Global Ecology and Biogeography

WILEY

Global Ecology and Biogeography | A Journal of Macroecology

RESEARCH ARTICLE OPEN ACCESS

Soil Plant Growth-Promoting Bacterial Diversity Changes With Land Use Intensity and Environmental Conditions

Syrie M. Hermans[1] | Hannah L. Buckley[1] | Bradley S. Case[1] | Fiona Curran-Cournane[2] | Matthew Taylor[3] | Gavin Lear[4]

[1]School of Science, Auckland University of Technology, Auckland, New Zealand | [2]Joint Evidence Data and Insights, Ministry for the Environment, Auckland, New Zealand | [3]Waikato Regional Council, Hamilton, New Zealand | [4]School of Biological Sciences, University of Auckland, Auckland, New Zealand

Correspondence: Syrie M. Hermans (syrie.hermans@aut.ac.nz)

Received: 15 May 2024 | **Revised:** 11 May 2025 | **Accepted:** 5 July 2025

Handling Editor: Brody Sandel

Funding: This work was supported by Royal Society Te Apārangi, Rutherford Postdoctoral Fellowship.

Keywords: environmental variation | nitrogen-fixing bacteria | phosphate solubilising bacteria | plant-microbe interactions | potassium solubilising bacteria

ABSTRACT

Aim: Plant growth-promoting bacteria (PGPB) play crucial roles in supporting plant growth and, therefore, in undisturbed ecosystems and agricultural systems. We aimed to understand how these microbial communities change under different land use and environmental conditions. This is an important prerequisite to utilising the positive impact PGPB may have for sustainable food production.

Location: 537 sites across Aotearoa New Zealand.

Time Period: 2013–2018.

Major Taxa Studied: Plant growth-promoting bacteria (PGPB).

Methods: We surveyed the PGPB in indigenous and exotic plantation forests, sheep and beef grasslands, dairy pastures and horticulture sites.

Results: PGPB community alpha-diversity increased with land use intensity, and the greatest portion of explainable variation in alpha-diversity was accounted for by soil nutrients, metal concentrations, and unexplained spatial patterns. Variation in PGPB community composition, on the other hand, was highest in the forest and horticulture sites and lowest in the grazed pastures. The variation was best accounted for by shared variation among land use, soil nutrients and soil metal concentrations. The relative abundance of nitrogen-fixing PGPB taxa decreased with land use intensity, largely driven by a decrease in Rhizobiales. In contrast, taxa in the order Bacillales, known for phosphate and potassium solubilisation, increased in relative abundance. Key environmental variables limiting the distributions of specific PGPB taxa included soil pH, several nutrients and the concentrations of cadmium and zinc.

Main Conclusions: Overall, we showed that PGPB show distinct patterns in response to land use and soil environmental variables, and these results contribute towards an understanding of the interplay between how we use our soil, their physicochemical properties and the function of the microbial communities within them. This increased understanding of the distribution of PGPB is crucial for advancing our ability to optimise and take advantage of the benefits these bacteria bring to both natural and agricultural land.

1 | Introduction

Plant growth-promoting bacteria (PGPB) are either free-living soil microbes or associated with the plant rhizosphere and help promote plant growth, confer resistance to biotic stresses such as pathogens or increase tolerance to abiotic stresses such as drought (Ramakrishna et al. 2019). To enhance plant growth, PGPB that improve the access of plants to key nutrients are crucial. For example, the importance of nitrogen-fixing bacteria has long been appreciated, especially given the importance of nitrogen as a mineral nutrient for plant growth (Isobe and Ohte 2014). Likewise, phosphorous and potassium are key plant nutrients which support plant growth and development, but large proportions of these minerals in the soil are insoluble and, therefore, inaccessible to plants; phosphorous and potassium solubilising PGPB are therefore crucial to deliver these macronutrients to plants (Billah et al. 2019; Ahmad et al. 2016). Given they are fundamental to sustaining and improving plant growth, PGPB are vital for supporting agricultural industries and natural ecosystems (Lacava et al. 2022; Zeng et al. 2022). Understanding what impacts their diversity, abundance and composition could unlock mechanisms that ensure these key microorganisms are utilised to realise optimal outputs and enhance crop production.

There is plenty of evidence of the benefits of PGPB for plant growth. Inoculating maize and sorghum with PGPB increases growth and nitrogen use efficiencies; the outcomes may depend on whether or not nitrogen fertiliser is also applied, but a positive impact may be observed regardless (Aquino et al. 2021). Likewise, lima beans inoculated with a PGPB *Bacillus* species showed better growth responses, even when compared to plant growth following nitrogen additions (Lima et al. 2016). Potassium solubilising bacteria isolated from cereal crops have been demonstrated to positively impact shoot length, plant biomass and the concentrations of carotenoids and sugars in plant biomass (Kaur et al. 2021). The amount of fertiliser needed can be reduced by adding PGPB consortia without affecting crop yield and indirect enhancement of nitrogen uptake by plants is observed when inoculating with PGPB not known to be capable of fixing nitrogen (Adesemoye et al. 2009). Likewise, in natural ecosystems, PGPB are likely to have vital roles in protecting and enhancing plant growth and their largely untapped microbial diversity could also serve as a reservoir for PGPB discovery (Lacava et al. 2022). Indeed, Lisboa et al. (2021) found that almost half of the strains associated with a tropical vascular plant were able to perform nutrient solubilisation and pathogen antagonisation potential was high too. However, while the impact of PGPB on plant growth has been well studied, less is known about the wider distributions PGPB communities present in soil and how their abundance, diversity and composition change under differing environmental conditions.

The composition of soil bacterial communities is shaped by a plethora of different factors; spatial, climatic and soil environmental variables all interact to determine what bacterial communities look like at different locations (Hermans et al. 2017; Yang et al. 2021, 2022; Karimi et al. 2018). Large-scale studies offer the ability to determine how natural or human-induced changes such as climate warming, carbon dioxide increases, changes in precipitation, fertilisation rates and land use changes impact microbial communities. Such studies have been responsible for highlighting that bacterial richness and turnover rates correlate with variation in soil variables (Terrat et al. 2017; Ranjard et al. 2013) and revealing how factors that vary only on a larger scale, such as land use, soil texture, soil nutrients and climate impact bacterial communities (Karimi et al. 2018; Terrat et al. 2017; Griffiths et al. 2011). A meta-analysis examining how microbial communities respond to large-scale changes driven by human activity revealed distinctions between rare and common taxa, with the former being more sensitive (Zhou et al. 2020). Given that different subsets of the microbial community clearly respond differently to anthropogenic-driven changes, more can be learned about groups of taxa by focussing specifically on them in large-scale studies.

Understanding the distribution of PGPB is crucial to allow us to take full advantage of the benefits these microorganisms can provide to help ensure food security in the future. Comparing the diversity and composition of these communities in large-scale studies and different land uses will provide novel insights into how soil environments, spatial variation and land use intensity impact the distribution of PGPB. Therefore, we conducted a large-scale investigation of key PGPB taxa in the soils of five different land use types to determine (1) how the alpha-diversity of PGPB differs between land use types and soil environmental variables, (2) what factors shape the composition of PGPB communities and (3) what factors limit the distribution of individual PGPB taxa.

2 | Methods

2.1 | Sampling and DNA Processing

Soil samples were collected and processed as described previously (Hermans et al. 2017; Hermans, Buckley, Case, et al. 2020). Briefly, the samples were collected between 2013 and 2018 from ten regions across Aotearoa New Zealand, covering approximately 196,000 km^2 of land (Figure 1). While samples were collected over a five-year period, previous analyses have shown that there is very minimal impact of time on the bacterial communities at these sites (Hermans, Buckley, Curran-Cournane, et al. 2020). A total of 537 sites were sampled and classified as belonging to one of five land uses, following national guidelines (Hill and Sparling 2009): indigenous forest ($n = 51$), exotic plantation forest (predominantly *Pinus radiata* plantation; $n = 58$), sheep and beef pastures ($n = 149$), dairy pastures ($n = 153$) or horticulture ($n = 126$; including arable). Soil samples (0–10 cm depth) were collected every 10 m along a 50-m transect at each site for microbial analyses, every 2 m for soil chemical analyses and every 15 m for soil physical analyses. The starting point of each transect was selected haphazardly, before the transect was established in a straight-line direction that would best capture the variation in the environment (e.g., running perpendicular to a slope, fence line or other topographic features, while avoiding areas such as water troughs, gates or passageways that would not be representative). Microbial samples were processed individually, soil chemical samples were combined into a single

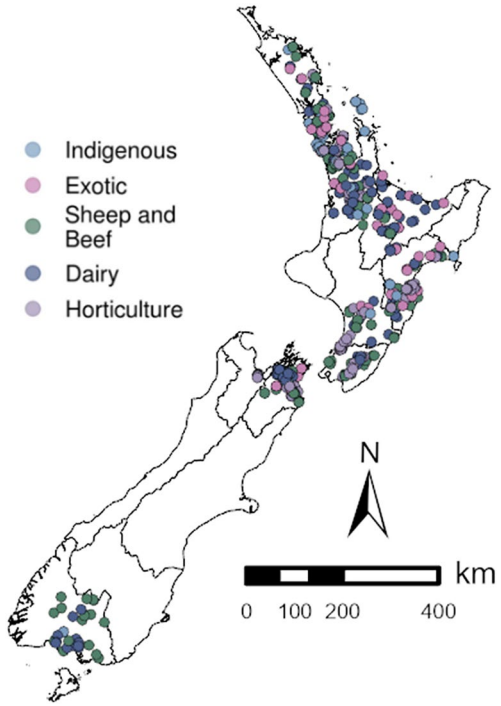

FIGURE 1 | The distribution of the sites across Aotearoa New Zealand. Sites were classified as belonging to one of four land uses: Indigenous forest, exotic plantation forest, sheep and beef pastures, dairy pastures or horticulture.

sample, and soil physical samples were measured individually and averaged to obtain one value per site.

Sample analysis for chemical and physical indicators was conducted by IANZ accredited laboratories using the methodology outlined in the National Environmental Monitoring Standards for Soil Quality and Trace elements (National Environmental Monitoring Standard 2022). Briefly, after samples were dried and sieved upon arrival in the lab, total C and N were determined by Dumas dry combustion of soil samples on an industry-accepted elemental analyser. Anaerobic mineralisable nitrogen (AMN) was measured by the change in the extractable ammonium-N after anaerobic incubation. Soil pH was determined by glass electrode from a suspension of soil and distilled water. Olsen P was measured following extraction of soil in sodium bicarbonate. For heavy metals, soil samples were digested in hydrochloric and nitric acid before total recoverable concentrations were determined in the digest by ICP-MS or a similarly accurate instrument. Finally, bulk density was measured on a weight basis to a volume equivalent and air-filled macroporosity (soil pores $>30\,\mu m$ in diameter) was measured on tension tables at −10.

Molecular microbial analysis was conducted as described previously (Hermans et al. 2017). Briefly, for each replicate at each site, DNA was extracted from the samples using the DNeasy PowerSoil-htp DNA extraction kit (Qiagen, previously MoBio) as per the manufacturer's instructions with minor modifications. The V3-V4 region of the bacterial 16S rRNA gene was then amplified from each DNA extract using the 341F and 785R primer pair (Klindworth et al. 2013) before normalised PCR products were barcoded (Nextera XT dual indices, Illumina Inc., USA), pooled and sequenced. Sequencing was done on an Illumina MiSeq instrument using V3 chemistry to generate 2×300 bp reads; multiple sequencing runs were performed, each with ~384 samples. Full sampling, sample processing, DNA extraction and amplicon preparation methods are detailed in the previously published studies (Hermans et al. 2017; Hermans, Buckley, Case, et al. 2020). Sequence data was deposited in the NCBI Sequence Read Archive (SRA) repository under accession numbers PRJNA323375 and PRJNA578562.

2.2 | Bioinformatic and Statistical Analyses

All bioinformatic and statistical analyses were performed in R version 4.2.2 (R Core Team 2022). DADA2 (Callahan et al. 2016) was used for quality filtering, denoising and amplicon sequence variant (ASV) inference from the DNA sequence data, as well as chimaera removal and taxonomic assignment. Specifically, the first 25 bp, which included the primers, were trimmed off the reads and then reads were truncated to 280 bp (forward reads) or 260 bp (reverse reads). Reads with more than two expected errors were discarded, and reads were truncated at the first instance where the quality score was equal to or less than two. After applying the DADA2 core algorithm to call ASVs, forward and reverse reads were merged. Chimeric ASVs were removed before taxonomic assignment against the Silva v 138.1 taxonomic reference database (Quast et al. 2013). ASVs that were not classified as bacterial, mitochondrial, or chloroplast were removed. Replicate samples per site ($n=5$) were merged for each site; sites for which not all five replicates were available, either due to insufficient PCR product or low sequence reads, were excluded from the analysis. Further, samples with less than 10,000 reads after combining replicates were also excluded, after which singletons (ASVs that only occurred once across the entire dataset) were removed. We then used cumulative sum scaling (CSS), implemented using the metagenomeSeq package (Paulson et al. 2013). From this ASV table, we filtered out all ASVs which were classified as taxa previously described as plant-growth-promoters in the literature and grouped them by their functional category (Table S1) (Orozco-Mosqueda et al. 2021). Ultimately, 537 sites were used in the analyses as they met the replicate number and sequencing depth threshold and had a complete set of environmental data available (Table S2). These sites comprised 51 indigenous sites, 58 exotic plantation forest sites, 149 sheep and beef pastures, 153 dairy pastures and 126 horticulture sites. For most analyses, the PGPB ASV table was used; however, the ASV table with all bacterial ASVs (including PGPB) was used in a subset of analyses to provide comparisons between the patterns in the PGPB and total bacterial communities. For downstream analyses, we ranked the five land uses from lowest to highest intensity, based on the degree of human input associated with each land use (e.g., the amount of fertiliser use, pesticide and herbicide use and soil disturbance) as well as the soil chemistry results (Figure S1).

Shannon's diversity for each PGPB community at each site was calculated using the 'diversity' function from the vegan package (Oksanen et al. 2017). The 'stat_compare_means' function from the ggpubr package was used to perform the Kruskal–Wallis test on Shannon's diversity scores for the different land use categories; Dunn's test for multiple comparisons with

Bonferroni corrections was performed using the dunn test package (Dinno 2017) and function of the same name. Shannon's diversity scores were also used as the response variable in variance partitioning analyses, performed as previously described (Lear et al. 2013). Response variables were grouped into 'land use', 'soil nutrients', 'soil metals' and 'space' for variance partitioning (Table S2). Variance partitioning was also performed on Shannon's diversity scores for the total bacterial communities at each site compared with the PGPB subset. Variance partitioning was repeated on subsets of sites containing all the samples from within each land use separately.

Pairwise differences in the PGPB community composition among different sites were visualised using nonmetric multidimensional scaling (nMDS) of the Bray–Curtis dissimilarity matrix and performed using the 'metaMDS' function in the vegan package. Permutational multivariate analysis of variance (PERMANOVA) was conducted using the 'adonis' command from vegan, 'betadisper' from the same package was used to assess the homogeneity of groups dispersions. The variance partitioning described above was then used to explain the variation in two response variables: (i) the Bray-Curtis pairwise dissimilarity matrix and (ii) the mean pairwise Bray–Curtis dissimilarity of each site to all other sites. We also visualised all pairwise Bray–Curtis dissimilarity scores between sites from the same land use and evaluated the statistical significance using Kruskal-Wallis and Dunn's test, as described above. Finally, to visualise the compositional differences as relative abundances of taxa across the different land uses, the average abundance of all PGPB ASVs were calculated per land use, and the order-level assignments of these ASVs was plotted. Additionally, we plotted the functional categories of these ASVs (Table S1).

To confirm that the unequal sampling depth per land use (indigenous forest = 51, exotic plantation forest = 58, sheep and beef pastures = 149, dairy pastures = 153 and horticulture 126) was not skewing our results, we randomly subsampled our sites to include exactly 51 sites per land use and repeated the alpha-diversity and beta-diversity analyses on this subset.

The specificity package (Darcy et al. 2022) was used to assess which environmental variables (Table S2) were impacting the PGPB ASVs' distributions across the sites. Briefly, this package applies Rao's Quadratic Entropy (Rao 1982, 2010) to calculate the specificity of ASVs to many different environmental variables. Only ASVs which occurred in at least 10% of sites were included in the analyses. A statistically significant specificity score indicates that an individual ASV's occurrence range across a given environmental gradient was smaller than expected by chance. The analysis was performed on all the sites together, as well as for all sites from each land use separately. After identifying all ASVs with a significant specificity score for each environmental variable, we determined the functional category of that ASV based on the taxonomic assignment to a certain PGPB genus (Table S1).

3 | Results

We sampled soil bacterial communities at 537 sites across Aotearoa New Zealand (Figure 1). Sites were classified as belonging to one of five land use types: indigenous forest ($n = 51$), exotic plantation forest (predominantly *Pinus radiata* plantation; $n = 58$), sheep and beef pastures ($n = 149$), dairy pastures ($n = 153$) or horticulture ($n = 126$). Based on the degree of human intervention and management practices, these land uses represent increasing land use intensity from low to high intensity (indigenous forests < exotic plantation forests < sheep and beef pastures < dairy pastures < horticulture), and each land use was characterised by a unique soil physicochemical profile (Figure S1).

Across the normalised dataset were 3046 ASVs classified within plant growth-promoting bacterial (PGPB) genera (~2% of total ASVs; Table S1). On average, these ASVs comprised ~8% of the total bacterial community, with horticulture sites having the lowest average abundance and exotic plantation forests and dairy sites having the highest (Figure S2, Table S3).

3.1 | PGPB Diversity Increases With Land Use Intensity

Soil PGPB community diversity, measured using Shannon's diversity index, increased as land use became more intensive (Figure 2A), and this pattern remained when accounting for differences in sample size across the land uses (Figure S3a). Indigenous forests, exotic plantation forests, and sheep and beef farms contained PGPB communities with significantly lower diversity than dairy and horticulture sites (Dunn's test $p < 0.01$ for all pairwise comparisons). Further, horticulture sites contained significantly more diverse communities than dairy sites (Dunn's test $p < 0.01$).

Only a small portion of the variation in PGPB alpha-diversity across all land uses could be explained by the available metadata (Figure 2B). The largest amount of variation was explained by the variable groups 'metals' (4%), 'nutrients' (3%), 'space' (2%) and a combination of 'land use type' and 'nutrients' (2%). The amount of variation in PGPB community diversity explained by nutrients was much higher than for the overall bacterial community diversity, where land use and 'space' explained more variation in diversity than for the PGPB community subset (Figure 2B). Differences exist in the amount of variation explained by each variable, or combination of variables, when looking at the alpha-diversity of sites within each land use (Figure S4). 'Nutrients' explained the largest portion of variation in alpha-diversity for indigenous forest sites (20%), while 'space' explained the largest portion of variation in alpha-diversity for horticulture (8%), dairy (9%) and sheep and beef (16%) sites. In exotic forest sites, 'metals' explained the largest portion of variation in alpha-diversity (14%).

3.2 | PGPB Community Composition Differs Across Different Land Uses

The composition of soil PGPB communities was significantly different across the five land uses (Figure 3A, PERMANOVA $p < 0.001$, $R^2 = 0.19$) and this pattern remained when accounting for differences in sample size across the land uses (Figure S3b, PERMANOVA $p < 0.001$, $R^2 = 0.22$). However,

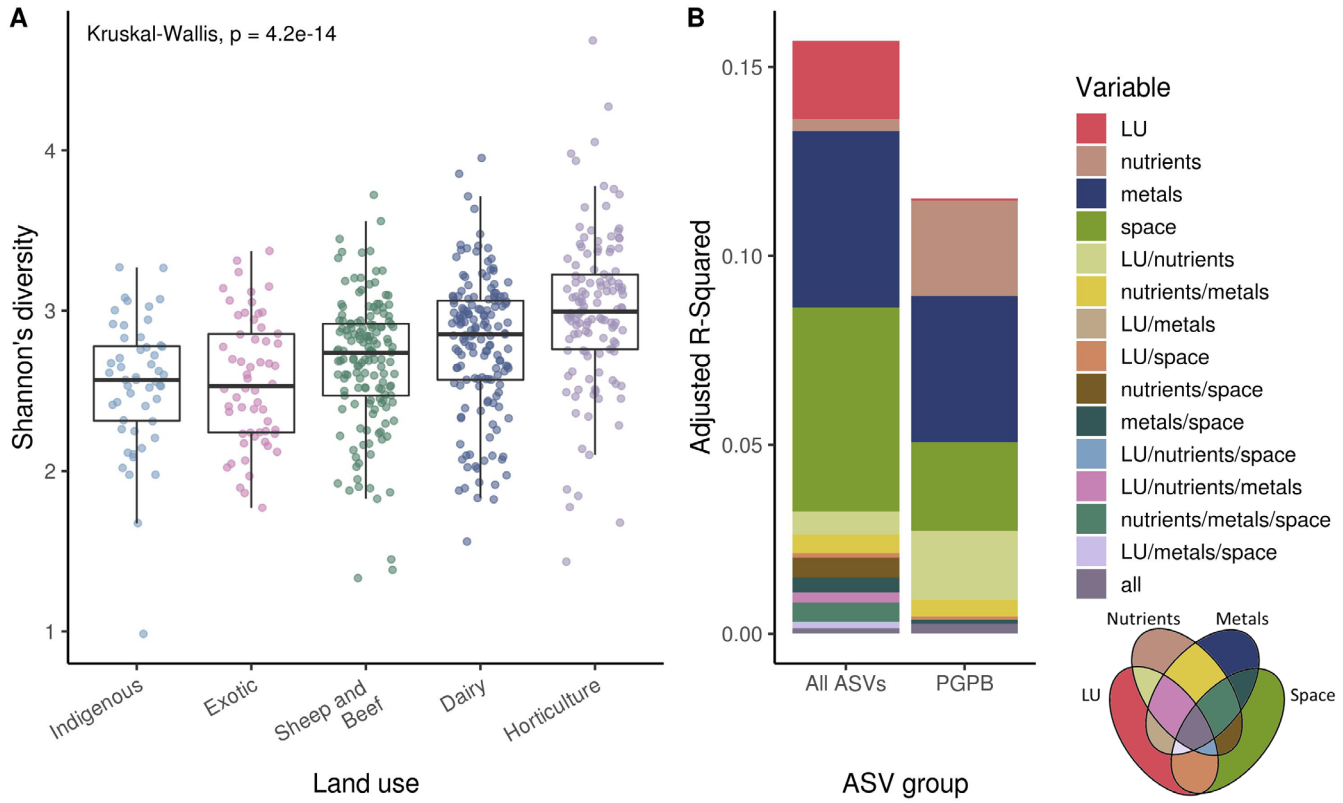

FIGURE 2 | Patterns in alpha diversity for PGPB ASVs across the different land uses and sites. (A) The diversity (Shannon's diversity index) of PGPB communities across the five land uses sampled. Land uses are ordered from least to most intensive. Boxes represent the interquartile range (IQR, 25%–75% of the data). Median values are indicated by the bar within each box, and whiskers show the values within 1.5 times the IQR; all other values are outliers and are shown as points. Kruskal–Wallis test was used to assess the significance of the differences; results from Dunn's test for pairwise comparisons are provided in Table S4. (B) The results of partial regression analysis show the proportion of variation in PGPB diversity (Shannon's diversity index) attributed to each group of explanatory variables or combination of groups. A '/' in the legend indicates shared variation between different variables. Venn diagram visually illustrates the overlaps between variable groups and the corresponding colour on the bar chart. Individual explanatory variables included in each group are described in Table S2.

some or all of this difference could be attributed to differences in the homogeneity of dispersion, which also varied significantly between land uses ($p < 0.001$). Indeed, overall, the dissimilarity of PGPB communities within each land use varied significantly (Figure 3C; Dunn's test $p < 0.001$ for all pairwise comparisons) and this pattern remained when accounting for differences in sample size across the land uses (Figure S3c). Within land use, variation was lowest for the sheep, beef and dairy sites and highest for the horticulture sites (Figure 3C). Overall, the variation in beta-diversity was largely attributed to the interactions between variable groups 'land use', 'nutrients' and 'metals' (15%), and 'land use' and 'nutrients' (9%) as well as the individual effects of variable groups 'land use' (8%) and nutrients (6%) (Figure 3B). Similar patterns were observed for the entire soil bacterial communities (Figure 3B). Within each land use, 'nutrients' explained the greatest portion of variation in beta-diversity for indigenous (12%) and exotic (12%) forests, dairy (9%) and horticulture (8%) sites (Figure S4). Variation in beta-diversity among the sheep and beef sites was most explained by 'space' (9%) (Figure S4).

When considering each site's average pairwise dissimilarity, which is a measure of the degree to which the bacterial community at a site is an outlier (higher) or modal (lower) compared to the average composition of all sites, the amount explained by the shared variable groups 'land use', 'nutrients' and 'metals' was much smaller for the PGPB communities (10%) compared to that for the entire bacterial communities (19%; Figure 3B).

3.3 | Taxonomic Differences Across Land Uses

The proportion of PGPB classified as *Bacillales* and *Flavobacteriales* increased with land use intensity, while *Rhizobiales* and *Corynebacteriales* decreased with increasing land use intensity (Figure 4A). This pattern remains largely consistent when considering the abundance of PGPB relative to the entire bacterial community (Figure S5). Given the roles these taxa are known to play in positively impacting plant growth (Table S1), these taxonomic differences translate into a reduction in the abundance of nitrogen-fixing PGPB when we compare indigenous forests and low-intensity exotic plantation forestry land uses to more intensive land uses, where more taxa contribute to phosphate and potassium solubilisation (Figure 4B). *Burkholderiales*, which are considered potassium solubilisers in a plant growth context, made up 10%–15% of the PGPB communities in the forest land uses (indigenous forest and exotic plantation forestry) but had a much lower abundance (< 2%) in the other land uses. Conversely, Micrococcales and Flavobacteriales were scarce in the forest land uses (< 0.6% and

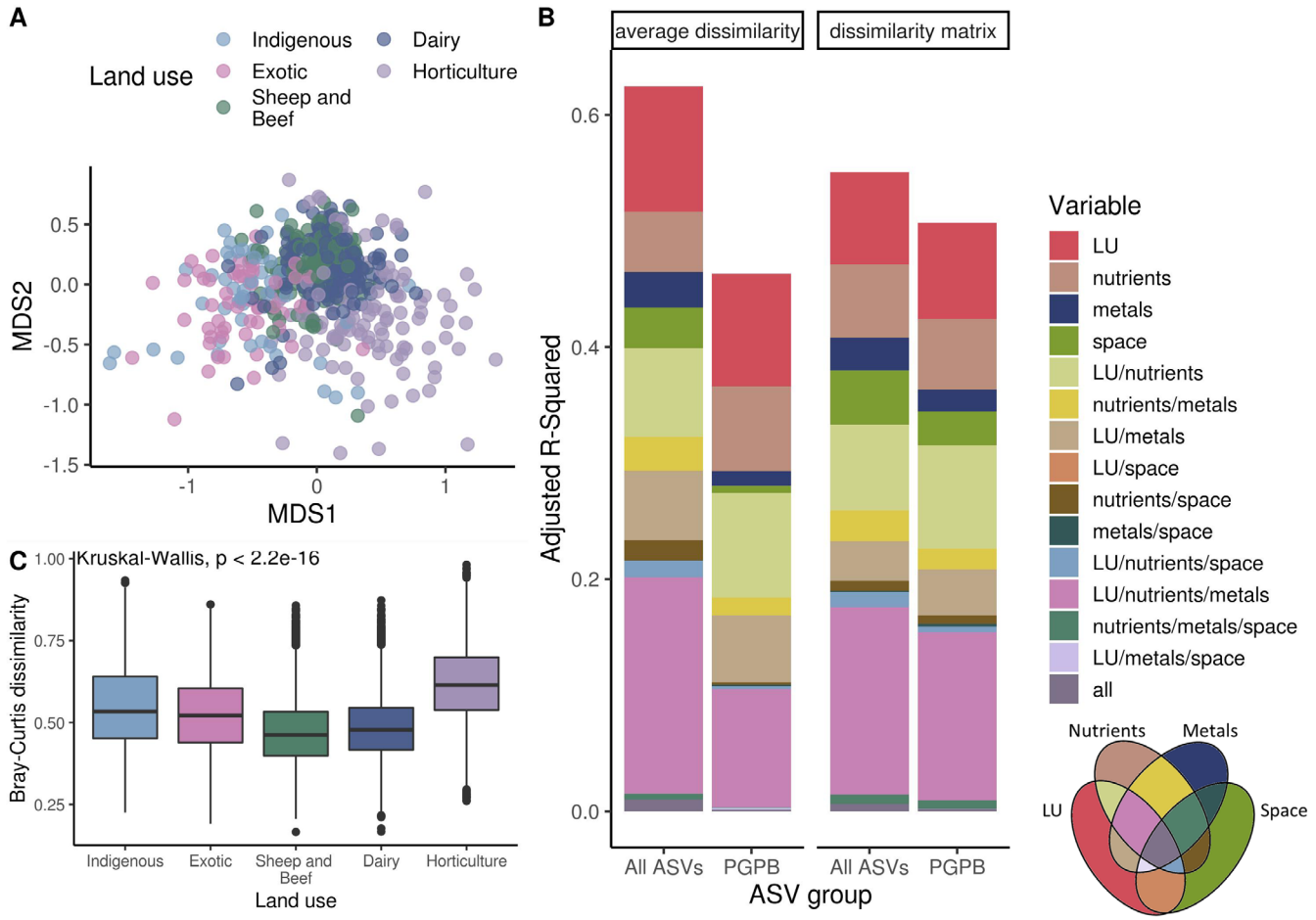

FIGURE 3 | Patterns in beta diversity for PGPB ASVs across the different land uses and sites. (A) Relative compositional differences (Bray–Curtis dissimilarity) between PGPB community composition at sites with different land uses. (B) Amount of variation attributed to each group of explanatory variables (Table S2) individually or in combination with each other for each site's average Bray–Curtis dissimilarity to all other sites or the Bray–Curtis dissimilarity matrix. Results are shown for both the PGPB community subset and the entire bacterial community. Venn diagram insert shows the overlapped groups represented by each colour, as described in the figure legend. (C) Summary of the pairwise dissimilarity scores for all sites from the same land use type. Land uses are ordered from least to most intensive. Boxes represent the interquartile range (IQR, 25%–75% of the data). Median values are indicated by the bar within each box, and whiskers show the values within 1.5 times the IQR; all other values are outliers and are shown as points. Kruskal–Wallis test was used to assess the significance of the differences; Dunn's test confirmed that all pairwise comparisons were significantly different ($p < 0.001$).

< 1.5%, respectively) but made up 3%–5% and 6%–11%, respectively, in the other land uses.

3.4 | Environmental Variables Restricting the Distribution of PGPB

We used specificity analyses (Darcy et al. 2022) to determine which variables most strongly influenced PGPB's environmental distributions across the sites. This test will highlight all ASVs with a distribution across the sites which occurred across a smaller environmental gradient than expected by chance; the range occupied by each ASV will vary, and some may be limited to lower values, while others are limited to intermediate or higher values. Overall, the occurrence of PGPB ASVs was limited by pH, the C:N and Olsen P concentration, as indicated by those ASVs occupying a narrower range of these variables than expected by chance (Figure 5A). A smaller number of ASVs showed specificity to a specific total nitrogen or macroporosity range. Finally, out of the five heavy metals we measured, only cadmium and zinc concentrations limited the distribution of PGPB (Figure 5A). At the land-use level, only a small number of variables influenced the distribution of a small number of PGPB ASVs (Figure S6). For indigenous forests, the occurrence of PGPB ASVs was limited by pH and C:N; in exotic forests it was C:N and zinc; in sheep and beef sites it was only C:N (Figure S6). For dairy sites, microporosity, chromium and zinc limited the distribution of PGPB, and in horticulture sites it was pH, total nitrogen and cadmium. For all variables that limited the distribution of PGPB ASVs across all the sites, those classified as phosphate-solubilising PGPB were the most common (Figure 5B). The 'other' category of PGPB was highly represented among ASVs limited by zinc concentrations. At the same time, only a few ASVs classified as potassium solubilising PGPB were limited by any of the measured variables (Figure 5B). Around 35% of all the ASVs that showed specificity to a measured environmental variable were limited by at least one soil nutrient variable and heavy metal; roughly the same number were limited only by one or more soil nutrient variables (Figure 5C).

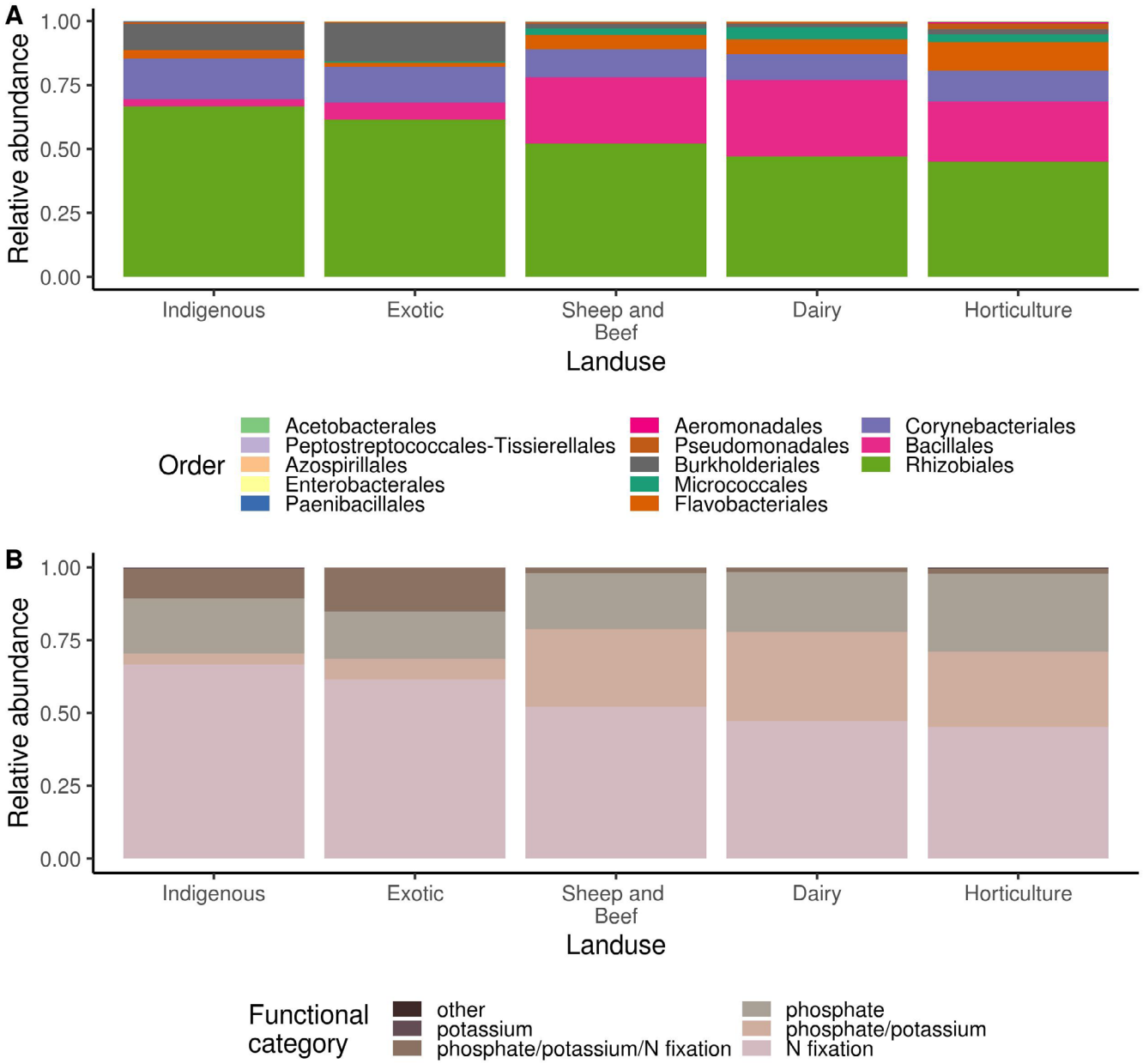

FIGURE 4 | Averaged relative abundance of ASVS from different (A) PGPB orders or (B) PGPB functional categories across the different land use types. Land use is ordered from least to most intensive.

4 | Discussion

Using a national dataset of over 500 sites across various land uses, we show the relationship between land use, environmental variables and the diversity and composition of plant growth-promoting bacteria (PGPB). The alpha-diversity of PGPB communities increased as land use intensity increased, from indigenous undisturbed sites to managed forest, pastures and horticultural sites. Low- and high-intensity land uses had higher beta-diversity than moderate-intensity pasture sites, and soil environmental variables largely drove these patterns. Soil pH, key nutrients and specific heavy metals were identified as limiting the distribution of PGPB ASVs and, therefore, shaping the PGPB communities across the sampled sites. Overall, there were key differences between the patterns in PGPB communities and the entire bacterial community, highlighting the importance of investigating biogeographic patterns of functionally important taxa.

Land use and management practices change the soil environment; the pH, nutrient content, soil physical structure and presence of contaminants or heavy metals are all variables that can be directly and indirectly altered by anthropogenic activity (During 1984; Drewry et al. 2004, 2015; Constancias et al. 2013). The degree of human intervention, and therefore the overall impact and changes caused in the soil environment, varies by land use and management practices. The land uses included here vary from no or very low inputs (indigenous and exotic plantation forests) to moderate or high inputs (grazed pastures and horticulture). We consider horticulture to be the most intensive land use due to the greater inputs, in terms of fertiliser use, pesticide application and soil disturbance for

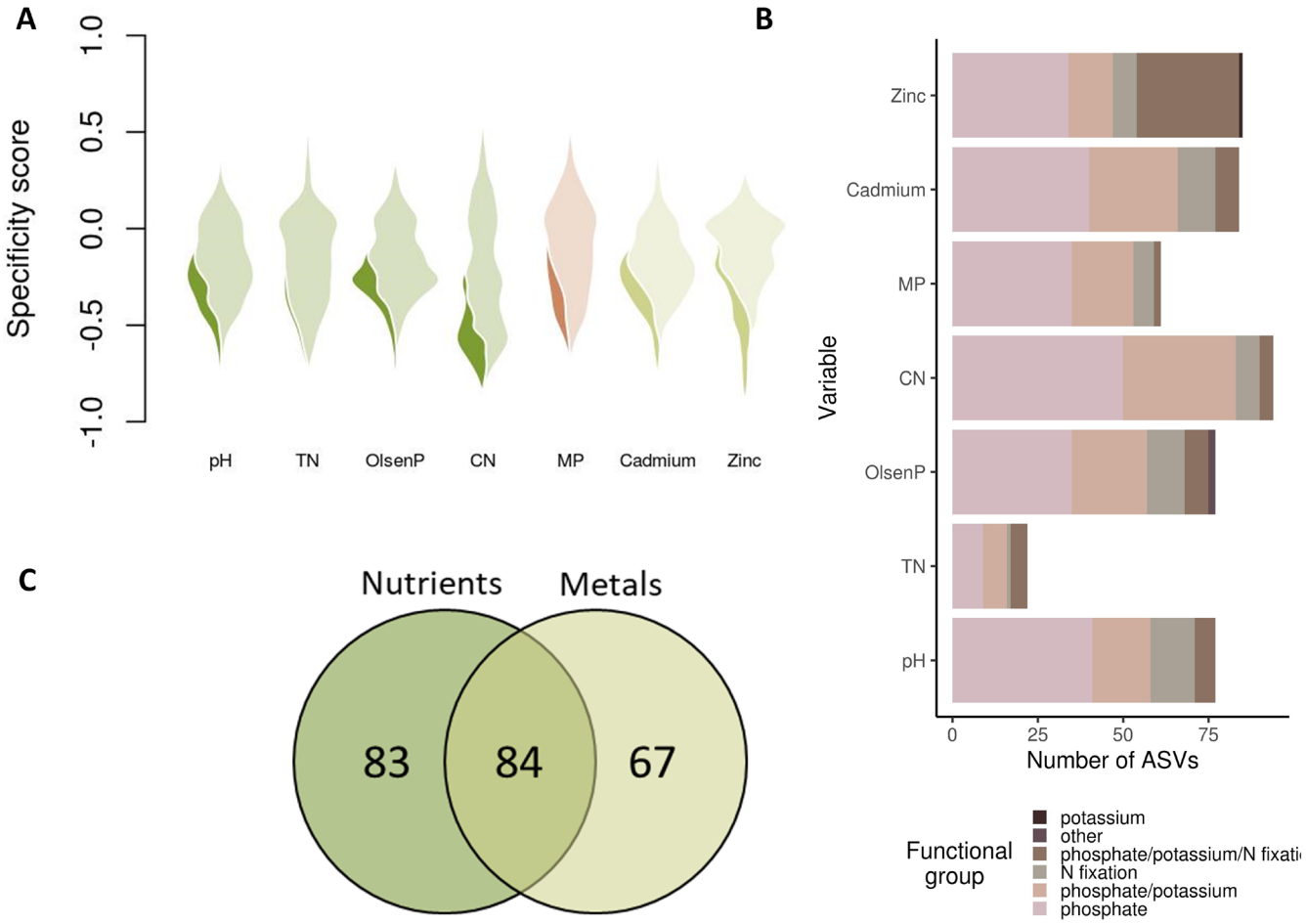

FIGURE 5 | Environmental variables which influenced the distribution of PGPB ASVs across all sites. (A) Number of ASVs that showed specificity for each environmental variable. Darker portions of the violin plots represent statistically significant specificity scores (narrower range of the environmental variable occupied than expected by chance). Variables from Table S2 that are not shown here had no statistically significant ASVs. (B) The functional group category for each PGPB ASV with a significant specificity score for each environmental variable and (C) the number of shared and unique ASVs with a significant specificity score for the nutrient (pH, TN, OlsenP, C:N and microporosity [MP]) and metals (Cadmium and Zinc) variables.

example through cultivation, associated with this land use (Jwaideh et al. 2022; Wainwright et al. 2014; Lillywhite 2014). The PGPB communities in our dataset showed increased alpha-diversity with increasing land use intensity; however, the beta-diversity within each land use did not follow this pattern. Instead, the moderate intensity pasture soils showed lower beta-diversity. This suggests that while this land use selects for a more diverse PGPB community, it also selects for a more consistent PGPB consortium. The horticultural sites, on the other hand, also selected for a more diverse PGPB community, but the community selected for varied between sites. Finally, indigenous and exotic plantation forest sites selected for less diverse PGPB, which were also more different from site to site. While this makes sense for the indigenous forest sites, which can vary widely in their plant communities along the latitudinal gradient we sampled (Leathwick et al. 1996), it is surprising given the exotic plantation forests were all dominated by the same pine species; however, the understory plant species will vary among sites (Brockerhoff et al. 2003), which could explain this pattern.

The observed increase in PGPB diversity with increasing land use intensity corresponds to a decrease in plant diversity, from heterogeneous forests to lower diversity grasslands or monospecific cropping systems. This contradicts the increase in overall bacterial diversity observed with increasing plant diversity (Wu et al. 2022), suggesting that the PGPB communities might respond differently to lower plant diversity; however, in our study, plant diversity and land use intensity are confounded. It has previously been shown that global change factors driven by human activities, which reduce the biodiversity of above-ground species, do not negatively affect microbial biodiversity (Zhou et al. 2020). Similar to what we observed, land use changes from native ecosystems to productive land are associated with increased bacterial alpha-diversity (Zhou et al. 2020), and globally, pasture systems have been shown to contain more diverse bacterial communities than forests (Walters and Martiny 2020). Importantly, we only observed this trend for the PGPB community, not the entire microbial community. This highlights the importance of focusing research efforts on functional subsets of the microbial

communities, especially those of ecological significance or those supporting agricultural industries.

As reported in many soil microbial community studies, at both large (Hermans et al. 2017; Terrat et al. 2017; Griffiths et al. 2011, 2015; Zhou et al. 2020; Fierer and Jackson 2006) and small (Rousk et al. 2010; Zhalnina et al. 2015; Kang et al. 2021) scales, soil pH was identified as a key variable impacting the distribution of PGPB. Deterministic processes more strongly drive bacterial community assembly in acidic or alkaline soils, while communities in neutral soils are dominated by stochastic assembly processes (Tripathi et al. 2018). While most studies have assessed the full microbial community, nitrogen-fixing prokaryotic communities specifically have also previously been shown to correlate with soil pH at a global scale (Sepp et al. 2023). While soil pH may have a direct impact on bacterial cells, for example, through its role in membrane-bound proton pumps and protein stability (Booth 1985; Naz et al. 2022), interactions between pH and other soil variables, including the effects it has on the bioavailability of nutrients and heavy metals, may also explain some of the patterns (Zhalnina et al. 2015; Brady and Weil 2008). Indeed, it has been shown that the outcome of any human-induced global change factor on the microbial community was related to the impact that the variable had on pH (Zhou et al. 2020). In our study, pH also differed significantly for all pairwise comparisons among land uses, except for between indigenous and exotic plantation forests. Some of the differences observed between land uses could be partly due to the impact of soil pH on the PGPB communities. Statistically, the converse could be true, whereby some of the impacts we can attribute to pH might be larger outcomes of the differences among the land uses. However, soil pH has previously been shown to explain variation in the composition and diversity of rhizosphere microbial communities, many of which would be considered PGPB (Fan et al. 2017). Further, the activity of phosphorous solubilising PGPB is altered by soil pH, with more acidic soils resulting in higher phosphorous concentrations in maize leaf tissues, indicating increased activity from phosphorous solubilising PGPB (Inagaki et al. 2015). It is, therefore, most likely that the relationships observed in our study between soil pH and PGPB community composition are driven at least partly by soil pH variation among sites and land uses.

Unsurprisingly, the PGPB communities in this study, many of which are directly or indirectly involved in making nutrients available to plants, showed strong relationships with soil nutrient content. This was true when assessing the PGPB in general, as well as assessing variation in the beta-diversity of PGPB within each land use. At global scales, nitrogen-fixing prokaryote diversity correlates with soil nitrogen content (Sepp et al. 2023). The frequency that genes involved in soil nitrogen cycling are detected in a sample is largely explained by soil carbon and nitrogen concentrations (Nelson et al. 2016). We have previously shown that the abundance of the PGPB genus *Bradyrhizobium* decreases with increasing Olsen P (biologically available phosphorus) (Hermans et al. 2017). In grasslands across the USA, UK and South Africa, phosphorous solubilising bacteria reduce in abundance with nitrogen addition. The soil carbon:phosphorous ratio was an important variable for explaining the variation in the abundance of these bacteria (Widdig et al. 2019). The relationship between phosphorous-solubilising bacteria and soil nutrients has also been demonstrated using culture-based methods targeting these bacteria (Janati et al. 2023). We observed the amount of variation in composition of PGPB to be explained by soil nutrients to a similar extent as the complete bacterial communities. This is likely due to the strong general relationship between soil bacteria and nutrients. For example, previously, 27% of the variability in rhizosphere bacterial communities, many of which are likely to be PGPB, has been explained by the soil chemistry alone; the C:N ratio of the soils was particularly important (Ma et al. 2019). Human-driven changes in soil nutrient content are also known to impact bacterial communities, with the addition of nitrogen and phosphorus fertilisers resulting in a consistent shift of bacterial community composition and functional potential across global grassland sites (Leff et al. 2015), and bacterial diversity and composition are strongly driven by the ratio of carbon, nitrogen and phosphorus in the soil (Delgado-Baquerizo et al. 2017). The relationship between PGPB, soil nutrients and plant growth is, therefore, likely complex and bidirectional; understanding these relationships is crucial to harnessing the full potential of PGPB to support crop growth.

This study took advantage of an existing dataset, which was extremely valuable due to the spatial scale covered, the number of samples included and the soil metadata available. However, the study is not without its limitations. The original study was not conducted with PGPB in mind, so sampling procedures were arguably not optimal for investigating these communities. Importantly, the soil samples consisted of bulk soil, which included plant roots and the rhizosphere. It has been shown that rhizosphere soils contain very different microbial communities than bulk soil, especially in terms of diversity, which decreases with distance from the root (Fan et al. 2017). Further, the bacteria living inside the roots, which are impacted by many factors, including the surrounding soil environment (Gaiero et al. 2013) could also have been captured by our sampling and DNA extraction protocols. The response of microbial communities in the rhizosphere and bulk soil to specific management practices such as tilling is also known to vary (Yang et al. 2013). Since our study sampled these community types simultaneously, some patterns may have been missed due to combining these distinct communities at the sampling stage. However, since the soil surrounding the rhizosphere can act as an important 'source' of rhizosphere bacteria (Zarraonaindia et al. 2015), it is equally important to understand how PGPB in this zone respond to land use and environmental changes; further research to investigate these communities simultaneously but separately could shed further important insights. Additionally, we rely solely on literature-based evidence for the plant-growth promoting properties of the taxa we included in our research. While this evidence is robust, and well documented (Orozco-Mosqueda et al. 2021), the research could still benefit from validation through the application of 'omics methods (Singh et al. 2022) to confirm the activity of the bacteria shows similar patterns to the taxonomic patterns we observed.

It is increasingly being appreciated that biological data, such as the composition of microbial communities, might serve as a much more suitable predictor for soil health metrics than physicochemical properties (Hermans, Buckley, Case, et al. 2020; Wilhelm et al. 2022). Focussing these efforts on specific

functional subgroups, such as PGPB, may ensure such monitoring efforts are optimal for predicting agriculturally important outcomes associated with soil health. The work presented here provides strong evidence that directly or indirectly, PGPB communities respond to the way we use our land. Exploring these communities under more specific land management strategies might highlight important ways they can indicate the health and productive potential of our agricultural soils. Such research would benefit from an experimental approach, which would be a more effective way to establish causality (Shaffer and Johnson 2008). Further, understanding which PGPB are present in our soils, why they are there, and what they are doing, builds the foundations for utilising these communities in the future to improve plant growth and crop yield, especially under environmental pertubations (Igiehon and Babalola 2018). Understanding which conditions favour certain PGPB is vital background knowledge for creating 'microbial consortia' that can be applied to increase crop yield while having other positive impacts like increasing carbon sequestration. PGPB are likely a crucial component of increasing carbon sequestration through increased utilisation of carbon for root growth while maintaining or improving crop yield (Jansson et al. 2021).

Overall, the results here build an understanding of the interplay between how we use our soil, the physicochemical properties of those soils, and the PGPB communities present within them. While PGPB showed some patterns similar to what has been observed for microbial communities, such as their relationship with soil pH, other patterns were unique to this subset of microbes. Given that the abundance and diversity of PGPB are crucial for supporting and improving plant growth in productive land uses, insights into factors that impact their distribution can help optimise the microbial communities serving this function.

Author Contributions

F.C.-C. and M.T. facilitated the sample collection. S.M.H., H.L.B., B.S.C. and G.L. designed the research. S.M.H. performed the research and conducted the data analyses with assistance from B.S.C. and H.L.B. S.M.H. drafted the manuscript; all authors reviewed and edited it.

Acknowledgements

We wish to thank the regional councils and unitary authorities from the following regions for the collection of soil samples and soil metadata, and the farmers and landowners for site access: Northland, Auckland, Waikato, Bay of Plenty, Hawkes Bay, Horizons, Wellington, Tasman, Marlborough, Canterbury and Southland. We also acknowledge using the New Zealand eScience Infrastructure (NeSI) high-performance computing facilities as part of this research. New Zealand's national facilities are provided by NeSI and funded jointly by NeSI's collaborator institutions and through the Ministry of Business, Innovation & Employment's Research Infrastructure programme. S.M.H. is supported by a Rutherford Postdoctoral Fellowship administered by the Royal Society Te Apārangi. Open access publishing facilitated by Auckland University of Technology, as part of the Wiley - Auckland University of Technology agreement via the Council of Australian University Librarians.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

This study utilised two previously published datasets for which the sequence data were accessed from the NCBI Sequence Read Archive (SRA) repository under accession numbers PRJNA323375 and PRJNA578562. R codes used for this manuscript are available in Appendix.

References

Adesemoye, A. O., H. A. Torbert, and J. W. Kloepper. 2009. "Plant Growth-Promoting Rhizobacteria Allow Reduced Application Rates of Chemical Fertilizers." *Microbial Ecology* 58: 921–929. https://doi.org/10.1007/s00248-009-9531-y.

Ahmad, M., S. M. Nadeem, M. Naveed, and Z. A. Zahir. 2016. "Potassium-Solubilizing Bacteria and Their Application in Agriculture." In *Potassium Solubilizing Microorganisms for Sustainable Agriculture*, edited by V. S. Meena, B. R. Maurya, J. P. Verma, and R. S. Meena, 293–313. Springer India. https://doi.org/10.1007/978-81-322-2776-2_21.

Aquino, J. P. A., J. E. L. Antunes, A. Bonifácio, et al. 2021. "Plant Growth-Promoting Bacteria Improve Growth and Nitrogen Metabolism in Maize and Sorghum." *Theoretical and Experimental Plant Physiology* 33: 249–260. https://doi.org/10.1007/s40626-021-00209-x.

Billah, M., M. Khan, A. Bano, T. U. Hassan, A. Munir, and A. R. Gurmani. 2019. "Phosphorus and Phosphate Solubilizing Bacteria: Keys for Sustainable Agriculture." *Geomicrobiology Journal* 36: 904–916. https://doi.org/10.1080/01490451.2019.1654043.

Booth, I. R. 1985. "Regulation of Cytoplasmic pH in Bacteria." *Microbiological Reviews* 49: 359–378.

Brady, N. C., and R. R. Weil. 2008. *The Nature and Properties of Soils*. 14th ed. Prentice Hall.

Brockerhoff, E. G., C. E. Ecroyd, A. C. Leckie, and M. O. Kimberley. 2003. "Diversity and Succession of Adventive and Indigenous Vascular Understorey Plants in *Pinus radiata* Plantation Forests in New Zealand." *Forest Ecology and Management* 185: 307–326. https://doi.org/10.1016/S0378-1127(03)00227-5.

Callahan, B. J., P. J. McMurdie, M. J. Rosen, A. W. Han, A. J. A. Johnson, and S. P. Holmes. 2016. "DADA2: High Resolution Sample Inference From Illumina Amplicon Data." *Nature Methods* 13: 581–583. https://doi.org/10.1038/nmeth.3869.

Constancias, F., N. C. Prévost-Bouré, S. Terrat, et al. 2013. "Microscale Evidence for a High Decrease of Soil Bacterial Density and Diversity by Cropping." *Agronomy for Sustainable Development* 34: 831–840. https://doi.org/10.1007/s13593-013-0204-3.

Darcy, J. L., A. S. Amend, S. O. I. Swift, P. S. Sommers, and C. A. Lozupone. 2022. "Specificity: An R Package for Analysis of Feature Specificity to Environmental and Higher Dimensional Variables, Applied to Microbiome Species Data." *Environmental Microbiomes* 17: 34. https://doi.org/10.1186/s40793-022-00426-0.

Delgado-Baquerizo, M., P. B. Reich, A. N. Khachane, et al. 2017. "It Is Elemental: Soil Nutrient Stoichiometry Drives Bacterial Diversity." *Environmental Microbiology* 19: 1176–1188. https://doi.org/10.1111/1462-2920.13642.

Dinno, A. 2017. "Dunntest: Dunn's Test of Multiple Comparisons Using Rank Sums." *R Package Version* 1: 1.

Drewry, J., F. Curran-Cournane, M. Taylor, and B. Lynch. 2015. "Soil Quality Monitoring Across Land Uses in Four Regions: Implications for Reducing Nutrient Losses and for National Reporting." In *Moving Farm Systems to Improved Attenuation*, edited by L. D. Currie and L. L. Burkitt, 1–14. Fertilizer and Lime Research Centre, Massey University.

Drewry, J. J., R. P. Littlejohn, R. J. Paton, P. L. Singleton, R. M. Monaghan, and L. C. Smith. 2004. "Dairy Pasture Responses to Soil Physical Properties." *Soil Research* 42: 99–105. https://doi.org/10.1071/SR03055.

During, C. 1984. *Fertilisers and Soils in New Zealand Farming*. Sigma Print Limited.

Fan, K., C. Cardona, Y. Li, et al. 2017. "Rhizosphere-Associated Bacterial Network Structure and Spatial Distribution Differ Significantly From Bulk Soil in Wheat Crop Fields." *Soil Biology and Biochemistry* 113: 275–284. https://doi.org/10.1016/j.soilbio.2017.06.020.

Fierer, N., and R. B. Jackson. 2006. "The Diversity and Biogeography of Soil Bacterial Communities." *PNAS* 103: 626–631. https://doi.org/10.1073/pnas.0507535103.

Gaiero, J. R., C. A. McCall, K. A. Thompson, N. J. Day, A. S. Best, and K. E. Dunfield. 2013. "Inside the Root Microbiome: Bacterial Root Endophytes and Plant Growth Promotion." *American Journal of Botany* 100: 1738–1750. https://doi.org/10.3732/ajb.1200572.

Griffiths, R. I., B. C. Thomson, P. James, T. Bell, M. Bailey, and A. S. Whiteley. 2011. "The Bacterial Biogeography of British Soils." *Environmental Microbiology* 13: 1642–1654. https://doi.org/10.1111/j.1462-2920.2011.02480.x.

Griffiths, R. I., B. C. Thomson, P. Plassart, et al. 2015. "Mapping and Validating Predictions of Soil Bacterial Biodiversity Using European and National Scale Datasets." *Applied Soil Ecology* 97: 61–68. https://doi.org/10.1016/j.apsoil.2015.06.018.

Hermans, S. M., H. L. Buckley, B. S. Case, F. Curran-Cournane, M. Taylor, and G. Lear. 2017. "Bacteria as Emerging Indicators of Soil Condition." *Applied and Environmental Microbiology* 83: e02826-16. https://doi.org/10.1128/AEM.02826-16.

Hermans, S. M., H. L. Buckley, B. S. Case, F. Curran-Cournane, M. Taylor, and G. Lear. 2020. "Using Soil Bacterial Communities to Predict Physico-Chemical Variables and Soil Quality." *Microbiome* 8: 79. https://doi.org/10.1186/s40168-020-00858-1.

Hermans, S. M., H. L. Buckley, F. Curran-Cournane, M. Taylor, and G. Lear. 2020. "Temporal Variation in Soil Bacterial Communities Can Be Confounded With Spatial Variation." *FEMS Microbiology Ecology* 96: fiaa192. https://doi.org/10.1093/femsec/fiaa192.

Hill, R. B., and G. P. Sparling. 2009. "Soil Quality Monitoring." In *Land and Soil Monitoring: A Guide for SoE and Regional Council Reporting*. Land Monitoring Forum.

Igiehon, N. O., and O. O. Babalola. 2018. "Rhizosphere Microbiome Modulators: Contributions of Nitrogen Fixing Bacteria Towards Sustainable Agriculture." *International Journal of Environmental Research and Public Health* 15: 574. https://doi.org/10.3390/ijerph15040574.

Inagaki, A. M., V. F. Guimaraes, C. L. M. Do, et al. 2015. "Maize Initial Growth With the Inoculation of Plant Growth-Promoting Bacteria (PGPB) Under Different Soil Acidity Levels." *Australian Journal of Crop Science* 9: 271–280. https://doi.org/10.3316/informit.118919752985563.

Isobe, K., and N. Ohte. 2014. "Ecological Perspectives on Microbes Involved in N-Cycling." *Microbes and Environments* 29: 4–16. https://doi.org/10.1264/jsme2.ME13159.

Janati, W., R. Bouabid, K. Mikou, L. E. Ghadraoui, and F. Errachidi. 2023. "Phosphate Solubilizing Bacteria From Soils With Varying Environmental Conditions: Occurrence and Function." *PLoS One* 18: e0289127. https://doi.org/10.1371/journal.pone.0289127.

Jansson, C., C. Faiola, A. Wingler, et al. 2021. "Crops for Carbon Farming." *Frontiers in Plant Science* 12: 636709. https://doi.org/10.3389/fpls.2021.636709.

Jwaideh, M. A. A., E. H. Sutanudjaja, and C. Dalin. 2022. "Global Impacts of Nitrogen and Phosphorus Fertiliser Use for Major Crops on Aquatic Biodiversity." *International Journal of Life Cycle Assessment* 27: 1058–1080. https://doi.org/10.1007/s11367-022-02078-1.

Kang, E., Y. Li, X. Zhang, et al. 2021. "Soil pH and Nutrients Shape the Vertical Distribution of Microbial Communities in an Alpine Wetland." *Science of the Total Environment* 774: 145780. https://doi.org/10.1016/j.scitotenv.2021.145780.

Karimi, B., S. Terrat, S. Dequiedt, et al. 2018. "Biogeography of Soil Bacteria and Archaea Across France." *Science Advances* 4: eaat1808. https://doi.org/10.1126/sciadv.aat1808.

Kaur, T., R. Devi, D. Kour, A. Yadav, and A. N. Yadav. 2021. "Plant Growth Promotion of Barley (*Hordeum vulgare* L.) by Potassium Solubilizing Bacteria With Multifarious Plant Growth Promoting Attributes." *Plant Science Today* 8: 17–24. https://doi.org/10.14719/pst.1377.

Klindworth, A., E. Pruesse, T. Schweer, et al. 2013. "Evaluation of General 16S Ribosomal RNA Gene PCR Primers for Classical and Next-Generation Sequencing-Based Diversity Studies." *Nucleic Acids Research* 41, no. 1: e1. https://doi.org/10.1093/nar/gks808.

Lacava, P. T., A. C. Bogas, and F. d. P. N. Cruz. 2022. "Plant Growth Promotion and Biocontrol by Endophytic and Rhizospheric Microorganisms From the Tropics: A Review and Perspectives." *Frontiers in Sustainable Food Systems* 6: 796113. https://doi.org/10.3389/fsufs.2022.796113.

Lear, G., V. Washington, M. Neale, B. Case, H. Buckley, and G. Lewis. 2013. "The Biogeography of Stream Bacteria." *Global Ecology and Biogeography* 22: 544–554. https://doi.org/10.1111/geb.12046.

Leathwick, J. R., D. Whitehead, and M. McLeod. 1996. "Predicting Changes in the Composition of New Zealand's Indigenous Forests in Response to Global Warming: A Modelling Approach." *Environmental Software* 11: 81–90. https://doi.org/10.1016/S0266-9838(96)00045-7.

Leff, J. W., S. E. Jones, S. M. Prober, et al. 2015. "Consistent Responses of Soil Microbial Communities to Elevated Nutrient Inputs in Grasslands Across the Globe." *PNAS* 112: 10967–10972. https://doi.org/10.1073/pnas.1508382112.

Lillywhite, R. 2014. "Horticulture and the Environment." In *Horticulture: Plants for People and Places*, edited by G. R. Dixon and D. E. Aldous, vol. 2: Environmental Horticulture, 603–617. Springer. https://doi.org/10.1007/978-94-017-8581-5_1.

Lima, E. F., V. P. d. C. Neto, J. M. de Araujo, F. d. A. Neto, A. Bonifacio, and A. C. Rodrigues. 2016. "Varieties of Lima Bean Shows Different Growth Responses When Inoculated With Bacillus sp., a Plant Growth-Promoting Bacteria." *Bioscience Journal* 32: 1221–1233. https://doi.org/10.14393/BJ-v32n5a2016-32932.

Lisboa, P. H. G., P. H. M. de Andrade, P. C. Machado, C. P. de Sousa, and P. T. Lacava. 2021. "Isolation and In Vitro Screening of Plant Growth-Promoting Rhizobacteria From Solanum Lycocarpum St. Hil., an Endemic Plant of the Brazilian Tropical Savannah." *AJMR* 15: 253–261. https://doi.org/10.5897/AJMR2021.9524.

Ma, S., P. De Frenne, N. Boon, et al. 2019. "Plant Species Identity and Soil Characteristics Determine Rhizosphere Soil Bacteria Community Composition in European Temperate Forests." *FEMS Microbiology Ecology* 95: fiz063. https://doi.org/10.1093/femsec/fiz063.

National Environmental Monitoring Standard. 2022. "Soil Quality and Trace Elements Sampling, Measuring, and Managing Soil Quality and Trace Element Data."

Naz, M., Z. Dai, S. Hussain, et al. 2022. "The Soil pH and Heavy Metals Revealed Their Impact on Soil Microbial Community." *Journal of Environmental Management* 321: 115770. https://doi.org/10.1016/j.jenvman.2022.115770.

Nelson, M. B., A. C. Martiny, and J. B. H. Martiny. 2016. "Global Biogeography of Microbial Nitrogen-Cycling Traits in Soil." *PNAS* 113: 8033–8040. https://doi.org/10.1073/pnas.1601070113.

Oksanen, J., G. Blanchet, M. Friendly, et al. 2017. "Vegan: Community Ecology Package. R Package Version 2.4–2." https://CRAN.R-project.org/package=vegan.

Orozco-Mosqueda, M. D. C., A. Flores, B. Rojas-Sánchez, et al. 2021. "Plant Growth-Promoting Bacteria as Bioinoculants: Attributes and

Challenges for Sustainable Crop Improvement." *Agronomy* 11: 1167. https://doi.org/10.3390/agronomy11061167.

Paulson, J. N., O. C. Stine, H. C. Bravo, and M. Pop. 2013. "Differential Abundance Analysis for Microbial Marker-Gene Surveys." *Nature Methods* 10: 1200–1202. https://doi.org/10.1038/nmeth.2658.

Quast, C., E. Pruesse, P. Yilmaz, et al. 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. 2022. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/.

Ramakrishna, W., R. Yadav, and K. Li. 2019. "Plant Growth Promoting Bacteria in Agriculture: Two Sides of a Coin." *Applied Soil Ecology* 138: 10–18. https://doi.org/10.1016/j.apsoil.2019.02.019.

Ranjard, L., S. Dequiedt, N. Chemidlin Prévost-Bouré, et al. 2013. "Turnover of Soil Bacterial Diversity Driven by Wide-Scale Environmental Heterogeneity." *Nature Communications* 4: 1434. https://doi.org/10.1038/ncomms2431.

Rao, C. R. 1982. "Diversity and Dissimilarity Coefficients: A Unified Approach." *Theoretical Population Biology* 21: 24–43. https://doi.org/10.1016/0040-5809(82)90004-1.

Rao, C. R. 2010. "Quadratic Entropy and Analysis of Diversity." *Sankhya* 72: 70–80. https://doi.org/10.1007/s13171-010-0016-3.

Rousk, J., E. Bååth, P. C. Brookes, et al. 2010. "Soil Bacterial and Fungal Communities Across a pH Gradient in an Arable Soil." *ISME Journal* 4: 1340–1351. https://doi.org/10.1038/ismej.2010.58.

Sepp, S.-K., M. Vasar, J. Davison, et al. 2023. "Global Diversity and Distribution of Nitrogen-Fixing Bacteria in the Soil." *Frontiers in Plant Science* 14: 1100235. https://doi.org/10.3389/fpls.2023.1100235.

Shaffer, T. L., and D. H. Johnson. 2008. "Ways of Learning: Observational Studies Versus Experiments." *Journal of Wildlife Management* 72: 4–13. https://doi.org/10.2193/2007-293.

Singh, J., D. K. Saini, R. Kashyap, et al. 2022. "14—Omics Technologies for Agricultural Microbiology Research." In *Trends of Applied Microbiology for Sustainable Economy Developments in Applied Microbiology and Biotechnology*, edited by R. Soni, D. C. Suyal, A. N. Yadav, and R. Goel, 343–394. Academic Press. https://doi.org/10.1016/B978-0-323-91595-3.00015-X.

Terrat, S., W. Horrigue, S. Dequietd, et al. 2017. "Mapping and Predictive Variations of Soil Bacterial Richness Across France." *PLoS One* 12: e0186766. https://doi.org/10.1371/journal.pone.0186766.

Tripathi, B. M., J. C. Stegen, M. Kim, K. Dong, J. M. Adams, and Y. K. Lee. 2018. "Soil pH Mediates the Balance Between Stochastic and Deterministic Assembly of Bacteria." *ISME Journal* 12: 1072–1083. https://doi.org/10.1038/s41396-018-0082-4.

Wainwright, H., C. Jordan, and H. Day. 2014. "Environmental Impact of Production Horticulture." In *Horticulture: Plants for People and Places*, edited by G. R. Dixon and D. E. Aldous, vol. 1: Production Horticulture, 503–522. Springer. https://doi.org/10.1007/978-94-017-8578-5_15.

Walters, K. E., and J. B. H. Martiny. 2020. "Alpha-, Beta-, and Gamma-Diversity of Bacteria Varies Across Habitats." *PLoS One* 15: e0233872. https://doi.org/10.1371/journal.pone.0233872.

Widdig, M., P.-M. Schleuss, A. R. Weig, et al. 2019. "Nitrogen and Phosphorus Additions Alter the Abundance of Phosphorus-Solubilizing Bacteria and Phosphatase Activity in Grassland Soils." *Frontiers in Environmental Science* 7: 185. https://doi.org/10.3389/fenvs.2019.00185.

Wilhelm, R. C., H. M. van Es, and D. H. Buckley. 2022. "Predicting Measures of Soil Health Using the Microbiome and Supervised Machine Learning." *Soil Biology and Biochemistry* 164: 108472. https://doi.org/10.1016/j.soilbio.2021.108472.

Wu, L., Y. Zhang, X. Guo, et al. 2022. "Reduction of Microbial Diversity in Grassland Soil Is Driven by Long-Term Climate Warming." *Nature Microbiology* 7: 1054–1062. https://doi.org/10.1038/s41564-022-01147-3.

Yang, G., M. Ryo, J. Roy, et al. 2022. "Multiple Anthropogenic Pressures Eliminate the Effects of Soil Microbial Diversity on Ecosystem Functions in Experimental Microcosms." *Nature Communications* 13: 4260. https://doi.org/10.1038/s41467-022-31936-7.

Yang, Q., X. Wang, and Y. Shen. 2013. "Comparison of Soil Microbial Community Catabolic Diversity Between Rhizosphere and Bulk Soil Induced by Tillage or Residue Retention." *Journal of Soil Science and Plant Nutrition* 13: 187–199. https://doi.org/10.4067/S0718-95162013005000017.

Yang, T., N. Lupwayi, S.-A. Marc, K. H. M. Siddique, and L. D. Bainard. 2021. "Anthropogenic Drivers of Soil Microbial Communities and Impacts on Soil Biological Functions in Agroecosystems." *Global Ecology and Conservation* 27: e01521. https://doi.org/10.1016/j.gecco.2021.e01521.

Zarraonaindia, I., S. M. Owens, P. Weisenhorn, et al. 2015. "The Soil Microbiome Influences Grapevine-Associated Microbiota." *MBio* 6: e02527-14. https://doi.org/10.1128/mBio.02527-14.

Zeng, Q., X. Ding, J. Wang, X. Han, H. M. N. Iqbal, and M. Bilal. 2022. "Insight Into Soil Nitrogen and Phosphorus Availability and Agricultural Sustainability by Plant Growth-Promoting Rhizobacteria." *Environmental Science and Pollution Research* 29: 45089–45106. https://doi.org/10.1007/s11356-022-20399-4.

Zhalnina, K., R. Dias, P. D. de Quadros, et al. 2015. "Soil pH Determines Microbial Diversity and Composition in the Park Grass Experiment." *Microbial Ecology* 69: 395–406. https://doi.org/10.1007/s00248-014-0530-2.

Zhou, Z., C. Wang, and Y. Luo. 2020. "Meta-Analysis of the Impacts of Global Change Factors on Soil Microbial Diversity and Functionality." *Nature Communications* 11: 3072. https://doi.org/10.1038/s41467-020-16881-7.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.