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Water hyacinth (*Eichhornia crassipes*) mulch and urea interactions shape soil biota and nitrogen cycling

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ABSTRACT

Organic amendments influence soil biological activity and nutrient availability depending on their composition and decomposition rate, and invasive plants such as water hyacinth (*Eichhornia crassipes*), one of the world's most widespread aquatic weeds, represent a potential source of nutrient-rich organic matter that can be repurposed as a soil amendment. This study tested the effects of water hyacinth mulch, a nutrient-rich and rapidly decomposable biomass, compared with woody mulch and an unmulched control across macadamia, lychee, and grazing systems in subtropical Queensland, Australia. Plots received mulch with or without ^{15}N-labelled urea, and soil bacteria, fungi, and nematodes were characterised using metabarcoding to assess treatment effects on microbial communities and nitrogen dynamics over seven weeks. Water hyacinth mulch reduced bacterial diversity but increased bacterial-feeding nematodes and shifted fungal composition toward saprotrophic decomposers. Bulk soil $\delta\ ^{15}$N was lower under water hyacinth mulch in fertilised macadamia soils, suggesting faster nitrogen turnover at that site, though no isotopic effect was detected at the lychee or pasture sites. These microbial shifts are consistent with accelerated nutrient mineralisation driven by labile organic matter, though effects on nitrogen cycling were context-dependent and require validation through direct process measurements. Combining water hyacinth mulch with more recalcitrant organic inputs may help moderate mineralization rates and improve nutrient use efficiency. Extended field trials are needed to evaluate whether these short-term responses translate to sustained improvements in soil function and long-term fertility.

1. Introduction

Organic amendments such as mulches, composts, and biochars improve soil health by enriching nutrients and organic matter, enhancing aggregation, porosity, and water retention, reducing erosion, and shaping microbial communities, with the effects depending on amendment characteristics (Blanchy et al., 2023; Deshoux et al., 2023; Breza and Grandy, 2025). Nutrient-rich materials that decompose quickly, such as green mulches, manures, or food waste composts, support rapid microbial turnover, stimulate mineralisation, and release nutrients in the short term (Zechmeister-Boltenstern et al., 2015; Luo et al., 2018; Islam et al., 2026). Inputs that are more resistant to decomposition, including woody residues, crop stubbles, or biochars, persist because they contain high levels of lignin and cellulose or, in the case of biochars, aromatic carbon structures formed during pyrolysis; these compounds decompose slowly and contribute to long-term soil carbon pools while improving cation exchange capacity (Wang et al., 2016; Shu et al., 2022; Breza and Grandy, 2025). The balance between fast and slow cycling components determines the timing of nutrient supply (Nicolardot et al., 2001; Chen et al., 2014; Sari et al., 2022), and consequently the resilience of soils to drought, erosion, and disturbance, because stable organic matter enhances aggregation, water retention, and nutrient buffering, while fresh inputs sustain microbial activity and short-term fertility that helps soils recover quickly from stress (Abdallah et al., 2021; Shu et al., 2022; Ma et al., 2024). Outcomes depend on local soil, climate, and land use, so the same amendment can perform differently across regions. Barriers to broader use include variable availability and quality, high transport and application costs, unacceptable odour, and competition with other demands such as livestock feed or bioenergy, which often limit farmers' ability to adopt amendments even when they are agronomically effective (Viaene et al., 2016; Hijbeek et al., 2019; Pergola et al., 2020).

Water hyacinth (*Eichhornia crassipes*) is one of the world's most invasive aquatic plants, forming dense mats that disrupt aquatic ecosystems, fisheries, and water infrastructure (Villamagna and Murphy, 2010; Abba and Sankarannair, 2024). At the same time, its prolific

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Table 1
Soil physicochemical properties (mean ± SD) for each mulch treatment across three agricultural sites in subtropical Queensland, Australia. Values are from plots without urea addition (n = 5 per treatment per site). Control = unmulched; WH = water hyacinth mulch; Wood = woody mulch. EC = electrical conductivity; CEC = cation exchange capacity; Org C = organic carbon.

	Pasture			Macadamia			Lychee		
Parameter	Control	WH	Wood	Control	WH	Wood	Control	WH	Wood
pH ($CaCl_2$)	5.92 ± 0.04	5.86 ± 0.09	5.94 ± 0.33	6.24 ± 0.52	6.62 ± 0.04	6.46 ± 0.09	5.60 ± 0.00	6.38 ± 0.51	5.58 ± 0.24
pH (H_2O)	6.54 ± 0.09	6.34 ± 0.11	6.60 ± 0.37	6.58 ± 0.72	7.00 ± 0.00	7.22 ± 0.18	6.48 ± 0.08	7.22 ± 0.53	6.44 ± 0.09
EC (dS/m)	0.39 ± 0.06	0.47 ± 0.08	0.30 ± 0.07	1.91 ± 1.01	0.55 ± 0.00	0.29 ± 0.05	0.10 ± 0.01	0.21 ± 0.06	0.15 ± 0.04
Total N (%)	0.079 ± 0.012	0.083 ± 0.012	0.097 ± 0.023	0.168 ± 0.030	0.223 ± 0.010	0.130 ± 0.000	0.091 ± 0.005	0.084 ± 0.003	0.077 ± 0.010
Total C (%)	1.56 ± 0.09	1.60 ± 0.19	1.70 ± 0.20	2.80 ± 0.47	3.60 ± 0.32	2.20 ± 0.00	1.46 ± 0.09	1.42 ± 0.32	1.24 ± 0.11
C:N ratio	19.8 ± 2.3	19.4 ± 0.9	18.4 ± 2.9	18.0 ± 0.0	16.5 ± 0.6	17.0 ± 0.0	16.0 ± 0.0	18.6 ± 4.9	16.3 ± 0.6
P Colwell (mg/kg)	34 ± 13	29 ± 8	49 ± 9	86 ± 13	83 ± 3	73 ± 10	58 ± 3	86 ± 26	77 ± 4
K ($cmol^+/kg$)	0.56 ± 0.29	1.16 ± 0.38	1.21 ± 0.32	1.40 ± 0.11	2.94 ± 0.98	1.17 ± 0.16	0.66 ± 0.00	2.55 ± 0.24	1.23 ± 0.23
Ca ($cmol^+/kg$)	18.60 ± 0.55	17.60 ± 0.89	18.60 ± 0.89	13.16 ± 1.01	13.51 ± 2.52	14.18 ± 0.94	5.95 ± 0.57	2.94 ± 0.27	3.00 ± 0.47
Mg ($cmol^+/kg$)	13.20 ± 0.45	12.20 ± 0.84	12.20 ± 0.84	6.78 ± 1.05	6.99 ± 0.64	6.45 ± 1.39	1.39 ± 0.21	1.81 ± 0.42	1.36 ± 0.18
CEC ($cmol^+/kg$)	33.18 ± 0.70	31.62 ± 1.12	32.10 ± 0.67	21.92 ± 1.92	24.43 ± 1.08	21.47 ± 3.11	7.77 ± 0.48	7.55 ± 0.87	5.82 ± 0.40
Org C (%)	1.30 ± 0.19	1.34 ± 0.17	1.44 ± 0.18	2.38 ± 0.50	3.11 ± 0.09	1.95 ± 0.05	1.36 ± 0.10	1.09 ± 0.05	1.10 ± 0.13
NO_3^--N (μg/g)	17.0 ± 8.9	26.4 ± 12.7	14.6 ± 11.5	6.8 ± 3.5	27.6 ± 13.3	11.0 ± 0.0	12.1 ± 1.6	40.6 ± 2.7	27.4 ± 16.0
NH_4^+-N (μg/g)	2.96 ± 1.29	3.96 ± 1.86	2.82 ± 1.08	6.84 ± 1.10	5.18 ± 0.27	4.40 ± 1.22	2.82 ± 0.63	1.70 ± 0.12	2.58 ± 0.46

growth and high nutrient content make it a potential organic resource (Irewale et al., 2024; Canning, 2025; Kassa et al., 2025). Studies in Asia and Africa have shown that composted or vermi-composted water hyacinth can improve soil fertility and crop yields (Mahanta et al., 2012; Yadav and Garg, 2013; Goswami et al., 2017; Ibrahim, 2024), while water hyacinth biochar has been reported to increase pH, water holding capacity and retention (Bao et al., 2021; He et al., 2022; Gezahegn et al., 2025). Water hyacinth amendments have been shown to modify soil conditions in ways that increase microbial biomass, stimulate enzyme activities such as dehydrogenase and phosphatase, and support shifts in microbial community balance, including changes in the bacteria-to-fungi ratio (Mahanta et al., 2012; Ramdas et al., 2017; Patra et al., 2022). Compared to traditional woody mulches, water hyacinth is rich in nitrogen, phosphorus, and soluble carbon but low in lignin and fibre, providing a readily available substrate that accelerates decomposition, stimulates microbial turnover, and alters nitrogen and carbon mineralisation rates (Duryea et al., 1999; Valenzuela-Solano and Crohn, 2006; Canning, 2025). Field-scale trials, however, remain scarce, and most studies are short-term or confined to single crop systems, leaving uncertainty about how responses generalise across agricultural contexts (Canning, 2025).

Microbial communities underpin key soil functions including decomposition, nutrient cycling, and plant-soil interactions, making their response to organic amendments central to understanding and managing soil nutrient cycling and biological function. Because nitrogen fertilisers strongly shape microbial processes and influence whether applied nitrogen is retained or lost, understanding how mulches interact with fertiliser inputs is critical. Stable isotope tracers such as ^{15}N-labelled fertiliser offer a direct way to track nitrogen retention and turnover, yet they have rarely been used to assess mulching with invasive plant biomass. Beyond these biological processes, managing water hyacinth also offers a circular economy opportunity whereby harvested weeds from nutrient-enriched waterways are applied as an agricultural amendment, returning nutrients to farmland, reducing fertiliser costs, and mitigating impacts on aquatic ecosystems (Harun et al., 2021; He et al., 2022; Irewale et al., 2024).

The extent to which these effects occur across different farming systems remains uncertain and shifts in soil microbial communities may have positive or negative consequences for soil function. For example, increases in microbial biomass or nutrient mineralisation can enhance fertility, whereas shifts toward opportunistic or imbalanced communities may increase nutrient losses, reduce stability or promote pests and diseases. To address this, the present study compared water hyacinth mulch, woody mulch, and a no-mulch control across three agricultural settings in subtropical Queensland: a macadamia farm, a lychee orchard, and a livestock grazing pasture. Specifically, the study aimed to:

1. Assess how mulch type and nitrogen addition influence soil microbial diversity, composition, and functional traits.
2. Assess how mulch type influences ^{15}N fate in soil using ^{15}N-enriched urea tracers as an indicator of nitrogen turnover dynamics.

This study contributes several methodological strengths to the existing literature, including a field-scale design replicated across three contrasting agricultural systems, high-resolution metabarcoding of bacteria, fungi, and nematodes with functional trait annotation, and the use of ^{15}N-labelled urea to directly trace nitrogen fate alongside community-level data, an approach rarely applied to invasive plant biomass amendments.

2. Methods

2.1. Study sites and experimental design

The experiment was conducted across three agricultural sites near Rockhampton, Queensland, Australia: a macadamia farm (grey clay soil), a lychee orchard (brown clay soil), and a livestock grazing pasture (grey sandy loam soil). At each site, 2 × 2 m plots received either water hyacinth (WH) mulch, woody mulch, or a no-mulch control, each with 10 replicate plots arranged in a randomized layout, this yielded 30 plots per site and a total of 90 plots across the entire experiment. At the macadamia and lychee orchards, plots were positioned halfway between trees along orchard rows, while at the grazing site livestock were excluded from the plots. WH mulch used raw water hyacinth that was sourced from Murray Lagoon near Rockhampton, pressed and mulch to remove excess water and reduce size, then solarised under a tarp for four weeks (C:N ratio 17.8). Woody mulch was provided by Rockhampton Regional Council from their vegetative waste (C:N ratio 79.2). Half of the plots received 50 kg N/ha of ^{15}N-labeled urea (5%) dissolved in 2 L of MilliQ water, applied using an electric hand sprayer over bare soil as a fine mist, immediately followed by hand application of a 5 cm layer of mulch to ensure soil contact and minimize urea spillover.

Each treatment combination was replicated five times with treatments randomly assigned. Mulch and urea treatments were applied on 30 May 2024, and left undisturbed for seven weeks, after which composite soil samples were taken on 18 July 2024. The mulch layer was carefully removed at each sampling point to expose the soil surface before coring. Cores were mixed and immediately chilled for transport to the laboratory. Soil samples consisted of five randomly collected soil cores per plot (70 mm diameter corer), taken to a depth of 20 cm, mixed, and immediately chilled for transport to the laboratory. Laboratory analysis included assessments of soil chemistry, ^{15}N fate, and microbial community structure and functional traits through metabarcoding. This experimental design facilitated examination of how mulch type, nitrogen application, and land use influenced microbial community composition, functional traits, and nitrogen dynamics across varied management contexts.

2.2. *Soil physicochemistry*

Soil samples were analysed by a NATA-accredited, ASPAC-certified laboratory (Table 1). Measurements included pH (water and $CaCl_2$), electrical conductivity, major nutrients (nitrate, ammonium, phosphorus by Colwell), exchangeable cations (Ca, K, Mg, Na) with CEC and Ca:Mg ratio, and trace elements (Cu, Fe, Mn, Zn, B, S, Cl). Total carbon and nitrogen were measured by combustion to calculate C:N ratio, and soil texture and colour were recorded.

Subsamples were also sent to the JCU Advanced Analytical Centre's to assess the $\delta^{15}N$ content using a Finnegan Delta-V gas source mass spectrometer coupled to a Costech elemental analyser. Additional subsamples were sent to Metagen Australia for measurement of soil enzyme activities (phosphatase and β-glucosidase).

Soil $\delta^{15}N$ and enzyme activities were analysed using linear mixed-effects models with Mulch treatment (control, water hyacinth, wood) as a fixed effect and Urea (applied or not applied) and Vegetation type (Pasture, Lychee, Macadamia) as random intercepts. This accounts for the experimental design in which ^{15}N-labelled urea was applied to half the plots at each site to trace nitrogen fate, with untreated control plots serving as a baseline to account for background ^{15}N variation, and responses are assessed across multiple agricultural systems.

To identify site-specific treatment effects, pairwise Wilcoxon tests were also conducted within each vegetation type for plots receiving ^{15}N-labelled urea (Urea = Yes), accounting for the limited sample size ($n = 5$ per treatment per site) and non-normal distribution of stable isotope data. P-values were adjusted for multiple comparisons using the Benjamini-Hochberg method. All analyses were conducted in R 4.4.3 using the lme4 and lmerTest packages (Bates et al.; Kuznetsova et al., 2017; R Core Team, 2025).

2.3. *DNA extraction, processing & metabarcoding*

Soil samples from each plot were sent to Metagen Australia for metabarcoding of bacteria, fungi and nematodes using the following methods:

DNA was extracted from 10 g soil subsamples using a modified version of the modular universal DNA extraction protocol (Sellers et al., 2018). Soil was homogenized with garnet sand and lysis buffer using a SPEX 2010 Geno Grinder (SPEX SamplePrep, NJ) at 1700 strokes per minute for 5 min. After centrifugation, the supernatant was treated with a flocculant to remove humic acid contaminants, centrifuged again, and DNA was recovered from 10 ml of the supernatant using SPRI beads (Oberacker et al., 2019). DNA quality and concentration were assessed using the Quantifluor dsDNA system (Promega, MI) and gel electrophoresis to ensure adequate yield and purity for subsequent metabarcoding.

Eukaryotic and bacterial/archaeal communities were characterized through metabarcoding. The primer sets NF1/18S2rB (Porazinska et al.,

Table 2
Functional traits assessed for bacteria, fungi, and nematodes, with associated justifications highlighting their roles in soil ecosystem processes, nutrient cycling, plant health, and biosecurity.

	Trait	Justification
Bacteria	Ureolysis	Converts urea to ammonia, enhancing nitrogen availability.
	Nitrification	Converts ammonia to nitrate, improving plant-available nitrogen.
	Nitrate Denitrification	Reduces nitrate to N_2, limiting leaching but potentially releasing N_2O.
	Nitrogen Fixation	Converts atmospheric N_2 to ammonia for plant uptake.
	Iron Respiration	Cycles iron and associated nutrients, stabilises soils, and mediates redox processes.
	Methanotrophy	Oxidises methane to CO_2, reducing greenhouse gas emissions.
	Chitinolysis	Breaks down chitin, aiding organic matter turnover.
	Cellulolysis	Degrades cellulose, supporting decomposition and carbon cycling.
	Fermentation	Enables anaerobic breakdown of organic matter.
	Aromatic Compound Degradation	Breaks down complex aromatics, reducing soil pollutants.
	Hydrocarbon Degradation	Degrades hydrocarbons, supporting soil remediation.
	Human Pathogenic Capacity	Indicates potential for human pathogens in soil.
	Animal Parasites or Symbionts	Reflects potential animal pathogens or symbionts, affecting biosecurity.
Fungi	Soil Saprotroph	Decomposes organic material, enhancing nutrient availability and soil structure.
	Decay Substrate: Leaf/Fruit/Seed	Targets specific decaying substrates, contributing to organic matter turnover.
	Decay Type: Chitinolytic	Specializes in breaking down chitin, supporting nutrient recycling in soil.
	Arbuscular Mycorrhizal	Forms symbiotic relationships with plants, improving nutrient and water uptake.
	Ectomycorrhizal	Enhances phosphorus uptake for host plants, benefiting tree and shrub health.
	Root Endophyte	Lives within roots, providing benefits like disease resistance and growth promotion.
	Root-Associated Endophyte Interaction	Provides plant roots with enhanced resilience against pathogens and nutrient uptake.
	Leaf/Fruit/Seed Pathogenic Capacity	Indicates potential plant disease risk in soil, affecting agricultural productivity.
	Root Pathogenic Capacity	Reflects risk of root diseases that could reduce plant growth and yield.
	Wood Pathogenic Capacity	Affects woody plants, posing risks for forest health and timber productivity.
	Nematophagous	Acts as a biological control against nematodes, contributing to biosecurity and crop health.
	Filamentous Mycelium	Contributes to soil structure and moisture retention.
	Partly Aquatic	Adapts to fluctuating water levels, supporting resilience in variable moisture environments.
	Opportunistic Human Parasite	Reflects potential human health risks in soil, important for biosecurity.
	Foliar Endophyte	Interacts with plant leaves, potentially affecting plant health and human exposure.
Nematodes	Feeding Group (AP, BF, EF, FF, PF, Omn, Pred, MN)	Feeding groups reflect the trophic roles of nematodes in soil food webs. For example, bacterivores (BF) and fungivores (FF) regulate microbial populations and nutrient turnover;

(*continued on next page*)

Table 2 (*continued*)

Trait	Justification
	plant feeders (PF) affect crop health and nutrient flows; omnivores (Omn) and predators (Pred) influence higher trophic dynamics; animal parasites (AP) and marine nematodes (MN) indicate biosecurity risks or environmental filtering.
Coloniser-Persister Score (AvCP)	CP values describe the life-history strategy of nematode taxa, ranging from r-selected colonisers (CP1) to K-selected persisters (CP5). Average CP (AvCP) provides an indicator of community maturity, soil disturbance, and ecological resilience.

2009) and Pro341F/Pro805R (Takahashi et al., 2014) were used to amplify 18S and 16S rRNA genes, respectively, for eukaryotes and prokaryotes, while Nemf/18Sr2b (Sikder et al., 2020) targeted soil nematodes. DNA amplification was conducted in two stages, following the Illumina protocol for dual-indexed amplicons to enable sample multiplexing. In the first PCR, 25 cycles amplified target regions; in the second, 15 cycles incorporated dual indexes for each sample. Fluorimetry (Quantifluor dsDNA) was used to standardize the concentration of final amplicons, which were then pooled at equimolar concentrations, purified with SPRI beads, normalized to 10 nM, and sequenced on an Illumina MiSeq (2 ×300 bp) at the IMB Sequencing Facility, University of Queensland.

Raw sequences were demultiplexed with DeML (Renaud et al., 2015). Amplicon sequence variants (ASVs) were generated using DADA2 (Callahan et al., 2016) in R version 3.5.1. For 18S and 16S reads, forward and reverse reads were truncated at 270 bp and 240 bp, respectively, with stringent error thresholds (2 expected errors for forward, 3 for reverse in 16S; 3 for forward, 4 for reverse in 18S) to minimize erroneous sequences. Chimeras were identified and removed using DADA2's "removeBimeraDenovo" function with the "consensus" method. Taxonomy was assigned to genus level for 16S using the Silva database version 128 (Quast et al., 2013) and to species level for 18S using the PR2 database version 4.12 (Guillou et al., 2013).

2.4. *Ecological community analysis*

All analyses were performed in R 4.4.3 (R Core Team, 2025) using microeco (Liu et al., 2021), vegan (Dixon and Palmer, 2003; Oksanen et al., 2007), lme4 and lmerTest (Bates et al.; Kuznetsova et al., 2017), and indicspecies (Cáceres and Legendre, 2009). Amplicon sequence variant (ASV) data for bacteria, fungi, and nematodes were each processed separately in microeco, with cumulative sum scaling (CSS) applied to normalise sequencing depth and taxa summarised at the genus level.

Alpha diversity (Shannon index) was calculated for each community type and analysed with linear mixed models including mulch, urea, and their interaction as fixed factors, and site (vegetation type) as a random effect. Post-hoc comparisons among treatment combinations were performed with estimated marginal means using the emmeans package (Lenth, 2025). Marginal R^2 (variance explained by fixed effects) and conditional R^2 (variance explained by fixed and random effects) were obtained with MuMIn (Barton, 2025).

Community composition was assessed using Permutational Multivariate Analysis of Variance (PERMANOVA) on Bray-Curtis dissimilarities, with mulch, urea, and their interaction included as fixed factors, and vegetation accounted for as a blocking factor using conditioning. Ordinations were performed with distance-based redundancy analysis (db-RDA) conditioned on vegetation to visualise and test treatment effects. The Envfit function was used to correlate the relative abundance of key traits (Table 2) and environmental variables to each ordination, with fitted vectors corrected using the Benjamini-Hochberg (BH) procedure. Functional traits were assigned with microeco using the FAPROTAX (Functional Annotation of Prokaryotic Taxa) database for bacteria (Louca et al., 2016) and FungalTraits for fungi (Põlme et al., 2020). For nematodes, traits assessed included their functional feeding group and coloniser-persister scores (CP-scores) and were assigned using the Nemaplex database (Bongers and Ferris, 1999, 2010; Ferris, 1999, 2010). Environmental variables included soil nutrients (P [Colwell], K [AmAcet], Total N, C:N ratio, Cl^-, and cation exchange capacity [CEC]), soil enzyme activities (phosphatase and β-glucosidase), and stable isotope composition ($\delta^{15}N$). Following ordination, differential abundance analysis was performed using a generalized linear mixed model with a beta distribution (GLMM-beta) implemented in the glmmTMB R package (Brooks et al., 2017) to identify taxa whose relative abundance differed among mulch and urea treatments, including their interaction, with vegetation type included as a random effect. Indicator species analysis was conducted using the multipatt function in the indicspecies package (Cáceres and Legendre, 2009), with presence-absence data and 999 permutations, to identify taxa indicative of water hyacinth mulch plots relative to all other treatments. Multipatt computes the IndVal statistic, which combines specificity (exclusivity to a treatment) and fidelity (consistency within that treatment), and evaluates it using permutation tests, where treatment labels are randomly reassigned (999 permutations) to generate a null distribution from which p-values are derived. Groups identified with permutation tests at $p < 0.05$ and IndVal stat ≥ 0.7 were considered indicators. For all taxa-level differential abundance and indicator species analyses, p-values were adjusted for multiple comparisons using the Benjamini–Hochberg false discovery rate procedure.

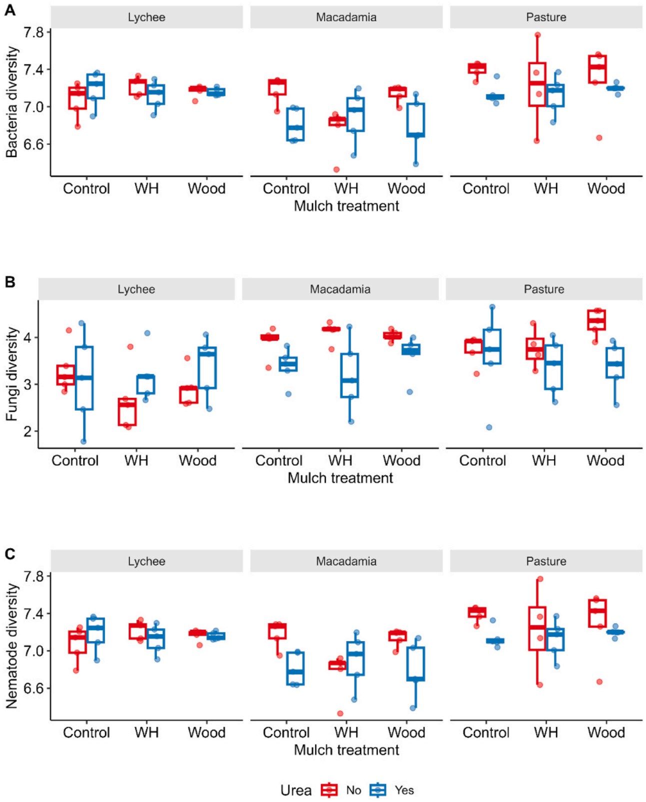


Fig. 1. Shannon diversity of (A) bacteria, (B) fungi, and (C) nematodes across mulch and urea treatments (red = no urea; light blue-green = urea applied), facetted by vegetation type.

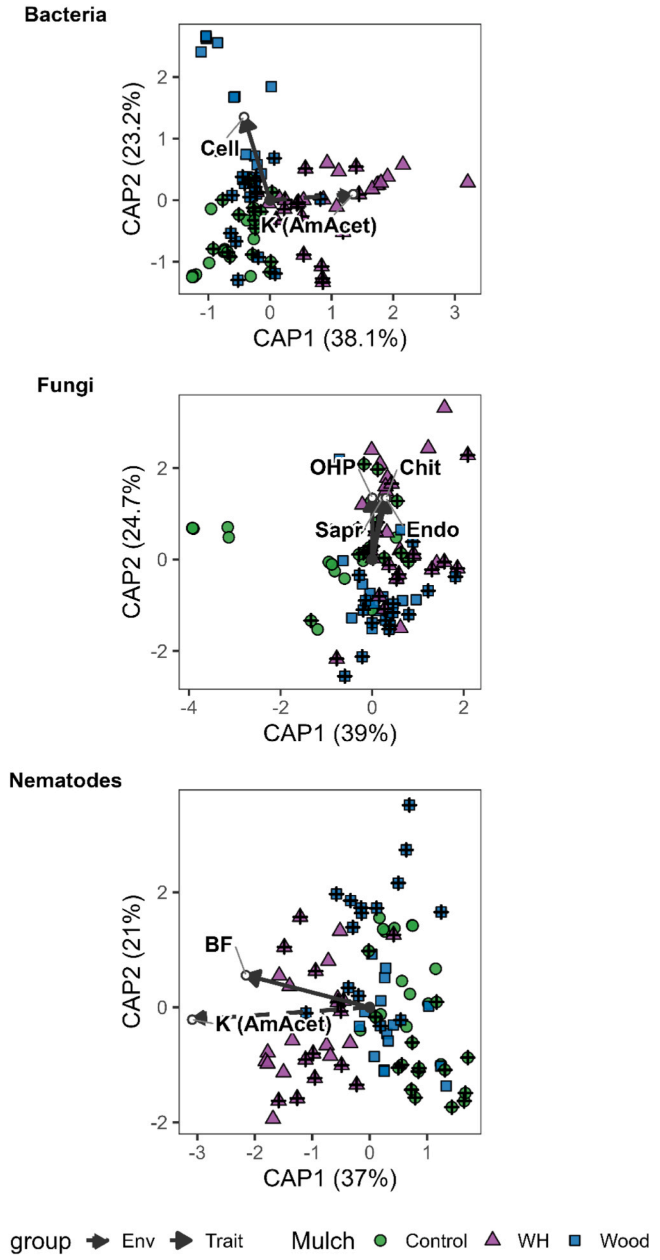


Fig. 2. Ordinations of bacterial, fungal, and nematode community composition using distance-based redundancy analysis (db-RDA) showing the effects of mulch and urea after conditioning on vegetation. Points were coloured and shaped by mulch treatment (Control = green circle, Water hyacinth = purple triangle, Wood = blue square) and urea treatment (cross-overlay = urea applied). Significant trait vectors are shown as solid arrows and soil environmental variables as dashed arrows.

3. Results

3.1. Ecological communities

3.1.1. Bacteria

Bacterial communities showed lower alpha diversity under water hyacinth mulch and urea addition, and differed in composition among mulch treatments, urea levels, and their interaction, with water hyacinth mulch associated with higher relative abundance of Gammaproteobacteria (e.g. Cellvibrionaceae, TRA3–20), Bacteroidetes, and Acidobacteria lineages.

Shannon diversity was lower under water hyacinth mulch (-0.20 ± 0.08, p = 0.020) and with urea addition (-0.17 ± 0.08, p = 0.040), while woody mulch did not differ from the control (-0.02 ± 0.08, p = 0.84). The mulch × urea interaction was not detected (p = 0.089), and Tukey-adjusted pairwise comparisons showed no significant differences among individual contrasts (p > 0.17; Fig. 1).

Table 3
Indicator taxa (ASVs) showing strong and significant association with water hyacinth mulch (indicator value ≥ 0.7, p ≤ 0.05). Bacterial, fungal, and nematode families are listed with representative genera. Where genus-level classification was unavailable, taxa are noted as 'Genus unspecified'. Max IndVal and Mean IndVal represent the maximum and mean indicator values across ASVs within each family. N ASVs indicates the number of amplicon sequence variants within each family group.

Group	Family	Genus	Max IndVal	Mean IndVal	N ASV
Bacteria	TRA3–20	Genus unspecified	0.932	0.932	1
Bacteria	BIrii41	Genus unspecified	0.917	0.917	1
Bacteria	Cellvibrionaceae	*Cellvibrio*	0.895	0.879	3
Bacteria	Microscillaceae	Genus unspecified	0.887	0.836	3
Bacteria	Blastocatellaceae	Genus unspecified	0.883	0.883	1
Bacteria	Dongiaceae	*Dongia*	0.883	0.883	1
Bacteria	Opitutaceae	*Lacunisphaera*	0.883	0.883	1
Bacteria	Hyphomonadaceae	*SWB02*	0.875	0.875	1
Bacteria	Fibrobacteraceae	Genus unspecified	0.863	0.863	1
Bacteria	Xanthomonadaceae	*Arenimonas*	0.850	0.840	2
Bacteria	Pedosphaeraceae	Genus unspecified	0.824	0.824	1
Bacteria	Unknown_Family	Genus unspecified	0.820	0.820	1
Bacteria	Solibacteraceae_ (Subgroup_3)	*PAUC26f*	0.791	0.791	1
Bacteria	Flavobacteriaceae	*Confluentibacter*	0.785	0.785	1
Bacteria	Rhizobiaceae	Genus unspecified	0.762	0.762	1
Bacteria	Sphingomonadaceae	*Sphingopyxis*	0.757	0.757	1
Fungi	Sordariomycetes	*Verticillium*	0.775	0.739	2
Fungi	Chytridiomycetes	Genus unspecified	0.767	0.767	1
Nematode	Panagrolaimidae	*Halicephalobus*	0.776	0.750	4

Bacterial community composition was influenced by mulch, urea, and their interaction (PERMANOVA, p = 0.001 for all terms), with mulch explaining a larger proportion of variation than urea (Fig. 2). A db-RDA conditioned on vegetation confirmed treatment-related separation of communities (F = 2.65, p = 0.001; CAP1 23.2%, CAP2 38.1% of constrained variance). Envfit analyses indicated significant correlations between bacterial community structure and potassium availability ($r^2 = 0.44$, $p_{adj} = 0.005$), and functional traits including cellulolysis ($r^2 = 0.30$, $p_{adj} = 0.003$) and methanotrophy ($r^2 = 0.26$, $p_{adj} = 0.003$; BH-adjusted; Fig. 2). Several additional traits and environmental variables were significantly correlated but had $r^2 < 0.4$ and are not shown in the ordination for clarity.

Indicator species analysis identified several bacterial lineages strongly associated with water hyacinth mulch (stat ≥ 0.7; Table 3). These indicators spanned multiple phyla, with the strongest associations observed for Gammaproteobacteria, including Cellvibrionaceae (stat up to 0.90), TRA3–20 (0.93), and Xanthomonadaceae (0.85), alongside representatives of Bacteroidetes (Microscillaceae, Flavobacteriaceae) and Acidobacteria (Solibacteraceae, Blastocatellaceae).

Differential abundance GLMMs showed broad shifts under water hyacinth mulch, with copiotrophic Gammaproteobacteria and Bacteroidota increasing (e.g., *Cellvibrio*, *Lysobacter*, *Flavobacterium*, *Gemmatimonas*, *Cupriavidus*) and oligotrophic Actinobacteriota declining (e.g. *Conexibacter*; Fig. 3). Urea addition was additionally associated with higher relative abundance of *Flavitalea* and *Lysobacter* and lower

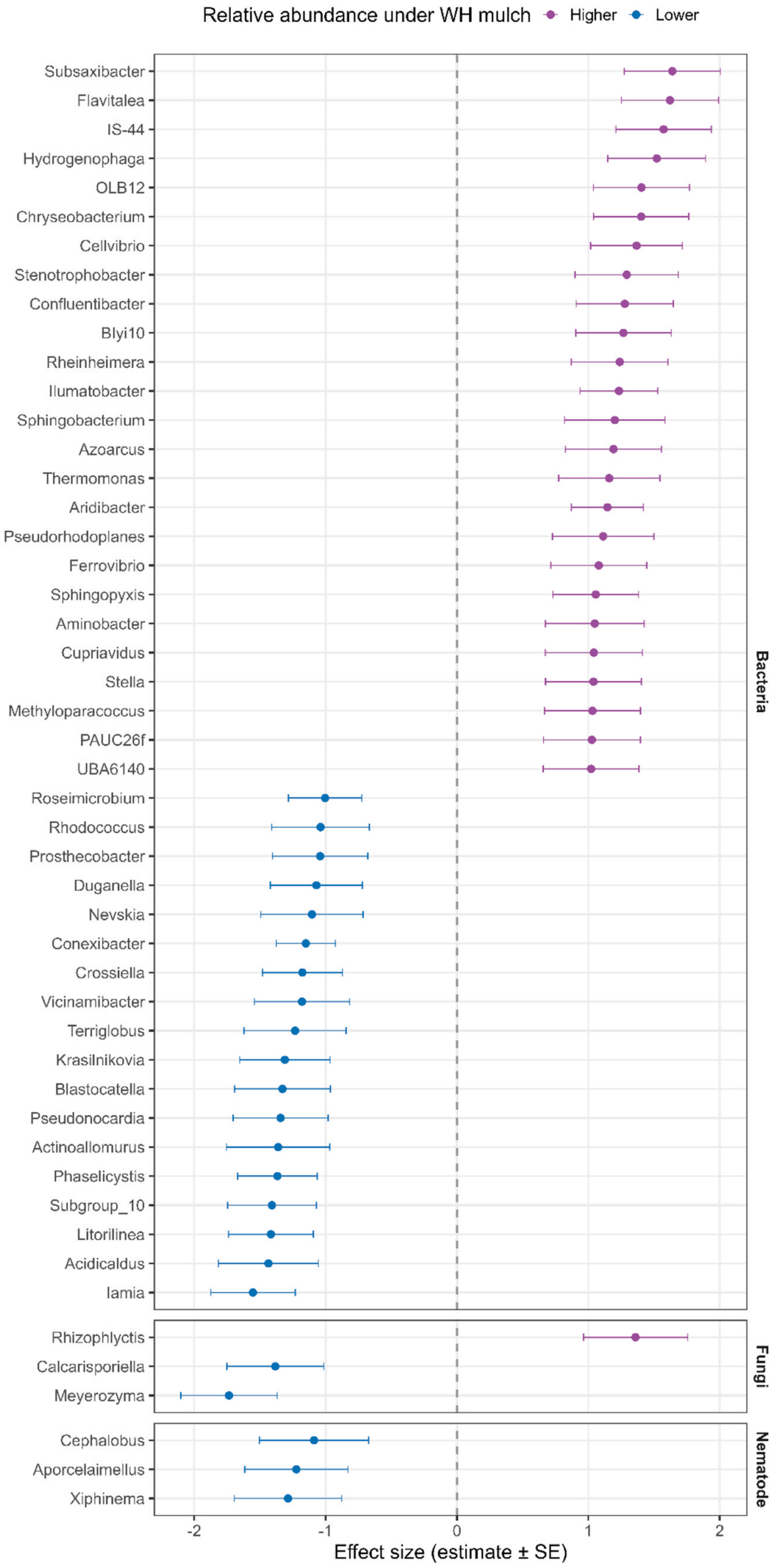


Fig. 3. Effect sizes (estimate ± SE) from generalised linear mixed models (GLMM-beta) for taxa with absolute effect size ≥ 1 under water hyacinth mulch relative to the unmulched control, for bacteria and fungi and nematodes (unadjusted $p < 0.05$). Purple indicates higher and blue indicates lower relative abundance under water hyacinth mulch. Vegetation type was included as a random effect.

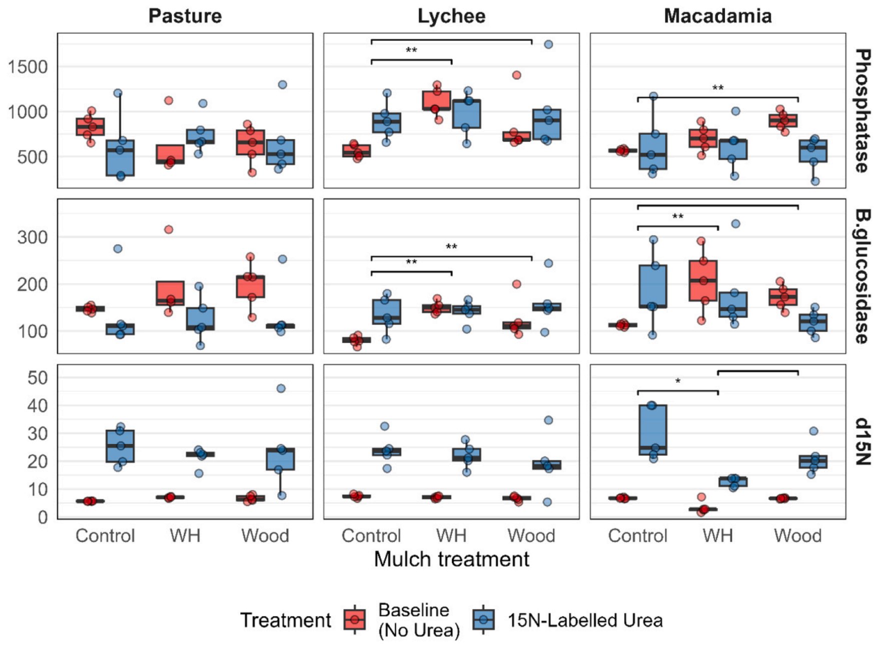


Fig. 4. Soil $\delta^{15}N$ recovery and enzyme activity after seven weeks by mulch treatment across three agricultural systems. Boxplots show $\delta^{15}N$ and soil enzyme activities (phosphatase and β-glucosidase) under three mulch treatments: Control (no mulch), WH (water hyacinth mulch), and Wood (woody mulch), comparing plots receiving ^{15}N-labelled urea (red) with unfertilised control plots (blue). Panels are faceted by agricultural system. Asterisks indicate significant pairwise differences within systems (Wilcoxon tests, $p < 0.05$, BH-adjusted).

abundance of several poorly resolved lineages (e.g., Berkelbacteria, OM190; all BH-adjusted $p < 0.05$). Additional indicator taxa and differential abundance results are reported in Supporting Information File S1.

3.1.2. *Fungi*

Fungal alpha diversity was unchanged by mulch or urea treatments, while community composition differed with mulch type and urea addition, with water hyacinth mulch associated with saprotrophic, chitinolytic, root-associated endophytic, and partly aquatic fungal taxa.

Fungal Shannon diversity did not differ among mulch treatments or with urea addition (all $p > 0.19$). Interaction effects were negligible ($p > 0.92$). Fixed effects explained little variation in diversity (marginal $R^2 = 0.06$), with most variance attributable to site differences (conditional $R^2 = 0.29$). Tukey-adjusted pairwise comparisons among treatment combinations showed no difference among contrasts ($p > 0.18$; Fig. 1).

Fungal community composition varied with mulch and urea (PERMANOVA, mulch $p = 0.001$; urea $p = 0.005$), while the mulch × urea interaction was marginal ($p = 0.053$). A db-RDA conditioned on vegetation confirmed treatment-related separation of communities ($F = 2.06$, $p = 0.001$; CAP1 39.0%, CAP2 24.7% of constrained variance). Envfit analyses indicated significant correlations between fungal community structure and chitinolytic ($r^2 = 0.41$, $p_{adj} = 0.003$), root-associated endophytic ($r^2 = 0.41$, $p_{adj} = 0.003$), partly aquatic ($r^2 = 0.41$, $p_{adj} = 0.003$), saprotrophic ($r^2 = 0.39$, $p_{adj} = 0.003$), and opportunistic fungal traits ($r^2 = 0.39$, $p_{adj} = 0.003$; BH-adjusted; Fig. 2). Additional traits including filamentous growth form, leaf/fruit/seed decay, and plant pathogenic capacity, and environmental variables potassium and chloride, were also significant but had $r^2 < 0.4$ and are not shown in the ordination.

Indicator species analysis identified fungal lineages within Sordariomycetes (Ascomycota) and Chytridiomycetes (Chytridiomycota) as associated with water hyacinth mulch plots (stat = 0.71–0.77; Table 3). One additional indicator could not be resolved beyond higher taxonomic ranks.

Differential abundance GLMMs identified *Rhizophlyctis* as higher under water hyacinth mulch, while *Apiotrichum*, *Meyerozyma*, *Penicillium*, *Minutisphaera*, and *Calcarisporiella* were lower (BH-adjusted $q < 0.05$; Fig. 3; Supporting Information File S1).

3.1.3. *Nematodes*

Nematode alpha diversity was lower with urea addition, and community composition differed among mulch treatments and mulch × urea combinations, with water hyacinth mulch associated with higher relative abundance of bacterial-feeding nematodes (Panagrolaimidae).

Nematode Shannon diversity was lower with urea addition (-0.35 ± 0.15, $p = 0.023$), while values under water hyacinth and woody mulch were similar to the control (both $p > 0.36$). No mulch × urea interaction was detected ($p > 0.24$). Fixed effects explained limited variation in diversity (marginal and conditional $R^2 = 0.15$), and Tukey-adjusted contrasts indicated generally small differences among treatment combinations, with higher diversity in unmulched control plots compared to wood mulch with urea ($p = 0.009$; Fig. 1).

Nematode community composition varied with mulch ($p = 0.001$) and the mulch × urea interaction ($p = 0.003$), while the main effect of urea was marginal ($p = 0.063$). A db-RDA conditioned on vegetation confirmed treatment-related separation of communities ($F = 2.13$, $p = 0.001$; CAP1 37.0%, CAP2 21.0% of constrained variance). Envfit analyses indicated significant correlations between nematode community structure and bacterial-feeding guild abundance ($r^2 = 0.34$, $p_{adj} = 0.005$), potassium availability ($r^2 = 0.34$, $p_{adj} = 0.005$), chloride ($r^2 = 0.24$, $p_{adj} = 0.005$), plant-feeding guild abundance ($r^2 = 0.18$, $p_{adj} = 0.005$), and fungal-feeding guild abundance ($r^2 = 0.11$, $p_{adj} = 0.018$; BH-adjusted; Fig. 2).

No nematode taxa were differentially abundant after BH correction; at unadjusted $p < 0.05$, *Oscheius* and *Filenchus* were higher and *Alaimus* lower under water hyacinth mulch (Fig. 3). Indicator analysis identified Panagrolaimidae as consistently associated with water hyacinth mulch plots (mean IndVal = 0.75; Table 3). Additional differentially abundant taxa are reported in Supporting Information File S1.

3.2. Nitrogen fate and enzyme concentrations

Soil δ^{1} ^{5}N recovery was lower under water hyacinth mulch than under unmulched controls, with this difference restricted to fertilised macadamia soils and not detected in lychee or pasture systems (Fig. 4). Enzyme activities (phosphatase and β-glucosidase) showed stronger responses in unfertilised plots, with both enzymes elevated under mulch treatments in lychee and macadamia soils, but these responses were not sustained when urea was applied.

Overall, soil δ^{15}N was lower under water hyacinth mulch compared to unmulched controls (estimate = −4.26 ± 1.49‰, t = -2.865, p = 0.005), while woody mulch showed no significant effect (estimate = −2.46 ± 1.49‰, t = -1.658, p = 0.101). A linear mixed-effects model with Mulch as a fixed effect and Urea and Vegetation type as random intercepts indicated that variation in δ^{15}N recovery was strongly structured by fertilisation and site. Phosphatase activity increased under water hyacinth mulch but did not reach significance in the global model (estimate = 104.99 ± 69.59 nmol g^{-1} h^{-1}, t = 1.509, p = 0.135), while β-glucosidase was significantly elevated under water hyacinth mulch (estimate = 33.03 ± 14.02 nmol g^{-1} h^{-1}, t = 2.355, p = 0.021). However, these enzyme responses were site- and fertilisation-specific: significant differences ($p \leq 0.012$) occurred only in unfertilised plots in Lychee and Macadamia soils, with no sustained responses in fertilised plots (all $p > 0.690$).

Site-specific pairwise comparisons showed that differences in δ^{15}N among mulch treatments occurred only in Macadamia soil (Fig. 4). In plots receiving ^{15}N-labelled urea, δ^{15}N was lower under water hyacinth mulch (12.6 ± 1.67‰) than under Control (29.6 ± 9.58‰; contrast estimate = 4.26 ± 1.49‰, t = 2.865, p = 0.014) and Woody mulch (21.1 ± 5.92‰; contrast estimate = 4.26 ± 1.49‰, t = 2.865, p = 0.018; Tukey-adjusted pairwise comparisons). No significant differences in δ^{15}N among mulch treatments were detected in Lychee or Pasture soils (all $p > 0.42$). Baseline δ^{15}N in unfertilised control plots was similar across sites and mulch types (24.0 ± 7.0‰).

4. Discussion

4.1. Microbial diversity

Overall, plots with water hyacinth mulch had lower bacterial diversity than plots without mulch or with woody mulch, and this pattern was unaltered by the application of urea. Reduced bacterial diversity suggests that a smaller set of dominant taxa were able to outcompete others under the nutrient-rich conditions created by WH inputs. While such dominance can drive rapid turnover and short-term gains in carbon and nitrogen mineralisation, it may also destabilise the community by reducing functional redundancy and increasing the likelihood of chaotic oscillations/boom-bust dynamics (Moore et al., 2007; Bardgett and Caruso, 2020; Philippot et al., 2021). In less diverse systems, soil processes may become more dependent on the performance of a few opportunistic taxa, increasing the likelihood of boom-bust cycles as these dominant groups rise quickly when resources are abundant but collapse when conditions shift (Moore et al., 2007; Bardgett and Caruso, 2020; Philippot et al., 2021). While some strong interactions are necessary for efficient food web cycling, a balance is needed as more stable food webs tend to have many weak interactions that can buffer impacts and dampen boom-bust cascades (Ulanowicz et al., 2009; Rooney and McCann, 2012; Mougi and Kondoh, 2016; Canning and Death, 2017; Gutgesell et al., 2024). Fungal and nematode diversity was unaffected by mulch, suggesting either stronger buffering or slower turnover in these groups. By contrast, urea reduced bacterial and nematode diversity across all treatments, reflecting a homogenising effect of high nitrogen inputs. This pattern indicates that while mulch effects may be subtle or delayed, nutrient enrichment more strongly erodes response diversity, increasing productivity in the short term but potentially reducing resilience to disturbance.

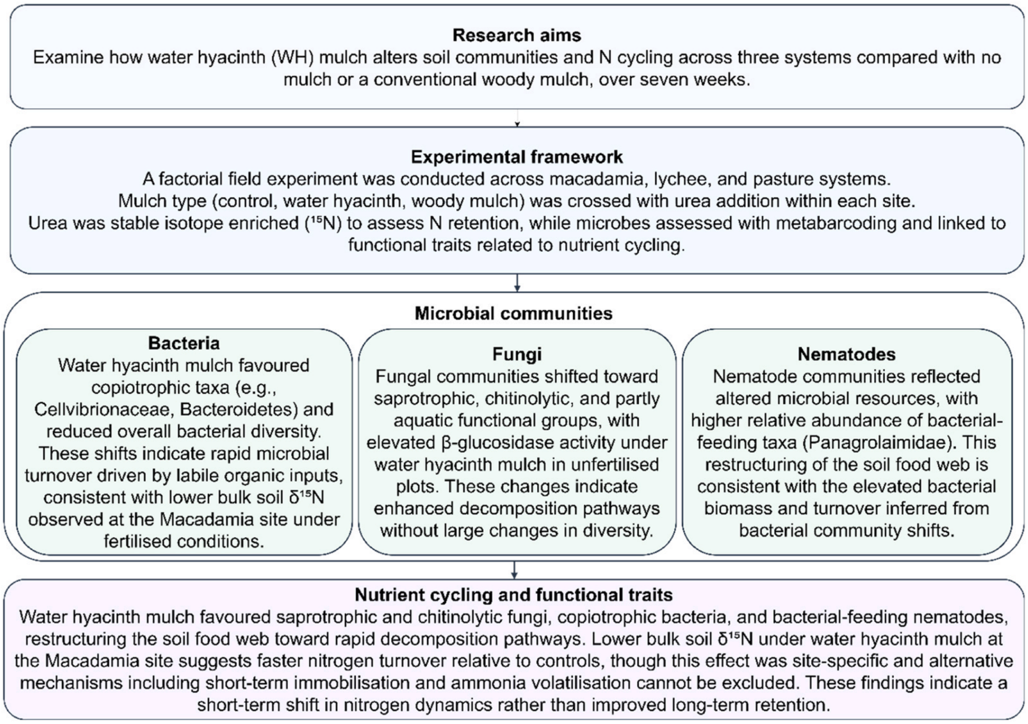
4.2. Microbial community composition

While differences in Shannon diversity were patchy across treatments, the composition of communities was consistently affected by both mulch and urea and their interaction - with the interactions for fungi and the urea effect for nematodes being marginal. The higher potassium concentrations observed under water hyacinth mulch likely reflect the release of soluble K accumulated in plant biomass while growing in waterways. This increased nutrient input coincided with shifts in fungal traits, including greater relative abundance of taxa associated with chitin degradation, partly aquatic environments, root-associated endophytism, and taxa with human pathogenic capacity. These shifts likely reflect both substrate-driven changes in resource availability and source-driven introductions of taxa associated with water hyacinth tissues and its aquatic origin.

Increased microbial turnover under WH mulch could have generated both structural residues (e.g., chitin from fungal cell walls or invertebrate fragments) that favour chitinolytic fungi and elevated bacterial biomass that supports bacterial-feeding nematodes (Olander and Vitousek, 2000; Puissant et al., 2021; Xing et al., 2022). WH roots are also known to host diverse fungal assemblages, including root-associated endophytes, and its aquatic origin may have introduced additional aquatic taxa, with the moist mulch-soil interface providing conditions for their persistence (Dagno et al., 2012; Yirefu et al., 2017). Although bacterial trait profiles did not differ among treatments, the combination of reduced bacterial diversity under WH and unchanged trait proportions is consistent with an increase in absolute bacterial abundance that is not detectable with relative amplicon data. Such a bottom-up increase would plausibly explain the higher abundance of bacterial-feeding nematodes observed under WH (Puissant et al., 2021; Xing et al., 2022), a mechanism that would require validation through absolute bacterial quantification alongside nematode counts.

The higher relative abundance of fungi annotated as having human pathogenic capacity likely reflects fungal assemblages naturally associated with water hyacinth tissues, which are known to host diverse opportunistic taxa including *Alternaria*, *Fusarium*, and *Aspergillus* spp. (Yirefu et al., 2017; Tasew and Wendimagegnehu, 2022), as well as microbes accumulated from upstream human and livestock activities in waterways. Differential abundance analysis identified *Exophiala* and *Verticillium* as positively associated with water hyacinth mulch plots, both of which include lineages with opportunistic pathogenic capacity (Klosterman et al., 2009; Kirchhoff et al., 2019). However, FungalTraits (Põlme et al., 2020) guild assignments reflect ecological classification based on known pathogenic potential rather than active health risk, and these taxa function primarily as opportunistic decomposers in nutrient-rich, disturbed soil environments.

Enzyme activities provide complementary evidence for differential microbial processing across sites. In unfertilised plots, phosphatase and β-glucosidase activities were significantly elevated under both water hyacinth and woody mulch in Lychee and Macadamia soils, suggesting stimulation of microbial decomposition and nutrient mobilisation in response to labile organic matter inputs. However, these enzyme responses were suppressed when urea was applied, indicating that exogenous nitrogen availability overrides the enzymatic response to mulch inputs. This pattern suggests that enzyme activity is sensitive to nutrient stoichiometry and that high nitrogen inputs may reduce microbial investment in acquiring nutrients from organic substrates. From a practical perspective, the suppression of enzyme activity under fertilisation indicates that nutrient availability from water hyacinth mulch decomposition may be constrained when synthetic nitrogen is applied, potentially reducing the benefit of the amendment if applied concurrently with urea. Conversely, applying water hyacinth mulch in unfertilised contexts could enhance phosphatase and glucosidase activity, accelerating organic matter decomposition and nutrient release, a potential advantage in systems with limited external inputs. The elevated β-glucosidase activity under water hyacinth mulch in unfertilised plots is



Research aims

Examine how water hyacinth (WH) mulch alters soil communities and N cycling across three systems compared with no mulch or a conventional woody mulch, over seven weeks.

Experimental framework

A factorial field experiment was conducted across macadamia, lychee, and pasture systems. Mulch type (control, water hyacinth, woody mulch) was crossed with urea addition within each site. Urea was stable isotope enriched (^{15}N) to assess N retention, while microbes assessed with metabarcoding and linked to functional traits related to nutrient cycling.

Microbial communities

Bacteria

Water hyacinth mulch favoured copiotrophic taxa (e.g., Cellvibrionaceae, Bacteroidetes) and reduced overall bacterial diversity. These shifts indicate rapid microbial turnover driven by labile organic inputs, consistent with lower bulk soil $\delta^{15}N$ observed at the Macadamia site under fertilised conditions.

Fungi

Fungal communities shifted toward saprotrophic, chitinolytic, and partly aquatic functional groups, with elevated β-glucosidase activity under water hyacinth mulch in unfertilised plots. These changes indicate enhanced decomposition pathways without large changes in diversity.

Nematodes

Nematode communities reflected altered microbial resources, with higher relative abundance of bacterial-feeding taxa (Panagrolaimidae). This restructuring of the soil food web is consistent with the elevated bacterial biomass and turnover inferred from bacterial community shifts.

Nutrient cycling and functional traits

Water hyacinth mulch favoured saprotrophic and chitinolytic fungi, copiotrophic bacteria, and bacterial-feeding nematodes, restructuring the soil food web toward rapid decomposition pathways. Lower bulk soil $\delta^{15}N$ under water hyacinth mulch at the Macadamia site suggests faster nitrogen turnover relative to controls, though this effect was site-specific and alternative mechanisms including short-term immobilisation and ammonia volatilisation cannot be excluded. These findings indicate a short-term shift in nitrogen dynamics rather than improved long-term retention.

Fig. 5. Conceptual synthesis integrating experimental design, microbial and faunal trait responses, and stable isotope evidence to summarise the effects of water hyacinth mulch on soil nitrogen cycling.

consistent with accelerated carbon mineralisation, providing a process-level link to the faster nitrogen turnover inferred from the isotope data at the Macadamia site. The site-specificity of enzyme responses present in Lychee and Macadamia but absent in Pasture mirrors the microbial community patterns and supports the interpretation that soil properties constrain the magnitude of decomposition responses to organic amendments.

4.3. Nitrogen fate and turnover

Stable isotope evidence indicated that water hyacinth mulch altered nitrogen fate in a context-dependent manner, consistent with the community-level shifts in bacteria, fungi, and nematodes described above. Bulk soil $\delta^{15}N$ was lower under water hyacinth mulch relative to unmulched controls, with this effect confined to fertilised macadamia soils. No $\delta^{15}N$ differences were detected in lychee or pasture systems, and woody mulch had no effect across sites. The reduced $\delta^{15}N$ recovery observed under water hyacinth mulch in macadamia soils is consistent with faster nitrogen turnover rather than increased soil retention. However, alternative mechanisms could also account for lower bulk soil $\delta^{15}N$. Short-term microbial immobilisation of fertiliser-derived nitrogen into biomass with a lower $\delta^{15}N$ signature could transiently reduce bulk soil values without reflecting genuine acceleration of turnover rates. Increased ammonia volatilisation, which preferentially removes ^{14}N and enriches residual soil nitrogen, would be expected to increase rather than decrease $\delta^{15}N$, making this mechanism less consistent with the observed pattern. Leaching of ^{15}N-enriched nitrate below the sampling depth (20 cm) remains possible and cannot be excluded without deeper soil sampling or resin bags. Disentangling these pathways would require direct measurement of gross mineralisation and nitrification rates, or resin-based capture of leached nitrogen, in future experiments.

Water hyacinth mulch supplies readily decomposable carbon and nutrients that stimulate microbial activity and mineralisation, consistent with the enrichment of saprotrophic fungi, copiotrophic bacterial taxa, and bacterial-feeding nematodes observed here, all of which are associated with rapid nutrient processing rather than long-term stabilisation. Because bulk $\delta^{15}N$ integrates nitrogen transformations over time it is relatively insensitive to short-term fluxes, yet the observed depletion under water hyacinth mulch aligns with this trait-based evidence of accelerated turnover. Rapid decomposition of water hyacinth mulch supplies labile carbon and nutrients and moderates soil microclimate, conditions that favour microbial activity and promote faster nitrogen turnover through microbial and plant pathways (Balasubramanian et al., 2013; Ranu et al., 2022).

4.4. Management implications and limitations

From a management perspective, blending water hyacinth with more recalcitrant organic amendments, such as woody mulches or compost, may help balance rapid nutrient release with longer-term carbon persistence. Aligning mulch application with peak crop nitrogen demand may further maximise uptake efficiency and reduce potential losses (Canning, 2025). Longer-term field experiments are required to quantify optimal blending ratios, crop-specific responses, and sustained nutrient use efficiency under combined labile and recalcitrant mulch inputs (Begum et al., 2021; Ranu et al., 2022).

Several limitations should be noted when interpreting these findings. This experiment was conducted over seven weeks, capturing early microbial and nutrient responses rather than long-term soil health outcomes such as organic carbon sequestration or sustained nitrogen retention. The observed shifts in microbial traits and $\delta^{15}N$ thus reflect short-term changes in nitrogen turnover, not persistent changes in soil carbon stocks. Nonetheless, this timeframe is broadly aligned with common fertiliser management practices, as split nitrogen applications in perennial and horticultural systems are typically applied at intervals of approximately four to eight weeks, making the results directly relevant to management decision windows. Future work should also incorporate direct measures of gross mineralisation and nitrification rates to disentangle the nitrogen turnover mechanisms inferred here from isotope and trait-based evidence. Longer-term experiments are required to determine whether repeated or blended applications of water hyacinth mulch lead to stabilisation of carbon and nitrogen pools or whether rapid turnover dominates over time.

5. Conclusion

Water hyacinth mulch consistently altered soil microbial communities across sites and was associated with shifts in nitrogen cycling indicators at one site, with effects varying markedly among agricultural systems (Fig. 5). In Macadamia soils, water hyacinth mulch was associated with lower bulk soil $\delta^{15}N$ recovery under fertilised conditions, suggesting faster nitrogen turnover, coupled with shifts toward fast-growing bacteria and saprotrophic fungi. Bacterial diversity decreased under WH, while nematode diversity declined with urea addition regardless of mulch type; however, WH enriched bacterial-feeding nematodes. These microbial shifts suggest accelerated nitrogen turnover from organic matter decomposition, which may increase nutrient loss risk if applications are not timed to match crop nitrogen demand. In contrast, lychee and pasture soils showed no significant $\delta^{15}N$ response to water hyacinth mulch, suggesting that the isotopic signal of altered nitrogen fate was not detectable across all systems, possibly reflecting differences in soil properties, baseline microbial communities, or decomposition rates among sites. The practical implication is that WH amendment can accelerate short-term nitrogen turnover in specific soil types (Macadamia), but sustained benefits require matching application rates and timing to crop nitrogen demand. Longer field trials are needed to determine whether these shifts translate to crop productivity and whether repeated WH applications maintain or destabilize microbial function.

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Declaration of Competing Interest

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2026.110448.

Data availability

Raw data available from Figshare at https://doi.org/10.6084/m9.figshare.30918899

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