community in a tropical peatland is unaffected by drainage and forest fires in a tropical peat soil. Soil Sci. Plant Nutr. 60: 577–585. doi.org/10.1080/00380768.2014.922034

Artiningsih, T., Tuah, S.J., Mirmanto, E., Osaki, M. 2000. Survey of peat soil in Sebangau-Kahayan Water Catchment, central Kalimantan for laccase producing fungi and their organic decomposing ability. In: Proceedings of the International Symposium on Tropical Peatlands. Bogor, Indonesia, pp. 61–67.

Aw, Y.K., Ong, K.S., Lee, L.H., Cheow, Y.L., Yule, C.M., Lee, S.M. 2016. Newly isolated *Paenibacillus tyrfis* sp. nov., from Malaysian tropical peat swamp soil with broad spectrum antimicrobial activity. Front. Microbiol. 7: 219. doi.org/10.3389/fmicb.2016.00219

Blodau, C. 2002. Carbon cycling in peatlands – A review of processes and controls. Environ. Rev. 10: 111–134. doi.org/10.1139/a02-004

Boonmak, C., Khunnamwong, P., Limtong, S. 2020. Yeast communities of primary and secondary peat swamp forests in southern Thailand. Antonie van Leeuwenhoek 113: 55–69. doi.org/10.1007/s10482-019-01317-0

Cameron, C.C., Esterle, J.S., Palmer, C.A. 1989. The geology, botany and chemistry of selected peat-forming environments from temperate and tropical latitudes. Int. J. Coal Geol. 12: 105–156. doi.org/10.1016/0166-5162(89)90049-9

Chantavorakit, T., Klaysubun, C., Duangmal, K. 2021. *Streptomyces acididurans* sp. nov., isolated from peat swamp forest soil. Int. J. Syst. Evol. Microbiol. 71: 004849. doi.org/10.1099/ijsem.0.004849

Chimner, R.A., Ewel, K.C. 2005. A tropical freshwater wetland: II. Production, decomposition, and peat formation. Wetl. Ecol. Manag. 13: 671–684. oi.org/10.1007/s11273-005-0965-9

Cole, L.E., Bhagwat, S.A., Willis, K.J. 2019. Fire in the swamp forest: Palaeoecological insights into natural and human-induced burning in intact tropical peatlands. Front. For. Glob. Change. 2: 1–15. doi.org/10.3389/ffgc.2019.00048

Dej-Adisai, S., Basow, N., Wattanapiromsakul, C., Nuankaew, W., Kang, T.H. 2021. Effect of isolated soil fungi from Sirindhorn Peat Swamp Forest Narathiwat province, Thailand on tyrosinase enzyme and melanin content. Chiang Mai J. Sci. 48: 27–41.

Dobrovol'skaya, T.G., Golovchenko, A.V., Zvyagintsev, D.G. 2014. Analysis of ecological factors limiting the destruction of high-moor peat. Eurasian Soil Sci. 47: 182–193. doi.org/10.1134/S106422931403003X

Dom, S.P., Ikenaga, M., Lau, S.Y.L., et al. 2021. Linking prokaryotic community composition to carbon biogeochemical cycling across a tropical peat dome in Sarawak, Malaysia. Sci. Rep. 11: 6416. doi.org/10.1038/s41598-021-81865-6

Fell, J.W., Boekhout, T., Fonseca, A., Scorzetti, G., Statzell-Tallman, A. 2000. Biodiversity and systematics of basidiomycetous yeasts as determined by large-subunit rDNA D1/D2 domain sequence analysis. Int. J. Syst. Evol. Microbiol. 50: 1351–1371. doi.org/10.1099/00207713-50-3-1351

Firdaus, M.S., Gandaseca, S., Ahmed, O.H. 2011. Effect of drainage and land clearing on selected peat soil physical properties of secondary peat swamp forest. Int. J. Phys. Sci. 6: 5462–5466.

Hankaew, M.C. 2000. Successional trend of peat swamp forests at Phru Toh Daeng and Phru Kuan Kreng, Southern Thailand. Ph.D. thesis, Graduate School, Kasetsart University. Bangkok, Thailand.

Jackson, C.R., Raub, S. 2010. The microbial ecology of peat swamp forests. In: Veress, B., Szigethy, J. (Eds.). Horizons in Earth Science Research, Vol. 2. Nova Science Publishers Inc. New York, NY, USA, pp.165–180.

Jackson, C.R., Liew, K.C., Yule, C.M. 2009. Structural and functional changes with depth in microbial communities in a tropical Malaysian peat swamp forest. Microb. Ecol. 57: 402–412. doi.org/10.1007/s00248-008-9409-4

Jaiboon, K., Lertwattanasakul, N., Limtong, P., Limtong, S. 2016. Yeasts from peat in a tropical peat swamp forest in Thailand and their ability to produce ethanol, indole-3-acetic acid and extracellular enzymes. Mycol. Prog. 15: 755–770. doi.org/10.1007/s11557-016-1205-9

Kaewwichian, R., Khunnamwong, P., Jindamorakot, S., Lertwattanasakul, N., Limtong, S. 2018. *Cryptotrichosporon siamense* sp. nov., a ballistoconidium-forming yeast species in Trichosporonales isolated from natural habitats in Thailand. Int. J. Syst. Evol. Microbiol. 68: 2473–2477. doi.org/10.1099/ijsem.0.002858

Kanitjinda, N., Phuangcharoen, W., Suwanmanee, A., et al. 2016. Rayong Botanical Garden "Wetland 1000 year old Melaleuca forest. Nature and Environment. 5: 4–14. [in Thai]

Kanokratana, P., Uengwetwanit, T., Rattanachomsri, U., et al. 2011. Insights into the phylogeny and metabolic potential of a primary tropical peat swamp forest microbial community by metagenomic analysis. Microb. Ecol. 61: 518–528. doi.org/10.1007/s00248-010-9766-7

Kanti, A., Sudiana, I.M. 2019. Fungal diversity and its functions in tropical peatlands as plant growth promoting microorganism or associated with green house emission. IOP Conf. Ser. Earth Environ. Sci. 308: 012073. doi: 10.1088/1755-1315/308/1/012073

Khunnamwong, P., Limtong, S. 2018. *Saturnispora kantuleensis* f.a., sp. nov., a novel yeast species isolated from peat in a tropical peat swamp forest in Thailand. Int. J. Syst. Evol. Microbiol. 68: 1160–1164. doi.org/10.1099/ijsem.0.002641

Kiheri, H., Velmala, S., Pennanen, T., et al. 2020. Fungal colonization patterns and enzymatic activities of peatland ericaceous plants following long-term nutrient addition. Soil Biol. Biochem. 147: 107833. doi.org/10.1016/j.soilbio.2020.107833

Kitson, E., Bell, N.G. 2020. The response of microbial communities to peatland drainage and rewetting: a review. Front. Microbiol. 11: 582812. doi.org/10.3389/fmicb.2020.582812

Klaysubun, C., Butdee, W., Suriyachadkun, C., Igarashi, Y., Duangmal, K. 2023. *Streptomyces silvisoli* sp. nov., a polyene producer, and *Streptomyces tropicalis* sp. nov., two novel actinobacterial species from peat swamp forests in Thailand. Int. J. Syst. Evol. Microbiol. 73: 006063. doi.org/10.1099/ijsem.0.006063

Klaysubun, C., Srisuk, N., Duangmal, K. 2022a. *Kitasatospora humi* sp. nov., isolated from a tropical peat swamp forest soil, and proposal for the reclassification of *Kitasatospora psammotica* as a later heterotypic synonym of *Kitasatospora aureofaciens*. Int. J. Syst. Evol. Microbiol. 72: 005356. doi.org/10.1099/ijsem.0.005356

Klaysubun, C., Srisuk, N., Duangmal, K. 2022b. *Streptomyces humicola* sp. nov., a novel actinobacterium isolated from peat swamp forest soil in Thailand. Int. J. Syst. Evol. Microbiol. 72: 005665. doi.org/10.1099/ijsem.0.005665

Klaysubun, C., Lipun, K., Duangmal, K. 2020. *Pseudonocardia acidicola* sp. nov., a novel actinomycete isolated from peat swamp forest soil. Int. J. Syst. Evol. Microbiol. 70: 5648–5653. doi.org/10.1099/ijsem.0.004459

Kurtzman, C.P., Robnett, C.J. 1998. Identification and phylogeny of ascomycetous yeasts from analysis of nuclear large subunit (26S) ribosomal DNA partial sequences. Antonie van Leeuwenhoek 73: 331–371. doi.org/10.1023/A:1001761008817

Lamit, L.J., Romanowicz, K.J., Potvin, L.R. et al. 2021. Peatland microbial community responses to plant functional group and drought are depth-dependent. Mol. Ecol. 30: 5119–5136. doi.org/10.1111/mec.16125

Latiff, A. 2005. An overview of the significant findings of the biodiversity expedition to the peat swamp forest of Sungai Bebar, Pahang. In: Latiff, A., Hamzah, K.A., Ahmad, N., Said, M.N.M., Toh, A.N., Gill, S.K. (Eds.). Biodiversity Expedition Sungai Bebar, Pekan, Pahang: Summary Findings. Peat Swamp Forest Project, UNDP/GEF Funded, in collaboration with the Pahang Forestry Department and University Kebangsaan, Selangor, Malaysia. pp. 3–7.

Le Geay, M., Lauga, B., Walcker, R., Jassey, V.E. 2024. A meta-analysis of peatland microbial diversity and function responses to climate change. Soil Biol. Biochem. 189: 109287. doi.org/10.1016/j.soilbio.2023.109287

Limtong, S., Kaewwichian, R., Yongmanitchai, W., Kawasaki, H. 2014. Diversity of culturable yeasts in phylloplane of sugarcane in Thailand and their capability to produce indole-3-acetic acid. World J. Microbiol. Biotechnol. 30: 1785–1796. doi.org/10.1007/s11274-014-1602-7

Limtong, S., Nasanit, R. 2017. Phylloplane yeasts in tropical climates. In: Buzzini, P., Lachance, M.A., Yurkov, A. (Eds.). Yeasts in Natural Ecosystems: Diversity. Springer. Cham, Switzerland, pp. 199–223.

Lipun, K., Chantavorakit, T., Mingma, R., Duangmal, K. 2020. *Streptomyces acidicola* sp. nov., isolated from a peat swamp forest in Thailand. J. Antibiot. 73: 435–440. doi.org/10.1038/s41429-020-0294-5

Murdiyarso, D., Saragi-Sasmito, M.F., Rustini, A. 2019. Greenhouse gas emissions in restored secondary tropical peat swamp forests. Mitig. Adapt. Strateg. Glob. Change. 24: 507–520. doi.org/10.1007/s11027-017-9776-6

Nasanit, R., Imklin, N., Limtong, S. 2020. Assessment of yeasts in tropical peat swamp forests in Thailand. Mycol. Prog. 19: 1559–1573. doi.org/10.1007/s11557-020-01646-9

Nichols, J.E., Peteet, D.M. 2019. Rapid expansion of northern peatlands and doubled estimate of carbon storage. Nat. Geosci. 12: 917–921. doi.org/10.1038/s41561-019-0454-z

Nookongbut, P., Kantachote, D., Khuong, N.Q., Sukhoom, A., Tantirungkij, M., Limtong, S., 2019. Selection of acid-resistant purple nonsulfur bacteria from peat swamp forests to apply as biofertilizers and biocontrol agents. J. Soil Sci. Plant Nutr. 19: 488–500. doi.org/10.1007/s42729-019-00044-9

Nottingham, A.T., Scott, J.J., Saltonstall, K., Broders, K., Montero-Sanchez, M., Püspök, J., Bååth, E., Meir, P. 2022. Microbial diversity declines in warmed tropical soil and respiration rise exceed predictions as communities adapt. Nat. Microbiol. 7: 1650–1660. doi.org/10.1038/s41564-022-01200-1

Nuyim, T. 2003. Guideline on Peat Swamp Forests Rehabilitation and Planting in Thailand. Percetakan Warisan Sdn. Kuala Lumpur, Malaysia.

Ong, C.S., Juan, J.C., Yule, C.M. 2015. Litterfall production and chemistry of *Koompassia malaccensis* and *Shorea uliginosa* in a tropical peat swamp forest: Plant nutrient regulation and climate relationships. Trees 29: 527–537. doi.org/10.1007/s00468-014-1130-y

Ong, K.S., Aw, Y.K., Lee, L.H., Yule, C.M., Cheow, Y.L., Lee, S.M. 2016. *Burkholderia paludis* sp. nov., an antibiotic-siderophore producing novel *Burkholderia cepacia* complex species, isolated from Malaysian tropical peat swamp soil. Front. Microbiol. 7: 2046. doi.org/10.3389/fmicb.2016.02046

Page, S.E., Rieley, J.O., Wüst, R. 2006. Lowland tropical peatlands of Southeast Asia. In: Martini, I.P., Martínez-Cortizas, A., Chesworth, W. (Eds.). Developments in Earth Surface Processes. Elsevier. Amsterdam, the Netherlands, pp. 145–172.

Phengkhlai, C., Niyomtham, C., Uejirakarn, W. 1991. Peat Swamp Forest Plant Species of Narathiwat, Phikulthong Study and Development Center, Royal Initiative Project, Narathiwat. So Somboon Publishing. Bangkok, Thailand. [in Thai]

Pinnoi, A., Lumyong, S., Hyde, K.D., Jones, E.G. 2006. Biodiversity of fungi on the palm *Eleiodoxa conferta* in Sirindhorn Peat Swamp Forest, Narathiwat, Thailand. Fungal Divers. 22: 205–218.

Pinruan, U., Sakayaroj, J., Jones, E.G., Hyde, K.D. 2004. Aquatic fungi from peat swamp palms: *Phruensis brunneispora* gen. et sp. nov. and its hyphomycete anamorph. Mycologia. 96: 1163–1170.

Polburee, P., Lertwattanasakul, N., Limtong, P., Groenewald, M., Limtong, S. 2017. *Nakazawaea todaengensis* f.a., sp. nov., a novel yeast isolated from a peat swamp forest in Thailand. Int. J. Syst. Evol. Microbiol. 67: 2377–2382. doi.org/10.1099/ijsem.0.001961

Posa, M.R.C., Wijedasa, L.S., Corlett, R.T. 2011. Biodiversity and conservation of tropical peat swamp forests. Biosci. 61: 49–57. doi.org/10.1525/bio.2011.61.1.10

Preston, M.D., Smemo, K.A., McLaughlin, J.W., Basiliko, N. 2012. Peatland microbial communities and decomposition processes in the James Bay Lowlands, Canada. Front. Microbiol. 3: 19875. doi.org/10.3389/fmicb.2012.00070

Rezanezhad, F., Price, J.S., Quinton, W.L., Lennartz, B., Milojevic, T., Van Cappellen, P. 2016. Structure of peat soils and implications for water storage, flow and solute transport: A review update for geochemists. Chem. Geol. 429: 75–84. doi.org/10.1016/j.chemgeo.2016.03.010

Rieley, J., Page, S. 2016. Tropical peatland of the world. In: Osaki, M., Tsuji, N. (Eds.). Tropical Peatland Ecosystems. Springer. Tokyo, Japan, pp. 3–32.

Rieley, J.O., Ahmad-Shah, A.A., Brady, M.A. 1996. The extent and nature of tropical peat swamps. In: Maltby, E., Immirzi, C.P., Safford, R.J. (Eds.). Tropical Peatlands of Southeast Asia. International Union for Conservation of Nature. Gland, Switzerland, pp. 17–53.

Robinson, C.H., Ritson, J.P., Alderson, D.M. et al. 2023. Aspects of microbial communities in peatland carbon cycling under changing climate and land use pressures. Mires Peat. 29: 2.

Roslan, M.A.M., Amirudin, N.A., Abidin, Z.A.Z., Omar, S.M. 2015. Isolation of bacteria from the acidic peat swamp forest soil and their lignin degradation potential. J. Teknol. 77: 77–81.

Rydin, H., Jeglum, J. 2006. The Biology of Peatlands. Oxford University Press. Oxford, UK.

Santisuk, T., Niyomtham, C. 1985. Peat Swamp Forests in Thailand and Problem of Conservation. Siam Society. Bangkok, Thailand. [in Thai]

Skogen, K., Helland, H., Kaltenborn, B. 2018. Concern about climate change, biodiversity loss, habitat degradation and landscape change: embedded in different packages of environmental concern? J. Nat. Conserv. 44: 12–20. doi.org/10.1016/j.jnc.2018.06.001

Simbolon, H., Marmanto, E. 1999. Checklist of plant species in the peat swamp forest of Central Kalimantan, Indonesia. In: Proceedings of the International Symposium on Tropical Peatlands. Bogor, Indonesia, pp. 179–190.

Stivrins, N., Ozoloa, I., Galka, M., et al. 2017. Drivers of peat accumulation rate in a raised bog: impact of drainage, climate, and local vegetation composition. Mires Peat. 19: 8.

Swails, E., Frolking, S., Deng, J., Hergoualc'h, K. 2024. Degradation increases peat greenhouse gas emissions in undrained tropical peat swamp forests. Biogeochemistry 167: 59–74. doi.org/10.1007/s10533-023-01110-2

Teo, W.F.A., Lipun, K., Srisuk, N., Duangmal, K. 2021. *Amycolatopsis acididurans* sp. nov., isolated from peat swamp forest soil in Thailand. J. Antibiot. 74: 199–205. doi.org/10.1038/s41429-020-00382-2

Teo, W.F.A., Srisuk, N., Duangmal, K. 2020. *Amycolatopsis acidicola* sp. nov., isolated from peat swamp forest soil. Int. J. Syst. Evol. Microbiol. 70: 1547–1554. doi.org/10.1099/ijsem.0.003933

Mašínová, T., Bahnmann, B.D., Větrovský, T., Tomšovský, M., Merunková, K., Baldrian, P. 2017. Drivers of yeast community composition in the litter and soil of a temperate forest. FEMS Microbiol. Ecol. 93: fiw223. doi.org/10.1093/femsec/fiw223

Thormann, M.N., Rice, A.V., Beilman, D.W. 2007. Yeasts in peatlands: A review of richness and roles in peat decomposition. Wetlands 27: 761–773. doi.org/10.1672/0277-5212(2007)27[761:YIPARO]2.0.CO;2

Too, C.C., Keller, A., Sickel, W., Lee, S.M., Yule, C.M. 2018. Microbial community structure in a Malaysian tropical peat swamp forest: The influence of tree species and depth. Front. Microbiol. 9: 410666. doi.org/10.3389/fmicb.2018.02859

Too, C.C., Ong, K.S., Yule, C.M., Keller, A. 2021. Putative roles of bacteria in the carbon and nitrogen cycles in a tropical peat swamp forest. Basic Appl. Ecol. 52: 109–123. doi.org/10.1016/j.baae.2020.10.004

Tripathi, B.M., Song, W., Slik, J.W.F., Sukri, R.S., Jaafar, S., Dong, K., Adams, J.M. 2016. Distinctive tropical forest variants have unique soil microbial communities, but not always low microbial diversity. Front. Microbiol. 7: 376. doi.org/10.3389/fmicb.2016.00376

United Nations Development Programme. 2006. Malaysia's peat swamp forests conservation and sustainable use. UNDP. Kuala Lumpur, Malaysia.

Voglmayr, H., Yule, C.M. 2006. *Polyancora globosa* gen sp. nov., and aeroaquatic fungus from Malaysian peat swamp forests. Mycol. Res. 110: 1242–1252. doi.org/10.1016/j.mycres.2006.07.001

Wang, H., Tian, J., Chen, H., Ho, M., Vilgalys, R., Bu, Z.J., Liu, X., Richardson, C.J. 2021. Vegetation and microbes interact to preserve carbon in many wooded peatlands. Commun. Earth Environ. 2: 67. doi.org/10.1038/s43247-021-00136-4

Whitmore, T.C. 1975. Tropical Rain Forests of the Far East. Clarendon Press. Oxford, UK.

Wieder, R.K., Vitt, D.H., Benscoter, B.W. 2006. Peatlands and the Boreal Forest. In: Wieder, R.K., Vitt, D.H. (Eds.). Boreal Peatland Ecosystems. Springer Berlin Heidelberg. Berlin, Germany, pp. 1–8.

Yu, Z., Joos, F., Bauska, T.K., et al. 2021. No support for carbon storage of > 1,000 GtC in northern peatlands. Nat. Geosci. 14: 465–467. doi.org/10.1038/s41561-021-00769-2

Yule, C.M., Lim, Y.Y., Lim, T.Y. 2016. Degradation of tropical Malaysian peatlands decreases levels of phenolics in soil and in leaves of *Macaranga pruinosa*. Front. Earth Sci. 4: 45. doi.org/10.3389/feart.2016.00045

Yule, C.M., Gomez, L.N. 2009. Leaf litter decomposition in a tropical peat swamp forest in Peninsular Malaysia. Wetl. Ecol. Manag. 17: 231–241. doi.org/10.1007/s11273-008-9103-9

Yule, C.M. 2010. Loss of biodiversity and ecosystem functioning in Indo-Malayan peat swamp forests. Biodivers. Conserv. 19: 393–409. doi.org/10.1007/s10531-008-9510-5

Yurkov, A. 2017. Yeasts in forest soils. In: Buzzini, P., Lachance, M.A., Yurkov, A. (Eds.). Yeasts in Natural Ecosystems: Diversity. Springer. Cham, Switzerland, pp. 87–116.

Zhao, L., Li, J., Tian, N., Li, G., Sheng, L., He, C., Bian, H. 2024. Effect of experimental warming on dissolved organic matter and bacterial diversity in a forest swamp soil. Ecol. Indic. 158: 111375. doi.org/10.1016/j.ecolind.2023.111375

Zhou, Z., Wang, C., Luo, Y. 2020. Meta-analysis of the impacts of global change factors on soil microbial diversity and functionality. Nat. Commun. 11: 3072. doi.org/10.1038/s41467-020-16881-7