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Macrofungal diversity in three protection forests of Sambas District, West Kalimantan, Indonesia

LAILI FITRI YENI♥, MAS AKHBAR FATURRAHMAN, AHMAD ALOY SAPUTRA, KHAIRI, RISKA MAULIDYA
Study Program of Biology Education, Department of Mathematics and Natural Sciences Education, Faculty of Teacher Training and Education,
Universitas Tanjungpura. Jl. Prof. Dr. H. Hadari Nawawi, Pontianak 78124, West Kalimantan, Indonesia.
Tel.: +62-561-739630, Fax.: +62-561-739637, ♥email: laili.fitri.yeni@fkip.untan.ac.id

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Abstract. *Yeni LF, Faturrahman MA, Saputra AA, Khairi, Maulidya R. 2025. Macrofungal diversity in three protection forests of Sambas District, West Kalimantan, Indonesia. Biodiversitas 26: 4309-4323.* The Gunung Pemangkat Protection Forest (GPPF), Gunung Majau Protection Forest (GMPF), and Gunung Sekadau Protection Forest (GSPF) in Sambas District, West Kalimantan, Indonesia, are three tropical rainforests whose macrofungal communities remain undocumented. This study aimed to investigate the previously unexplored macrofungal diversity in GPPF, GMPF, and GSPF. Field surveys were conducted along zigzag transects to systematically record macrofungi. Identification was based on macromorphological features and confirmed with online taxonomic databases. Environmental factors were measured to characterize habitat conditions. Subsequently, the spatial distribution of macrofungi was analyzed and mapped. A total of 94 macrofungal species from 30 families across Ascomycota and Basidiomycota were recorded: 44 species from 23 families in GPPF, 42 from 20 families in GMPF, and 54 from 22 families in GSPF. Polyporaceae was the most species-rich family. Most taxa were saprophytic and predominantly associated with wood debris, while a smaller number occurred on decomposing litter and soil. Parasitic and mutualistic types were recorded only occasionally. Favorable environmental factors—warm temperatures, high humidity, slightly acidic soils, and low light intensity—likely supported macrofungal growth. Spatial analysis revealed a clumped distribution pattern associated with microhabitat variability and substrate availability. More than half of the macrofungi identified at the species level possess nutritional or medicinal value, underscoring their socio-economic importance. This study provides the first inventory of macrofungi in these forests, filling a critical knowledge gap in the region and extending beyond previous reports from Borneo, especially West Kalimantan. Systematic sampling in GPPF, GMPF, and GSPF revealed a broader spectrum of diversity and confirmed these forests as key reservoirs of macrofungal richness. The findings establish a critical baseline for ecological studies and emphasize the importance of conservation in these protection areas. More broadly, the study advances understanding of tropical fungi in Southeast Asia and underscores their role in long-term biodiversity management.

Keywords: Forest ecology, fungal diversity, macrofungal guild, substrate preference, tropical rainforest

Abbreviations: GMPF: Gunung Majau Protection Forest, GPPF: Gunung Pemangkat Protection Forest, GSPF: Gunung Sekadau Protection Forest

INTRODUCTION

Borneo, one of the world's richest tropical biodiversity hotspots, faces major conservation challenges due to limited data on forest conditions and biodiversity (Budiharta and Meijaard 2017). Land conversion further accelerates habitat loss and species decline (Willard et al. 2022). In this context, protection forests have become increasingly vital. These state-owned lands, managed by government authorities with community involvement, curb deforestation by prohibiting logging, resource extraction, agriculture, mining, and infrastructure development (Liu et al. 2022; Parera et al. 2022). Their establishment preserves habitats and ecological connectivity, strengthening biodiversity conservation (Gunawan et al. 2024). However, knowledge of key taxa in these ecosystems remains uneven: vascular plants and vertebrates are relatively well studied, while fungi—particularly macrofungi—remain underexplored.

Macrofungi, or mushrooms, are visible members of the kingdom Fungi that produce spore-bearing fruiting bodies (Harun et al. 2024; Suryani et al. 2024). They are vital to forest ecosystems as decomposers, pathogens, and nutrient recyclers (Gafforov et al. 2020). Many also form mycorrhizae, which enhances nutrient uptake and plant regeneration (Nordin et al. 2024), making them keystone species for soil fertility, productivity, and carbon cycling. By 2017, only 2,273 fungal species had been recorded in Indonesia—just 0.15% of global estimates at the time—with most records from Java (Retnowati and Rugayah 2019). Against recent global accounts of 140,000 described fungal species (Hyde et al. 2024), the 2017 Indonesian record would equal about 1.6%, underscoring both advances in global documentation and persisting national gaps. However, the overall fungal diversity of Indonesia remains insufficiently documented, and, as noted by Putra et al. (2022), the country still lacks a comprehensive national checklist, unlike neighboring Malaysia and Vietnam.

Macrofungal diversity faces significant global threats that are often overlooked in conservation strategies. Anthropogenic pressures such as urbanization degrade habitats (Nordin et al. 2024). This affects macrofungal abundance through reduced substrate richness, which is further influenced by species traits (Ye et al. 2019; Shuhada et al. 2020). Climate change further affects fungal phenology, distribution, and virulence (George et al. 2025). These global threats also impact Borneo's protection forests, evidenced by habitat loss and biodiversity declines from infrastructure expansion (Spencer et al. 2023) and climate change (Scriven et al. 2015), worsened by fires and invasive species (Tuah et al. 2020). Without macrofungi, forests lose ecosystem services such as timber production and carbon storage (Niego et al. 2023). Their exclusion from biodiversity assessments leaves fungi underrepresented in policies, increasing the risk of unnoticed declines.

This study focuses on West Kalimantan, particularly the three primary protection forests of Sambas District—Gunung Pemangkat Protection Forest (GPPF), Gunung Majau Protection Forest (GMPF), and Gunung Sekadau Protection Forest (GSPF)—which remain unexplored for macrofungal diversity. These relatively undisturbed mountainous forests, with dense canopy cover, varied topography, and diverse substrates, provide ecological niches supporting rich macrofungal communities. Moreover, they act as refuges for many organisms and maintain ecological connectivity in a landscape increasingly affected by anthropological pressures, highlighting their global significance for tropical biodiversity conservation. Documenting macrofungal diversity here provides essential data for conservation planning and sustainable management. Notably, Yunida et al. (2014) represent the only study in Sambas protection forests, while other studies in West Kalimantan, such as Sumarni et al. (2017), Zulpitasari et al. (2019), and Widyastuti and Yeni (2022), provide a regional context.

Systematic documentation of macrofungi supports conservation (Nacua et al. 2018), indicates ecosystem health (Md Noordin et al. 2024), and reveals their ecological and applied importance (Gafforov et al. 2023). Gafforov et al. (2025) stated that fungal taxa in tropical montane regions remain underdocumented, with many species likely undescribed. Based on the background, this study is guided by the central question: How does macrofungal diversity vary across the protection forests of GPPF, GMPF, and GSPF in Sambas District? To address this, four objectives are pursued: (i) to examine species composition, substrate preferences, and ecological guilds of macrofungi; (ii) to investigate habitat conditions influencing macrofungal diversity; (iii) to analyze spatial distribution patterns in relation to habitat conditions, substrate availability, and spore dispersal; and (iv) to assess the potential uses of documented macrofungi, emphasizing their ecological and socio-economic value. Documenting macrofungal diversity in Borneo is crucial to safeguard biodiversity and forest health against ongoing environmental change, anthropogenic pressures, species loss, and ecosystem degradation.

MATERIALS AND METHODS

Study sites

The study was conducted in three protection forests in Sambas District, West Kalimantan, Indonesia: GPPF, GMPF, and GSPF (Figure 1). Macrofungal sampling was conducted in January to February 2023. The GPPF covers ± 237 hectares at 350 metres above sea level, located in Pemangkat District (01°15'11.6"N, 109°10'24.9"E). The GMPF covers ± 523 ha at 150 metres above sea level, located in Dare Nandung Hamlet of the Sempalai Sebedang Village, Sebawi District (1°12'15"N, 109°13'28"E). The GSPF covers ± 4,148.401 hectares at 150-500 metres above sea level, located in Madak Village, Subah District (1°10'53"N, 109°17'54"E). All three protection forests exhibit typical lowland tropical rainforest vegetation.

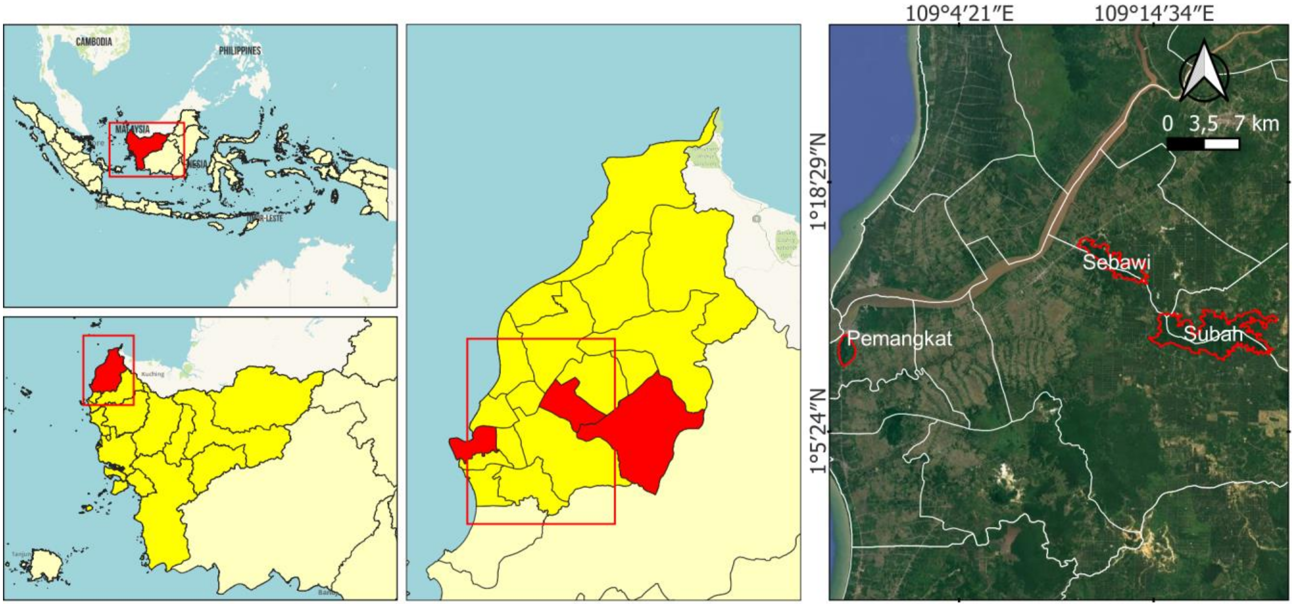

Figure 1. Study sites in GPPF, GMPF, and GSPF, Sambas District, West Kalimantan Province, Indonesia

Procedures

Field survey and sampling

Preliminary observations were conducted to ascertain the most suitable locations for sampling and the optimal cruising paths. The sampling location is selected from a path that allows accessibility of the area and the presence of fungi (Kinge et al. 2017). Sampling was conducted using a zigzag transect method with 2-meter margins on either side. The zigzag roaming method obtains data representing each macrofungi habitat spread across the study site (Widyastuti and Yeni 2022). Moreover, this method was chosen because the zigzag path increases the likelihood of capturing a wider range of microhabitats compared to straight transects, thereby improving representativeness. Sampling effort was standardized by establishing five transects of approximately 1 km in each forest, surveyed once during a six-week simultaneous sampling period. This ensured equal observer effort and minimized temporal bias. Systematic presence-based recording along fixed transects was conducted by documenting all fruiting bodies encountered, without selective collection, to minimize observer bias.

Each macrofungus found was documented using a camera in its natural habitat. Each macrofungus sample was then collected from the substrate where the fruiting bodies were found. Macrofungal family locations were recorded using a Garmin eTrex 10 GPS device. Environmental parameters—air temperature, soil properties, air humidity, and light intensity—were measured with calibrated instruments: GEA Medical S-006 alcohol thermometer, Yieryi 4-in-1 soil survey instrument, TFA Dostmann 30.5013 thermo-hygrometer, and Smart Sensor AS803 luxmeter. All instruments were calibrated before each sampling session following standard protocols to ensure data accuracy. Environmental factors were measured at each point where a macrofungus was found, whether under a canopy or in open areas, to capture the specific conditions of its microhabitat.

Macrofungal identification based on morphology

The morphological identification of macrofungi was based on macroscopic characteristics observed in fresh specimens. Key diagnostic features recorded included: substrate type, as macrofungi exhibit substrate specificity (decomposing litter, soil, or wood debris); pileus characters: shape, size (diameter), surface texture, margin, color (in young and mature stages), hygroscopic properties, and moisture level; hymenophore features: type (lamellae, pores, or spines), attachment to the stipe (free, adnate, decurrent, etc.), spacing, length, and edge morphology; stipe characteristics: shape, color (in both young and mature stages), length and diameter, surface texture, insertion on substrate, presence of veils (partial or universal), and attachment type; other features: texture, odor, and taste (if applicable and safe to assess); and spore prints, which were collected on white and/or black paper to help determine spore color as an additional identification aid. Identification was carried out using standard mycological references, including Largent et al. (1977), Largent and Stuntz (1986), Arora (1986), Lodge et al. (2004), and Læssøe (2013). Taxonomic names were verified and updated using online databases Index Fungorum (indexfungorum.org) and MycoBank (mycobank.org). While morphological identification was the primary approach, the integration of molecular techniques is recommended in future studies to resolve cryptic taxa and improve taxonomic resolution.

Data analysis

Data were analyzed descriptively based on taxonomic groups, substrate types, ecological guilds, and recorded habitat conditions. As individual counts and population sizes were unavailable, diversity indices (e.g., Shannon, Simpson) were not calculated. Instead, analyses focused on species presence and spatial distribution patterns. Spatial distribution patterns of macrofungal families across the three protection forests were visualized using Quantum Geographic Information System (QGIS, version 3.36) software based on the GPS coordinates recorded. Coordinate data were imported in Comma Separated Values format and subsequently converted to a Shapefile, then projected to the WGS84 coordinate system (EPSG:4326), as our sole purpose was to visualize the sampling locations according to the original data without modifying their spatial distribution. Although formal spatial analyses (such as nearest neighbor analysis) were not conducted, the mapped distributions suggest a clumped pattern warranting further study with advanced methods. In addition, the potential uses of documented macrofungi were analyzed through a review of published scientific articles, highlighting their ecological roles and socio-economic importance.

RESULTS AND DISCUSSION

Macrofungal diversity

A total of 94 macrofungal species from 30 families within Ascomycota and Basidiomycota were recorded across GPPF, GMPF, and GSPF. Species richness and taxonomic composition varied by site, with GSPF showing the highest diversity (54 species from 22 families), followed by GPPF (44 species from 23 families) and GMPF (42 species from 20 families). These differences likely reflect site-specific variations in forest structure, microclimate, and substrate availability. This study presents the first in-depth and systematic inventory of macrofungi in the three protection forests of Sambas District, contributing a significant set of new records that enrich the current understanding of macrofungal diversity in West Kalimantan. Beyond serving as a baseline inventory, these findings highlight the ecological significance of macrofungi and emphasize the urgent need to include them in integrated conservation frameworks alongside plants and animals in Borneo. Recognizing macrofungi as key components of forest ecosystems is essential for holistic biodiversity protection, sustainable management, and the resilience of tropical forests under increasing anthropogenic pressures.

The results of this study complement previous studies on macrofungal diversity in Borneo, such as Noverita and Setia (2019), who recorded 87 species in the peat swamp forests of Kapuas Hulu, West Kalimantan, and Md Noordin et al. (2024), who identified 28 species in the Lentang Forest Reserve, Pahang, Malaysia. Moreover, this study adds to the growing body of studies on macrofungal diversity in West Kalimantan's protection forests. Previous studies reported 15 species in Bukit Rentap Protection Forest (Sumarni et al. 2017), 29 species in Bukit Wangkang Protection Forest (Zulpitasari et al. 2019), and 53 species in Bukit Penintin Protection Forest (Widyastuti and Yeni 2022). In addition, 32 genera were recorded in Bukit Baka Bukit Raya National Park (Harun et al. 2024). These findings underscore the variability of macrofungal communities across different areas in Borneo, highlighting the ecological importance of preserving diverse habitats to support fungal biodiversity and the need for continued exploration to fill existing knowledge gaps. However, this study did not include molecular identification, which may have underestimated cryptic species. Future studies should apply molecular barcoding, particularly the Internal Transcribed Spacer sequencing, to validate morphological identifications and reveal hidden taxa. Additionally, the sampling strategy might not have captured all taxa, particularly ephemeral species or those with strong seasonal occurrences, potentially leading to an incomplete representation of the macrofungal community.

Phylum-level composition

Macrofungal communities across all three protection forests were dominated by Basidiomycota, with 41, 39, and 51 species recorded in GPPF, GMPF, and GSPF, respectively, while only three Ascomycota species were observed at each site (Figure 2). This pattern aligns with previous findings by Kerfahi et al. (2016) and Song et al. (2019), who observed similar patterns in forested ecosystems. Basidiomycota and Ascomycota are both key fungal lineages found in soil and root-associated ecosystems, though Basidiomycota typically show greater abundance in warm and humid climates (Wang et al. 2021). The dominance of Basidiomycota is primarily due to their key role in decomposing wood and organic matter, as they efficiently break down lignocellulosic materials common in forests (de Figueiredo et al. 2021). In contrast, Ascomycota species typically specialize in degrading cellulose and hemicellulose and are less efficient at lignin decomposition (Manici et al. 2024). Kerfahi et al. (2016) noted that limited lignin-rich substrates can restrict Basidiomycota abundance, highlighting their substrate preference. The Basidiomycota phylum features a reproductive structure called the basidium, which produces spores on its surface, facilitating more effective spore dispersal into the surrounding environment. In contrast, the Ascomycota phylum has an ascus structure, resulting in less efficient spore dispersal than the basidium. Additionally, developing hyphae and spores dispersed by air play a crucial role in enabling these fungi to adapt to terrestrial environments (Hurdeal et al. 2021).

Family and species-level composition

Macrofungal diversity in the three protection forests was high, as illustrated in Figure 3 and detailed in Table 1. GPPF recorded 44 species from 23 families, GMPF had 42 species from 20 families, and GSPF exhibited the most tremendous diversity with 54 species spanning 22 families. These results highlight the ecological diversity of each site, where different microhabitats and substrates sustain a broad spectrum of fungal species. The significantly greater species richness in GSPF indicates more favorable or diverse habitat conditions for macrofungal colonization and development.

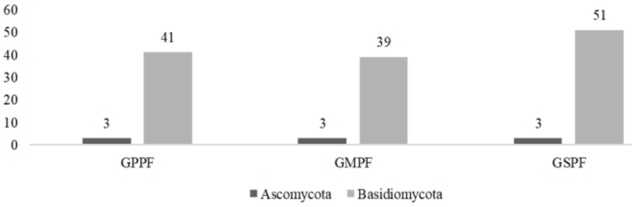

Figure 2. Macrofungal diversity in GPPF, GMPF, and GSPF based on the phyla present

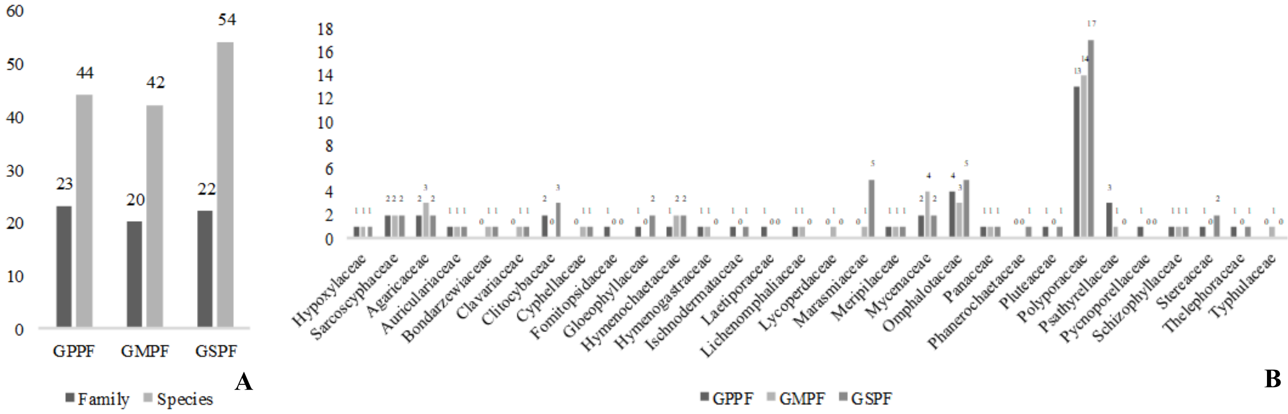

Figure 3. A. Number of macrofungal families and species in GPPF, GMPF, and GSPF, B. Number of species per family

Table 1. Macrofungal diversity in GPPF, GMPF, and GSPF

Family	Species	Location(s) present			Local name	Substrate(s)	Ecological guild
		GPPF	GMPF	GSPF			
			Ascomycota				
Hypoxylaceae	*Daldinia concentrica* (Bolton) Ces. & De Not.	✓	✓	✓	*Kulat kancing*	WD	S
Sarcoscyphaceae	*Cookeina speciosa* (Fr.) Dennis	-	✓	✓	*Kulat mangkok*	WD	S
	Cookeina sulcipes (Berk.) Kuntze	✓	-	-	*Kulat mangkok*	WD	S
	Cookeina tricholoma (Mont.) Kuntze	✓	✓	✓	*Kulat mangkok*	WD	S
			Basidiomycota				
Agaricaceae	*Cyathus striatus* Willd.	✓	✓	-	Unknown	WD	S
	Lepiota sp.1	-	✓	✓	*Kulat palngi*	WD	S
	Lepiota sp.2	✓	-	✓	*Kulat menahun*	WD	S
	Leucocoprinus sp.	-	✓	-	*Kulat tahun abu*	WD	S
Auriculariaceae	*Auricularia auricula-judae* (Bull.) Quél.	✓	✓	✓	*Kulat tembibir*	WD	S
Bondarzewiaceae	*Heterobasidion* sp.	-	✓	✓	Unknown	WD	P
Clavariaceae	*Ramariopsis* sp.	-	✓	✓	*Kulat tandok rusa*	WD	S
Clitocybaceae	*Clitocybe* sp.1	-	-	✓	*Kulat cawan*	WD	S
	Clitocybe sp.2	✓	-	✓	*Kulat cawan*	WD	S
	Clitocybe sp.3	✓	-	-	Unknown	WD	S
	Collybia sp.	-	-	✓	*Kulat payung*	WD	S
Cyphellaceae	*Cheimonophyllum candidissimum* (Berk. & M.A. Curtis) Singer	-	✓	✓	*Kulat bunge*	WD	S
Fomitopsidaceae	*Fomitopsis* sp.	✓	-	-	*Kulat kipas*	WD	S
Gloeophyllaceae	*Gloeophyllum* sp.1	✓	-	✓	*Kulat kayu*	WD	S
	Gloeophyllum sp.2	-	-	✓	Unknown	WD	S
Hymenochaetaceae	*Coltricia* sp.	-	✓	✓	*Kulat juang*	WD	S
	Hymenochaete sp.	✓	✓	-	Unknown	WD	S
	Xanthoporia sp.	-	-	✓	Unknown	WD	S
Hymenogastraceae	*Gymnopilus* sp.1	-	✓	-	Unknown	WD	S
	Gymnopilus sp.2	✓	-	-	Unknown	WD	S
Ischnodermataceae	*Ischnoderma* sp.	✓	-	✓	Unknown	WD	S
Laetiporaceae	*Phaeolus* sp.	✓	-	-	Unknown	WD	S
Lichenomphaliaceae	*Lichenomphalia* sp.	✓	✓	-	*Kulat ae' bak*	WD	M
Lycoperdaceae	*Lycoperdon perlatum* Pers.	-	✓	-	*Kulat bintik putih*	DL	S
Marasmiaceae	*Campanella* sp.1	-	-	✓	*Kulat buih*	WD	S
	Campanella sp.2	-	-	✓	*Kulat bunge*	WD	S
	Marasmius sp.1	-	-	✓	*Kulat rambut*	DL	S
	Marasmius sp.2	-	-	✓	Unknown	DL	S
	Tetrapyrgos sp.	-	✓	✓	*Kulat sunguro*	DL	S
Meripilaceae	*Rigidoporus microporus* (Sw.) Overeem	✓	✓	-	*Kulat kappah*	WD	P
	Rigidoporus ulmarius (Sowerby) Imazeki	-	-	✓	Unknown	WD	P
Mycenaceae	*Hemimycena* sp.	-	✓	✓	*Kulat payung*	WD	S
	Mycena sp.1	✓	✓	-	*Kulat bintang*	WD	S
	Mycena sp.2	-	✓	-	*Kulat temukut*	DL	S
	Mycena sp.3	✓	-	-	Unknown	DL	S
	Mycena sp.4	-	-	✓	*Kulat tanggoi*	DL	S
	Panellus sp.	-	✓	-	Unknown	WD	S
Omphalotaceae	*Collybiopsis* sp.1	✓	-	✓	*Kulat padi*	WD	S
	Collybiopsis sp.2	-	-	✓	*Kulat kapor*	WD	S
	Collybiopsis sp.3	-	-	✓	*Kulat abu*	WD	S
	Gymnopus sp.1	-	✓	-	Unknown	WD	S
	Gymnopus sp.2	-	✓	✓	Unknown	DL	S
	Gymnopus sp.3	✓	-	-	*Kulat koko*	DL	S
	Gymnopus androsaceus (L.) Della Magg. & Trassin.	✓	✓	-	Unknown	S	S
	Gymnopus foetidus (Sowerby) P.M. Kirk	-	-	✓	Unknown	WD	S
	Mycetinis sp.	✓	-	-	*Kulat paying*	DL	S
Panaceae	*Cymatoderma elegans* Jungh.	✓	✓	-	Unknown	WD	S
	Panus sp.	-	-	✓	*Kulat parut*	WD	S
Phanerochaetaceae	*Hapalopilus* sp.	-	-	✓	Unknown	WD	S
Pluteaceae	*Pluteus cervinus* (Schaeff.) P.Kumm.	✓	-	✓	Unknown	WD	S
Polyporaceae	*Cerioporus varius* (Pers.) Zmitr. & Kovalenko	-	-	✓	Unknown	WD	S

Family	Species	Location(s) present			Local name	Substrate(s)	Ecological guild
		GPPF	GMPF	GSPF			
	Daedaleopsis sp.1	✓	-	-	Unknown	WD	S
	Daedaleopsis sp.2	-	-	✓	*Kulat papan*	WD	S
	Earliella sp.	✓	-	-	Unknown	WD	S
	Fabisporus sanguineus (L.) Zmitr.	✓	-	✓	*Kulat limau*	WD	S
	Favolus tenuiculus P.Beauv.	-	✓	✓	*Kulat minyak*	WD	S
	Fomes sp.1	-	-	✓	Unknown	WD	S
	Fomes sp.2	-	-	✓	*Kulat batu*	WD	S
	Ganoderma applanatum (Pers.) Pat.	✓	✓	✓	*Kulat hati luka laki*	WD	S
	Ganoderma australe (Fr.) Pat.	✓	-	-	Unknown	WD	S
	Ganoderma lucidum (Curtis) P.Karst.	-	✓	✓	*Kulat badal ayam*	WD	S
	Ganoderma resinaceum Boud.	-	✓	✓	*Kulat hati ayam*	WD	S
	Lentinus crinitus (L.) Fr.	✓	-	-	Unknown	WD	S
	Lentinus sajor-caju (Fr.) Fr.	✓	-	-	Unknown	WD	S
	Lentinus squarrosulus Mont.	✓	-	-	*Kulat putih*	WD	S
	Lenzites sp.	-	✓	-	*Kulat kayu*	WD	S
	Microporus sp.	-	✓	✓	*Kulat kipas*	WD	S
	Microporus xanthopus (Fr.) Kuntze	-	✓	✓	Unknown	WD	S
	Podofomes sp.	-	-	✓	Unknown	WD	S
	Polyporus sp.1	-	✓	-	Unknown	WD	S
	Polyporus sp.2	-	✓	-	Unknown	WD	S
	Pseudofavolus tenuis (Fr.) G.Cunn.	-	✓	✓	*Kulat sarang wanyek*	WD	S
	Sanguinoderma rugosum (Blume & T.Nees) Y.F.Sun, D.H.Costa & B.K.Cui	✓	✓	✓	*Kulat hati luka laki*	WD, S	S
	Trametes sp.	-	✓	-	*Kulat merah*	WD	S
	Trametes elegans (Spreng.) Fr.	✓	✓	-	Unknown	WD	S
	Trametes gibbosa (Pers.) Fr.	-	-	✓	Unknown	WD	S
	Trametes hirsuta (Wulfen) Lloyd	-	-	✓	*Kulat telinge barok*	WD	S
	Trametes pubescens (Schumach.) Pilát	✓	-	-	Unknown	WD	S
	Trametes variegata (Berk.) Zmitr., Wasser & Ezhov	✓	✓	-	*Kulat kayu*	WD	S
	Trametes versicolor (L.) Lloyd	✓	-	✓	*Kulat kayu*	WD	S
Psathyrellaceae	*Coprinellus* sp.1	✓	-	-	Unknown	WD	S
	Coprinellus sp.2	✓	-	-	Unknown	WD	S
	Psathyrella sp.	✓	✓	-	*Kulat taon batang pisang*	WD	S
Pycnoporellaceae	*Pycnoporellus* sp.	✓	-	-	*Kulat kayu*	WD	S
Schizophyllaceae	*Schizophyllum commune* Fr.	✓	✓	✓	*Kulat karang*	WD	S
Stereaceae	*Stereum ostrea* (Blume & T.Nees) Fr.	✓	-	✓	*Kulat sisik*	WD	S
	Stereum rugosum Pers.	-	-	✓	*Kulat kerak*	WD	S
Thelephoraceae	*Thelephora caryophyllea* (Schaeff.) Pers.	✓	-	-	Unknown	S	M
	Thelephora terrestris Ehrh. ex Fr.	-	-	✓	*Kulat sisik tenggiling*	WD	M
Typhulaceae	*Typhula* sp.	-	✓	-	*Kulat jarum*	S	S

Note: DL: decomposing litter, S: soil, WD: wood debris for substrate types; M: mutualistic, P: parasitic, S: saprophytic for ecological guilds

Among the recorded families, Polyporaceae was the most species-rich, contributing 30 species: 13 in GPPF, 14 in GMPF, and 17 in GSPF. This aligns with broader trends in tropical Asia, where Polyporaceae are among the most diverse and ecologically dominant fungal families (Zhao et al. 2024). The Polyporaceae family is highly adaptable and resilient, which enables them to thrive in various ecological niches. Furthermore, the fruiting bodies of these organisms can withstand prolonged periods of desiccation, demonstrating their resilience to environmental stresses. This phenomenon can be attributed to their saprophytic lifestyle (Runnel et al. 2021) and the rigidity of their fruiting bodies, which are known to resist rapid decomposition (Joshi et al. 2021). This durability helps them survive longer and remain present in forest litter and on decaying wood. Fruitbodies of several macrofungal species found in the sites are presented in Figure 4.

Figure 4. Fruitbodies of several macrofungal species found in GPPF, GMPF, and GSPF: A. *Cookeina tricholoma* (Mont.) Kuntze, B. *Auricularia auricula-judae* (Bull.) Quél., C. *Trametes versicolor* (L.) Lloyd, D. *Lentinus crinitus* (L.) Fr., E. *Cyathus striatus* Willd., F. *Daldinia concentrica* (Bolton) Ces. & De Not., G. *Schizophyllum commune* Fr., H. *Ramariopsis* sp. (scale bar = 1 cm)

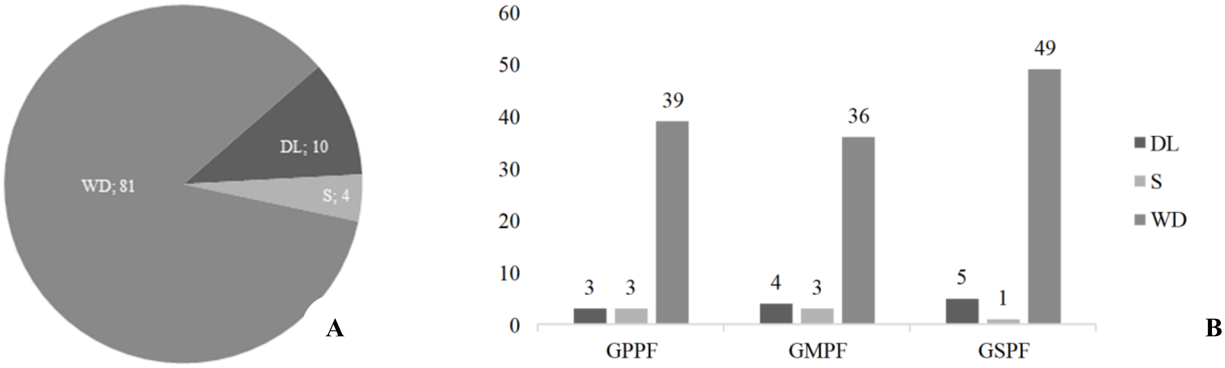

Figure 5. A. Macrofungal substrates in GPPF, GMPF, and GSPF, B. Number of species by substrate type (DL: decomposing litter, S: soil, WD: wood debris)

Substrate preferences

Each macrofungal species possesses distinct habitat preferences. Substrate types are pivotal in their growth and development (Suryani et al. 2024). Macrofungal diversity in the three protection forests was identified on three substrates: decomposing litter, soil, and wood debris (Table 1; Figure 5). Of the 94 species identified, 81 species (86.17%) were associated with wood debris, 10 species (10.63%) with decomposing litter, and 4 species (4.25%) with soil. Across all study sites, wood debris consistently supported the highest number of macrofungal species, with 39 species in GPPF, 36 in GMPF, and 49 in GSPF. In contrast, soil was the least colonized substrate, with only 3 species in GPPF, 3 in GMPF, and 1 in GSPF. Decomposing litter supported a small but increasing number of species from 3 in GPPF, 4 in GMPF, to 5 in GSPF. These results indicate that wood debris is the most favorable substrate for macrofungal growth in all three forest types. The predominance of wood debris as the primary substrate for macrofungi aligns with findings from numerous studies, including Nacua et al. (2018), Rahmawati et al. (2018), Zulpitasari et al. (2019), Daud et al. (2021), Widyastuti and Yeni (2022), Md Noordin et al. (2024), and Nordin et al. (2024).

The strong predominance of wood-inhabiting macrofungi highlights the key role of coarse woody debris in shaping macrofungal diversity in the study sites. Substrate complexity and availability, particularly of deadwood, are known to enhance fungal richness by providing diverse ecological niches (Shuhada et al. 2020). Wood decomposition is essential for forest nutrient cycling, soil formation, and carbon turnover (Wei 2021), processes in which macrofungal diversity is a significant biological agent (Niego et al. 2023). Interestingly, only one species—*Sanguinoderma rugosum* (Blume & T.Nees) Y.F.Sun, D.H.Costa & B.K.Cui—was observed growing on more than one substrate type. This species was found on both wood debris and soil, indicating a degree of ecological plasticity. *Sanguinoderma rugosum* has been observed to grow in humid and humus soil (Seng et al. 2017) and is also known to colonize dead coniferous wood (Hapuarachchi et al. 2018), reflecting its broad environmental tolerance.

Macrofungal ecological guilds

Ecologically, most terrestrial macrofungi can be categorized into three guilds: saprophytic, parasitic, and mutualistic (Martin and Tan 2025). In this study, all three ecological guilds were represented. Based on the inventory results, the majority of macrofungi—88 species (93.62%)—were saprophytic, while 3 species (3.19%) were parasitic, and the remaining 3 species (3.19%) were mutualistic. Most saprophytic macrofungi and all parasitic macrofungi (*Heterobasidion* sp., *Rigidoporus microporus* (Sw.) Overeem, and *Rigidoporus ulmarius* (Sowerby) Imazeki), were found on wood debris substrates. This finding is consistent with the statement by Ahmadni et al. (2024), which notes that macrofungi fruiting on decaying wood substrates can exhibit saprophytic or parasitic lifestyles.

The three macrofungal species classified as mutualistic were further divided into two types. The first type is ectomycorrhizal macrofungi, represented by *Thelephora caryophyllea* (Schaeff.) Pers., which fruits on soil, and *Thelephora terrestris* Ehrh. ex Fr., which fruits on wood debris. The genus *Thelephora* is generally known to form ectomycorrhizal associations with a wide range of host plants, but it is also capable of causing white rot (Liu et al. 2021). The second type consists of macrofungi associated with lichens, represented by *Lichenomphalia* sp., that grow on wood debris. *Lichenomphalia* Redhead, Lutzoni, Moncalvo & Vilgalys species form associations with unicellular green algae belonging to the genus *Coccomyxa* Schmidle, 1901 (Sandoval-Leiva et al. 2017). The presence of *Lichenomphalia* in the GPPF and GMPF indicates that the ecosystems in these protection forests remain relatively clean and stable, considering that lichens are highly sensitive to air pollution.

However, the representation of mutualistic macrofungi was very limited. The low occurrence of ectomycorrhizal macrofungi can be attributed to the scarcity of suitable host trees, as highlighted by Song et al. (2019) and Ye et al. (2019). Similarly, the poor representation of lichen-associated macrofungi, exemplified by *Lichenomphalia*, is likely shaped by several ecological and biological constraints. A key factor is the high specificity of symbiotic associations with particular algal partners, which, combined with narrow ecological niche specialization and limited adaptability to diverse habitat conditions, restricts their distribution (Rolshausen et al. 2018, 2020; Zuo et al. 2023). In addition, complex interactions with other microorganisms within lichen communities may further influence their abundance and persistence (Suryanarayanan and Thirunavukkarasu 2017). Abiotic factors such as microclimatic variation, substrate characteristics, and disturbance regimes likely impose additional constraints. These complexities were not examined in depth here and therefore warrant further studies to elucidate the mechanisms underlying the rarity of mutualistic fungi in protection forests.

Overall, the dominance of saprophytic macrofungi across all sites reflects a strong dependency on decomposing organic matter, particularly wood. At the same time, the minimal representation of parasitic and mutualistic guilds may be influenced by host availability and specific habitat conditions. The difference between the proportions of saprophytic, parasitic, and mutualistic macrofungal species highlights the functional composition of macrofungal communities in the studied forests. It underscores the importance of substrate type in shaping ecological guild dynamics.

Macrofungal habitat conditions

The three protection forests—GPPF, GMPF, and GSPF—shared similar environmental features, such as leaf-littered floors, fallen and decaying logs, hilly landscapes, and layered vegetation ranging from tall canopy trees over 30 meters to dense understory plants (Figure 6). These features are typical of tropical rainforest ecosystems and provide microhabitats favorable for macrofungal development. This observation aligns with the assertions put forth by Hu et al. (2022), who emphasized that vegetation structure, topography, and microclimatic conditions significantly influence macrofungal occurrence and diversity.

Five physicochemical parameters were measured to evaluate the ecological suitability of these forests for macrofungal growth and development: air and soil temperature, air humidity, soil pH, and light intensity (Figure 7). The air temperatures ranged from 26-31°C in GPPF, 29-32°C in GMPF, and 25-32°C in GSPF. Corresponding soil temperatures showed minor variations: 25-30°C in GPPF, 25-28°C in GMPF, and 25-29°C in GSPF. These values tend to fall within the optimal growth range for most macrofungal species. Macrofungi have been found to thrive at temperatures ranging from 16-30°C (Muzaki et al. 2024). A significant positive correlation between temperature, precipitation, and the fruiting of saprophytic macrofungi was demonstrated (Hu et al. 2022), as temperature influences metabolic processes and protein functions essential to fungal growth and development (Bakar et al. 2020). Mycelial growth of many fungal species occurs efficiently within the 5-30°C range (Back et al. 2015).

Figure 6. Environmental features in: A. GPPF, B. GMPF, C. GSPF

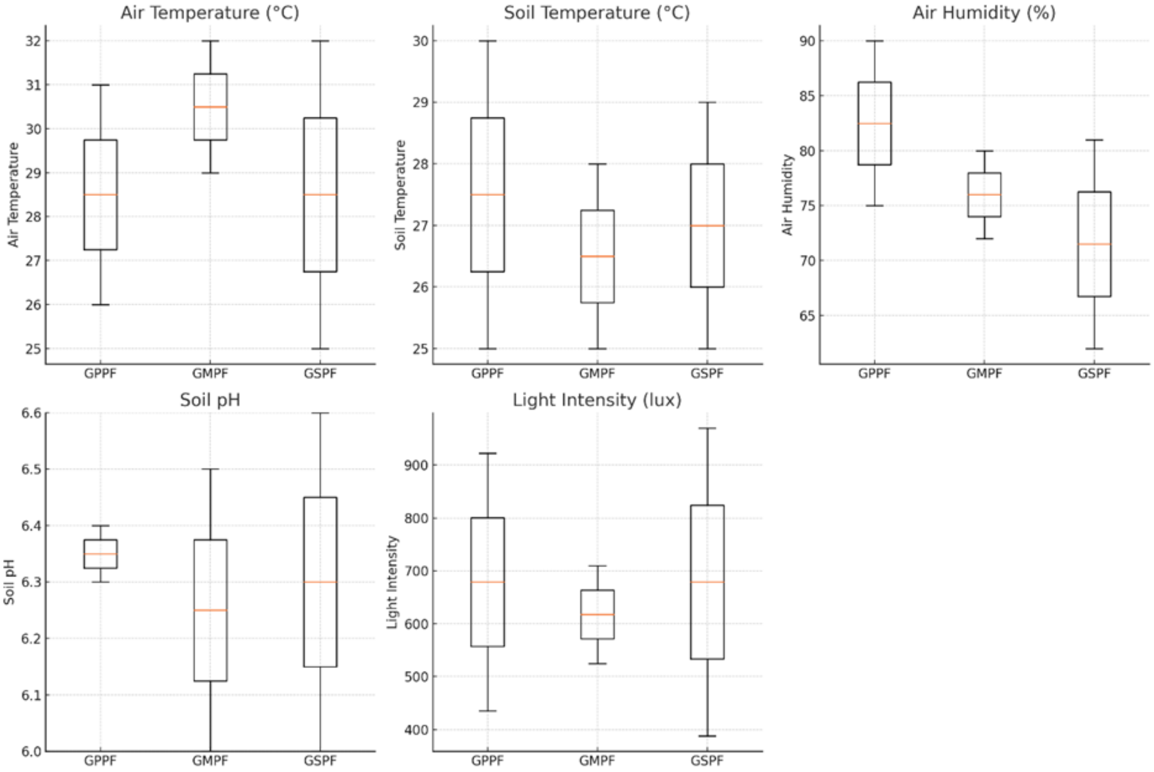

Figure 7. Environmental factors measurement results

The air humidity levels in the three protection forests were favorable for macrofungal growth, ranging from 75-90% in GPPF, 72-80% in GMPF, and 62-81% in GSPF. Macrofungi typically thrive at a humidity level of 80-95% (Muzaki et al. 2024). The positive association between humidity and fungal diversity is well-documented (Hu et al. 2022). High air humidity in GPPF, GMPF, and GSPF was attributable to the dense vegetation characteristic of the three designated protection forests. A significantly higher humidity level characterises the forest air than in open areas. This phenomenon is attributed to the continuous evaporation of water from the vegetation, which maintains a moist microclimate near the forest floor (Ren et al. 2020).

The soil pH levels across the three protection forests were slightly acidic: 6.3-6.4 in GPPF, 6.0-6.5 in GMPF, and 6.0-6.6 in GSPF. These values are consistent with those reported for tropical rainforest soils, which typically range from pH 4.3-6.5 (Nacua et al. 2018). Most fungal species exhibit optimal growth at pH values ranging from 3.0-8.5 (Mustafa et al. 2023). Substrate pH significantly affects macrofungal growth and carbon source utilization (Putra et al. 2023). It also influences the growth and sporulation of saprophytic and pathogenic fungi, with many species requiring specific pH ranges for optimal development (Mustafa et al. 2023).

The light intensity varied slightly between sites: 436-922 lux in GPPF, 525-710 lux in GMPF, and 388-970 lux in GSPF. Light is an important environmental cue in fungi, regulating primordia initiation and fruiting body development (Yue et al. 2022). The relatively low light intensity levels measured across all sites are due to the dense canopy, which limits light penetration to the forest floor. Increased light intensity can lead to higher evaporation rates and reduced humidity, which may, in turn, suppress macrofungal diversity (Putra et al. 2023).

Although the environmental factors measured across the three protection forests generally fall within optimal ranges for macrofungal growth, species richness varies among the sites, indicating the potential influence of microclimatic conditions on macrofungal diversity. The potential for such influence is supported by the findings of Pérez-Rosas et al. (2022), which demonstrate significant variation in macrofungal diversity across different vegetation types, consequently affecting local environmental factors. The GSPF exhibited the highest richness, with 54 species from 22 families, despite having the lowest air humidity range (62-81%) among the three protection forests. This suggests that factors other than humidity, such as broader light intensity variation (388-970 lux) and possibly greater microhabitat heterogeneity, may contribute to the higher diversity observed at this study site. The wide range of light availability in GSPF could support both shade-loving and more light-tolerant fungal species, enabling the coexistence of a broader spectrum of taxa. In contrast, the GPPF recorded the second-highest species richness (44 species from 23 families) and had the highest relative humidity (75-90%) and moderately stable temperature conditions (25-31°C). The high humidity in GPPF aligns with existing literature that identifies moisture as a key driver of fungal fruiting and mycelial activity, suggesting a positive correlation between ambient humidity and macrofungal richness in this site. The GMPF, with the lowest richness (42 species from 20 families), had the most stable but slightly narrower environmental ranges, including air humidity

(72-80%) and light intensity (525-710 lux), which may reflect less environmental variability and possibly reduced niche diversity for macrofungi. Soil pH across all sites ranged from 6.0 to 6.6 and remained within suitable limits for macrofungal development. This suggests that pH may not have been a limiting factor for species richness in this context. These findings suggest that macrofungal diversity is likely influenced by a combination of factors, where humidity and light variability appear to correspond most strongly with inter-site differences in species richness.

Macrofungal spatial distribution patterns

Biotic and abiotic factors influence the spatial distribution patterns of macrofungi in natural ecosystems. Distribution patterns are generally categorized into three distinct types: random, uniform, and clumped (Odum 1959). This study analyzed the spatial occurrence of macrofungal families in GPPF, GMPF, and GSPF using QGIS mapping (Figure 8). The spatial mapping revealed that macrofungal taxa were unevenly distributed, displaying a clumped pattern, typical of heterogeneous forest environments. Similar clumped patterns appeared in other studies, though not as consistently. For example, Izati et al. (2020) and Sharma et al. (2022) discovered that most taxa were clumped, while some displayed different distribution patterns. In contrast, our study showed that all taxa had a fully clumped distribution.

The clumped distribution patterns observed can be attributed to the variable and non-uniform nature of environmental factors and nutrient availability, which exhibit significant variations even within limited geographical areas (Hartini et al. 2021). Environmental factors in GPPF, GMPF, and GSPF show variations, albeit not significant. The distribution of substrate, especially deadwood and decaying organic material, is irregular across the forest floor and plays a crucial role in determining where macrofungi can establish and produce fruiting bodies. Moreover, microclimatic factors like moisture levels, shading, and slight temperature fluctuations—even as minimal as 0.1°C—can markedly influence fungal metabolism and development, leading to the uneven distribution of species (Rahmawati et al. 2018). For example, shaded valleys tend to hold more moisture and support distinct fungal communities than ridges exposed to sunlight. Variations in elevation and slope within these forests create environmental layers that promote spatial differentiation (Rahman et al. 2021). In support of this, Caiafa et al. (2017) demonstrated a significant positive correlation between macrofungal richness and elevation. Overall, these factors collectively generate clumped distributions, with macrofungi concentrated in microhabitats characterized by higher substrate availability, areas where canopy openings create favorable light and airflow conditions, and micro-sites that retain moisture longer, supporting fungal growth and reproduction.

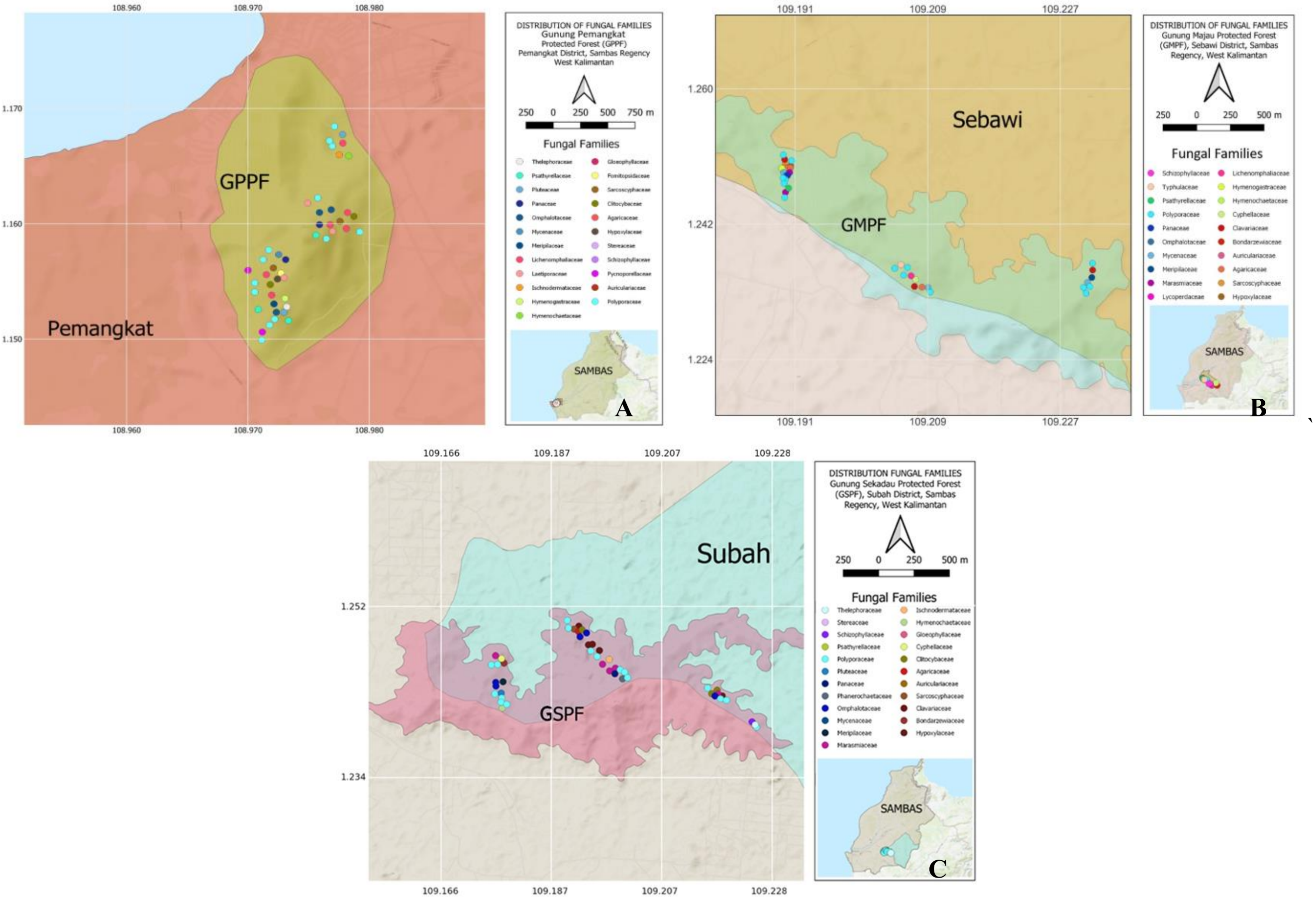

Figure 8. Macrofungal spatial distribution patterns in: A. GPPF, B. GMPF, C. GSPF

Ecological overlap and divergence were evident in the fungal families recorded. Eleven families—Agaricaceae, Auriculariaceae, Hymenochaetaceae, Hypoxylaceae, Meripilaceae, Mycenaceae, Omphalotaceae, Panaceae, Polyporaceae, Sarcoscyphaceae, and Schizophyllaceae—were common to all three protection forests, reflecting taxa that are well-adapted to a wide range of substrates and microhabitats. In contrast, several families displayed localized or site-restricted distributions. Fomitopsidaceae, Laetiporaceae, and Pycnoporellaceae occurred exclusively in GPPF, suggesting specialized habitat requirements or limited spore dispersal. Lycoperdaceae and Typhulaceae were found only in GMPF, while Phanerochaetaceae was unique to GSPF. Other families, such as Clitocybaceae, Gloeophyllaceae, and Stereaceae, were shared between only two sites, indicating intermediate distribution breadths and potential ecological filtering.

These distribution patterns support the notion that macrofungal communities are influenced by niche factors, such as substrate specialization and microclimate preferences, and by limitations in spore dispersal. Wind, insects, or animals spread spores, and forest features like canopy density and wind pathways can either aid or restrict their movement. For instance, the denser canopy in GSPF helps maintain humidity, benefiting certain wood-decaying fungi missing in more open or disturbed sites. The variation in family diversity and their uneven distribution across sites highlight subtle ecological boundaries within the larger tropical forest ecosystem of Sambas District. Beyond providing a biodiversity baseline, these spatial patterns carry important conservation implications. The protection forests acts as vital refuges for macrofungal diversity, particularly for species with limited ranges or specific habitat requirements. Importantly, the status of these forests as designated protection areas minimizes anthropogenic pressures such as logging, land clearing, and human settlement, thereby preserving microhabitat integrity and allowing natural ecological processes to shape fungal community structures. The study by Yu et al. (2021) showed a positive relationship between macrofungal distribution patterns probability and human activity. Recording these patterns is essential for ongoing ecological monitoring, especially in the face of climate change or habitat disruption.

Macrofungal potential uses

Macrofungal diversity plays a vital ecological and economic role in forest ecosystems, particularly in protected areas where biodiversity conservation is prioritized. Beyond their ecological importance, many macrofungal species have potential applications in daily life, such as food and medicine. Table 2 presents the mushroom specimens successfully identified to the species level and their documented food and/or medicinal values, where applicable.

The potential uses of the macrofungal species identified in this study are emphasized in their established roles as food and medicine, supported by documented ethnomycological studies and empirical reports of medicinal applications. In many regions, macrofungi are regarded as one of the most popular non-timber forest products (NTFPs) with significant economic value for local livelihoods (Kewessa et al. 2023), particularly in supporting food security and traditional healthcare systems. As noted by Teke et al. (2018), macrofungi have a long-standing association with humankind and exert profound biological and economic impacts. Their uses as NTFPs in daily life are deeply rooted in the traditional knowledge of indigenous communities, forming the basis of ethnomycology. Ethnomycology plays a critical role in understanding the cultural interactions between humans and fungi (Faturrahman and Yeni 2024; Yeni et al. 2025). These interactions generate insights into diverse uses of macrofungi, ranging from food and medicine to recreational purposes, ecological indicators, ceremonial practices, and local beliefs (Ríos-García et al. 2023). Recognizing these roles places macrofungi within broader conservation narratives, particularly in Borneo, where macrofungi represent important NTFPs that can strengthen community-based conservation strategies and livelihood resilience. Therefore, documenting macrofungal diversity is essential not only for ecological understanding but also for enhancing human well-being.

More than half of the macrofungi identified at the species level in GPPF, GMPF, and GSPF are recognized for their nutritional or medicinal value, underscoring their importance in both dietary and pharmacological contexts. Edible mushrooms are among the most valuable natural resources, serving as a significant nutritional source for much of the global population, while many species also possess medicinal properties due to their bioactive compounds (Živković et al. 2021; Gafforov et al. 2023; Yusran et al. 2024a). Notably, genera such as *Ganoderma* P.Karst., *Rigidoporus* Murrill, and *Trametes* Fr. are well-represented in medicinal uses. The presence of commonly consumed edible species such as *Auricularia auricula-judae* (Bull.) Quél., *Cookeina tricholoma* (Mont.) Kuntze, *Lentinus crinitus* (L.) Fr., and *Schizophyllum commune* Fr. highlights the potential to develop local food resources, particularly in forest-adjacent communities. Meanwhile, the species *Cheimonophyllum candidissimum* (Berk. & M.A. Curtis) Singer, *Cymatoderma elegans* Jungh., *Gymnopus foetidus* (Sowerby) P.M.Kirk, and *T. caryophyllea* remain underexplored, with their potential uses listed as unknown, indicating opportunities for future bioprospecting and pharmacological screening.

Overall, the potential uses of macrofungi extend beyond their essential ecological roles that underpin forest ecosystem health. In addition to contributing to nutrient cycling, soil fertility enhancement, and carbon dynamics regulation, macrofungi provide significant benefits to human well-being, including sources of nutrition, traditional medicine, and bioactive compounds for pharmaceutical applications (Mishra and Shankar 2025). Integrating the conservation and sustainable utilization of macrofungi into forest management strategies is therefore imperative. Preserving macrofungal diversity not only sustains ecosystem services and strengthens climate resilience but also supports local communities reliant on edible and medicinal species. Recognizing the multifunctional roles of macrofungi can further guide policymakers and conservation practitioners in developing interventions that balance ecological preservation with socio-economic development. By incorporating macrofungal diversity into forest conservation planning, it becomes possible to simultaneously safeguard ecosystem integrity, promote sustainable resource use, and advance broader objectives, including food security, traditional healthcare, and climate change mitigation.

In conclusion, this study systematically documents the macrofungal diversity in GPPF, GMPF, and GSPF, comprising 94 species from 30 families within Ascomycota and Basidiomycota. It provides the first baseline assessment of macrofungal diversity in the three primary protection forests of Sambas District, highlighting the ecological significance and potential conservation value of these communities. While some taxa were unique to individual sites, the overall diversity underscores the importance of habitat heterogeneity and substrate availability. Most species were saprophytic and closely associated with wood debris, emphasizing the critical role of deadwood in sustaining macrofungal communities and maintaining ecosystem health and resilience in tropical forests. Furthermore, the evaluation of their potential uses in food and medicine demonstrates that macrofungi contribute not only to ecological functioning but also to human livelihoods as important NTFPs with socio-economic roles. Notably, several species remain unassessed for their nutritional or medicinal potential, representing significant opportunities for future studies and sustainable utilization.

Table 2. Macrofungal potential uses

Species	**Potential uses**			**Reference(s)**
	Food	**Medicine**	**Unknown**	
Auricularia auricula-judae (Bull.) Quél.	✓			Yeni et al. (2025)
Cerioporus varius (Pers.) Zmitr. & Kovalenko		✓		Sevindik (2019)
Cheimonophyllum candidissimum (Berk. & M.A. Curtis) Singer			✓	None (potential not yet evaluated)
Cookeina speciosa (Fr.) Dennis		✓		Yusran et al. (2024b)
Cookeina sulcipes (Berk.) Kuntze	✓			Yeni et al. (2025)
Cookeina tricholoma (Mont.) Kuntze	✓			Yeni et al. (2025)
Cyathus striatus Willd.		✓		Fares et al. (2022)
Cymatoderma elegans Jungh.			✓	None (potential not yet evaluated)
Daldinia concentrica (Bolton) Ces. & De Not.		✓		Teke et al. (2018)
Fabisporus sanguineus (L.) Zmitr.	✓			Yusran et al. (2024a)
Favolus tenuiculus P.Beauv.	✓			Teke et al. (2018)
Ganoderma applanatum (Pers.) Pat.		✓		Teke et al. (2018)
Ganoderma australe (Fr.) Pat.		✓		Zhou et al. (2022)
Ganoderma lucidum (Curtis) P.Karst.		✓		Živković et al. (2021)
Ganoderma resinaceum Boud.		✓		Sipping et al. (2022)
Gymnopus androsaceus (L.) Della Magg. & Trassin.		✓		Song et al. (2018)
Gymnopus foetidus (Sowerby) P.M.Kirk			✓	None (potential not yet evaluated)
Lentinus crinitus (L.) Fr.	✓			Ríos-García et al. (2023)
Lentinus sajor-caju (Fr.) Fr.	✓			Yeni et al. (2025)
Lentinus squarrosulus Mont.	✓	✓		Teke et al. (2018)
Lycoperdon perlatum Pers.	✓			Živković et al. (2021)
Microporus xanthopus (Fr.) Kuntze		✓		Yeni et al. (2025)
Pluteus cervinus (Schaeff.) P.Kumm.	✓			Daud et al. (2021)
Pseudofavolus tenuis (Fr.) G.Cunn.		✓		Umeyama et al. (2014)
Rigidoporus microporus (Sw.) Overeem		✓		Oba et al. (2020)
Rigidoporus ulmarius (Sowerby) Imazeki		✓		Oba et al. (2020)
Sanguinoderma rugosum (Blume & T.Nees) Y.F.Sun, D.H.Costa & B.K.Cui		✓		Chan et al. (2025)
Schizophyllum commune Fr.	✓			Yeni et al. (2025)
Stereum ostrea (Blume & T.Nees) Fr.		✓		Tian et al. (2020)
Stereum rugosum Pers.		✓		Tian et al. (2020)
Thelephora caryophyllea (Schaeff.) Pers.			✓	None (potential not yet evaluated)
Thelephora terrestris Ehrh. ex Fr.		✓		Radulović et al. (2005)
Trametes elegans (Spreng.) Fr.		✓		Awala and Oyetayo (2015)
Trametes gibbosa (Pers.) Fr.		✓		Knežević et al. (2015)
Trametes hirsuta (Wulfen) Lloyd		✓		Knežević et al. (2015)
Trametes pubescens (Schumach.) Pilát		✓		Im et al. (2016)
Trametes variegata (Berk.) Zmitr., Wasser & Ezhov		✓		Silva et al. (2009)
Trametes versicolor (L.) Lloyd		✓		Teke et al. (2018)

Despite these insights, several limitations should be acknowledged. Sampling was conducted over a relatively short period, potentially overlooking seasonal variation in fruiting patterns. Identification relied primarily on morphological characters, which may underestimate species richness due to cryptic taxa, and spatial analysis was limited to basic occurrence mapping without detailed statistical evaluation. Future studies should adopt long-term monitoring frameworks to capture temporal shifts in macrofungal diversity and distribution in response to seasonal changes and anthropogenic pressures, integrating molecular and anatomical identification techniques, advanced spatial analyses, and systematic ethnomycological surveys. Incorporating local knowledge can enhance biodiversity monitoring and support participatory conservation strategies, ensuring sustainable utilization of macrofungal resources. Additionally, further investigation into the functional redundancy and uniqueness within macrofungal guilds is needed to understand how the loss of specific species may impact ecosystem resilience. To enable rigorous quantitative assessments of diversity, future studies are encouraged to collect quantitative data suitable for statistical analyses.

The results have clear implications for forest management and conservation policy in Borneo. Preserving fungal diversity, recognizing macrofungi as indicators of forest biodiversity, and integrating them into management planning can enhance ecosystem services, strengthen climate resilience, and support local communities dependent on edible and medicinal fungi. By establishing this baseline, the study contributes novel data that can inform regional biodiversity strategies and guide interventions that balance ecological preservation with socio-economic development. Ultimately, macrofungi represent both a critical component of tropical forest ecosystems and a key resource for sustainable development, underscoring their central role in maintaining biodiversity and ecosystem resilience in the region.

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