UMAR HUSSAINI BIN TARMIZI

MASTER OF SCIENCE

2025

DIVERSITY, COMPOSITION AND ACTIVITY OF SOIL BIOTA FROM DIFFERENT CONTRASTING HABITATS OF TERENGGANU, MALAYSIA

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Thesis Submitted in Fulfilment of the Requirement for the Master of Science in the Institute of Tropical Biodiversity and Sustainable Development Universiti Malaysia Terengganu

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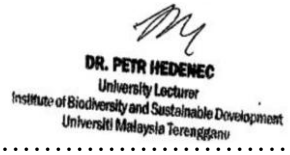

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DEDICATION

This work is dedicated to my beloved family, whose unwavering support and encouragement have been my guiding light throughout this journey.

To my mother, Jamilah binti Ani, whose love, strength, and sacrifices have been a constant source of inspiration.

To my father, Tarmizi bin Awang Hamat, whose wisdom, patience, and unwavering support have been my foundation.

To my friends, whose constant support, camaraderie, and understanding have been invaluable, especially during the most challenging times.

To my mentors and teachers whose invaluable guidance and insightful feedback were essential to this work.

May Allah bless

Abstract of thesis presented to the Senate of Universiti Malaysia Terengganu in fulfilment of the requirements for the degree of Master of Science

DIVERSITY, COMPOSITION AND ACTIVITY OF SOIL BIOTA FROM DIFFERENT CONTRASTING HABITATS OF TERENGGANU, MALAYSIA

UMAR HUSSAINI BIN TARMIZI

DECEMBER 2025

Main Supervisor : **Petr Heděnec, Ph.D**

Co-Supervisor : **Amirah Alias, Ph.D**

School/Institute : **Institute of Tropical Biodiversity and Sustainable Development**

Tropical soil biodiversity remains poorly understood compared to temperate and boreal regions, despite its critical role in maintaining ecosystem functioning such as organic matter transformation and regulating climate processes. Although numerous studies on soil biodiversity have been conducted in Malaysia, information on belowground communities across different natural and anthropogenic habitats in Terengganu remains understudied. Addressing this regional gap is important for conserving biodiversity, enhancing soil functions such as organic matter transformation, as well as informing sustainable land-use practices. This study examined the diversity, composition, and metabolic activity of soil bacteria, fungi, and soil meso- and macrofauna across natural and anthropogenic habitats in Terengganu using a combination of amplicon sequencing, greenhouse gas (GHG) flux measurements, volatile organic compound (VOC) profiling, and litterbag experiments. Results showed that tropical rainforests harbored the highest microbial and faunal diversity, whereas urban soils showed the lowest biodiversity. Soil texture emerged as the primary environmental factor influencing the structure of soil communities, and both taxonomic and functional groups varied distinctly among habitats. GHG

emissions and VOC profiles differed across land-use types, reflecting changes in microbial metabolic activity. Litterbag experiments revealed significant differences in decomposition rates among habitats, incubation periods, and accessibility for soil meso and macrofauna. Soil macrofauna accelerated decomposition in permaculture systems, whereas mesofauna played a greater role in urban soils, likely because urban soils support fewer large soil invertebrates but still maintain active mesofaunal communities. Overall, faunal effects became more pronounced with longer incubation periods. These findings highlight the complex relationships between soil biota and environmental factors in tropical ecosystems and demonstrate the key contribution of soil organisms to litter decomposition and ecosystem processes. This research expands understanding of tropical soil biodiversity in Terengganu, underscores its ecological importance, and provides baseline knowledge to guide conservation, land-use management, and climate change mitigation strategies.

Abstrak tesis yang dikemukakan kepada Senat Universiti Malaysia Terengganu sebagai memenuhi keperluan untuk Ijazah Sarjana Sains

DIVERSITI, KOMPOSISI DAN AKTIVITI BIOTA TANAH DARIPADA HABITAT BERBEZA DI TERENGGANU, MALAYSIA

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Kepelbagaian biodiversiti tanah tropika masih kurang difahami berbanding kawasan beriklim sederhana dan boreal, walaupun ia memainkan peranan penting dalam mengekalkan fungsi ekosistem seperti penguraian bahan organik dan pengawalan proses iklim. Walaupun banyak kajian mengenai biodiversiti tanah telah dijalankan di Malaysia, maklumat tentang komuniti bawah tanah merentasi habitat semula jadi dan antropogenik di Terengganu masih kurang diterokai. Menangani jurang pengetahuan ini penting bagi pemuliharaan biodiversiti, meningkatkan fungsi tanah seperti penguraian bahan organik, serta memberi panduan kepada amalan guna tanah yang lestari. Kajian ini meneliti kepelbagaian, komposisi dan aktiviti metabolik bakteria tanah, kulat, mesofauna dan makrofauna tanah merentasi habitat semula jadi dan antropogenik di Terengganu dengan menggunakan gabungan kaedah penjujukan amplicon, pengukuran fluks gas rumah hijau (GHG), pemprofilan sebatian organik meruap (VOC), dan eksperimen ”litterbag”. Hasil kajian menunjukkan bahawa hutan hujan tropika mempunyai kepelbagaian mikrob dan fauna yang tertinggi, manakala tanah ”urban” menunjukkan tahap biodiversiti yang paling rendah. Tekstur tanah muncul sebagai faktor persekitaran utama yang mempengaruhi struktur komuniti tanah, dan kumpulan taksonomi serta fungsi berbeza dengan jelas antara habitat. Pelepasan GHG dan profil VOC turut berbeza mengikut jenis guna tanah,

mencerminkan perubahan dalam aktiviti metabolik mikrob. Eksperimen ”litterbag” menunjukkan perbezaan ketara dalam kadar penguraian antara habitat, tempoh inkubasi, serta tahap kebolehcapaian oleh mesofauna dan makrofauna tanah. Makrofauna tanah mempercepatkan penguraian dalam sistem permakultur, manakala mesofauna memainkan peranan lebih besar dalam tanah bandar, kemungkinan kerana tanah bandar menyokong bilangan invertebrata besar yang lebih sedikit tetapi masih mengekalkan komuniti mesofauna yang aktif. Secara keseluruhannya, kesan fauna menjadi lebih ketara dengan tempoh inkubasi yang lebih panjang. Penemuan ini menekankan hubungan kompleks antara biota tanah dan faktor persekitaran dalam ekosistem tropika serta menunjukkan sumbangan penting organisma tanah terhadap penguraian sampah daun dan proses ekosistem. Kajian ini memperluas pemahaman tentang biodiversiti tanah tropika di Terengganu, menegaskan kepentingan ekologinya, dan menyediakan pengetahuan asas untuk membimbing usaha pemuliharaan, pengurusan guna tanah, serta strategi mitigasi perubahan iklim.

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Thank you all for your support and contributions.

APPROVALS

I certify that an Examination Committee has met on 25th June 2025 to conduct the final examination of Full Name, on his Master thesis entitled **"DIVERSITY, COMPOSITION AND ACTIVITY OF SOIL BIOTA FROM DIFFERENT CONTRASTING HABITATS OF TERENGGANU, MALAYSIA"** in accordance with the regulations approved by the Senate of Universiti Malaysia Terengganu. The Committee recommends that the candidate be awarded the relevant degree. The members of the Examination Committee are as follows:

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This thesis has been accepted by the Senate of Universiti Malaysia Terengganu in fulfilment of the requirement for the degree of Master of Science.

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Universiti Malaysia Terengganu

Date:

DECLARATION

I hereby declare that the thesis is based on my original work except for quotations and citations which have been duly acknowledged. I also declare that it has not been previously or concurrently submitted for any other degree at UMT or other institutions.

UMAR HUSSAINI BIN TARMIZI

Date: 7/12/2025

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LIST OF ABBREVIATIONS

AM	Arbuscular Mycorrhizas
ANOVA	Analysis of Variance
CH_4	Methane
CO_2	Carbon Dioxide
ddH_2O	Double-distilled Water
DNA	Deoxyribonucleic Acid
ECM	Ectomycorrhizas / Ectomycorrhizal Fungi
FRGS	Fundamental Research Grant Scheme
GC–MS	Gas Chromatography–Mass Spectrometry
GHG	Greenhouse Gas
GHGs	Greenhouse Gases
ITS	Internal Transcribed Spacer
MARA	Majlis Amanah Rakyat
MOHE	Ministry of Higher Education
N	Nitrogen
N_2O	Nitrous Oxide
NMDS	Non-Metric Multidimensional Scaling
OM	Organic Matter
OTU	Operational Taxonomic Unit
P	Phosphorus
PCA	Principal Component Analysis
PCR	Polymerase Chain Reaction
POM	Particulate Organic Matter
SHS	Static Headspace Sampling

SOM	Soil Organic Matter
spp.	Multiple Species
TN	Total Nitrogen
TOC	Total Organic Carbon
UMT	Universiti Malaysia Terengganu
VOC	Volatile Organic Compound
VOCs	Volatile Organic Compounds

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CHAPTER 1

INTRODUCTION

1.1 Background of the Study

Soil biotas comprise a diverse community of organisms that are broadly categorized into microflora, microfauna, mesofauna, and macrofauna, each playing distinct ecological roles. Soil biodiversity plays a crucial role in maintaining ecosystem functions and services such as nutrient release, litter decomposition and the transformation of soil organic matter (Guerra et al., 2021). The microflora, including bacteria, fungi, actinomycetes, algae, and cyanobacteria, contribute significantly to nutrient cycling, soil structure formation, organic matter decomposition, and plant health (Chen et al., 2024; Fierer, 2017; Frouz, 2018; Guerra et al., 2021). Microfauna, primarily protozoa and nematodes, regulate microbial populations and facilitate nutrient mineralization, while mesofauna such as mites and springtails contribute to organic matter fragmentation and enhance microbial activity (Coleman et al., 2018). The macrofauna, including earthworms, termites, ants, and beetles, improve soil aeration, aggregation, and nutrient redistribution through bioturbation (Lavelle et al., 2006). Together, these organisms form a complex, interdependent system that regulate essential soil processes and contribute to the overall resilience of terrestrial ecosystems (Kiprotich et al., 2025). Studying soil biota provides vital insights into maintaining soil health, ensuring food security, and promoting sustainable land management under changing environmental conditions (Bardgett & van der Putten, 2014).

Research on soil biota in tropical countries has gained significant attention, reflecting growing recognition of its role in ecosystem functioning, soil fertility, and climate regulation. A comprehensive systematic review of soil ecosystem services in tropical regions by Rodrigues et al. (2021) emphasized the complexity of soil biotic interactions and their contributions to carbon sequestration, nutrient cycling, and resilience to land degradation. A study by Fujii et al. (2018) that focused on plant–soil interactions reveals that tropical ecosystems maintain high biodiversity partly due to dynamic feedback between plants and soil organisms. Their findings suggest that soil microbial communities mediate key ecological processes like decomposition and nitrogen fixation, thereby supporting biodiversity in nutrient-poor tropical soils. In addition, Gomes et al. (2017) examined the impact of environmental stressors and contaminants on tropical soil organisms by assessing the ecotoxicological risks of emerging pollutants such as microplastics and pesticides, noting that tropical soils are particularly vulnerable due to intense agricultural activities and weak regulatory enforcement. Furthermore, addressing the integration of local ecological knowledge that remains limited, Pauli et al. (2016) highlighted that farmers in tropical regions possess valuable experiential knowledge of soil fauna and fertility management, yet such insights are rarely incorporated into formal scientific research. Bridging this gap could enhance the co-production of knowledge for sustainable soil management in tropical agroecosystems. In summary, research on soil biota underscores that tropical soil biota underpins critical ecosystem services but remains underexplored relative to temperate regions.

In Malaysia, research on soil biota has expanded significantly in recent decades. Studies have examined soil microorganisms, mesofauna, and macrofauna across diverse ecosystems, including rainforests, plantations, peatlands, mangroves, and agricultural fields, in Kedah, Perak, Selangor, Sarawak and Sabah (Ahmad et al., 2023; Chin & Wong, 2022; Jeyanny et al., 2018; Kerfahi et al., 2016; Tripathi et al., 2012, 2013). These studies consistently highlight the high diversity of soil microbial communities, with pH, land use, and soil properties being key drivers of community composition and function (Ahmad et al., 2023; Chen et al., 2024; Kerfahi et al., 2016; Tripathi et al., 2012, 2013). Land-use changes, particularly forest conversion to oil palm and rubber plantations, have been shown to shift the composition of microbial

and faunal communities, though not always reducing overall diversity (Yang et al., 2023; Zhang et al., 2022). However, existing studies are often geographically concentrated and do not adequately cover the full range of environmental settings across the country. In particular, the research on soil biota in the eastern part of peninsular Malaysia, such as Terengganu state, remains understudied. This lack of baseline information on soil biota presents a significant gap in understanding how soil biodiversity varies spatially within Terengganu and how it may be affected by local anthropogenic pressures such as land development, agriculture, and urban expansion.

1.2 Problem Statement and Justification

The studies in Terengganu often focus on soil chemistry or aboveground diversity (Khairil et al., 2015; Mahmud et al., 2020; Rawi & Shahrudin, 2021). The state's soils, particularly in tropical forests and coastal vegetation, tend to be more nutrient-poor, sandy, and acidic compared to other Malaysian regions (Kamoona et al., 2023; Rawi & Shahrudin, 2021). These unique edaphic conditions likely influence the composition of both plant and soil communities. With little emphasis on the extremely rich but almost unknown belowground biodiversity, our understanding of the diversity and ecological roles of soil microorganisms, mesofauna, and macrofauna in this region remains limited. In addition, methodological challenges, such as underrepresentation of certain taxa, absence of standardized protocols, and the lack of long-term, large-scale studies, further constrain our understanding. Without such data, it is challenging to make informed decisions regarding land use, conservation planning, or biodiversity management that are specific to Terengganu’s context. Therefore, efforts to map soil biodiversity, quantify functional diversity, and mitigate anthropogenic pressures are essential to ensuring tropical Terengganu soils continue to sustain agriculture, forest productivity, and climate regulation. Collaborative, interdisciplinary, and locally informed studies are crucial for advancing the ecological and practical understanding of tropical soil biota.

1.3 Research Questions

The research questions are as follows:

1. How do soil bacteria, fungi and soil meso and macro fauna vary between natural and anthropogenic tropical ecosystems across Terengganu, Malaysia, and what patterns emerge along the land-use intensity gradient?
2. How variations in soil physico-chemical properties influence the diversity, abundance, and community composition of soil biota (bacteria, fungi and soil meso and macrofauna) across contrasting natural and anthropogenic habitats in tropical ecosystems?
3. How do differences in soil microbial community structure and soil properties affect microbial metabolic activity, as indicated by species-specific VOCs and greenhouse gas fluxes, along a gradient of land-use intensity?
4. How do variations in soil diversity influence litter decomposition rates across natural and anthropogenic habitats in tropical ecosystems?

1.4 Objectives

This study specifically embarks to: -

1. To assess the diversity and structure of soil biota in soils taken from various contrasting natural and anthropogenic habitats across Terengganu.
2. To examine how variations in soil physico-chemical properties shape the diversity, abundance, and community structure of soil biota across contrasting natural and anthropogenic habitats in tropical ecosystems.
3. To detect and analyse activity of soil microbiota using species-specific Volatile Organic Compounds (VOCs) as well as greenhouse gas fluxes (GHG) by soil bacteria and fungi.
4. To investigate effect of soil fauna on litter decomposition rates using field litterbag experiment on different natural and anthropogenic sites across Terengganu Malaysia.

1.5 Hypotheses

1. We expect that variations in the diversity, community composition and activity of bacteria, fungi and soil meso and macro fauna across natural and anthropogenic habitats will reflect the gradient of land-use intensity, with natural sites maintaining more stable soil conditions compared to anthropogenic habitats.
2. We hypothesize that the differences in diversity, abundance, and activity of soil bacteria, fungi, and soil meso and macrofauna in soils from natural and anthropogenic habitats are expected to be primarily driven by variation in soil physico-chemical properties, such as texture, pH, nutrient levels, organic matter content, and moisture availability.
3. We hypothesize that the metabolic activity of soil microbial communities based on analyses of VOCs and GHG fluxes will differ significantly between natural and anthropogenic habitats. These differences will be reflected in distinct profiles of species-specific VOCs and greenhouse gas fluxes, corresponding to the microbial composition and environmental conditions of each habitat.
4. We hypothesize that the presence of soil animals will lead to higher rates of litter decomposition compared to conditions where soil animals are absent. Specifically, litterbags designed to allow access to a greater diversity or broader range of soil biota, such as microfauna, mesofauna, and macrofauna, are expected to experience more rapid decomposition, due to the enhanced physical fragmentation and microbial stimulation facilitated by these organisms.

CHAPTER 2

LITERATURE REVIEW

2.1 Soil Biota

Soils host a large diversity of organisms. For example, a single gram of Chernozem soil hosts thousands of microbial species (Fierer, 2017). Soil biota encompass a vast diversity of organisms that inhabit the soil, ranging from microscopic microbes to larger invertebrates. They are broadly classified into microflora, microfauna, mesofauna, and macrofauna (Swift et al., 1979), each performing distinct but interconnected ecological roles (Figure 2.1). This classification not only highlights the size diversity but also reflects the functional roles these organisms play in maintaining soil health and ecosystem balance (Coleman & Wall, 2015; Lavelle, 1997; Menta, 2012).

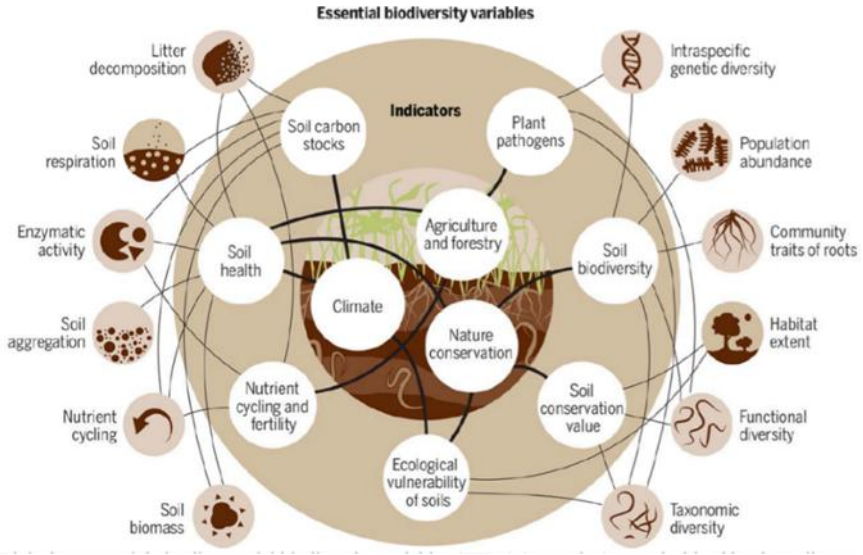

Figure 2.1 Schematic diagram of ecosystem functions and services (Guerra et al. 2021)

The microflora or microbiota refers to the community of microscopic organisms, including bacteria, fungi, actinomycetes, algae, and cyanobacteria. These microorganisms are central to nutrient cycling, organic matter decomposition, and the maintenance of soil fertility. For instance, actinobacteria and cyanobacteria are also significant due to their roles in decomposing complex organic materials and nitrogen fixation, respectively (Bhatti et al., 2017; Massey & Davis, 2023). Soil microbiotas play several vital ecological roles, including nutrient cycling, where they decompose organic matter and release essential nutrients like nitrogen, phosphorus, and sulphur back into the soil for plant absorption. They also contribute to the formation of humus, which improves soil structure and fertility, and enhances soil aggregation and stability, leading to better water retention and aeration. Additionally, certain soil microbiota forms symbiotic relationships with plants, promoting growth and providing protection against pathogens, while others inhibit the growth of soil-borne diseases, thereby contributing to plant health (Almario et al., 2022; Lazcano et al., 2021). Despite their importance, studying soil microbiota remains challenging because only a small fraction, approximately 5% is cultivable using traditional methods. However, advancements in DNA sequencing methods have greatly improved our ability to characterize soil microbial communities beyond cultivable species (Garg et al., 2024). Additionally, instrumental techniques such as gas chromatography-mass spectrometry (GC-MS) allow researchers to study the metabolic products of soil biota and assess their functional activity, providing deeper insights into their ecological roles (Withers et al., 2020).

Soil fauna are animals, primarily invertebrates, inhabiting the soil. They consist of various functional and trophic groups, including bacterial feeders, fungal feeders, predators, saprophages, herbivores, and omnivores. Soil fauna is involved in key ecosystem processes such as nutrient release or decomposition and transformation of soil organic matter (Heděnec et al., 2022a). The soil microfauna are animals with a body width smaller than 0.2 mm (Swift et al., 1979). These microscopic animals, typically less than 0.1 mm in size, are essential for nutrient cycling and decomposition, as they feed on microorganisms and help break down organic matter. Microfauna includes protozoa, nematodes, tardigrades, and small unsegmented worms. Protozoa, as single-celled organisms, are a major component of soil microfauna and play a vital

role in nutrient cycling by feeding on smaller microorganisms that decompose organic material. Soil microfauna are primarily filtrators or microbial feeders, consuming bacteria, fungi, and other microorganisms (Devetter et al., 2017). Nematodes (roundworms) are another abundant group that inhabit water films or pore spaces in leaf litter and soil, contributing to soil health and nutrient availability (Pires et al., 2023). Tardigrades (phylum Tardigrada), often referred to as water bears, are eight-legged arthropods that are also part of the soil microfauna. Soil microfauna are top consumers of highly diverse groups of bacteria, fungi, and other microeukaryotes (Zawierucha et al., 2022). Additionally, various microscopic, unsegmented worms can be found within the soil ecosystem. Protists or microeukaryotes (Figure 2.2) are highly diverse groups within the microfauna, exhibiting a wide trophic range from autotrophic to heterotrophic modes of nutrition (Geisen et al., 2017). They acquire nutrients from dissolved compounds in the soil solution or by breaking down organic matter. As key consumers of bacteria, protists play a crucial role in regulating microbial biomass and nutrient cycling in soil ecosystems (Bodur et al., 2024; Liao et al., 2024).

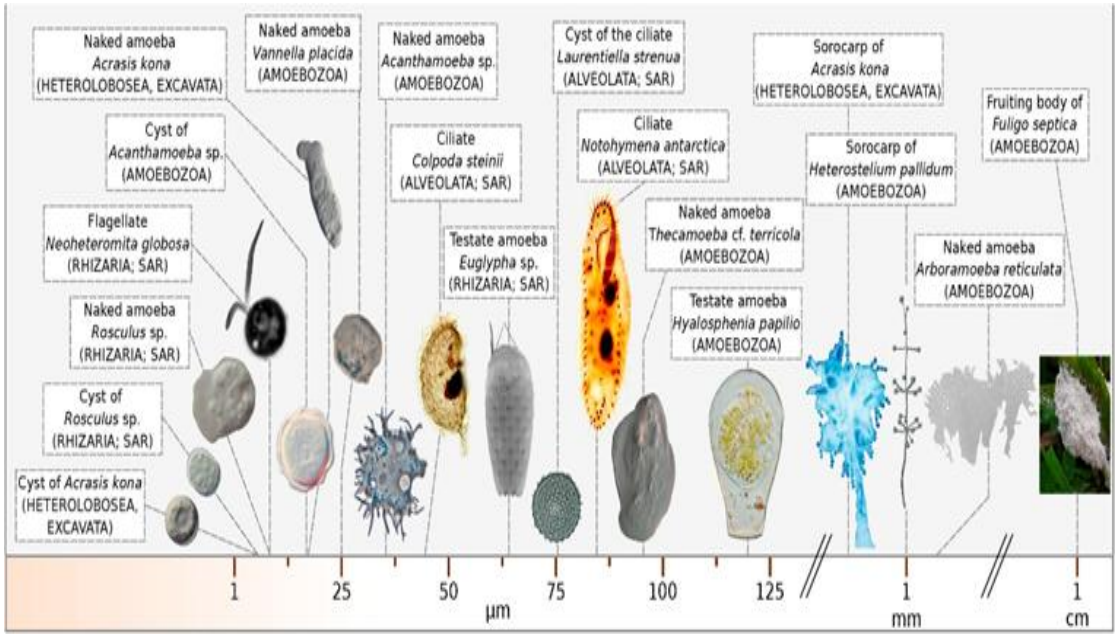

Figure 2.2 Soil harbours a wide variety of free-living protists (Geisen et al., 2017)

Meanwhile, the mesofauna are animals with a body width larger than 0.2 mm but smaller than 2 mm (Swift et al., 1979) that inhabit the soil and litter layers of terrestrial ecosystems (Ortiz-Ramírez et al., 2024). The most common groups of mesofauna are Acari (mites; Figure 2.3) and Collembola (springtails; Figure 2.4), which also play crucial roles in soil ecosystem functioning; the group also includes enchytraeids (Figure 2.5), proturans (Figure 2.6), and diplurans (Figure 2.7) (Ortiz-Ramírez et al., 2024). Acari and Collembola are often used as bioindicators of soil quality and ecosystem health due to their sensitivity to disturbances (George et al., 2017). Within Acari, the main subgroups found in soil include Mesostigmata, Prostigmata, Oribatida, and Astigmata, while common families within the Collembola order include Isotomidae and Entomobryidae (Marian et al., 2018). Mesofauna serve as a crucial link between microfauna and macrofauna, contributing significantly to organic matter decomposition, nutrient cycling, and the maintenance of soil structure (Zagatto et al., 2019), although their direct impact on organic matter breakdown may be limited compared to microorganisms in some agricultural soils. Soil mesofauna also contributes to the dispersion of soil microorganisms by transferring on their bodies (Frouz, 2018). Mesofauna also improves the turnover of organic matter and decomposition processes in soils. Mesofauna are mainly predators or saprophagous, and some of them are parasites. They feed on soil bacteria and fungi and thus indirectly affect the transformation of organic matter. Some groups of soil mesofauna are characterized due to interactions with microorganisms associated with their digestive tract. Soil mesofauna use soil pores as habitats and thus play an important role in the formation and improvement of soil aggregates (Frouz, 2018). Their abundance and diversity are strongly influenced by soil properties, land use, management practices, and environmental conditions, making them sensitive indicators of soil health and ecosystem change (Arboláez et al., 2023; Vanolli et al., 2024).

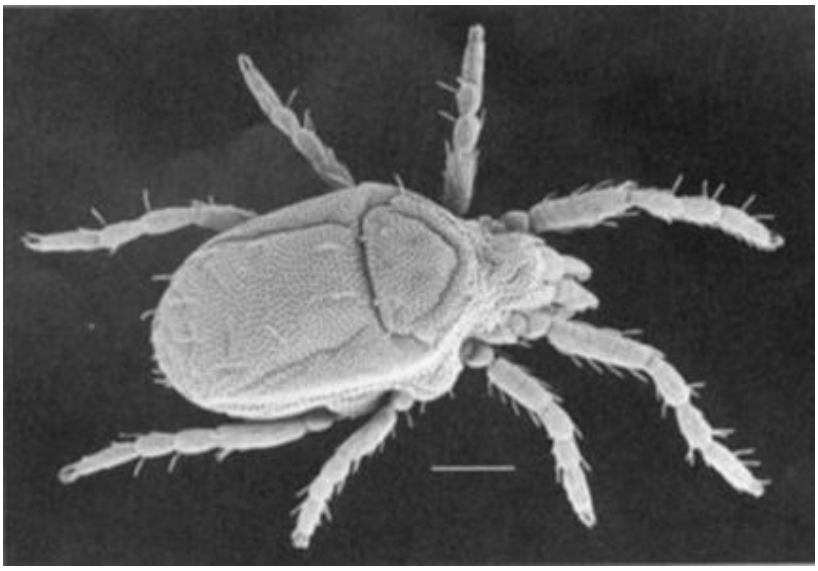

Figure 2.3 Free-living yellow moss mite (Acari: Penthalodidae, Stereotydeus sp.),

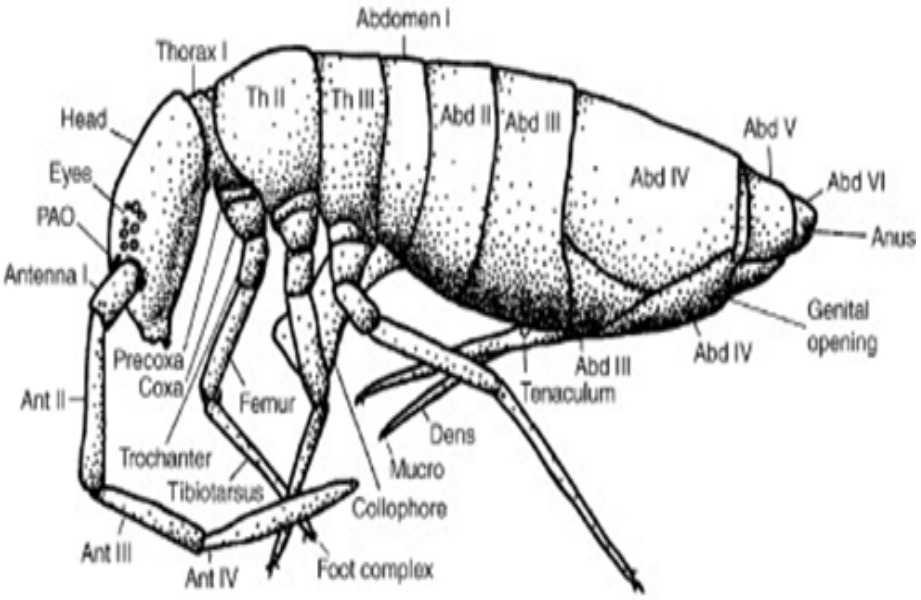

Figure 2.4 Typical collembola anatomy (Christiansen et al., 2009).

Figure 2.5 Enchytraeid worms (Zanella et al., 2018)

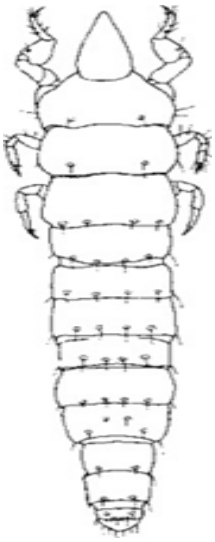

Figure 2.6 Proturan (Gibb & Oseto, 2020)

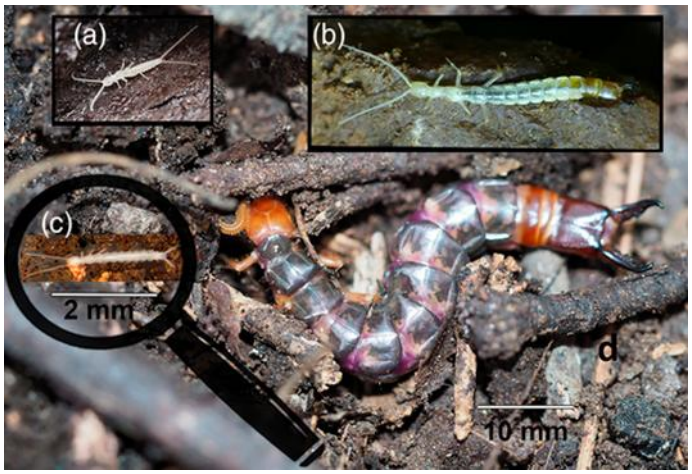

Figure 2.7 Overview of Diplura habitus. (a) Campodeidae; (b) Japygidae; (c) Projapygidae and (d) Heterojapygidae. Scale bars: (a), (b) and (d) = 10 mm; (c) = 2 mm (Sendra et al., 2021).

At the larger end of the spectrum, the macrofauna - including earthworms, termites, ants, beetles, and other invertebrates - are often referred to as "ecosystem engineers." They mix and aerate the soil, form aggregates, and enhance organic matter incorporation, thereby improving soil porosity and fertility (Lavelle et al., 2006). The soil macrofauna comprises a diverse group of invertebrates with body widths between 2 mm and 2 cm (Gongalsky, 2021; Sofo et al., 2020) that inhabit the soil and litter layers. They actively shape soil properties via their building activity by creating tunnels and pores (Frouz, 2018). This group includes earthworms, ants, termites, beetles, millipedes, centipedes, and various insect larvae (Gongalsky, 2021; Lavelle et al., 2022; Sofo et al., 2020). Earthworms, termites, and ants are considered the most important macrofauna components due to their abundance and crucial soil-forming roles. Macrofauna play a vital role in organic matter breakdown, nutrient cycling, and interacting with microorganisms to enhance soil health and productivity (Sofo et al., 2020). Their activities promote litter decomposition, incorporate organic matter into the soil, and regulate soil structure and water regimes (Cheik et al., 2019; Frouz, 2018). Macrofauna are sensitive to soil conditions and can serve as indicators of soil quality (Lavelle et al., 2022; Silva et al., 2021). Despite their importance, research on soil macrofauna is challenged by their taxonomic diversity and the need for specialized identification, leading to underrepresentation in some ecological studies (Gongalsky, 2021). Collectively, these biotic groups form a complex and interactive community that underpins soil health, fertility, and ecosystem stability. Understanding their

composition and functions is essential for sustainable agriculture, environmental conservation, and global biogeochemical balance (Bardgett & van der Putten, 2014).

2.2 Diversity of Soil Biota in Tropical Regions

Tropical soils harbour extremely rich microbial communities. A large survey of soils from Thailand, Malaysia, Indonesia, and the Philippines identified about 11,893 bacterial species across 558 samples (Likhitrattanapisal et al., 2021). Dominant bacterial phyla include Proteobacteria, Actinobacteria, Firmicutes, Bacteroidetes, and Cyanobacteria (Likhitrattanapisal et al., 2021). Bacterial diversity in these soils is strongly influenced by soil chemistry: more neutral pH soils tend to support higher bacterial richness, while lower pH decreases bacterial diversity (Tripathi et al., 2016). Tropical forests with high plant diversity also tend to support abundant bacterial communities due to producing different quality leaf litter and root exudates (Prommer et al., 2020), although specific drivers of soil microbial diversity like pH, moisture, and carbon are often site-specific.

Tropical forest soils also host diverse fungal communities. Common functional groups are saprotrophic fungi, the decomposers of litter and wood, symbiotic fungi such as mycorrhizal fungi that associate with roots, and pathogenic fungi that infect plants or soil animals (Liu et al., 2022). These groups can be very speciose in rainforests. For example, Indonesian lowland rainforests showed extremely high fungal richness, and even after conversion to oil palm or rubber plantations, the taxonomic diversity remained high (Brinkmann et al., 2019). Instead of large losses in richness, conversion to monoculture tended to shift the community composition; mycorrhizal fungi declined while saprotrophs and pathogens increased (Brinkmann et al., 2019). This implies that the original forests harboured many specialized symbiotic fungi. In fact, global reviews suggest tropical soils often have lower fungal richness than temperate or boreal soils (Li et al., 2022). Nevertheless, tropical soil still contains a very large number of fungal species. A few studies noted that rich tropical plant communities support abundant soil fungi (Barberán et al., 2015; Peay et al., 2013).

Tropical soils have a high diversity of soil animals. In a classic study of African rainforest soils, 200 nematode individuals from a single soil core yielded an average of 61 species (range 49–89) (Bloemers et al., 1997). Across multiple sites in that study, researchers recorded 431 nematode species (and ~194 genera). These nematodes represent all trophic levels: bacterial-feeders, fungal-feeders, plant-parasites, and predators. Importantly, nematode diversity remained very high even under disturbance: only the most extreme land use (slash-and-burn and clearcutting) reduced richness significantly, up to 40% of primary forest levels (Bloemers et al., 1997), still in managed or disturbed tropical lands, abundance is generally lower than in undisturbed forests, but still substantial (Wang et al., 2022)

2.2.1 Human activities affect the diversity of soil biota

Intensive agriculture consistently reduces soil biodiversity, leading to less complex soil food webs, lower species richness, and functional homogenization across regions (Berkelmann et al., 2020; Peng et al., 2024; Tsiafouli et al., 2015). Agricultural intensification increases the abundance of certain microbial groups, for example, Acidobacteria, Actinobacteria, and Proteobacteria in croplands, while depleting others, and often reduces the diversity of rare or specialist taxa (Berkelmann et al., 2020; Peng et al., 2024; Romdhane et al., 2022; Xue et al., 2023). However, some studies report that agricultural soils can exhibit high microbial diversity, particularly in the early years following land-use change or under less intensive management, though this diversity may be functionally redundant or less resilient (Mendes et al., 2015; Nabi et al., 2022; Yoon et al., 2024). Management practices play a critical role, with one study reporting that crop rotation promotes greater soil bacterial and fungal diversity (Romdhane et al., 2022). While many studies highlight declines in diversity, others indicate that some microbial or faunal groups might thrive in plantation environments, leading to increases in overall diversity or functional diversity (Lee-Cruz et al., 2013; Mishra et al., 2023). For example, some anthropogenic habitats such as monoculture tree plantations may harbour higher fungal biomass, including soil-borne pathogens, potentially attracting fungal-feeding organisms such as Collembola and Oribatida (Meyer et al., 2020).

Urbanization significantly alters soil biota by changing land use, increasing pollution, and modifying soil properties, which together reshape the diversity and composition of soil organisms. Studies show that urbanization often reduces the richness of soil invertebrates and nematodes, particularly specialist species, while favouring generalists that can thrive in disturbed environments, leading to a loss of biodiversity and community specialization (Coulibaly et al., 2025; Szabo et al., 2016; Zheng et al., 2024). Soil microbial communities also shift in response to urbanization, with changes in dominant groups and altered community structures, often driven by factors like soil pH, nutrient levels, and heavy metal contamination (Fu et al., 2023; Gao et al., 2023; Li et al., 2023; Yi et al., 2022). In some cases, urban soils may exhibit higher microbial diversity, especially in peri-urban areas, but the stability and complexity of these communities tend to decrease compared to rural soils (Gao et al., 2023; Li et al., 2023). Urban green spaces and parks can support diverse microbial and faunal communities, sometimes comparable to or exceeding those in less disturbed environments, but urbanization also favours generalist species and reduces the abundance of specialists, leading to functional homogenization (Coulibaly et al., 2025; Joimel et al., 2017; Schittko et al., 2022; Scholier et al., 2023). Pollution, soil sealing, and construction activities can further alter soil properties and biota, sometimes reduce overall diversity or shift community structure (Greinert, 2015; Greinert et al., 2024).

2.3 Physico-Chemical Properties of Soils Influence the Soil Biota

Recent studies repeatedly find that soil physicochemical factors such as moisture and pH strongly influence microbial communities in tropical soils (Santillán et al., 2021; Tripathi et al., 2012; Zhao et al., 2020). Soil pH is often the major factor influencing microbial diversity in soils (Sawada et al., 2021; Yang et al., 2021). In tropical systems, even small changes in pH can significantly alter the bacterial community. For instance, soils with higher pH generally support higher bacterial OTU richness (Liu et al., 2020; Sawada et al., 2021; Tripathi et al., 2016). Furthermore, study by Sawada et al. (2021) showed that converting lowland forest to Acacia plantation raised soil pH and subsequently increased overall bacterial diversity in one soil type. In contrast, acidification tends to reduce bacterial richness (Wan et al., 2020). Similarly, soil pH can influence the structure of fungal communities by altering the

availability of nutrients or by creating physiological limitations that affect fungal growth (Li et al., 2020). For example, studies in tea plantations and agricultural soils found that the relative abundance of saprotrophs increased with higher pH (Du et al., 2022; Li et al., 2020, p. 202). Study by Brinkmann et al. (2019) from Indonesia reported that soil pH was among the best predictors of fungal community differences across land uses. In contrast, another more recent study by Luo et al. (2021) reported that pH did not play a significant role in shaping fungal community composition.

Nutrient levels are also key driver that shapes soil bacterial and fungal community. Higher soil organic carbon generally increases microbial biomass and can support greater diversity of both bacteria and fungi, by providing source of energy (Chen et al., 2024). Nitrogen and phosphorus availability further influence communities. The extremely low P in soils tends to select for microbes and symbionts that oligotrophic life strategies, such as certain Rhizobiales, Actinomycetales, and Acidobacteriales (Bergkemper et al., 2016; Oliverio et al., 2020). Fungi are more sensitive toward changes in phosphorus level in soil compared to bacteria (Liu et al., 2018). Low soil phosphorus conditions select for fungi that are efficient at phosphorus acquisition and recycling, such as ectomycorrhizal and arbuscular mycorrhizal fungi (Khalid et al., 2021; Zheng & Song, 2022). Conversely, bacterial diversity has a non-linear response toward nitrogen level in soil (Liu et al., 2020). Bacterial diversity is stable at low N levels but drops sharply once a critical N threshold is exceeded (Liu et al., 2020; Song et al., 2023). High N input lowers soil pH, which is the primary driver of reduced bacterial diversity (He et al., 2021; Liu et al., 2020; Song et al., 2023; Yang et al., 2025; Yang et al., 2024). The relative abundance of Proteobacteria increased significantly, whereas that of Acidobacteria declined with elevated nitrogen inputs (Song et al., 2023). For fungi, elevated N level reduced fungal diversity and altered community structure (Azwa et al., 2022; Chen et al., 2020). Nitrogen addition can increase the relative abundance of Basidiomycota, Mortierellomycota and Rozellomycota and decrease Ascomycetes (He et al., 2021; Wang et al., 2021). High level of nitrogen generally decreases nematode diversity mainly due to soil acidification, increased ammonium, and reduced microbial biomass, which disrupt nematode habitats and food resources (Liang et al., 2020; Nisa et al., 2021; Xing et al., 2023; Yang et al., 2025).

In tropical systems and beyond, increased soil organic matter (SOM) usually correlates with higher bacterial richness, reflecting more available niches and energy sources. For example, Tian et al. (2018) found bacterial richness and phylogenetic diversity to be significantly higher in temperate (organic matter-rich) forests than in tropical ones. In tropical montane study, soil bacterial diversity increased linearly over 60 to 80 years of forest recovery, parallel to rising SOM (Sniegocki et al., 2022). Interestingly, different study report that arid, carbon-poor soils have higher diversity-to-biomass ratios than carbon-rich soils, implying that extreme carbon limitation can elevate diversity relative to biomass (Bastida et al., 2021). Overall, though, a lack of OM usually constrains bacterial diversity, while increasing OM fosters richer bacterial communities (Sniegocki et al., 2022; Tian et al., 2018). Fungi similarly benefit from high OM. In tropical forests, soils with greater litter inputs and OM generally support more diverse fungal assemblages. For instance, in a Chinese subtropical forest, fungal richness in the organic horizon (rich in OM) was much higher than in the mineral horizon (Luo et al., 2021). In the Bornean forest study, fungal diversity increased with forest age as litter layers built up (Sniegocki et al., 2022). Disturbance or low-OM environments often cause fungal homogenization: cleared or cultivated tropical soils showed lower fungal diversity and fewer ectomycorrhizal taxa than intact forests (Sniegocki et al., 2022).

Soil moisture also mediates diversity. Bacteria are more sensitive to both short-term and long-term changes in soil moisture than fungi (Jiao et al., 2021, 2023; Yang et al., 2021). Bacterial diversity and community structure shift quickly with changes in moisture in soil, while fungi tend to be more stable under the same conditions (P. Jiao et al., 2021, 2023). In one study, increasing the soil moisture leads to dominant bacterial species converted from Actinobacteria to Alphaproteobacteria and Acidobacteria (Jiao et al., 2023). Saturated or poorly drained forest soils such as peat swamps host distinct communities, often with anaerobic microbes or methanogens (Pan et al., 2021; Yang et al., 2025). Studies across various ecosystems show that nematode diversity and abundance increase with higher soil moisture. For example, the highest nematode trophic levels and diversity were observed at around 30% soil moisture, and nematode diversity indices were higher in moist forest soils compared to drier alpine soils (Ding et al., 2024; Nisa et al., 2021; G. Zhang et al., 2020).

Soil texture, defined by the proportions of sand, silt, and clay, plays a significant but complex role in shaping the diversity of soil bacteria, fungi and soil mesofauna. In one study, microbial abundance increased with decreasing particle size, due to the greater surface area available for colonization and the higher water retention capacity associated with increased clay content (Obayomi et al., 2021). Gammaproteobacteria was significantly higher in clay soil while the Bacteriodetes taxa was more abundant in low clay soils (Obayomi et al., 2021). Fungal diversity is less consistently affected by texture compared to bacterial diversity (Seaton et al., 2020). Some studies show a positive correlation with sand content, while others find little or no effect (Seaton et al., 2020; Xia et al., 2020). For soil arthropods such as oribatid mites, collembolans or isopods, some study shows positive correlation between sandy soil and abundance of meso and macro-arthropods in soil (Dunxiao et al., 1999; Zhang et al., 2024). Despite clear evidence, the effects of soil properties on soil biota in the eastern part of Peninsular Malaysia, particularly in Terengganu, remain elusive.

2.3.1 Physico-chemical properties of soils in the tropics

Tropical soils are generally highly weathered and acidic, often and often less fertile compared to soils in temperate zone such as cambisol or chernozem (Lie et al., 2023; Likhitrattanapisal et al., 2021; Mani & Cao, 2019; Tripathi et al., 2016; Wei et al., 2020). Intense leaching in the humid tropics releases aluminium and iron into soils, which then fix phosphorus into insoluble forms which leads to many humid tropical soils to have very low plant-available P (Cunha et al., 2022; Soong et al., 2020; Tiessen, 2005). Typical topsoil pH in tropical forests is extremely acidic. In a study of tropical Asian rainforests, average soil pH in primary and secondary forest was only about 3.9–4.4 (Mani & Cao, 2019; Tripathi et al., 2016). One study even reveal the tropical soil pH can goes as low as 3.2 (Tripathi et al., 2016). Such low pH significantly limits nutrient availability (Neina, 2019)

Organic matter (OM) in tropical soils tends to rapid turnover due to warm temperatures and moisture. Undisturbed forests accumulate litter, but stable soil

organic carbon (SOC) is often modest due high decomposition rates and due to high rainfall. For instance, in Northeast Thailand undisturbed tropical forest topsoil contained about 15.4 g/kg total C (1.54%) (Zhou et al., 2019).Tropical forest soils often have similarly low total nitrogen while secondary forests sometimes show higher soil N and P than old grow. For example, one study found secondary-forest soils had 2.6 g/kg N compared to 2.1 g/kg in primary forest, and 0.4 g/kg P and 0.3 g/kg respectively (Mani & Cao, 2019). This likely reflects nutrient release from cleared biomass and lighter uptake in early successional vegetation.

Variation in soil electrical conductivity and salinity in natural tropical sites depending on geographical location but are usually very low , since high rainfall flushes salts (Perri et al., 2022). In tropical coastal regions and river deltas, soil salinity can be high due to seawater intrusion, rising sea levels, and tidal flooding (Hoa et al., 2019; Szabo et al., 2016).

Soil texture in tropical regions is highly variable depending on the bedrock, but tropical soils often range from sandy to clay, with a significant presence of clay-rich soils. For example, soils in the Mun River basin of Thailand were mostly sandy loam or silty loam in the surface horizons (Zhou et al., 2019). Many tropical soils, especially in forested and weathered regions, are clay-rich like in Amazonia forest in Pará, Brazil (Pavão et al., 2024).

Soils in tropical rainforests, like the Amazon, maintain high moisture content throughout the year due to frequent rainfall and deep soil profiles. For example, mean soil moisture values in Amazonian forests can range from about 0.38 to 0.53 m^3/m^3 (volumetric water content) (Bruno et al., 2006). In tropical dry forests or semi-arid regions, soil moisture is more variable. During the rainy season, soils can become quite moist, but they dry out significantly during prolonged dry periods (Negrón-Juárez et al., 2020).

In Malaysia, the natural forest and wetland soils are very acidic (Isa et al., 2023). Typical pH values in primary tropical rainforests range from 3.5 to 5.5. For example, lowland dipterocarp forest soils in the Peninsular were measured at pH less

than 5.5 (Zaidey et al., 2010), and a mature Putrajaya urban rainforest averaged pH 4.69 (Isa et al., 2023). Montane forest soils in Sabah had pH 4.21 to 5.71 (Suhaili et al., 2021). In tropical peat swamp forests, soils are even more acidic with typical tropical peat soils have pH around 2.9 to 3.5 (Richard et al., 2015; Sahabudin et al., 2022). Low pH is due to high rainfall leaching and accumulation of organic acids which results in high exchangeable Al and H saturation and very low base saturation in the soil (Naz et al., 2022; Neina, 2019). Interestingly, there are site that are slightly acidic, just below the pH of 7, as observed in Matang Mangrove Forest Reserve in Kuala Sepetang, Perak (Azwa et al., 2022).

Organic matter (OM) content shows wide range in tropical soils of Malaysia depending on the input of organic matter produced by aboveground vegetation (Zaidey et al., 2010). Soils under rainforests usually have modest level of OM largely in the humus layer as seen in lowland dipterocarp soils (Zaidey et al., 2010). In contrast, peat swamp soils are high in OM (Sahabudin et al., 2022). For example, a study of Sarawak peat swamp found soil organic matter ≈97–98 % with total C ≈48–49 % (Salimin et al., 2010). Also, chemical composition of aboveground vegetation shapes content of OM. Litter with high C:N ratio support accumulation of OM in soils due to slow decomposition (Salimin et al., 2010). For example, peat soils have extremely high C:N (Salimin et al., 2010). Soil texture in upland forests is typically sandy loam to clay loam with many upland soils derive from sandstone and are sandy with low clay content (Karam et al., 2017; Keng et al., 2020). In undisturbed forest soils, clay content consists of low-activity clays like kaolinite and iron oxides (Zaidey et al., 2010).

Natural forest soils in Malaysia are extremely nutrient-poor (Hamdan & Bumham, 1996; Kamoona et al., 2023). In undisturbed dipterocarp forests, total N and available P are very low and exchangeable bases are low (Zaidey et al., 2010). In another study, a Putrajaya forest had mean extractable P 2.2 mg/kg (Isa et al., 2023). Nutrients are largely tied up in biomass and organic matter, and surface soils often have high Al that binds P. Tropical peat swamp soils likewise have low mineral nutrient concentrations, in one Sarawak peat study, total N was 0.79±0.06 %, total P 219.20±18.79 mg/L, and exchangeable K 330.60±20.66 mg/L (Salimin et al., 2010).

All natural inland Malaysian soils showed less soil salinity and conductivity, whereas coastal mangroves can exceed the moderate saline threshold. An example in a study reveals low land forest reserve to have conductivity ranging from 0.28 (dS/m) to 0.54 (dS/m) while highland forest reserve have conductivity ranging from 0.28 (dS/m) to 0.31 (dS/m) (Karam et al., 2017). On the other hand, sites that were closed to the coastal line have moderate to high conductivity and salinity due to saltwater intrusion (Azwa et al., 2022; Jeyanny et al., 2018).

2.4 The Metabolic Activities of Soil Biota

Soil biota are fundamental drivers of ecosystem processes. Soil biota perform essential functions in nutrient cycling, organic matter decomposition, and the regulation of soil structure and fertility. Microorganisms drive the decomposition of plant residues and soil organic matter, releasing nutrients and stabilizing soil carbon (Crowther et al., 2019; Hu et al., 2024; Maron et al., 2018; Morrissey et al., 2023; Wu et al., 2024). Bacteria utilize easily degradable substrates such as glucose and starch, whereas fungi decompose more recalcitrant compounds such as lignin and cellulose (Wang & Kuzyakov, 2024). Bacteria are often classified as copiotrophic or oligotrophic: copiotrophs are fast-growing taxa that thrive in high-nutrient environments, while oligotrophs are slow-growing taxa adapted to nutrient-poor conditions and low pH (Yao et al., 2017). Fungi can be divided into saprotrophic forms, which degrade organic matter, and symbiotic mycorrhizal fungi, which include arbuscular mycorrhizas (AM) associated with most herbaceous plants and ectomycorrhizas (ECM) associated with many woody species (Tedersoo et al., 2020; Valášková et al., 2007). Other large group of fungi represents plant and fungal pathogens which are important agricultural pests (Tedersoo et al., 2020). In contrast, some of the fungal pathogens can regulate insect pests and thus serves as an natural regulator of pest's population.

Soil fauna also plays a critical role in regulating microbial activity and shaping soil organic matter dynamics. Mesofauna (e.g., mites, springtails) are primarily microbial feeders that influence decomposition indirectly by modifying microbial

populations, while macrofauna (e.g., earthworms, termites, ants) are mainly litter feeders that affect decomposition directly through litter fragmentation (T. Liu et al., 2019; Lubbers et al., 2020). Both groups include herbivores and predators, forming complex trophic interactions within soil food webs. For instance, insect predators also regulate decomposition indirectly via their predatory effect on soil decomposers (Frouz, 2018). Typically, spiders or centipedes often regulates population of millipedes and termites. By altering soil structure and resource availability, mesofauna and macrofauna interact with microbial communities to accelerate nutrient mineralization and maintain ecosystem functioning (Wang et al., 2024).

Soil biota, in particular soil bacteria is also central to the production and consumption of greenhouse gases (GHGs). Microbial communities mediate carbon dioxide (CO_2) release via respiration during mineralization of their substrate, methane (CH_4) production via methanogenesis, and nitrous oxide (N_2O) emissions through denitrification processes (Bahram et al., 2022; Tian et al., 2019). Environmental factors such as fertilization, irrigation, and pollution can alter microbial community structure and functional gene abundance, thereby affecting GHG fluxes (B. Gao et al., 2022; Ma et al., 2021; You et al., 2022). Soil microorganisms are both sources and sinks of VOCs. Reduced microbial diversity tends to increase total VOC emissions but decreases the diversity of VOCs produced (Abis et al., 2020). Specific microbial taxa, such as Proteobacteria, Bacteroidetes, and fungi, are positively correlated with VOC production (Abis et al., 2020; Graham et al., 2024). Microbial diversity and community composition are key determinants of decomposition rates and carbon cycling. High microbial diversity enhances the decomposition of both labile and recalcitrant carbon sources, stabilizes soil organic carbon, and increases ecosystem resilience to environmental change (Maron et al., 2018; H. Wu et al., 2024; Xu et al., 2021). Soil fauna further modulate these processes by influencing microbial activity and the physical structure of soil organic matter (Liu et al., 2019).

Advancements in the detection and characterization of volatile organic compounds (VOCs) have facilitated a deeper understanding of soil microbial metabolism. VOCs, produced as metabolic by-products of bacteria and fungi, serve as indicators of microbial functional diversity and activity in soils (Jiao et al., 2023;

Lemfack et al., 2018). Profiling VOC emissions enables the generation of community-level taxonomic and functional signatures, providing evidence of the chemical diversity of microbial volatiles and their involvement in long-distance interactions and communication (Choudoir et al., 2019; Guo et al., 2021; Weisskopf et al., 2021). Fungi, in particular, release a broad spectrum of VOCs that mediate interactions with plants, insects, and other microorganisms (Guo et al., 2021).

Certain volatile organic compounds (VOCs), including diethyl sulphide and isopropanol, have been identified as markers of anthropogenic influences such as agriculture, industrial activity, and urban development (Liu et al., 2020). However, knowledge of how VOC profiles relate to specific soil organism groups, particularly in tropical ecosystems, remains limited. Greenhouse gas (GHG) fluxes, including carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O), also serve as indicators of microbial metabolic activity in soils, as their production and consumption are closely associated with microbial processes (Heděnec et al., 2017, 2018; Jin et al., 2023; Chen et al., 2022). For instance, drying and subsequent rewetting of soils have been shown to increase GHG emissions through enhanced bacterial activity (Heděnec et al., 2018). Combining VOC analysis with GHG monitoring, DNA sequencing, and soil physico-chemical measurements can provide a more integrated view of microbial community dynamics under varying environmental conditions.

2.5 Soil Biota Influence Litter Decomposition

Soil microbes, bacteria and fungi, are the primary agents of organic matter decomposition, with bacteria often dominating the breakdown of labile (easily degradable) substrates and fungi specializing in more recalcitrant (complex) compounds like lignin (Jílková et al., 2019; Wang & Kuzyakov, 2024). High microbial diversity is consistently linked to enhanced decomposition rates and greater ecosystem stability, particularly under environmental stress or changing conditions (M. Hu et al., 2024). Functional redundancy exists, but keystone taxa, specific bacteria or fungi, can disproportionately drive decomposition processes (Wang et al., 2025; Yang et al., 2021) Soil fauna, such as earthworms, isopods, termites, ants and millipedes,

contribute by fragmenting litter, enhancing microbial access, and directly digesting organic matter, often accelerating decomposition rates (Frouz et al., 2007; Heděnec et al., 2022b; Tan et al., 2020). The presence and abundance of these groups can shift decomposition pathways and rates, with macrofauna like earthworms significantly increasing the rate of organic matter breakdown (Frouz et al., 2007; Pant et al., 2017). Litterbag experiments involve enclosing plant litter in mesh bags of different pore sizes to control which soil organisms can access the material. This method is widely used to quantify the role of soil meso- and macrofauna in litter decomposition. For example, Peguero et al. (2019) used fine (70 μm) and coarse (7 mm) mesh bags in Amazonian forests to show that meso- and macrofauna substantially accelerate decomposition in nutrient-poor soils. Similarly, Homet et al. (2021) applied litterbags with different mesh sizes in Mediterranean woodlands and found that mesofauna modulated decomposition under drought. In cropland systems, Cassani et al. (2021) demonstrated faster litter decay in coarse-mesh bags that allowed access by all soil fauna. These studies confirm that litterbags are a reliable tool to partition faunal contributions to decomposition. Despite increasing evidence, the effects and contribution of soil meso and macrofauna to litter decomposition rates in different contrasting habitats remains elusive in comparison to temperate and boreal zone

2.6 Methods for Studying Soil Biota

Over the past decades, a wide array of methods has been developed to assess the taxonomic and functional diversity of soil organisms, ranging from routine morphological identification to advanced molecular, biochemical, physiological, and imaging techniques. Recent reviews emphasize that no single method can fully capture the large biodiversity of complex soil ecosystem,, and thus integrative approaches are increasingly recommended to overcome the limitations of individual techniques (Geisen et al., 2019; Lahlali et al., 2021; Römbke et al., 2018). Traditional morphological identification remains a cornerstone for studying soil fauna, such as earthworms, nematodes, and arthropods. These methods involve direct observation, sorting, and taxonomic identification using microscope (Geisen et al., 2019; Jänsch et al., 2025). While effective for larger organisms, they are time-consuming, require taxonomic expertise, and may miss cryptic or microscopic taxa (Geisen et al., 2019).

Recent studies compare morphological with DNA-based identification, finding that molecular methods often detect more species, but both approaches are complementary (Jänsch et al., 2025).

Molecular methods have transformed soil biota research, enabling the detection and characterization of unculturable microorganisms. Techniques include DNA/RNA extraction, PCR amplification of marker genes like 16S/18S rRNA, DNA metabarcoding, metagenomics, and metatranscriptomics (Daniel, 2005; Dopheide et al., 2019; Francioli et al., 2021; Lahlali et al., 2021; Wydro, 2022). These approaches provide high-resolution data on community composition, diversity, and functional potential. However, they are subject to biases from DNA extraction, PCR, and bioinformatics pipelines, and may not always reflect active functions (Dopheide et al., 2019; Francioli et al., 2021). Integrative approaches, such as combining metagenomics with cultivation or biochemical and physiological assays, are increasingly applied in research of complex soil organisms (Lahlali et al., 2021). Biochemical and physiological methods assess microbial biomass, activity, and functional diversity. Common techniques include phospholipid fatty acid analysis (PLFA), enzyme activity assays, analyses of VOCs, soil respiration measurements (including in situ GHG measurements), and stable isotope probing (Kandeler, 2015; Pérez-Guzmán et al., 2021; Potapov et al., 2019). For example, PLFA analyses provides detailed insight into bacterial or fungal biomass based on concentration of membrane phospholipids specific for bacteria and fungi. Similarly, enzyme assay methods provide information on metabolic activity of bacteria and fungi based on substrate specific enzyme reaction. Similarly, analyses of GHG or specific VOCs can reflect metabolic activity of certain microbial taxa such as methanogens, denitrifiers and thus can provide important information about microbial activity of soil (Abis et al., 2020; Graham et al., 2024). These methods provide insights into microbial community structure, metabolic activity, and nutrient cycling. While they offer functional information, they may lack taxonomic resolution and can be influenced by soil properties and environmental conditions (Kandeler, 2015; Pérez-Guzmán et al., 2021; Potapov et al., 2019).

CHAPTER 3

METHODOLOGY

3.1 Sampling Location and Sampling Design

Our study was conducted at eight distinct locations across Terengganu state in Malaysia, spanning approximately 40–50 km apart, to assess soil biota communities and their diversity in relation to specific soil conditions along a gradient from natural to anthropogenic habitats (Table 3.1). These sites were selected to encompass a wide range of environmental conditions, from pristine ecosystems to intensively managed landscapes, allowing us to examine how land-use changes and soil properties influence soil biota diversity and composition. Natural habitats included secondary forest on Bidong Island; Jambu Bongkok, a coastal lowland peat forest; primary tropical rainforest surrounding Tasik Kenyir, and Setiu, a tropical wetland with exceptionally high moisture and organic matter content. These sites represent key reference ecosystems that support diverse and largely undisturbed soil biota communities. Anthropogenic sites represented a gradient of land use intensity, including an extensive paddy field in Jerteh district with a seasonally waterlogged soils rich in available phosphorus; industrial oil palm plantation in Permaisuri with moderate soil moisture and organic content; a durian orchard in Besut district with moderate organic matter and well-drained soils; and the UMT campus, an urban park with compacted soils and low organic matter. Detailed description of selected location is provided in Table 3.1.

Six plots (25 × 25 m) were established at each sampling location, spaced approximately 150–200 meters apart. To minimize spatial variation, all samples for different analyses were collected from the same designated plots. From each plot, six compact soil blocks (10 × 10 cm) were collected using a shovel from the mineral topsoil (0–15 cm depth, after removing aboveground vegetation and litter) between February and April 2022 and combined into a single composite sample per plot for soil physicochemical analyses. The soil cores were taken at 1.5 m from the tree trunks to

avoid the effect of a throughfall on soil microclimatic conditions. These samples were immediately transported to the Ecological Laboratory at Universiti Malaysia Terengganu (UMT). Soil physico-chemical parameters—including soil moisture content, pH, salinity, total organic carbon (TOC), total nitrogen (TN), and plant-available phosphorus (P)—were measured for each composite sample. For DNA extraction, six soil cores (2 cm diameter, 0–15 cm depth) were collected from each plot using an iron corer during the same period and combined into one composite sample per plot. These samples were stored at −20 °C for downstream molecular analyses. Soil fauna sampling was carried out in three randomly selected plots (25 × 25 m) per site, spaced 150–200 meters apart. Composite soil samples from three replicates per plot were collected for the extraction of soil mesofauna and macrofauna. For volatile organic compound (VOC) analysis, three random plots per site (25 × 25 m), also spaced 150–200 meters apart, were selected. Soil samples were collected in triplicate using an iron corer (2 cm diameter, 0–15 cm depth), combined into a composite sample per plot, wrapped in aluminium foil, and stored in plastic ziplock bags at −80 °C for downstream analysis.

Table 3.1 Geographical coordinates, dominant vegetation and soil types of natural and anthropogenic habitats across peninsular Malaysia

Sampling locations	Current habitat type	Former habitat type	Land use	MAT (°C)	MAP (mm)	Latitude	Longitude	Dominant tree vegetation	Dominant understory vegetation	Dominant soil type (World Reference Base for Soil Resources)
Bidong Island	Secondary forest (1980)+	Tropical island vegetation and farmland (papaya, tapioca, banana)	Natural	27.6	2,458	5.613	103.065	*Dipterocarpus* sp., *Shorea* sp., *Gluta* sp.	*Asplenium* sp., *Baccaurea* sp., *Licuala* sp.	Arenosols
Jambu Bongkok	Peat forest *	Peat forest	Natural	27.8	2,500	4.930	103.351	*Shorea sp., Gluta* sp., *Acacia mangium*	*Calamus* sp., *Asplenium* sp.,	Histosol
Setiu	Tropical wetland*	Tropical wetland	Natural	27.3	2,450	5.630	102.783	*Accacia mangium, Melaleuca cajuputi, Rhizophora apiculata*	*Nephrolepis* sp., *Cyperus* sp., *Scleria* sp.	Gleysol
Tasik Kenyir	Primary forest*	Primary forest	Natural	26.9	2,680	4.945	102.592	*Shorea* sp, *Macaranga sp. Dipterocarpus* sp.	*Globba* spp., *Selaginella wildenowii, Dracaena* sp., *Calamus* sp.	Ferralsols
Jerteh	Paddy field (1960)	Primary forest	Anthropogenic	28	2,455	5.764	102.580	*Oryza sativa*	*Lemna* sp., *Cyperus* sp.	Fluvisols
Permai suri	Oil palm plantation (1970)	Tropical wetland	Anthropogenic	27.9	2,490	5.633	102.723	*Elaeis guineensis*	*Nephrolepis* sp., *Imperata cylindrica, Mucuna pruriens*	Acrisols
Besut UMT campus	Durian orchard (1970)	Primary forest	Anthropogenic	27.5	2,555	5.751	102.617	*Durio zibethicus*	*Nephrolepis sp., Imperata cylindrica, Mucuna pruriens*	Acrisols
	Urban park (1990)	Coastal swamp vegetation	Anthropogenic	28	2,911	5.412	103.088	*Syzygium grande, Cyrtophyllum fragrans, Casuarina equisetifolia, Calophyllum inophyllum, Cinnamomum iners, Callerya artopurpurea*	*Mikania micrantha, Homalomena sagitifolia, Paspalum conjugatum*	Arenosol

+Bidong Island, a former refugee hotspot during the Vietnam War, was abandoned in the 1980s and left to natural succession. The number in the brackets indicate year of the conversion. Asterisks indicate natural sites with age long age > 500 years. (MAT - Mean annual temperature, MAP - Mean annual precipitation

3.2 Soil Biota Diversity and Composition Assessment

3.2.1 Soil bacteria and fungi

Six soil cores were collected from each site for both bacterial and fungal analyses. The soil samples were homogenized, sieved, and prepared for DNA extraction to assess microbial diversity and composition. A total of 0.25 g of sieved and homogenized soil was used for DNA extraction using the DNeasy PowerSoil Pro Kits (QIAGEN, Germany) following the manufacturer instructions. The extracted genomic DNA was evaluated for purity and concentration using Nanodrop spectrophotometry. The DNA was diluted to a concentration of 10 ng/μL and stored at -20°C for downstream analyses.

In sequencing for bacterial communities, primers 515F and 909R were used to target the 16S rRNA V4-V5 region (Caporaso et al., 2010). The PCR mixture (25 μL) contained 12.5 μL 2x Taq MasterMix, 1 μL each of forward and reverse primers, 9.5 μL ddH_2O, and 1 μL DNA template (10 ng/μL). PCR conditions included an initial denaturation at 94°C for 3 min, followed by 30 cycles of 94°C for 40 s, 56°C for 60 s, and 72°C for 60 s, with a final extension at 72°C for 10 min. Two PCR reactions were performed per sample, and the products were pooled.

For fungal communities sequencing, the ITS4 and gITS7F primers (Ihrmark et al., 2012) were used to target the ITS gene regions. The PCR mixture (25 μL) contained 12.5 μL 2x Taq MasterMix, 1 μL each of forward and reverse primers, 9.5 μL ddH_2O, and 1 μL DNA template (10 ng/μL). PCR conditions were as follows: initial denaturation at 94°C for 5 min, followed by 34 cycles of 94°C for 30 s, 56°C for 30 s, and 68°C for 45 s, with a final extension at 72°C for 10 min. Two PCR reactions were conducted per sample, and the products were pooled. The TruSeq® Illumina TruSeq kit was used to build sequencing library. The sequencing library was sequenced using Illumina NovaSeq sequencer at Chengdu Institute of Biology, Chinese Academy of Sciences.

For the sequencing data processing, paired-end sequencing reads were assembled using FLASh (Magoč & Salzberg, 2011), followed by stringent quality control and filtering via the QIIME bioinformatics pipeline (Caporaso et al., 2010). Chimeric sequences were identified and removed with the Usearch tool (Edgar, 2013). Operational Taxonomic Units (OTUs) were delineated at a 97% sequence similarity threshold using the cd-hit algorithm (Edgar, 2013).

Taxonomic classification of bacterial sequences was performed against the Silva v132 database (Yilmaz et al., 2014), while fungal taxa were annotated using the UNITE database (Nilsson et al., 2019). In total, approximately 1,000,000 bacterial (16S rRNA gene) and 250,000 fungal (ITS2) sequence reads were clustered into 50,000 and 8,000 OTUs, respectively. To mitigate sequencing biases, singleton reads were excluded, and bacterial and fungal datasets were rarefied to 20,000 and 5,000 sequences per sample, respectively.

Bacterial functional groups were classified based on established literature (Bastian et al., 2009; Fierer et al., 2007), with Bacteroidota, Alphaproteobacteria, and Gammaproteobacteria designated as copiotrophs, whereas Deltaproteobacteria, Actinomycetota, and Acidobacteriota were categorized as oligotrophs (Bastian et al., 2009; Fierer et al., 2007). Fungal functional assignments were derived from the FungalTraits database (Põlme et al., 2020). The raw sequencing data have been deposited in the European Nucleotide Archive under accession number PRJEB80237.

3.2.2 Soil fauna

Soils from each location were taken using a shovel from a 10 x 10 cm square area of soil to a depth of 5 cm with 3 replicates from 3 subplots. Soil mesofauna was extracted by dry extraction method using a modified Berlese-Tullgren extractor for three days (Pande & Berthet, 1973; Sortwell, 1984). This modified Berlese-Tullgren are made with a strainer and pot without holes (Figure 3.1). Soils were placed on the strainer which was placed the pot containing mixture of soap and water. Due to the breaking of surface tension of the water by the soap, the soil mesofauna specimens

were trapped. The trapped specimens (Figure 3.2) were collected using plastic pipette with the aid of dissecting microscope and further stored and preserved in 70% ethanol (Figure 3.3) for later identification (Peng et al., 2022).

Figure 3.1 Modified Berlese-Tulgren extractor

Figure 3.2 Soil mesofauna from the modified Berlese-Tullgren extractor under dissecting microscope to be collected

Figure 3.3 Stored extracted soil fauna in 70% ethanol

Next, for the soil macrofauna, a soil block with approximate size 25 cm x 25 cm and 5 cm depth were taken using shovel. It was then transferred to ecological lab of FSSM for immediate processing. Soil macrofauna from those soil block was obtained using hand sorting method (Ruiz et al., 2008; Smith et al., 2008; Swift et al., 1979). Soil animals were grouped into 16 taxonomic categories at the family, order, subclass, or class level. These included mesofauna such as Collembola, Acari, Diplura, Symphyla, Pauropoda, and Protura, as well as macrofauna such as Lumbricidae, Diplopoda, Isoptera, Isopoda, Aranea, Chilopoda, Formicidae, Coleoptera, Blattodea, and other insects including larvae. In addition, the soil fauna community was organised into seven functional groups: Predators, Omnivores, Saprophages (Macrofauna), Saprophages (Mesofauna), Total Macrofauna, Total Mesofauna, and Total Fauna (Filser et al., 2016; Orgiazzi et al., 2016; Ruiz et al., 2008; Swift et al., 1979).

3.2.3 Data analysis

Alpha diversity was assessed to quantify patterns of species richness and community complexity across the different habitats. All analyses were performed in R Studio (R version 4.1.1; R Core Team) using the vegan package (Oksanen et al., 2015)

3.3 Soil Physicochemical Analysis

Soil moisture content was determined gravimetrically by oven-drying samples at 105°C to constant weight. Soil pH, salinity and conductivity was measured using a Horiba LAQUA PH210 pH meter (Figure 3.5) with a 1:5 soil-to-water ratio. Total Organic Carbon (TOC) and Total Nitrogen (TN) were quantified using an Elementar UNICUBE® (Figure 3.4) organic elemental analyser, employing helium as the carrier gas. Soil texture (percentages of sand, silt, and clay) was determined via the standard sedimentation method (Beretta et al., 2014). Plant-available phosphorus (P) was analysed spectrophotometrically (Shimadzu UV-1800) following Bray-1 extraction. Soil organic matter (OM) content was determined by loss-on-ignition at 400°C for 12 hours.

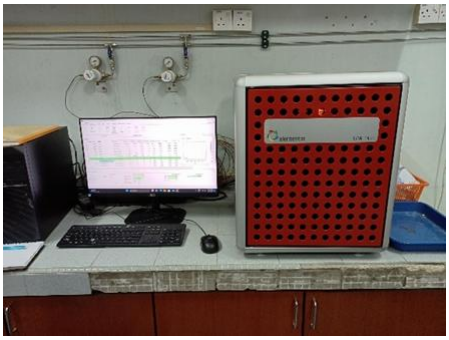

Figure 3.4 Elementar UNICUBE®

Figure 3.5 Horiba LAQUA PH210

3.3.1 Data analysis of soil parameters

Statistical analyses were carried out in R Studio using R version 4.1.1 (R Core Team, 2025). Differences in soil physico-chemical properties were examined using a two-way ANOVA, and significant effects were further evaluated with a Tukey HSD post-hoc test to compare locations and land-use types.

3.4 Microbial Activity Measurement

Soil VOCs and GHGs were measured to assess the metabolic activities of soil microorganisms. VOCs represent volatile by-products of microbial metabolism, especially from fermentative or stress pathways, and provide a non-destructive fingerprint of active biochemical processes in soil (Choudoir et al., 2019; Insam & Seewald, 2010). Greenhouse gases (CO_2, CH_4, N_2O) reflect core microbial biogeochemical cycles: CO_2 arises from microbial respiration, CH_4 indicates methanogenesis or methanotrophy under varying redox conditions, and N_2O signals nitrification/denitrification activity (Kuusemets et al., 2025; H. Wang et al., 2022; Wangari et al., 2022). Together, these measurements serve as functional indicators of carbon and nitrogen cycling processes, allowing comparison of microbial metabolic activity across different soil habitats and land-use regimes.

3.4.1 Volatile organic compounds (vocs) extraction

We selected soils from 3 subplots of each site. 30 grams of these soils were collected from each subplot and filled into glass vials, as shown in Figure 3.6, before being send to laboratory at Universiti Kebangsaan Malaysia (UKM) for further analysis.

Static headspace sampling (SHS) technique (Kremser et al., 2016; Voice & Kolb, 1993) were used to measure volatile organic compounds (VOCs) from soil samples. A 5 g portion of soil is placed in a 2 mL glass vial. The vial is then sealed

with an airtight septum to prevent VOC loss. Samples are incubated at a controlled temperature (e.g., 25–40°C) for 24 hours to allow VOCs to accumulate in the headspace. After incubation, a headspace sampler or a gas-tight syringe is used to extract the gaseous phase from the vial. This sample is injected into a gas chromatograph (GC) equipped with a suitable detector (e.g., flame ionization detector or mass spectrometer) for VOC separation and quantification. The GC conditions, such as carrier gas flow, column type, and oven temperature, are optimized based on the expected VOC profile.

Subsequently, VOC fluxes (VF; µg m-2 h-1) were calculated according to the following equation:

$$VF = \frac{(Cout \times Cin) \times Qin}{SAsoil}$$

where Cout (µg L^{-1}) represents the concentration of VOCs at the outlet of the sample, Cin (µg L^{-1}) indicates the VOC concentration in the purified air entering the system, Qin (L h^{-1}) refers to the inflow rate into the soil collars, and SA soil (m^2) denotes the soil surface area within the collars. Volatile organic compounds (VOCs) of biological origin, specifically those produced by bacteria and fungi, were identified using the microbial volatile compound database mVOC 2.0 (Lemfack et al., 2018).

Figure 3.6 Prepared soil in glass vial for VOCs analysis

3.4.2 Greenhouse gas extraction

To measure CH_4, CO_2, and N_2O emissions from soil, greenhouse gas sampling was conducted using closed chamber techniques. At each site, three chambers were placed on separate subplots, where they were left undisturbed for 1 hour to allow the accumulation of gases emitted from the soil (Figure 3.7). After this incubation period, gas samples were extracted from the chambers using a syringe with a needle attachment and transferred into airtight glass vials for storage and transport.

The collected gas samples were then analysed using Agilent 7890 gas chromatography (GC) at the Environmental Analytical Chemistry Laboratory UMT. The GC was equipped with detectors specific for CH_4 (flame ionization detector, FID), CO_2, and N_2O (electron capture detector, ECD). Calibration was performed using standard gas mixtures provided by Linde Malaysia. The GC conditions, including column type, temperature, and carrier gas flow, were optimized to ensure accurate separation and quantification of the greenhouse gases.

Figure 3.7 Chamber used for greenhouse gas extraction

Emission rates were calculated by considering the change in gas concentration over time, the volume of the chamber, and the surface area of the soil. GHG fluxes were calculated by determining the change in gas concentration over time. The GHGs flux (in µg C m^{-2} h^{-1} for CO_2 and CH_4, and µg N m^{-2} h^{-1} for N_2O) was calculated using the following formula:

$$GHG\ flux = \frac{MV \times S \times P \times V}{A \times R \times T}$$

Where;

M = molecular weight of GHGs (C-CO_2=12, C-CH_4=12, N_2-N_2O=28),

S = slope of the gas concentration over time (µL L^{-1} hr^{-1}),

P = assumed atmospheric pressure = 1 atm,

V = volume of static-chamber headspace (m3),

R = universal gas constant (0.0821 L atm K^{-1} mol^{-1}),

T = field temperature (K).

3.4.3 Data analysis for metabolic activity study

All statistical analyses were conducted in R Studio using R version 4.1.1. Data visualisations were produced with the ggplot2 package (Wickham, 2016). The effects of sampling location and land-use type on VOC fluxes and greenhouse gas emissions were evaluated using the Kruskal–Wallis test implemented in the vegan package (Oksanen, 2015). Principal component analysis (PCA) was applied to illustrate patterns in VOC concentrations and soil physico-chemical properties. Analysis of dissimilarities (PerMANOVA) was used to examine how VOC profiles varied across locations and land-use categories. To identify key soil properties influencing the greenhouse gas emissions, random forest analysis was performed using the rfPermute package (Liu et al., 2020). Relationships between VOC community composition and microbial communities were assessed using the Mantel test.

3.5 Litterbags Experiment

While diversity assessments and soil physico-chemical measurements were conducted at eight sites, the litterbag experiment was restricted to three representative sites: an urban park, a primary forest, and a permaculture garden. This was due to two constraints: first, constructing and deploying litterbags at all eight sites would have been logistically demanding and prohibitively expensive; second, the three selected sites span a gradient of land-use intensity, from minimally disturbed forest, through a semi-managed permaculture system, to heavily modified urban soil, providing a meaningful comparison of how soil fauna influence litter decomposition across contrasting environments. This targeted approach allowed us to maintain experimental quality, ensure replication within each site, and generate results that reflect both ends of the land-use spectrum as well as an intermediate condition.

The selected sites are Universiti Malaysia Terengganu (UMT) campus, Taman Negara Pahang Permaculture, and the Lake Kenyir tropical forest. Two of these sites correspond to locations from the diversity survey (though different plots were used to avoid disturbance), while the permaculture site was included specifically to represent an anthropogenic habitat with low-intensity management practices such as the use of

animal manure as fertilizer. It is important to note that although the UMT campus and Lake Kenyir sites were also included in other parts of the study, the litterbag experiment was conducted in separate plots within these sites to ensure independence from the other experimental setups. The geographical locations of the litterbag experiment sites are illustrated in Figure 3.8.

Figure 3.8 Site selection for litterbag experiment

We tested the effect of soil animals on decomposition of leaf litter by using three types of litterbags with different mesh sizes. Nylon net with 2 mm mesh size accessible for soil mesofauna, nylon net with 2 mm mesh size and with 2 cm holes which accessible to both mesofauna and macrofauna, and litterbags made from fabric with 0.1 mm mesh size as a control (Burtis et al., 2024).

Leaflitters were collected from various tree from Botanical Garden in UMT campus. The dominant trees are Dipterocarpus, Shorea, Lithocarpus, Pometia, Artocarpus, and Maniltoa while dominant understory vegetation is from the family of Zingiberaceae and Annonaceae. It then was oven dried for overnight. The dried leaflitters were weight at exact 5 grams and were put into all litterbags. The litterbags were then placed at the selected three sites as shown in Figure 3.9, Figure 3.10, and Figure 3.11. In total, 54 litterbags, consisting of six replicates, with different mesh sizes (18 accessible for macrofauna, 18 accessible for mesofauna, and 18 control litterbags) were place at each site (Figure 3.12). The incubation period were set for 3 months because of the tropical climate, the decomposition was expected to be rapid compared to temperate regions.

Figure 3.9 Litterbags setup in Tasik Kenyir forest

Figure 3.10 Litterbags setup on UMT campus

Figure 3.11 Litterbags setup in Pahang permaculture

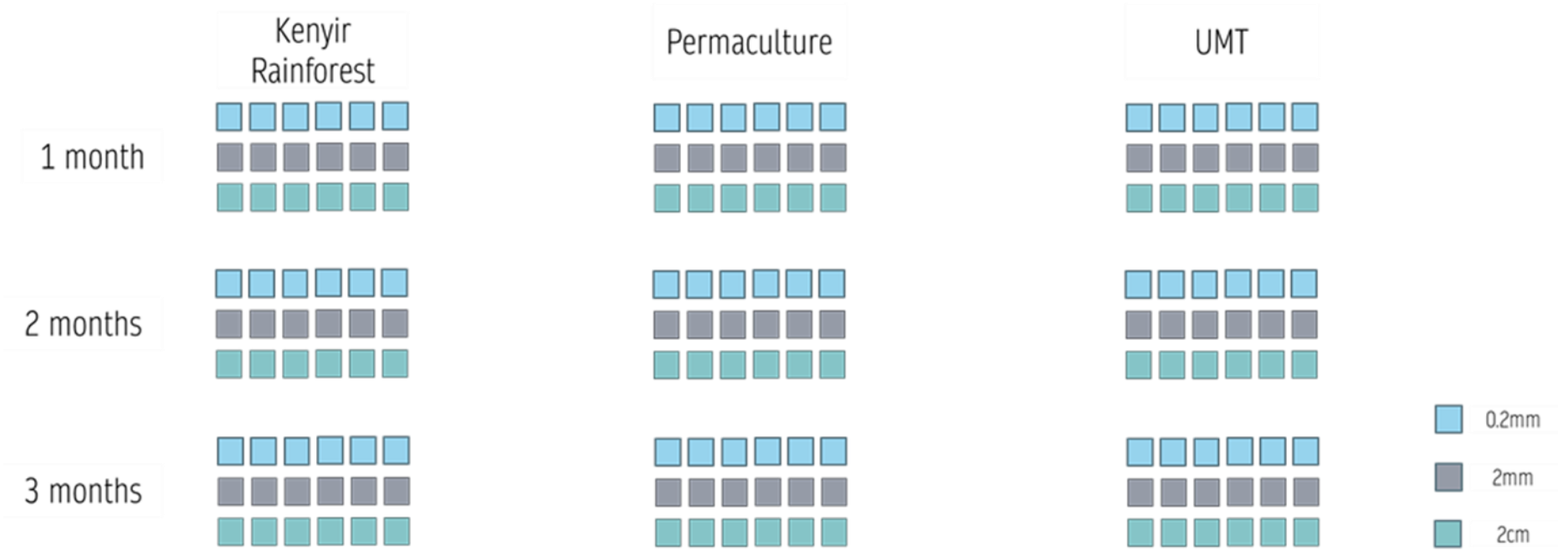

Figure 3.12 Layout of litterbag experiment showing total number of litterbags used in three selected sites to be incubated for predetermined periods.

3.5.1 Soil faunal extraction from litterbags experiments sites

Soil samples for mesofauna were collected using a shovel by removing 10 × 10 cm soil blocks to a depth of 5 cm. Three intact soil cores were obtained from each litterbag site for each of the three incubation months, yielding a total of 27 samples. Mesofauna were extracted via a dry extraction technique using a modified Berlese–Tullgren funnel over three days (Pande & Berthet, 1973), with specimens trapped in detergent water and subsequently preserved in 70% ethanol for later identification (Peng et al., 2022a). Macrofauna were sampled using the hand-sorting method. At each site, a 25 × 25 cm soil monolith (5 cm deep) was collected alongside the mesofauna samples, resulting in another 27 monoliths across all sites and sampling periods. These monoliths were transported to the laboratory and processed immediately by manually extracting all fauna larger than 2 mm (Ruiz et al., 2008; Swift et al., 1979). All soil animals were identified to one of 16 taxonomic groups at the family, order, subclass, or class level, including Collembola, Acari, Diplura, Symphylla, Pauropoda, Protura, Lumbricidae, Diplopoda, Isoptera, Isopoda, Araneae, Chilopoda, Formicidae, Coleoptera, other insects, and Blattodea (excluding Isoptera). Additionally, soil fauna was assigned to seven functional categories: Predators, Omnivores, Saprophages (Macrofauna), Saprophages (Mesofauna), Macrofauna total, Mesofauna total, and Total fauna (Filser et al., 2016; Orgiazzi et al., 2016; Swift et al., 1979).

3.5.2 Data analysis for litterbag study

litterbag experiment, we used a logarithmic regression to fit the temporal trend of mass loss for each species and mesh size across three sampling locations. The decomposition rate (decomposition constant) (k value) was calculated according to a single exponential model for comparisons among different litterbags and sampling locations (Peng et al., 2022). Specifically, we calculated the k value (months−1) using the equation:

$$k = -\frac{1}{t}\ln\left(\frac{M_t}{M_0}\right)$$

where M0 is the initial litter dry mass (g) and Mt is the dry mass at sampling time t (month). The effects of litterbag mesh size, sampling locations, sampling times and their interactions on the percentage of mass loss were assessed using a linear regression model. The Analyses of Variance (ANOVA) were used to compare the mean percentage of mass loss and decomposition rate between three different sampling locations, followed by post hoc test (Tukey's Honest Significant Difference) for observed means. To test how access of meso- and macrofauna modulates litter decomposition rate (k) as assessed using different litterbag mesh sizes, effect sizes were calculated as a proxy. All statistical analyses and graphical representations were conducted using the R-Studio program (R Core Team, 2025) with the assistance of the "vegan" and "ggplot2" packages (Oksanen et al., 2012; Wickham, 2014).

CHAPTER 4

RESULTS

4.1 Diversity and Composition of Soil Biota

4.1.1 Diversity of soil biota

The alpha diversity indices of bacteria, fungi, and soil fauna varied considerably among the different land-use types across Peninsular Malaysia (Table 4.1). For bacterial communities, richness and diversity were generally high across all habitats, though significant differences were detected among sites ($p < 0.001$). The primary forest exhibited the highest bacterial richness (5721 ± 153), followed closely by the oil palm plantation (5463 ± 263), whereas the peat forest (3788 ± 133) and urban park (4116 ± 636) supported markedly lower bacterial richness. The Shannon diversity index reflected a similar pattern, with the primary forest showing the highest diversity (11.1 ± 0.1), indicating both a greater number and evenness of bacterial taxa compared to other sites. Although the Simpson index values were uniformly high (0.995–0.998) across all habitats, suggesting highly even bacterial assemblages, no significant differences were observed among land-use types for this metric. When comparing broad categories, natural and anthropogenic habitats did not differ significantly in bacterial diversity ($p > 0.05$), though mean values were slightly higher in the former (4815 ± 208 vs. 4556 ± 169).

In contrast, fungal communities exhibited more pronounced variation among habitats. Fungal richness was highest in the primary forest (789 ± 66) and tropical

wetland (626 ± 16), while substantially lower values were observed in the urban park (352 ± 54) and peat forest (400 ± 27) ($p < 0.001$). The Shannon index mirrored these trends, with the primary forest (7.3 ± 0.3) displaying significantly greater fungal diversity than other habitats, suggesting a well-balanced and species-rich community structure. The Simpson index ranged from 0.793 to 0.974, indicating moderate variability in community evenness among sites. Although the ANOVA for natural versus anthropogenic habitats was not significant, the mean diversity values again favored natural systems (6.0 ± 0.3 vs. 5.8 ± 0.2).

The soil fauna showed the strongest response to land-use changes, with highly significant differences in all indices ($p < 0.01$). Species richness peaked in the primary forest (9 ± 2) and tropical wetland (6 ± 1) but declined sharply in the peat forest (3 ± 1) and durian orchard (3 ± 0). The Shannon index similarly indicated that primary forest soils supported the most diverse and evenly distributed faunal communities (2.0 ± 0.2), whereas the durian orchard had the lowest diversity (0.7 ± 0.1). Simpson index values ranged widely (0.409–0.832), again highlighting a loss of evenness and dominance of few species in disturbed systems. However, when pooled by land-use category, natural and anthropogenic sites did not differ significantly, although mean values were slightly higher in natural soils (0.664 ± 0.046 vs. 0.644 ± 0.051).

Overall, primary forests consistently supported the highest microbial and faunal diversity, while peat forests and urban parks exhibited the lowest levels across all taxa. Agricultural systems such as paddy fields, oil palm plantations, and orchards maintained intermediate levels of diversity, suggesting that moderate management intensity may allow partial recovery or persistence of soil biota. The consistent ranking of primary forests as the most biodiverse habitat across bacteria, fungi, and fauna underscores the crucial role of intact forest ecosystems in maintaining soil ecological integrity. Conversely, anthropogenic disturbance appears to disproportionately affect fungi and fauna, which showed greater sensitivity to land-use conversion compared to bacterial communities.

Table 4.1 Alpha diversity indices (mean±SE) of bacteria, fungi and soil fauna from soils among various natural and anthropogenic habitats across peninsular Malaysia.

	Sites									Land use		
Alpha diversity indices	Secondary forest	Peat forest	Tropical wetland	Primary forest	Paddy field	Oil palm	Durian orchard	Urban park	ANOVA	Anthropogenic	Natural	ANOVA
Bacteria: Richness	4707±104b	3788±133c	4008±150bc	5721±153a	4983±328	5463±263ab	4699±154b	4116±636c	***	4815±208	4556±169	ns
Bacteria: Shannon	10.5±0.1b	10.0±0.1b	10.2±0.1ab	11.1±0.1a	10.7±0.2b	11.0±0.2ab	10.2±0.2b	10.2±0.4b	***	10.5±0.1	10.5±0.1	ns
Bacteria: Simpson	0.996±0.000	0.997±0.000	0.997±0.000	0.998±0.000	0.997±0.001	0.998±0.001	0.995±0.001	0.996±0.001	ns	0.996±0.000	0.997±0.000	ns
Fungi: Richness	414±56c	400±27c	626±16b	789±66a	533±23c	517±68c	503±43c	352±54d	***	476±28	557±40	ns
Fungi: Shannon	4.6±0.6c	5.8±0.3c	6.3±0.1b	7.3±0.3a	6.6±0.1b	5.5±0.6c	5.5±0.4c	5.5±0.5c	**	5.8±0.2	6.0±0.3	ns
Fungi: Simpson	0.793±0.080	0.938±0.015	0.952±0.006	0.974±0.007	0.968±0.004	0.886±0.051	0.885±0.050	0.915±0.030	ns	0.913±0.019	0.914±0.024	ns
Fauna: Richness	4±1c	3±1d	6±1b	9±2a	4±0c	6±0b	3±0d	5±1c	**	5±1	6±1	ns
Fauna: Shannon	1.1±0.1c	1.1±0.2bc	1.2±0.3b	2.0±0.2a	1.1±0.1c	1.7±0.0ab	0.7±0.1d	1.5±0.2b	**	1.3±0.1	1.4±0.1	ns
Fauna: Simpson	0.619±0.034c	0.623±0.063c	0.582±0.147c	0.832±0.024a	0.608±0.029	0.810±0.008a	0.409±0.082d	0.750±0.046b	**	0.644±0.051	0.664±0.046	ns

Beta diversity analysis using non-metric multidimensional scaling (NMDS; Figure 4.1), based on Hellinger-transformed Bray-Curtis dissimilarities, revealed distinct variations in the beta diversity of bacterial, fungal, and soil fauna communities across different land use types and between natural and anthropogenic habitats. For bacterial communities, the NMDS plot clearly separated natural from anthropogenic habitats. Natural sites exhibited greater similarity among themselves, indicating lower beta diversity compared to anthropogenic sites.

For bacterial communities, the NMDS ordination clearly separated natural and anthropogenic habitats along the primary axis, indicating strong compositional turnover linked to habitat modification. Natural sites formed compact clusters, suggesting greater similarity in bacterial assemblages and thus lower beta diversity under undisturbed conditions. Conversely, samples from anthropogenic habitats were more widely scattered, reflecting increased community heterogeneity and higher beta diversity. This pattern likely arises from spatial variability in soil disturbance, nutrient enrichment, and microhabitat heterogeneity commonly associated with agricultural or human-impacted sites. Environmental vector fitting revealed that soil texture (clay, silt, sand), moisture, and nutrient concentrations (total nitrogen and total phosphorus) were major correlates of bacterial community variation. Clay and moisture gradients were positively associated with natural habitats, whereas sand content and higher pH values aligned with anthropogenic sites, suggesting that soil structure and fertility mediate bacterial assemblage composition.

For fungal communities, the NMDS ordination also showed a pronounced separation between natural and anthropogenic habitats, though with a slightly broader overlap than in bacterial assemblages. Natural sites were again more tightly clustered, indicating compositional stability, likely maintained by more consistent organic matter quality and microclimatic conditions. In contrast, anthropogenic sites exhibited greater dispersion, suggesting the proliferation of habitat-generalist or disturbance-tolerant taxa in response to altered soil conditions. Fungal communities appeared particularly responsive to moisture and nutrient gradients, as indicated by the direction and strength of the corresponding vectors, emphasizing their dependence on soil organic content and water availability

The soil fauna communities displayed a somewhat weaker but still evident separation between habitat types. The distribution pattern suggests that while soil fauna are influenced by similar environmental gradients as microbes, their community structure is additionally modulated by habitat complexity and resource availability. The NMDS plot showed that sand content was the strongest environmental factor shaping faunal assemblages, with coarser soils typically associated with anthropogenic habitats, while finer, moister soils characterized natural sites. The looser clustering of fauna in the ordination space suggests that faunal communities are more spatially heterogeneous, reflecting both dispersal limitations and the influence of microhabitat variation.

Overall, the NMDS analyses reveal that natural habitats support more compositionally homogeneous bacterial, fungal, and soil faunal communities, consistent with stable environmental conditions and reduced disturbance. In contrast, anthropogenic habitats promote higher beta diversity, reflecting heterogeneous soil conditions and altered resource distributions caused by land-use change. Across all community types, gradients of soil texture, moisture, pH, and nutrient status were key determinants of compositional differences, highlighting the pivotal role of soil physicochemical properties in structuring belowground biodiversity. These results demonstrate that environmental filtering and anthropogenic disturbance jointly drive community turnover across ecosystems, emphasizing the ecological consequences of land-use transformation on soil biological integrity.

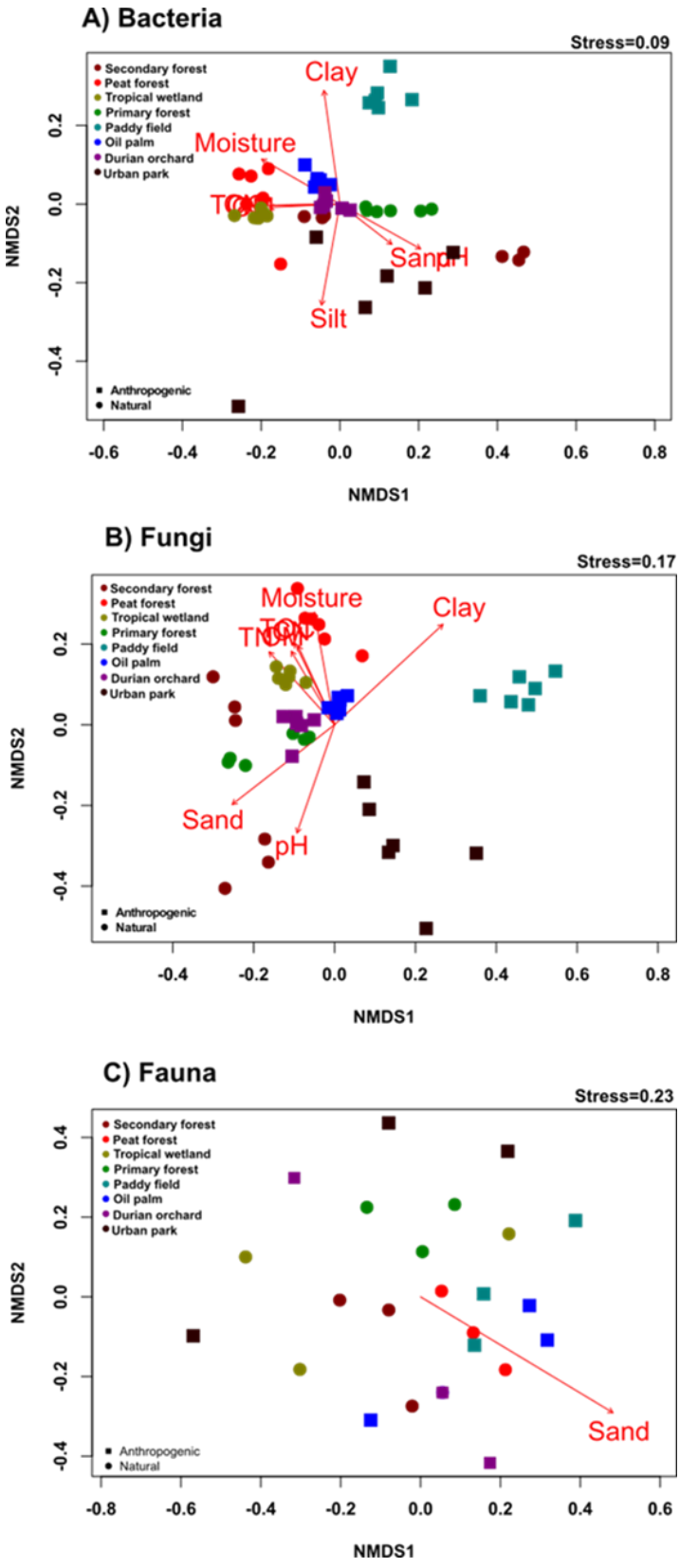

Figure 4.1 The NMDS diagram of community structure of soil prokaryotes (A), fungi (B) and soil meso and macrofauna (C) among various sampling locations and land use management.

4.1.2 Composition of soil biota

The composition of the bacterial community was predominantly characterized by Proteobacteria and Planctomycetota, with Acidobacteriota and Actinomycetota also contributing substantially to overall diversity (Figure 4.2A). Although these phyla occurred across all habitat types, their relative abundances varied markedly along a clear land-use gradient that reflected a broader biodiversity hierarchy: primary forest > wetland > secondary forest > agricultural systems > urban habitats. Soils from primary rainforest and durian orchards contained significantly higher proportions of Proteobacteria ($p < 0.001$), whereas paddy fields, oil palm plantations, and urban parks exhibited elevated levels of Chloroflexi ($p < 0.001$). Despite these patterns, no statistically significant differences emerged between natural and anthropogenic habitats when compared as broad categories, suggesting that fine-scale environmental heterogeneity plays a critical role. Life-history trends further revealed that oligotrophic bacteria, indicative of nutrient-limited or more structurally stable soils, were most abundant in urban parks, peat forests, and secondary forests (Figure 4.2D). This pattern aligns with a soil health gradient mirroring land-use intensity, wherein primary forests maintain balanced microbial networks, agricultural systems exhibit increasingly specialized functional dominance, and urban soils show functional narrowing and greater dominance by stress-tolerant taxa.

In the fungal community, Ascomycota was the most prevalent phylum, followed by Basidiomycota, although their relative abundances varied substantially among habitats (Figure 4.2B). Basidiomycota reached its highest relative abundance in durian orchards, whereas Ascomycota was most dominant in tropical wetlands. These differences reflect variation in moisture, substrate type, and vegetation composition across the land-use categories. Functionally, the fungal assemblage encompassed ectomycorrhizal fungi (ECM), animal parasites, plant pathogens, and a variety of saprotrophic group (Figure 4.2E). ECM fungi were most abundant in secondary forests, tropical wetlands, and oil palm plantations, whereas soil saprotrophs dominated in primary forests, durian orchards, and urban parks. Importantly, these shifts illustrate functional trade-offs associated with land-use change: as human modification intensifies, fewer fungal taxa perform a narrower range of ecological roles, reducing redundancy and potentially undermining long-term soil resilience.

The soil fauna community displayed substantial taxonomic variation across habitats, reflecting strong responses to local microhabitat conditions (Figure 4.2C). Symphyla were significantly more abundant in tropical wetlands, while Isopoda and Diplopoda were most numerous in primary forests, which provided deeper litter layers and greater structural complexity. Coleoptera occurred in highest abundance in oil palm plantations, and Formicidae populations were significantly larger in tropical wetlands and primary forests than in urban parks, orchards, and plantations. These patterns further reinforce the biodiversity hierarchy, with primary forests supporting the broadest representation of soil fauna groups and urban soils supporting the narrowest. The pronounced turnover among sites highlights the sensitivity of soil fauna to environmental degradation and the disproportionate loss of key taxa in highly modified landscapes.

Functional characterization of soil fauna revealed that saprophages constituted the most abundant trophic group, including both mesofauna and macrofauna (Figure 4.2F). Primary forests supported the highest abundance of saprophagous macrofauna, consistent with their rich litter inputs and well-developed detrital food webs. In contrast, oil palm plantations were dominated by omnivores, indicative of simplified food-web structure and reduced functional redundancy. These results together confirm that soil functional integrity closely mirrors biodiversity loss, with the strongest, most complex functional networks occurring in minimally disturbed ecosystems. The statistically significant differences indicated across multiple panels (denoted by asterisks) collectively demonstrate that land-use type has a pronounced effect on community structure. This reinforces the broader ecological conclusion that alterations in biodiversity at multiple trophic levels translate directly into shifts in soil ecosystem functioning and resilience.

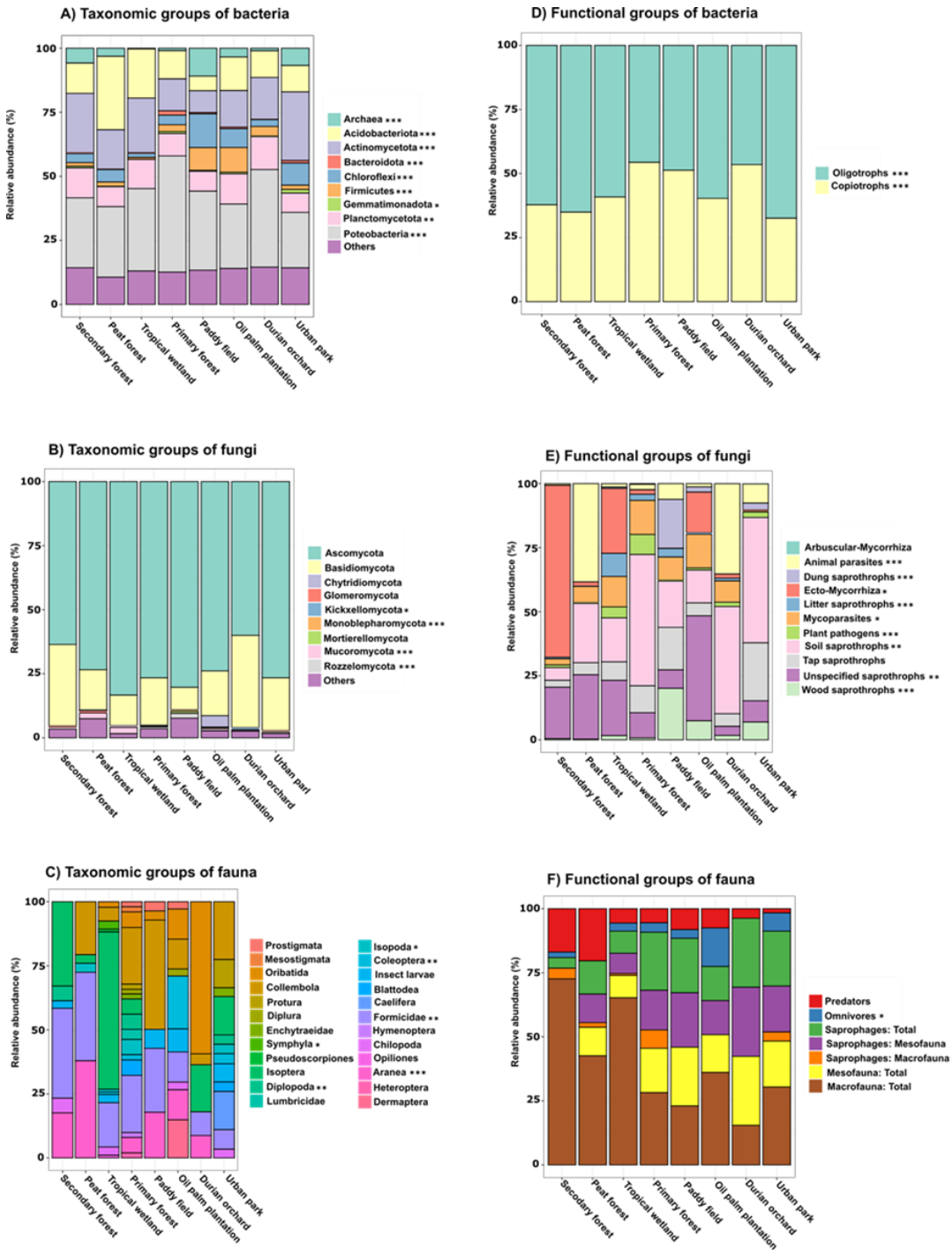

Figure 4.2 Relative abundances of taxonomic (A-C) and functional (D-F) groups of soil bacteria, fungi and fauna (meso-and macrofauna) among various habitats across peninsular Malaysia. Asterisks indicate statistically significant differences *$p < 0.05$; **$p < 0.01$.

When comparing natural and anthropogenic soils (Figure 4.3), clear differences emerged across all biological domains, bacteria, fungi, and soil fauna, indicating consistent ecological restructuring with land-use change. Among bacteria, Acidobacteriota exhibited the highest relative abundance in natural soils, reflecting the dominance of oligotrophic, slow-growing taxa adapted to low-nutrient, organic-rich environments. In contrast, Archaea, Chloroflexi, and Firmicutes were more abundant in anthropogenic soils, a pattern consistent with increases in copiotrophic and disturbance-tolerant groups documented in managed or fertilized systems. These shifts support the broader interpretation that natural soils promote conservative nutrient cycling, whereas anthropogenic soils favor taxa associated with faster, more open nutrient cycles.

Within the fungal community, Mortierellomycota and Mucoromycota were more abundant in natural sites, whereas mycorrhizal fungi, particularly ectomycorrhizal (ECM) taxa, were also enriched in natural soils compared to anthropogenic soils. Conversely, saprotrophic fungi were markedly more abundant in anthropogenic sites, indicating a transition from symbiosis-dominated to decomposition-dominated systems. This aligns with the interpretation that land-use conversion leads to a reduction in mutualistic fungi and an increase in fast-growing saprotrophs and potential pathogens, signalling a functional shift and a decline in soil ecosystem stability.

For soil fauna, Formicidae were the most abundant group in natural soils, representing a taxon often associated with structurally complex, undisturbed habitats. Predators and saprophagous macrofauna also exhibited higher relative abundances in natural soils, reflecting the presence of a more balanced and multi-layered soil food web. Anthropogenic soils, in contrast, showed evidence of trophic simplification, consistent with the dominance of disturbance-tolerant, generalist taxa reported in previous analyses. These differences reinforce the broader ecological pattern that natural soils support higher functional diversity and redundancy, whereas anthropogenic soils host simplified communities with reduced ecosystem multifunctionality.

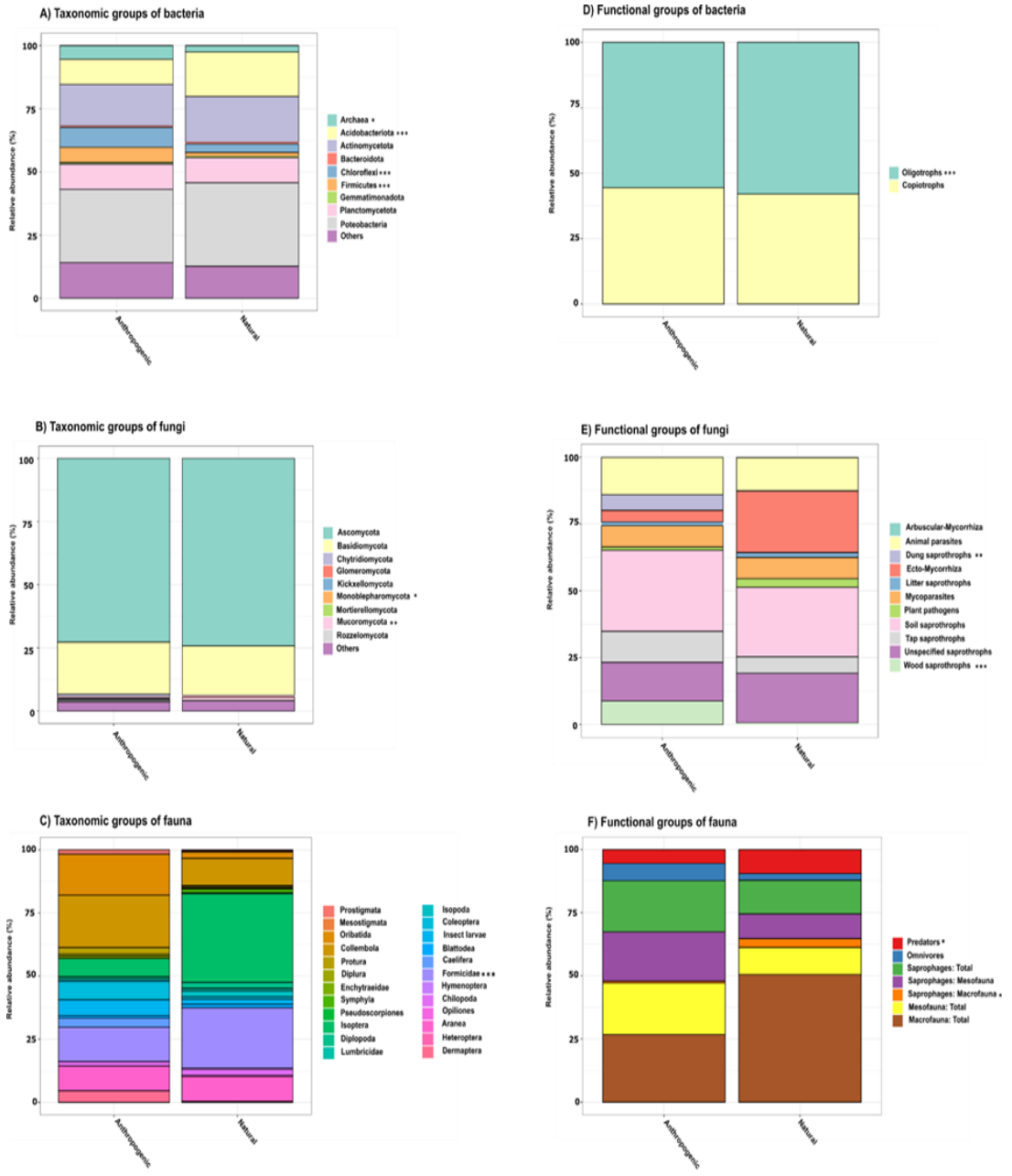

Figure 4.3 Relative abundances of taxonomic (A-C) and functional (D-F) groups of soil prokaryotes, fungi and soil meso and macrofauna between natural and anthropogenic sites Malaysia. Asterisks indicate statistically significant differences *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$. Same letters indicate statistical homogenous groups.

4.2 Effects of Soil Physico-Chemical Properties on Diversity and Composition of Soil Biota

4.2.1 Soil physico-chemical properties

Significant differences in soil physico-chemical properties were detected between natural and anthropogenic habitats (Table 4.1). Compared with anthropogenic sites, natural sites had significantly higher moisture (33.7 ± 5.2%), conductivity (52.4 ± 5.8 μS·cm⁻¹), salinity (33.5 ± 3.7 mg·kg⁻¹), total organic carbon (TOC) (9.4 ± 2.6%), total nitrogen (TN) (0.11 ± 0.01% vs 0.05 ± 0.01%; $p < 0.001$), organic matter (OM) (18.2 ± 4.6% vs 4.5 ± 0.6%; $p < 0.01$), C:N ratio (6.6 ± 1.5 vs 2.7 ± 0.2; $p < 0.05$), sand (42.3 ± 2.0% vs 33.8 ± 1.0%; $p < 0.001$) and silt (39.3 ± 2.0% vs 31.8 ± 2.2%; $p < 0.05$). In contrast, anthropogenic sites had significantly higher clay (34.5 ± 2.6%) and available phosphorus (P) (16.1 ± 1.9 mg kg⁻¹). Soil pH did not differ significantly between groups (natural 5.5 ± 0.2, anthropogenic 5.3 ± 0.1; ns).

Within anthropogenic sites, oil palm plantations had the highest available P (262 ± 47 mg kg⁻¹) and the highest clay content (48.0 ± 12.0%); paddy fields also showed high clay (42.0 ± 10.5%) and relatively high moisture (26.5 ± 3.3%). Among anthropogenic land uses, oil palm and paddy were the wettest (oil palm 28.3 ± 7.3%; paddy 26.5 ± 3.3%), whereas urban parks were the driest (7.0 ± 1.0%). Urban parks had the highest silt within anthropogenic sites (50.0 ± 12.5%) and the highest pH among anthropogenic sites (5.9 ± 0.2). Durian orchards had the highest OM and moderate conductivity within anthropogenic sites (OM 7.9 ± 1.7%; conductivity 39.9 ± 9.2 μS·cm⁻¹). Oil palm soils had the lowest OM (2.1 ± 0.4%) and low TN (0.04 ± 0.02%).

Within natural sites, tropical wetlands were extreme: highest moisture (70.6 ± 5.7%), highest conductivity (74.4 ± 13.8 μS·cm⁻¹), highest salinity (47.6 ± 8.8 mg·kg⁻¹), highest TOC (25.1 ± 4.6%), highest TN (0.14 ± 0.02%), highest OM (47.8 ± 10.3%), highest C:N ratio (172 ± 15), and high available P (21.1 ± 2.8 mg kg⁻¹), and

the lowest pH (4.2 ± 0.1). Peat forest had very high silt (50.0 ± 12.5%) and elevated OM (13.8 ± 6.3%). Primary forest had the highest sand among natural sites (55.0 ± 13.8%) and shared the highest pH (6.3 ± 0.1) with secondary forest. Secondary forest showed comparatively low moisture (9.3 ± 2.1%), low clay (11.0 ± 2.8%) and intermediate TOC and OM.

When comparing each property, moisture shows a clear ecological gradient. Natural habitats, particularly tropical wetlands, retain substantially more water because of persistent saturation and slower drainage, while anthropogenic habitats such as urban parks exhibit strong drying due to soil compaction, reduced canopy cover, and managed landscaping. This pattern emphasises how land modification alters hydrology and reduces the soil's ability to store water.

Soil pH varies mainly with vegetation type and hydrology. Natural sites span from acidic wetlands (pH ~4) to mildly acidic forests (pH ~6.3), reflecting organic acid accumulation and leaching. Anthropogenic soils cluster within a similar acidic range, but with less variation, likely reflecting disturbance, input of fertilisers, and reduced organic accumulation. The absence of a significant difference between groups suggests pH is driven more by inherent parent material and specific land-use practices than by the natural–anthropogenic divide.

Conductivity and salinity are elevated in wetter, organic-rich natural environments. Tropical wetlands show the highest values, consistent with solute concentration under reducing, slow-draining conditions. Anthropogenic soils, by contrast, exhibit lower conductivity due to higher clay compaction, faster percolation after rainfall, and reduced organic inputs. These patterns highlight how hydrology and organic matter jointly drive ionic composition.

Total organic carbon (TOC) is strongly shaped by litter inputs and decomposition regimes. The extreme TOC in tropical wetlands reflects slow anaerobic decomposition; peat forest also retains substantial carbon. Anthropogenic habitats consistently show depleted TOC, reflecting biomass removal, tillage, and rapid decomposition under disturbance. This demonstrates that natural habitats function as

important carbon reservoirs, whereas anthropogenic landscapes lose soil carbon rapidly.

Total nitrogen (TN) mirrors TOC patterns. Natural habitats accumulate more nitrogen because of continuous organic inputs and slower mineralisation, while anthropogenic soils, especially oil palm, show nitrogen depletion due to harvesting, fertiliser-driven nutrient imbalances, and lower biomass turnover. This reinforces the link between nitrogen cycling and carbon dynamics across land uses.

The C:N ratio underscores contrasting decomposition environments. Tropical wetlands exhibit exceptionally high C:N, characteristic of carbon-rich, nitrogen-limited, slow-decomposition systems. Forests maintain moderate C:N values consistent with balanced litter turnover. Anthropogenic habitats have uniformly low C:N ratios, signalling nitrogen-poor, carbon-depleted soils that cycle organic matter rapidly and lack long-term stabilisation pathways.

Available phosphorus (P) is strongly influenced by fertiliser practices. Anthropogenic sites show higher P, driven especially by oil palm plantations—indicating external inputs and possible P accumulation in clay-rich soils. Natural habitats have lower P except tropical wetlands, where organic matter and hydrology concentrate nutrients. This contrast highlights how fertiliser dependency reshapes soil nutrient balance in human-modified landscapes.

Organic matter (OM) patterns closely follow TOC and TN. Natural systems maintain much higher OM because of continuous litterfall and minimal disturbance. Anthropogenic soils lose OM through ploughing, erosion, and reduced biomass return. Extremely high OM in tropical wetlands further reflects persistent waterlogging and inhibited decomposition. OM therefore acts as a strong diagnostic indicator distinguishing intact from disturbed ecosystems.

Texture (sand–silt–clay fractions) shows that natural habitats lean towards sandier profiles, especially primary forests, supporting better drainage and lower compaction. Anthropogenic habitats show higher clay content, reflecting soil selection

for agriculture, compaction from machinery, or sediment redeposition. Higher clay in paddy and oil palm soils influences water retention, nutrient binding, and P accumulation. Silt peaks in peat forest and urban parks, showing how organic material and managed landscaping shape intermediate textures.

Overall, these results indicate that natural habitats tend to have sandier, more moist, and more organic-rich soils, whereas anthropogenic habitats are generally clay-rich and phosphorus-rich but lower in organic matter and moisture.

Table 4.2 Physico-chemical properties (mean±SE) from soils among various natural and anthropogenic habitats across peninsular Malaysia.

	Natural habitats				Anthropogenic habitats					Land use		
Soil properties	Secondary forest	Peat forest	Tropical wetland	Primary forest	Paddy field (After-harvest)	Oil palm plantation	Durian orchard	Urban park	ANOVA	Anthropogenic	Natural	ANOVA
Moisture (%)	9.3±2.1d	28.2±7.1b	70.6±5.7a	26±2.7b	26.5±3.3b	28.3±7.3b	18.0±1.4c	7.0±1.0d	***	20.0±2.6b	33.7±5.2a	*
pH	6.3±0.6a	5.3±0.3b	4.2±0.1c	6.3±0.1a	5.1±0.2b	5.6±0.1ab	4.6±0.1bc	5.9±0.2ab	***	5.3±0.1	5.5±0.2	ns
Conductivity (µS·cm−1)	29.6±4.6c	50.3±11.1b	74.4±13.8a	55.4±8.9b	33.4±3.2c	24.4±3.2c	39.9±9.2bc	36.0±8.7bc	**	33.4±3.4b	52.4±5.8a	**
Salinity (mg·kg−1)	18.0±3.0c	32.2±7.1b	47.6±8.8a	35.5±5.7b	21.4±2.1c	15.6±2.0c	25.5±5.9bc	23.1±5.6bc	**	21.4±2.2b	33.5±3.7a	**
TOC (%)	1.4±0.4b	9.2±5.7ab	25.1±4.6a	1.9±0.5b	1.6±0.2b	1.0±0.2c	1.6±0.3bc	1.3±0.2c	***	1.4±0.1b	9.4±2.6a	**
TN (%)	0.1±0.01ab	0.1±0.03ab	0.14±0.02a	0.07±0.002b	0.06±0.03c	0.04±0.02c	0.05±0.01c	0.05±0.01c	***	0.05±0.01b	0.11±0.01a	***
C:N ratio	13±3c	54±23b	172±15a	25±5c	25±2c	25±6c	33±4bc	26±3c	***	2.7±0.2b	6.6±1.5a	*
P (mg kg -1)	7.4±0.6bc	5.4±0.8c	21.1±2.8a	5.9±0.8c	13.2±2.2ab	26.2±4.7a	13.1±2.2ab	11.8±3b	***	16.1±1.9a	10±1.5b	*
OM (%)	3.8±0.6c	13.8±6.3ab	47.8±10.3a	7.2±1.9b	4.3±0.2b	2.1±0.4c	7.9±1.7ab	3.8±1.0c	***	4.5±0.6b	18.2±4.6a	**
Sand (%)	43.0±10.8ab	28.0±7.0c	43.0±10.8ab	55.0±13.8a	34.0±8.5b	26.0±6.5c	40.0±10.0b	35.0±8.8bc	***	33.8±1.0b	42.3±2.0a	***
Silt (%)	46.0±11.5ab	50.0±12.5a	36.0±9.0b	25.0±6.3c	24.0±6.0c	26.0±6.5c	27.0±6.8c	50.0±12.5a	***	31.8±2.2b	39.3±2.0a	*
Clay (%)	11.0±2.8d	22.0±5.5b	21.0±5.3c	20.0±5.0c	42.0±10.5a	48.0±12.0a	33.0±8.3ab	15.0±3.8c	***	34.5±2.6a	18.5±0.9b	***

Asterisks indicate statistically significant differences: *p < 0.05; **p < 0.01; ***p < 0.001. Same letters indicate statistically homogeneous groups. TOC – Total Organic Carbon; TN – Total Nitrogen; C:N – Carbon-to-Nitrogen ratio; P – Available Phosphorus; OM – Organic Matter (based on loss on ignition).

4.2.2 Effects of soil physico-chemical properties on diversity and composition of soil biota

Random Forest models were used to identify the relative importance of soil properties in predicting the alpha diversity of bacteria, fungi, and soil fauna (Figure 4.4). The models revealed that each biological group responded to a distinct set of environmental controls, reflecting the ecological strategies and habitat requirements of microorganisms and soil animals.

For bacterial alpha diversity (Figure 4.4A), soil pH emerged as the most influential predictor, followed by total organic carbon (TOC) and moisture content. This pattern is consistent with global evidence that pH is the dominant regulator of bacterial community structure due to its strong effects on enzyme activity, nutrient solubility, and cell membrane stability. Organic carbon and moisture were also important, as they provide energy substrates and regulate oxygen availability, thereby shaping the balance between aerobic and anaerobic bacterial guilds. Other variables such as texture and conductivity contributed minimally to bacterial diversity, acting primarily through indirect effects on aeration and nutrient diffusion.

For fungal alpha diversity (Figure 4.4B), soil organic matter was the strongest driver, with C:N ratio and soil moisture also contributing substantially. Fungi depend heavily on organic substrates for energy, and variations in carbon quality and nutrient stoichiometry regulate the prevalence of different functional groups (e.g., lignin-degrading Basidiomycota vs. fast-growing Ascomycota). Moisture further modulated fungal diversity by influencing hyphal growth and oxygen availability. Phosphorus showed moderate importance, reflecting its role in plant–fungal symbioses, where elevated P levels can weaken mycorrhizal associations. Consistent with previous findings, pH played a weaker role for fungi than for bacteria due to their broader physiological tolerance to acidity.

For soil fauna (Figure 4.4C), soil texture (particularly clay and sand proportions) and moisture content were the primary determinants of diversity. These

factors regulate the physical habitat structure, such as pore connectivity, aeration, and mobility pathways, on which meso- and macrofauna depend. High organic matter and total nitrogen also contributed to faunal diversity by supporting microbial prey and detrital resources. In contrast, pH and electrical conductivity exhibited only minor importance, exerting indirect influence through their effects on microbial communities and soil chemical conditions.

Overall, the Random Forest analysis revealed clear functional differentiation among soil biotic groups. Bacterial diversity was shaped mainly by chemical constraints (pH, carbon availability); fungal diversity by resource quality and nutrient balance (OM, C:N, moisture); and faunal diversity by physical habitat characteristics (texture, moisture) and organic resources. These findings highlight the multidimensional nature of soil environments, where chemical, physical, and biological factors interact to control biodiversity across trophic levels.

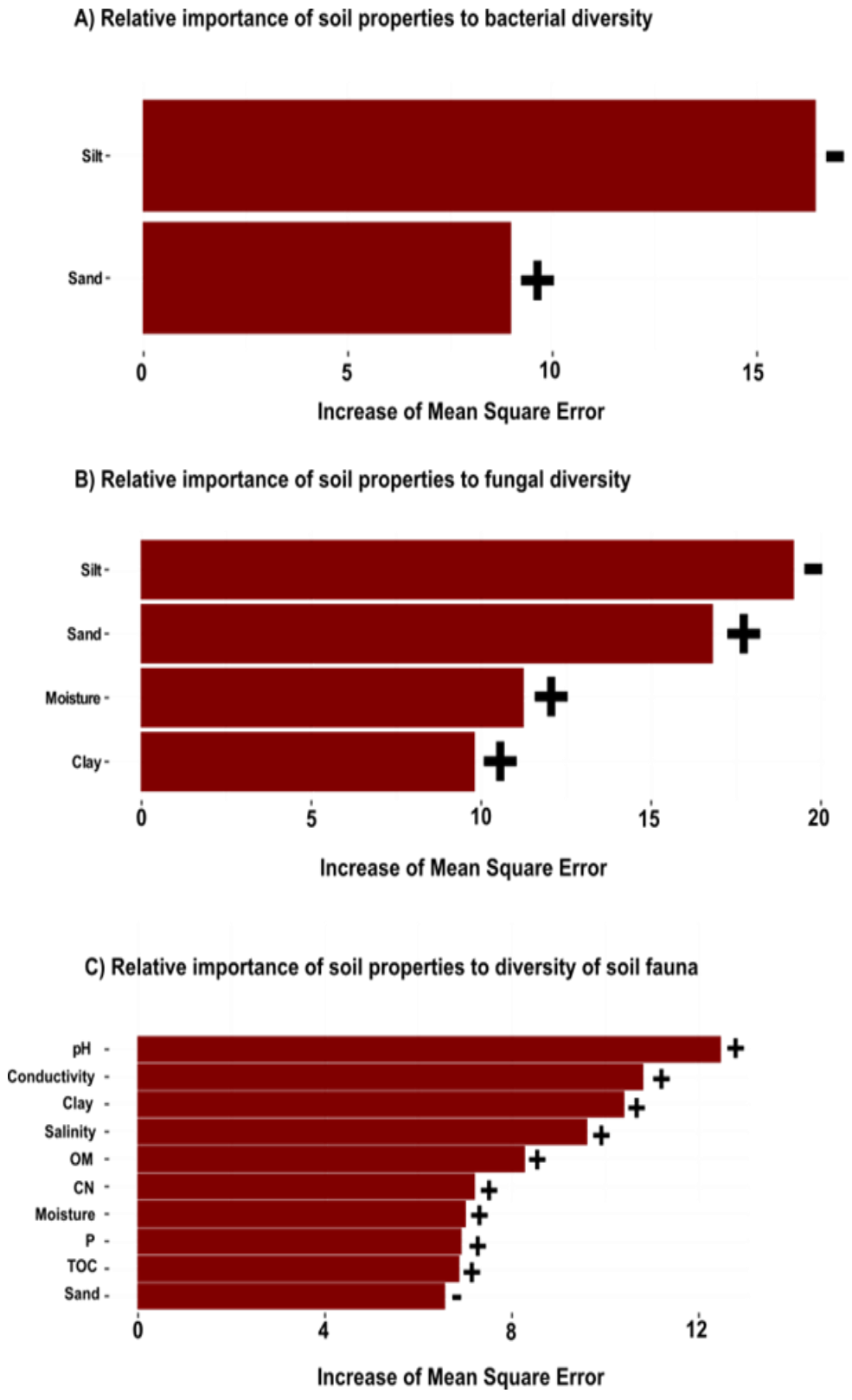

Figure 4.4 Relative importances of soil properties to soil (A) bacterial, (B) fungal, and (C) faunal diversity.

Figure 4.5 shows the NMDS diagram of the community structure of soil biota among various sampling locations and land use management. Moisture and soil texture emerged as the most significant environmental factors shaping the beta diversity of bacterial communities (Figure 4.5A). Sites characterized by higher moisture and clay content supported distinct bacterial assemblages that clustered together in ordination space, clearly separated from communities associated with sandier and more silt-rich soils. This pattern indicates that bacterial community structure is tightly linked to water availability and the physical properties of the soil matrix, which influence microbial habitat stability and organic matter retention.

Fungal beta diversity (Figure 4.5B) was also strongly influenced by moisture, clay content, organic matter–related variables (TOC, TN, OM, C:N), and pH. Fungal communities in wetter, clay-rich soils formed coherent clusters, reflecting similar community structures across these environments. In contrast, fungal assemblages associated with sandier, higher-pH soils were more widely spread in ordination space, suggesting greater heterogeneity in community composition under drier, more disturbed or nutrient-altered conditions. The strong alignment of fungal communities with moisture and organic matter axes underscores their sensitivity to resource availability and substrate quality.

In comparison, the NMDS analysis of soil meso- and macrofauna (Figure 4.5C) showed weaker separation between natural and anthropogenic habitats. Only sand content appeared as a significant environmental driver of faunal beta diversity. Sites with higher sand proportions formed distinct clusters, indicating that soil texture—and thus the physical structure of the soil environment—is a primary determinant of faunal community patterns. This suggests that soil fauna respond less to chemical gradients than microbes and more to habitat structure, pore space, and moisture retention governed by soil texture.

These NMDS trends were supported by PerMANOVA analyses based on Hellinger-transformed Bray–Curtis distances. Site-specific environmental conditions explained substantial proportions of variation in bacterial ($R^2 = 0.37$, $p = 0.001$), fungal ($R^2 = 0.38$, $p = 0.001$), and soil fauna ($R^2 = 0.39$, $p = 0.004$) communities,

demonstrating that local environmental heterogeneity plays a major role in structuring soil biota. Land-use type also had a significant, though smaller, effect on community composition for bacteria ($R^2 = 0.07$, $p = 0.001$), fungi ($R^2 = 0.06$, $p = 0.001$), and fauna ($R^2 = 0.09$, $p = 0.03$), indicating that broader ecosystem management practices further contribute to differences in soil community structure across the landscape.

Overall, these findings highlight a consistent pattern: microbial communities are strongly shaped by moisture, organic matter, and soil texture, while soil fauna respond mainly to the physical structure associated with sandy soils. Natural ecosystems with higher moisture and greater organic accumulation support more cohesive microbial communities, whereas anthropogenic soils with sandier textures and higher pH values exhibit more variable or simplified community structures.

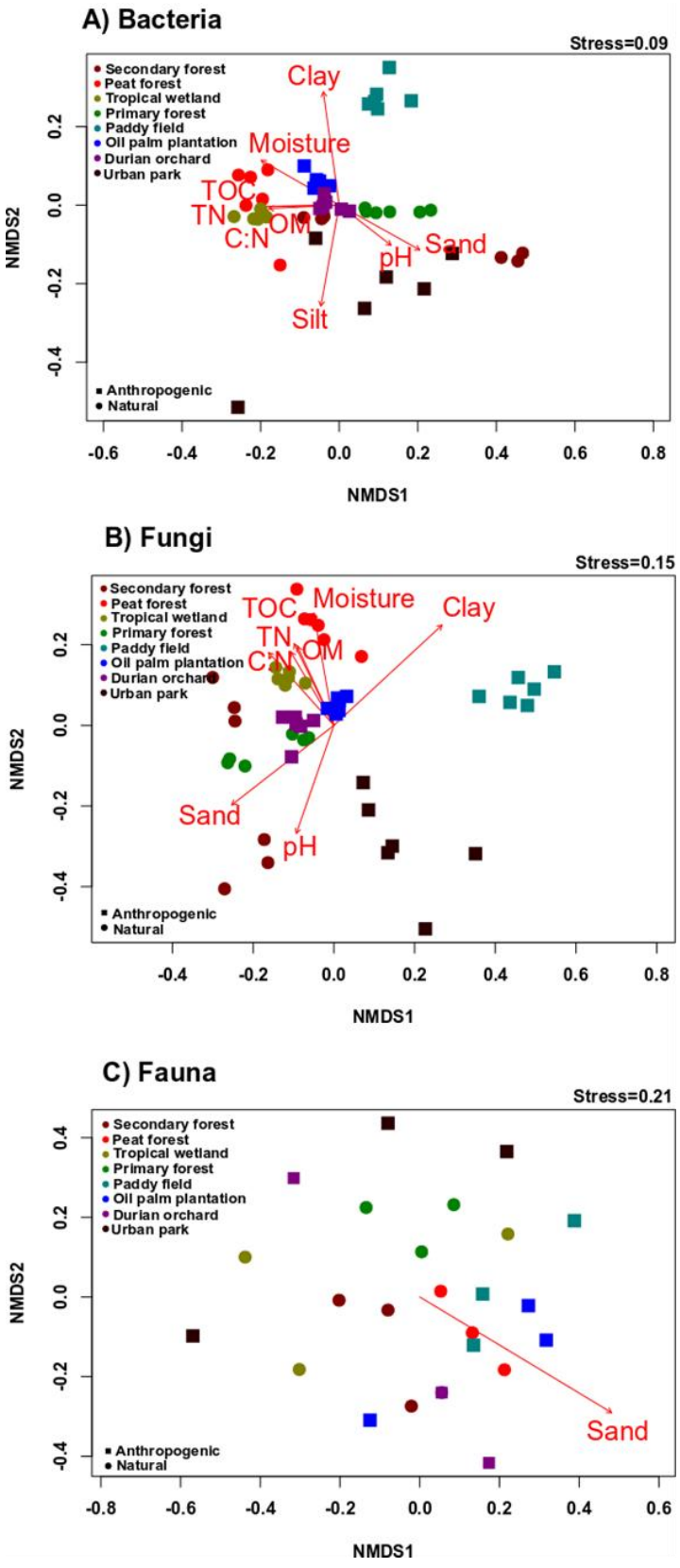

Figure 4.5 The NMDS diagram of community structure of soil prokaryotes (A), fungi (B) and soil meso and macrofauna (C) among various sampling locations and land use management. Only significant environmental variables are shown in the figure.

4.3 Soil Biota Metabolic Activity

4.3.1 Volatile organic compounds (VOCs)

Table 4.3 shows the Volatile Organic Compounds (VOCs) across eight sampling sites in Terengganu. Across the sites, most VOCs showed no statistically significant differences in concentration, indicating high within-site variability and considerable overlap among ecosystems. However, three aromatic compounds—toluene, p-xylene, and benzoic acid—exhibited clear and significant variation across land uses ($p < 0.01$ for toluene and p-xylene; $p < 0.05$ for benzoic acid). These compounds were consistently and markedly higher in natural soil systems, namely secondary forest, peat forest, tropical wetland, and primary forest, compared to the anthropogenic sites. Toluene concentrations in natural soils ranged between 1.16 and 2.00 ppb, while anthropogenic soils showed markedly reduced levels, with several sites registering a complete absence of this compound. A similar pattern occurred for p-xylene, which was present in all natural soils but entirely absent from paddy, oil palm plantation, orchard, and urban soils. Benzoic acid followed the same trend, with the highest concentration recorded in the primary forest (1.7 ± 0.339 ppb) and negligible or zero values in most managed landscapes.

These significant patterns reflect strong ecological differentiation between natural and anthropogenic soils. The elevated presence of toluene and p-xylene in forested and wetland sites aligns with the role of these aromatic hydrocarbons as microbial secondary metabolites, commonly produced by Actinobacteria, Basidiomycota, and other decomposer guilds involved in lignin degradation and aromatic compound turnover. Their suppression in agricultural and urban soils suggests a disturbance-driven decline in oxidative decomposition pathways, consistent with reduced organic matter inputs, lower functional diversity, and more compact or nutrient-limited soil conditions. Benzoic acid displayed a similar natural-soil dominance; as a co-metabolite of fungal and bacterial lignin breakdown, its abundance in forested soils indicates active processing of plant-derived aromatic substrates, whereas its near absence in anthropogenic soils signifies a loss of these metabolic capacities.

Beyond the significant compounds, broader VOC patterns further distinguished natural from anthropogenic systems. Natural soils exhibited higher chemical richness, including carboxylic acids (e.g., acetic acid, dodecanoic acid), aromatics (benzene, benzaldehyde), and various fatty acids. These compounds are typically associated with microbial respiration, secondary metabolism, and lipid turnover, reflecting the metabolic complexity supported by soils with higher organic matter and more diverse microbial communities. In contrast, anthropogenic soils showed a simplified VOC profile dominated by stress-related aldehydes and alcohols (e.g., hexanal, acetaldehyde, isopropyl alcohol), suggesting a shift towards stress physiology rather than decomposition-driven biochemical activity. This simplification corresponds with the reduced microbial diversity and lower organic carbon content documented for managed sites, as reported in related soil physicochemical data (Tables 4.1–4.2).

Wetland and peat soils presented intermediate patterns, emitting both aromatic compounds and unique metabolites such as methyl salicylate, which appeared almost exclusively in the tropical wetland. This compound, associated with fungal fermentation and potential plant–microbe signalling under high moisture conditions, reflects the partially anaerobic character of these environments. The presence of siloxanes (e.g., cyclotrisiloxane hexamethyl) across several sites, though not significant, may represent low-level environmental contamination or saprophytic by-products, as commonly noted in aerated soils.

Overall, the VOC dataset demonstrates that natural ecosystems possess a diverse and functionally rich microbial metabolic signature, characterised by abundant aromatic and carboxylic acid emissions linked to organic matter decomposition. Meanwhile, anthropogenic land uses exhibit a simplified and stress-oriented VOC profile, indicative of reduced microbial functional diversity and diminished lignocellulolytic activity. These findings position toluene, p-xylene, and benzoic acid as strong biochemical indicators of forest soil integrity, microbial functional richness, and overall ecosystem metabolic health.

Table 4.3 Volatile Organic Compounds (VOCs) across eight sampling sites in Terengganu.

	Sites								Land use			
VOCs (ppb)	Secondary Forest	Peat forest	Tropical wetland	Primary forest	Paddy	Oilpalm plantation	Durian	Urban	Kruskal-Wallis	Anthropogenic	Natural	Kruskal-Wallis	Microorganisms emitting the compound
Isobutane	0.437±0.437	0±0	0±0	0.51±0.51	0.413±0.413	0±0	0.433±0.433	0±0	ns	0.212±0.143	0.237±0.16	ns	Bacteria
Pentane	0.47±0.47	0±0	0.733±0.585	0±0	0±0	0±0	0±0	0.283±0.283	ns	0.071±0.071	0.301±0.186	ns	Bacteria/Fungi
Acetic acid	4.367±1.004	4.4±3.103	2.617±1.256	4.56±1.52	5.127±0.695	3.44±0.956	3.757±1.177	4.437±1.923	ns	4.19±0.577	3.986±0.847	ns	Bacteria
1,3,5 Cycloheptatriene	0.473±0.473	0±0	0±0	0.477±0.477	0.727±0.606	0±0	0±0	0.2±0.2	ns	0.232±0.163	0.238±0.16	ns	Bacteria
Cyclotrisiloxane hexamethyl	2.223±1.34	6.897±1.719	1.6±0.916	3.587±0.903	3.787±1.262	2.703±0.557	2.133±1.772	1.207±0.623	ns	2.458±0.571	3.577±0.82	ns	Bacteria
2,6,6 Trimethylbicyclo,3,1,1.hept.-2-ene	1.853±1.476	0±0	0.387±0.387	0±0	0±0	0±0	0±0	0±0	ns	0±0	0.56±0.398	ns	Bacteria/Fungi
Benzoic_acid-2-trimethylsilyl-oxytrimethylsilyl-ester	1.407±0.414	0.473±0.473	0.497±0.405	0.227±0.227	0±0	0.35±0.35	0.587±0.587	0.437±0.254	ns	0.343±0.168	0.651±0.215	ns	Bacteria/Fungi
Tridecanoic acid	0.177±0.177	0.653±0.653	0±0	0±0	0.36±0.36	0±0	0.957±0.957	0.443±0.443	ns	0.44±0.259	0.208±0.165	ns	Bacteria
Ethylene oxide	4.837±3.098	0±0	0.4±0.4	2.637±2.637	2.113±2.113	0±0	0±0	0±0	ns	0.528±0.528	1.968±1.049	ns	Fungi
nHexane	0.823±0.823	2.223±1.801	2.18±1.94	1.3±0.858	2.01±0.57	0±0	0.49±0.49	1.09±0.342	ns	0.898±0.286	1.632±0.644	ns	Fungi
Benzene	2.25±1.192	2.663±2.663	1.437±0.743	2.85±0.139	0.243±0.243	1.623±0.924	1.507±1.126	1.12±0.665	ns	1.123±0.382	2.3±0.663	ns	Fungi
Toluene	2±1.163	1.503±0.86	1.723±0.99	1.163±0.641	0±0	0.597±0.597	0.64±0.375	0±0	ns	0.309±0.177b	1.598±0.409 a	**	Bacteria/Fungi
Hexanal	0.3±0.3	0.477±0.238	0±0	0.36±0.195	0.67±0.165	0.147±0.147	0.237±0.237	0±0	ns	0.263±0.102	0.284±0.106	ns	Bacteria
pXylene	0.813±0.813	0.663±0.43	0.45±0.45	0.87±0.476	0±0	0±0	0±0	0±0	ns	0±0b	0.699±0.246 a	**	Bacteria/Fungi
1-Hexanol-2-ethyl	2.297±1.248	1.82±0.996	0±0	1.247±1.247	0±0	1.067±1.067	1.073±1.073	2.453±0.463	ns	1.148±0.428	1.341±0.503	ns	Bacteria/Fungi
Decanal	0.057±0.345	0±0	0.63±0.13	0.79±0	0±0	1.87±1.827	0±0.28	0.377±0	ns	0.562±0.476	0.369±0.112	ns	Bacteria/Fungi
nHexadecanoic_acid	0.653±0.345	0±0	0.253±0.13	0±0	0±0	2.157±1.827	0.553±0.28	0±0	ns	0.678±0.476	0.227±0.112	ns	Bacteria/Fungi
Dodecanoic acid	1.23±1.23	0.607±0.607	0±0	0.69±0.69	0.467±0.467	1.747±0.545	2.67±0.451	1.45±1.45	ns	1.583±0.429	0.632±0.353	ns	Bacteria/Fungi
Nonanal	0.463±0.463	0±0	0±0	0±0	0.88±0.88	1.66±0.942	0±0	0.557±0.557	ns	0.774±0.35	0.116±0.116	ns	Bacteria/Fungi
Benzoic acid	0.817±0.817 b	0.88±0.441b	0±0d	1.7±0.339a	0±0d	0±0d	0.213±0.213 c	0±0d	*	0.053±0.053b	0.849±0.278 a	*	Bacteria/Fungi
Tetradecanoic acid	0.38±0.38	0±0	0.447±0.447	0±0	0±0	2.383±2.383	2.217±0.164	3.82±3.234	ns	2.105±0.951	0.207±0.14	ns	Bacteria/Fungi
Heptanal	0±0	0.133±0.133	0.043±0.043	0.44±0.273	0±0	0.2±0.2	0±0	0±0	ns	0.05±0.05	0.154±0.083	ns	Bacteria/Fungi
Isopropyl Alcohol	0±0	1.157±1.157	0±0	0±0	0±0	2.11±2.11	0±0	0.503±0.503	ns	0.653±0.531	0.289±0.289	ns	Bacteria/Fungi
Benzene_1,3 dimethyl	0±0	0.357±0.357	0±0	0±0	0±0	0±0	1.093±0.716	0±0	ns	0.273±0.209	0.089±0.089	ns	Fungi
1 Octene	0±0	0.083±0.083	0±0	0±0	0.177±0.177	0±0	0.27±0.27	0±0	ns	0.112±0.077	0.021±0.021	ns	Bacteria/Fungi
Benzaldehyde	0±0	0.563±0.563	0±0	1.813±0.912	1.57±0.786	0.94±0.94	1.363±0.392	1.547±1.547	ns	1.355±0.436	0.594±0.319	ns	Fungi
Acetaldehyde	0±0	1.933±1.933b	0±0d	2.583±1.356 b	8.567±2.718a	1.33±1.33c	2.013±1.259 b	1.45±0.488c	*	3.34±1.154	1.129±0.612	ns	Bacteria/Fungi
Ethyl Chloride	0±0	0±0	0.263±0.263	0.273±0.273	0±0	0±0	0±0	3.67±3.67	ns	0.918±0.918	0.134±0.09	ns	Bacteria/Fungi
3H.3a-7-Methanoazulene	0±0	0±0	0.733±0.733	1.07±1.07	0±0	0±0	0.433±0.433	0±0	ns	0.108±0.108	0.451±0.31	ns	Fungi
Butanal	0±0	0±0	0±0	0.427±0.427	0±0	0.417±0.417	0.1±0.1	0.313±0.313	ns	0.208±0.124	0.107±0.107	ns	Bacteria/Fungi
Octanal	0±0	0±0	0.133±0.133	0.48±0.48	0±0	0.487±0.487	0.317±0.317	0±0	ns	0.201±0.139	0.153±0.122	ns	Bacteria/Fungi
1H Cycloprop-e-azulene-1a	0±0	0±0	1.367±1.367	0±0	0±0	10.18±6.365	8.22±8.22	0±0	ns	4.6±2.623	0.342±0.342	ns	Fungi
Methyl salicylate	0±0c	0±0c	4.833±2.474a	0±0	0±0c	0±0c	0±0c	0.227±0.227b	*	0.057±0.057	1.208±0.822	ns	Bacteria/Fungi
Pentanal	0±0	0±0	0.073±0.073	0±0	0.497±0.249	0.34±0.34	0±0	0±0	ns	0.209±0.111	0.018±0.018	ns	Bacteria/Fungi
Silanediol dimethyl	0±0	0±0c	0±0c	0±0c	0.113±0.113b	0.45±0.235a	0±0c	0±0c	*	0.141±0.079	0±0	ns	Bacteria

Principal Component Analysis (PCA) revealed clear differentiation in soil VOC fluxes across natural and anthropogenic habitats in Terengganu (Figure 4.6). The ordination showed a distinct separation between natural ecosystems and disturbed sites, demonstrating that VOC composition is strongly structured by land-use type. Natural habitats, including the primary forest, peat forest, tropical wetland, and secondary forest, clustered in regions associated with chemically diverse compounds such as benzoic acid, methyl salicylate, ethylbenzene, and other aromatic and acid-based volatiles. These VOCs are characteristic of lignin degradation, fungal metabolism, and complex plant–soil interactions, reflecting the high organic matter availability, stable moisture regimes, and rich microbial networks typical of natural forest and wetland systems. This pattern is consistent with the interpretation that natural soils act as biochemical "hotspots," releasing a broad spectrum of VOCs through both aerobic and anaerobic pathways.

In contrast, anthropogenic habitats, including durian orchards, oil palm plantations, paddy fields, and urban parks, clustered together on the opposite side of the PCA space and were associated with a narrower suite of VOCs, including compounds such as silanediol dimethyl, various aldehydes, and sporadic hydrocarbons. These VOCs typically indicate soil disturbance, reduced microbial functional diversity, and contamination or chemical alteration linked to fertilization, pesticide use, and reduced plant diversity. The paddy field exhibited the lowest VOC concentrations overall, likely due to sustained waterlogging and limited volatilization under low-oxygen conditions. Oil palm plantations formed a particularly distinct cluster, influenced by their high sand content, reduced carbon inputs, and simplified vegetation structure, reinforcing their metabolically constrained status relative to natural ecosystems.

Environmental variables significantly influenced VOC patterns across the study sites. Soil pH, total nitrogen (TN), total organic carbon (TOC), moisture, and elements of soil texture exhibited strong correlations with VOC composition. Sites with elevated pH and TN, primarily anthropogenic habitats, were associated with VOCs such as isopropanol and xylene, which are often linked to stress responses or anthropogenic chemical inputs. Conversely, habitats with high TOC and moisture,

especially peat forests and wetlands, were associated with compounds such as methyl salicylate and ethylbenzene, consistent with microbial fermentation, redox-driven metabolism, and higher rates of organic matter turnover. These patterns align with broader ecological gradients, where OM, C:N:P ratios, and moisture availability structure the underlying microbial processes that generate VOCs.

The PCA therefore reflects a clear land-use intensity gradient. Natural soils exhibited high chemical richness, diverse VOC spectra, and strong contributions from both aerobic and anaerobic microbial pathways. Wetland and peat soils showed transitional signatures, combining forest-like aromatic compounds with unique anaerobic volatiles. In contrast, anthropogenic soils demonstrated simplified VOC profiles dominated by low-diversity metabolites, indicating reduced ecosystem functionality and microbial metabolic collapse. These VOC patterns mirror documented changes in soil biodiversity, organic matter content, and nutrient status across the same habitats.

The Mantel test further supported the link between soil VOCs and biological communities. VOC composition showed significant positive correlations with bacterial community composition ($r = 0.24$, $p = 0.001$) and fungal communities ($r = 0.08$, $p = 0.02$). This indicates that shifts in microbial assemblages correspond with measurable changes in soil VOC emissions, reinforcing the role of VOCs as functional indicators of microbial activity and ecosystem integrity across the land-use gradient.

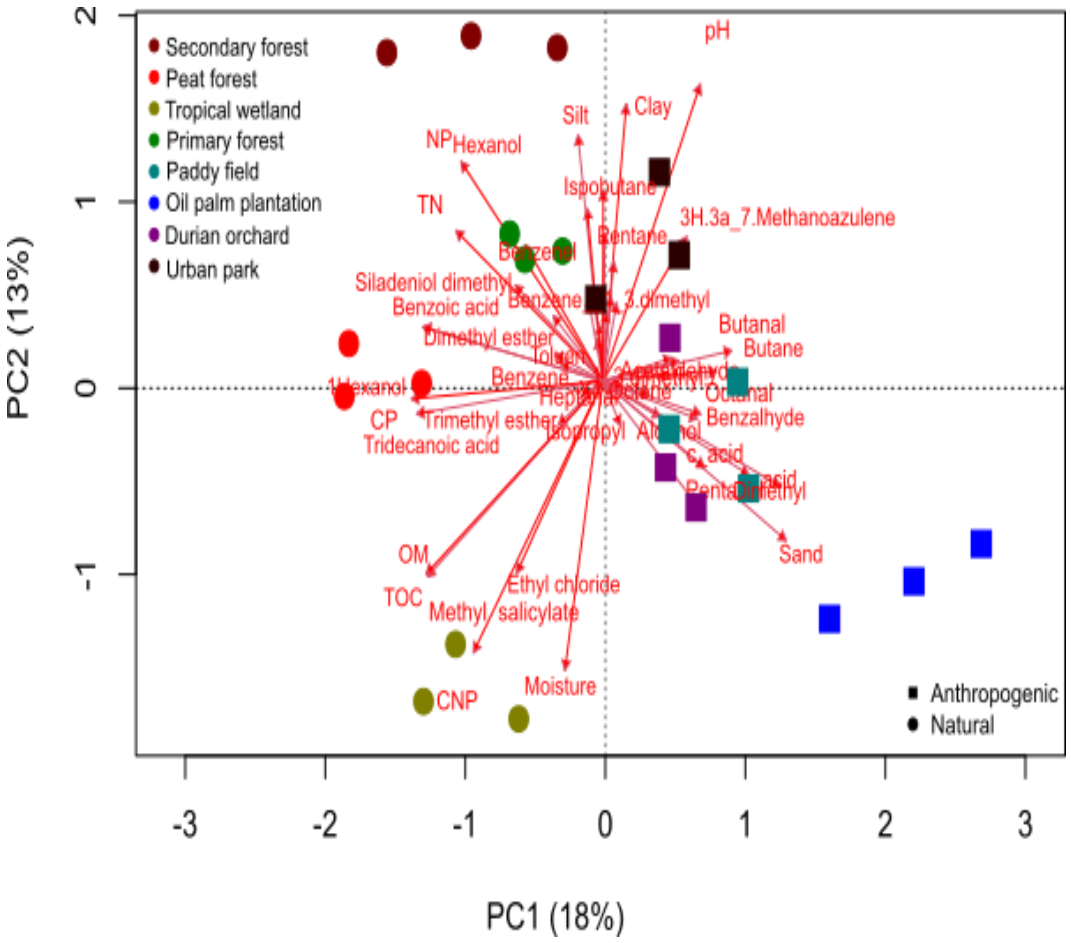

Figure 4.6 The concentrations of VOCs in soils from different anthropogenic and natural habitats across Terengganu.

4.3.2 Greenhouse gas fluxes

Figures 4.7A–C show that soil greenhouse gas (GHG) fluxes differed significantly across the eight ecosystems examined. Methane (CH_4) emissions varied strongly among sites ($P < 0.001$; Figure 4.7A). The peat forest and secondary forest exhibited the highest CH_4 fluxes, reflecting their high organic matter content and reduced soil aeration. Paddy fields and primary forests showed moderate CH_4 release, whereas oil palm plantations, durian orchards, and urban parks recorded the lowest fluxes. Significant differences were also observed for carbon dioxide (CO_2) emissions ($P < 0.001$; Figure 4.7B). The secondary forest, tropical wetland, and oil palm plantation produced the highest CO_2 fluxes, indicative of elevated microbial and root respiration. Peat forest and primary forest showed intermediate CO_2 emissions, while the paddy field, durian orchard, and urban park had the lowest respiration rates.

For nitrous oxide (N_2O), emissions also varied significantly among sites ($P < 0.001$; Figure 4.7C). The oil palm plantation was the dominant N_2O source, followed by the tropical wetland, consistent with enhanced nitrification–denitrification under nutrient-enriched or intermittently anaerobic soils. Moderate fluxes were detected in the peat and secondary forests, whereas primary forest, paddy field, durian orchard, and urban park showed minimal N_2O emissions.

When GHG fluxes were grouped by land-use category, only CH_4 showed a significant difference, with natural ecosystems emitting more CH_4 than anthropogenic systems ($P < 0.05$; Figure 4.7D). No significant differences were detected for CO_2 or N_2O between land-use types (Figures 4.7E–F), indicating that these gases respond more strongly to local soil conditions than to broad land-use classifications. An analysis identified soil clay content as the strongest predictor of CH_4, CO_2, and N_2O fluxes (Figures 4.7G–I). This was followed by available phosphorus (P) and total nitrogen (TN), which were consistently the second and third most influential predictors across all gases. Textural components (silt, sand) and soil moisture had comparatively smaller effects. The dominance of clay suggests that soil physical structure, which regulates aeration and microbial habitat, is a central control on GHG production across these ecosystems.

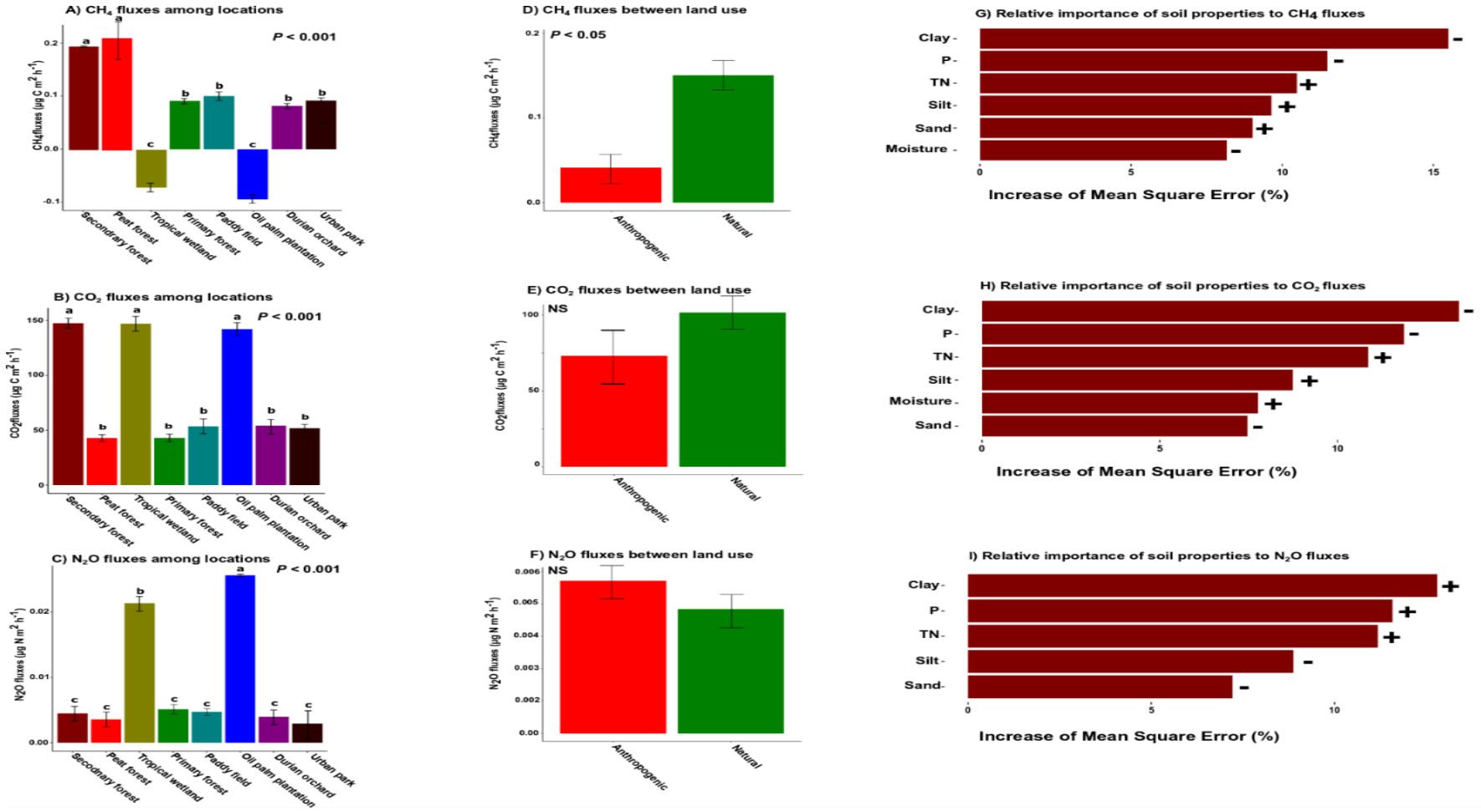

Figure 4.7 Greenhouse gas emissions among various sampling locations and land use management, as well as factors shaping greenhouse gas emissions. Asterisms indicate statistically significant differences *p<0.05; **p<0.01; ***p<0.001. Same letters indicate statistical homogenous groups.

4.4 Influence of Soil Fauna on Litter Decomposition

4.4.1 Decomposition rates in litterbags of different mesh sizes

The litter decomposition rates differed strongly across sites and litterbag mesh sizes, with clear temporal patterns emerging over the incubation period (Figure 4.8A). Across all three ecosystems, mass loss followed a characteristic negative exponential trajectory, although the strength of these relationships varied by location. In the urban soil, decomposition proceeded slowly and with comparatively high variability. In contrast, both the permaculture and tropical forest sites exhibited faster and more predictable decomposition dynamics, with consistently high model fits. In all sites, macrofauna-accessible litterbags showed the steepest decay curves, while control bags, restricting meso- and macrofauna, retained substantially more material over time.

Figure 4.8B shows that when data were aggregated across sites, litterbag mesh size exerted a significant effect on decomposition rates ($P<0.01$). Macrofauna bags decomposed significantly faster than both mesofauna and control treatments, while mesofauna bags displayed intermediate levels of mass loss. This pattern demonstrates the functional contribution of larger soil fauna, whose access to the litter markedly accelerated decomposition relative to bags that excluded them.

Site effects on decomposition were also pronounced ($P<0.001$). Decomposition rates were highest in the tropical forest, followed closely by the permaculture system (Figure 4.8C). Both sites formed a common statistical group, indicating similarly high levels of biological activity. The urban soil, however, exhibited significantly lower decomposition rates than the other two ecosystems. This suggests reduced soil biological quality and potentially less favourable microenvironmental conditions for detritivores and microbial communities.

Taken together, the results show that both faunal access and site characteristics strongly govern litter decomposition. While the presence of macrofauna consistently enhanced mass loss across all locations, the magnitude of this effect was strongly modulated by ecosystem type. The tropical forest and permaculture systems supported rapid and predictable decay, whereas the urban soil constrained decomposition regardless of fauna size class. These combined patterns reflect the interacting influences of decomposer community structure and broader environmental conditions on litter turnover.

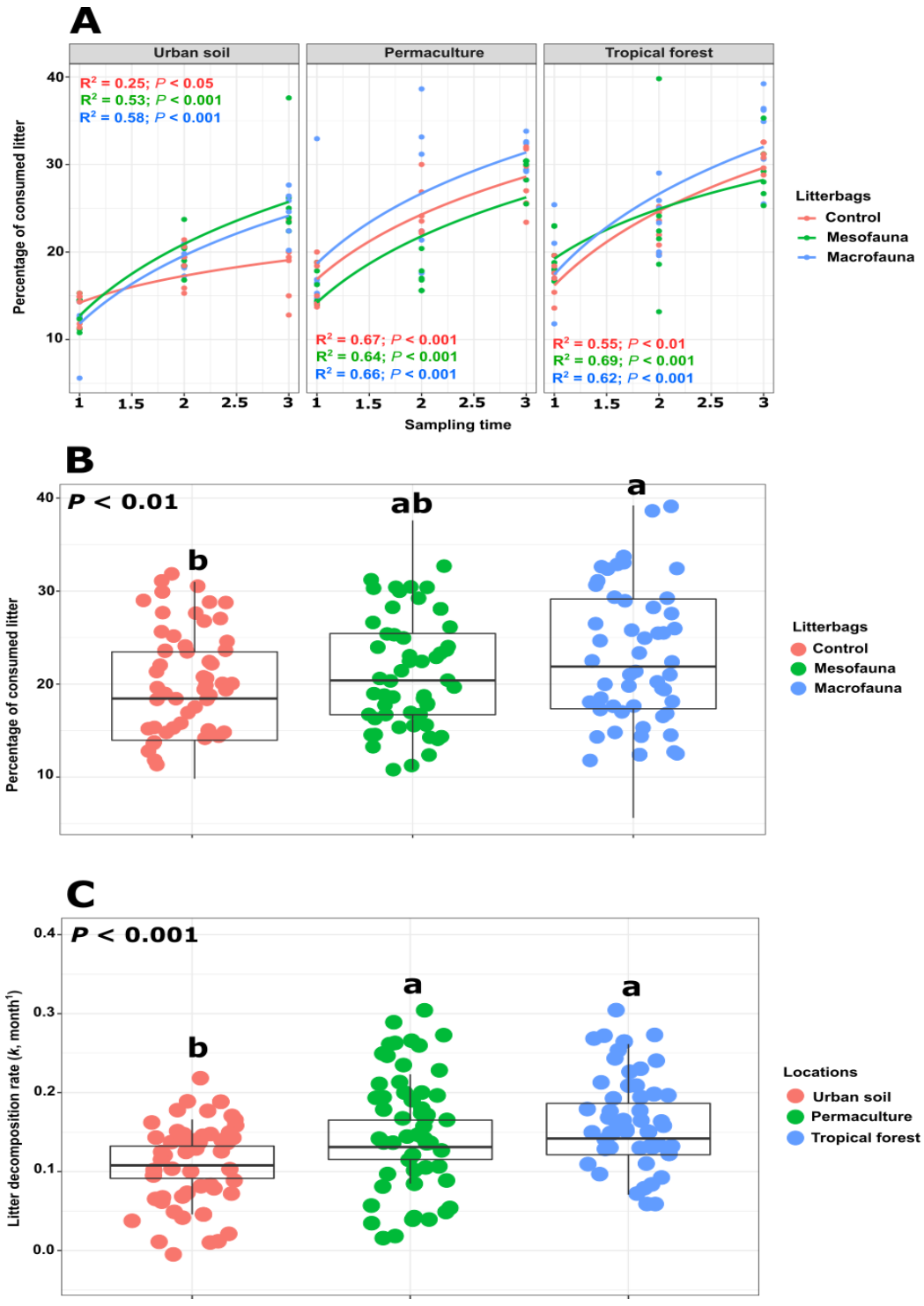

Figure 4.8 Litter decomposition dynamics and rates across land-use types and litterbag mesh sizes. (A) Litter mass loss increased with time across the three sites (Urban soil, Permaculture, and Tropical Forest) and litterbag types (Control, Mesofauna, Macrofauna). Exponential decay models show higher R^2 values and faster decomposition in Permaculture and Tropical Forest soils. (B) Comparison of decomposition rates (k) among litterbag mesh sizes indicates that larger mesh sizes (Macrofauna) promote greater mass loss. (C) Comparison of k values among sites shows faster decomposition in Permaculture and Tropical Forest soils than in Urban soil.

4.4.2 Abundance of soil fauna taxonomic and functional groups at litterbags Sites

Figure 4.9 summarizes the relative abundances of soil fauna functional groups across the three study locations and throughout the three-month litterbag incubation period. Clear differences in community composition were observed among sites (Figure 4.9A). In the top panel, tropical forest soils exhibited the highest functional diversity, with substantial contributions from mesofauna, macrofauna, and saprophagous groups, as well as a noticeable presence of predators and omnivores. Permaculture soils showed a similarly balanced composition, dominated by macrofauna and saprophages, while predators and omnivores occurred in lower proportions. In contrast, the urban soil supported a more restricted functional assemblage, with mesofauna and macrofauna comprising most of the community and comparatively lower proportions of saprophages and predators.

Temporal patterns in functional composition, shown in the lower panel, reveal consistent shifts over the three sampling periods (Figure 4.9B). In Month 1, functional groups varied markedly among sites, with tropical forest samples displaying the greatest representation of predators and saprophagous fauna, whereas the urban soil showed the lowest functional diversity. By Month 2, saprophagous groups increased in all locations, particularly in the permaculture and tropical forest soils, contributing to a more similar overall community structure between these two sites. Macrofauna remained consistently abundant across all months. By Month 3, community composition stabilized, with the tropical forest maintaining the broadest distribution of functional groups and the urban soil retaining the narrowest. Across all months, the permaculture and tropical forest sites showed comparable functional group distributions, while the urban soil consistently differed from the other two systems.

Overall, the patterns in Figure 4.9 demonstrate clear spatial and temporal variation in soil fauna functional groups, with natural and permaculture systems supporting more functionally diverse soil communities throughout the decomposition period than the urban soil.

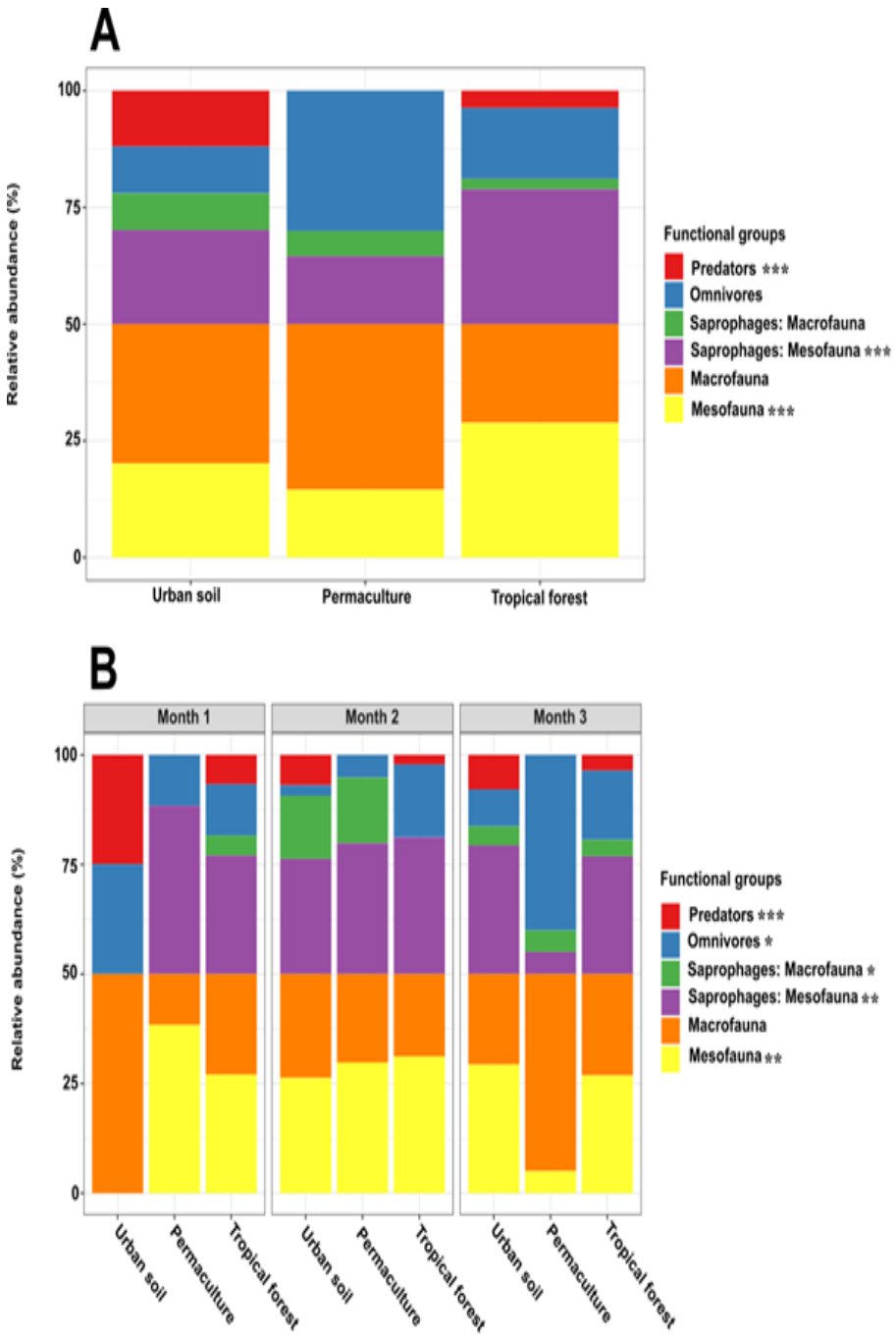

Figure 4.9 Relative abundances of soil fauna functional groups across locations (A) and sampling periods (B). *P < 0.05, **P < 0.01, *P < 0.001.

Table 4.4 presents the abundances of soil fauna taxonomic and functional groups across the three litterbag locations and sampling periods, revealing clear spatial and temporal differences in community structure. Across sites, the tropical forest consistently supported the highest abundances of mesofauna, including Collembola (84 ± 15) and Acari (74 ± 15), both significantly greater than values in permaculture and urban soils (ANOVA: $p < 0.001$). Several taxa, such as Diplura and Isoptera, were found predominantly or exclusively in the tropical forest, further distinguishing it from the other sites. Permaculture generally exhibited intermediate abundances and shared many functional characteristics with the tropical forest, including high saprophagous mesofauna, while also hosting unique groups such as Symphylla and Pauropoda. In contrast, the urban soil contained the lowest overall faunal abundances (150 ± 15), with reduced representation of key detritivore groups and the absence of several microarthropod taxa.

Temporal patterns across the three sampling months also showed significant variation. Early samples (Month 1) exhibited comparatively low mesofauna counts, with Collembola and Acari increasing sharply by Month 2 (74 ± 18.9 and 70 ± 13, respectively), marking the peak of mesofauna activity during the experiment (ANOVA: $p < 0.01$). Month 2 also showed the highest saprophagous mesofauna abundance (144 ± 30), while macrofauna groups such as Lumbricidae peaked during Months 2 and 3. Total fauna increased from Month 1 (158 ± 16) to Month 2 (243 ± 47) and remained high in Month 3 (298 ± 53), with both later months significantly exceeding early abundances (ANOVA: $p < 0.05$). Functional group patterns mirrored these trends, with saprophages, particularly mesofauna, showing strong site and time effects, and omnivores achieving their highest values in Month 3.

Overall, Table 4.4 shows that both site type and sampling time strongly influenced the abundance and distribution of soil fauna. The tropical forest and permaculture sites consistently supported richer and more abundant communities than the urban soil, while faunal activity increased markedly through time, peaking during the middle and late stages of the decomposition process.

Table 4.4 Abundances of soil fauna taxonomic and functional groups across three litterbags locations and sampling periods.

	Locations				Sampling times			
Group	Urban soil	Permaculture	Tropical rain forest	ANOVA	Month 1	Month 2	Month 3	ANOVA
Collembola	33.0±10b	17±1.8c	84±15a	***	20±6c	74±18.9a	40±8b	***
Acari	20±6c	46±4b	74±15a	***	27±9c	70±13a	44±9b	**
Diplura	0.±0b	0±0b	20±10a	*	20±10a	0±0b	0±0b	*
Symphylla	0±0b	3±2a	0±0b	*	3±2a	0±0b	0±0b	*
Pauropoda	0±0b	4±2a	0±0b	*	4±2a	0±0b	0±0b	*
Protura	7±4a	0±0b	0±0b	*	0±0b	0.0±0b	7±4a	*
Lumbricidae	20±10a	19±5a	0±0b	*	0±0c	30±9a	9±5b	***
Diplopoda	4±2	0±0	3±2		3±2	0±0	4±2	
Isoptera	0±0c	4±2b	11±3a	***	4±2b	0±0c	11±3a	***
Isopoda	0.0±0.0b	3±2a	0±0b	*	0±0b	0±0b	3±2a	*
Araneae	29±8a	0±0c	19±3b	***	30±9a	12±3b	6±2b	***
Chilopoda	7±2a	0±0c	3±2b	***	0±0b	3±2a	7±2a	***
Formicidae	20±8	124±60	50±15		30±6	40±18	124±60	
Coleoptera	3±2b	0±0b	20±6a	***	3±2	7±3	13±7	
Insect others	3±2c	13±2b	20±5a	***	7.6±2b	6.4±2b	22±4a	***
Blattodea	4±2	8±2	3±2		7±2a	0±0b	8±2a	**
Predators	36±6a	0±0c	23±2b	***	30±9a	16±4b	13±3b	***
Omnivores	30±8	145±63	93±12		48±4b	53±22b	168±58a	*
Saprophages: Macrofauna	24±9	26±7	14±4		7±3b	30±9a	27±6a	*
Saprophages: Mesofauna	60.7±16b	70.±8b	177±21a	***	74.±19b	144±30a	91±15b	**
Macrofauna total	90±10	171±68	130±8		84±14	100±17	208±60	
Mesofauna total	61±16b	70±8b	177±21a	***	74±19b	144±30a	91±15b	**
Total fauna	150.±15b	242±63a	307±29a	*	158±16b	243±47a	298±53a	*

CHAPTER 5

DISCUSSION

5.1 Variation in Diversity, Composition and Activity of Soil Biota Across a Land-Use Intensity Gradient

5.1.1 Diversity and composition of soil biota across Terengganu

Our study demonstrated significant differences in soil microbial and faunal diversity among various natural and anthropogenic habitats in the tropical region of Peninsular Malaysia. The primary forest exhibited the highest diversity of both microbial and faunal communities, whereas the urban park showed the lowest. The elevated diversity observed in the primary rainforest around Tasik Kenyir is likely associated with its high plant diversity, which supplies a wide range of resources for soil biota through leaf litter of varying quality and diverse root exudates. Plant-derived organic matter provides essential substrates for microbial and faunal communities, creating diverse ecological niches and supporting complex soil food webs (Fujii & Takeda, 2010; Urbanová et al., 2015). Furthermore, substrate quality likely influences the diversity of decomposer communities, including bacteria, fungi, and soil fauna (Freschet et al., 2012). Conversely, the low diversity observed in the urban park is probably a result of frequent anthropogenic disturbances, such as construction, pollution, and soil compaction, which degrade soil structure, reduce organic matter input, and disrupt habitat conditions, thereby constraining soil organism diversity and abundance (Delgado-Baquerizo et al., 2021).

These observations, at first, align with our hypothesis that variations in bacterial, fungal, and soil faunal communities reflect a gradient of land-use intensity, with less-disturbed natural habitats supporting richer and more stable soil biotic communities compared to intensively managed sites. However, when habitats were broadly classified as natural versus anthropogenic, overall diversity did not differ significantly. –We hypothesize that while land-use changes significantly affect the diversity of soil biota, the extent to which these changes influence diversity may vary between sites (Phillips et al., 2017). Additionally, we suggest that functional redundancy may occur, where the overall diversity remains constant, but the composition of soil biota shifts (Lammel et al., 2015; Ulanowicz, 2018).

While land-use changes clearly alter community composition and relative abundances. Surprisingly, we found higher abundances of Oribatida and Collembola in the durian orchard and paddy field in comparison to natural habitats. This may be associated with elevated levels of available phosphorus, which enhances microbial activity and supports greater populations of microbial-feeding fauna (Crowther & A'Bear, 2012; Harrop-Archibald et al., 2016; Meyer et al., 2020; Simpson et al., 2012). Additionally, some anthropogenic habitats such as monoculture tree plantations may harbour higher fungal biomass, including soil-borne pathogens, potentially attracting fungal-feeding organisms such as Collembola and Oribatida (Meyer et al., 2020).

Land use also shaped soil biotic communities. Bacterial assemblages in primary forest and durian orchard soils contained higher proportions of Proteobacteria, which thrive in nutrient-rich microsites (Lin et al., 2021). Fungal communities showed clear habitat-specific patterns, with Ascomycota and Basidiomycota dominant across sites, while Mucoromycota and Rozellomycota varied among habitats. Soil fauna in natural ecosystems included more saprophagous macrofauna, likely linked to steady litter inputs and root exudates (Barajas-Guzmán & Alvarez-Sánchez, 2003), whereas anthropogenic habitats, such as oil palm plantations, supported more omnivorous and generalist taxa like Coleoptera.

Natural soils also had higher relative abundances of oligotrophic bacteria and ectomycorrhizal (ECM) fungi, which are typical of nutrient-limited but stable

environments and the presence of suitable host plants. Although oil palm usually associates with arbuscular mycorrhizas (Phosri et al., 2010), unexpectedly high ECM fungal abundances were detected in oil palm soils, possibly due to ECM-associated understory vegetation (Corrales et al., 2018). In contrast, anthropogenic soils were dominated by saprotrophic fungi and copiotrophic bacteria, which reflect rapid organic matter turnover and frequent disturbance. The greater abundance of saprophages in natural habitats, together with increased predator numbers in wetlands and primary forests, indicates how abiotic factors and continuous resource availability shape soil biodiversity (Brunbjerg et al., 2017, 2020).

Overall, these findings partially support our hypothesis that soil bacterial, fungal, and faunal diversity, abundance, and activity differ substantially between natural and anthropogenic ecosystems. The richer and more functionally active communities in natural habitats are likely promoted by higher environmental stability, greater plant diversity, and favourable soil conditions, particularly pH, organic matter content, and texture.

5.1.2 Metabolic activity and litter decomposition

The metabolic activity of soil biota, particularly microbial respiration and gas fluxes, varied significantly across land-use types and environmental gradients. This aligns with our third hypothesis that natural and anthropogenic habitats differ not only in microbial community composition but also in their metabolic activity, reflected in distinct VOC and GHG profiles. Our findings highlight the complex interactions between soil physico-chemical properties and microbial functional responses, supporting the view that land-use change not only alters biodiversity but also modulates ecosystem functioning through shifts in metabolic processes.

Our study examined volatile organic compounds (VOCs) as indicators of microbial metabolic activity. VOCs play a central role in microbial interactions, soil food web signalling, and plant-microbe communication (Choudoir et al., 2019; Jiao et al., 2023). We observed substantial variation in VOC profiles across sites, with natural

soils exhibiting more diverse and stable VOC signatures compared to anthropogenic soils, directly supporting our third hypothesis. Although the total number of detected VOCs was lower than reported in some temperate studies, the patterns we observed suggest that VOCs can reflect underlying microbial community dynamics and functional responses to environmental stressors (Guo et al., 2021). Microbial VOC production is closely tied to bacterial and fungal community structure, particularly during early growth phases when community-level interactions are most active. In this context, land-use intensity appears to simplify VOC profiles by reducing microbial diversity and altering metabolic outputs. For example, fungal-dominated communities in natural forests may contribute unique VOCs associated with saprotrophic activity, whereas urban and agricultural soils, characterized by reduced diversity and more copiotrophic microbial communities, exhibit limited VOC complexity.

In addition to VOCs, we studied Greenhouse gas (GHG) emissions, including methane (CH_4), carbon dioxide (CO_2), and nitrous oxide (N_2O), and found that they were strongly influenced by local environmental conditions and land-use intensity. Notably, higher methane emissions were observed in peat-dominated environments such as tropical wetland, where saturated soils promote anaerobic conditions that favour methanogenesis by archaea (Conrad, 2007; Serrano-silva et al., 2014). This is consistent with previous research indicating that high water tables and poor oxygen diffusion in peat soils create ideal conditions for methane production. Conversely, negative methane fluxes in tropical wetlands and oil palm plantations suggest active methane oxidation by methanotrophs in well-aerated surface soils, especially in zones experiencing fluctuating water levels that permit aerobic-anaerobic transitions (Cai et al., 2016; Ishikura et al., 2019).

The unexpectedly high CH_4 emissions recorded in the secondary forest may be explained by microbial degradation of sulphur compounds, particularly dimethyl sulphide, a process known to release methane under certain tropical conditions (Deschaseaux et al., 2022). This observation suggests a potential link between sulphur and carbon cycling that merits further investigation, especially in coastal and island soils where such microbial pathways may be more active.

Carbon dioxide fluxes were highest in forested and wetland environments, likely due to increased organic matter input and variable water levels, which create conditions favourable for microbial respiration. In these systems, aerobic microbes decompose litter and soil organic matter, releasing CO_2 through heterotrophic respiration. In contrast, poorly aerated or waterlogged soils support anaerobic metabolism, often shifting the balance toward CH_4 production (Ishikura et al., 2019; Qian et al., 2022; Wang et al., 2021). Similarly, elevated N_2O emissions in oil palm plantations and paddy fields likely result from intensified nitrogen cycling via microbial nitrification and denitrification, processes stimulated by synthetic fertilizer inputs and episodic wet-dry conditions (Peng et al., 2011; Ramirez et al., 2010).

The activity of soil meso- and macrofauna, expressed as a litter mass loss, increased progressively over the three-month incubation period. The observed increase in decomposition over time is likely attributable to the gradual colonization and activity of soil animals, which enhance litter breakdown as incubation progresses. The warm and humid tropical climate is expected to promote decomposition more effectively than drier or colder biomes (Frouz et al., 2015; Heděnec et al., 2022b; Wall et al., 2008). Consistently stable moisture and temperature regimes in tropical environments may further accelerate the physiological activity of both soil fauna and microbiota, potentially resulting in elevated decomposition rates (Peguero et al., 2019; Powers et al., 2009).

Our findings demonstrate that litterbags accessible to macrofauna experienced significantly greater mass loss compared with control litterbags, whereas no significant difference was observed relative to mesofauna-accessible litterbags. These results support our hypothesis: soil animal presence clearly enhanced litter decomposition, but the effect was primarily driven by macrofauna rather than by the combined access of all size groups as predicted. The strong influence of macrofauna highlights their role in fragmenting coarse organic material, thereby increasing the surface area available for microbial decomposition (Frouz, 2018; Fujii et al., 2018; García-Palacios et al., 2013). Our findings are consistent with previous litterbag studies across diverse habitats with varying vegetation types (Peguero et al., 2019; Peng, Holmstrup, Schmidt, et al., 2022), although in our study significant litter mass loss was restricted

to treatments accessible to macrofauna. This suggests that organism body size influences decomposition rates through higher consumption per unit body mass, as demonstrated by Ardestani et al. (2019), who found that larger soil animals consumed more litter relative to their body weight than smaller organisms.

Decomposition rates did not differ significantly between tropical forest and permaculture sites. Soil fauna positively influences litter decomposition in both habitats but also indicates that the strength and drivers of this effect vary among ecosystems. In highly biodiverse tropical forests, factors such as microbial activity and environmental conditions may play a more dominant role in decomposition (García-Palacios et al., 2013; Wall et al., 2008), whereas in managed permaculture systems with lower biodiversity, macrofauna contributions to litter breakdown appear more pronounced. Effect size analysis further supports this, showing that macrofauna exerted the strongest influence on litter mass loss in permaculture systems.

5.2 Soil Properties Shape Diversity, Composition and Activity of Soil Biota Across Sites and Land-Use Types

5.2.1 Changes of soil properties

Tropical wetland, a natural wetland and peat-dominated area, exhibited the highest soil moisture content (70.6%), while urban areas showed the lowest (7.0%). This stark contrast is consistent with the expectation that proximity to water bodies and dense vegetative cover in tropical wetland promotes water retention and reduces evapotranspiration (Xiao-Dong et al., 2011; T. Zhao et al., 2020). In contrast, urban environments are typically characterized by impervious surfaces, limited vegetation, and increased water runoff, which inhibit infiltration and reduce soil water availability (Peng et al., 2015; Shi et al., 2016). Agricultural sites such as paddy fields and oil palm plantations displayed intermediate moisture levels, which likely reflect irrigation and site-specific water management strategies. These results align with global findings that land management practices play a key role in modifying soil hydrology (Feng et al., 2022).

Soil pH ranged from strongly acidic in tropical wetlands (pH 4.2) to nearly neutral in secondary and primary forests (pH 6.3). The acidic nature of tropical wetland soils can be attributed to organic acid production from slow decomposition of organic matter under waterlogged, anaerobic conditions common in peatlands (Ferreira et al., 2007; Qadafi et al., 2023). Furthermore, Tropical wetland's high organic matter content, combined with the potential presence of sulphides in mangrove-influenced zones, may contribute additional acidity via sulfuric acid formation when exposed to oxygen. In contrast, secondary forest's near-neutral pH may be due to long-standing afforestation and the presence of buffering minerals such as calcium carbonate from underlying parent materials (Hong et al., 2018; Luo et al., 2015). Agricultural soils, particularly in oil palm plantations, displayed slightly acidic pH (~5.6), likely driven by the use of nitrogen-based fertilizers, which release hydrogen ions during nitrification and can lead to long-term acidification (Dal Molin et al., 2020; J. Hu et al., 2022).

Measurements of conductivity and salinity also revealed marked differences between sites. Tropical wetland recorded the highest values (74.4 µS/cm conductivity and 47.6 mg/L salinity), which likely reflect the influence of coastal proximity and periodic saltwater intrusion. Coastal soils are particularly susceptible to salt accumulation, which can alter microbial and plant community composition and reduce productivity (Servais et al., 2019). In contrast, urban soils had the lowest values, potentially due to increased leaching from rainfall and limited salt inputs. Agricultural soils exhibited variable salinity, with elevated levels in paddy fields likely resulting from fertilizer inputs and evapo-concentration in poorly drained areas, consistent with reports from irrigated landscapes (Tomaz et al., 2020).

Organic matter indicators, total organic carbon (TOC), total nitrogen (TN), and C:N ratios, also varied significantly. Natural sites like tropical wetland showed high TOC (25.1%) and TN (0.14%), reflecting consistent organic input and limited disturbance. This finding aligns with studies indicating that forest and wetland soils often accumulate organic matter due to continuous litterfall and slower decomposition under moist or anoxic conditions (Kumar et al., 2017; Novara et al., 2015). In contrast, oil palm plantations had the lowest TOC (1.0%), likely a consequence of repeated

harvesting, removal of biomass, and minimal organic residue return to the soil (Clarke et al., 2021). Urban and agricultural land uses, by disrupting the soil carbon cycle, can reduce microbial food sources and compromise soil structure and fertility. The high C:N ratio in Tropical wetland (17.2) indicates slow decomposition and potential nitrogen immobilization, a common trait in organic-rich, water-saturated environments (Li et al., 2019).

Soil texture also emerged as a key driver of physico-chemical variability. Primary forest had the highest sand content (55.0%), promoting aeration and drainage but potentially limiting water and nutrient retention (Wang et al., 2022). Tropical wetland, with higher clay content (21.0%), retained more water and nutrients, supporting the observed high moisture and TOC levels. However, excessive clay may impede aeration and root penetration, posing challenges for plant and microbial activity if not balanced (Tahir & Marschner, 2017). Peat forest had the highest silt content (50.0%), suggesting loamy textures favourable for plant growth due to their balance of aeration, water retention, and nutrient availability (Eyong & Ofem, 2020).

5.2.2 Effect of soil properties on diversity, composition and metabolic activity of soil biota

Random forest analyses showed that soil texture was an important factor influencing bacterial and fungal diversity, reflecting its role in influencing aeration, water retention, and nutrient availability. Natural habitats with coarse-textured soils, such as the primary forest at Tasik Kenyir, likely supported more diverse microbial communities due to improved pore structure and reduced compaction (Qian et al., 2022). In contrast, soil faunal communities were more strongly associated with pH and electrical conductivity, which may affect fauna indirectly through changes in vegetation composition and microbial resources. Litter inputs and soil microorganisms, therefore appear to play a central role in sustaining faunal diversity (Fierer et al., 2009; Frouz, 2018; Fujii et al., 2018).

Community differences between natural and anthropogenic habitats were clear. Beta diversity of bacteria and fungi was most closely linked to pH, total organic carbon

(TOC), C:N ratio, and soil texture. These findings are consistent with studies in other tropical ecosystems where pH and TOC are repeatedly identified as major drivers of microbial community structure (Lauber et al., 2009; Rousk et al., 2010; Vasar et al., 2022). Soil pH influences microbial communities by altering nutrient solubility and overall chemical conditions (Kemmitt et al., 2006; Wu et al., 2017), while TOC, TN, and C:N ratios promote microbial growth and diversity (Liu et al., 2019). In contrast, soil fauna was influenced mainly by sand content, which improves permeability and reduces physical resistance to movement. Sandy soils provide larger pores that allow macrofauna and mesofauna to burrow and access resources more effectively (Frouz, 2018; Swift et al., 1979; Xin et al., 2012).

5.3 Limitations, Implications, and Future Research Directions

This study offers valuable insights into soil ecosystem dynamics; however, it is subject to several limitations inherent in both the methodologies employed and the study's scope. Methodologically, the exclusion of microfauna such as nematodes, mainly due to very specific extraction methods using Bauermann extraction method and due to difficulties in microscopic observation represents a significant constraint. Moreover, DNA-based microbial identification may detect relic DNA from inactive or dead organisms, potentially confounding assessments of active microbial communities. Although RNA-based approaches provide a more accurate representation of metabolically active microbes, they are limited by lower extraction efficiency and higher financial costs. While metagenomics allows for more comprehensive insights into microbial functional potential, its utility is often constrained by financial and analytical demands.

The assessment of litter decomposition based solely on mass loss also presents limitations, as it does not distinguish among the underlying processes, such as microbial mineralization, leaching, or physical fragmentation (Frouz, 2018; Kampichler & Bruckner, 2009). Additionally, the use of litterbags can create artificial microclimatic conditions and restrict faunal access, thereby deviating from natural decomposition dynamics. The complex roles of soil fauna, which may either stimulate

or inhibit microbial activity depending on species and environmental context, further complicate interpretation (Angst et al., 2024; Frouz, 2018). Analysis of volatile organic compounds (VOCs) also remains constrained by compound specificity and the absence of standardized protocols. The spatial and temporal dimensions of the study impose further limitations. By focusing on selected sites within Peninsular Malaysia, the findings may not reflect the broader heterogeneity of tropical ecosystems. The relatively short duration of the decomposition experiment captures only initial stages and may not adequately represent long-term trends. Additionally, seasonal variability in soil properties, biotic communities, and ecological processes was not explicitly incorporated into the study design.

Despite these limitations, the findings have significant implications for land management, conservation, ecological restoration, and the broader understanding of ecosystem functioning. The observed substantial influence of land use on soil physicochemical properties, biodiversity, and ecosystem processes highlights the urgent need for sustainable land-use practices. In agricultural systems, strategies such as crop rotation, organic amendments, and conservation tillage have the potential to mitigate soil degradation, enhance fertility, and support biodiversity, thereby promoting long-term sustainability (Jaziri et al., 2022; Malobane et al., 2020). Urban land management should prioritize green infrastructure and permeable surfaces to enhance soil health and hydrological regulation (Buzzard et al., 2021). Furthermore, the conservation of natural habitats is imperative. These ecosystems harbour high levels of biodiversity and support critical functions such as carbon sequestration, nutrient cycling, and organic matter decomposition. They also act as reservoirs of ecological resilience. Findings from degraded sites underscore the necessity for restoration efforts focused on improving soil health through increased organic matter input, reduced chemical application, and effective erosion control, ultimately enhancing biodiversity and ecosystem resilience. Understanding the interconnections between litter decomposition and nutrient cycling, soil fertility (de Vries et al., 2013; Edlinger et al., 2023), crop resilience (Delgado-Baquerizo et al., 2020; Griffiths et al., 2000; Vannier et al., 2019), and greenhouse gas (GHG) fluxes is critical for developing informed strategies for climate change mitigation and adaptation.

Several promising avenues for future research arise from both the findings and limitations of this study. Long-term monitoring across seasons and land-use types is essential for capturing temporal variability and ecosystem resilience. Investigating the specific impacts of diverse land management practices on soil biodiversity and function can inform the development of context-specific best practices that balance agricultural productivity with ecological integrity. Future research should incorporate more advanced analytical techniques, including RNA-based analyses to identify active microbial taxa, stable isotope tracing to elucidate nutrient pathways and food web interactions, and metagenomics to explore functional potential (Baldrian, 2017; Sultana et al., 2019; L. Zhang et al., 2020). There is also a need to explicitly include microfauna in assessments and to examine the functional roles and interactions of distinct soil faunal groups within the soil food web. Enhancing VOC analysis methodologies could increase their applicability as non-invasive indicators of microbial activity and soil health. Finally, more integrative approaches that combine aboveground and belowground data will be critical for elucidating the feedback mechanisms that drive ecosystem structure and function. Addressing these research priorities will contribute to a more comprehensive understanding of tropical soil ecosystems and support the development of evidence-based strategies for their conservation and sustainable management

CHAPTER 6

CONCLUSION AND RECOMMENDATIONS

This study provides clear evidence that soil biodiversity and associated ecosystem functions in tropical habitats are influenced by gradients of land-use intensity and habitat characteristics. The findings support the first hypothesis, indicating that variations in bacterial, fungal, and soil faunal communities follow a gradient of land-use intensity, with relatively undisturbed natural habitats sustaining more diverse and stable soil biotic assemblages than intensively managed sites.

The results also offer partial support for the second hypothesis, which proposed that the diversity, abundance, and activity of soil bacteria, fungi, and animals would differ markedly between natural and anthropogenic habitats. Although natural ecosystems generally supported richer and more functionally active soil communities, these differences were not uniform across all taxa or sampling locations. This suggests that soil properties, nutrient availability, and vegetation composition interact with land-use type to influence belowground community structure and function.

The third hypothesis is supported by evidence that the metabolic activity of soil microbial communities varies significantly between natural and anthropogenic habitats. Distinct profiles of species-specific volatile organic compounds (VOCs) and greenhouse gas (GHG) fluxes corresponded with differences in microbial composition and local environmental conditions, demonstrating that land-use change can alter functional attributes of soil microbial assemblages.

Finally, the findings provide partial support for the fourth hypothesis, which predicted that the presence of soil animals would enhance litter decomposition.

Litterbags permitting access to a broader range of soil biota, including microfauna, mesofauna, and macrofauna, generally decompose at faster rates. However, the strength of this effect varied among sites, indicating that soil faunal activity is moderated by microclimatic factors and litter quality.

Overall, this research highlights the importance of environmental stability, vegetation diversity, and habitat heterogeneity in sustaining diverse and functionally active soil communities. The study contributes valuable baseline information on tropical soil biodiversity and function, with implications for ecosystem management, biodiversity conservation, and future research examining how land-use change shapes belowground ecological processes.

Future research should continue to investigate the complex interactions between soil physicochemical properties, microbial communities, mesofauna, macrofauna, and ecosystem processes. Long-term and broad-scale studies are needed to understand how these interactions regulate decomposition, nutrient cycling, and greenhouse gas fluxes. Examining how soil fauna respond to environmental factors such as soil moisture and nutrient content can inform management strategies designed to enhance litter decomposition and nutrient turnover. Applying advanced molecular techniques that distinguish active from inactive microbial taxa and integrating functional measures such as metabolic activity will strengthen the link between biodiversity and ecosystem function in tropical soils.

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APPENDICES

Appendix 1

Abundance of soil meso and macrofauna (mean±SE) from soils among various natural and anthropogenic habitats across Terengganu, Malaysia

	Natural habitats				Anthropogenic habitats					Land use		
Fauna (individuals m^{-2})	Secondary forest	Peat forest	Tropical wetland	Primary forest	Paddy fiel	Oil palm plantation	Durian orchard	Urban park	Kruskal-Wallis	Anthropogenic	Natural	Kruskal-Wallis
Prostigmata	0±0	0±0	0±0	14±13	15±14	14±13	0±0	0±0	ns	7±5	4±4	ns
Mesostigmata	0±0	0±0	0±0	15±14	0±0	0±0	0±0	0±0	ns	0±0	4±4	ns
Oribatida	0±0	0±0	29±29	44±44	15±15	58±29	189±170	0±0	ns	66±43	18±13	ns
Collembola	0±0	88±67	73±73	161±59	176±76	58±39	14±14	89±44	ns	84±27	81±30	ns
Protura	0±0	0±0	0±0	15±15	0±0	0±0	0±0	43±25	ns	11±8	4±4	ns
Diplura	0±0	0±0	0±0	13±13	0±0	14±14	0±0	0±0	ns	3±3	3±3	ns
Enchytraeidaa	0±0	0±0	0±0	14±14	0±0	0±0	0±0	14±14	ns	3±3	4±4	ns
Symphyla	0±0b	0±=0b	43±25a	0±0b	0±0b	0±0b	0±0b	0±0b	*	0±0	11±8	ns
Pseudoscorpiones	0±0	0±0	15±15	0±0	0±0	0±0	0±0	0±0	ns	0±0	4±4	ns
Isoptera	165±139	14±14	835±815	43±2	0±0	0±0	59±59	59±39	ns	29±17	264±203	ns
Diplopoda	29±14b	0±0c	0±0c	43±2a	0±0c	0±0c	0±0c	15±15bc	**	4±4	18±6	ns
Lumbricidae	0±0	0±0	0±0	29±29	0±0	0±0	0±0	0±0	ns	0±0	7±7	ns
Isopoda	0±0	15±15b	14±14b	43±2a	0±0c	0±0c	0±0c	14±14b	*	4±4	18±6	ns
Coleoptera	0±0c	0±0c	13±13bc	15±15bc	0±0c	102±39a	0±0c	15±15bc	ns	29±16	7±5	ns
Insect larvae	15±15b	0±0c	44±26a	0±0c	30±30	45±45a	0±0c	28±14ab	*	26±13	15±8	ns
Blattodea	0±0	0±0	0±0	44±44	0±0	0±0	0±0	15±15	ns	4±4	11±11	ns
Caelifera	0±0	0±0	0±0	0±0	0±0	0±0	0±0	59±59	ns	15±15	0±0	ns
Formicidae	175±44b	147±15b	235±39a	162±29b	103±53bc	58±15c	29±15c	30±30c	**	55±16b	180±18a	***
Hymenoptera	0±0	0±0	0±0	14±14	0±0	0±0	0±0	0±0	ns	0±0	4±4	ns
Chilopoda	29±29	0±0	44±25	0±0	0±0	15±15	0±0	13±13	ns	7±5	18±10	ns
Opiliones	0±0	0±0	14±14	0±0	0±0	0±0	0±0	0±0	ns	0±0	4±4	ns
Aranea	88±0b	161±15a	0±0	44±25	73±29b	58±15bc	28±14c	0±0	***	40±11	73±19	ns
Heteroptera	0±0	0±0	0±0	14±14	0±0	0±0	0±0	0±0	ns	0±0	4±4	ns
Dermaptera	0±0b	0±0b	0±0b	0±0b	0±0b	74±39a	0±0b	0±0b	*	18±13	0±0	ns
Functional groups												
Predators	117±29	161±15	103±65	88±67	73±29	73±15	28±14	13±13	ns	47±11b	117±23a	*
Omnivores	15±15c	0±0	58±29b	59±59b	30±30bc	147±30a	0±0	58±13b	*	59±19	33±16	ns
Saprophages total	29±14	103±64	159±77	362±72	190±89	130±24	203±164	175±87	ns	175±45	163±46	ns

Saprophages_Meso	0±0	88±67	145±81	248±102	190±89	130±24	203±164	146±73	ns	167±44	120±41	ns
Saprophages: Macro	29±14b	15±15c	14±14c	115±30a	0±0d	0±0d	0±0d	29±15b	***	7±5b	43±15a	*
Mesofauna	0±0	88±67	160±77	277±116	205±78	144±28	203±164	146±73	ns	174±43	131±45	ns
Macrofauna	500±114	337±38	1199±807	452±51	206±52	352±51	116±30	248±77	ns	231±35	622±202	ns
Fauna	500±114	425±102	1360±798	728±166	411±63	496±58	319±154	393±141	ns	405±52	753±209	ns

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Umar Hussaini bin Tarmizi, born on 27 January 1998, is a master student with a fervent interest in biodiversity and botany. His journey in the world of science began early, inspired by the captivating documentaries of National Geographic and Discovery Channel, which his parents regularly tuned into. This early exposure to the wonders of natural science ignited a deep passion for life science.

Umar's formal education began at Sekolah Kebangsaan Mulong 1, followed by Sekolah Menengah Kebangsaan Mulong, where he completed his secondary education in 2015. He furthered his studies at Universiti Teknologi MARA, obtaining a diploma in pharmacy in 2019 and a Bachelor of Science in Biology in 2022. Currently, he is advancing his study through a Master of Science in Environmental Science at Universiti Malaysia Terengganu.

Driven by a lifelong fascination with the natural world and a desire to contribute to the field of biodiversity, Umar aspires to become an expert in his field, echoing the inspiring figures he once admired on television.

Publications

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