Received: 9 July 2025 | Accepted: 21 April 2026

DOI: 10.1002/2688-8319.70266

RESEARCH ARTICLE

Ecological Solutions and Evidence

Floodplain reforestation reduces nitrate loss through soil microbial pathways

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Funding information
Greening Australia, Grant/Award Number: 11360

Handling Editor: Jia Pu

Abstract

1. Reducing nutrient losses from agricultural catchments is critical for improving water quality issues in rivers, estuaries and oceans. Floodplain reforestation has been proposed as a potential nature-based solution to reducing nutrient loss. However, the underlying microbial and nutrient mechanisms of floodplains remain poorly understood.
2. We conducted a field experiment in North Queensland comparing nitrate leaching and soil microbial assemblages (bacteria, fungi, nematodes) between intensively farmed sugarcane and adjacent mature *Melaleuca* forest restored on floodplain land. Five nitrate application rates (0–100 kg N/ha) were applied to replicate 4 m × 4 m plots, with nitrate leaching assessed using ion-exchange resins and microbial communities characterised by amplicon-based metabarcoding.
3. Nitrate leaching increased linearly with fertiliser load in sugarcane plots but remained low and unresponsive to load in the *Melaleuca* forest. Differences were attributed to higher soil organic carbon in *Melaleuca* plots, supporting decomposer-dominated microbial communities that immobilise nitrogen during organic matter breakdown, in contrast to sugarcane soils dominated by ammonia-oxidising bacteria that rapidly convert ammonium to leachable nitrate.
4. Microbial community composition differed significantly by vegetation type across all three taxonomic groups. *Melaleuca* plots were enriched in bacterial decomposer traits including chitinolysis and cellulolysis, while sugarcane plots were dominated by nitrification-associated taxa, with these functional differences correlated with measured nitrate leaching and organic matter decomposition rates. Fungal communities in sugarcane plots were dominated by disturbance-tolerant Ascomycota, while *Melaleuca* plots supported more stable Basidiomycota-rich assemblages. Nematode diversity increased with nitrate loading but was lower in *Melaleuca* soils.
5. Soil microbial communities showed strong concordance in compositional shifts across bacteria, fungi and nematodes, suggesting coordinated food web responses to vegetation type and nitrogen load. Functional trait analysis revealed that microbial traits, rather than diversity alone, may better explain nitrate retention and loss dynamics.
6. *Practical implication*: Reforesting floodplains with native vegetation such as *Melaleuca* can significantly reduce nitrate leaching by promoting microbial

processes that retain nitrogen. These findings support the use of floodplain restoration as a nature-based solution for improving water quality outcomes. Microbial traits potentially offer practical indicators for monitoring the effectiveness of restoration and indication of ecosystem services.

KEYWORDS
floodplain restoration, Great Barrier Reef water quality, ion exchange resin, metabarcoding, nitrate leaching, nitrogen cycling, nitrogen enrichment, soil microbes

1 | INTRODUCTION

The eutrophication of freshwater, estuarine and marine ecosystems from excessive use of fertilisers on land has become one of the planet's most ubiquitous adverse human impacts (Jwaideh et al., 2022; Maure et al., 2021; McDowell et al., 2020). The type of land use and particular management practices have a pivotal role in shaping the microbial assemblages of that land and their capacity to control nitrogen cycling (Bissett et al., 2011; Cookson et al., 2007; Zhao et al., 2024). Excess nitrogen from fertilisers can leach or volatilise, contributing to water pollution and greenhouse gas emissions (Jones et al., 2014; Jwaideh et al., 2022; Menegat et al., 2022). However, the extent of these losses depends not only on soil properties and hydrology but also on the composition and functions of soil microbes (Huddell et al., 2023; Krüger et al., 2021; Liu et al., 2025).

Land use change involving the conversion of one vegetation type to another can influence microbial community structure and function, altering nitrogen retention and loss pathways (Wan et al., 2021; Xue et al., 2022; Yang et al., 2023). Aside from the influence of land slope and soil type, vegetation type is highly influential on nitrogen retention and removal (Hill, 2019; Lv & Wu, 2021; Walton et al., 2020). Vegetation type affects soil microbial assemblages through differences in root exudates, root structure, organic matter inputs and associated shifts in soil chemistry and moisture (Jin et al., 2017; Saleem et al., 2018; Zhang et al., 2017). These factors, in turn, modulate microbial-driven nitrogen cycling processes such as nitrification, denitrification and nitrogen fixation (Das et al., 2022; Li, Tian, et al., 2019; Zhao et al., 2021). Evidence from the riparian buffer literature suggests that forested riparian buffers have greater denitrification and plant nitrogen removal rates than grass. In early forest growth stages, nutrient removal from plant growth is high, while in mature forests, the high levels of soil carbon, leaf litter, and root exudates promote greater denitrification (Lyu et al., 2021; Zhang et al., 2010). Furthermore, plant residues differ between vegetation types, which then affects the soil microbial assemblages and their ability to support denitrification (Audet et al., 2021; Rich et al., 2003; Truu et al., 2020). For example, Rich et al. (2003) compared the denitrifying communities from adjacent meadow and forest soils in Oregon, USA. They observed distinct denitrifier communities according to vegetation type and site, with a significant shift in the proportional abundances of dominant denitrifying genotypes from meadow to forest soils, and a corresponding order of magnitude higher denitrifying enzyme activity (used as a proxy for denitrification) at the meadow sites than the forest sites. Understanding how land use and nitrogen inputs interact with soil microbes is therefore critical for optimising management strategies that enhance soil fertility and ultimately protect water quality.

When land is converted to cropping, soils are frequently tilled, kept in monocultures and enriched with inorganic fertilisers, which can also disturb and alter the diversity and composition of soil microbial communities (Li et al., 2020; Puissant et al., 2021; Vukicevich et al., 2016). High nutrient availability can favour copiotrophic, fast-growing bacteria specialising in nitrogen transformation, potentially outcompeting slower growing or more specialised microbes and reducing soil microbial diversity (Liu et al., 2020; Shao et al., 2025; Wang et al., 2021). Forested ecosystems have comparatively limited nutrient availability, less frequent disturbance, greater structural complexity and a higher abundance of organic inputs from leaf litter and woody debris. These conditions support greater fungal biomass, more diverse nematode and bacterial communities supported by heterogeneous resources (Martens et al., 2004; Peng et al., 2021; Shi et al., 2019). As a result, forest soil biota can exhibit greater functional redundancy, resilience to environmental fluctuation and nitrogen retention capacity (Delgado-Baquerizo et al., 2020; Li, He, et al., 2019; Rodriguez-Ramos et al., 2021). For example, Li, He, et al. (2019) found that converting subtropical forest to agriculture reduced fungal and bacterial nitrate immobilisation by 81% and 61%, respectively. The bacterial decline was potentially driven by lower soil organic carbon (SOC) and carbon-to-nitrogen (C/N) ratios, while the fungal decline may also reflect increased pH and available phosphorus. Ultimately, long-term reductions in disturbance frequency, diversification of plant inputs and rebuilding of soil organic matter are key strategies to foster microbial communities that improve nitrogen retention and soil health.

In regions where the degradation of water quality from agricultural practices needs to be mitigated, such as in Australia's Great Barrier Reef (GBR) catchment, understanding how different vegetation types influence microbial nitrogen cycling is particularly important. Excess nitrogen from intensive agriculture, including sugarcane cultivation, is a major contributor to water quality degradation in the GBR, promoting algal blooms, reducing water clarity and promoting the growth of pests like the Crown of Thorns starfish

(Lewis et al., 2024; McCloskey et al., 2021). As a result, significant efforts are being made to reduce nitrogen loss, including policy interventions and incentive-based programmes (Coggan et al., 2021; Hamman et al., 2022; van Grieken et al., 2019). For example, Queensland's Reef Credit Scheme provides financial incentives for land management changes that demonstrably improve water quality, including practices that reduce dissolved inorganic nitrogen loss (Eco-Markets, 2020; GreenCollar, 2017). Given that much of the nitrogen transported to the GBR occurs during flood events, strategies that enhance nitrogen retention in flood-prone areas are particularly relevant (Brodie et al., 2012; Davis et al., 2017).

Floodplains act as temporary nitrogen sinks during flood events, where vegetation type plays a critical role in determining whether nitrogen is retained through plant uptake and microbial denitrification or lost through leaching to groundwater (Gordon et al., 2020; Kretz et al., 2021; Noe & Hupp, 2009). While considerable attention has been made to the role of riparian zones in water quality improvement, the effectiveness of broader floodplain reforestation in reducing nitrogen loss remains underexplored (Gordon et al., 2020; Lyu et al., 2021; Zhang et al., 2010). Floodplain reforestation may be a strategy to reduce nitrogen transport to downstream ecosystems (Kaden et al., 2023). While similar to riparian zones, floodplain terraces often become waterlogged and ponded for short periods after a flood has receded, with floodwaters either slowly leaching, draining or evaporating, whereas riparian zones on sloped embankments do not remain ponded after floodwater recession. Reforested floodplains can remove nitrogen delivered from floods through denitrification and vegetation sequestration (Gordon et al., 2020). Denitrification occurs when denitrifying bacteria decompose leaf litter and associated organic matter in hypoxic environments where metabolism relies on nitrate reduction instead of oxygen, such as when nitrate-laden water leaches through the soil column (Li et al., 2022; Pan et al., 2022). Yet, the extent to which forests support microbial assemblages that enhance nitrogen removal, such as nitrogen delivered from floodwater, relative to existing agricultural land uses, remains poorly understood.

In Australia's GBR catchment, *Melaleuca* forests, which historically covered extensive floodplain areas in the region (that are now dominated by sugarcane), have the ability to enhance nitrogen retention through plant uptake and microbial denitrification (Adame et al., 2019, 2020). Reforesting marginal or retired agricultural land to *Melaleuca*-dominated systems has been proposed as a strategy to reduce nitrogen loss and improve hydrological and ecological functions (Canning, 2025; Waltham et al., 2020, 2021). However, the extent to which reforested *Melaleuca* forests influence microbial assemblages and nitrogen cycling, particularly in comparison to sugarcane, remains unclear. By comparing microbial community composition, nitrogen metabolism traits and nitrate leaching rates between these two land uses, this study aims to assess whether transitioning from sugarcane to *Melaleuca* enhances nitrogen removal from floodwaters. Specifically, the following questions were examined:

1. Do nitrate leaching rates differ with application rates between sugarcane and reforested *Melaleuca* systems?
2. Do soil biological communities (bacteria, fungi and nematodes) differ between sugarcane and reforested *Melaleuca* systems following nitrate application?
3. Are potential differences in soil communities most strongly linked with metabolic traits, soil chemistry or nitrate leaching rates?

2 | MATERIALS AND METHODS

2.1 | Study site

The experiment occurred at a sugarcane farm adjacent to Palm Creek in Forrest Beach, Queensland. Palm Creek is a lowland distributary of the Herbert River, which is a 288-km long river that drains a catchment area of 9842 km^2. Headwaters begin in the National Parks across the Great Dividing Range within the Atherton Tablelands, travel through primarily mixed cropping and dairy farming and then drain intensive sugarcane cropping in the lowland coastal areas near Ingham. The site (EPSG:4326; Lat: −18.728, Long: 146.264) floods during the wet season with nitrate-laden water draining from the upstream sugarcane fields (Mitchell et al., 1997; Vilas et al., 2020; Yao et al., 2021). Within the site, the experiment covered 1 ha of sugarcane and an adjacent 1 ha of mature *Melaleuca* forest that had been restored in the early 1990s. The dominant geology at the site is Quaternary coastal and estuarine sediments, with soils largely composing clay on river alluvial plains (Grundy et al., 2015; McKenzie et al., 2012). As a result, the site is typical of the coastal sugarcane farms within Queensland's wet tropics where *Melaleuca* forests have the potential to be restored (Waltham et al., 2021). Permission to use the study site for the experiment was obtained from the landholder (John Cardillo) via Greening Australia prior to commencement.

2.2 | Experiment

Nitrate leaching from topsoil was examined over 6 weeks after nitrate application, at five load rates, across randomised soil plots (4 m × 4 m) within the sugarcane and mature *Melaleuca* forest. The experiment was conducted for 6 weeks between 11 November 2022 and 23 December 2022 to capture the onset of monsoonal rains when most nutrients are mobilised but ended shortly before any flooding. Nitrogen was applied as potassium nitrate (KNO_3) dissolved in 10 L of water, evenly sprayed over the trial plots using an electronic spray gun. Application rates were 0 kg N/ha (control), 25 kg N/ha, 50 kg N/ha, 75 kg N/ha and 100 kg N/ha, with plots replicated at three random locations across each of the sugarcane and *Melaleuca* patches, yielding a total of 30 plots. Soil chemistry and biota were assessed in each plot immediately prior to nitrate application and again 6 weeks after the experiment end using an ion-exchange method detailed below.

2.3 | Soil chemistry and decomposition

To characterise the soil within each plot, a standard agricultural soil test measuring nutrients and other key properties was conducted at the beginning and end of the experiment. Within each plot, five randomly located soil cores were collected to a depth of 20 cm, pooled, thoroughly mixed and analysed for a common suite of agronomic analytes at the Environmental Analysis Laboratory at Southern Cross University (File S1).

As the addition of nitrogen can promote the decomposition of organic detritus, potentially mineralising organic nitrogen that contributes to leaching, wood decomposition was also assessed. Wood decomposition rates were compared between plots by burying wooden stirring sticks (~15 cm × 1.5 cm × 0.2 cm) under 10 cm of soil at three random locations within each plot. Decomposition was measured by subtracting the dried mass at completion from the initial dry mass after drying the sticks for 3 days at 70°C. Similar methods have previously found that these decomposition measures are concordant with measures of natural decomposition (Arroita et al., 2012; Leifheit et al., 2015; Ostertag et al., 2008).

2.4 | Assessment of nitrate leaching

Nitrate leaching from topsoil (at 30 cm depth) over the study period was estimated using the ion-exchange resin method, with one resin bag buried in the centre of each plot prior to the nitrogen application. Ion-exchange resins are increasingly used in both agricultural (e.g. Hess et al., 2020; Karhu et al., 2021; Woodward et al., 2022) and ecological studies (Borken & Matzner, 2004; Guerrieri et al., 2021; Ibrahim et al., 2021) to assess nitrate leaching and have been shown to be effective compared to the more traditional lysimeter methods (Pampolino et al., 2000; Wey et al., 2021). Unlike lysimeters, resins passively capture nitrate over time, providing an integrated measure of leaching between sampling periods, which is particularly useful in environments where nitrate loss can be highly variable. Additionally, given the flood-prone nature of the study site and the associated challenges of access, ion-exchange resins offer a practical alternative to in situ sensors, reducing the risk of equipment loss or damage and eliminating the need for frequent site visits (Qian & Schoenau, 2002).

The ion-exchange resin approach involved burying meshed bags (50 cm^2) containing 50 g of nitrate-selective ion exchange resin (Resinex NR-1) at a depth of 30 cm below undisturbed soil accessed via a replaced soil core (as in Singh et al., 2018) and left in situ for the 6-week experimental period. Resinex NR-1 is a high purity, premium grade, cross-linked polystyrene divinylbenzene resin that is highly selective for nitrate ions, even with high background sulphate. It has also been shown to have very low nitrate displacement (and consequently greater nitrate retention) by organic material (Edgar & Boyer, 2022). A nitrate-selective resin was necessary given that the sites examined are coastal with the potential for interference from high sulphate soils. In the laboratory, nitrate in the resin was extracted by adding 200 mL of 2 M KCl and agitated for 2 h at 300 rpm, with the filtrate analysed for nitrate using UV spectrophotometry following the American Public Health Association et al. (2017) protocols. Given the strong bind between nitrate and resin, not all the nitrate could be recovered from the extraction; calibration adjustments were thus required.

A calibration relationship between nitrate applied to resin and that recovered was derived with a lab recovery experiment. Twenty-two sterilised plastic jars containing 50 g of Resinex NR-1 were spiked with differing quantities of nitrate-N, delivered as potassium nitrate (KNO_3) dissolved in 100 mL of milli-Q water. Nitrate spikes included three replicates of the following quantities: 0, 18, 36, 66, 88, 109 and 131 mg NO_3^--N, along with an additional single trial of 175 mg NO_3^--N. Spiked samples were agitated for 1 h at 300 rpm and then left for 24 h for nitrate binding prior to extraction testing. To extract nitrate from the resin, the supernatant was drained from the resin and the resin then mixed with 200 mL of 2 M KCl for 2 h at 300 rpm. The nitrate concentration within the extractant was then quantified using UV spectrophotometry with a detection limit of 0.01 mg/L. Linear regression forced through the origin was used to characterise the relationship between nitrate spiked and nitrate recovered (slope = 0.434, $R^2 = 0.99$, $F_{1,21} = 1977$, $p < 0.001$), indicating a mean recovery rate of 43.4% across the calibration range (0–175 mg NO_3^--N). All field extraction values were divided by this recovery factor to estimate true nitrate leached. Repeatability was high, with coefficients of variation across replicated spike levels ranging from 0.7% to 5.3%.

Linear regression, using R 4.3.3 (R Core Team, 2025), was used to examine whether nitrate leaching rates differed between nitrogen application rates and/or vegetation type.

2.5 | Soil metabarcoding

A portion of each soil sample was also sent to Metagen Australia for metabarcoding of eukaryotic, bacterial/archaeal and nematode communities using the following primer sets: NF1/18S2rB (Porazinska et al., 2009), Pro341F/Pro805R (Takahashi et al., 2014) and Nemf/18Sr2b (Sikder et al., 2020) for eukaryotic, bacterial/archaeal and nematode communities, respectively.

DNA was extracted from 10 g subsamples of soil using a modification of the modular universal DNA extraction protocol (Sellers et al., 2018). Briefly, this involved 10 g soil samples being mixed with sterile garnet sand and lysis buffer before being processed in a SPEX 2010 Geno Grinder homogeniser (SPEX SamplePrep, NJ) at 1700 strokes per minute for 5 min. After centrifugation to remove soil particles, 9 mL of the supernatant was treated with a flocculant solution designed to remove humic acid contaminants. Samples were again centrifuged, and DNA was recovered from 10 mL of the supernatant using SPRI beads (Oberacker et al., 2019). The purified DNA was then eluted in 200 µL of Tris–HCl pH 8.0 and was assessed for yield and quality using the Quantifluor® DNA system (Promega, MI) and agarose gel electrophoresis.

A two-step PCR protocol was used to generate dual-indexed amplicons adapted from the Illumina protocol for 16S

Metagenomic Sequencing Library Preparation (three technical PCR replicates). For the first PCR, each reaction contained 2 μL of template DNA, 4 μL 5× MyTaq Red PCR buffer, 0.5 μM of each gene-specific primer and 0.2 μL MyTaq DNA polymerase in a total volume of 20 μL. PCR conditions were 95°C for 3 min, 25 cycles of 95°C for 30 s, 52°C for 30 s and 72°C for 40 s and a final extension step at 72°C for 5 min. Amplicons from PCR1 were diluted 1 in 10 in 10 mM Tris–HCl pH 8.0. Dual indexed PCR amplicons were produced using 2 μL diluted PCR1 amplicon as template DNA, 0.5 μM of each index primer, 5 μL 5× MyTaq Red PCR buffer and 0.2 μL MyTaq DNA polymerase in a final volume of 25 μL. PCR conditions for the second PCR were 95°C for 3 min, 15 cycles of 95°C for 30 s, 65°C for 30 s, 72°C for 40 s, followed by a final extension at 72°C for 5 min. The concentration of PCR amplicons was then measured by fluorimetry using the Quantifluor dsDNA system. Amplicons were then pooled at equimolar concentrations, purified using SPRI beads normalised to a concentration of 10 nM and sequenced by the IMB Sequencing Facility at the University of Queensland on an Illumina MiSeq (2 × 300 bp).

Sequences were demultiplexed with DeML (Renaud et al., 2015). Sequence variants and taxonomic inference were done in the DADA2 package within R 3.5.1 (Callahan et al., 2016; R Core Team, 2025). Briefly, the read pairs were truncated to 270 and 240 bp for 18S and 16S amplicons. For the 16S amplicon, reads were removed if the expected errors in the forward reads exceeded 2 and, in the reverse, if they exceeded 3. For the 18S amplicon, the cut-off for expected errors was 3 in the forward read and 4 in the reverse. For both amplicons, chimeras were identified and removed with the 'consensus' method of the 'removeBimeraDenovo' function. The naïve Bayesian Classifier was used to assign taxonomy to genus level for the 16S amplicon with version 128 of the Silva reference database (Quast et al., 2013) and to species level with the PR2 database version 4.12 (Guillou et al., 2013) for the 18S amplicon using the 'assignTaxonomy' function of DADA2 (Callahan et al., 2016).

2.6 | Data analysis of biotic assemblages

Raw amplicon sequence variant (ASV) data were processed separately for bacterial (16S), fungal (18S) and nematode (metabarcoding) datasets. Each dataset was normalised using cumulative sum scaling (CSS) prior to analysis of diversity and composition. CSS was used to account for differences in sequencing depth while retaining data, reducing biases from uneven sampling effort. All analysis was carried out using the microeco and vegan packages in R 4.3.3 (Liu et al., 2021; Oksanen et al., 2026; R Core Team, 2025).

Shannon diversity was calculated for bacterial, fungal and nematode assemblages using CSS-normalised ASV counts using the lme4 package in R 4.3.3 (Kuznetsova et al., 2017; R Core Team, 2025), Mixed effects linear regression models were used to assess the effects of nitrate load (kg N/ha) and land use (sugarcane or *Melaleuca*) on the Shannon's diversity of each assemblage. Plot was included as a random effect to account for repeated sampling before and after nitrate application. All pre-application samples were assigned a nitrate load of 0 kg N/ha.

Using the vegan package, distance-based redundancy analysis (db-RDA) with Bray–Curtis dissimilarity was used on post-application data to assess assemblage differences (relative ASV abundance following CSS normalisation) by nitrate load and land use. Pairwise similarity in the structure of bacterial, fungal and nematode ordinations was evaluated using Procrustes analysis with the protest function (permutations = 999). The *envfit* function identified post-application correlations between ordination axes and soil indicators or functional traits using permutation tests ($n = 999$). PERMANOVA was conducted on the joint pre- and post-application data, with plot included as a strata term to account for repeated measures, to assess community differences before and after nutrient application. Soil process indicators assessed in the *envfit* analysis included the nitrate leaching rate, decomposition rate and the post-experiment differences in total carbon, total nitrogen and carbon:nitrogen ratio from their pre-experiment baseline. Functional trait gradients were evaluated using the relative abundance of taxa classified with a given trait or guild (e.g. nitrogen fixation) using the FAPROTAX database for bacteria (Louca et al., 2016; Sansupa et al., 2021), the FUNGuild database for fungi (Nguyen et al., 2016) and the Nemaplex database for nematodes (Ferris, 1999). While the trait databases store data on many traits, only those considered highly relevant for nitrogen processes were examined (Table 1). Nematodes were classified based on their feeding groups (e.g. bacterivores, fungivores, plant parasites, omnivores, predators) and coloniser–persister (CP) scores ranging from 1 (*r*-strategists) to 5 (*K*-strategists), which reflect life-history traits and sensitivity to disturbance (Bongers & Bongers, 1998; Ferris et al., 2001). Bacterivores with low CP scores often dominate nutrient-enriched soils and can accelerate nitrogen mineralisation through microbial grazing, while higher CP nematodes may indicate stable, resource-limited conditions and slower nutrient cycling (Bongers & Bongers, 1998; Ferris et al., 2001; Ferris & Bongers, 2006).

Differential abundance of microbial taxa in response to nitrogen load and land use was assessed using the glmm_beta method in the microeco package, which fits generalised linear mixed models with a beta distribution using the glmmTMB package (Brooks et al., 2017; McGillycuddy et al., 2025). Relative abundance (bounded 0–1) was modelled with nitrogen load and vegetation type as fixed effects, and plot as a random effect to account for repeated sampling before and after nitrate application. Pre-application samples were assigned a nitrogen load of 0 kg N/ha. Taxon-level estimates and *p*-values for fixed effects were obtained directly from the fitted models and then corrected for multiple testing using the Benjamini–Hochberg method.

3 | RESULTS

3.1 | Soil chemistry and nitrate leaching

All soil samples had similar texture, nitrate-N (4.58 ± 2.33 mg/kg in cane; 4.72 ± 2.53 mg/kg in *Melaleuca*) and total C:N (15.14 ± 0.95 in cane; 15.07 ± 0.92 in *Melaleuca*). Relative to the *Melaleuca* plots, the

TABLE 1 Summary of microbial functional traits assessed in this study, including bacterial and fungal processes relevant to nitrogen cycling, organic matter decomposition and soil nutrient dynamics.

	Traits	Description
Bacteria	Ureolysis	Converts urea to ammonia, contributing to nitrogen availability and soil fertility.
	Nitrate respiration	Uses nitrate as a terminal electron acceptor under anoxic conditions, reducing nitrate leaching and contributing to nitrogen loss pathways.
	Nitrogen respiration	Includes pathways for reducing nitrate/nitrite to nitrogen gas, completing denitrification.
	Nitrate reduction	Reduces nitrate to nitrite; a key step in both denitrification and dissimilatory nitrate reduction pathways.
	Nitrogen fixation	Converts atmospheric nitrogen (N_2) into ammonia, supplying nitrogen to plants in nitrogen-poor soils.
	Nitrification	Oxidises ammonia to nitrate via nitrite; increases nitrogen availability but can contribute to leaching.
	Aerobic ammonia oxidation	Converts ammonia to nitrite in oxygenated soils; the first step of nitrification.
	Aerobic nitrite oxidation	Converts nitrite to nitrate, completing aerobic nitrification.
	Chitinolysis	Degrades chitin from fungal cell walls and arthropods, aiding nutrient turnover.
	Cellulolysis	Breaks down cellulose from plant residues, contributing to carbon cycling.
	Fermentation	Anaerobic degradation of organic matter, producing substrates for other anaerobes.
Fungi	Soil saprotroph	Decomposes organic matter in soil, releasing nutrients for plant uptake.
	Plant saprotroph	Breaks down dead plant material, contributing to carbon cycling and soil formation.
	Endophyte	Lives within plants without causing harm; can enhance plant growth, nutrient uptake and stress resistance.
	Arbuscular mycorrhizal (AM)	Forms mutualistic associations with most crops; improves phosphorus and water uptake.
	Ectomycorrhizal (ECM)	Associates with many trees; enhances nitrogen and phosphorus uptake in forest soils.
	Wood saprotroph	Degrades lignin and cellulose in wood, playing a key role in carbon turnover in forest systems.

cane sites had slightly higher pH in water (4.85 ± 0.20 vs. 4.11 ± 0.06) but slightly lower pH in $CaCl_2$ (3.95 ± 0.07 vs. 4.00 ± 0.06), lower electrical conductivity (0.18 ± 0.13 vs. 3.03 ± 0.48 dS/m), lower ammonium-N (2.80 ± 0.78 vs. 6.72 ± 1.54 mg/kg), lower cation exchange capacity (CEC) (7.75 ± 0.71 vs. 24.34 ± 3.42 cmol(+)/kg) and lower organic carbon (2.31 ± 0.23% vs. 6.22 ± 1.17%) (File S1).

Nitrate leaching increased with nitrogen load in sugarcane plots ($\beta = 1.48$, $t = 8.48$, $p < 0.001$), but the relationship was significantly weaker in *Melaleuca* plots (interaction: $\beta = -1.33$, $t = -5.40$, $p < 0.001$; Figure 1). There was no significant difference in baseline nitrate leaching between vegetation types ($\beta = 9.87$, $t = 0.65$, $p = 0.52$). The overall model was significant ($F_{(3,26)} = 38.3$, $p < 0.001$; $R^2 = 0.82$).

3.2 | Soil microbial communities

Diversity of bacteria and fungi was not linked with nitrate load or vegetation type (Bacteria: nitrate load: $t = 1.98$, df $= 56$, $p = 0.053$; vegetation: $t = -0.18$, df $= 56$, $p = 0.857$; fungi: nitrate load: $t = -1.61$, df $= 56$, $p = 0.113$; vegetation: $t = 0.23$, df $= 56$, $p = 0.817$). In contrast, nematode diversity increased with nitrate load and was lower in *Melaleuca* plots (nitrate load: $t = 4.52$, df $= 42.88$, $p < 0.001$; vegetation: $t = -3.20$, df $= 27.31$, $p = 0.003$; Figure 2).

The db-RDAs indicated that community composition across all three taxonomic groups was primarily structured by vegetation type, with additional gradients within each vegetation type linked to nitrate load (Figure 3; Table 2). For bacteria, multiple functional traits were significantly associated with vegetation type differences: ureolysis ($r^2 = 0.39$, $p = 0.011$), nitrification ($r^2 = 0.36$, $p = 0.011$), chitinolysis ($r^2 = 0.30$, $p = 0.011$), cellulolysis ($r^2 = 0.46$, $p = 0.011$), aerobic ammonia oxidation ($r^2 = 0.30$, $p = 0.011$) and aerobic nitrite oxidation ($r^2 = 0.34$, $p = 0.011$). Bacterial community composition was also significantly correlated with environmental variables: nitrate leaching ($r^2 = 0.38$, $p = 0.038$), mass loss ($r^2 = 0.50$, $p = 0.020$) and total carbon difference ($r^2 = 0.50$, $p = 0.020$). For fungi, no functional traits were significantly associated with the RDA axes. However, several environmental variables were nitrate leaching ($r^2 = 0.52$, $p = 0.0025$), mass loss ($r^2 = 0.68$, $p = 0.0025$) and total nitrogen difference ($r^2 = 0.36$, $p = 0.020$). For nematodes, no functional traits were significantly associated with community composition. However, nitrate leaching ($r^2 = 0.38$, $p = 0.038$) and mass loss ($r^2 = 0.50$, $p = 0.020$) were significantly correlated with differences between vegetation types.

Procrustes tests indicated strong concordance in community composition patterns among the three groups: bacteria and fungi ($r = 0.86$, $p = 0.001$), bacteria and nematodes ($r = 0.77$, $p = 0.001$) and fungi and nematodes ($r = 0.83$, $p = 0.001$).

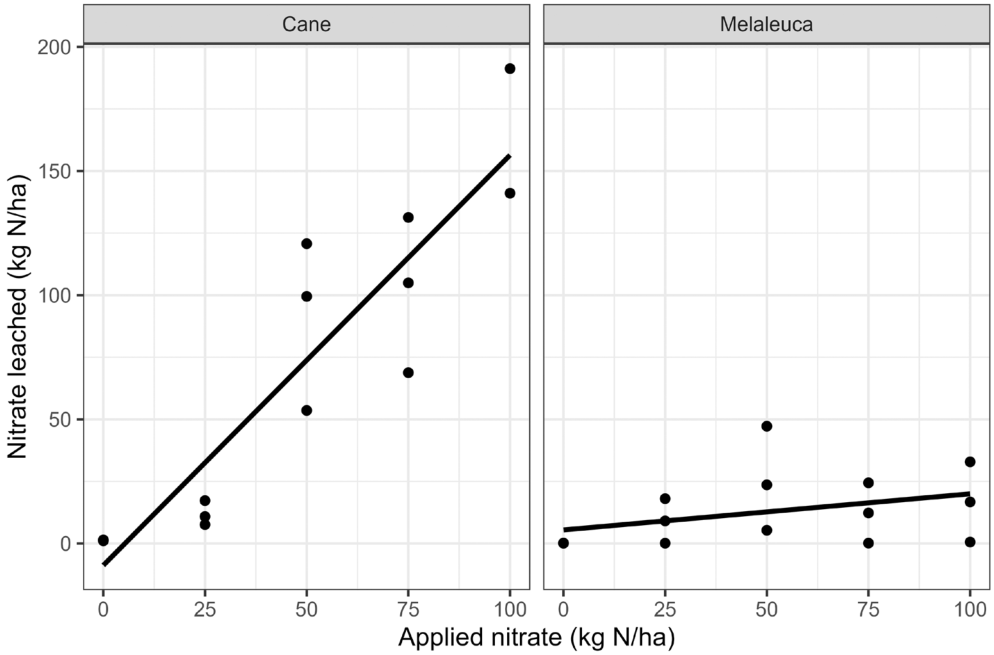


FIGURE 1 The relationships between the applied nitrate applied to plots versus the nitrate leached across plots in the sugarcane field and the restored *Melaleuca* patch.

Volcano plots highlighting the relative influence of each genus in differentiating between vegetation and nitrogen treatments for the three assemblages, as determined using generalised linear mixed models, are shown in Figure 4 and File S2.

4 | DISCUSSION

4.1 | Nitrate retention mechanisms

Nitrate leaching increased linearly with higher nitrogen load in sugarcane plots but was much lower in the reforested *Melaleuca* plots. Higher organic carbon and complex litter inputs in *Melaleuca* plots supported microbial communities dominated by decomposers (chitinolytic and cellulolytic bacteria), which retain nitrogen in biomass during organic matter breakdown (Adame et al., 2019; Hanrahan et al., 2018; Orr et al., 2007). Root systems of mature *Melaleuca* will also be more extensive and deeper than those of sugarcane, improving nitrate uptake and contributing to nitrate retention. While the *Melaleuca* plots had higher CEC, this alone does not explain the lower leaching, as higher CEC can sometimes result in increased nitrate availability for leaching. Rather, the consistent difference in organic carbon between vegetation soil types provides a stronger explanation, as carbon availability supports microbial immobilisation of nitrogen during decomposition of complex organic substrates (Adame et al., 2019; Di & Cameron, 2016; Shrestha et al., 2014). Reforestation of these floodplains clearly alters their functioning and improves the ability to reduce nitrogen losses in the surrounding agricultural landscapes. Active replanting or simply removing barriers that could restrict inundation of existing floodplain forests is a promising nature-based solution to the issue of agricultural eutrophication of receiving waterways (Gergel et al., 2005; Shrestha et al., 2014; Welti et al., 2012).

4.2 | Microbial community responses to vegetation type and nitrogen enrichment

In this study, nitrate addition did not lead to significant short-term changes in the diversity of bacteria or fungi in either the sugarcane or reforested *Melaleuca* plots. While some global meta-analyses have shown that nitrogen fertilisation can reduce microbial diversity (Yang et al., 2022), particularly at high rates or over longer periods, other studies highlight that diversity is not a consistent predictor of microbial functional or compositional change (Bebber & Richards, 2022; Zhou et al., 2020).

In contrast, nematode diversity increased with nitrate loading and was lower in reforested *Melaleuca* plots. This pattern aligns with studies suggesting that nematodes, particularly lower trophic levels like bacterivores, can respond positively to increased resource availability under nitrogen enrichment (Azpilicueta et al., 2014; Song et al., 2016). Global syntheses show that nematode diversity often declines with high nitrogen addition, especially in cold or dry regions (Xing et al., 2022), but can increase in warm, moist systems as in our study site. The elevated nitrate leaching in the sugarcane plots may have stimulated microbial activity and created a resource-rich environment favouring opportunistic nematode taxa. In contrast, the lower diversity in *Melaleuca* plots could reflect more stable, resource-limited conditions or suppression of certain trophic groups due to the differing microbial communities, root structures and/or soil chemical properties. Alternatively, ammonium toxicity has also

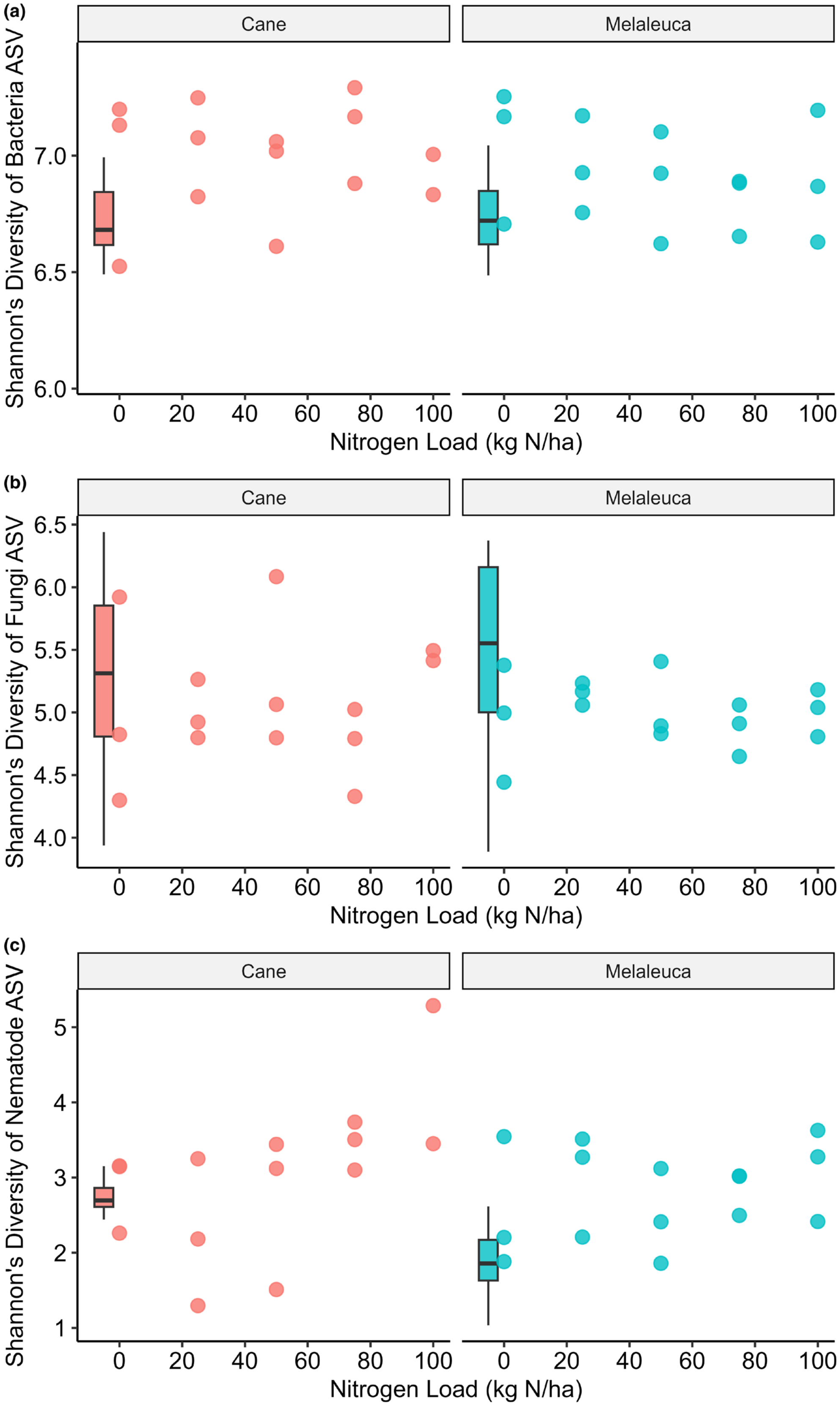
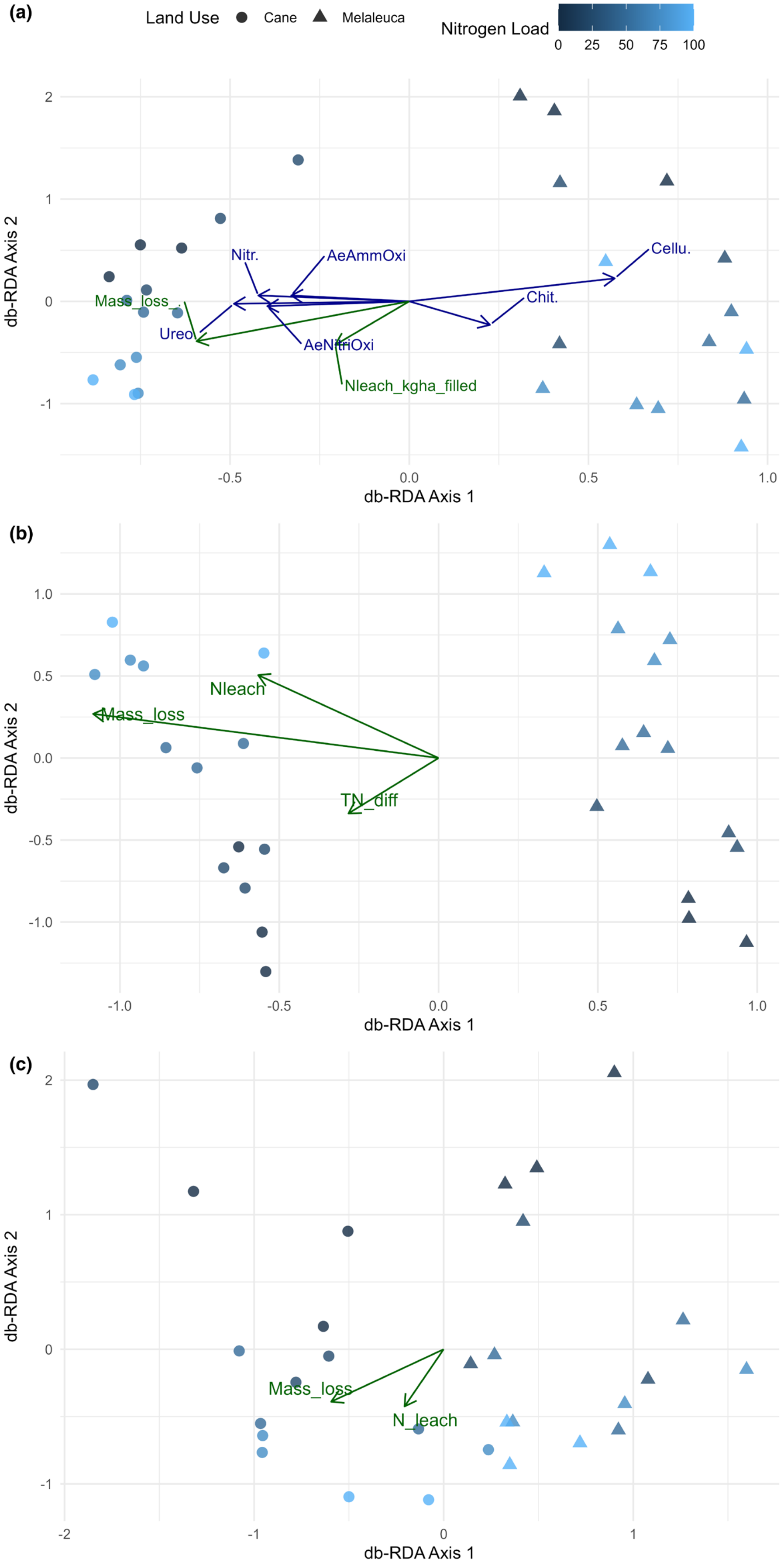


FIGURE 2 Shannon diversity of (a) bacterial, (b) fungal and (c) nematode amplicon sequence variants (ASVs) across a nitrate application gradient in plots from the sugarcane field (red) and the restored *Melaleuca* patch (blue). Boxplots summarise diversity before nitrate application, while dots show plot-level diversity 6 weeks after application.

FIGURE 3 Distance-based redundancy analysis (db-RDA) plots showing (a) bacterial, (b) fungal and (c) nematode community composition 6 weeks after nitrate application. Colour gradient represents nitrate application rate (light to dark blue: 0–100 kg N/ha). Circles indicate sugarcane plots; triangles indicate *Melaleuca* plots. Blue arrows show traits with correlated relative abundance; green arrows show correlated environmental variables.



been proposed as a driver of nematode suppression under nitrogen addition (Wei et al., 2012). The substantially higher ammonium concentrations in *Melaleuca* plots (6–7 mg/kg) compared to sugarcane plots (2–3 mg/kg) suggest that toxicity effects may have contributed to reduced diversity, potentially through selective suppression of sensitive trophic groups or altered microbial interactions (Oka, 2010; Su et al., 2017; Wei et al., 2012). Clearly, nematodes are responsive indicators of nutrient enrichment, but further work is needed to understand exactly how they respond to differences in vegetation, moisture and nutrient enrichment.

The db-RDA results for bacterial assemblages revealed strong associations between community composition, environmental gradients and functional traits. *Melaleuca* plots were enriched in decomposer traits (chitinolysis and cellulolysis), supported by generalist decomposer taxa including Sporosarcina (Firmicutes), Bacteroidetes and Deltaproteobacteria that retain nitrogen in biomass during slow breakdown of woody litter. In contrast, sugarcane plots were consistently dominated by Nitrosococcus (Nitrosococcaceae), a rapid ammonia-oxidising bacterium (AOB) that dominates in fertilised, disturbed soils, across all nitrogen application rates. The consistent enrichment of *Nitrosococcus* in sugarcane soils, combined with the linear increase in nitrate leaching with applied nitrogen, suggests that active nitrification by this AOB is the primary driver of rapid ammonium-to-nitrate conversion and subsequent nitrate loss. In contrast, *Sporosarcina* and Bacteroidetes-dominated *Melaleuca* soils retain nitrogen in microbial biomass during slow organic matter breakdown, reducing nitrate availability for leaching (Chisholm et al., 2024; Di et al., 2009). Functional trait assessment from metabarcoding is inferential rather than direct measurement of process rates. Nitrification rates or enzyme assays could provide complementary validation. However, the strong correlation between bacterial community composition and measured nitrate leaching ($r^2=0.38$, $p=0.038$), combined with consistent enrichment of taxa with known metabolic capabilities (*Nitrosococcus* for nitrification, *Sporosarcina* and Bacteroidetes for chitinolysis and cellulolysis), provides ecological coherence to the mechanistic interpretation. Even gene-level approaches face similar limitations as gene presence does not ensure expression under field conditions. Nonetheless, differences in functional traits from shifts in community may provide better insight into the observed difference in nitrogen fate than nitrogen input rate or diversity metrics alone. The correlations between nitrate leaching and both fungal ($r^2=0.52$, $p=0.003$) and nematode ($r^2=0.38$, $p=0.038$) community composition further support this interpretation, suggesting that the observed differences in nitrogen fate are reflected coherently across multiple trophic levels rather than being an artefact of bacterial community analysis alone.

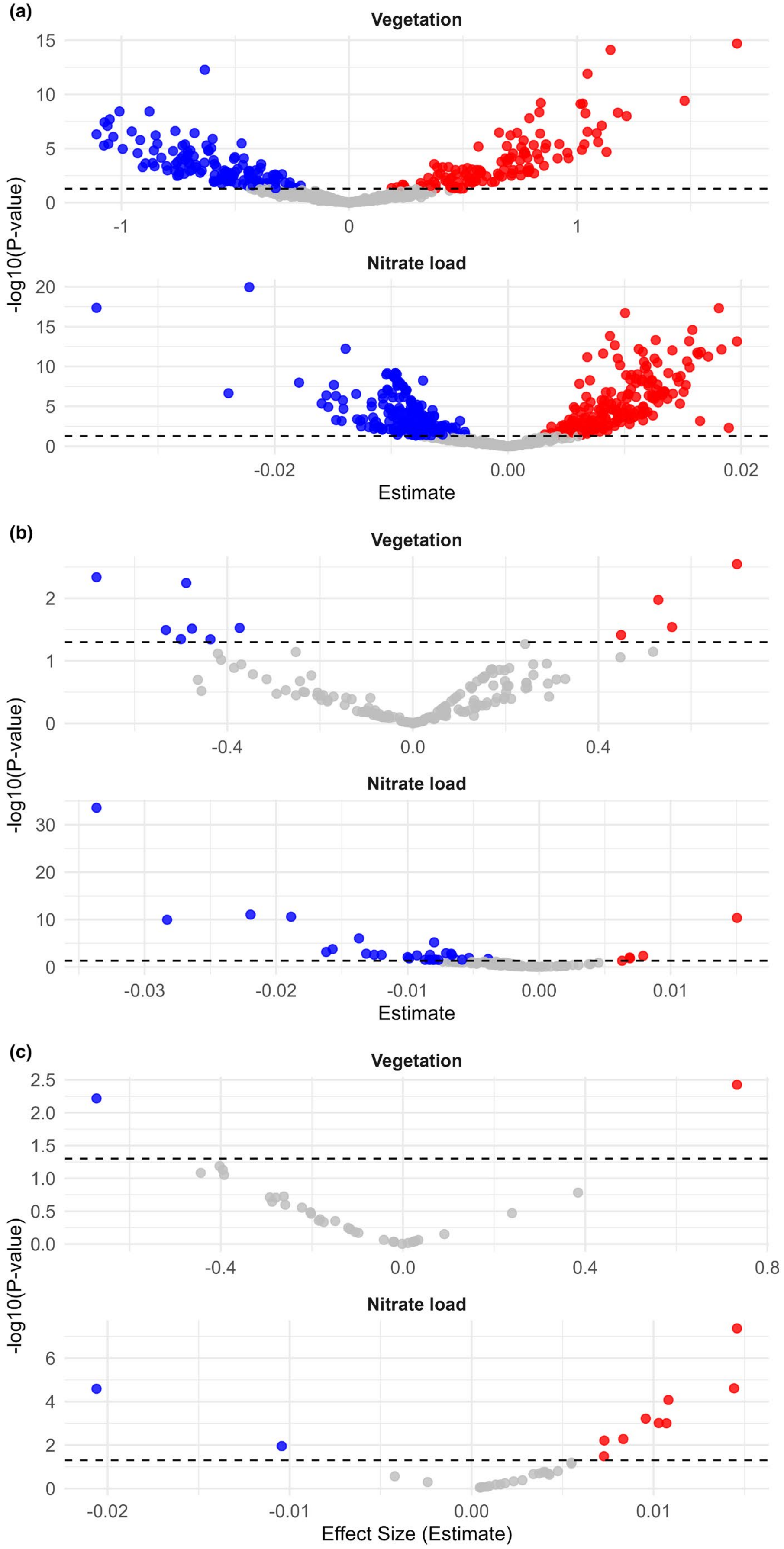
Fungal community composition varied significantly with nitrate load and vegetation type, yet their role in mediating nitrate retention remains unclear relative to other drivers. Sugarcane plots showed higher nitrate leaching, mass loss and total nitrogen change, consistent with nutrient turnover under disturbance and fertilisation. These plots were dominated by stress-tolerant Ascomycota such as *Penicillium* and *Exophiala*, consistent with *r*-strategist fungi that proliferate in disturbed, nutrient-rich environments (Allison et al., 2007; Bai et al., 2022; Liu et al., 2022). In contrast, *Melaleuca* plots supported higher relative abundance of Basidiomycota and litter-associated Ascomycota genera, aligning with more stable *K*-strategist fungal communities known to dominate in undisturbed systems and contribute to organic matter retention (Liu et al., 2022; Manici, Caputo, De Sabata, & Fornasier, 2024; Manici, Caputo, Fornasier, et al., 2024). While relative ASV abundance of functional traits was not associated with community composition, this may reflect a signal-to-noise problem arising from high functional variability within taxonomic groups or incomplete trait databases.

The Ascomycota:Basidiomycota (A:B) ratio, although not directly assessed here, has been proposed as a qualitative indicator of soil carbon cycling and afforestation effectiveness (Manici, Caputo, Fornasier, et al., 2024). Given the observed correlation between mass loss and nitrate leaching in our study, the A:B ratio may also hold

TABLE 2 PERMANOVA results testing the marginal effects of nitrate load and vegetation type on bacterial, fungal and nematode community composition using Bray–Curtis dissimilarities. *p*-values reflect the independent contribution of each predictor while accounting for the other, based on 999 permutations stratified by sampling waypoint.

Taxon	Factor	*F*	df	R^2	*p*
Bacteria	Nitrate load	15.47	1, 56	0.187	0.001
	Vegetation	11.18	1, 56	0.135	0.001
Fungi	Nitrate load	4.31	1, 56	0.068	0.001
	Vegetation	2.71	1, 56	0.043	0.001
Nematodes	Nitrate load	6.2	1, 56	0.093	0.001
	Vegetation	4.85	1, 56	0.072	0.001

FIGURE 4 Volcano plots showing differentially abundant genera for (a) bacteria, (b) fungi and (c) nematodes in response to nitrate load and vegetation type (*Melaleuca* vs. sugarcane) 6 weeks after nitrate application. Each panel displays model estimates (effect sizes) on the *x*-axis and negative log-transformed unadjusted *p*-values on the *y*-axis. Red points indicate genera with significant increases, blue points indicate significant decreases and grey points are not statistically significant ($p \geq 0.05$). The dashed line denotes the $p=0.05$ threshold. Results are based on GLMMs fitted to cumulative sum scaling (CSS)-normalised data with plot included as a random effect to account for repeated sampling before and after nitrate application.


(a)
Vegetation
15
10
5
0
-1
0
1
Nitrate load
20
15
10
5
0
-0.02
0.00
0.02
Estimate
-log10(P-value)
(b)
Vegetation
2
1
0
-0.4
0.0
0.4
Nitrate load
30
20
10
0
-0.03
-0.02
-0.01
0.00
0.01
Estimate
-log10(P-value)
(c)
Vegetation
2.5
2.0
1.5
1.0
0.5
0.0
-0.4
0.0
0.4
0.8
Nitrate load
6
4
2
0
-0.02
-0.01
0.00
0.01
Effect Size (Estimate)
-log10(P-value)

potential as an indicator of nitrate loss risk, warranting further investigation. Basidiomycota are often associated with stable, *K*-strategist communities and complex organic matter decomposition, whereas Ascomycota tend to dominate in disturbed or nutrient-enriched systems (Liu et al., 2022; Manici, Caputo, De Sabata, & Fornasier, 2024; Manici, Caputo, Fornasier, et al., 2024). A shift towards Ascomycota dominance may therefore reflect reduced organic matter retention and increased nutrient turnover, both of which could contribute to nitrate leaching. If supported by further research, the A:B ratio could offer a simple, scalable proxy for fungal contributions to nutrient retention under different land use or fertiliser regimes.

Beyond decomposition, long-term shifts in fungal communities could alter soil structural properties that affect nitrate retention. Fungi contribute to soil aggregation via traits such as dense hyphal networks and low leucine aminopeptidase activity (Lehmann et al., 2020). If nitrate enrichment selectively favours *r*-strategist fungi with limited structural contributions, this could impair aggregate stability and reduce the soil's physical capacity to retain nitrate over time. This may reduce the soil's structural capacity to retain nitrate, particularly when combined with other stressors such as reduced precipitation that further destabilise aggregates and diminish glomalin-related proteins (Huang et al., 2022). Nitrogen addition may also stabilise recalcitrant organic matter fractions while reducing overall respiration and microbial activity in bulk soils (Swanston et al., 2004). These findings raise concern that nitrate-driven fungal shifts could degrade soil structure and compromise long-term nitrate retention, warranting further research.

While nematode CP scores and trophic composition were not significantly associated with nitrogen load or vegetation type, nematode community composition was correlated with both nitrate leaching and wood mass loss. This suggests a response to underlying shifts in soil nutrient dynamics not captured by existing trait groupings. Previous studies have shown that nitrogen enrichment reduces total nematode diversity and suppresses herbivores, omnivores and predators, while favouring bacterivores in a non-linear fashion, potentially due to ammonium toxicity and altered microbial food resources (Bongers & Ferris, 1999; Wei et al., 2012). These responses can differ seasonally or contextually across systems (Liang et al., 2009; McSorley, 2012), limiting the predictive power of trophic categories. Buchan et al. (2013) also found that free-living nematode additions enhanced nitrifier abundance and nitrate levels, though causality remained unclear. Despite the absence of detectable trait-level shifts in this study, the congruent structuring of bacterial, fungal and nematode assemblages across nitrate and vegetation gradients points to coordinated reorganisation of soil food webs in response to nitrogen loading.

4.3 | Long-term stability and climate considerations

The long-term stability of microbial communities in restored *Melaleuca* systems remains an open question. The short duration of this study precludes direct assessment of temporal community stability. When stability is examined indirectly by comparing the degree of compositional change in response to nitrogen enrichment as a press disturbance, both vegetation types showed similar sensitivity. Communities shifted comparably along the nitrogen gradient in the db-RDA, and the absence of significant CP score differences between vegetation types provides no evidence that the two systems differ in successional maturity or disturbance history as captured by that metric. Rather, vegetation type established fundamentally different community states with distinct taxonomic composition and functional trait profiles that persisted across the nitrogen gradient, consistent with vegetation acting as a strong environmental filter on baseline community composition. Regular cultivation in sugarcane fields periodically resets soil communities, meaning that, at any given point, the sugarcane system likely occupies an earlier and more variable seral stage position compared to *Melaleuca*, where communities can develop continuously without disturbance-driven resetting. Whether the nitrate retention capacity observed here persists over longer timeframes remains unknown, as both this study and existing assessments of denitrification in *Melaleuca* systems rely on snapshot measurements that cannot capture temporal variation in process rates. Longer term sampling across multiple cultivation cycles and disturbance events would be needed to characterise this temporal variability and its consequences for nitrogen cycling.

Future research should investigate how the frequency, duration and extent of inundation potentially shape microbial nitrogen cycling. Hydrological modifications, such as bund walls or drainage channels, may disrupt microbial processes critical for denitrification and nitrate retention. Repeated nitrogen deposition (such as from regular floods) may favour denitrifiers, enhancing denitrification potential during high nitrogen inputs (Kong et al., 2010; Li et al., 2022; Wang et al., 2018), whereas infrequent inputs may act as pulse disturbances that, over time, shift into press disturbances, restructuring microbial networks (Li et al., 2021; Philippot et al., 2021). As climate change alters rainfall and flood regimes, it will be essential to understand how these dynamics interact with vegetation and soil biota. This is particularly important in flood-prone systems, where drying–rewetting cycles and vegetation-driven microbial selection may influence both nitrogen retention and loss pathways over time (Gordon et al., 2008; Hansen et al., 2019). While nitrogen enrichment can increase mineral-associated carbon (Beillouin et al., 2023; Xu et al., 2021), in soils with high C:N ratios, it may initially stimulate microbial decomposition and accelerate the loss of particulate organic matter, potentially reducing total SOC and compromising nitrogen retention through decreased aggregation and microbial immobilisation (Cui et al., 2022; Huang et al., 2022; Zhang & Shangguan, 2023). Practical and affordable indicators of nitrate retention and removal are also needed to demonstrate restoration performance, with microbial indicators showing promise in this context. Future research should validate candidate taxa and traits across diverse soil types, vegetation communities and hydrological conditions, linking microbial composition to measured nitrate fluxes over time to ensure indicators are reliable, scalable and suitable for integration into practical monitoring and ecosystem service payment schemes.

Climate projections for the Far North Queensland region indicate that tropical cyclones are expected to become less frequent but more intense, accompanied by reduced average rainfall, fewer heavy precipitation days, more consecutive dry days and rising temperatures of 1.1°C–3.2°C by 2090 depending on emissions scenario, suggesting flood events may deliver larger pulse nitrogen loads with longer and hotter dry intervals between them (State of Queensland, 2024). However, observed trends in severe tropical cyclones making landfall along the GBR coastline over the past five decades show that the most recent decade recorded more severe events than the previous two combined, with the highest intensity cyclone on record occurring during 2010–2019 (Duke et al., 2024). Longer dry intervals and higher temperatures between flood events may alter soil moisture regimes and microbial community composition, potentially reducing denitrification capacity and nitrogen immobilisation ahead of the next flood pulse, and therefore compromising the ability of reforested floodplains to respond to nitrate-laden floodwaters when they arrive. Conversely, more intense flood events delivering larger nitrogen pulses may periodically overwhelm even well-functioning microbial communities. These dynamics reinforce rather than diminish the case for floodplain reforestation as the organic carbon-rich soils and decomposer-dominated communities of mature *Melaleuca* systems are likely more buffered against such fluctuations than disturbed agricultural soils, though empirical testing across flood events of varying intensity remains a priority.

4.4 | Management and economic implications

Our results indicate that reforesting floodplains can enhance soil microbial pathways that mitigate nitrogen losses from floods, benefiting downstream ecosystems like the GBR (Adame et al., 2019; Davis et al., 2017). However, while large areas are suitable for restoration (Canning, 2025; Canning & Duke, 2026; Waltham et al., 2021), the economic feasibility of scaling up floodplain reforestation depends on the funding mechanisms used. Active restoration of *Melaleuca* forests and woodlands across Australia has been estimated at AU$5648 per ha for cleared land in 2020 dollars, with landscape-scale restoration across approximately 17,600 ha estimated at approximately AU$29 million net present value excluding land purchase and landholder stewardship costs, and carbon market revenue potentially covering 77%–302% of restoration costs depending on carbon pricing scenarios (Mappin et al., 2022). In the GBR sugarcane context, modelling by Kandulu et al. (2018) suggests that the broader environmental benefits of reducing nitrogen loss through land use change consistently exceed the private profit reductions farmers would incur, yet without compensation, farmers have little financial incentive to change, highlighting the need for incentive-based interventions that transfer some of the societal benefit back to landholders. However, single-outcome payment for ecosystem service schemes, such as those focused solely on carbon or water quality, often struggle with financial viability, high assessment costs and difficulties demonstrating additionality, particularly for the variable and spatially complex processes such as denitrification that underpin the benefits observed in this study (Canning et al., 2021). More integrated funding approaches that value multiple ecosystem services, such as common asset trusts modelled on Latin American water funds which pool investment across multiple services and reduce administrative burden through bundled payments and landscape-scale planning, will be needed to scale up floodplain reforestation efforts at the scale required to deliver meaningful water quality outcomes for the GBR while explicitly managing potential trade-offs (Canning et al., 2021; Salzman et al., 2018).

Managing these trade-offs will require consideration of the full range of ecosystem service outcomes from floodplain reforestation. The decomposer-dominated microbial communities of *Melaleuca* soils, reflected in significant correlations between mass loss and community composition across all three taxonomic groups, could periodically mobilise nitrogen during dry intervals between flood events, while the anaerobic conditions that promote denitrification may also stimulate methane and nitrous oxide production, potentially offsetting water quality benefits with greenhouse gas costs. These trade-offs do not diminish the value of floodplain reforestation as a nitrogen management strategy but highlight the importance of accounting for multiple ecosystem service outcomes when designing and evaluating restoration programmes.

AUTHOR CONTRIBUTIONS

Adam Canning conceptualised the idea, conducted field experiments, analysed the data and wrote the manuscript. Michelle Tink conducted all nitrate assessments, including deriving the nitrate recovery from resin calibration and edited the manuscript.

ACKNOWLEDGEMENTS

The authors thank Lynise Wearne and Greening Australia for financial support and John Cardillo for granting access to his property for this experiment. Open access publishing facilitated by James Cook University, as part of the Wiley - James Cook University agreement via the Council of Australasian University Librarians

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Raw data are available from a Figshare repository: https://doi.org/10.6084/m9.figshare.32143024.v1(Canning, 2026).

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REFERENCES

Adame, M. F., Franklin, H., Waltham, N. J., Rodriguez, S., Kavehei, E., Turschwell, M. P., Balcombe, S. R., Kaniewska, P., Burford, M. A., & Ronan, M. (2019). Nitrogen removal by tropical floodplain wetlands through denitrification. *Marine and Freshwater Research*, *70*(11), 1513–1521. https://doi.org/10.1071/Mf18490

Adame, M. F., Reef, R., Wong, V. N. L., Balcombe, S. R., Turschwell, M. P., Kavehei, E., Rodríguez, D. C., Kelleway, J. J., Masque, P., & Ronan, M. (2020). Carbon and nitrogen sequestration of floodplain wetlands in tropical Australia. *Ecosystems*, *23*(2), 454–466. https://doi.org/10.1007/s10021-019-00414-5

Allison, S. D., Hanson, C. A., & Treseder, K. K. (2007). Nitrogen fertilization reduces diversity and alters community structure of active fungi in boreal ecosystems. *Soil Biology and Biochemistry*, *39*(8), 1878–1887. https://doi.org/10.1016/j.soilbio.2007.02.001

American Public Health Association, American Water Works Association, & Federation, W. E. (2017). *Standard methods for the examination of water and wastewater* (23rd ed.). A. P. H. Association.

Arroita, M., Aristi, I., Flores, L., Larranaga, A., Diez, J., Mora, J., Romani, A. M., & Elosegi, A. (2012). The use of wooden sticks to assess stream ecosystem functioning: Comparison with leaf breakdown rates. *Science of the Total Environment*, *440*, 115–122. https://doi.org/10.1016/j.scitotenv.2012.07.090

Audet, J., Olsen, T. M., Elsborg, T., Baattrup-Pedersen, A., & Riis, T. (2021). Influence of plant habitats on denitrification in lowland agricultural streams. *Journal of Environmental Management*, *286*, 112193. https://doi.org/10.1016/j.jenvman.2021.112193

Azpilicueta, C. V., Aruani, M. C., Chaves, E., & Reeb, P. D. (2014). Soil nematode responses to fertilization with ammonium nitrate after six years of unfertilized apple orchard. *Spanish Journal of Agricultural Research*, *12*(2), 353–363. https://doi.org/10.5424/sjar/2014122-4634

Bai, L., Zhang, X., Li, B., Sun, F., Zhao, X., Wang, Y., Lu, Z., Zhang, D., & Fang, J. (2022). Fungal communities are more sensitive to nitrogen fertilization than bacteria in different spatial structures of silage maize under short-term nitrogen fertilization. *Applied Soil Ecology*, *170*, 104275. https://doi.org/10.1016/j.apsoil.2021.104275

Bebber, D. P., & Richards, V. R. (2022). A meta-analysis of the effect of organic and mineral fertilizers on soil microbial diversity. *Applied Soil Ecology*, *175*, 104450. https://doi.org/10.1016/j.apsoil.2022.104450

Beillouin, D., Corbeels, M., Demenois, J., Berre, D., Boyer, A., Fallot, A., Feder, F., & Cardinael, R. (2023). A global meta-analysis of soil organic carbon in the Anthropocene. *Nature Communications*, *14*(1), 3700. https://doi.org/10.1038/s41467-023-39338-z

Bissett, A., Richardson, A. E., Baker, G., & Thrall, P. H. (2011). Long-term land use effects on soil microbial community structure and function. *Applied Soil Ecology*, *51*, 66–78. https://doi.org/10.1016/j.apsoil.2011.08.010

Bongers, T., & Bongers, M. (1998). Functional diversity of nematodes. *Applied Soil Ecology*, *10*(3), 239–251. https://doi.org/10.1016/S0929-1393(98)00123-1

Bongers, T., & Ferris, H. (1999). Nematode community structure as a bioindicator in environmental monitoring. *Trends in Ecology & Evolution*, *14*(6), 224–228. https://doi.org/10.1016/s0169-5347(98)01583-3

Borken, W., & Matzner, E. (2004). Nitrate leaching in forest soils: An analysis of long-term monitoring sites in Germany. *Journal of Plant Nutrition and Soil Science*, *167*(3), 277–283. https://doi.org/10.1002/jpln.200421354

Brodie, J. E., Kroon, F. J., Schaffelke, B., Wolanski, E. C., Lewis, S. E., Devlin, M. J., Bohnet, I. C., Bainbridge, Z. T., Waterhouse, J., & Davis, A. M. (2012). Terrestrial pollutant runoff to the Great Barrier Reef: An update of issues, priorities and management responses. *Marine Pollution Bulletin*, *65*(4–9), 81–100. https://doi.org/10.1016/j.marpolbul.2011.12.012

Brooks, M. E., Kristensen, K., Van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Machler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, *9*(2), 378–400. https://doi.org/10.32614/RJ-2017-066

Buchan, D., Gebremikael, M. T., Ameloot, N., Sleutel, S., & De Neve, S. (2013). The effect of free-living nematodes on nitrogen mineralisation in undisturbed and disturbed soil cores. *Soil Biology and Biochemistry*, *60*, 142–155. https://doi.org/10.1016/j.soilbio.2013.01.022

Callahan, B. J., McMurdie, P. J., Rosen, M. J., Han, A. W., Johnson, A. J., & Holmes, S. P. (2016). DADA2: High-resolution sample inference from Illumina amplicon data. *Nature Methods*, *13*(7), 581–583. https://doi.org/10.1038/nmeth.3869

Canning, A. (2026). *Dataset: Floodplain reforestation reduces nitrate loss through soil microbial pathways (Version 1)*. figshare. https://doi.org/10.6084/m9.figshare.32143024.v1

Canning, A. D. (2025). Scoping the suitability of water-tolerant species of trees for swamp restorations across Australia and its Great Barrier Reef catchment. *Restoration Ecology*, *33*(3), e14375. https://doi.org/10.1111/rec.14375

Canning, A. D., & Duke, N. C. (2026). Assessing threats and rehabilitation opportunities for mangrove-saltmarsh blue carbon ecosystems. *Ocean and Coastal Management*, *271*, 107974. https://doi.org/10.1016/j.ocecoaman.2025.107974

Canning, A. D., Jarvis, D., Costanza, R., Hasan, S., Smart, J. C. R., Finisdore, J., Lovelock, C. E., Greenhalgh, S., Marr, H. M., Beck, M. W., Gillies, C. L., & Waltham, N. J. (2021). Financial incentives for large-scale wetland restoration: Beyond markets to common asset trusts. *One Earth*, *4*(7), 937–950. https://doi.org/10.1016/j.oneear.2021.06.006

Chisholm, C., Di, H., Cameron, K., Podolyan, A., Shen, J., Zhang, L., Sirisena, K., & Godsoe, W. (2024). Contrasting response of comammox *Nitrospira*, ammonia oxidising bacteria, and archaea to soil pH and nitrogen inputs. *Science of the Total Environment*, *924*, 171627. https://doi.org/10.1016/j.scitotenv.2024.171627

Coggan, A., Thorburn, P., Fielke, S., Hay, R., & Smart, J. C. R. (2021). Motivators and barriers to adoption of improved land management practices. A focus on practice change for water quality improvement in Great Barrier Reef catchments. *Marine Pollution Bulletin*, *170*, 112628. https://doi.org/10.1016/j.marpolbul.2021.112628

Cookson, W. R., Osman, M., Marschner, P., Abaye, D. A., Clark, I., Murphy, D. V., Stockdale, E. A., & Watson, C. A. (2007). Controls on soil nitrogen cycling and microbial community composition across land use and incubation temperature. *Soil Biology and Biochemistry*, *39*(3), 744–756. https://doi.org/10.1016/j.soilbio.2006.09.022

Cui, J., Zhu, R., Wang, X., Xu, X., Ai, C., He, P., Liang, G., Zhou, W., & Zhu, P. (2022). Effect of high soil C/N ratio and nitrogen limitation caused by the long-term combined organic-inorganic fertilization on the soil microbial community structure and its dominated SOC decomposition. *Journal of Environmental Management*, *303*, 114155. https://doi.org/10.1016/j.jenvman.2021.114155

Das, P. P., Singh, K. R., Nagpure, G., Mansoori, A., Singh, R. P., Ghazi, I. A., Kumar, A., & Singh, J. (2022). Plant-soil-microbes: A tripartite interaction for nutrient acquisition and better plant growth for sustainable agricultural practices. *Environmental Research*, *214*(Pt 1), 113821. https://doi.org/10.1016/j.envres.2022.113821

Davis, A. M., Pearson, R. G., Brodie, J. E., & Butler, B. (2017). Review and conceptual models of agricultural impacts and water quality in waterways of the Great Barrier Reef catchment area. *Marine and Freshwater Research*, *68*(1), 1–19. https://doi.org/10.1071/Mf15301

Delgado-Baquerizo, M., Reich, P. B., Trivedi, C., Eldridge, D. J., Abades, S., Alfaro, F. D., Bastida, F., Berhe, A. A., Cutler, N. A., Gallardo, A., Garcia-Velazquez, L., Hart, S. C., Hayes, P. E., He, J. Z., Hseu, Z. Y., Hu, H. W., Kirchmair, M., Neuhauser, S., Perez, C., … Singh, B. K. (2020). Multiple elements of soil biodiversity drive ecosystem functions across biomes. *Nature Ecology & Evolution*, *4*(2), 210–220. https://doi.org/10.1038/s41559-019-1084-y

Di, H. J., & Cameron, K. C. (2016). Inhibition of nitrification to mitigate nitrate leaching and nitrous oxide emissions in grazed grassland: A review. *Journal of Soils and Sediments*, *16*(5), 1401–1420. https://doi.org/10.1007/s11368-016-1403-8

Di, H. J., Cameron, K. C., Shen, J. P., He, J. Z., & Winefield, C. S. (2009). A lysimeter study of nitrate leaching from grazed grassland as affected by a nitrification inhibitor, dicyandiamide, and relationships with ammonia oxidizing bacteria and archaea. *Soil Use and Management*, *25*(4), 454–461. https://doi.org/10.1111/j.1475-2743.2009.00241.x

Duke, N., Canning, A., & MacKenzie, J. (2024). More intense severe tropical cyclones in recent decades cause greater impacts on mangroves bordering Australia's Great Barrier Reef. In E. Wolanksi & M. Kingsford (Eds.), *Oceanographic processes of coral reefs* (2nd ed.). CRC Press.

Eco-Markets, A. (2020). *Reef credit as market-based incentive mechanism*. Eco-Markets Australia.

Edgar, M., & Boyer, T. H. (2022). Nitrate adsorption and desorption during biological ion exchange. *Separation and Purification Technology*, *285*, 120363. https://doi.org/10.1016/j.seppur.2021.120363

Ferris, H. (1999). *NEMAPLEX: The nematode-plant expert information system*. University of California. http://nemaplex.ucdavis.edu/

Ferris, H., & Bongers, T. (2006). Nematode indicators of organic enrichment. *Journal of Nematology*, *38*(1), 3–12. https://www.ncbi.nlm.nih.gov/pubmed/19259424

Ferris, H., Bongers, T., & de Goede, R. G. M. (2001). A framework for soil food web diagnostics: Extension of the nematode faunal analysis concept. *Applied Soil Ecology*, *18*(1), 13–29. https://doi.org/10.1016/S0929-1393(01)00152-4

Gergel, S. E., Carpenter, S. R., & Stanley, E. H. (2005). Do dams and levees impact nitrogen cycling? Simulating the effects of flood alterations on floodplain denitrification. *Global Change Biology*, *11*(8), 1352–1367. https://doi.org/10.1111/j.1365-2486.2005.00966.x

Gordon, B. A., Dorothy, O., & Lenhart, C. F. (2020). Nutrient retention in ecologically functional floodplains: A review. *Water*, *12*(10), 2762. https://doi.org/10.3390/w12102762

Gordon, H., Haygarth, P. M., & Bardgett, R. D. (2008). Drying and rewetting effects on soil microbial community composition and nutrient leaching. *Soil Biology and Biochemistry*, *40*(2), 302–311. https://doi.org/10.1016/j.soilbio.2007.08.008

GreenCollar. (2017). *GreenCollar Reef Credits* (Vol. 2018).

Grundy, M. J., Rossel, R. A. V., Searle, R. D., Wilson, P. L., Chen, C., & Gregory, L. J. (2015). Soil and landscape grid of Australia. *Soil Research*, *53*(8), 835–844. https://doi.org/10.1071/Sr15191

Guerrieri, R., Templer, P., & Magnani, F. (2021). Canopy exchange and modification of nitrogen fluxes in forest ecosystems. *Current Forestry Reports*, *7*(3), 115–137. https://doi.org/10.1007/s40725-021-00141-y

Guillou, L., Bachar, D., Audic, S., Bass, D., Berney, C., Bittner, L., Boutte, C., Burgaud, G., de Vargas, C., Decelle, J., Del Campo, J., Dolan, J. R., Dunthorn, M., Edvardsen, B., Holzmann, M., Kooistra, W. H., Lara, E., Le Bescot, N., Logares, R., … Christen, R. (2013). The Protist ribosomal reference database (PR2): A catalog of unicellular eukaryote small sub-unit rRNA sequences with curated taxonomy. *Nucleic Acids Research*, *41*, D597–D604. https://doi.org/10.1093/nar/gks1160

Hamman, E., Brodie, J., Eberhard, R., Deane, F., & Bode, M. (2022). Regulating land use in the catchment of the Great Barrier Reef. *Land Use Policy*, *115*, 106001. https://doi.org/10.1016/j.landusepol.2022.106001

Hanrahan, B. R., Tank, J. L., Dee, M. M., Trentman, M. T., Berg, E. M., & McMillan, S. K. (2018). Restored floodplains enhance denitrification compared to naturalized floodplains in agricultural streams. *Biogeochemistry*, *141*(3), 419–437. https://doi.org/10.1007/s10533-018-0431-4

Hansen, S., Froseth, R. B., Stenberg, M., Stalenga, J., Olesen, J. E., Krauss, M., Radzikowski, P., Doltra, J., Nadeem, S., Torp, T., Pappa, V., & Watson, C. A. (2019). Reviews and syntheses: Review of causes and sources of NO emissions and NO leaching from organic arable crop rotations. *Biogeosciences*, *16*(14), 2795–2819. https://doi.org/10.5194/bg-16-2795-2019

Hess, L. J. T., Hinckley, E. L. S., Robertson, G. P., & Matson, P. A. (2020). Rainfall intensification increases nitrate leaching from tilled but not no-till cropping systems in the US Midwest. *Agriculture Ecosystems & Environment*, *290*, 106747. https://doi.org/10.1016/j.agee.2019.106747

Hill, A. R. (2019). Groundwater nitrate removal in riparian buffer zones: A review of research progress in the past 20 years. *Biogeochemistry*, *143*(3), 347–369. https://doi.org/10.1007/s10533-019-00566-5

Huang, B., Yan, G., Liu, G., Sun, X., Wang, X., Xing, Y., & Wang, Q. (2022). Effects of long-term nitrogen addition and precipitation reduction on glomalin-related soil protein and soil aggregate stability in a temperate forest. *Catena*, *214*, 106284. https://doi.org/10.1016/j.catena.2022.106284

Huddell, A., Ernfors, M., Crews, T., Vico, G., & Menge, D. N. L. (2023). Nitrate leaching losses and the fate of (15)N fertilizer in perennial intermediate wheatgrass and annual wheat - A field study. *Science of the Total Environment*, *857*(Pt 1), 159255. https://doi.org/10.1016/j.scitotenv.2022.159255

Ibrahim, M. H., Metali, F., U Tennakoon, K., & Sukri, R. S. (2021). Impacts of invasive acacias on ion deposition in a coastal Bornean tropical heath forest. *Journal of Forest Research*, *27*(1), 20–27. https://doi.org/10.1080/13416979.2021.1965700

Jin, K., White, P. J., Whalley, W. R., Shen, J., & Shi, L. (2017). Shaping an optimal soil by root-soil interaction. *Trends in Plant Science*, *22*(10), 823–829. https://doi.org/10.1016/j.tplants.2017.07.008

Jones, L., Provins, A., Holland, M., Mills, G., Hayes, F., Emmett, B., Hall, J., Sheppard, L., Smith, R., Sutton, M., Hicks, K., Ashmore, M., Haines-Young, R., & Harper-Simmonds, L. (2014). A review and application of the evidence for nitrogen impacts on ecosystem services. *Ecosystem Services*, *7*, 76–88. https://doi.org/10.1016/j.ecoser.2013.09.001

Jwaideh, M. A. A., Sutanudjaja, E. H., & Dalin, C. (2022). Global impacts of nitrogen and phosphorus fertiliser use for major crops on aquatic biodiversity. *International Journal of Life Cycle Assessment*, *27*(8), 1058–1080. https://doi.org/10.1007/s11367-022-02078-1

Kaden, U. S., Schulz-Zunkel, C., Fuchs, E., Horchler, P., Kasperidus, H. D., de Moraes Bonilha, O., Rupp, H., Tschikof, M., Weigelhofer, G., Hein, T., & Scholz, M. (2023). Improving an existing proxy-based approach for floodplain denitrification assessment to facilitate decision making on restoration. *Science of the Total Environment*, *892*, 164727. https://doi.org/10.1016/j.scitotenv.2023.164727

Kandulu, J., Thorburn, P., Biggs, J., & Verburg, K. (2018). Estimating economic and environmental trade-offs of managing nitrogen in Australian sugarcane systems taking agronomic risk into account. *Journal of Environmental Management*, *223*, 264–274. https://doi.org/10.1016/j.jenvman.2018.06.023

Karhu, K., Kalu, S., Seppänen, A., Kitzler, B., & Virtanen, E. (2021). Potential of biochar soil amendments to reduce N leaching in boreal field conditions estimated using the resin bag method. *Agriculture Ecosystems & Environment*, *316*, 107452. https://doi.org/10.1016/j.agee.2021.107452

Kong, A. Y. Y., Hristova, K., Scow, K. M., & Six, J. (2010). Impacts of different N management regimes on nitrifier and denitrifier communities and N cycling in soil microenvironments. *Soil Biology and Biochemistry*, *42*(9), 1523–1533. https://doi.org/10.1016/j.soilbio.2010.05.021

Kretz, L., Bondar-Kunze, E., Hein, T., Richter, R., Schulz-Zunkel, C., Seele-Dilbat, C., van der Plas, F., Vieweg, M., & Wirth, C. (2021). Vegetation characteristics control local sediment and nutrient retention on but not underneath vegetation in floodplain meadows. *PLoS One*, *16*(12), e0252694. https://doi.org/10.1371/journal.pone.0252694

Krüger, M., Potthast, K., Michalzik, B., Tischer, A., Küsel, K., Deckner, F. F. K., & Herrmann, M. (2021). Drought and rewetting events enhance nitrate leaching and seepage-mediated translocation of microbes from beech forest soils. *Soil Biology and Biochemistry*, *154*, 108153. https://doi.org/10.1016/j.soilbio.2021.108153

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, *82*(13), 1–26. https://doi.org/10.18637/jss.v082.i13

Lehmann, A., Zheng, W., Ryo, M., Soutschek, K., Roy, J., Rongstock, R., Maaß, S., & Rillig, M. C. (2020). Fungal traits important for soil aggregation. *Frontiers in Microbiology*, *10*, 2904. https://doi.org/10.3389/fmicb.2019.02904

Leifheit, E. F., Verbruggen, E., & Rillig, M. C. (2015). Arbuscular mycorrhizal fungi reduce decomposition of woody plant litter while increasing soil aggregation. *Soil Biology and Biochemistry*, *81*, 323–328. https://doi.org/10.1016/j.soilbio.2014.12.003

Lewis, S., McCloskey, G., Bainbridge, Z., Davis, A., Bartley, R., & Turner, R. (2024). Sediment and nutrient flux from land. In *Oceanographic processes of coral reefs* (pp. 126–142). CRC Press.

Li, B.-B., Roley, S. S., Duncan, D. S., Guo, J., Quensen, J. F., Yu, H.-Q., & Tiedje, J. M. (2021). Long-term excess nitrogen fertilizer increases sensitivity of soil microbial community to seasonal change revealed by ecological network and metagenome analyses. *Soil Biology and Biochemistry*, *160*, 108349. https://doi.org/10.1016/j.soilbio.2021.108349

Li, X. B., He, H. B., Zhang, X. D., Yan, X. Y., Six, J., Cai, Z. C., Barthel, M., Zhang, J. B., Necpalova, M., Ma, Q. Q., & Li, Z. A. (2019). Distinct responses of soil fungal and bacterial nitrate immobilization to land conversion from forest to agriculture. *Soil Biology and Biochemistry*, *134*, 81–89. https://doi.org/10.1016/j.soilbio.2019.03.023

Li, Y. Z., Song, D. P., Liang, S. H., Dang, P. F., Qin, X. L., Liao, Y. C., & Siddique, K. H. M. (2020). Effect of no-tillage on soil bacterial and fungal community diversity: A meta-analysis. *Soil & Tillage Research*, *204*, 104721. https://doi.org/10.1016/j.still.2020.104721

Li, Z., Tang, Z., Song, Z., Chen, W., Tian, D., Tang, S., Wang, X., Wang, J., Liu, W., Wang, Y., Li, J., Jiang, L., Luo, Y., & Niu, S. (2022). Variations and controlling factors of soil denitrification rate. *Global Change Biology*, *28*(6), 2133–2145. https://doi.org/10.1111/gcb.16066

Li, Z., Tian, D., Wang, B., Wang, J., Wang, S., Chen, H. Y. H., Xu, X., Wang, C., He, N., & Niu, S. (2019). Microbes drive global soil nitrogen mineralization and availability. *Global Change Biology*, *25*(3), 1078–1088. https://doi.org/10.1111/gcb.14557

Liang, W. J., Lou, Y. L., Li, Q., Zhong, S., Zhang, X. K., & Wang, J. K. (2009). Nematode faunal response to long-term application of nitrogen fertilizer and organic manure in Northeast China. *Soil Biology and Biochemistry*, *41*(5), 883–890. https://doi.org/10.1016/j.soilbio.2008.06.018

Liu, C., Cui, Y., Li, X., & Yao, M. (2021). Microeco: An R package for data mining in microbial community ecology. *FEMS Microbiology Ecology*, *97*(2), fiaa255. https://doi.org/10.1093/femsec/fiaa255

Liu, H., Gao, X., Li, C., Cai, Y., Song, X., & Zhao, X. (2025). Intercropping increases plant water availability and water use efficiency: A synthesis. *Agriculture*, *Ecosystems & Environment*, *379*(9), 109360. https://doi.org/10.1016/j.agee.2024.109360

Liu, T., Wu, X., Li, H., Ning, C., Li, Y., Zhang, X., He, J., Filimonenko, E., Chen, S., Chen, X., Gibson, D. J., Kuzyakov, Y., & Yan, W. (2022). Soil quality and r – K fungal communities in plantations after conversion from subtropical forest. *Catena*, *219*, 106584. https://doi.org/10.1016/j.catena.2022.106584

Liu, W., Jiang, L., Yang, S., Wang, Z., Tian, R., Peng, Z., Chen, Y., Zhang, X., Kuang, J., Ling, N., Wang, S., & Liu, L. (2020). Critical transition of soil bacterial diversity and composition triggered by nitrogen enrichment. *Ecology*, *101*(8), e03053. https://doi.org/10.1002/ecy.3053

Louca, S., Parfrey, L. W., & Doebeli, M. (2016). Decoupling function and taxonomy in the global ocean microbiome. *Science*, *353*(6305), 1272–1277. https://doi.org/10.1126/science.aaf4507

Lv, J., & Wu, Y. B. (2021). Nitrogen removal by different riparian vegetation buffer strips with different stand densities and widths. *Water Supply*, *21*(7), 3541–3556. https://doi.org/10.2166/ws.2021.119

Lyu, C. J., Li, X. J., Yuan, P., Song, Y. H., Gao, H. J., Liu, X. L., Liu, R. X., & Yu, H. B. (2021). Nitrogen retention effect of riparian zones in agricultural areas: A meta-analysis. *Journal of Cleaner Production*, *315*, 128143–128143. https://doi.org/10.1016/j.jclepro.2021.128143

Manici, L. M., Caputo, F., De Sabata, D., & Fornasier, F. (2024). The enzyme patterns of Ascomycota and Basidiomycota fungi reveal their different functions in soil. *Applied Soil Ecology*, *196*, 105323. https://doi.org/10.1016/j.apsoil.2024.105323

Manici, L. M., Caputo, F., Fornasier, F., Paletto, A., Ceotto, E., & De Meo, I. (2024). Ascomycota and Basidiomycota fungal phyla as indicators of land use efficiency for soil organic carbon accrual with woody plantations. *Ecological Indicators*, *160*, 111796. https://doi.org/10.1016/j.ecolind.2024.111796

Mappin, B., Ward, A., Hughes, L., Watson, J. E. M., Cosier, P., & Possingham, H. P. (2022). The costs and benefits of restoring a continent's terrestrial ecosystems. *Journal of Applied Ecology*, *59*(2), 408–419. https://doi.org/10.1111/1365-2664.14008

Martens, D. A., Reedy, T. E., & Lewis, D. T. (2004). Soil organic carbon content and composition of 130-year crop, pasture and forest land-use managements. *Global Change Biology*, *10*(1), 65–78. https://doi.org/10.1046/j.1529-8817.2003.00722.x

Maure, E. R., Terauchi, G., Ishizaka, J., Clinton, N., & DeWitt, M. (2021). Globally consistent assessment of coastal eutrophication. *Nature Communications*, *12*(1), 6142. https://doi.org/10.1038/s41467-021-26391-9

McCloskey, G. L., Baheerathan, R., Dougall, C., Ellis, R., Bennett, F. R., Waters, D., Darr, S., Fentie, B., Hateley, L. R., & Askildsen, M. (2021). Modelled estimates of dissolved inorganic nitrogen exported to the Great Barrier Reef lagoon. *Marine Pollution Bulletin*, *171*, 112655. https://doi.org/10.1016/j.marpolbul.2021.112655

McDowell, R. W., Noble, A., Pletnyakov, P., Haggard, B. E., & Mosley, L. M. (2020). Global mapping of freshwater nutrient enrichment and periphyton growth potential. *Scientific Reports*, *10*(1), 3568. https://doi.org/10.1038/s41598-020-60279-w

McGillycuddy, M., Popovic, G., Bolker, B. M., & Warton, D. I. (2025). Parsimoniously fitting large multivariate random effects in glmmTMB. *Journal of Statistical Software*, *112*(1), 1–19. https://doi.org/10.18637/jss.v112.i01

McKenzie, N., Jacquier, D., Maschmedt, D., Griffin, E., & Brough, D. (2012). *The Australian soil resource information system (ASRIS) technical specifications* (Revised Version 1.6).

McSorley, R. (2012). Ecology of the dorylaimid omnivore genera. *Nematology*, *14*(6), 645–663. https://doi.org/10.1163/156854112x651168

Menegat, S., Ledo, A., & Tirado, R. (2022). Greenhouse gas emissions from global production and use of nitrogen synthetic fertilisers in agriculture. *Scientific Reports*, *12*(1), 14490. https://doi.org/10.1038/s41598-022-18773-w

Mitchell, A. W., Bramley, R. G. V., & Johnson, A. K. L. (1997). Export of nutrients and suspended sediment during a cyclone-mediated flood event in the Herbert River catchment, Australia. *Marine and Freshwater Research*, *48*(1), 79–88. https://doi.org/10.1071/Mf96021

Nguyen, N. H., Song, Z. W., Bates, S. T., Branco, S., Tedersoo, L., Menke, J., Schilling, J. S., & Kennedy, P. G. (2016). FUNGuild: An open annotation tool for parsing fungal community datasets by ecological guild. *Fungal Ecology*, *20*, 241–248. https://doi.org/10.1016/j.funeco.2015.06.006

Noe, G. B., & Hupp, C. R. (2009). Retention of riverine sediment and nutrient loads by coastal plain floodplains. *Ecosystems*, *12*(5), 728–746. https://doi.org/10.1007/s10021-009-9253-5

Oberacker, P., Stepper, P., Bond, D. M., Hohn, S., Focken, J., Meyer, V., Schelle, L., Sugrue, V. J., Jeunen, G. J., Moser, T., Hore, S. R., von Meyenn, F., Hipp, K., Hore, T. A., & Jurkowski, T. P. (2019). Bio-on-magnetic-beads (BOMB): Open platform for high-throughput nucleic acid extraction and manipulation. *PLoS Biology*, *17*(1), e3000107. https://doi.org/10.1371/journal.pbio.3000107

Oka, Y. (2010). Mechanisms of nematode suppression by organic soil amendments-A review. *Applied Soil Ecology*, *44*(2), 101–115. https://doi.org/10.1016/j.apsoil.2009.11.003

Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Borman, T., Carvalho, G., Chirico, M., De Caceres, M., … Weedon, J. (2026). *vegan: Community ecology package* (version R package version 2.8–0). https://vegandevs.github.io/vegan/

Orr, C. H., Stanley, E. H., Wilson, K. A., & Finlay, J. C. (2007). Effects of restoration and reflooding on soil denitrification in a leveed Midwestern floodplain. *Ecological Applications*, *17*(8), 2365–2376. https://doi.org/10.1890/06-2113.1

Ostertag, R., Marín-Spiotta, E., Silver, W. L., & Schulten, J. (2008). Litterfall and decomposition in relation to soil carbon pools along a secondary forest chronosequence in Puerto Rico. *Ecosystems*, *11*(5), 701–714. https://doi.org/10.1007/s10021-008-9152-1

Pampolino, M. F., Urushiyama, T., & Hatano, R. (2000). Detection of nitrate leaching through bypass flow using pan lysimeter, suction cup, and resin capsule. *Soil Science and Plant Nutrition*, *46*(3), 703–711. https://doi.org/10.1080/00380768.2000.10409135

Pan, B. B., Xia, L. L., Wang, E. L., Zhang, Y. S., Mosier, A., Chen, D. L., & Lam, S. K. (2022). A global synthesis of soil denitrification: Driving factors and mitigation strategies. *Agriculture Ecosystems & Environment*, *327*(11), 107850. https://doi.org/10.1016/j.agee.2021.107850

Peng, S. M., Liu, W., Xu, G., Pei, X. J., Millerick, K., & Duan, B. L. (2021). A meta-analysis of soil microbial and physicochemical properties following native forest conversion. *Catena*, *204*, 105447. https://doi.org/10.1016/j.catena.2021.105447

Philippot, L., Griffiths, B. S., & Langenheder, S. (2021). Microbial community resilience across ecosystems and multiple disturbances. *Microbiology and Molecular Biology Reviews*, *85*(2), e00026-20. https://doi.org/10.1128/MMBR.00026-20

Porazinska, D. L., Giblin-Davis, R. M., Faller, L., Farmerie, W., Kanzaki, N., Morris, K., Powers, T. O., Tucker, A. E., Sung, W., & Thomas, W. K. (2009). Evaluating high-throughput sequencing as a method for metagenomic analysis of nematode diversity. *Molecular Ecology Resources*, *9*(6), 1439–1450. https://doi.org/10.1111/j.1755-0998.2009.02611.x

Puissant, J., Villenave, C., Chauvin, C., Plassard, C., Blanchart, E., & Trap, J. (2021). Quantification of the global impact of agricultural practices on soil nematodes: A meta-analysis. *Soil Biology and Biochemistry*, *161*, 108383. https://doi.org/10.1016/j.soilbio.2021.108383

Qian, P., & Schoenau, J. J. (2002). Practical applications of ion exchange resins in agricultural and environmental soil research. *Canadian Journal of Soil Science*, *82*(1), 9–21. https://doi.org/10.4141/S00-091

Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., Peplies, J., & Glockner, F. O. (2013). The SILVA ribosomal RNA gene database project: Improved data processing and web-based tools. *Nucleic Acids Research*, *41*, D590–D596. https://doi.org/10.1093/nar/gks1219

R Core Team. (2025). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Renaud, G., Stenzel, U., Maricic, T., Wiebe, V., & Kelso, J. (2015). deML: Robust demultiplexing of Illumina sequences using a likelihood-based approach. *Bioinformatics*, *31*(5), 770–772. https://doi.org/10.1093/bioinformatics/btu719

Rich, J. J., Heichen, R. S., Bottomley, P. J., Cromack, K., Jr., & Myrold, D. D. (2003). Community composition and functioning of denitrifying bacteria from adjacent meadow and forest soils. *Applied and Environmental Microbiology*, *69*(10), 5974–5982. https://doi.org/10.1128/AEM.69.10.5974-5982.2003

Rodriguez-Ramos, J. C., Cale, J. A., Cahill, J. F., Jr., Simard, S. W., Karst, J., & Erbilgin, N. (2021). Changes in soil fungal community composition depend on functional group and forest disturbance type. *New Phytologist*, *229*(2), 1105–1117. https://doi.org/10.1111/nph.16749

Saleem, M., Law, A. D., Sahib, M. R., Pervaiz, Z. H., & Zhang, Q. M. (2018). Impact of root system architecture on rhizosphere and root microbiome. *Rhizosphere*, *6*, 47–51. https://doi.org/10.1016/j.rhisph.2018.02.003

Salzman, J., Bennett, G., Carroll, N., Goldstein, A., & Jenkins, M. (2018). The global status and trends of payments for ecosystem services. *Nature Sustainability*, *1*(3), 136–144. https://doi.org/10.1038/s41893-018-0033-0

Sansupa, C., Wahdan, S. F. M., Hossen, S., Disayathanoowat, T., Wubet, T., & Purahong, W. (2021). Can we use functional annotation of prokaryotic taxa (FAPROTAX) to assign the ecological functions of soil bacteria? *Applied Sciences*, *11*(2), 688. https://www.mdpi.com/2076-3417/11/2/688

Sellers, G. S., Di Muri, C., Gómez, A., & Hänfling, B. (2018). Mu-DNA: A modular universal DNA extraction method adaptable for a wide range of sample types. *Metabarcoding and Metagenomics*, *2*, e24556. https://doi.org/10.3897/mbmg.2.24556

Shao, H., Wang, H. M., Delgado-Baquerizo, M., Dai, X. Q., Meng, S. W., Kardol, P., Wang, Y. X., Chen, F. S., Kou, L., Gao, D. C., & Fu, X. L. (2025). Nutrient enrichment shapes litter micro-food webs in a subtropical plantation. *Forest Ecology and Management*, *580*, 122545. https://doi.org/10.1016/j.foreco.2025.122545

Shi, L., Dossa, G. G. O., Paudel, E., Zang, H., Xu, J., & Harrison, R. D. (2019). Changes in fungal communities across a Forest disturbance gradient. *Applied and Environmental Microbiology*, *85*(12), e00080-00019. https://doi.org/10.1128/AEM.00080-19

Shrestha, J., Niklaus, P. A., Pasquale, N., Huber, B., Barnard, R. L., Frossard, E., Schleppi, P., Tockner, K., & Luster, J. (2014). Flood pulses control soil nitrogen cycling in a dynamic river floodplain. *Geoderma*, *228*, 14–24. https://doi.org/10.1016/j.geoderma.2013.09.018

Sikder, M. M., Vestergård, M., Sapkota, R., Kyndt, T., & Nicolaisen, M. (2020). Evaluation of metabarcoding primers for analysis of soil nematode communities. *Diversity*, *12*(10), 388. https://www.mdpi.com/1424-2818/12/10/388

Singh, G., Kaur, G., Williard, K., Schoonover, J., & Kang, J. (2018). Monitoring of water and solute transport in the Vadose zone: A review. *Vadose Zone Journal*, *17*(1), 160058. https://doi.org/10.2136/vzj2016.07.0058

Song, M., Li, X. M., Jing, S. S., Lei, L. J., Wang, J. L., & Wan, S. Q. (2016). Responses of soil nematodes to water and nitrogen additions in an old-field grassland. *Applied Soil Ecology*, *102*, 53–60. https://doi.org/10.1016/j.apsoil.2016.02.011

State of Queensland. (2024). *Climate change in the far north region*.

Su, L. X., Shen, Z. Z., Ou, Y. N., Tao, C. Y., Ruan, Y. Z., Li, R., & Shen, Q. R. (2017). Novel soil fumigation strategy suppressed plant-parasitic nematodes associated with soil nematode community alterations in the field. *Applied Soil Ecology*, *121*, 135–142. https://doi.org/10.1016/j.apsoil.2017.09.039

Swanston, C., Homann, P. S., Caldwell, B. A., Myrold, D. D., Ganio, L., & Sollins, P. (2004). Long-term effects of elevated nitrogen on forest soil organic matter stability. *Biogeochemistry*, *70*(2), 229–252. https://doi.org/10.1023/B:BIOG.0000049341.37579.86

Takahashi, S., Tomita, J., Nishioka, K., Hisada, T., & Nishijima, M. (2014). Development of a prokaryotic universal primer for simultaneous analysis of bacteria and archaea using next-generation sequencing. *PLoS One*, *9*(8), e105592. https://doi.org/10.1371/journal.pone.0105592

Truu, M., Nolvak, H., Ostonen, I., Oopkaup, K., Maddison, M., Ligi, T., Espenberg, M., Uri, V., Mander, U., & Truu, J. (2020). Soil bacterial and archaeal communities and their potential to perform N-cycling processes in soils of boreal forests growing on well-drained peat.

Frontiers in Microbiology, *11*, 591358. https://doi.org/10.3389/fmicb.2020.591358

van Grieken, M. E., Roebeling, P. C., Bohnet, I. C., Whitten, S. M., Webster, A. J., Poggio, M., & Pannell, D. (2019). Adoption of agricultural management for Great Barrier Reef water quality improvement in heterogeneous farming communities. *Agricultural Systems*, *170*, 1–8. https://doi.org/10.1016/j.agsy.2018.12.003

Vilas, M. P., Thorburn, P. J., Fielke, S., Webster, T., Mooij, M., Biggs, J. S., Zhang, Y. F., Adham, A., Davis, A., Dungan, B., Butler, R., & Fitch, P. (2020). 1622WQ: A web-based application to increase farmer awareness of the impact of agriculture on water quality. *Environmental Modelling & Software*, *132*, 104816. https://doi.org/10.1016/j.envsoft.2020.104816

Vukicevich, E., Lowery, T., Bowen, P., Urbez-Torres, J. R., & Hart, M. (2016). Cover crops to increase soil microbial diversity and mitigate decline in perennial agriculture. A review. *Agronomy for Sustainable Development*, *36*(3), 1–14. https://doi.org/10.1007/s13593-016-0385-7

Waltham, N., Canning, A., Smart, J., Hasan, S., Curwen, G., & Waterhouse, J. (2020). *Scoping land conversion options for high DIN risk, low-lying sugarcane, to alternative use for water quality improvement in dry tropics catchments*.

Waltham, N. J., Wegscheidl, C., Volders, A., Smart, J. C. R., Hasan, S., Ledee, E., & Waterhouse, J. (2021). Land use conversion to improve water quality in high DIN risk, low-lying sugarcane areas of the Great Barrier Reef catchments. *Marine Pollution Bulletin*, *167*, 112373. https://doi.org/10.1016/j.marpolbul.2021.112373

Walton, C. R., Zak, D., Audet, J., Petersen, R. J., Lange, J., Oehmke, C., Wichtmann, W., Kreyling, J., Grygoruk, M., Jablonska, E., Kotowski, W., Wisniewska, M. M., Ziegler, R., & Hoffmann, C. C. (2020). Wetland buffer zones for nitrogen and phosphorus retention: Impacts of soil type, hydrology and vegetation. *Science of the Total Environment*, *727*, 138709. https://doi.org/10.1016/j.scitotenv.2020.138709

Wan, X. H., Chen, X. L., Huang, Z. Q., & Chen, H. Y. H. (2021). Global soil microbial biomass decreases with aridity and land-use intensification. *Global Ecology and Biogeography*, *30*(5), 1056–1069. https://doi.org/10.1111/geb.13282

Wang, H., He, X., Zhang, Z. F., Li, M. G., Zhang, Q., Zhu, H. Y., Xu, S. T., & Yang, P. W. (2021). Eight years of manure fertilization favor copiotrophic traits in paddy soil microbiomes. *European Journal of Soil Biology*, *106*, 103352. https://doi.org/10.1016/j.ejsobi.2021.103352

Wang, J., Chadwick, D. R., Cheng, Y., & Yan, X. (2018). Global analysis of agricultural soil denitrification in response to fertilizer nitrogen. *Science of the Total Environment*, *616–617*, 908–917. https://doi.org/10.1016/j.scitotenv.2017.10.229

Wei, C., Zheng, H., Li, Q., Lu, X., Yu, Q., Zhang, H., Chen, Q., He, N., Kardol, P., Liang, W., & Han, X. (2012). Nitrogen addition regulates soil nematode community composition through ammonium suppression. *PLoS One*, *7*(8), e43384. https://doi.org/10.1371/journal.pone.0043384

Welti, N., Bondar-Kunze, E., Tritthart, M., Pinay, G., & Hein, T. (2012). Nitrogen dynamics in complex Danube River floodplain systems: Effects of restoration. *River Systems*, *20*(1–2), 71–85. https://doi.org/10.1127/1868-5749/2011/0047

Wey, H., Hunkeler, D., Bischoff, W. A., & Bunemann, E. K. (2021). Field-scale monitoring of nitrate leaching in agriculture: Assessment of three methods. *Environmental Monitoring and Assessment*, *194*(1), 4. https://doi.org/10.1007/s10661-021-09605-x

Woodward, E., Raij-Hoffman, I., Scow, K., & Tautges, N. (2022). Alfalfa reduces winter nitrate leaching relative to organic and conventional annual vegetable systems: Resin bag field measurements and modeling with HYDRUS-1D. *Journal of Soil and Water Conservation*, *77*(5), 450–465. https://doi.org/10.2489/jswc.2022.00155

Xing, W., Lu, X. M., Niu, S. L., Chen, D. M., Wang, J. S., Liu, Y., Wang, B. X., Zhang, S., Li, Z. L., Yao, X. J., Yu, Q., & Tian, D. S. (2022). Global patterns and drivers of soil nematodes in response to nitrogen enrichment. *Catena*, *213*, 106235. https://doi.org/10.1016/j.catena.2022.106235

Xu, C., Xu, X., Ju, C., Chen, H. Y. H., Wilsey, B. J., Luo, Y., & Fan, W. (2021). Long-term, amplified responses of soil organic carbon to nitrogen addition worldwide. *Global Change Biology*, *27*(6), 1170–1180. https://doi.org/10.1111/gcb.15489

Xue, P., Minasny, B., & McBratney, A. B. (2022). Land-use affects soil microbial co-occurrence networks and their putative functions. *Applied Soil Ecology*, *169*, 104184. https://doi.org/10.1016/j.apsoil.2021.104184

Yang, Y., Chai, Y., Xie, H., Zhang, L., Zhang, Z., Yang, X., Hao, S., Gai, J., & Chen, Y. (2023). Responses of soil microbial diversity, network complexity and multifunctionality to three land-use changes. *Science of the Total Environment*, *859*(1), 160255. https://doi.org/10.1016/j.scitotenv.2022.160255

Yang, Y., Chen, X., Liu, L., Li, T., Dou, Y., Qiao, J., Wang, Y., An, S., & Chang, S. X. (2022). Nitrogen fertilization weakens the linkage between soil carbon and microbial diversity: A global meta-analysis. *Global Change Biology*, *28*(21), 6446–6461. https://doi.org/10.1111/gcb.16361

Yao, L., Adame, M. F., & Chen, C. (2021). Resource stoichiometry, vegetation type and enzymatic activity control wetlands soil organic carbon in the Herbert River catchment, North-East Queensland. *Journal of Environmental Management*, *296*, 113183. https://doi.org/10.1016/j.jenvman.2021.113183

Zhang, R., Vivanco, J. M., & Shen, Q. (2017). The unseen rhizosphere root-soil-microbe interactions for crop production. *Current Opinion in Microbiology*, *37*, 8–14. https://doi.org/10.1016/j.mib.2017.03.008

Zhang, X., Liu, X., Zhang, M., Dahlgren, R. A., & Eitzel, M. (2010). A review of vegetated buffers and a meta-analysis of their mitigation efficacy in reducing nonpoint source pollution. *Journal of Environmental Quality*, *39*, 76–84. https://doi.org/10.2134/jeq2008.0496

Zhang, Y., & Shangguan, Z. (2023). Long-term N addition accelerated organic carbon mineralization in aggregates by shifting microbial community composition. *Agriculture, Ecosystems & Environment*, *342*, 108249. https://doi.org/10.1016/j.agee.2022.108249

Zhao, M., Zhao, J., Yuan, J., Hale, L., Wen, T., Huang, Q., Vivanco, J. M., Zhou, J., Kowalchuk, G. A., & Shen, Q. (2021). Root exudates drive soil-microbe-nutrient feedbacks in response to plant growth. *Plant, Cell & Environment*, *44*(2), 613–628. https://doi.org/10.1111/pce.13928

Zhao, Y. P., Wang, Z. H., Cai, K., Wang, S. L., Wright, A. L., & Jiang, X. J. (2024). Stability of nitrogen-cycling microbial communities and impact on microbial nitrogen function under different land use practices. *Applied Soil Ecology*, *204*, 105729. https://doi.org/10.1016/j.apsoil.2024.105729

Zhou, Z., Wang, C., & Luo, Y. (2020). Meta-analysis of the impacts of global change factors on soil microbial diversity and functionality. *Nature Communications*, *11*(1), 3072. https://doi.org/10.1038/s41467-020-16881-7

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

File S1. Summary tables of soil analytes from five pooled 0–20 cm samples within each plot prior to nitrate application with the cane and *Melaleuca* sites.

File S2. Summary tables of differential abundance model outputs from glmmTMB beta regression models, presented separately for bacteria, fungi and nematodes. Each table lists taxon-level estimates of fixed effects (intercept, nitrogen load, vegetation type), along with standard error, and *p*-value. Models were fitted using CSS-normalised relative abundance (bounded 0–1), with plot included as a random effect to account for repeated sampling before and after nitrate application. Pre-application samples were assigned a nitrogen load of 0 kg N/ha.

How to cite this article: Canning, A., & Tink, M. (2026). Floodplain reforestation reduces nitrate loss through soil microbial pathways. *Ecological Solutions and Evidence*, *7*, e70266. https://doi.org/10.1002/2688-8319.70266