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Unveiling the mycobiome of ecological importance from termitarium soils

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Abstract

Background Termitarium is an intricate biological home with exceptional physicochemical soil properties and numerous beneficial microbiomes. The termitarium microbiome plays a role in several bionetwork processes. It contributes significantly to sustainable agriculture, forestry, and horticulture. In contrast to the immense number of research works focusing on termitarium bacteria and archaea, the amount of study about termitarium fungal communities is limited. This is despite the fact that fungi significantly contribute to the cycling of energy and matter on Earth. Thus, this study investigates the metagenomic datasets from termitarium soil collected from agricultural soils, to obtain a depiction of their mycobiome of ecological importance.

Results Our dataset showed that Ascomycota was the most rank phylum, while Basidiomycota was the next in rank. Specifically, we identified numerous fungi of commercial importance, for example, producers of cellulases and cellulosomes. This was strengthened with the presence of functional genes/enzymes capable of promoting plant growth traits and defence system. Analysis further shown that soil properties influenced the distribution of fungal communities. Magnesium, nitrogen, and potassium, for example, were observed to be among the best predictor of fungal distribution and explained 87.40% of the total variation.

Conclusion This study epitomize further insights into the mycobiome of termitarium soils that are of ecological interest. Again, with some of our sequences assembled as uncategorized fungi, further studies are recommended for the evaluation of the metabolic potentials of these fungi as there is a possibility of the discovery of new fungi or genes of industrial or environmental applications.

Keywords Biotechnology, Metagenomics, Mycobiome, Termitarium: termites

Introduction

Termites are known as “ecosystem engineers” since they stimulate soil changes by engineering the soil (Enagbonma et al. 2020b). Termites like *Coptotermes* sp. are common bio-agents that cause significant chemical and physical transformations to subtropical and tropical soils

(Enagbonma and Babalola 2020). *Coptotermes* sp. have a global distribution, inhabiting Australia, Asia, Africa, and the Americas (Scheffrahn 2023). Their underground colonies and tunnel networks earn them the nickname “subterranean termites” (Cornelius and Gallatin 2015). Beyond their reputation as pests, *Coptotermes* species play a vital ecological role in enhancing soil quality (Kanyi 2022; Chouvinc et al. 2016). Through their burrowing activities, they mix and aerate soil, enhancing its structure and allowing better penetration of air, water, and nutrients (Lee et al. 2015). By breaking down organic matter, they recycle essential nutrients like nitrogen,

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phosphorus, and potassium, making them available to plant life (Cornelius and Osbrink 2011). Termite mounds and tunnels also introduce a unique blend of soil, saliva, and feces, enriching the soil with organic matter (Subi and Sheela 2020). This amendment improves soil fertility, texture, and water retention capabilities. Furthermore *Coptotermes* species influence the soil microbiome, modulating the activity of bacteria and fungi that drive decomposition and nitrogen fixation, (Cheik et al 2019; Li and Greening 2022). Their underground infrastructure can alter soil hydrology, creating pathways for water infiltration and storage, which reduces erosion and runoff (Marsh et al. 2021). While their destructive potential is significant, recognizing the ecological benefits of *Coptotermes* species can foster a greater appreciation for their role in maintaining soil health and ecosystem balance (Marsh et al. 2021). Sound knowledge about the role of termites in soil biology is crucial for understanding the intricacy and interdependence of soil bionetworks. While some farmers normally see termites as pests due to the damage they can cause to wooden structures and crops, but they play significant role in sustaining soil health and plant growth (Enagbonma et al. 2021). Termites are examples of soil bioturbators that play essential roles in promoting soil nutrients and decomposing organic materials to forms plants can use (Enagbonma et al. 2021; Zeng et al. 2023; Lopez-Hernandez 2023). Concerning the high nutrients accrued in termitarium, reviewers have recommended that termitarium soils could be a good soil amendment for improving cultivated soils. Actually, local people of Asia and Africa now practice the application of termitarium soils for enhancing agricultural topsoil (Chisanga et al. 2020a, b; Enagbonma and Babalola 2020; Adebajo et al. 2021). Termites affect ecological functions by constructing subterranean galleries and mounds to defend themselves from biotic and abiotic stressors while they search for food (Jouquet et al. 2016; Enagbonma and Babalola 2019). Due to the rich soil nutrients embedded in termitarium (Schaefer et al. 2016), their soils have been reviewed by several researchers to be a “gold mine” for bacterial diversity (Enagbonma et al. 2020a), archaeal diversity (Wakung’oli et al. 2020) and soil invertebrates (Enagbonma and Babalola 2022). However, for mycobiome (that is the fungal component of the microbiome), there is little or no information on their structure and function. Fungi are organisms mainly found in subaerial and subsoil habitats (López-Archilla et al. 2004; Jiao and Lu 2020) and contribute a key role as decomposers (Alori et al. 2017; Feng et al. 2022), and they use organic materials as vital source of energy (Singara Charya 2015). Furthermore, fungi play a fundamental part in conserving soil structure because of their recurrent production of exopolymer and filamentous branching (Miller and Jastrow 2000). Fungi function as

ecosystem regulators in their environments, play a huge part in organic matter breakdown, and are of agricultural importance (Li et al. 2021; Kavanagh 2017). In symbiotic relationships with roots, some fungi can enhance survival and protect plants against pathogens and drought (Frąc et al. 2018). Plant growth-promoting fungi (PGPF) are gaining substantial attention in biotechnology (Adeleke and Babalola 2021; Imade and Babalola 2021), because of their uses as biological inoculants. PGPF have the potential of promoting plants function and play a role in food additives, pharmaceuticals and aromas production as they also can suppress plant pathogens (Saxena et al. 2015; Chuang et al. 2020). With inadequate data on the ecological roles of mycobiome present in the termitarium soil, this study made an extensive effort to profile comprehensively the taxonomic composition and structure plus the functional role of fungal communities from termitarium soils. To achieve our aim and to overcome the limitation of culture-dependent approach, we used the shotgun sequencing method to fully characterize fungal communities in termitarium soils. Shotgun sequencing is a method for profiling the sequence of whole genomes and total chromosomes by creating random fragments of DNA, assembled by computers that arrange the fragments by locating overlapping ends (Bista et al. 2018). In this research work we tested two hypotheses: (i) termitarium soils are hotspot for fungi like *Aspergillus*, *Penicillium*, *Arthroderma*, *Trichoderma*, *Chaetomium* and *Penicillium* which possess genes/enzymes that are of agriculturally, industrially, and environmentally importance (ii) termites’ activities influence magnesium, potassium, and nitrogen that subsequently have an effect on soil fungal community structure.

Materials and methods

Study sites and soil sampling

We mined 50 g of soils from the bottom of the termitariums (i.e. 0 cm) to 15 cm downward (in August 2017) where the *Coptotermes* species (identified based on method earlier used by Arif et al. (2019) build nests-like cartons and where their bioturbation had influence (Enagbonma et al. 2021). The identification of *Coptotermes* species was determined through integrating both physical characteristics and behavioral traits. Morphological examinations focused on various attributes, including body proportions, head morphology, mandible structure, antennal characteristics, and wing morphology (in alates). Additionally, soldier termites were identified by their distinctive head and mandible shapes. Behavioral observations, on the other hand, centered on foraging patterns, dietary preferences, nesting habits, tunnel architecture, and social hierarchy. By combining these two approaches, a comprehensive understanding of *Coptotermes* species was achieved (Table S1). A soil

auger (5 m in width) was used for collecting eight soil samples from termitarium (for each termitarium, we took 3 replicates, that were assembled into one prior to examination) from the sampled areas (T1-T8) in North-West Province, South Africa (25°27'11.2" S 26°07'33.8" E; 25°26'13.5" S 26°05'50.4" E). Each termitarium was about 2 m apart from the others and they were inhabited by *Coptotermes* species. We decided not to present the adjacent soils data in this research because this study is not a comparative study rather, we focus at unveiling the mycobio-ome of biotechnological significance from termitarium soils. The South African region rims with Botswana and is demarcated by shrubs, few trees and mountain towards the North-east. The temperature of this region varies between 3° to 21 °C in winter and 17° to 31 °C in summer and annually it rains about 360 mm with the highest in the fourth and tenth month (Enagbonma and Babalola 2023). The soils were stored in coolers during sampling and transportation to the laboratory. The samples arrived the laboratory same day that we collected the samples for further investigation. Samples were later stored at 4 °C for 14 days (at 4 °C it slows down the growth of microorganisms, therefore preserving the original microbial community and preventing changes in the sample's composition) prior to DNA mining and the evaluation of physico-chemical parameters respectively.

Analyses of termitarium soil properties

The physico-chemical components of the soils were estimated within two weeks of sampling. 20 g of each soil sample were dried, grounded and sieved (2 mm sieve) to eradicate unsolicited materials. Hydrometer techniques (Faé et al., 2019) were used to determine the particle size and they were allotted for textural classes. Textural classes were calculated in line with the stipulations of the United State Department of Agriculture which is as follows: sand particles, silt and clay particles range from 2.0 to 0.05 mm, 0.05 to 0.002 mm and <0.002 mm respectively. Soil pH was measured by using a pH-meter (Globe Scientific Digital Auto pH Meter, 018-G) (Enagbonma et al. 2019). Soil total nitrogen (N) was measured via the Kjeldhal method (Muwawa et al. 2010). Exchangeable calcium (Ca), magnesium (Mg) and potassium (K), were calculated after extraction (Enagbonma et al. 2024) using 1 mol.dm⁻³ NH₄CH₃CO₂ at neutral (i.e. 7) pH. A flame photometer (PFP-7 Industrial Flame Photometer) was used for reading the exchangeable K while an Atomic Absorption Spectrophotometer (Thermo Scientific Atomic Absorption Spectrophotometer Model-AA301) machine was used in reading the replaceable Mg and Ca (Deke et al. 2016). The amount of available phosphorus (P) in the soil samples was estimated by using a spectrophotometer (Aarson Digital UV Visible Spectrophotometer, Model: RSCH-352) while organic carbon was

measured in line with the method previously used by Walkley and Black (1934) and Shi et al. (2011).

Molecular procedures and assessment

Total genomic DNA was mined from 0.25 g of each soil sampled from termitarium with the aid of PowerSoil® DNA isolation kit (MoBio laboratories, CA, USA) by using the company's manual. The data generated from the extracted DNA were produced via shotgun sequencing method at the Molecular Research LP (Texas, USA). DNA concentration was evaluated by fluorescence using the Quant-iT PicoGreen dsDNA kit (Invitrogen, California, USA); assessment of fluorescence was done using a DQ 300 fluorometer (Hoefer Scientific Instruments, San Francisco, California, USA). Libraries were organized using 50 ng of DNA from each samples by means of the Nextera DNA Sample Preparation Kit (Illumina). Library insert size was decided by Experion Automated Electrophoresis Station (Bio-Rad). Library insert sizes varied from 300 to 850 bp (average 500 bp). Individually, library was loaded to a six hundred Cycles v3 Reagent cartridge (Illumina) and the sequencing was done using a 2×250 bp sequencing carried out on the Illumina MiSeq.

Metagenome annotation analyses and data analyses and visualization

Individual raw metagenome sequences were analyzed using the MG-RAST (Meyer et al. 2008; Glass et al. 2010). The raw sequences underwent quality control for the exclusion of artificial, host-specific species and indistinct base pairs sequences and to get rid of sequences with a length >2σ (standard deviations) from the mean. Sequences annotation was done through BLAT against M5NR databank (Kent 2002; Wilke et al. 2012), a platform that offers nonredundant incorporation of many databases. Fungal taxonomy and functional annotation were carried out using SEED Subsystem (a regularly updated combination of genomic data with API, a web front end, a genome database, and server scripts. It is employed by several researchers for predicting gene functions and determining new pathways) (Overbeek et al. 2013). An expected value (e value) of 0.1×10⁻⁴, the least identity of 60%, and a highest alignment length of 15 bp were the limits applied for assigning fungal classifications. Sequences gained from prokaryotes, viruses and eukaryote (except fungi) were rejected and fungal sequences were retained since they are the focal point of this research. In order to curtail the influence of experimental errors, the homogeneous option of MG-RAST was turned on. The fungal tables gotten afterwards were categorized to their individual taxa levels for statistical determinations and unclassified reads were also kept. Subsequently, the abundances were converted into percentages. The abundance of fungi at phylum, class and

genus levels were depicted through the Circos software and Shinyheatmap (both available at <http://circos.ca/> and <http://www.heatmapper.ca/expression/> respectively) (Khomtchouk et al. 2017; Enagbonma and Babalola 2020). Our used sequences can be found in the NCBI repository using PRJNA526912 as the bioproject numbers. The effect of physico-chemical properties on the distribution of fungal communities between the termitarium was also carried out via the canonical correspondence analysis (CCA) based on a Bray-curtis distance matrix CANOCO 5 (Microcomputer Power, Ithaca, NY).

Result

Physico-chemical characterization of the termitarium soils

Physicochemical examination of termitarium soil different between samples T1 – T8 (Table 1). However, the amount of exchangeable Mg, exchangeable K, sand, clay, silt, and exchangeable Ca were high in termitarium soil.

General analyses of sequencing data of termitarium soils across the sites

The information of the sequence read upon uploading into the MGRAST sever and post quality control information of sequences as well as the aligned sequences are reported in Table S2. The number of sequences uploaded ranged from 5,583,309 (T7) to 7,775,745 (T6) for the soil samples. Following preprocessing, the remaining sequences ranged from 5,228,212 (T7) to 7,376,055 (T4). Notably, the mean G+C content decreased from 65.88% before preprocessing to 59.5% after preprocessing.

Structural distribution of fungi across the soils from termitarium

Seven fungi at the phylum level were observed in termitarium soil samples with Basidiomycota (which had a minimum value of 7.59% in T3 and a maximum value of 92.66% in T4) predominated the termitarium and this was followed by Ascomycota (which had a minimum value of 7.20% in T4 and a maximum value of 90.02% in T2) (Fig. 1). Blastocladiomycota, (which had a minimum value of 0% in T2, T4, T5, T7, and T8 and a maximum

value of 0.04% in T1) Microsporidia (which had a minimum value of 0.01% in T4 and a maximum value of 0.61% in T2), Glomeromycota (which had a minimum value of 0% in T2, T5, T7, and T8 and a maximum value of 0.28% in T1), Chytridiomycota (which had a minimum value of 0% in T2 and T3 and a maximum value of 0.08% in T1), and Neocallimastigomycota (which had a minimum value of 0% in T2, T3 T6, T7, and T8 and a maximum value of 0.08% in T1) were the other phyla present in termitarium soils, while other were grouped as unclassified fungi (Fig. 1). At the class level, 16 fungi were identified in termitarium soils (Fig. 2). The relative abundance of *Agaricomycetes* (which had a minimum value of 6.70% in T3 and a maximum value of 93.18% in T4) predominated in the termitarium soils, followed by *Eurotiomycetes* (which had a minimum value of 1.99% in T4 and a maximum value of 41.77% in T2), *Sordariomycetes* (which had a minimum value of 2.38% in T4 and a maximum value of 35.37% in T6), *Dothideomycetes* (which had a minimum value of 0.38% in T4 and a maximum value of 10.46% in T1), *Saccharomycetes* (which had a minimum value of 0.31% in T4 and a maximum value of 7.33% in T1) and *Leotiomycetes* (which had a minimum value of 0.48% in T4 and a maximum value of 3.42% in T1) (Fig. 2). In the genus level, *Aspergillus* (which had a minimum value of 2.92% in T4 and a maximum value of 57.25% in T8) had the highest abundance in the termitarium soils, followed by *Sordaria* (which had a minimum value of 2.55% in T4 and a maximum value of 29.46% in T6), *Nectria* (which had a minimum value of 1.49% in T4 and a maximum value of 8.87% in T3), *Metarhizium* (which had a minimum value of 1.58% in T5 and a maximum value of 8.31% in T2) and *Magnaporthe* (which had a minimum value of 0.66% in T8 and a maximum value of 4.57% in T2) (Fig. 3).

Functional genes observed from the termitarium soil

Analysis showed that adenylate cyclase (which had a minimum value of 33.03 in T6 and a maximum value of 60.58 in T1) predominated the termitarium soils and this was followed by squalene–hopene cyclase (EC 5.4.99.17)

Table 1 Physico-chemical properties of termitarium soils

Site	T1	T2	T3	T4	T5	T6	T7	T8
Sand (%)	71	70	66	53	65	25	30	71
Silt (%)	8	9	6	13	12	29	30	8
Clay (%)	21	21	28	34	23	49	40	21
Exchangeable Potassium (mg/L)	507	304	276	487	403	459	489	359
Exchangeable Calcium (mg/L)	1500	1278	2215	2525	1790	2237	2417	2507
Exchangeable Magnesium (mg/L)	253	503	672	872	632	535	647	675
pH	4.89	4.79	5.52	5.21	4.21	4.52	5.11	4.06
Total Nitrogen (%)	0.13	0.07	0.07	0.1	0.14	0.09	0.1	0.07
Available Phosphorus (mg/L)	1	0	0	0	1	0	1	1
OC (%)	0.1	0.1	0.1	0.94	0.1	0.1	0.1	0.1

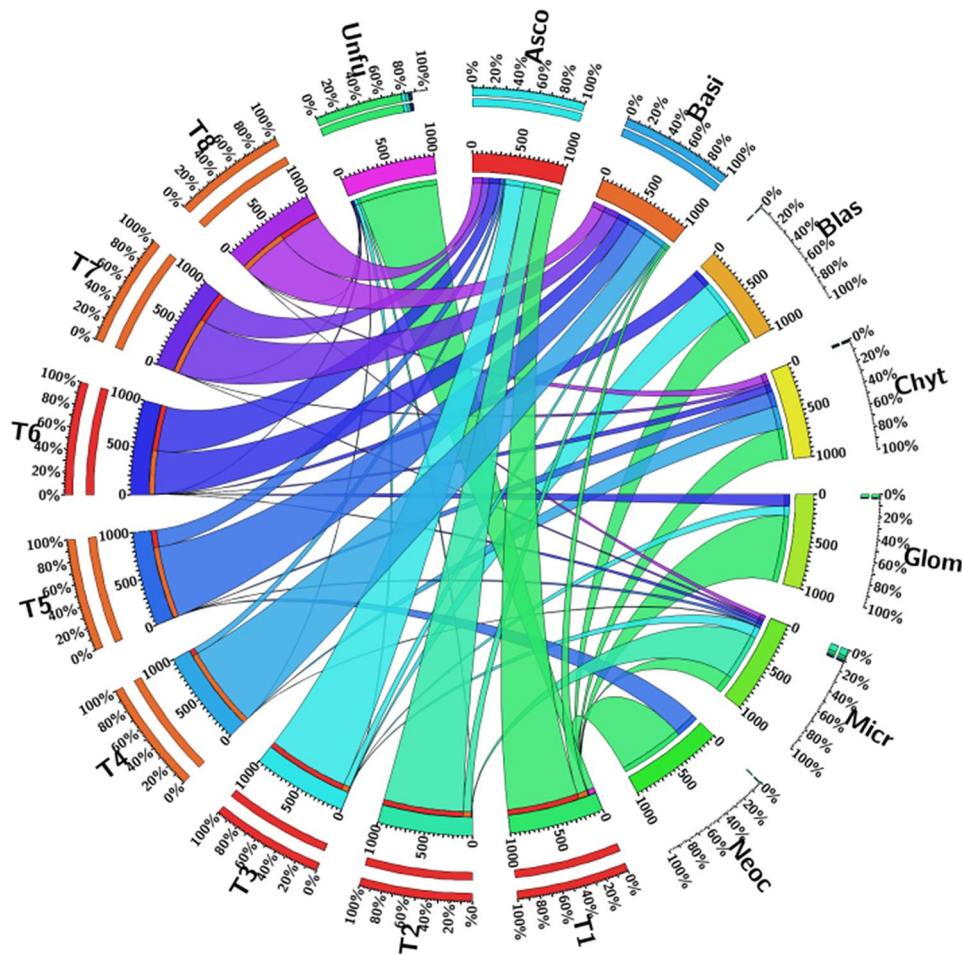


Fig. 1 The rank-abundance of the mycobiome at phylum level in the termitarium soils visualized with the help of Circos software. Asco=Ascomycota, Basi=Basidiomycota, Blas=Blastocladiomycota, Micr=Microsporidia, Glom=Glomeromycota, Chyt=Chytridiomycota, Neoc=Neocallimastigomycota and Unfu=Unclassified fungi

(which had a minimum value of 14.82% in T4 and a maximum value of 29.50 in T2). Furthermore, analysis showed that termitarium soils have other functional genes that encode alpha-glucuronidase (EC 3.2.1.139) (which had a minimum value of 3.54 in T2 and a maximum value of 7.44 in T7), beta-glucuronidase (EC 3.2.1.31) (which had a minimum value of 0.10 in T7 and a maximum value of 2.42 in T4), endoglucanase (EC 3.2.1.4) (which had a minimum value of 2.35 in T1 and a maximum value of 6.42 in T6), endoglucanase (which had a minimum value of 0 in T7 and T8 and a maximum value of 0.34 in T2), 1-aminocyclopropane-1-carboxylate deaminase (EC 3.5.99.7) (which had a minimum value of 0.10 in T7 and a maximum value of 8.22% in T4), alpha-N-acetylglucosaminidase (EC 3.2.1.50) (which had a minimum value of 0.31 in T2 and a maximum value of 24.09 in T5), putative cytochrome P450 Igra (which had a minimum value of 0.10 in T8 and a maximum value of 0.77 in T6), and Xylanase (which had a minimum value of 2.51 in T8 and a maximum value of 6.01 in T7) (Fig. 4).

The effects of physico-chemical parameters on fungal community distribution

To determine the effect of the soil physicochemical properties on the distribution of fungal communities, CCA was carried out. The entire soil physicochemical parameters in Table 1 were utilized in plotting the CCA with CCA 1 and CCA 2 explained 73.15 and 21.75% variation respectively (Fig. 5). Ascomycota, Microsporidia, Blastocladiomycota, Glomeromycota, and Neocallimastigomycota were found to be positively correlated with Ca, N, K, sand, and pH and negatively correlated with clay, silt, OC, and Mg. Also, Chytridiomycota, and Basidiomycota positively correlated with clay, silt, OC, and Mg and negatively correlated with Ca, N, K, pH and sand. Magnesium (Mg) (p-value=0.044), Nitrogen (N) (p-value=0.012) and Potassium (K) (p-value=0.034), had significant influence on the distribution of fungal communities (Fig. 5; Table 2).

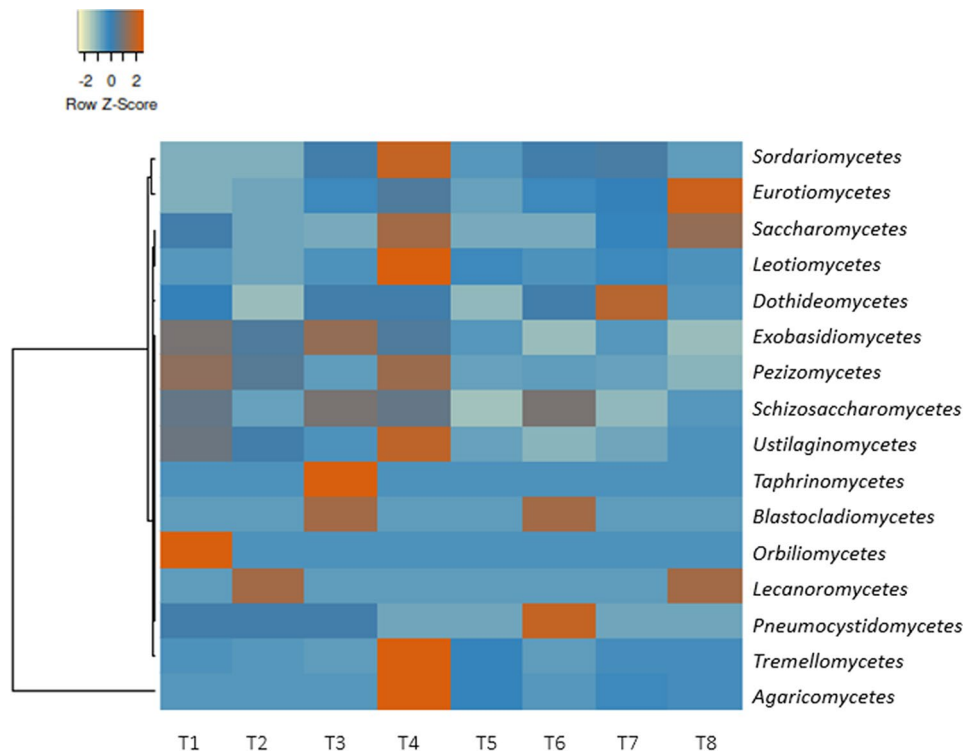


Fig. 2 The rank abundance of the mycobiome at class level in the termitarium soils visualized with the help of heatmap. The gauge-block signifies colour concentration gradient that symbolized the comparative rank of the mycobiome at class level as transformed by the standard (Z) score

Discussion

While termite positive impacts on soil are significant for ecosystem health, certain species can have negative effects on human structures and agriculture. Striking a balance between appreciating termites' ecological contributions and managing its potential risks is key to maintaining a healthy soil and its microbiome. Metagenomic studies provide a broader knowledge of diverse microbial associations inhabiting different environments (Martin et al. 2018). With the shotgun sequencing methodology, we characterized the mycobiome in termitarium soils. Firstly, we theorized that the termitarium soils are hotspot for fungi of ecological importance. This was justified with the presence and dominance of *Aspergillus*, *Sordaria*, *Nectria*, *Metarhizium*, *Magnaporthe*, *Arthroderma*, *Trichoderma*, *Chaetomium*, and *Penicillium*, which are of agriculturally, industrially, and environmentally significant from termitarium soils (Fig. 3). This result supported Makonde et al. (2017) research which reported the presence of *Aspergillus*, *Chaetomium*, *Fusarium*, and *Phaeosphaeria* in termite mound soils when the used the 454 pyrosequencing-based analysis of the internal transcribed spacer (ITS) gene sequences to compare the fungi communities among the termite gut, mound soils and the surrounding soils. Also, Ganesan et al. (2010) reported the presence *Penicillium*, *Chaetomium*, *Trichoderma* and *Aspergillus* in termite mound soils.

Fungi contribute a vital role in providing numerous nutrients like manganese, zinc, iron, phosphorus and potassium to the plants which are typically inaccessible (Adedayo and Babalola 2023; Gianinazzi et al. 2010). For instance, strains of *Aspergillus* and *Penicillium* has been reported by Mittal et al. (2008) as good phosphate-solubilizing fungi by promoting the growth and seed of *Cicer arietinum* when inoculated with *Aspergillus awamori* and *Penicillium citrinum*. Furthermore, *Trichoderma* is an imperative biocontrol agent for controlling plant diseases as it can activate disease-fighting mechanisms within plants and protect against pathogens (Manzar et al. 2022) while some *Trichoderma* strains and *Aspergillus* have been described to produce phytohormones like siderophores, a chemical that embody the uptake of iron as well as other vital elements such as arsenic, nickel, zinc, copper, and magnesium and also a potential biocontrol agent against harmful phytopathogens (Hung and Rutgers 2016; Kumar et al. 2017). Although some strains of *Sordaria* have been reported by Bolívar-Anillo et al. (2024) to exhibits significantly in vitro effects, inhibiting *Botrytis cinerea* growth however, Campbell (2013) warns that *Sordaria fimicola* strain could impact negatively on fecundity and herbivory of *Bromus tectorum* and transit through the alimentary canal of sheep thereby provide a substantial impediment to the application of this fungus as a biological control agent. Some strains of *Nectria*

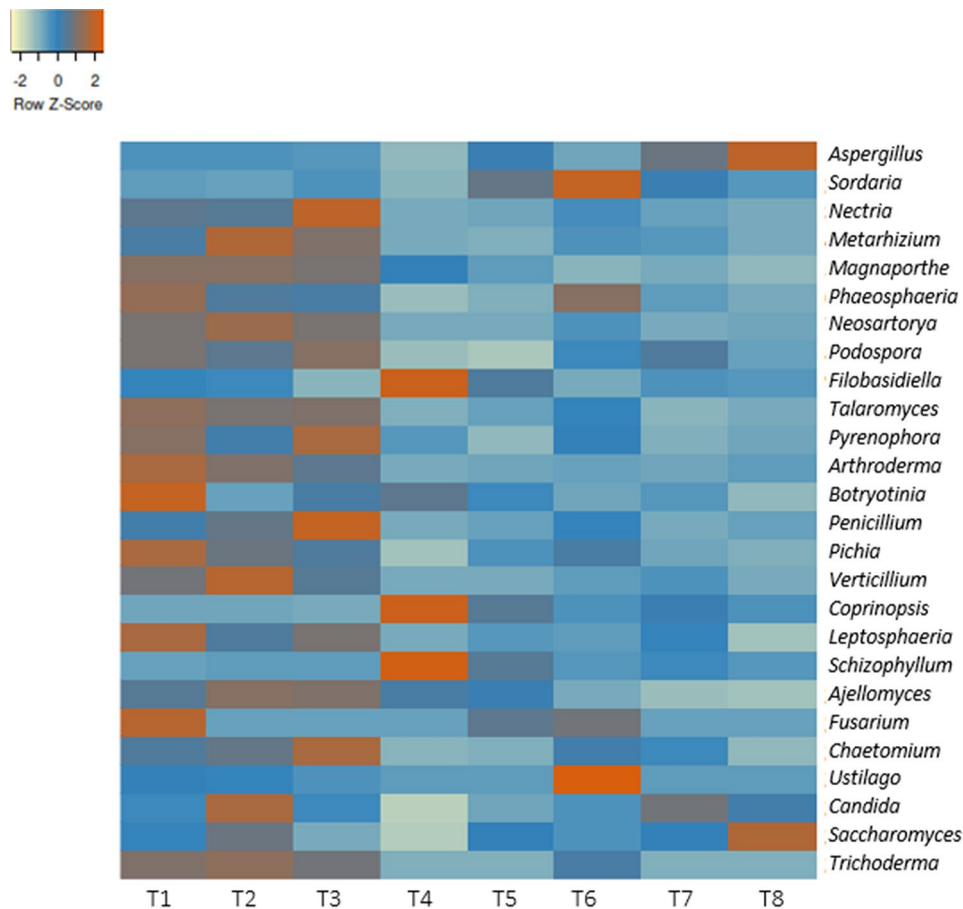


Fig. 3 The rank abundance of the mycobiome at genus level in the termitarium soils visualized with the help of heatmap. The gauge-block signifies colour concentration gradient that symbolized the comparative rank of the mycobiome at class level as transformed by the standard (Z) score

precisely *N. haematococca* has been reported by Rodriguez-Carres et al. (2008) to possess a unique chromosome that contains genes responsible for its ability to infect peas. Interestingly, this chromosome also carries a trait that enhances the fungus's competitiveness in the pea rhizosphere, allowing it to outcompete other microorganisms. Furthermore, *Metarhizium* species facilitate complex relationships with their surroundings, yielding beneficial outcomes for their perennial plant partners while concurrently harming ephemeral insect hosts. Notably, their broad-spectrum insecticidal capabilities safeguard plants and generate a nitrogen surplus, which the fungus exchanges with the plant for carbon resources (Sheng et al. 2022). Nevertheless, it is important to note that certain fungal taxa observed from this study could pose a dual threat, harboring potential risks for both human and animal health (notably mycotoxin-producing species like *Talaromyces*, *Penicillium*, and *Aspergillus*) as well as for agricultural productivity (including plant pathogens like *Botryotinia*, *Verticillium*, *Magnaporthe*, *Fusarium*, and *Ustilago*). For instance, *Magnaporthe* sp. (like *Magnaporthe oryzae*), a highly destructive fungal

organism, wreaks havoc on various plant species, particularly crucial food crops such as rice, wheat, pearl millet, and finger millet, leading to blast diseases that result in significant agricultural losses and economic repercussions (Zhang et al. 2022).

Functional analysis showed that termitarium soils have enzymes/genes of industrial importance like alpha-glucuronidase (EC 3.2.1.139) and beta-glucuronidase (EC 3.2.1.31) which are exogenous markers that might be employed to detect and track specific *Trichoderma* isolates in agro-ecosystems (Guzmán-Guzmán et al. 2023; Kour et al. 2019), endoglucanase (EC 3.2.1.4) which aid in cellulose hydrolysis, 1-aminocyclopropane-1-carboxylate deaminase (EC 3.5.99.7) that stimulate the enlargement of plant root (Saravanakumar et al. 2018). Furthermore, our functional analysis shows the presence of genes encoding adenylate cyclase, which is responsible for plant sprouting and development, mycoparasitism and secondary metabolism (Yang et al. 2016; Speckbacher and Zeilinger 2018), alpha-N-acetylglucosaminidase (EC 3.2.1.50) which is essential for chitinase induction by chitin (Ronceret et al. 2008), and squalene-hopene

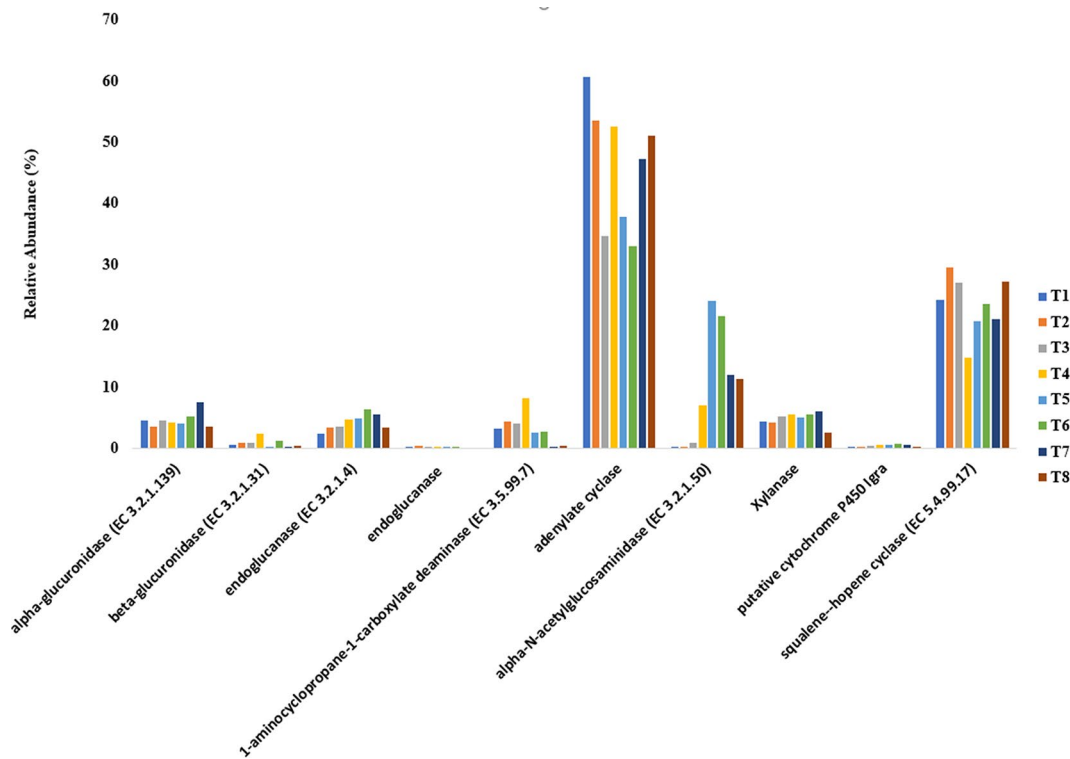


Fig. 4 The rank abundance of the mycobiome functional genes in the termitarium soils

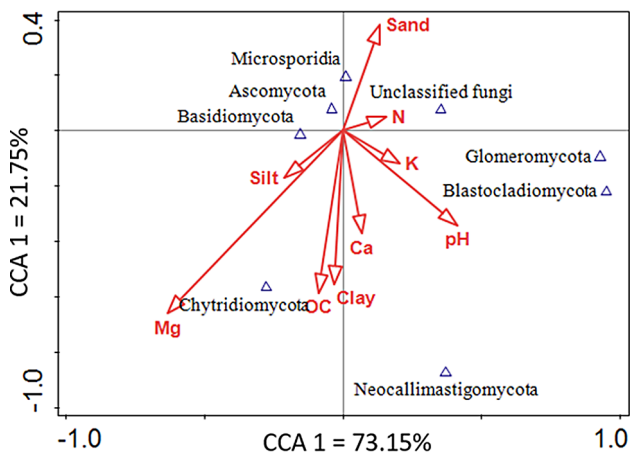


Fig. 5 The effect of soil physicochemical factors on fungal community distribution

cyclase (EC 5.4.99.17) which contributes to the activation of defense system in plants (Ronceret et al. 2008). PGPF with varied growth traits are ecologically safe as well as expected choices to substitute synthetic fertilizers (Ahmed et al. 2019; Emmanuel and Babalola 2020). Plant growth promoting fungi has been found to produce biological chemicals that are of industrial importance (Tiwari et al. 2020; Olowe et al. 2022a; Nimsi et al. 2023). For examples, *Trichoderma* sp. were recounted to release volatile organic compounds to prompt plant responses (Nieto-Jacobo et al. 2017; Olowe et al. 2022b), while *Chaetomium* produce amylase, cellulose and protease which are enzymes needed for industrial purposes (Ahmed et al. 2017; Abdel-Azeem et al. 2016). Furthermore, lipolytic activity has been recounted in *Aspergillus* sp., *Candida* sp., *Penicillium* sp., *Saccharomyces* sp., and *Trichoderma* sp. (Venkatesagowda et al. 2012). With few

Table 2 Forward selection result of physical and chemical variables in the environment which explained the distribution of fungi in their community

Physicochemical properties	Explains (%)	Contribution (%)	pseudo-F	P-value
exchangeable Mg	63	63	10.2	0.044
Total N	18.8	18.8	5.2	0.012
OC	6.2	6.2	2.1	0.158
pH	2.6	2.6	0.8	0.446
exchangeable K	6.3	6.3	4.1	0.034
Silt	2.6	2.6	5.4	0.17
exchangeable Ca	0.5	0.5	<0.1	1

of our sequences assembled as uncategorized fungi, further studies are recommended for the evaluation of the metabolic potentials of these fungi as there is a possibility of the discovery of new fungi or genes of environmental applications.

We also postulated that termite activities in soil (like the burrowing activities that aid soil mixing and aeration) could impact soil physico-chemical properties. This could be held accountable for the variances in the fungal distribution among termitarium soils. With the low values of nitrogen, phosphorus and organic carbon recorded in this study (Table 1) and with similar low values of nitrogen, phosphorus and organic carbon reported by Mosaku et al. (2024) when they evaluated the soil quality in termite mounds and adjacent soils, it will be difficult to support the claim that termitarium soil is nutrient hotspot (Dhembare and Pokale 2013; Menichetti et al. 2014). Knowing that nitrogen, phosphorus, and organic carbon are crucial for plant growth, supporting photosynthesis, energy transfer, and soil structure, respectively (Masowa et al. 2023; Jiaying et al. 2022; Gunina and Kuzyakov 2022). The CCA plot (Fig. 5), indicated that fungal societies shifted with soil physical and chemical parameters. The length of the vector Mg (axis 1) was positively linked with Ascomycota, Basidiomycota and Microsporidia and negatively correlated with Blastocladiomycota, Glomeromycota, Chytridiomycota, and Neocallimastigomycota on axis 2. At phylum level, the CCA result revealed that Mg, N and K significantly explained the differences in the distribution of fungal communities more than the other variables since they explained 63.00%, 18.80% and 6.30% of the overall dissimilarity (Table 2; Fig. 4). Environmental properties are principal drivers of soil microbial distribution and the physico-chemical parameters of soil influence fungal diversity (Liu et al. 2015; Lladó et al. 2018). This revealed that the physico-chemical properties of the soils in this research affected the comparative abundance and distribution of the fungi in the different environments.

Conclusion

Shotgun metagenomics was very useful in this investigation in profiling the mycobiome of ecological importance in termitarium soils. Our result shows fungi and their functional genes/enzymes with multifunctional potentials which are not just agriculturally and industrially importance but are ecological significant. Furthermore, our CCA analysis showed that, soil physicochemical parameters impacted the fungal distribution. The occurrence of sequences allotted to uncategorized fungi, could suggest the presence of novel fungi, which could be useful for agro-industrial purposes as well, biotechnology.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13213-024-01779-2>.

Supplementary Material 1

Author contributions

BJE managed the literature searches, wrote the first draft of the manuscript, performed the analyses, and interpreted results. S.C. carried out the laboratory work and assisted in the analysis. A.E.A. proofread the draft while O.O.B. is the principal investigator, who thoroughly critiqued, rewrote some aspects of the manuscript and funded the totality of the research. All authors approved the article for publication.

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Data availability

Sequences used in this study have been deposited in the Sequence Read Archive (SRA) of the National Center for Biotechnology Information (NCBI) under the bioproject number PRJNA526912.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

All authors affirm that they have no competing interests.

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