

Mulching of post-harvest residues and delayed planting improves fungal biodiversity in South African *Eucalyptus* plantations and enhances plantation productivity

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ABSTRACT

Short-rotation *Eucalyptus* plantations provide essential forest products, with productivity and soil health influenced by residue management and planting strategies. This study examined the effects of burning or mulching post-harvest residue followed by immediate versus delayed planting on soil fungal biodiversity, soil properties, and tree growth across four sites in KwaZulu-Natal, South Africa. Plots were planted either three months ('immediate') or six months ('delayed') after treatment implementation. Volume measurements assessed tree growth, and soil attributes, including moisture, temperature, and nutrient levels, were analyzed. Soil samples were collected in November 2019 and March 2022, and fungal communities were analyzed through high-throughput sequencing targeting the internal transcribed spacer 1 (ITS1) region. Data emerging from this study showed mulched plots had significantly higher tree volume, with delayed planting increasing productivity by 13.6 % at 24–36 months and 25 % at 36–48 months post-planting. Soil moisture was 1.3–2 times higher in mulched plots than in burnt plots. Mulching significantly reduced the maximum soil temperatures by 4.5–6.8 °C. Four months after treatment, burnt plots had higher pH (1.1-fold), carbon (2.2-fold), phosphate (1.6-fold) and manganese (2.5-fold). Initially, mulched plots had lower fungal biodiversity (0.81-fold) than burnt plots but surpassed them after 28 months (1.28-fold increase). Fungal community overlap declined from 83.28 % to 40.64 %, with mulching supporting higher saprotroph (1.3-fold) and symbiotroph (1.25-fold) abundances, while delayed planting increased pathotroph presence by 1.5-fold in burnt plots. These findings highlight the long-term benefits of mulching and delayed planting in enhancing fungal biodiversity, promoting beneficial microbial communities, and improving tree growth, contributing to more sustainable *Eucalyptus* plantation management.

1. Introduction

Continuous replanting of the same or similar tree species can degrade soil properties and reduce microbial biodiversity, ultimately affecting tree vigour (Bose et al., 2023a; Li et al., 2024). Retaining post-harvest residues can mitigate this impact by supporting microbial communities that enhance soil health and nutrient cycling (Bose et al., 2023b; Xiong et al., 2021). Fungi, in this regard, play a pivotal role.

Saprotrophs, as primary decomposers, break down organic residues, releasing nutrients for plant uptake (Lindahl et al., 2002), while symbiotrophs mobilize essential minerals such as nitrogen (N) and phosphorus (P) to improve plant absorption (Johnson et al., 2015; Philpott et al., 2018; Tedersoo and Bahram, 2019). However, post-harvest residues can also harbour soilborne pathogens, potentially increasing disease risk (Bockus and Shroyer, 1998; Kerdraon et al., 2019), although they may simultaneously support beneficial microbes that suppress

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pathogens (Bonanomi et al., 2007; Bose et al., 2023b).

From a forestry perspective, managing post-harvest residues is essential for sustainable soil management, replanting success, and fire prevention (Bose et al., 2023a; Bose et al., 2023b; Carlos Rodriguez et al., 2022; Skovsgaard et al., 2021; Xu et al., 2021). Common management strategies include burning, broadcasting (retaining residues intact), mulching, or collecting for bioenergy (Zitha et al., 2023). The choice of method depends on factors such as terrain, weather, residue volume, operational costs, and market demand (Becker and Keefe, 2020; Eckert et al., 2023; Jain et al., 2018). In South Africa, burning is the dominant practice, followed by broadcasting and mulching (Ramantwana et al., 2020).

Burning is often preferred for its cost-effectiveness compared to mechanical treatments like mulching (Ndlovu et al., 2019). It rapidly releases essential nutrients, such as N, P, and potassium (K), while ash deposition raises soil pH, reducing acidity and preventing aluminium toxicity (Aciego Pietri and Brookes, 2008; Certini, 2005; Chungu et al., 2020; James et al., 2018; Wan et al., 2001). Burning can also enhance soil microbial diversity in the short term by promoting certain fungi and nitrifying bacteria (Hart et al., 2005). However, it also poses significant risks, including uncontrolled fires, soil degradation, microbial biodiversity loss, and disruptions to geochemical cycles (Almeida et al., 2018; Zhu et al., 2021). High-temperature fires can volatilize carbon (C), N, and sulphur (S), reducing soil fertility and contributing to air pollution (Dutta et al., 2022; Fynn et al., 2003; Shinde et al., 2022). In contrast, broadcasting and mulching retain organic matter, reducing water loss, nutrient runoff, and soil erosion, thereby promoting long-term soil health (Juo and Manu, 1996; Li et al., 2020b).

Broadcasting positively influences soil health (Zitha et al., 2023). However, the intact post-harvest residues can take longer to decompose and can serve as a substrate for forest fires. Mulching is often considered a preferable alternative to broadcasting. In this method, post-harvest residues are mechanically shredded and evenly distributed across the plantation, accelerating decomposition, reducing fuel loads for forest fires, and improving access for replanting. Mulch also enhances soil health, reduces pest and disease pressure on crops, and fosters a diverse ecosystem of soil microbes. This practice reduces fire risk and fire intensity (Kalies and Yocom Kent, 2016; Stephens et al., 2012) as well as significantly improves soil structure and moisture retention while promoting a balanced and thriving soil microbiome (Wang et al., 2023; Xu et al., 2022). However, mulching is associated with higher capital expenditure, leading to increased operational costs (Abrantes et al., 2018; Lopes et al., 2020). Nevertheless, microbial decomposition of these organic substrates is a complex, insufficiently studied process (Spohn and Berg, 2023).

Organic matter decomposition is crucial for nutrient cycling and soil enrichment in forest ecosystems (Cleveland et al., 2011; Waring, 2013). While microbial biomass maintains stable C:N and C:P ratios globally (Cleveland and Liptzin, 2007; Xu et al., 2013), C-rich harvest residues can initially create nutrient imbalances due to low N and P availability (Spohn, 2020; Zechmeister-Boltenstern et al., 2015). Microbes adapt by adjusting biomass composition, increasing respiration, and selectively metabolizing organic matter that meets their nutrient demands (Arsuffi and Suberkropp, 1989; Spohn and Berg, 2023). As decomposition progresses, carbon loss releases N and P, making them available for plant uptake, while other nutrients, such as K, manganese (Mn), calcium (Ca), and magnesium (Mg), are either absorbed by plants, retained by soil minerals, or lost through leaching (Berg and McClaugherty, 2008; Blair, 1988; Osono and Takeda, 2004). These decomposition dynamics directly influence soil health and tree growth, underscoring the importance of effective post-harvest residue management.

Selecting an appropriate residue management strategy for short-rotation plantations is crucial for balancing sustainability and productivity, as it directly affects soil microbes, nutrient cycling, and ecosystem functioning. Unlike elsewhere in the world, in South Africa, research on residue management primarily examined its effects on the physical and

chemical properties of the soil, with little focus on soil-associated microbes. In particular, the effects of burning versus mulching on soil microbial diversity, nutrient availability, and tree vigour under local conditions remain poorly understood. To address this, we conducted a short-term study in South Africa to compare the effects of burning and mulching on soil fungi and tree productivity across four sites in KwaZulu-Natal. At each site, residues were either burnt or mulched, and trees were planted at two different time points, three months (immediate) and six months (delayed) after treatments. Using high-throughput sequencing, we assessed soil fungal biodiversity at two time points (November 2019 and March 2022). We hypothesized that (i) tree volume will be higher in mulched plots than in burnt plots over time, (ii) burnt plots will have higher initial soil nutrients, but nutrient availability will improve in mulched plots over time, (iii) mulching will enhance fungal diversity and create a distinct community composition, and (iv) fungal communities will develop differently across treatments due to vegetation growth and soil changes.

2. Materials and methods

2.1. Description of study sites

In April 2019, burnt and mulched study (BMS) sites were established at four locations in the Zululand District of KwaZulu-Natal, South Africa (Fig. 1A). The study sites included (i) Palm Ridge C09 (28°20'8.232"S, 32°14'19.824"E; MAP: 914 mm, MAT: 22 °C, 57 m ASL), (ii) Palm Ridge F14 (28°22'13.224"S, 32°12'50.939"E; MAP: 914 mm, MAT: 22 °C, 73 m ASL), (iii) Mavuya A32 (28°32'24.9"S, 32°11'7.547"E; MAP: 1082 mm, MAT: 22 °C, 40 m ASL), and (iv) Salpine E01 (28°33'36.648"S, 32°11'27.887"E; MAP: 1165 mm, MAT: 21 °C, 61 m ASL). Each site had the same soil type (major: Fernwood; minor: Oakleaf). At each study site, the compartments were unequally divided into four sub-plots, separated by 5 m buffer zones. Two larger plots, measuring 50 × 14 rows, were designated for 'mulched immediately planted' and 'burnt immediately planted' (Fig. 1B). In the 'mulched immediately planted' subplots, post-harvest residues were pulverized using a Tigercat® 4061-30 mulching head attached to a Tigercat® 760B mulcher (approximate particle size 12–80 mm × 9 mm × 2 mm), where the mulch was uniformly distributed across the plot area. In the 'burnt immediately planted' subplots, the residues were burnt. The remaining two smaller plots, measuring 10 × 14 rows, were used for 'mulched delay planted' and 'burnt delay planted' (Fig. 1B). Delayed treatment mimicked the gap between harvest and replanting in burning regimes, where residue burning is regulated to occur outside "fire seasons" and still requires dry conditions. Mulching skips this waiting period, offering faster re-establishment time frames, less weed control, and better planning. All sites received treatments (burnt or mulched) in April 2019. 'Immediate' plots were planted in July 2019, while delayed plots were planted in January 2020 (Fig. 1C). Regardless of treatments, all plots and the buffer zone were planted with a single genotype of *Eucalyptus grandis* × *E. urophylla*, at an escapement of 3 × 2 m (1667 stems per hectare).

2.2. Measurement of tree volume

Tree volumes from all four BMS sites were initially recorded in July 2020, seven months after planting the 'delay' plots. Subsequent recordings were done in September 2021, August 2022, and September 2023 (Fig. 1C). All the measurements were done at the center of the trial plot, measuring 6 × 6 rows of trees by the same team of field technicians from Sappi Forests South Africa. The measurement of the tree diameter at breast height (1.37 m; DBH) was done using a nylon diameter tape (d-tape). For accuracy, the nylon d-tape was calibrated against a steel d-tape in between plots. The tree height was determined using Vertex III and Transponder T3 instruments (Haglöf, Sweden) calibrated as per the manufacturer's guidelines. The estimation of stem volume for each

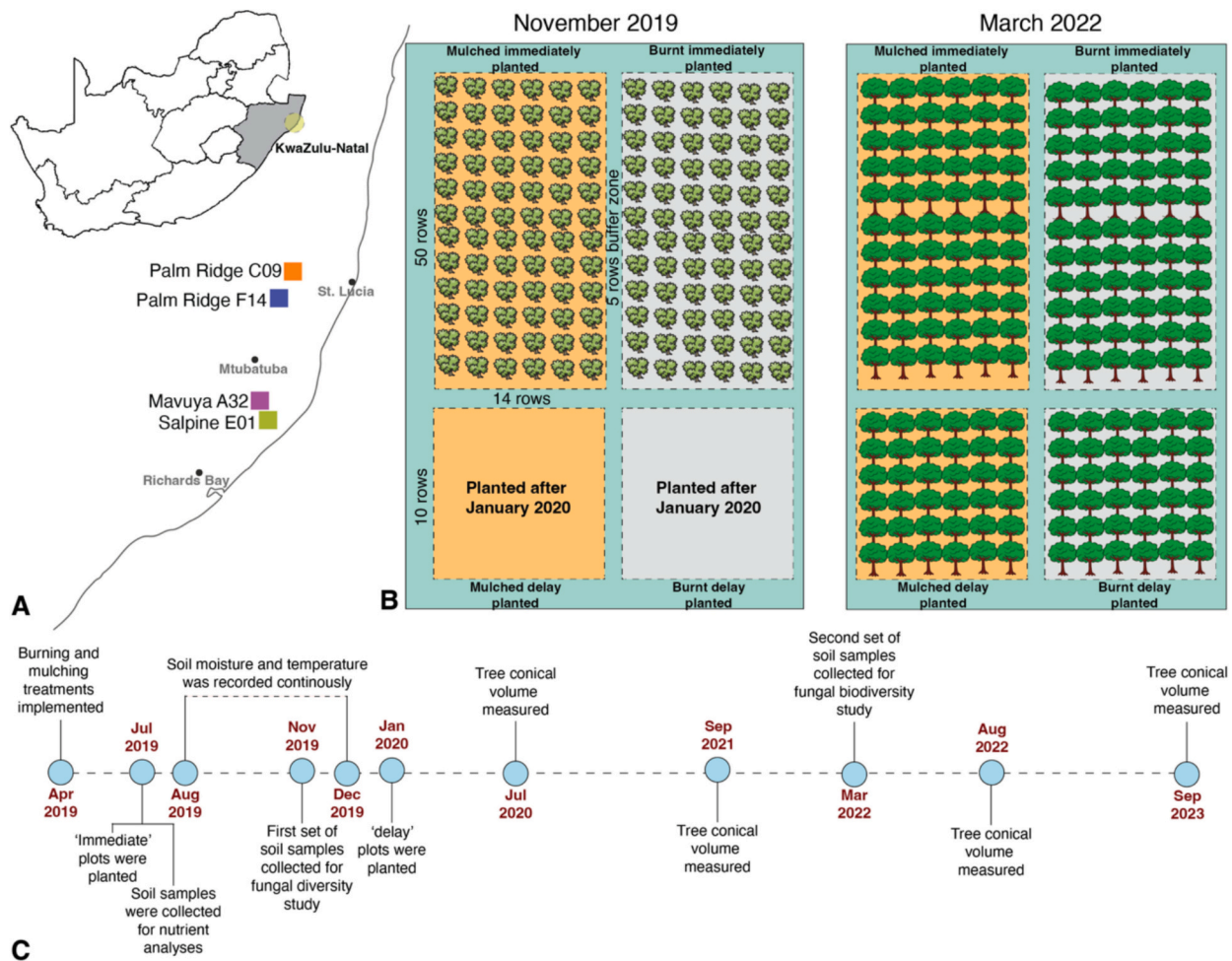


Fig. 1. Experimental design, site locations, and timeline of data collection. (A) Map showing the study sites in KwaZulu-Natal, South Africa. (B) Layout of experimental plots indicating mulching and burning treatments as well as immediate and delayed planting zones. (C) Timeline of key experimental activities between April 2019 to September 2023).

assessed tree was accomplished through the application of a conical form factor function, which was modified to account for taper (Clutter et al., 1983).

$$\text{Stem Volume (m}^3\text{)} = \pi \times \left(\frac{\text{DBH}}{200}\right)^2 \times \text{Ht} \times k$$

k is the taper correction factor (0.42) used to modify the conical function, accommodating for stem taper in rapidly growing trees, such as *Eucalyptus* species. The total stem volume for each tree was added up within each plot and subsequently standardized to a per-hectare measurement ($\text{m}^3 \text{ha}^{-1}$). Relative growth rates for each treatment at three and four years were calculated by dividing the difference in volume by the difference in time ($\delta \text{ volume (measurement2 - measurement1)}/\delta \text{ time (measurement2 - measurement1)}$).

2.3. Measurement of soil attributes

Following the burning and mulching of the post-harvest residues at each BMS site, the soil moisture, temperature, and chemistry were measured. Soil moisture levels were evaluated between August and December 2019 using a Delta PR2 SDI-12 soil moisture probe paired with an HH2 logging unit (Delta Devices Ltd., Cambridge, UK; Fig. 1C). An access tube extending 1 m into either the mulched or burnt plot was installed for data collection. Moisture readings were taken at depths of 0.1, 0.2, 0.3, 0.4, 0.6, and 1.0 m between August and December 2019 (Fig. 1C). For the same period, daily temperatures at the soil surface

were recorded using Thermochron iButtons (model DS1921G, Dallas Semiconductor, California, USA). Daily average, maximum, and minimum temperatures were derived from the recorded data.

Soil samples were collected from the burnt and mulched plots at all sites in July 2019 after the ‘immediate’ plots were planted (Fig. 1C). At each plot, three random points were sampled at soil depths of 0–0.2, 0.2–0.6, and 0.6–1.0 m to assess variations in organic matter (topsoil), root distribution zone (subsoil), and deeper soil properties. Samples from each depth layer within the plot were bulked for analysis. These samples were air-dried, milled to <2 mm, and analyzed for pH (using 1 M KCl and water), extractable base cations (Ca, Mg, K, Na), exchangeable acidity (using 1 M KCl), extractable P (using Bray 2), and micronutrients (using 1 M HCl extraction). Total C, N, and S were measured using a Leco Trumac CNS Analyser (Leco Corporation, Missouri, USA). Particle size analysis was conducted on selected soil samples using a dispersion and sedimentation method. The Institute for Commercial Forestry Research performed all analyses following the methods outlined by Donkin et al. (1993).

2.4. Collection of soil samples for cataloguing fungal biodiversity

Soils from these study sites were sampled at two time points in November 2019 and March 2022, 28 months later (Fig. 1C). At each time point, 80 soil samples were collected (5 soil samples per treatment \times 4 treatments \times 4 sampling sites). In total, 160 soil samples were collected for this study (80 soil samples per time point \times 2 time points).

During the first sampling in November 2019, composite soil samples were collected around the base of five randomly selected plants in ‘immediately planted’ sub-plots. In the ‘delayed planted’ plots where planting had not taken place yet, composite soil samples were collected from around five single points. Sampling points were at least 5 m away from the subplot boundaries. For each composite soil sample, the topsoil layer (0.01–0.015 m deep) was removed using a trowel, and samples were collected from four cardinal points around each plant (or point) at a depth of ~0.1 m, combined and thoroughly mixed. About 100 g of this soil mixture was stored in labelled 50 ml sterile collection tubes and placed in a 10 °C cool box. To avoid cross-contamination between sub-plots, the sampling equipment was surface sterilized using a 4 % (v/v) sodium hypochlorite solution followed by spraying with absolute ethanol and flame sterilization. In the March 2022 sampling, a similar strategy was employed, except for the ‘delay planted’ sub-plots. By then, these sub-plots were planted, and samples were collected from the base of the trees as previously described.

2.5. Extraction of DNA from soil samples

Soil samples collected at both time points were dried at 20–22 °C for two weeks inside a drying cabinet. About 50 g of each dried soil sample was pulverized using a Retsch® grinding jar attached to a Qiagen® TissueLyser II at a frequency of 20 oscillations per sec. DNA was extracted from 0.25 g of each pulverized soil sample using the Qiagen DNeasy® PowerSoil® Kit, following the manufacturer’s protocol. DNA extracted from soil samples was quantified using a Thermo Scientific NanoDrop® One spectrophotometer. For confirming the presence of fungal DNA, all samples were amplified using the fungal-specific primers ITS1F (5'-TTGGTCATTTAGAGGAAGTAA-3') (White et al., 1990) and ITS4 (5'-TCCTCCGTTATTGATGTC-3') (Gardes and Bruns, 1993). Each PCR reaction included 5 µl of 5× GoTaq Flexi Buffer (Promega, MI), 2.5 µl of 25 mM MgCl₂ (Promega, MI), 1.5 µl of 0.1 mM dNTPs (Promega, MI), 1 µl BSA (Amresco, OH), 1 U GoTaq Hot Start Polymerase (Promega, MI), 0.5 µl each of forward and reverse primers, 2 µl of soil DNA extract and the final volume was made up to 25 µl with PCR grade water. The amplifications were carried out with initial denaturation at 94 °C for 2 min, followed by 30 cycles of 94 °C for 30 s, 58 °C for 30 s, 72 °C for 1 min and final elongation at 72 °C for 7 min. PCR products were visualized using 1 % agarose gel electrophoresis. In the event of no bands being detected in any of the samples during gel electrophoresis, the DNA extraction process was repeated. The extracted DNA samples were subsequently stored at –20 °C until the preparation of fungal amplicon libraries.

2.6. High-throughput sequencing of DNA samples

Preparation of fungal amplicon libraries targeting the Internal Transcribed Spacer 1 (ITS1) region and Illumina MiSeq sequencing using v3 chemistry (paired-end, 2 × 300 bp) of the 160 soil DNA samples were outsourced to Macrogen, Inc. in Seoul, South Korea. For the preparation of amplicon libraries, fungal-specific primers ITS1F and ITS2 (5'-GCTGCGTTCTTCATCGATGC-3') (White et al., 1990) were used. The forward and reverse reads were deposited in the NCBI Sequence Read Archive (<https://submit.ncbi.nlm.nih.gov/subs/sra/>) under the accession number PRJNA1003671.

2.7. Analyses of high-throughput sequence data

The sequencing facility demultiplexed the Illumina MiSeq sequence data. The demultiplexed sequence data was analyzed using Quantitative Insights into Microbial Ecology 2 (QIIME 2) v 2023.5 (Bolyen et al., 2019). Data were analyzed using two approaches: merging the forward and reverse reads and using only the forward reads. The merging of forward and reverse reads was done using BBMerge v 35.85 (Bushnell et al., 2017). Irrespective of the pipelines, the ‘q2-dada2’ plugin

(Callahan et al., 2016) was used for denoising, trimming, deletion of chimeras and singletons, and read filtering. To assemble the reads into Operational Taxonomic Units (OTUs) with a 99 % sequence similarity, the ‘q2-vsearch’ plugin was used (Rognes et al., 2016). Subsequently, the ‘qiime feature-classifier’ plugin (Bokulich et al., 2018) was used to assign taxonomy to the OTUs. At this step, the UNITE fungal ITS database v16.10.2022 (Abarenkov et al., 2022) was used as the reference.

After comparing outcomes from both pipelines, over 30 % of total reads were lost during the merging of forward and reverse reads compared to using only forward reads. Consequently, further analyses were exclusively conducted based on the OTU table obtained from the analysis of forward reads.

2.8. Statistical analysis of soil attributes, growth data, and sequence data

All statistical analyses of soil properties and growth rates were conducted using generalized mixed effects models with the ‘nlme’ package in R v4.3.2, as the data was not normally distributed and contained pseudoreplication. Soil nutrients and growth rates across BMS sites were averaged and analyzed using the BMS sites as random effects. Soil moisture contents and temperatures were analyzed using the sampling dates as random effects.

The fungal microbiome data was statistically analyzed using MicrobiomeAnalyst. Low-count features were filtered based on the mean abundance value, with the minimum count set at four, while the low-variance features were removed based on the interquartile range. The remaining features were normalized using the total sum scaling (TSS). To analyze the soil fungal diversity, alpha diversity indices, including Shannon, Simpson and Chao1 (species richness), were calculated using the *t*-test/ANOVA as the statistical method. The experimental factors considered for these analyses were ‘sampling sites’, ‘treatments’ and ‘sampling time’.

To examine the soil fungal community composition across different ‘sampling sites’, ‘treatments’ and ‘sampling times’, a Principal Coordinate Analysis (PCoA) based on Bray-Curtis dissimilarity was used. Additionally, a Permutational Multivariate Analysis of Variance (PERMANOVA) was used to explore potential differences in community composition among the different ‘sampling sites’, ‘treatments’, and ‘sampling times’. In cases where the PCoA did not display a clear clustering of the data points, but the PERMANOVA yielded statistically significant results with a relatively small R-value, Permutational Multivariate Analysis of Dispersion (PERMDISP) was used to determine if the observed differences were primarily attributed to variations in data dispersion rather than actual differences in community structure. The taxonomic heat tree was built with Metacoder (Foster et al., 2017), available through MicrobiomeAnalyst.

2.9. Functional characterization of the fungal community

FUNGuild v1.1 (Nguyen et al., 2016) was used to identify the trophic mode and guilds of the fungal OTUs associated with each of the four treatments across four sample locations and two different sampling time points. In this analysis, two confidence levels, ‘highly probable’ and ‘probable’, were considered reliable. Any OTUs that could not be matched to known taxa in the database were categorized as ‘unassigned’. Trophic mode data from the four BMS sites were normalized using log transformations. Transformed data were analyzed using a three-factorial analysis of variance (soil treatment, planting date and sampling date), followed by a Tukey’s post-hoc test at a confidence level of 0.05. Data was analyzed using R v4.3.2 (R Core Team, 2023).

2.10. Fungal dynamics across treatment regimes and sampling times

This analysis aimed to compare the percentage abundance and composition of the top 10 most abundant fungal OTUs for each treatment regime across two different sampling time points. For this, the OTU

table was divided into eight sections, each presenting a treatment regime and sampling year. MicrobiomeAnalyst v 2.0 (Lu et al., 2023) was used to analyze each of these OTU tables. For all eight analyses, the ‘low count filter’ was set to 100, and the ‘low variance filter’ was set to 10 % based on the ‘inter-quantile range’. Default settings were maintained for data rarefying, data scaling, and data transformation. In the ‘core microbiome’ analysis, the taxonomic level was specified as ‘feature level’, sample prevalence was 30, relative abundance was 0.01, and data sub-setting was ‘all samples’. The resulting heat maps were exported and subsequently edited using an image editing tool.

3. Results

3.1. Impact of treatment and planting time on tree volume

Analysis of volume data revealed significant impacts of both treatment (burnt and mulched) and planting time (immediate and delayed) on tree vigour 24–36 months after planting (Fig. 2A). Mulched plots exhibited a higher volume ($2.3\text{--}2.7\text{ m}^3\text{ ha}^{-1}\text{ month}^{-1}$) than burnt plots ($1.8\text{--}2.2\text{ m}^3\text{ ha}^{-1}\text{ month}^{-1}$; $p = 0.01$). Delayed planting led to greater tree volume ($2.2\text{--}2.7\text{ m}^3\text{ ha}^{-1}\text{ month}^{-1}$) compared to immediate planting ($1.8\text{--}2.3\text{ m}^3\text{ ha}^{-1}\text{ month}^{-1}$; $p = 0.0003$; Fig. 2A). During the 36–48 months period, only planting time remained a significant factor. Regardless of whether the plots were burnt or mulched, delayed planting resulted in higher volumes ($2.2\text{--}2.6\text{ m}^3\text{ ha}^{-1}\text{ month}^{-1}$) than immediate planting ($1.7\text{--}2.1\text{ m}^3\text{ ha}^{-1}\text{ month}^{-1}$; $p = 0.0038$; Fig. 2B).

3.2. Effects of mulching and burning on soil moisture, temperature, and chemistry

Soil moisture levels in the first four months after treatments were implemented were 1.3–2 times higher in all mulched treatments compared to burnt treatments across four sampling sites. The differences were significant ($p < 0.05$) for all BMS sites, except for the Mavuya A32 site ($p = 0.058$) (Fig. 3A; Table S1). Mulched plots with delayed planting also showed consistently elevated moisture levels, possibly due to the absence of tree growth, but this was only significant at the Mavuya A32 site ($p = 0.03$) (Table S1).

Mulching significantly reduced surface temperatures in the first four months after the treatments were implemented, resulting in lower average soil surface temperatures at three sites except for the Palm Ridge C9 site. The temperature was $1.24\text{ }^\circ\text{C}$ lower in the mulched plots at Palm Ridge C09 in comparison to the burnt plots, a reduction of $3.13\text{ }^\circ\text{C}$ was observed at Palm Ridge F14, a reduction of $1.57\text{ }^\circ\text{C}$ was observed at Salpine E01, and the temperature was reduced by $1.83\text{ }^\circ\text{C}$ in mulched plots at Mavuya A32 ($p < 0.05$; Table S2). Also, mulching reduced daily temperature fluctuations compared to burnt sites. Mulching did not influence the recorded minimum temperatures at three of the sites but significantly reduced the maximum temperatures at three sites ($p < 0.001$), by approximately $4.5\text{ }^\circ\text{C}$ at Palm Ridge F14, by $5.2\text{ }^\circ\text{C}$ at Mavuya A32, and by $6.8\text{ }^\circ\text{C}$ at Salpine E01 (Fig. 3B). High surface temperatures above $30\text{ }^\circ\text{C}$ were regularly observed in burnt plots (Fig. 3B; Table S2).

Soil chemistry was analyzed after planting the ‘immediate’ plots at all four sites. Topsoil pH (H_2O) was about 1.1-fold higher in burnt plots

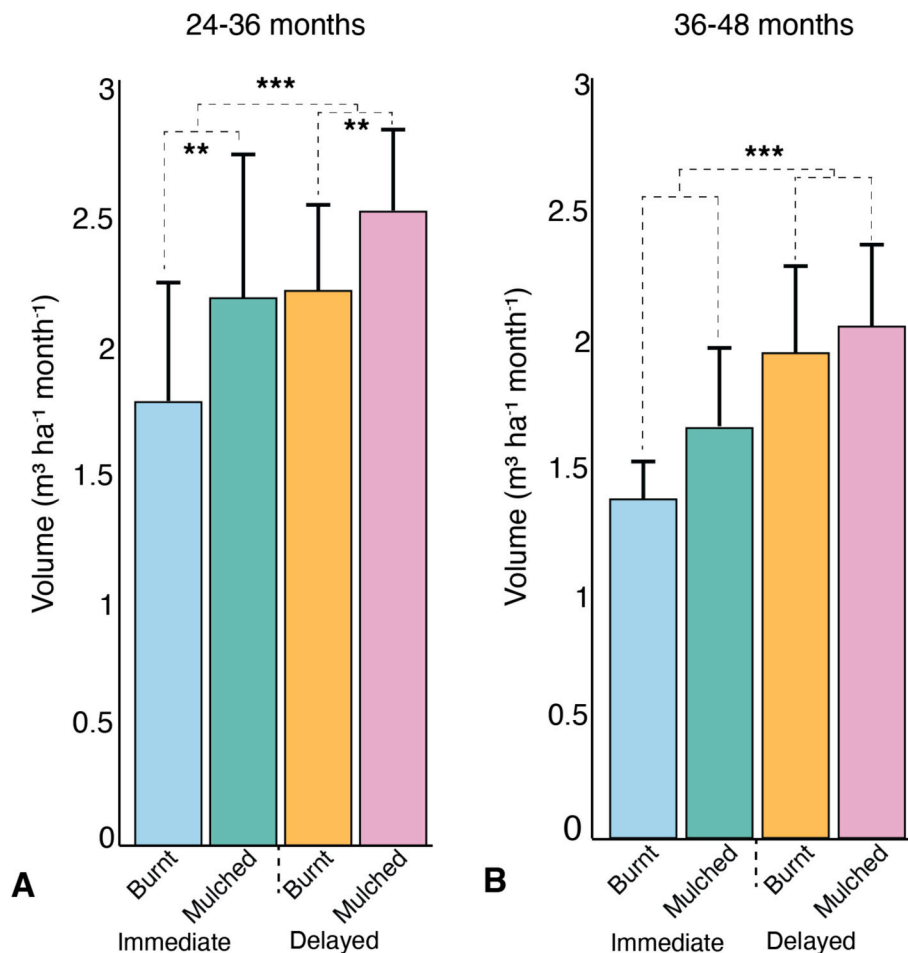


Fig. 2. Bar plots showing the incremental increase (m^3 per hectare per month) in average volume of *Eucalyptus* trees in the burnt versus mulched study. (A) 24–36 months post-planting, mulching coupled with delayed planting significantly improved tree vigour while (B) during the 36–48 months period, only delayed planting emerged as a significant factor influencing tree vigour.

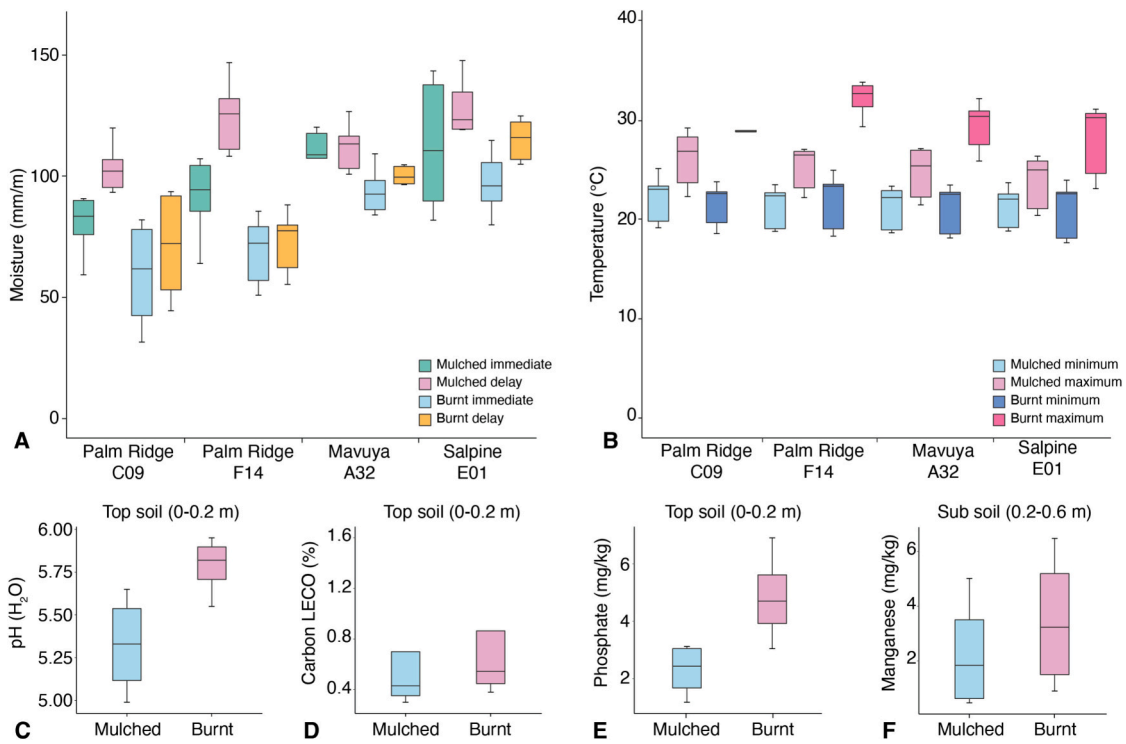


Fig. 3. Bar plots showing the effects of mulching and burning on selected significant soil attributes across four sampling sites (for details see Table S1–3). (A) Soil moisture content, (B) minimum and maximum soil temperatures, and (C–D) pH (h₂O), soluble carbon, phosphate, and manganese.

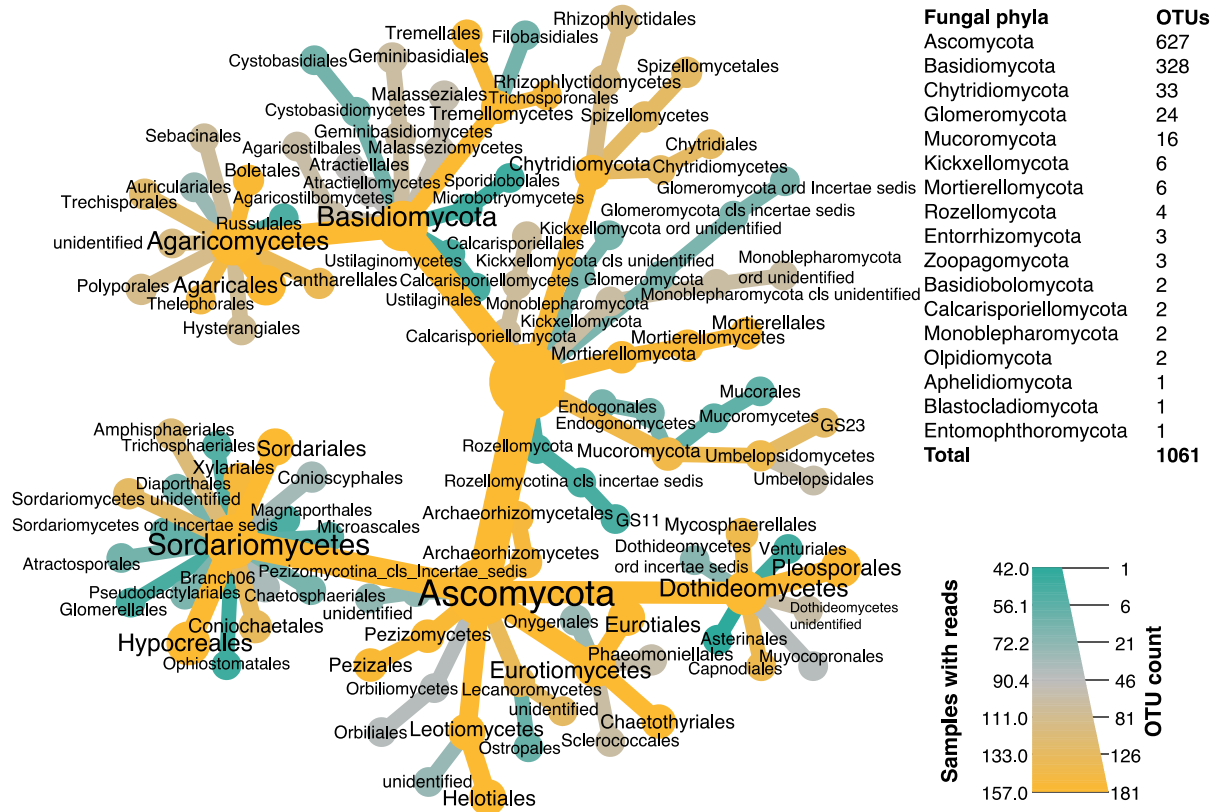


Fig. 4. The taxonomic composition of fungi in the soil from four treatment regimes up to the order level. The size of nodes and edges corresponds to the number of OTUs within each taxon, while the colour indicates the abundance of the taxon.

($p = 0.008$) compared to mulched plots, but this effect diminished in the subsoil (Fig. 3C; Table S3). In general, mineral nutrients were consistently lower in mulched soils compared to burned soils. Among these, P and C levels were approximately 2.2 ($p = 0.009$) and 1.6 ($p = 0.04$) times lower in the mulched topsoil (0–0.2 m) compared to its burnt counterpart (Fig. 3D, E). In the subsoil (0.2–1.0 m), nutrient levels were also marginally lower in the mulched treatment, but only Mn levels were about 2.5-fold lower in mulched versus burned treatments ($p = 0.04$; Fig. 3F).

3.3. Soil fungal community profile

High-throughput sequencing of 160 DNA samples extracted from soil collected at four BMS sites gave a total of 12,604,029 raw forward reads. After filtering the reads with ‘q2-dada2,’ 11,479,789 reads (91.08 %) were used for further analysis. A total of 1061 fungal OTUs were identified after de novo assembly and taxonomic assignment of these filtered reads. The fungal OTUs were predominantly represented by Ascomycota, accounting for 59.1 % (627 OTUs), followed by Basidiomycota with 30.9 % (328 OTUs) (Fig. 4; Table S4). Ascomycota was further classified into 13 classes and 70 orders, with a majority of the OTUs belonging to the Sordariomycetes (239), Dothideomycetes (205), and Eurotiomycetes (58) (Table S4). In contrast, Basidiomycota comprised 14 classes and 40 orders, with the most abundant OTUs in classes Agaricomycetes (214), Agaricostilbomycetes (48), and Atractiellomycetes (16) (Fig. 4; Table S4). ‘The remaining 10 % (106) of fungal OTUs were distributed across several phyla, including Chytridiomycota (33), Glomeromycota (24), Mucoromycota (16), and 11 others with fewer representatives (Fig. 4; Table S4).

Saprotrophs were significantly affected by both treatment type (burnt vs. mulched; $p = 0.01932$) and planting date (immediate vs. delayed; $p = 0.01534$; Fig. 5A). Mulched plots had 1.3 times more saprotrophs than burnt plots, while immediately planted plots had 1.25 times more saprotrophs than delayed planting (Fig. 5A). Symbiotrophs were significantly influenced by planting date ($p = 0.004784$) and sampling year (2019 vs. 2022; $p = 6.275e-10$; Fig. 5B). Immediately planted plots had 2.8 times more symbiotrophs than delayed planting. Additionally, symbiotroph abundance was 3.2 times higher in 2022 compared to 2019, indicating a strong effect of time on symbiotroph populations (Fig. 5B). Pathotrophs showed significant differences only between the two planting dates ($p = 0.04621$; Fig. 5C). Delayed planting had 1.5 times more pathotrophs than immediate planting.

3.4. Effect of sampling site on the diversity and community composition of soil fungi

The species richness of soil fungi did not show significant differences among the four sampling locations ($p > 0.05$; Fig. S1A). Similarly, the various sampling sites did not significantly affect the Shannon and Simpson indices ($p > 0.05$; Fig. S1B, C). The PCoA plots did not exhibit distinct clustering patterns based on site. However, PERMANOVA ($F = 2.9742$, $p = 0.001$; Fig. S1D) analyses indicated that the community composition of soil fungi was influenced by the ‘sampling sites’, but PERMDISP analyses did not support this hypothesis ($F = 4.0006$, $p = 0.009$; Fig. S1D).

3.5. Effect of treatment on the diversity and community composition of soil fungi

The species richness of soil fungi ($F = 9.8191$, $p = 7.6796e-05$) and Shannon index displayed a significant difference ($F = 5.008$, $p = 0.005$; Fig. S2) between treatments only at Palm Ridge F14, with no significant variation observed in other sampling locations (Fig. S2). The Simpson index was not significantly influenced by the ‘treatments’ at all sites ($p > 0.05$; Fig. S2).

In the PCoA plots, the data points from different soil treatment

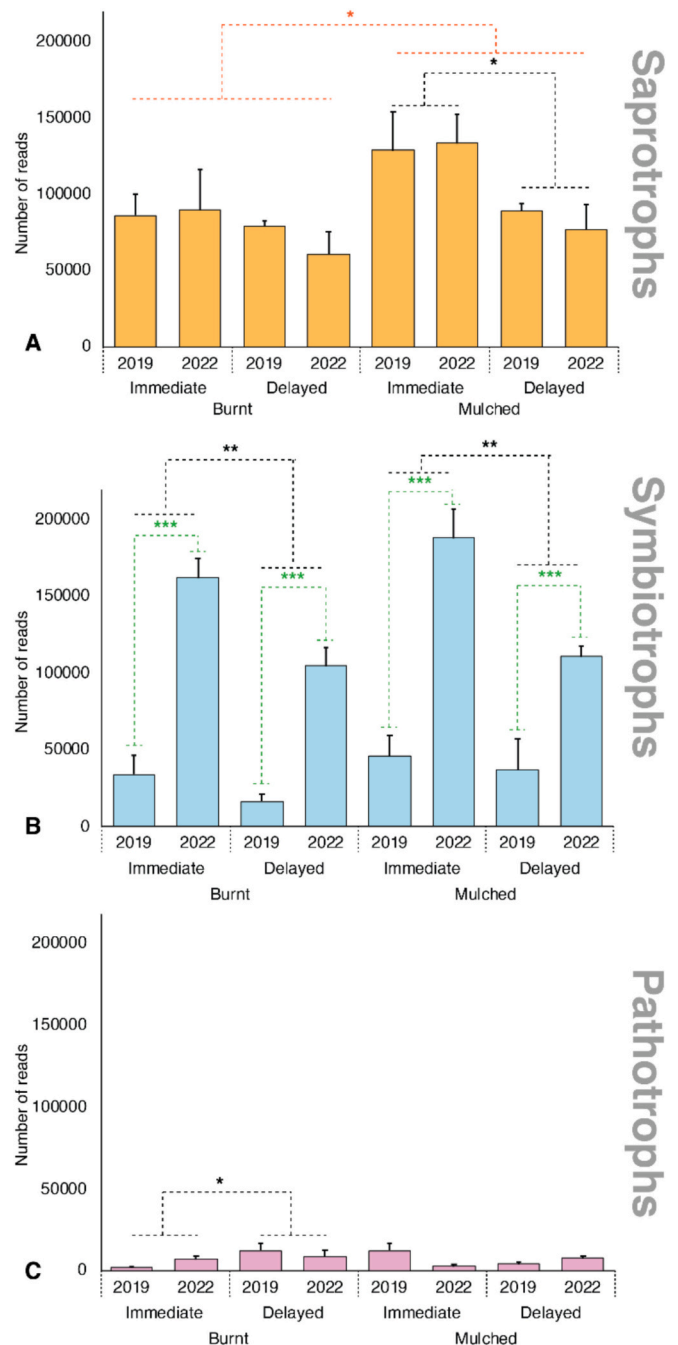


Fig. 5. Bar plots showing the prevalence of three predominant fungal trophic modes identified through FUNGuild analysis: saprotrophs, symbiotrophs, and pathotrophs. Saprotrophs were significantly affected by both treatments (burnt vs. mulched; orange line) and planting dates (immediate vs. delayed; black line). Symbiotrophs were significantly influenced by planting dates and sampling dates (2019 vs. 2022; green line). Pathotrophs exhibited significant differences only between the two planting dates.

regimes overlapped (Fig. 6). However, the PERMANOVA analysis indicates that the treatment regimes had a significant influence on the community composition of soil fungi at all sites (Table 1), though the percentage of statistical variance (r^2) was relatively low (Table 1). Additionally, the PERMDISP analysis showed that the differences observed by the PERMANOVA at all sampling sites were primarily attributed to significant variations in the fungal community composition ($F = 7.3211$; $p > 0.09$) rather than the dispersion of the samples.

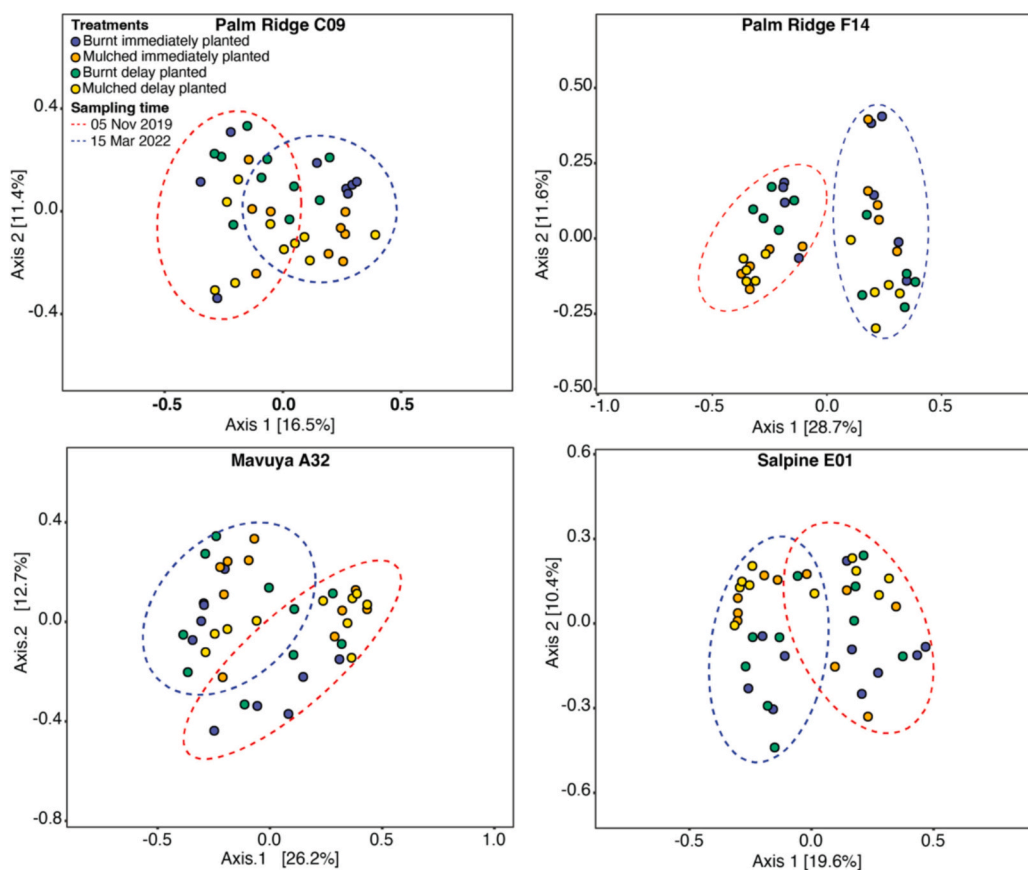


Fig. 6. Principal Coordinates Analysis (PCoA) of soil fungal community composition associated with four treatments (burnt immediately planted, mulched immediately planted, burnt delay planted, and mulched delay planted) across four different sampling sites. The data points are clustered based on sampling times (November 2019, and March 2022).

Table 1

The results of the PERMANOVA analyzing the influence of treatment and sampling time on soil fungal community composition associated with four burnt versus mulched trial sites.

Sites	Explanatory variables	df	F value	r ²	p-value
Palm Ridge C09	Treatments	3	1.7654	0.13478	0.001
Palm Ridge F14	Treatments	3	1.599	0.12054	0.035
Mavuya A32	Treatments	3	1.8528	0.13375	0.011
Salpine E01	Treatments	3	1.4547	0.10812	0.022
Palm Ridge C09	Sampling time points	1	5.514	0.13282	0.001
Palm Ridge F14	Sampling time points	1	13.4	0.26588	0.001
Mavuya A32	Sampling time points	1	8.4764	0.18238	0.001
Salpine E01	Sampling time points	1	7.1746	0.15882	0.001

3.6. Effect of sampling time on the diversity and community composition of soil fungi

The species richness (Chao1) of soil fungi was significantly different between the two sampling times (November 2019 and March 2022) at Palm Ridge C09 ($p = 0.0001$), Palm Ridge F14 ($p = 0.0171$), and Mavuya A32 ($p = 1.4434e-05$), while no significant variation was observed in Salpine E01 (Fig. S3). The Shannon and Simpson indices were significantly affected by the ‘sampling time’ at Palm Ridge C09 and F14 ($p > 0.05$; Fig. S3). However, these diversity indices showed no significant differences for Mavuya A32 and Salpine E01 ($p > 0.05$; Fig. S4).

The PCoA plots exhibited clear clustering patterns based on the soil sampling times, in November 2019 and March 2022 (Fig. 6), although there were some overlaps observed in the case of Palm Ridge C09, Mavuya A32, and Salpine E01 (Fig. 6). The PERMANOVA analysis confirmed the significant impact of sampling time on the community

composition of soil fungi across all sites (Table 1), and this finding was supported by the PERMDISP analysis ($F = 6.54336$; $p > 0.6$).

3.7. Soil fungal succession between 2019 and 2022

In 2019, primary colonizers in burnt subplots included saprotrophic fungi like *Aspergillus*, *Mortierella*, *Penicillium*, *Talaromyces*, and *Oidiodendron*, an ericoid mycorrhizal fungus (Perotto et al., 2002), and *Ruhlandiella*, an ectomycorrhizal fungus of *Eucalyptus* (Kraisitudomsook et al., 2019) (Fig. 7). Both these mycorrhizal fungi were already present in ‘delay’ plots awaiting *Eucalyptus* planting (Fig. 7). Later in 2022, ‘immediately’ planted plots had other *Eucalyptus* ectomycorrhizal taxa, such as *Ruhlandiella*, *P. marmoratus*, *Scleroderma*, and *Tomentella* (Bose et al., 2023b), along with various saprotrophs. In ‘delay’ planted plots, only *Ruhlandiella* among the ectomycorrhizal taxa was abundantly detected (Fig. 7). Rhizosphere-associated fungal taxa in the Archaeorhizomycetales (Rosling et al., 2011) were abundantly detected in both types of burnt plots at both sampling times (Fig. 7).

In 2019, Rozellomycota was the most abundant fungal taxon in both ‘immediately’ and ‘delay’ planted mulched plots (Fig. 7). *Oidiodendron* sp. and *Ruhlandiella* sp. were abundantly detected in both treatments. A genus of ‘black fungi’, *Cladophialophora* (Chang et al., 2023), was abundantly detected in both types of mulched plots (Fig. 7). Xylophagous fungi from the Basidiomycota, such as *Coniophora* and *Trechispora*, were also found in mulched plots. In 2022, *Ruhlandiella* emerged as the most abundant taxon in both types of mulched plots, with other ectomycorrhizal taxa such as *P. marmoratus*, *Scleroderma*, and *Tomentella*, although at a higher detection threshold than in ‘burnt’ plots (Fig. 7). Saprotrophs from the Basidiomycota, like *Coprinellus* and *Auriculariales*, and *Phoma*, a foliar pathogen of *Eucalyptus* species (Crous et al., 1989),

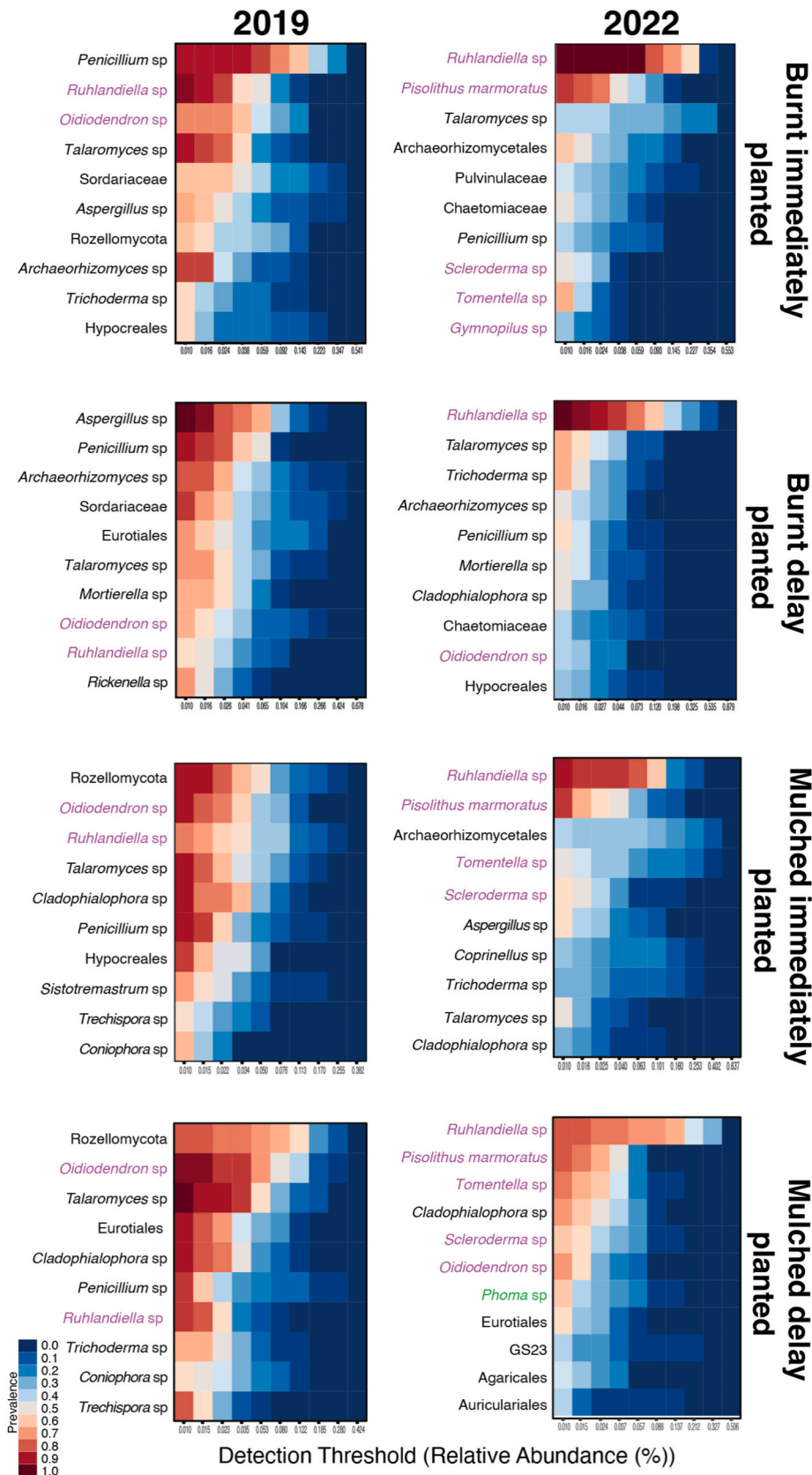


Fig. 7. Heat maps illustrate fungal succession within different treatment regimes at two soil sampling times. This analysis focused on the top ten most abundant taxa. If species-level taxonomy was unavailable for an OTU, the highest available taxonomic level was considered. Taxa names in purple fonts = symbiotrophs, black fonts = saprotrophs, green font = pathotrophs.

were commonly detected in 'mulched delay planted' plots (Fig. 7).

4. Discussion

This study investigated the effects of mulching and burning of post-harvest residues on soil properties, tree vigour, and soil fungal biodiversity across four study sites in KwaZulu-Natal planted with a hybrid genotype of *Eucalyptus*. Data emerging from this study showed that mulching increased soil moisture and reduced surface temperatures, with trees in mulched plots showing better vigour at mid-rotation (four years). Soil fungal biodiversity was higher in mulched, immediately planted plots. Additionally, fungal functional analysis revealed more saprotrophs and symbiotrophs in mulched plots, aligning with the expected long-term benefits of mulching. The delayed planting strategy improved tree vigour in both mulched and burned plots.

4.1. Impact of mulching and burning of post-harvest residue on soil attributes and tree vigour

At the BMS sites, mulched plots had 1.3–2 times higher soil moisture content and lower surface temperature (1.24–3.13 °C) compared to burnt plots. Mulching also significantly reduced maximum soil temperatures by 4.5–6.8 °C. This is in line with several previous studies that measured these parameters (Coello et al., 2018; Li et al., 2020b; Prosdocimi et al., 2016). Mulching acts as a protective layer on the soil that conserves moisture, moderates temperature extremes, suppresses weed growth, and prevents erosion (Amoroso et al., 2010; Fan et al., 2023; Li et al., 2021; Mechergui et al., 2021; Prosdocimi et al., 2016). In addition to these benefits, mulching also enriches the soil with saprotrophic fungi (Barreiro et al., 2016; Huang et al., 2008; Li et al., 2020a; Wang et al., 2020), which decompose the organic matter, thereby maintaining natural nutrient cycling processes that would otherwise be disrupted by the removal of plant residues (Bose et al., 2023a; Mechergui et al., 2021; Ngosong et al., 2019). Mulching thus mimics a slow-release fertilizer, while burning of post-harvest residues releases nutrients into the soil instantly, which can have both positive and negative impacts on soil properties and tree vigour (Kumaraswamy et al., 2014; Mendham et al., 2003).

At the start of the trial, compared to mulched plots, the burning of post-harvest residues in the BMS sites significantly increased soil pH (1.1 times) and some nutrients. Earlier studies have reported that post-burning labile N levels typically rise due to the release of ammonium from heated organic matter, stimulating the nitrification process and increasing ammonium and nitrate concentrations essential for plant growth (Certini, 2005; James et al., 2018; Wan et al., 2001). After a fire, soil pH increases due to ash deposition, which in turn mitigates aluminium toxicity associated with acidic soils and enhances soil biological recovery through increased levels of essential nutrients like K, Mg, and Ca (Aciego Pietri and Brookes, 2008; Chungu et al., 2020; Kim et al., 2011; Rout et al., 2001; Xue et al., 2014). This increase in pH also fosters a more favourable environment for soil bacteria involved in N cycling, further assisting tree growth and overall forest productivity (Aciego Pietri and Brookes, 2008; Arocena and Opio, 2003; Chungu et al., 2020; Neff et al., 2005; Rout et al., 2001). The burning of post-harvest residues also reduces the inoculum load of pathogenic microbes that could negatively impact subsequent rotations (Dutta et al., 2022). However, burning reduces soil fertility over time due to the leaching of minerals by rain, dispersion of ashes through wind and erosion, reduced infiltration due to hydrophobicity (Abdurrahman et al., 2020; Raza et al., 2022) and reduced water retention ability of the soil (Zhao et al., 2015). Burning of post-harvest residues can thus have positive and negative effects on soil fertility and tree vigour. The ambivalent effects of burning crop residues also extend to the tree species planted, as *Eucalyptus* trees are adapted to regular forest fires in their native range (Attiwill, 1994).

Tree volume measurements from the BMS sites showed that initially,

trees in the mulched plots had significantly higher volumes (2.3–2.7 m³ ha⁻¹ month⁻¹) at mid-rotation (four years) compared to those in the burnt plots (1.8–2.2 m³ ha⁻¹ month⁻¹). Despite being a fire-adapted species, mulching provided a more conducive soil environment for the growth of young *Eucalyptus* trees, possibly due to lower soil temperature fluctuations and higher water retention. In addition, nutrients from decaying plant material could have facilitated faster growth in mulched plots due to the mineralization of nutrients (Coello et al., 2018; Iqbal et al., 2020; Li et al., 2020b; Prosdocimi et al., 2016). However, the most significant factor influencing tree growth on the BMS sites was planting date, where delayed planting resulted in increased tree vigour (2.2–2.7 m³ ha⁻¹ month⁻¹) compared to immediate planting (1.8–2.3 m³ ha⁻¹ month⁻¹) that was sustained over the first four years, regardless of the soil treatment. It is well known that microbes selectively use minerals, especially nitrogen, from the soil during the initial breakdown of organic biomass with a high C:N ratio to supplement their needs (Arsuffi and Suberkropp, 1989; Spohn, 2020; Spohn and Berg, 2023; Zechmeister-Boltenstern et al., 2015). This immobilization of mineral nutrients results in an initial nutrient-deficient stage in the soil (Mendham et al., 2003). As the degradation of plant material and ash progresses, nutrients are released back into the soil by mineralization. Delaying planting thus allows trees to avoid the initial nutrient immobilization stage. Later, when most of the essential nutrients are available through the breakdown of organic matter and ash (Berg and McClaugherty, 2008; Blair, 1988), trees can utilize the mineralized nutrients and show improved vigour (Osono and Takeda, 2004).

4.2. Impact of burning and mulching of post-harvest residue on soil fungal biodiversity

The significant influence of residue management regimes and sampling times on soil fungal biodiversity can be attributed to the differences in the availability of organic substrates and nutrients in the mulched and burnt plots. At the start of the trial in 2019, the mulched plots had a higher soil fungal biodiversity than the burnt plots. The mulched plots were rich in organic residues, which harboured a greater biodiversity of soil fungi, such as saprotrophs and symbiotrophs, which often act as primary decomposers in an ecosystem (Baldrian, 2017a, 2017b; Talbot et al., 2008). In contrast, the burnt plots initially had higher soil nutrient content due to the combustion of the post-harvest residues, however, they lacked organic substrates. This limited the types of fungi that could colonize these plots (Dove and Hart, 2017), such as pyrophytic fungal species (Johnston et al., 2024; Tomao et al., 2020). Thus, burnt plots had lower fungal biodiversity, with only 96/130 exclusive OTUs compared to 257/210 in the mulched immediately planted plots.

In 2019, immediately planted plots after burning had slightly lower fungal biodiversity (434 OTUs) than those planted later (460 OTUs). In contrast, immediately planted mulched plots exhibited higher biodiversity (595 OTUs) compared to delayed plots (536 OTUs). This suggests that distinct factors influenced soil fungal biodiversity across these treatments. In the burnt plots, the difference in fungal OTUs between immediate and delayed planting is likely due to nutrient competition between *Eucalyptus* trees and soil fungi (Kuzyakov and Xu, 2013; Püschel et al., 2016; Zhu et al., 2016). Immediate planting limits fungal diversity because the trees compete for available nutrients, while delayed planting allows fungi to access these nutrients without competition, leading to greater diversity. Conversely, the higher fungal biodiversity in immediately planted mulched plots was mainly due to mycorrhizal OTUs. The presence of *Eucalyptus* likely enhances soil fungal biodiversity, particularly mycorrhizae (Liu et al., 2022; Teng et al., 2021). Thus, the contrasting patterns of fungal diversity in burnt and mulched plots highlight the complexity of soil fungal dynamics influenced by different treatments and planting strategies.

In 2022, the soil fungal communities in the burnt immediately planted and mulched immediately planted plots also showed distinct

differences. The mulched plots that were immediately planted had higher fungal biodiversity (564 OTUs) compared to the burnt counterpart (515 OTUs). Although both treatments shared 400 OTUs, the mulched plots had a higher number of exclusive fungal OTUs (164) compared to the burnt plots (115). This reinforces the observations from previous studies that retaining post-harvest residue improves the fungal biodiversity of soil over time (Bose et al., 2023a; Bose et al., 2023b; Huang et al., 2008; Ngosong et al., 2019), which leads to the establishment of a more diverse and stable fungal community, which is essential for maintaining soil health and ecosystem functioning (Zhang et al., 2020).

The fungal communities in the delayed planted plots sampled in 2022 had higher fungal biodiversity compared to the immediately planted plots. The recovery of fungal biodiversity in burnt delayed planted plots could be attributed to several factors. In 2022, these plots had trees that contributed to the improved soil fungal biodiversity compared to the 2019 sampling period, which took place before the delayed planting. Over two years, these trees deposited plant litter, which was left untouched to mimic natural conditions. This litter was colonized by soil fungi, enhancing their biodiversity and thereby partially offsetting the loss of fungal biodiversity caused by the burning of harvest residues (Ge et al., 2013; Giweta, 2020). Additionally, fungi from the mulched plots likely migrated to the burnt plots due to the presence of plant litter. This led to an increase in shared fungal OTUs between the burnt and mulched plots over time.

4.3. Impact of burning and mulching of post-harvest residue on fungal succession

In 2019, saprotrophs in the burnt plots included *Aspergillus*, *Mortierella*, *Penicillium*, *Talaromyces*, and many others. In post-fire conditions, the fungal biomass substantially decreases (Filialuna and Cripps, 2021; Pressler et al., 2019). This allows the colonization of early succession species, such as those saprotrophs detected in this study. These fungi are also affected by fire, but they seem to be more tolerant than other fungi, and they recover more rapidly (Filialuna and Cripps, 2021). However, due to limited data, specific responses of saprotrophs to fire are largely unknown (Kouki and Salo, 2020). Nevertheless, available evidence suggests saprotrophs play an important role as nutrient cyclers in post-fire conditions (Orumaa et al., 2022).

In the burned plots, we observed the presence of *Rhizoglyphus*, an ectomycorrhizal fungus typically associated with *Eucalyptus* species, as well as *Oidiodendron*, an ericoid mycorrhiza. The early establishment of mutualistic fungi is essential for the recovery of plant communities in fire-disturbed environments. The relative abundance and types of ectomycorrhizal fungi following a fire, for example, can be influenced by fungal morphology (mycelia, spores, heat-resistant reproductive propagules), functional associations, ability to break down post-fire resources, and exploration type (Agerer, 2001; Bowd et al., 2023; Olchowik et al., 2021). Among these, for example, post-fire conditions favour short-distance ectomycorrhizal fungi, which briefly respond to increased inorganic nutrients (Lilleskov et al., 2011; Wan et al., 2001). In contrast, long-distance ectomycorrhizal fungi, which require more C and specialize in organic N uptake, tend to dominate in later successional stages when below-ground C allocation increases (Lilleskov et al., 2011; Tedersoo and Smith, 2013). Thus, in 2022, a difference in mycorrhizal community was observed between burnt 'immediately' and 'delayed' planted plots. In 'immediately' planted plots, the introduction of *Eucalyptus* trees early led to the proliferation of additional ectomycorrhizal fungi such as *P. marmoratus*, *Scleroderma*, and *Tomentella*, alongside the saprotrophs initially identified. Conversely, in 'delayed' planted plots, *Rhizoglyphus* remained the predominant ectomycorrhizal fungus. Thus, we believe both abiotic conditions (Bowd et al., 2021; Bowd et al., 2023; Certini, 2005) and planting times following fire also play key roles in selecting saprotrophs and symbiotrophs in plantation soils.

In 2019, mulched plots were characterized by the abundant presence of saprotrophs from Ascomycota and Basidiomycota. At this time point, *Rhizoglyphus* was the only prominent mycorrhizal species detected in both 'immediately' and 'delayed' plots. However, by 2022, the fungal community in mulched plots had shifted, with *Rhizoglyphus* emerging as the most abundant taxon. This shift suggests that, over time, mulching improves symbiotic fungal biodiversity. Also, the detection of other ectomycorrhizal fungi, such as *P. marmoratus*, *Scleroderma*, and *Tomentella*, at higher levels than in burnt plots points to the effectiveness of mulching in creating a conducive environment for these beneficial fungi. These elevated levels of ectomycorrhizal fungi facilitate the uptake of P, N and immobile nutrients (Smith and Read, 2010), affect forest composition and nutrient cycling and therefore in turn impact plant productivity and health (Aerts, 2003; DeBellis et al., 2006; Natel and Neumann, 1992; Tedersoo et al., 2008; Twieg et al., 2007).

4.4. Effect of treatments on plant pathogenic fungi

In this study, both burnt and mulched plots had significantly lower levels of pathotrophs in the soil compared to saprotrophs and symbiotrophs. Despite this, several key *Eucalyptus* pathogens were detected in the soil, including those from families such as Botryosphaeriaceae, Ceratocystidaceae, Cryphonectriaceae, Elsinoaceae, Ophiostomataceae, Quambalariaceae, Schizoparmaceae, and Teratosphaeriaceae, among others. Although species-level identification of plant pathogenic fungal OTUs couldn't be achieved in this study, many fungi from these families are known to be established pathogens of *Eucalyptus* in both field and nursery settings in South Africa. Examples include *Coniella*, *Elsinoë*, *Lasiodiplodia*, *Neofusicoccum*, *Pseudocercospora*, *Quambalaria*, *Ramularia*, *Teratosphaeria*, and *Zasmidium*. Many of these were also detected in our previous soil fungal biodiversity study from South African *Eucalyptus* plantations (Bose et al., 2023b). In that study, we also observed that plots retaining intact post-harvest residues (broadcasted) generally had a lower percentage of pathotrophs compared to plots where the residue was removed and inorganic fertilizer was added. However, when comparing intact residue retention to mulching, we found that mulched plots in this study had significantly lower pathotroph levels than plots in the previous study where intact post-harvest residues were retained. This suggests mulching is a more effective strategy for reducing pathogen presence and promoting soil health compared to retaining intact post-harvest residues.

5. Conclusions

This study underscores the importance of post-harvest residue management in shaping soil fungal biodiversity and tree productivity within South African and global plantation forestry landscapes. While the burning of post-harvest residue is cost-effective and might present short-term benefits like increased labile N levels and reduced pathogenic microbes, its long-term consequences on soil health, biodiversity, and ecological sustainability may not be favourable. Mulching consistently showed superior benefits by enhancing soil moisture, moderating temperatures, promoting microbial activity, and fostering overall soil health.

Moving forward, global forestry stakeholders should consider adopting mulching practices. This shift is not merely an ecological imperative but also ensures long-term economic viability. By investing in mulching techniques, the forestry sector can strike a harmonious balance between production goals and ecological stewardship. Thus, in South Africa, most forestry companies have already begun implementing mulching where practical, such as on level land, although it remains challenging in mountainous or steep areas where mulchers cannot be used. Despite its higher initial costs, the data presented in this paper supports the continued shift towards mulching over burning, particularly in the context of climate change and its negative effect on air quality. South Africa is already experiencing shifts in rainfall patterns

and rising temperatures, making mulching an even more favourable option for maintaining soil health and reducing negative ecological impact. As this practice becomes more widespread, it is essential to continually refine and adapt these practices based on emerging research and local conditions. Furthermore, ongoing monitoring and adaptive management strategies will be crucial for optimising tree productivity while safeguarding soil health and biodiversity.

CRediT authorship contribution statement

Tanay Bose: Writing – review & editing, Writing – original draft, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Jolanda Roux:** Writing – review & editing, Resources, Conceptualization. **Louis Titchshall:** Writing – review & editing, Resources. **Steven B. Dovey:** Writing – review & editing, Resources. **Almuth Hammerbacher:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.apsoil.2025.106091>.

Data availability

The high-throughput sequencing data generated in this study is available in the NCBI Sequence Read Archive (<https://submit.ncbi.nlm.nih.gov/subs/sra/>) under accession number PRJNA1003671.

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