Soil microbial communities in Southeast Asian peatlands: a review

Christina Birnbaum[1,2,3,4], Anne Yalien Yusuf[4], Tri Wira Yuwati[5], Dony Rachmanadi[5],
Adi Kunarso[4,5], Mark T.L. Bonner,[4,6], Samantha P.P. Grover[4]

[1] School of Agriculture & Environmental Science, University of Southern Queensland, Toowoomba QLD, Australia
[2] Centre for Crop Health, University of Southern Queensland, Toowoomba QLD, Australia
[3] Centre for Sustainable Agricultural Systems, University of Southern Queensland, Toowoomba QLD, Australia
[4] Applied Chemistry and Environmental Science, STEM College, RMIT University Melbourne VIC, Australia
[5] Ecology and Ethnobiology, National Research and Innovation Agency (BRIN), Cibinong, Jawa Barat, Indonesia
[6] Centre for Agriculture and the Bioeconomy, Queensland University of Technology, Brisbane QLD, Australia

SUMMARY

Peatlands in Southeast Asia are considered biodiversity hotspots that contribute significantly to the global carbon cycle. Land-use change on these tropical peatlands alters chemical and physical properties of the peat which directly affect plant health and the composition, diversity and functioning of soil microbial communities. Soil microbial diversity in tropical peatlands is considerably less understood than in boreal peatlands. The aim of this study was to investigate published English-language literature on soil microbial communities in the peatlands of Indonesia, Malaysia and Brunei using a systematic quantitative literature review approach, focusing on their fungal, bacterial and archaeal soil or rhizosphere communities. Data extracted from the articles (published between 2001 and 2023) included the study location, peatland condition, peat depth, context of the research, soil microbial communities and microbial functions studied, and soil abiotic processes assessed. We found 75 studies that met the review criteria, of which the majority (45) were from Indonesia, 29 from Malaysia and one from Brunei. Soil bacteria were reported in 43 % compared to soil fungi in 32 % of these studies. Both bacteria and fungi were reported in 17 % of studies, while only 8 % of studies reported archaea, bacteria and fungi. Soil microbial functions were assessed in 52 % of studies, with considerable emphasis on enzyme activity, respiration and decomposition. Agriculture was the most common research focus (29 % of studies), followed by biodiversity (23 %) and forestry (8 %). Many studies integrated microbial richness and diversity metrics with putative functional attributes, which is an important step towards better understanding microbial activity in peatlands. Future challenges involve better understanding soil archaeal and fungal communities in Southeast Asian peatlands and the roles that they play in peatland ecosystem processes.

KEY WORDS: archaea, bacteria, fungi, tropical peat swamp, restoration

INTRODUCTION

Tropical peatlands are estimated to cover between 90 and 170 Mha and are predominantly located in South America, Southeast Asia and Central Africa (Gumbricht *et al*. 2017). The peatlands in Southeast Asia are located across Sumatra, Kalimantan and West Papua in Indonesia, as well as in Malaysia, Brunei and Papua New Guinea (Ribeiro *et al*. 2021). The peat swamp forests in Southeast Asia are biodiversity hotspots, whilst also providing important livelihoods for local communities through agricultural cultivation, forestry and fishing (Limin *et al.* 2007, Harrison 2013, Padfield *et al*. 2015, Yuwati *et al*. 2021, Omar *et al*. 2022). Many of these peatlands have undergone extensive land conversion to large-scale industrial plantations (Margono *et al*. 2014). Additional landscape transformation has occurred beyond tree planting due to the associated extensive drainage and subsequent recurrent fires (Hoscilo *et al*. 2011, Hooijer *et al*. 2012). The consequences of landscape transformation in tropical peat swamp forests include decline in forest cover, increased greenhouse gas emissions, reduction of carbon sequestration, carbon losses through aerobic peat decomposition, loss of ecosystem services and changes in composition, diversity and function of the soil microbial community (Gunarso *et al*. 2013, Dohong *et al*. 2018).

The largest national area (13.43 million ha) of tropical peatland is in Indonesia (87 %), although this may change in light of recent reports of large (16.7 million hectares) peat deposits in the Congo (Dargie *et al*. 2017, Crezee *et al*. 2022). In Indonesia, the peatland occurs predominantly on low-altitude coastal and sub-coastal areas of Sumatra (5.85 Mha, 43.5 %), Kalimantan (4.54 Mha, 33.8 %), Papua (3.01 Mha, 22.4 %) and Sulawesi (0.024 Mha, 0.3 %) (Wahyunto & Agus 2010, Page *et al*. 2011, Anda *et al*. 2021, Yuwati *et al*. 2021). Malaysia has approximately 2.6 Mha of peatland, of which 70 % is in Sarawak (Melling 2016). Tropical peatlands are also found in Thailand (40,000 ha), and to a lesser extent in Vietnam, Brunei and the Philippines (Ribeiro *et al*. 2021). Estimated to hold 85 % of the Southeast Asian carbon stock (Dohong *et al*. 2018), Indonesian peat swamp forests are a key reservoir for carbon storage in Southeast Asia. However, with the fourth largest population in the world (241 million in 2012), there are significant economic pressures for Indonesia to utilise tropical peatlands for livelihoods, which is often accompanied by considerable environmental degradation (Tilman *et al*. 2001). It is estimated that approximately 13 Mha of Indonesian peat swamp forest is now in a degraded condition, mainly due to logging, peatland fires, canal dredging and agricultural activities (Uda *et al*. 2017, Dohong *et al*. 2018). As a direct result of widespread peatland degradation, it has been estimated that carbon emissions have increased by 0.5 Pg C year^{-1} (van der Werf *et al*. 2009). Thus, tropical peatlands are at substantial risk of losing their biodiversity, ecosystem functions and ability to sequester carbon (Nurulita *et al*. 2016).

It is critical to develop land management protocols to facilitate conservation and restoration of degraded peatlands (Nurulita *et al*. 2016). Indonesia already has a target to restore 2.67 Mha of degraded peat by three main activities: rewetting, revegetating and revitalisation of livelihoods (BRG 2016, Yuwati *et al*. 2021). The aim of rewetting is to bring back the water table to a level near the soil surface by blocking primary, secondary and tertiary canals (Yuwati *et al*. 2021). Revegetation is prioritised in areas that have had repeated fires and where natural plant regeneration is slow to occur (Hoscilo *et al*. 2011, Blackham *et al*. 2013). Livelihood revitalisation is a central strategy in peat swamp forest restoration as it focuses on facilitating best land-use practices incorporating traditional knowledge amongst local communities (Silvianingsih *et al*. 2021). However, to achieve a successful restoration outcome, both aboveground and belowground components of the ecosystem should be considered. It is important to consider plant species diversity, climatic conditions, hydrological regime of the site, topography and soil biotic and abiotic properties (Gorham & Rochefort 2003).

Peatland degradation and associated land-use change considerably alter soil chemical and physical properties (Sinclair *et al.* 2020, Kunarso *et al*. 2022), which in turn directly affect plant health, soil abiotic properties and soil microbial composition, diversity and functioning (Puglisi *et al*. 2014, Strickman *et al*. 2016). Soil microbial communities are critical for healthy ecosystems as they support plant establishment and growth, perform critical ecosystem processes, e.g., soil organic matter decomposition and nutrient cycling. An approximately fivefold greater quantity of carbon is cycled through soil microbes annually than is emitted by all human fossil fuel use and cement manufacturing combined (Raich & Schlesinger 1992, Le Quéré *et al*. 2015). Soil bacteria can colonise dead wood and produce metabolites that support the growth of other beneficial soil organisms such as soil fungi (Clausen 1996, Roesch *et al*. 2007, Schmidt *et al*. 2007). Soil fungi play a key role in soil organic matter degradation in forest litter, with many fungi uniquely able to degrade recalcitrant substrates, specifically lignin and cellulose (Floudas *et al*. 2012). Many fungal species also form symbiotic relationships with plants, i.e., mycorrhizal associations that are beneficial to plants and provide protection against pathogens and drought relief. Thus, soil microbial communities play an important role in ecosystems, and incorporating belowground soil microbial communities into aboveground restoration planning and execution has the potential to improve overall restoration outcomes.

The soil microbial diversity in tropical peatlands is under-studied and considerably less understood than in boreal peatlands (Liu *et al*. 2019, Robinson *et al*. 2023). The aim of this study was to investigate published literature on soil microbial community diversity in Southeast Asian peatlands using a systematic quantitative literature review approach. The review focused on the archaeal, bacterial and fungal soil or rhizosphere communities in Indonesia, Malaysia and Brunei, where most of the Southeast Asian tropical peatlands are found.

METHODS

We performed a systematic quantitative literature review by searching the Scopus (Elsevier, Atlanta, U.S.A) and ISI Web of Knowledge (Core collection; Thomson Reuters, NY, U.S.A.) databases on 24 June 2024. Scopus was searched through title, abstract and keywords using the Boolean search string: (Indonesia* OR Brunei* OR Malaysia*) AND (peat* OR "peat land" OR "peatland" OR mire* OR mires OR swamp*) AND (fung* OR bacter* OR archaea* OR microb*) AND (soil* OR "bulk soil*" OR sediment* OR rhizosphere*). Items published during the 23 years from 2001 until June 2024 were included.

This search returned 255 articles (Figure 1). All articles were imported into Covidence (Covidence systematic review software, Veritas Health Innovation, Melbourne) for title, abstract and full text screening. Selection of studies was conducted following PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) protocols (http://www.prisma-statement.org), which are built into Covidence (Figure 1). We excluded 180 articles because they were either duplicates (35) or did not meet our inclusion criteria (145), which were:

1) study must have been conducted on peatlands, mires or swamps in Indonesia, Brunei or Malaysia; i.e., in effect, within the three land masses of Borneo, Sumatra and Peninsular Malaysia;
2) study must have been conducted under field conditions and soil samples collected directly from the field (i.e., not a laboratory or manipulative experiment); and
3) soil archaea, bacteria or fungi were analysed - for example, we excluded studies that assessed soil microbial communities on aboveground plant parts or did not report soil microbial communities.

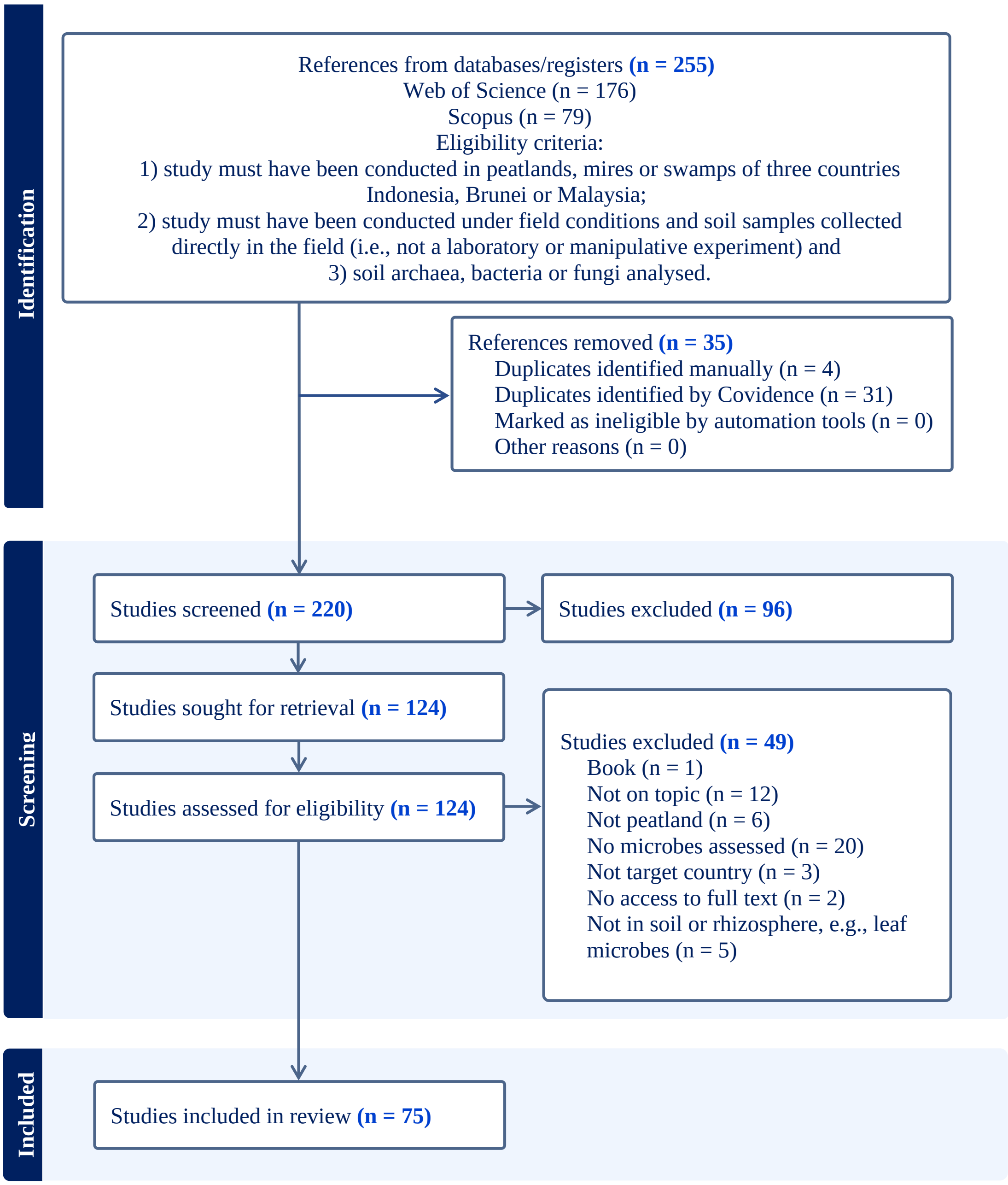

Figure 1. Modified PRISMA flow chart summarising the literature screening process.

Studies that met the selection criteria were then identified by full text review and used for data extraction and analysis (see Supplement). The following data were extracted from articles: location of the study; peatland condition (intact, degraded, restored or managed plantation/agriculture/paddy); peat depth; context of the research (agriculture, forestry, conservation, restoration, etc.); soil microbial communities studied (archaea, bacteria or fungi); microbial functions studied; and soil abiotic processes assessed. Additionally, the countries of the first and last authors' affiliations were recorded. All analyses and graphs were created using Microsoft Excel 365 (Version 2208, Microsoft Corporation).

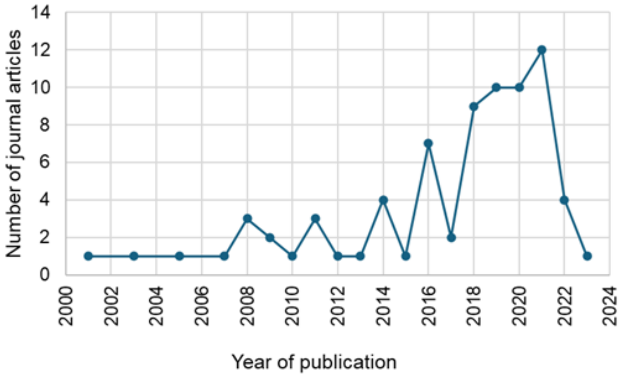

Figure 2. Number of journal articles on soil microbial communities in Southeast Asian tropical peatlands published between 2000 and 2023 (n = 75).

RESULTS

In total, we found 75 studies that met the criteria for this review (Figure 1 and Supplement). The average number of studies published on soil microbial communities in Southeast Asia between 2001 and 2024 was 3.8 per year, with a notable increase since 2016 (2016–2024 mean 6.9 per year) (Figure 2). We found one study from Brunei, 45 from Indonesia and 29 from Malaysia (Figure 3A). The analysis of author affiliations revealed that 40 % of first authors were based in Indonesia, 32 % in Malaysia and 12 % in Japan (see Supplement). The pattern was similar for last authors' affiliations.

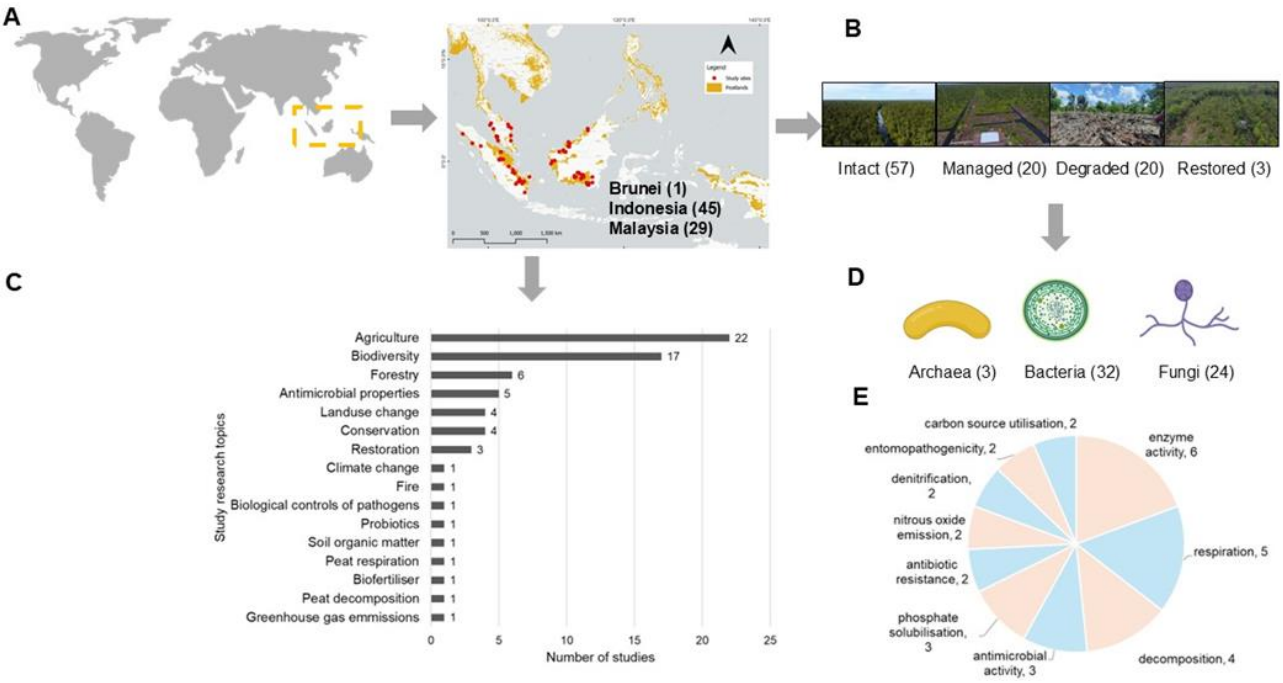

Figure 3. A) Distribution of tropical peatlands in Southeast Asia (brown) and locations of study sites from the 75 articles (published between 2000 and 2023) included in this review (red circles). The number of studies per country is shown in brackets. B) Peatland condition as reported in the 75 studies; the number of studies per category is shown in brackets. The 'managed' category refers to, e.g., plantation, agriculture or paddy field. All images supplied by Tri Wira Yuwati. C) Number of studies by research topic. D) Number of studies that focused solely on archaea, bacteria or fungal soil or rhizosphere communities. E) Results for ten soil microbial putative functions that were reported in ≥ 2 articles. For the full list of 24 putative functions reported, see Supplement. B and D created in BioRender.com.

Soil microbial communities were reported from 57 intact peatlands, 20 degraded peatlands, 20 managed peatlands and 3 restored peatlands (Figure 3B). The range of peat depth, reported in 49 % of studies (i.e., 37 studies), was 30–850 cm (see Supplement). Agriculture was the most common research topic (22 studies), followed by biodiversity (17) and forestry (6). Other research topics included antimicrobial properties, conservation, restoration, climate change, fire and peat decomposition (Figure 3C).

Peatland microbial communities

Soil microbial communities were reported predominantly from the bulk soil (62 studies), rhizosphere (six studies) or a combination of soil, rhizosphere and roots (seven studies). More than a quarter (33 %) of the studies analysed soil microbial communities using exclusively culture-based methods, while 19 studies used only sequencing and three studies used microbial community profiling methods (i.e., DGGE or T-RFLP) (see Supplement).

Archaea, bacteria and fungi were studied in 6 %, 43 % and 32 % of studies, respectively (Figure 3D). Archaeal, bacterial and fungal taxa were described collectively in 69 % of studies; bacteria and fungi were reported in 17 % of studies; while only 8 % of studies reported archaea, bacteria and fungi. More than half (68 %) of the reviewed studies reported microbial taxa at a taxonomic level. Specifically, 24 studies reported archaea, bacteria or fungi at species level, seven at genus level, two at family level, ten at Phylum level and two at kingdom or domain level, with 25 studies not reporting any taxonomic assignment of archaeal, bacterial or fungal species (see Supplement). We found six studies that assessed archaea (i.e., Crenarchaeota and/or Euryarchaeota), namely: Jackson *et al*. (2009); Nurulita *et al*. (2016); Ismail *et al*. (2017); Too *et al*. (2018, 2021); Dom *et al*. (2021); and Blewett *et al*. (2022).

Twenty-six of the reviewed studies described bacterial taxa. These included the Phyla Proteobacteria, Firmicutes, Bacteroidetes, Actinobacteria, Planctomycetes, Verrucomicrobia and Chloroflexi, three species of *Burkholderia* (*B. gladioli*, *B. paludis*, *B. unamae*), five species of *Bacillus* (*B. albus*, *B. cereus*, B. *stratosphericus*, *B. thuringiensis*, *B. tequilensis*), seven species of *Mycobacterium* (*M. avium*, *M. branderi*, *M. celatum*, *M. fragae*, *M. intracellulare*, *M. kyorinense*, *M. tuberculosis*), *Acidobacterium capsulatum*, *Lysinibacillus fusiformis*, *Aeromonas hydrophila*, *Escherichia coli*, *Pseudomonas aeruginosa*, *Klebsiella pneumoniae* and *Enterobacter cloacae* (see Supplement).

Fungal taxa were described in 19 studies. For example, four species of *Acaulospora* (*A. scrobiculata*, *A. bireticulata*, *A.mellea*, *A. laevis*) and three species of *Glomus* (*G. monosporum*, *G. constrictum*, *G. manihotis*) were described from Indonesian peatlands (Sefrila *et al*. 2021); while nine species of *Fusarium* (*F. solani*, *F. verticillioides*, *F. incarnatum*, *F. proliferatum*, *F. lateritium*, *F. oxysporum*, *F. rigidiuscula*, *F. chlamydosporum*, *F. camptoceras*) were reported from Malaysia (Zubi *et al*. 2021). Other fungal species included *Metarhizium anisopilae* and *Isaria amoenerosea* (Kin *et al*. 2017), along with *Annulatascus velatisporus*, *Beverwykella pulmonaria*, *Dactylella* sp., *Monodictys pelagica* and *Pleurophragmium* sp. (Fryar *et al*. 2005) from intact peatlands in Malaysia, *Pisolithus arhizus* (Turjaman *et al*. 2019) from restored peatlands in Indonesia and *Trichoderma asperellum* from degraded peatland in Indonesia (Subandar *et al.* 2021) (see Supplement).

Soil microbial functions were assessed in 39 (52 %) of the studies. Decomposition and respiration were collectively analysed in nine studies, followed by enzyme production, which was analysed in six studies. The remaining 16 soil microbial processes that were reported in two or more studies were carbon source utilisation, entomopathogenicity, denitrification, nitrous oxide emissions, antibiotic resistance, phosphate solubilisation and antimicrobial activity (Figure 3E).

Soil abiotic properties

Soil abiotic properties were reported in 64 % of studies. The three most reported soil abiotic properties were pH (45 studies), soil nitrogen (26 studies) and soil carbon (20 studies) (Figure 4). Other soil abiotic properties reported included soil moisture content, phosphorus, cation exchange capacity, soil temperature, loss on ignition, organic carbon, C:N ratio, bulk density, nitrate, magnesium, electrical conductivity and ammonium (Figure 4).

DISCUSSION

Previous reviews on soil microbial communities in Northern Hemisphere peatlands have acknowledged that, although progress has been made towards better understanding the structure of northern peatland microbial communities, more research is needed to relate the microbial community structure to ecosystem functions of peatlands (Andersen *et al*. 2013, Robinson *et al*. 2023). Similar reviews are lacking for tropical peatlands as there is currently a paucity of studies assessing soil microbial communities in tropical peatlands (Robinson *et al*. 2023). We found 75 studies that have described soil

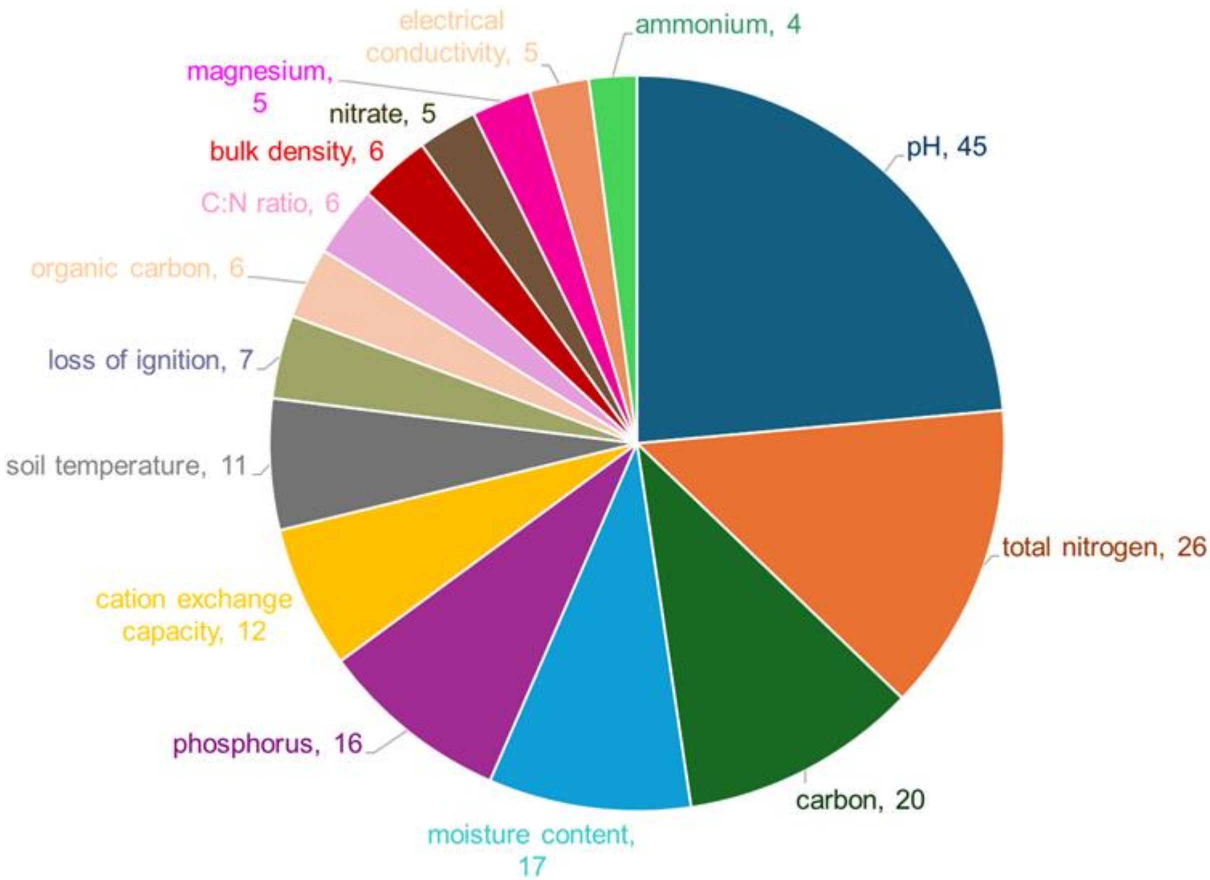

Figure 4. Soil abiotic properties from a total of 75 studies on soil microbial communities in tropical peatlands published between 2000 and 2023 that were included in the systematic review. Results are shown for 15 properties that were reported in ≥ 5 articles. For the full list of 39 soil abiotic properties reported, see Supplement.

microbial communities from Southeast Asian peatlands, with most reviewed studies from Indonesia, followed by Malaysia, and one study from Brunei.

One of the focus microorganism groups in this review was archaea, which are responsible for two main metabolic pathways in the global circulation of nutrients, namely methanogenesis and anaerobic methane oxidation (Eme & Doolittle 2015). Archaea, specifically Euryarchaeota, generate approximately 85 % of methane, a critical greenhouse gas, on the planet (Eme & Doolittle 2015). Tropical peat swamp forest soils have been reported to act as both sinks and sources of methane at different times of year and laboratory incubation experiments suggest that drainage and rewetting will affect methane fluxes substantially (Sakabe *et al*. 2018). We found only two studies that had assessed archaea (i.e., Crenarchaeota and Euryarchaeota) in Indonesian peatlands (Nurulita *et al*. 2016, Blewett *et al*. 2022) and four that dealt with archaea in Malaysian peatlands (Jackson *et al*. 2009, Ismail *et al*. 2017, Too *et al*. 2018, 2021 (same study site), Dom *et al*. 2021). Considering these findings and the important ecological role that archaea play in soils and associated ecosystem processes, a thorough understanding of the composition of archaea in tropical peat soils under different land uses remains elusive, and this topic warrants further research.

Bacterial taxa were described in 26 of the studies reviewed here. *Acidobacteria* and *Actinobacteria* are two of the major globally distributed bacterial phyla in soils and peatlands, thus their presence in tropical peatlands is expected (Barka *et al*. 2015, Dedysh & Damsté 2018). Among the described bacteria there were three nitrogen fixing genera (*Bradyrhizobium*, *Burkholderia*, *Mesorhizobium*). These nitrogen fixing bacteria have the capacity to colonise the rhizosphere and interact with leguminous plants by inducing the formation of root nodules where atmospheric nitrogen is fixed. Nitrogen is one of the major limiting nutrients to plant growth and thus the presence of these bacteria can contribute significantly to plant nitrogen acquisition (Franche *et al*. 2009). This is particularly relevant to the revegetation component of peatland restoration, where nitrogen limitation may be one of the factors affecting low success rates.

Among described fungi were several widespread fungal genera, such as *Aspergillus*, *Penicillium* and *Talaromyces*, that have been researched in fields such as food, indoor and medical mycology and biotechnology (Houbraken *et al*. 2020). Two arbuscular (*Acaulospora*, *Glomus*) and three typically ectomycorrhizal fungal genera (*Pisolithus*, *Scleroderma*, *Strobilomyces*) were described from Indonesian peatlands. Mycorrhizal fungi play an important beneficial role in plant growth as their presence in plant roots is correlated with an increase in uptake of immobile nutrients in the soil, especially phosphorus (Bolan 1991). Also among the fungi described were several known pathogenic genera, i.e., *Fusarium, Metarhizium* (entomopathogenic fungi) and *Neocosmospora* (Roberts & Leger 2004, Ma *et al*. 2013, Sandoval-Denis & Crous 2018). Notably, Liu *et al*. (2019) found that intact peat swamp forest supported a more diverse bacterial and fungal community than disturbed peat soil in Central Kalimantan (Indonesia). These authors also reported that fungal pathotrophs were significantly more abundant in disturbed peat soil than in intact peat swamp forest, suggesting that the disturbance of tropical peatland may lead to the introduction and spread of soil fungal diseases (Liu *et al*. 2019).

Soil microbial functions were assessed in 52 % of the studies. Most (15) of these studies reported decomposition, soil respiration and enzyme activity collectively, as these are common soil properties that can be measured under laboratory conditions. Decomposition is a critical ecosystem process in peat soil formation and peat accumulation. Peat is formed when the rate of organic matter accumulation exceeds the rate of decomposition (Leng *et al*. 2019). It has been reported that anthropogenic interventions, such as construction of drainage canals, has increased the rate of peat decomposition in Southeast Asian peatlands; thus, the predominant focus on studying decomposition in tropical peat swamp forests is to be expected (Leng *et al*. 2019). Microbial respiration is a major component of decomposition and was reported in five studies (Yanai *et al*. 2007, Husen & Agus 2011, Turjaman *et al*. 2011, Husen *et al*. 2014, Nurulita *et al*. 2016). Carbon dioxide is released from peat to the atmosphere via microbial respiration and there is an increasing number of studies that focus on assessing peat respiration in intact versus disturbed peatlands and the contribution of these carbon dioxide emissions to regional and global change (Husen *et al*. 2014). Despite the increasing number of studies assessing greenhouse gas emissions from tropical peatlands, we found that soil microbial communities were studied most in agricultural contexts (~ 1/3 of all studies). Agriculture forms an important part of people's livelihoods in tropical peatlands, predominantly via plantation and agricultural cultivation land use types (Hergoualc'h *et al*. 2018). Thus, the high number of published studies assessing microbial communities in agricultural contexts is not unexpected.

We found that 15 soil properties were reported in ≥ 5 articles. Similarly to Kunarso *et al*. (2022), we found that pH, carbon and nitrogen were the most studied soil abiotic properties. Changes in land use associated with tropical peat soil drainage have been reported to change nutrient concentrations and nutrient cycling as consequences of changes in vegetation composition and associated availability and turnover of organic matter (Könönen *et al*. 2015). The increasing trend of measuring both biological and chemical properties of peats within one study is promising, as successful restoration and sustainable management of peatlands requires a holistic understanding of biological, chemical and physical soil properties and how they relate to plant productivity.

In our review of soil microbial communities from tropical peat swamp forests, we found that approximately a quarter (33 %) of studies analysed soil microbial communities using exclusively culture-based methods and 19 studies used sequencing methodologies (see Supplement). Microbial analysis using cultures is important, however only a relatively small number of soil microbes are culturable and thus the true diversity of soil microbes using culture-dependent methods will be underestimated. For example, only 0.1–1 % of prokaryotes (bacteria and archaea) and 10–30 % of fungi are culturable using traditional microbiological methods (Magnuson & Lasure 2002, Culligan *et al*. 2014). High-throughput sequencing (HTS) provides advanced, high-quality methods for analysing microbiome structure and function from complex environmental DNA samples (Tedersoo *et al*. 2021). While HTS is becoming more affordable, the overall cost of sampling, DNA extraction, PCR and sequencing of bacterial and fungal DNA at a commercial laboratory is in the range AU$/US$ 50–120 per sample. The total expenses for a single analysis can quickly add up based on the number of samples, making it potentially unaffordable for many researchers and practitioners (Birnbaum & Trevathan-Tackett 2022). We advocate for increased international collaboration to enhance the study of microbial diversity in tropical peat swamp forests using the latest molecular tools.

It is important to acknowledge that studies on tropical peat soil microbial communities have also been published in non-English languages, e.g., Bahasa Indonesia; and in ‘grey’ literature, e.g., reports and conference proceedings which were not included here as these materials are not peer reviewed or accessible using online search engines. Including these materials would provide a more comprehensive review of current knowledge of soil microbial communities in tropical peatlands. This warrants further investigation.

To conclude, our review indicates that soil bacteria were studied more frequently than fungi, with agriculture being the main research focus, followed by biodiversity and forestry. Numerous studies integrated metrics of microbial richness and diversity with functional attributes, which is essential for comprehending microbial activity in peatlands. Overall, our results suggest that we have a limited understanding of tropical peatland soil microbial diversity and more research is needed, especially using high-throughput sequencing tools, to better understand the soil microbial diversity. Future research challenges involve deepening our understanding of archaeal and fungal communities in Southeast Asian tropical peatlands and their roles in ecosystem processes. The many research gaps offer new opportunities for researchers to contribute to both fundamental and applied knowledge through technological advances, collaborative efforts and increased understanding of the importance of soil microbial communities to peatland conservation and restoration success.

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AUTHOR CONTRIBUTIONS

Idea and conceptualisation: CB, TWY, DR, SPPG; data extraction and analysis: CB, AYY; writing of first draft: CB; data extraction and manuscript editing: AYY, TWY, DR, AK, MTLB, SPPG.

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Author for correspondence: Dr Christina Birnbaum, School of Agriculture & Environmental Science, University of Southern Queensland, West Street, Toowoomba 4350, Queensland, Australia.
Tel: +61 7 4631 2646; Email: christina.birnbaum@unisq.edu.au