

Relative to rainforests and grasslands, banana and sugarcane soils have half the microbial biomass and highly distinct bacterial and fungal communities

Henry W.G. Birt^{a,1}, Anthony B. Pattison^b, Yolima Carrillo^c, Scott N. Lieske^a, Rebecca Lyons^a, Hazel R. Lapis-Gaza^b, Jiarui Sun^a, Paul G. Dennis^{a,*}

^a School of the Environment, The University of Queensland, Turrbal Country, Brisbane, QLD, Australia

^b Department of Agriculture and Fisheries, Centre for Wet Tropics Agriculture, South Johnstone, QLD, Australia

^c Hawkesbury Institute for the Environment, Western Sydney University, Richmond, NSW, Australia

ARTICLE INFO

Keywords:

Microbiome
Land use
Microbial biomass
Bacteria
Fungi
Fusarium wilt
Banana
Sugarcane

ABSTRACT

Soil microbial communities mediate a range of ecosystem services and are impacted by land use. The Wet Tropics region of north Queensland, Australia, is a biodiversity hotspot with some of the world's oldest rainforests, but also has large areas converted for agriculture. We explored soil abiotic and biotic characteristics in 86 sites across four of the key land uses in this area: banana production, sugarcane production, grassland, and rainforest. Furthermore, we characterised sites where wild bananas were found in rainforests to bridge the associations found in natural and agricultural areas. Soil abiotic and biotic characteristics were found to differ between landuses, with commercial banana soils being the most distinct. Commercial banana and sugarcane soils had less soil carbon, and banana soils were also less acidic and had higher zinc and nitrate levels than other landuses. Interestingly, banana and sugarcane soils had half the microbial biomass of other landuses, including wild banana. The diversity of soil bacterial and fungal communities was also highly distinct in commercial banana soils, with significantly larger relative abundances of *Fusarium oxysporum*, a fungal species complex that includes important plant pathogens. Differences in soil biotic characteristics between landuses were significantly correlated with soil carbon, nitrogen, phosphorus, and pH. Our results demonstrate that land management can profoundly impact soil microbial communities, with potential consequences for ecosystem functioning.

1. Introduction

Soil bacteria and fungi underpin vital ecosystem services such as nutrient cycling, pathogen control and water purification (Saccá et al., 2017). These microbes are in turn influenced by anthropogenic land management (e.g., tillage; Nikitin et al., 2020), fertilisation (Bei et al., 2018), and monocropping (Shen et al., 2018), which influences their ability to perform ecosystem services with implications for global carbon stocks and climate change (Powlson et al., 2011). As >50 % of terrestrial ecosystems are influenced by anthropogenic management (Hooke et al., 2012), the impact of anthropogenic management on microbial ecosystem services globally could be substantial. To understand the impacts, a special focus should be placed on biodiversity hotspots as losses in ecosystem services here can result in a disproportionate loss in flora and fauna when compared to other areas (Marchese, 2015). Consequently, it is imperative to investigate various biodiversity

hotspots, as they can function as representative models for phenomena observed in hotspots globally.

The Queensland Wet Tropics, a UNESCO World Heritage area, encompasses diverse ecosystems like the Daintree rainforest, Great Barrier Reef and unique sclerophyll and mangrove forests (UNESCO, 2022; Richards and Day, 2018; Standing Committee, 2012; Roberts et al., 2021). However, these protected areas are also in the same biogeographical area as intensive agricultural sites including banana, sugarcane, and livestock production (Australian Banana Growers Council, 2020; Lavarack, 2016; Weber et al., 2021). While these industries support the local economy (Emtage and Herbohn, 2012), the impact they could have on soil microbes within this biodiversity hotspot are unclear. Elucidating the relationship between management and microbial ecosystem services in and around the Wet Tropics could unlock innovative strategies for managing vital services like disease control, pollution mitigation, and carbon sequestration (Bakker et al., 2018; Sanjuan

* Corresponding author.

E-mail address: p.dennis@uq.edu.au (P.G. Dennis).

¹ Current address: Department of Earth and Environmental Sciences, The University of Manchester, Manchester, UK.

et al., 2020; Bhattacharyya et al., 2022), with potential ramifications for climate dynamics (Harris et al., 2021). However, information on consistent microbial changes across landscapes is lacking, hindering effective management for both agriculture and regional conservation.

A study from sub-tropical Queensland, a climatic region to the south of The Wet Tropics, reported reduced organic P fractions, as well as altered bacterial diversity and phosphatase activity after converting natural ecosystems to crops (Zhang et al., 2021). Similarly, an Australia-

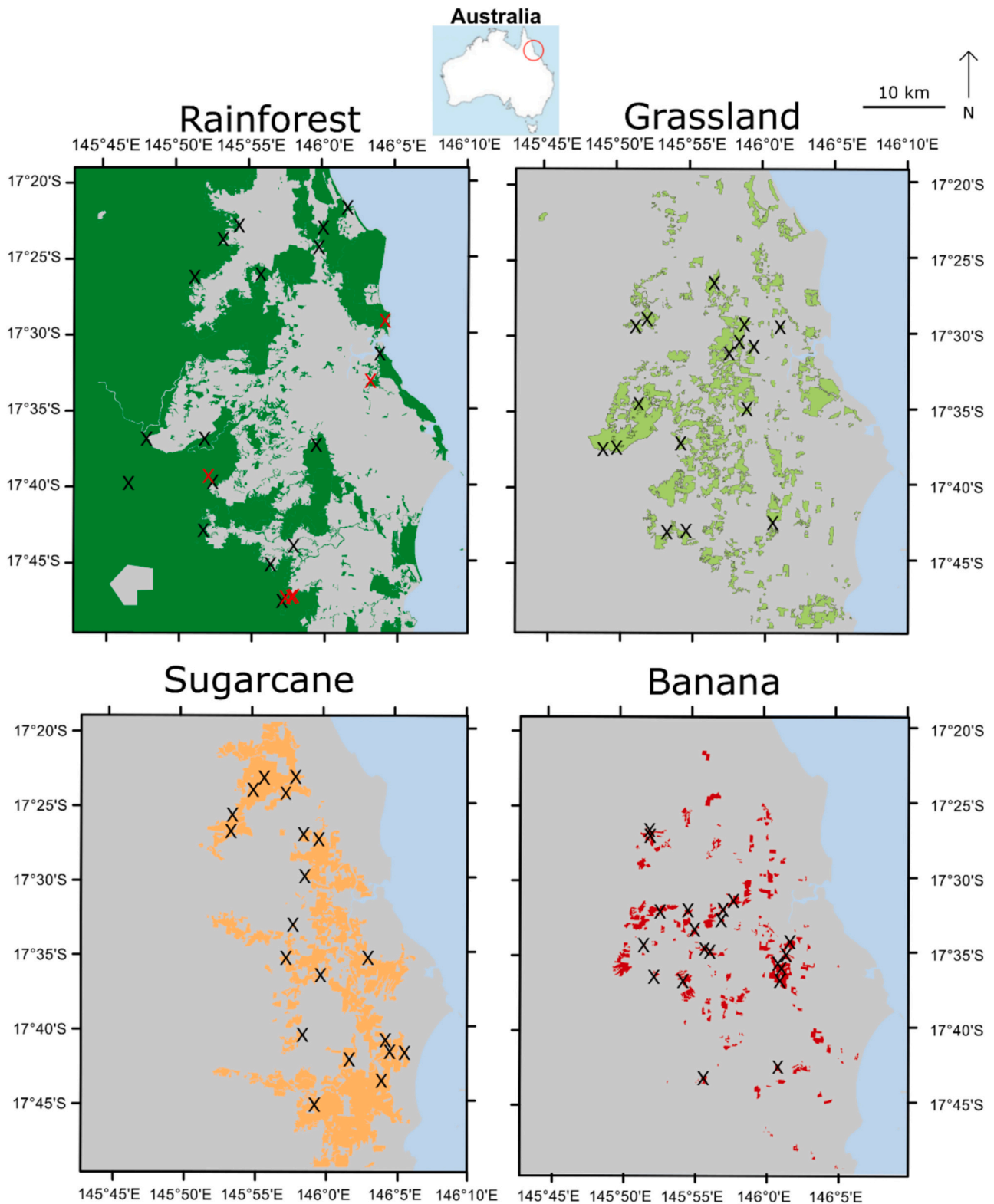


Fig. 1. The sample sites allocated by random stratified sampling to each land use in the study area. Black crosses indicate where samples were taken within a land use and highlighted areas show the extent of that land use in the study area. Red crosses indicate areas where wild banana were sampled in rainforest areas. Inset map of Australia shows the position of the study site nationally. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

wide study supported this, finding no link between soil microbial biodiversity and soil fertility in croplands while a clear link between these factors was present in natural ecosystems (Delgado-Baquerizo et al., 2017). This disruption highlights the impact of landuse change on soil biogeography. Nevertheless, while conversion to agricultural land has been shown to disrupt trends of soil biogeography, there is evidence that soil abiotic properties can explain a large proportion of the patterns of diversity of soil microbes within agricultural areas (Xue et al., 2018).

Here, we used a biogeographical approach to determine the impact of landuse on soil abiotic and biotic conditions in The Wet Tropics. By studying a variety of sites and increasing understanding about what may cause the distribution of microbes within them, we aimed to demonstrate that landuse within The Wet Tropics has consistent impacts on soil microbes. If this was true, management may be altered in the future to produce consistent beneficial effects for ecosystem conservation and resilience as well as agricultural management. We focused on four key landuses in the same landscape: banana production, sugarcane production, grassland, and rainforest. To bridge the associations between 'natural' and agricultural areas we also compared areas where wild bananas grow in rainforest areas. Finally, we conclude with a discussion of how changes observed within The Wet Tropics compares with other patterns of soil microbial biogeography.

2. Material and methods

2.1. Sample collection and study area

Details of the site selection are provided in our Supplementary methods. Briefly, 86 sites, comprising rainforest, grassland, sugarcane, and banana, were sampled using stratified random sampling within a 48 km × 56 km area of The Wet Tropics, North Queensland (Table S1 and Fig. 1). These landuses represent various levels of management intensity: banana and sugarcane sites are monocrops heavily managed with pesticide and fertiliser. Grassland sites were designated 'grazing under native vegetation' that were grassland sites with no or varying levels of grazing intensity, hereafter referred to as simply grassland. Rainforest sites were forested areas that were designated as national park, managed resource protection sites, or residual native cover. Although The Wet Tropics includes areas of mangrove and wet sclerophyll forest, exclusively notophyll rainforest areas were sampled. While these sites are relatively wild, it must be acknowledged that they are not entirely free of anthropogenic influence. For example, minor activities in rainforest areas include native tree planting, feral pig removal, and trail maintenance. Nineteen to twenty-one sites were sampled per land use. As the region is within the native range of two wild banana species: *Musa accuminata* subsp. *banksii* and *Musa jackeyi* (Office of the Gene Technology Regulator, 2023), banana sites included not only farms, but also six sites within rainforests at which soil was sampled around the base of wild banana plants. This design facilitated comparisons bananas in sites with high and negligible management intensity.

At each site, nine points were marked in a 3 m × 3 m grid covering 9 m². A 10 cm deep core was taken from each subsite, pooled into a composite sample, and then homogenised. Roots or other living material were removed. Samples were then transported to the lab in a cool box with ice until further processing on the same day. A sub-sample of the composite was dried in a 120 °C oven for 24 h for abiotic analysis, and the remaining soil was then frozen at -20 °C. DNA was extracted from frozen soil according to the method of Deng et al. (2010) with minor modifications (Supplementary Methods).

2.2. Soil physicochemical characteristics

Full details of our soil chemical analyses are provided in the Supplementary methods. Briefly, total organic carbon and total nitrogen were simultaneously determined in soil samples through high-

temperature (720 °C) catalytic combustion (Pt/Al₂O₃) oxidation on a Soli TOC® cube (Elementar Analysis Systems, Germany) (Pitt et al., 2003). Other key soil elements were determined using ICP-OES according to the method of Rayment and Lyons (2011) and a modified method of Baethgen and Alley (1989) was used to analyse water-extractable ions on a SEAL AQ2+ autoanalyser (Baethgen and Alley, 1989; USEPA, 1983).

2.3. Soil microbiological characteristics

Full details of our soil biological analyses are provided in the Supplementary methods. Briefly, microbial phospholipid fatty acids (PLFAs) were analysed as indicators of total microbial, bacterial, and fungal biomass in soil according to Buyer and Sasser (2012). In addition, the diversity of soil bacterial and fungal communities was characterised using 16S rRNA and ITS2 gene amplicon sequencing, respectively.

2.4. Statistical analysis

The influence of landuse on univariate response variables (alpha diversity and biomass) was assessed using ANOVA. The associations between these response variables and the abiotic predictor variables were assessed using multiple linear regression, with parsimonious models being identified using forward selection. Multivariate response data (community composition and abiotic variables) were analysed using PERMANOVA, ordination, and Mantel tests. Landuse was added as a variable to both univariate and multivariate models to assess its explanatory power. All statistical analyses were conducted using R (see Supplementary Methods for further details).

3. Results

3.1. Soil abiotic characteristics

Soil abiotic characteristics were significantly different between land uses (PERMANOVA: $R^2 = 26.34\%$, $F = 7.15$, $P < 0.001$; Fig. 2). The pH of commercial banana soils was significantly more alkaline than other landuses, except for wild banana (Table S3). Nitrate was considerably higher on average in banana soils than rainforest, grassland, or sugarcane areas, yet wild bananas were found to grow in much higher nitrate areas on average than those found in production areas (Table S3). Soil carbon was significantly reduced by 30 % in banana production areas relative to rainforest soils (Table S3). Zinc levels were also significantly higher in banana production areas than elsewhere (between 186 and 337 % higher on average, Table S3).

3.2. Soil microbial phospholipid fatty acids

PLFA analyses revealed lower microbial biomass in banana and sugarcane soils compared to rainforests. Reductions were 46.8 % and 60.1 % for total PLFAs, respectively; fungal PLFAs showed similar declines (50.4 % and 60.9 %, Fig. 3). While bacterial PLFAs decreased in banana soils (36.0 %), they remained higher than sugarcane (27.1 % lower than banana, 53.3 % lower than rainforest). Rainforest had the highest fungal:bacterial PLFA ratio, indicating a higher proportion of fungi. Grassland had a lower fungal:bacterial ratio than rainforest, while banana had the lowest, suggesting a dominance of bacteria (Fig. 3). No significant differences in total, microbial, bacterial or fungal PLFAs were observed between rainforest and grassland or wild banana sites.

Zinc was associated with a decline in biomass across total, bacterial, and fungal biomass (Table 1); however, this trend appeared to be driven by a small number of high zinc concentration sites (Figs. S1–S4). As such, zinc's overall influence on the final model was often small, represented by a small beta coefficient, despite being significant. Total nitrogen was associated with an increase in the amount of bacterial and total microbial biomass (Table 1, Figs. S1 and S2), while fungal biomass

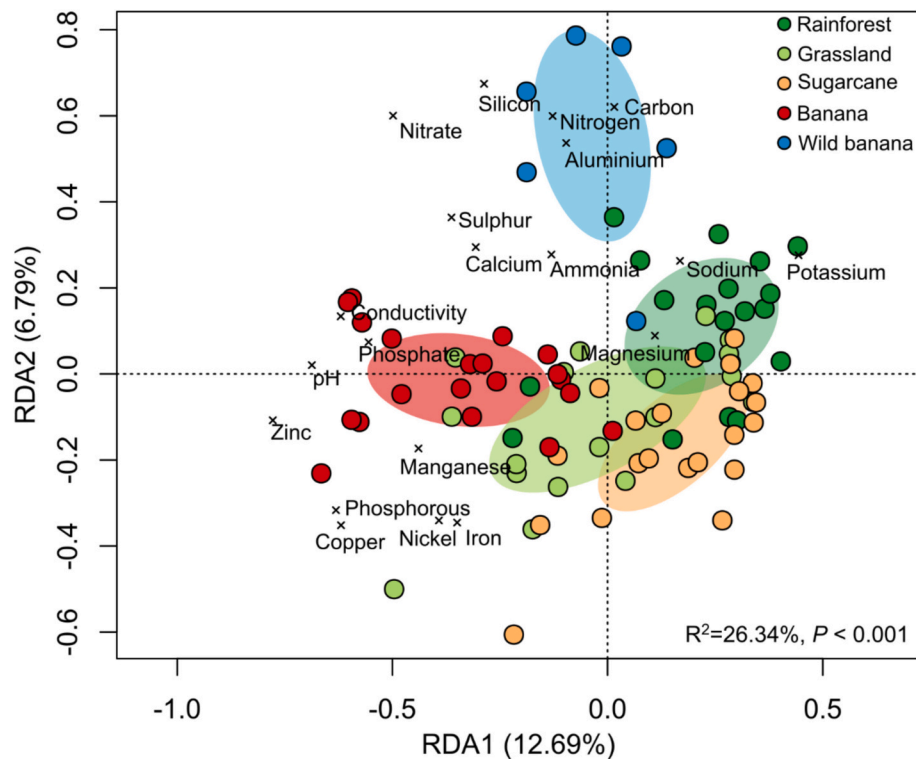


Fig. 2. Redundancy analysis (RDA) highlighting the differences in abiotic characteristics between various land use types. The ellipses represent standard deviations of the group centroids. Results from a PERMANOVA test comparing the differences between land uses in inset.

was associated with an increase in total carbon (Table 1, Fig. S3). Increases in soil aluminium were associated with increases in bacterial biomass (Table 1, Fig. S2). Soil pH was the most strongly associated variable with fungal:bacterial biomass (Fig. S4). As soils became more neutral, a lower fungi:bacterial biomass ratio was observed, suggesting more acidic soils favoured increases in the relative abundance of fungi. For all microbial biomass metrics, land use provided a significant explanation of the residual variation (Table 1).

3.3. Microbial community composition

Distinct fungal and bacterial communities were associated with each land use (Table 2, Fig. 4). Proteobacteria were the largest bacterial phylum found in all soils (Fig. S5), while Acidobacteriota formed a lower proportion of the community in sugarcane and banana soils. Actinobacteria were, on average, a larger proportion of the community in banana soils than in other land uses. For fungal classes, Sordariomycetes were dominant in sugarcane, banana, and wild banana soils while Agaricomycetes formed a greater proportion of the community in rainforest and grassland soils (Fig. S5).

Among the 433 bacterial OTUs showing significant differences in abundance across land uses, 15 had an average relative abundance exceeding 1 % in at least one land use (Fig. 5). These bacteria represented a diverse phylogenetic range, belonging to four distinct phyla. The decline of four differentially abundant Acidobacteriota OTUs was observed not only in sugarcane and banana sites but also in wild banana sites. In contrast, Nitrospirota OTUs displayed increased abundance in both banana and wild banana locations.

For fungal OTUs, 209 exhibited significantly different relative abundance between land uses; however, only 18 had an average abundance of >1 % in at least one land use (Fig. 6). Among these, three belonged to the Hypocreales order and were predominantly found in banana soils. One of these three was a *Fusarium oxysporum* (OTU1, Fig. 6). OTU1 relative abundance was 74 times greater in banana soils (6.7 % of reads on average) than rainforest areas (0.1 % of reads on

average, Fig. 6). Most of the differentially abundant unclassified fungi and three Agaricales were indicative of rainforest or wild banana soils.

3.4. Abiotic correlations with microbial diversity

Bacterial community composition could be significantly explained by change in a range of abiotic variables (Fig. 4). Nevertheless, land use could still significantly explain residual variation in models that included only abiotic variables (Table 1 and S4). Increased silicon, phosphorus, and soil pH were mainly associated with bacterial community composition from banana sites, with soil pH having the largest impact (Fig. 4, Table S4). Increased soil carbon was associated with bacterial community composition in wild banana and rainforest sites.

Significant variations in fungal community composition were also correlated with multiple abiotic variables (Tables 1 and S4). Again, when models incorporated only abiotic variables, land use accounted for a significant portion of the residual variation (Table S4). Zinc was most closely associated with banana sites and explained the most variation of any abiotic variable (Fig. 4, Table S4). Soil pH and conductivity was also associated with fungal community composition in banana sites (Fig. 4, Table S4). Increased potassium more associated with sugarcane and rainforest sites respectively, while reduced soil carbon was indicative of sugarcane fungal communities and increased soil carbon was associated with rainforest fungal communities (Fig. 4).

3.5. Soil microbial alpha diversity

According to Shannon's diversity, bacterial communities were more diverse in wild banana and banana soils than in other land uses (Table 2, Fig. S6). Abiotic variables predicted differences in bacterial alpha diversity; the residual variation could not be explained by different land uses (Table S4). Increases in soil pH, calcium, zinc, and silicon were all associated with an increase in bacterial Shannon diversity (Tables 2 and S4, Fig. S7). Increases in soil copper were associated with a modest decrease in bacterial Shannon diversity (Tables 1 and S4, Fig. S7).

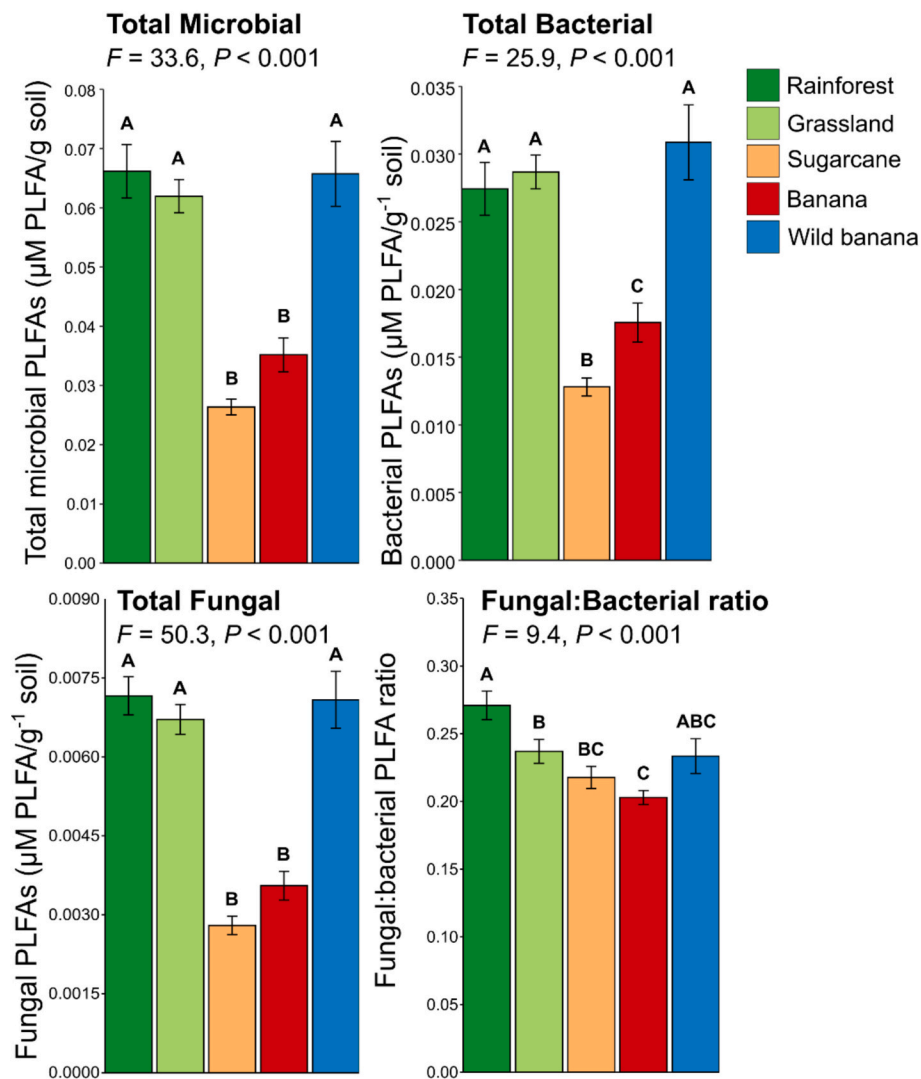


Fig. 3. Bar charts showing the difference in microbial biomass and biomass ratio between land uses in the Wet Tropics. Letters indicate significantly different groups according to post hoc analysis.

Fungal alpha diversity did not differ between land uses and there was no correlation between fungal Shannon diversity and soil abiotic variables (Table 2, Fig. S6).

4. Discussion

Anthropogenic land management like tillage, monoculture, and fertilisation impact soil microbial biodiversity, impacting on ecosystem services like nutrient and carbon storage. This study in Australia's Wet Tropics, a biodiversity hotspot, explored these effects and their potential wider consequences. Studying the Wet Tropics as a model can inform understanding of similar changes in other hotspots globally. Importantly, demonstrating these effects at the landscape scale provides evidence that consistent land management practices can be used to manage soil microbes across entire regions or large agricultural sectors.

4.1. Landuses exhibited characteristic soil abiotic profiles

Landuse significantly impacted soil abiotic properties across the study area. Notably, banana production areas exhibited more neutral pH (Fig. 2, Table S3), likely due to liming practices common for increasing nutrient availability (Pattison et al., 2008). This coincided with significantly higher nitrate levels in banana soils than the other three landuses

(Table S3), reflecting their nitrogen-intensive cropping systems. Compared to other crops, banana production generally employs higher nitrogen application (e.g., 400 kg N ha⁻¹ vs. 140–170 kg N ha⁻¹ for sugarcane; Canegrowers, 2020). Elevated phosphate, total phosphorous, and conductivity further support the influence of fertilisation on banana soils (Table S3). Interestingly, wild banana areas showed similar nitrate enrichment and slightly higher pH, potentially linked to disturbance-induced nutrient release, such as fire or fallen trees from storms (Marod et al., 2010).

Soil carbon and nitrogen was on average more than halved in sugarcane soils compared to rainforest areas and still drastically reduced even when compared to banana production areas (Table S3). This could be due to the intensive tillage required in sugarcane production to establish a suitable seed bed (Calcino et al., 2008; Skocaj et al., 2013). Furthermore, cane crop residue can sometimes be managed through controlled burns (Pinakana et al., 2023). Intense tillage and the burning of crop residue has been shown to decrease soil nitrogen and carbon storage in soils (Robertson and Thorburn, 2007; Singh and Rengel, 2007). By comparison, tillage in banana production and crop residues are left to decompose in-row which may account for the higher soil carbon and nitrogen seen in these soils (Geense et al., 2015). Vegetation burning has been shown to increase soil carbon in forests, but these prescribed burns are often less frequent, of lower intensity, and do

Table 1

A summary of significant abiotic variable model terms that explain changes in microbial community biotic variables between land uses. The last row indicates whether land use could be added as a significant term using a hierarchical ANOVA approach.

Abiotic variable	Biotic variable								Total
	Total microbial biomass	Total bacterial biomass	Total fungal biomass	Fungal: bacterial biomass ratio	Bacterial Shannon diversity	Bacterial community composition	Fungal Shannon diversity	Fungal community composition	
Aluminium	-	✓**	-	-	-	-	-	-	1
Calcium	-	-	-	-	✓**	-	-	-	1
Copper	-	-	-	-	✓*	✓*	-	-	2
Electrical conductivity	-	-	-	-	-	-	-	✓**	1
Manganese	-	-	-	✓*	-	-	-	-	1
Potassium	-	-	-	-	-	-	-	✓**	1
Phosphate	-	-	-	✓***	-	✓*	-	-	2
Phosphorus	-	-	-	-	-	✓***	-	-	1
Silicon	-	-	-	-	-	✓***	-	✓***	3
Soil pH	-	-	-	✓***	-	✓***	-	✓***	4
Total carbon	-	-	✓***	-	-	✓***	-	✓***	3
Total nitrogen	✓***	✓***	-	-	-	-	-	-	2
Zinc	✓***	✓**	✓***	✓***	✓*	✓***	-	✓***	7
Landuse explained residual?	✓***	✓***	✓***	✓*	-	✓***	-	✓***	-

Asterisks represent the significance of model terms ($P \leq 0.05^*$; $P \leq 0.01^{**}$; $P \leq 0.001^{***}$).

Table 2

The impact of land use on the alpha and beta diversity of soil microbial communities as represented by the Shannon Diversity Index and changes in Euclidean distance of Hellinger transformed OTU relative abundances. These were analysed using ANOVA and PERMANOVA, respectively.

Group	Shannon's diversity		Community composition		
	F value	P value	R ² (%)	F value	P value
Bacteria (16S)	9.5	<0.001***	27.89	7.8	<0.001***
Fungi (ITS)	0.3	0.844	18.94	4.7	<0.001***

Asterisks represent the significance of model terms ($P \leq 0.001^{***}$).

not clear all vegetation (Pellegrini et al., 2018).

4.2. Conversion to cropping halved microbial biomass

Cropland soils had half of the microbial biomass than rainforest and grassland soils (Fig. 3). This is consistent with previous findings (Chen et al., 2022). While Chen et al. (2022) reported a 70–75 % reduction, the

lower reduction in microbial biomass in our study (~50–60 % depending on land use conversion types) may be due to soil carbon accumulating less in the tropics and within this study we have seen clear correlations between soil carbon and microbial biomass (Crowther et al., 2019). Soil carbon and nitrogen are important drivers of microbial biomass (Chen et al., 2022). Both our study and that of Chen et al. (2022) found that increased soil nitrogen and carbon was associated with increased soil microbial biomass, although we found total nitrogen to have better correlation with bacterial biomass and carbon for fungal biomass (Figs. S2–S3). Further fractionation of carbon could reveal more specific trends. For example, labile carbon has been shown to drive microbial biomass trends more than more recalcitrant forms (Zhang et al., 2020; Pattison et al., 2008).

We also found that higher concentrations of zinc were associated with reduced microbial biomass. Their elevated levels in banana areas could be due to the use of zinc oxides in pesticides (Al Jabri et al., 2022). High zinc concentrations can affect microbial cell membranes, denature proteins, displace essential ions, affect nutrient uptake, and cause oxidative stress thus reducing microbial biomass (Cuajungco et al.,

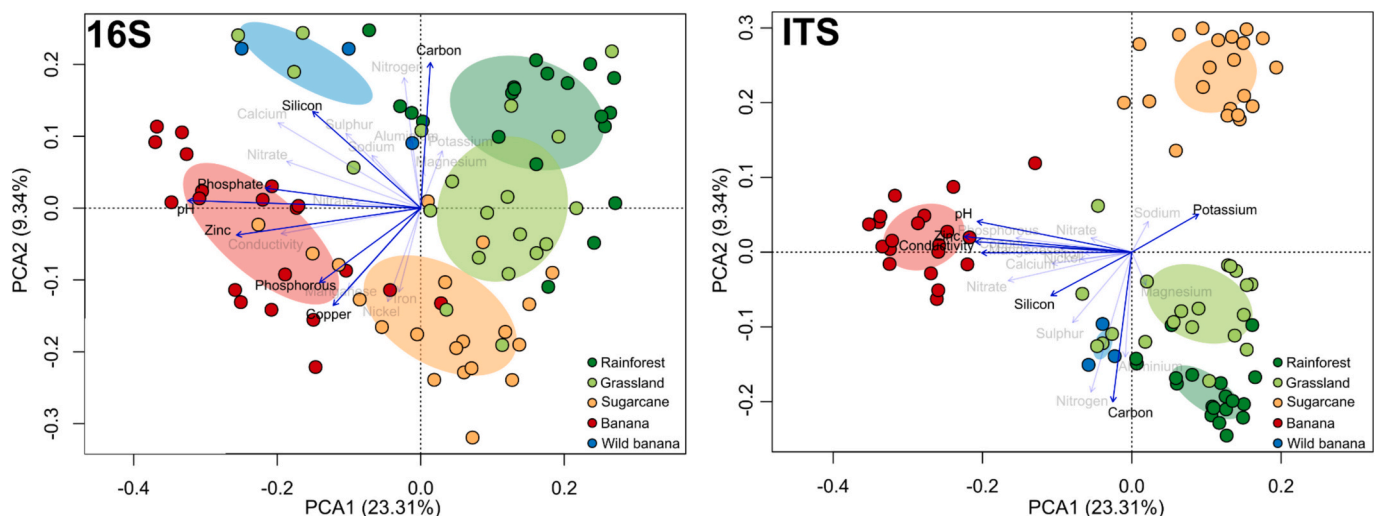


Fig. 4. Ordinations of principal coordinate analysis showing bacterial (16S rRNA genes), and fungal community composition (ITS2 genes). Solid arrows demonstrate the relationship between soil microbial communities and environmental variables. Faded arrows (e.g., Na, Ni) are non-significant associations with abiotic variables.

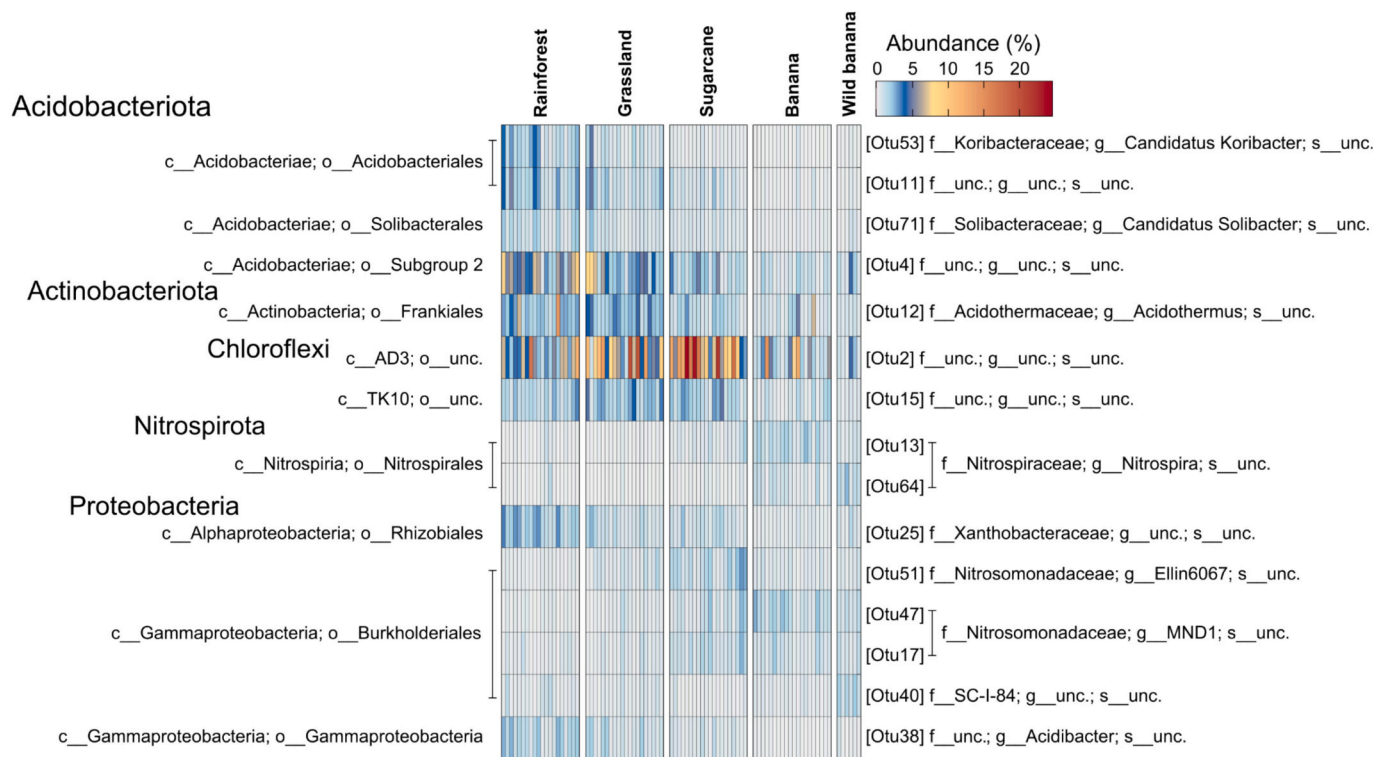


Fig. 5. A heatmap showing bacterial OTUs that were differentially abundant between land uses and had an average abundance ≥ 1 % within at least one land use.

2021). Other studies have found that zinc levels comparable to the higher end observed in our study (~ 350 – 600 mg kg⁻¹ soil) have also been associated with declines in microbial biomass (Barajas Aceves et al., 1999; Moffett et al., 2003).

Increases in soil pH in this study were associated with a decrease in fungal:bacterial biomass ratio (Fig. S6). This disagrees with an artificial pH gradient that found an increase in fungal dominance toward more neutral pHs (Rousk et al., 2009). However, it is noteworthy that banana soils tended to also be more neutral and therefore in our study pH is not decoupled from other management effects such as monocropping, tillage, and pesticide use that can also affect microbial biomass (Kabiri et al., 2016; Meyer et al., 2021; Mo et al., 2016).

After accounting for parsimonious soil abiotic variables, residual variation in soil microbial biomass could still be attributed to land use (Table 1). This suggests that land use alterations introduce changes not solely encapsulated by shifts in measured soil abiotic factors. Although data on the duration of monocropping was not collected during sampling, it is likely a significant factor influencing soil microbial biomass. For example, the rotation of banana production with other crops has been shown to significantly increase soil microbial biomass carbon by 8.6 %–40.5 % (Zhong et al., 2015). Similarly, sugarcane monocropping has been shown to reduce microbial biomass (Holt and Mayer, 1998). This has been attributed to other factors not analysed in this study including quantity and quality of litter, as well as soil temperature and moisture. Other effects such as the impact of tillage on soil aggregation, the distribution of organic matter and pesticides could also affect soil microbial biomass (Sun et al., 2011; Ullah and Dijkstra, 2019; Zuber and Villamil, 2016).

4.3. Land use change results in distinct communities

Regional-scale land use change shaped bacterial and fungal communities (Fig. 4, Table 2). This aligns with studies of land use in other tropical regions (Petersen et al., 2019) and New Zealand (Louison et al., 2023), suggesting conserved microbial biogeographic patterns based on land management. Decreases in Proteobacteria and Acidobacteria in the

shift from natural to cropped areas were consistent with previous studies indicating shared responses to land use change. Further work in The Wet Tropics could assess potential functional shifts linked to observed community changes.

Among OTUs, *Fusarium oxysporum* (OTU1) showed the strongest land-use association (Fig. 6). Consistent with Birt et al. (2023), *F. oxysporum* was also associated with various banana production soils. *F. oxysporum*'s pathogenicity traits (Nirmaladevi et al., 2016; Van Dam et al., 2016) likely mean it benefits from monocropping practices in these areas (Shen et al., 2018). Although elevated in wild bananas, its lower abundance relative to banana production areas, suggests suppressive factors in natural environments (Alabouvette, 1989). Despite its association with disease plants were healthy at sampling, highlighting the prevalence of non-pathogenic *F. oxysporum* forms (Nel et al., 2006).

Similar to changes in the total biomass of the community, total carbon, and pH were all correlated with communities from specific land uses. These variables have also been shown to correlate with community changes in a range of other studies on the impact of land use change on soil microbial communities (Berkelmann et al., 2020; Liu et al., 2022; Zhang et al., 2022). We also found that total phosphorus and phosphate was well correlated with bacterial and fungal community structure as reported previously (Fig. 4; Gumiere et al., 2019). Soil phosphorus is often unavailable to organisms due to factors such as pH, organic complexation, and clay adsorption (Frossard et al., 2000) and microbes have evolved specific strategies to acquire phosphorus from these unavailable forms (Richardson and Simpson, 2011). The introduction of phosphorus in readily assimilable forms can be advantageous to microbial populations that lack specialised mechanisms for accessing recalcitrant phosphorus sources; such specialisation often entails a metabolic fitness trade-off. As a result, shifts in microbial community composition and dynamics may occur in agricultural soils (Mori et al., 2018).

We did not find that land use change influenced fungal alpha diversity. This was surprising given other studies have reported land use conversion has influenced fungal alpha diversity through changes in soil structure and nutrients, notably available phosphorus (Liu et al., 2022;

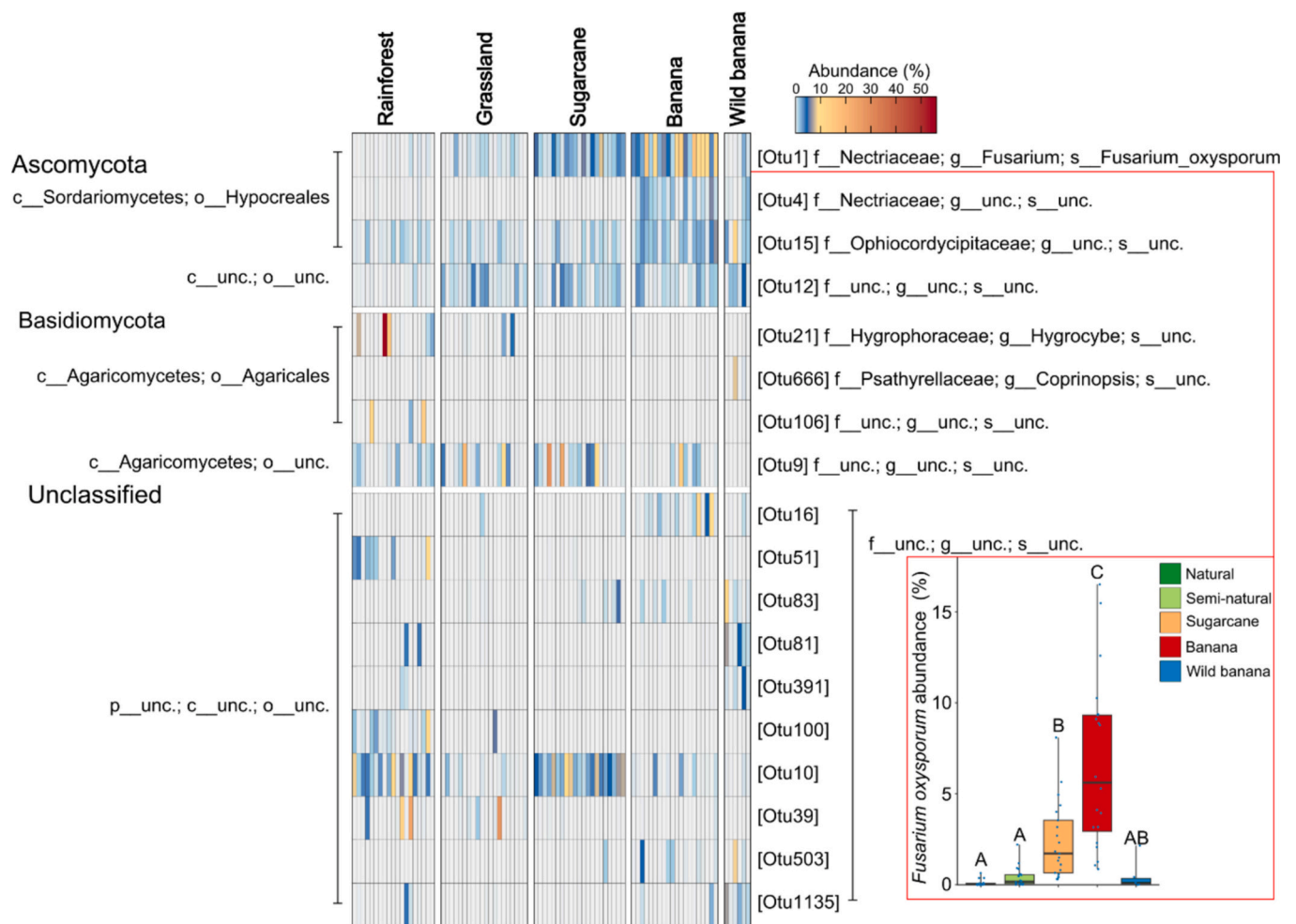


Fig. 6. A heatmap showing fungal OTUs that were differentially abundant between land uses and had an average relative abundance $\geq 1\%$ within at least one land use. Inset is a boxplot showing the difference between the relative abundance of OTU1 (*Fusarium oxysporum*) one of the most common fungal OTUs observed in the dataset. Different letters indicate significantly different relative abundance of OTU1 between land uses according to estimated marginal means post hoc with Benjamini-Hochberg corrections.

Berkelmann et al., 2020). *Fusarium* dominance in agricultural soils (Fig. 6) might have masked diversity changes. Alternatively, antagonistic effects of different land-use pressures (e.g., nutrient increase vs. tillage) could cancel out impacts on fungal diversity. Bacterial alpha diversity, solely explained by abiotic factors (Table 2), was positively associated with soil pH, calcium, and silicon, which were elevated in banana soils (Fig. S7). This is consistent with the fact that soil pH is a master regulator of soil bacterial diversity, with richness and evenness increasing from low to more neutral pH values.

5. Conclusions

This study provides important insights into the impact of land use on soil microbial communities in The Wet Tropics of Queensland, a biodiversity hotspot which may serve as a model for biodiverse areas elsewhere. We investigated this area as a loss of ecosystem services in biodiversity hotspots can affect a disproportionate number of species when compared to other areas. As such, it is important to understand how anthropogenic land management is influencing soil microbes in these areas. The findings of this study suggest that managed grassland, banana, and sugarcane production systems have led to changes in soil abiotic conditions, which correlate with reductions in microbial biomass and distinct microbial communities. Notable among these changes were changes in total soil carbon, nitrogen, and phosphorous as well as pH. These findings have implications for the management of soil microbial

communities in natural and agricultural systems and the provision of ecosystem services in agricultural lands. Future research might investigate the extent to which restoring abiotic factors to conditions observed in undisturbed regions influences the soil microbial biomass and community structure. Furthermore, landuse designations given in this study may be further broken-down into levels of intensity (e.g., conventional vs. organic agriculture, or grazing intensity within grasslands). Exploring these areas in this manner may reveal more nuanced effects. Finally, this work demonstrates that characteristic soil microbial communities can be formed at the landscape scale through management. Therefore, future work to manage microbial services in natural ecosystems at the regional scale or agriculture at the industry scale are likely viable through soil management.

Funding

This project was funded by Hort Innovation using the research and development banana industry levy and funds from the Australian Government, with co-investment from the Queensland Government and the University of Queensland, through the project BA14014 – *Fusarium* Wilt Tropical Race 4 Research Program.

CRediT authorship contribution statement

Henry W.G. Birt: Writing – review & editing, Writing – original

draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Anthony B. Pattison:** Writing – review & editing, Supervision, Resources, Project administration, Investigation, Funding acquisition, Conceptualization. **Yolima Carrillo:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Data curation. **Scott N. Lieske:** Writing – review & editing, Visualization, Software, Resources, Investigation, Formal analysis, Data curation, Conceptualization. **Rebecca Lyons:** Writing – review & editing, Project administration, Methodology, Investigation. **Hazel R. Lapis-Gaza:** Writing – review & editing, Resources, Methodology, Investigation. **Jiarui Sun:** Writing – review & editing, Software, Investigation, Data curation. **Paul G. Dennis:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Paul G. Dennis reports financial support was provided by Horticulture Innovation Australia Ltd. Henry W. G. Birt reports a relationship with Plantaigo Ltd. that includes: employment. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We gratefully acknowledge Jeff Daniells for his assistance in identifying wild banana plants, and the many land managers that enabled us to collect samples.

Additional information

HWGB is the Director of Plantaigo Ltd., a company that conducts research relating to natural sciences in the UK. The remaining authors have no conflicts of interest to declare.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.apsoil.2024.105750>.

Data availability

The amplicon sequences associated with this study have been deposited in the NCBI SRA under accession: SRR27665394 (16S) and SRR27665395 (ITS).

References

- Al Jabri, H., Saleem, M.H., Rizwan, M., Hussain, I., Usman, K., Alsafran, M., 2022. Zinc oxide nanoparticles and their biosynthesis: overview. *Life* 12 (4), 594. <https://doi.org/10.3390/life12040594>.
- Alabouvette, C., 1989. Manipulation of soil environment to create suppressiveness in soils. In: Tjamos, E.C., Beckman, C.H. (Eds.), *Vascular Wilt Diseases of Plants*. Springer, Berlin, pp. 457–478. https://doi.org/10.1007/978-3-642-73166-2_34.
- Australian Banana Growers Council, 2020. Economic Contribution. Our Industry. <https://abgc.org.au/our-industry/economic-contribution/>.
- Baethgen, W.E., Alley, M.M., 1989. A manual colorimetric procedure for measuring ammonium nitrogen in soil and plant kjeldahl digests. *Commun. Soil Sci. Plant Anal.* 20 (9–10), 961–969. <https://doi.org/10.1080/00103628909368129>.
- Bakker, P.A.H.M., Pieterse, C.M.J., de Jonge, R., Berendsen, R.L., 2018. The soil-borne legacy. *Cell* 172 (6), 1178–1180. <https://doi.org/10.1016/j.cell.2018.02.024>.
- Barajas Aceves, M., Grace, C., Ansorena, J., Dendooven, L., Brookes, P.C., 1999. Soil microbial biomass and organic C in a gradient of zinc concentrations in soils around a mine spoil tip. *Soil Biol. Biochem.* 31 (6), 867–876. [https://doi.org/10.1016/S0038-0717\(98\)00187-4](https://doi.org/10.1016/S0038-0717(98)00187-4).
- Bei, S., Zhang, Y., Li, T., Christie, P., Li, X., Zhang, J., 2018. Response of the soil microbial community to different fertilizer inputs in a wheat-maize rotation on a calcareous soil. *Agric. Ecosyst.* 260, 58–69. <https://doi.org/10.1016/j.agee.2018.03.014>.
- Berkelmann, D., Schneider, D., Meryandini, A., Daniel, R., 2020. Unravelling the effects of tropical land use conversion on the soil microbiome. *Environ. Microbiomes*. 15 (1), 1–18. <https://doi.org/10.1186/s40793-020-0353-3>.
- Bhattacharyya, S.S., Ros, G.H., Furtak, K., Iqbal, H.M.N., Parra-Saldívar, R., 2022. Soil carbon sequestration – an interplay between soil microbial community and soil organic matter dynamics. *Sci. Total Environ.* 815, e152928. <https://doi.org/10.1016/j.scitotenv.2022.152928>.
- Birt, H.W.G., Pattison, A.B., Skarshewski, A., Daniells, J., Raghavendra, A., Dennis, P.G., 2023. The core fungal microbiome of banana (*Musa* spp.). *Front. Microbiol.* 14. <https://doi.org/10.3389/fmicb.2023.1127779>.
- Buyer, J.S., Sasser, M., 2012. High throughput phospholipid fatty acid analysis of soils. *Appl. Soil Ecol.* 61, 127–130. <https://doi.org/10.1016/j.apsoil.2012.06.005>.
- Calcino, D., Schroeder, B., Hurney, A., Allsopp, P., 2008. *SmartCane Plant Cane Establishment and Management*. BSES Limited.
- Canegrowers, 2020. Nitrogen Management in the Queensland Sugarcane Industry. https://www.canegrowers.com.au/icms_docs/319512_nitrogen-management-in-the-queensland-sugarcane-industry.pdf.
- Chen, Q., Yang, F., Cheng, X., 2022. Effects of land use change type on soil microbial attributes and their controls: data synthesis. *Ecol. Indic.* 138, e108852. <https://doi.org/10.1016/j.ecolind.2022.108852>.
- Crowther, T.W., van den Hoogen, J., Wan, J., Mayes, M.A., Keiser, A.D., Mo, L., Averill, C., Maynard, D.S., 2019. The global soil community and its influence on biogeochemistry. *Science* 365 (6455), eaav0550. <https://doi.org/10.1126/science.aav0550>.
- Cuajungco, M., Ramirez, M., Tolmasky, M., 2021. Zinc: multidimensional effects on living organisms. *Biomedicines* 9 (2), e208. <https://doi.org/10.3390/biomedicines9020208>.
- Delgado-Baquerizo, M., Powell, J.R., Hamonts, K., Reith, F., Mele, P., Brown, M.V., Dennis, P.G., Ferrari, B.C., Fitzgerald, A., Young, A., Singh, B.K., Bissett, A., 2017. Circular linkages between soil biodiversity, fertility and plant productivity are limited to topsoil at the continental scale. *New Phytol.* 215 (3), 1186–1196. <https://doi.org/10.1111/nph.14634>.
- Deng, H., Zhang, B., Yin, R., Wang, H. li, Mitchell, S.M., Griffiths, B.S., Daniell, T.J., 2010. Long-term effect of re-vegetation on the microbial community of a severely eroded soil in sub-tropical China. *Plant and Soil* 328 (1), 447–458. <https://doi.org/10.1007/s11040-009-0124-9>.
- Emtage, N., Herbohn, J., 2012. Implications of landholders' management goals, use of information and trust of others for the adoption of recommended practices in the Wet Tropics region of Australia. *Landsc. Urban Plan.* 107 (4), 351–360. <https://doi.org/10.1016/j.landurbplan.2012.07.003>.
- Frossard, E., Condron, L.M., Oberson, A., Sinaj, S., Fardeau, J.C., 2000. Processes governing phosphorus availability in temperate soils. *J. Environ. Qual.* 29 (1), 15–23. <https://doi.org/10.2134/jeq2000.00472425002900010003x>.
- Geense, P., Pattison, A.B., Kukulies, T.L., Scholberg, J.M.S., Molina, A.B., 2015. Can changes in soil properties in organic banana production suppress fusarium wilt? *Nat. Resour. Oper.* 06 (03), 181–195. <https://doi.org/10.4236/nr.2015.63017>.
- Gumiere, T., Rousseau, A.N., da Costa, D.P., Cassetari, A., Cotta, S.R., Andreato, F.D., Gumiere, S.J., Pavinato, P.S., 2019. Phosphorus source driving the soil microbial interactions and improving sugarcane development. *Sci. Rep.* 9 (1), e4400. <https://doi.org/10.1038/s41598-019-40910-1>.
- Harris, N.L., Gibbs, D.A., Baccini, A., Birdsey, R.A., De Bruin, S., Farina, M., Fatoyinbo, L., Hansen, M.C., Herold, M., Houghton, R.A., Potapov, P.V., Suarez, D. R., Roman-Cuesta, R.M., Saatchi, S.S., Slay, C.M., Turubanova, S.A., Tyukavina, A., 2021. Global maps of twenty-first century forest carbon fluxes. *Nat. Clim. Chang.* 11 (3), 234–240. <https://doi.org/10.1038/s41558-020-00976-6>.
- Holt, J.A., Mayer, R.J., 1998. Changes in microbial biomass and protease activities of soil associated with long-term sugar cane monoculture. *Biol. Fertil. Soils* 27 (2), 127–131. <https://doi.org/10.1007/s003740050410>.
- Hooke, R. LeB, Martín-Duque, J.F., Pedraza, Javier, 2012. Land transformation by humans: a review. *GSA Today* 12 (12), 4–10. <https://doi.org/10.1130/GSAT151A.1>.
- Kabiri, V., Raiesi, F., Ghazavi, M.A., 2016. Tillage effects on soil microbial biomass, SOM mineralization and enzyme activity in a semi-arid Calcixerpts. *Agric. Ecosyst. Environ.* 232, 73–84. <https://doi.org/10.1016/j.agee.2016.07.022>.
- Lavarack, B., 2016. Review of the development of the co-products industry in Australia. *Proceedings of the International Society of Sugar Cane Technologists* 29, 1543–1550.
- Liu, G., Bai, Z., Cui, G., He, W., Kongling, Z., Ji, G., Gong, H., Li, D., 2022. Effects of land use on the soil microbial community in the Songnen grassland of Northeast China. *Front. Microbiol.* 13, e865184. <https://doi.org/10.3389/fmicb.2022.865184>.
- Louison, Z., Hermans, S.M., Buckley, H.L., Case, B.S., Taylor, M., Curran-Cournane, F., Lear, G., 2023. Land use modification causes slow, but predictable, change in soil microbial community composition and functional potential. *Environ. Microbiome.* 18 (1), e30. <https://doi.org/10.1186/s40793-023-00485-x>.
- Marchese, C., 2015. Biodiversity hotspots: a shortcut for a more complicated concept. *Glob. Ecol. Conserv.* 3, 297–309. <https://doi.org/10.1016/j.gecco.2014.12.008>.
- Marod, D., Pinyo, P., Duengkae, P., Hiroshi, T., 2010. The role of wild banana (*Musa acuminata* Colla) on wildlife diversity in mixed deciduous forest, Kanchanaburi province, Western Thailand. *Nat. Sci.* 44 (1), 35–43.
- Meyer, M., Diehl, D., Schaumann, G.E., Muñoz, K., 2021. Agricultural mulching and fungicides—impacts on fungal biomass, mycotoxin occurrence, and soil organic matter decomposition. *Environ. Sci. Pollut. Res.* 28 (27), 36535–36550. <https://doi.org/10.1007/s11356-021-13280-3>.

- Mo, A.S., Qiu, Z.Q., He, Q., Wu, H.Y., Zhou, X.B., 2016. Effect of continuous monocropping of tomato on soil microorganism and microbial biomass carbon. *Commun. Soil Sci. Plant Anal.* 47 (9), 1069–1077. <https://doi.org/10.1080/00103624.2016.1165832>.
- Moffett, B.F., Nicholson, F.A., Uwakwe, N.C., Chambers, B.J., Harris, J.A., Hill, T.C.J., 2003. Zinc contamination decreases the bacterial diversity of agricultural soil. *FEMS Microbiol. Ecol.* 43 (1), 13–19. <https://doi.org/10.1111/j.1574-6941.2003.tb01041.x>.
- Mori, T., Lu, X., Aoyagi, R., Mo, J., 2018. Reconsidering the phosphorus limitation of soil microbial activity in tropical forests. *Funct. Ecol.* 32 (5), 1145–1154. <https://doi.org/10.1111/1365-2435.13043>.
- Nel, B., Steinberg, C., Labuschagne, N., Viljoen, A., 2006. Isolation and characterization of nonpathogenic *Fusarium oxysporum* isolates from the rhizosphere of healthy banana plants. *Plant Pathol.* 55 (2), 207–216. <https://doi.org/10.1111/j.1365-3059.2006.01343.x>.
- Nikitin, D.A., Ivanova, E.A., Zhelezova, A.D., Semenov, M.V., Gadzhumarov, R.G., Tkhakakhova, A.K., Chernov, T.I., Ksenofontova, N.A., Kutovaya, O.V., 2020. Assessment of the impact of no-till and conventional tillage technologies on the microbiome of southern agrochernozeems. *Eurasian J. Soil Sci.* 53 (12), 1782–1793. <https://doi.org/10.1134/S106422932012008X>.
- Nirmaladevi, D., Venkataramana, M., Srivastava, R.K., Uppalapati, S.R., Gupta, V.K., Yli-Mattila, T., Clement Tsui, K.M., Srinivas, C., Niranjana, S.R., Chandra, N.S., 2016. Molecular phylogeny, pathogenicity and toxigenicity of *Fusarium oxysporum* f. sp. *Lycopersici*. *Sci. Rep.* 6 (1), e21367. <https://doi.org/10.1038/srep21367>.
- Office of the Gene Technology Regulator, 2023. *The Biology of Musa L. (Banana)*. Australian Government.
- Pattison, A.B., Moody, P.W., Badcock, K.A., Smith, L.J., Armour, J.A., Rasiah, V., Cobon, J.A., Gulino, L.-M., Mayer, R., Lindsay, S., 2008. Development of key soil health indicators for the Australian banana industry. *Appl. Soil Ecol.* 40, 155–164. <https://doi.org/10.1016/j.apsoil.2008.04.002>.
- Pellegrini, A.F.A., Ahlström, A., Hobbie, S.E., Reich, P.B., Nieradzki, L.P., Staver, A.C., Scharenbroch, B.C., Jumpponen, A., Anderegg, W.R.L., Randerson, J.T., Jackson, R. B., 2018. Fire frequency drives decadal changes in soil carbon and nitrogen and ecosystem productivity. *Nature* 553, 194–198. <https://doi.org/10.1038/nature24668>.
- Petersen, I.A.B., Meyer, K.M., Bohannan, B.J.M., 2019. Meta-analysis reveals consistent bacterial responses to land use change across the tropics. *Front. Ecol. Evol.* 7, e391. <https://doi.org/10.3389/fevo.2019.00391>.
- Pinakana, S.D., Robles, E., Mendez, E., Raysoni, A.U., 2023. Assessment of air pollution levels during sugarcane stubble burning event in La Feria, South Texas, USA. *Pollution* 3 (2), 197–219. <https://doi.org/10.3390/pollutants3020015>.
- Pitt, J.L., Provin, T.L., Hons, F.M., Dou, F., Waskom, J.S., 2003. Use of a total carbon/nitrogen analyzer for the determination of organic and inorganic carbon in soils, manure, and composts. In: *Meeting of ASA: Changing Sciences for a Changing World: Building a Broader Vision*. Denver, CO, Nov. 2–6.
- Powlson, D.S., Gregory, P.J., Whalley, W.R., Quinton, J.N., Hopkins, D.W., Whitmore, A. P., Hirsch, P.R., Goulding, K.W.T., 2011. Soil management in relation to sustainable agriculture and ecosystem services. *Food Policy* 36, S72–S87. <https://doi.org/10.1016/j.foodpol.2010.11.025>.
- Rayment, G.E., Lyons, D.J., 2011. *Soil Chemical Methods: Australasia*, vol. 3. CSIRO publishing.
- Richards, Z.T., Day, J.C., 2018. Biodiversity of the Great Barrier Reef—how adequately is it protected? *PeerJ* 6, e4747. <https://doi.org/10.7717/peerj.4747>.
- Richardson, A.E., Simpson, R.J., 2011. Soil microorganisms mediating phosphorus availability update on microbial phosphorus. *Plant Physiol.* 156 (3), 989–996. <https://doi.org/10.1104/pp.111.175448>.
- Roberts, P., Buhrich, A., Caetano-Andrade, V., Cosgrove, R., Fairbairn, A., Florin, S.A., Vanwezer, N., Boivin, N., Hunter, B., Mosquito, D., Turpin, G., Ferrier, Á., 2021. Reimagining the relationship between Gondwanan forests and Aboriginal land management in Australia's "Wet Tropics". *iScience* 24 (3), e102190. <https://doi.org/10.1016/j.isci.2021.102190>.
- Robertson, F.A., Thorburn, P.J., 2007. Management of sugarcane harvest residues: consequences for soil carbon and nitrogen. *Soil Res.* 45 (1), e13. <https://doi.org/10.1071/SR06080>.
- Rousk, J., Brookes, P.C., Bååth, E., 2009. Contrasting soil pH effects on fungal and bacterial growth suggest functional redundancy in carbon mineralization. *Appl. Environ. Microbiol.* 75 (6), 1589–1596. <https://doi.org/10.1128/AEM.02775-08>.
- Saccá, M.L., Barra Caracciolo, A., Lenola, M.D., Grenni, P., 2017. Ecosystem services provided by soil microorganisms. In: Lukac, M., Grenni, P., Gamboni, M. (Eds.), *Soil Biological Communities and Ecosystem Resilience*. Springer, Cham, pp. 9–24. https://doi.org/10.1007/978-3-319-63336-7_2.
- Sanjuan, J., Delgado, M.J., Girard, L., 2020. Editorial: microbial control of the nitrogen cycle. *Front. Microbiol.* 11, 950. <https://doi.org/10.3389/fmicb.2020.00950>.
- Shen, Z., Penton, C.R., Lv, N., Xue, C., Yuan, X., Ruan, Y., Li, R., Shen, Q., 2018. Banana fusarium wilt disease incidence is influenced by shifts of soil microbial communities under different monoculture spans. *Microb. Ecol.* 75 (3), 739–750. <https://doi.org/10.1007/s00248-017-1052-5>.
- Singh, B., Rengel, Z., 2007. The role of crop residues in improving soil fertility. In: Marschner, P., Rengel, Z., Varma, A. (Eds.), *Nutrient Cycling in Terrestrial Ecosystems*. Springer, Berlin, pp. 183–214. <https://doi.org/10.1007/978-3-540-68027-7>.
- Skocaj, D.M., Everingham, Y.L., Schroeder, B.L., 2013. Nitrogen management guidelines for sugarcane production in Australia: can these be modified for wet tropical conditions using seasonal climate forecasting? *Springer Sci. Rev.* 1 (1–2), 51–71. <https://doi.org/10.1007/s40362-013-0004-9>.
- Standing Committee on Climate Change, Environment and the Arts, 2012. *Case Studies on Biodiversity Conservation, volume 2. The Commonwealth of Australia*.
- Sun, B., Hallett, P.D., Caul, S., Daniell, T.J., Hopkins, D.W., 2011. Distribution of soil carbon and microbial biomass in arable soils under different tillage regimes. *Plant and Soil* 338 (1–2), 17–25. <https://doi.org/10.1007/s11104-010-0459-2>.
- Ullah, M., Dijkstra, F., 2019. Fungicide and bactericide effects on carbon and nitrogen cycling in soils: a meta-analysis. *Soil Syst.* 3 (2), 23. <https://doi.org/10.3390/soilsystems3020023>.
- UNESCO World Heritage Convention, 2022. *Wet Tropics of Queensland*. <https://whc.unesco.org/en/list/486>.
- USEPA, 1983. *Methods for chemical analysis of water and wastes*. In: *Environmental Protection*. USEPA, p. 491.
- Van Dam, P., Fokkens, L., Schmidt, S.M., Linmans, J.H.J., Kistler, H.C., Ma, L., Rep, M., 2016. Effector profiles distinguish formae speciales of *Fusarium oxysporum*. *Environ. Microbiol.* 18 (11), 4087–4102. <https://doi.org/10.1111/1462-2920.13445>.
- Weber, E.T., Catterall, C.P., Locke, J., Ota, L.S., Pridemore, B., Shirreffs, L., Talbot, L., Gordon, I.J., 2021. Managing a world heritage site in the face of climate change: a case study of the wet tropics in Northern Queensland. *Earth* 2, 248–271. <https://doi.org/10.3390/earth2020015>.
- Xue, P.P., Carrillo, Y., Pino, V., Minasy, B., McBratney, A.B., 2018. Soil properties drive microbial community structure in a large scale transect in south eastern Australia. *Sci. Rep.* 8, e11725. <https://doi.org/10.1038/s41598-018-30005-8>.
- Zhang, X., Chen, X., Liu, M., Xu, Z., Wei, H., 2020. Coupled changes in soil organic carbon fractions and microbial community composition in urban and suburban forests. *Sci. Rep.* 10 (1), e15933. <https://doi.org/10.1038/s41598-020-73119-8>.
- Zhang, Y., Finn, D., Bhattacharyya, R., Dennis, P.G., Doolette, A.L., Smernik, R.J., Dalal, R.C., Meyer, G., Lombi, E., Klysubun, W., Jones, A.R., Wang, P., Menzies, N. W., Kopitke, P.M., 2021. Long-term changes in land use influence phosphorus concentrations, speciation, and cycling within subtropical soils. *Geoderma* 393, e115010. <https://doi.org/10.1016/j.geoderma.2021.115010>.
- Zhang, T., Liu, Y., Sui, X., Frey, B., Song, F., 2022. Effects of land conversion on soil microbial community structure and diversity in Songnen Plain, Northeast China. *Sustainability* 14 (17), e10767. <https://doi.org/10.3390/su141710767>.
- Zhong, S., Zeng, H., Jin, Z., 2015. Soil microbiological and biochemical properties as affected by different long-term banana-based rotations in the tropics. *Pedosphere* 25 (6), 868–877. [https://doi.org/10.1016/S1002-0160\(15\)30067-9](https://doi.org/10.1016/S1002-0160(15)30067-9).
- Zuber, S.M., Villamil, M.B., 2016. Meta-analysis approach to assess effect of tillage on microbial biomass and enzyme activities. *Soil Biol. Biochem.* 97, 176–187. <https://doi.org/10.1016/j.soilbio.2016.03.011>.