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Patterns, Processes, and Predictions: Soil bacteria unique habitats along a megametre transect in Eastern Australia

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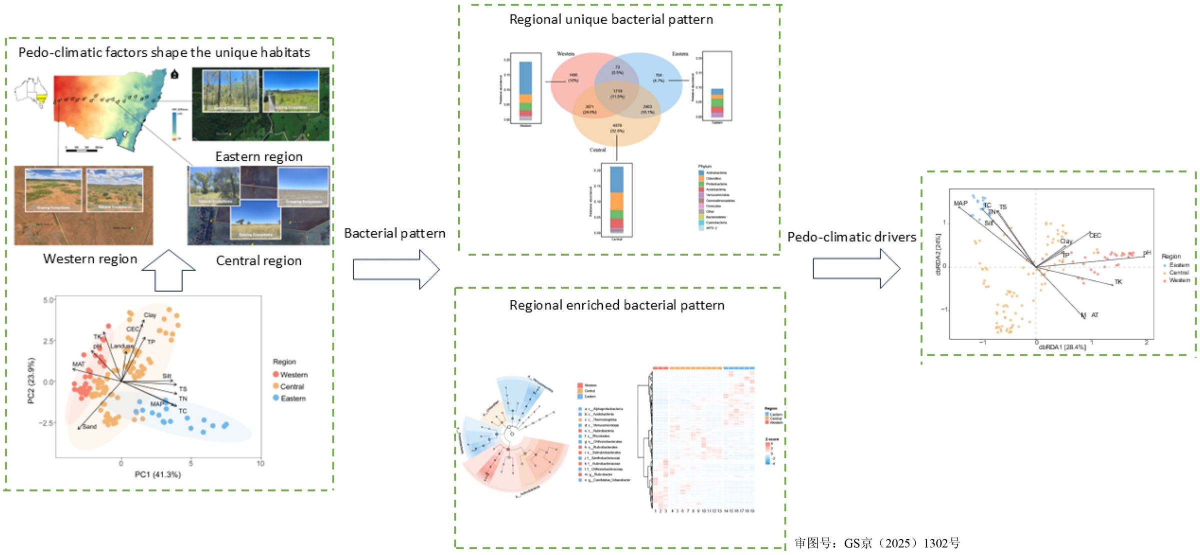
ABSTRACT



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- Bacteria distribution exhibited stronger regional preference even at high taxonomy.
- The increased land use intensity enhances the relative abundance of Actinobacteria and bacterial connectivity.
- Regionally unique bacterial taxa exhibit conserved adaptation to specific pedo-climatic thresholds, e.g., *Candidatus_Udaeobacter* for high precipitation, Rubrobacter for high pH.

Soil microbiomes play a crucial role in ecosystem functioning, yet knowledge about region-specific bacterial taxa across diverse soil types, particularly at a continental scale, remains uncertain. This study employs 16S rRNA sequencing to analyze 141 soil samples collected along a 1400 km transect in New South Wales, Australia, revealing distinct bacterial communities adapted to the varying climatic and soil conditions from east to west. The transect is characterised by three unique pedo-climatic zones: >900 mm mean annual precipitation in the eastern region, 900–300 mm in the central region, and <300 mm in the western region. These variations in climate and soil properties, particularly soil pH, organic carbon, and precipitation, significantly influence bacterial diversity and composition. We identified regionally enriched taxa, including *Verrucomicrobia* in the eastern, *Chloroflexi* in the central, and *Gemmatimonadetes* in the western, demonstrating the adaptation of microbial communities to local environmental conditions. Additionally, our findings show that increasing land use intensity, particularly in agricultural areas, correlates with higher *Actinobacteria* abundance and leads to more homogenised and interconnected microbial networks. This study provides new insights into the biogeography of soil bacteria in Australia, highlighting the importance of local environmental factors in shaping microbial community structure and offering valuable information for ecological and agricultural management strategies.

Keywords soil bacteria, land use, biogeography

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1 Introduction

Soil microorganisms rank among the most abundant and diverse organisms in terrestrial ecosystems. Remarkably, one gram of soil can harbour 10^5 to 10^6 unique “taxonomic groups” (Griffiths et al., 2016), yet a substantial portion of these microbial communities remain undescribed. These microbes are crucial to ecosystem processes, enhancing agricultural productivity and sustainability by regulating element cycling, carbon stabilisation and sequestration (Fierer, 2017; Bhattacharyya et al., 2022). Moreover, soil microbes impact animals and global food security through both direct and indirect influences (Fierer, 2017; Evangelista et al., 2024). Therefore, it is imperative to understand the factors and controls influencing the biogeographic patterns of soil microbes and their community distribution mechanisms.

“Everything is everywhere, but the environment selects” (Baas Becking, 1934) is a concept that has been supported by some studies on soil microbes (Rout and Callaway, 2012; Fondi et al., 2016). However, growing evidence, such as the strong geographical structure of soil microbes, contradicts this idea (Griffiths et al., 2011; Pino et al., 2019). It is clear that microbial diversity, geography, and soil properties are interconnected; however, the mechanisms governing the distribution of soil microbes are not yet fully understood. A large body of research conducted at both regional (Liu et al., 2014; Xue et al., 2018; Xia et al., 2020; Ramoneda et al., 2023) and global scales (Delgado-Baquerizo et al., 2016, 2018) has demonstrated that soil bacterial diversity and assemblages are influenced by soil pH (Ramoneda et al., 2023), soil texture (Xia et al., 2020), soil carbon content (Liu et al., 2014), climate (Xue et al., 2024), land use (Griffiths et al., 2011) and plant community (Delgado-Baquerizo et al., 2018). The distribution of bacteria is primarily an outcome of covarying pedo-climatic effects, which create supportable niches for their survival.

A biogeographic study in France revealed a patchy distribution pattern of soil microbial phyla, highlighting the role of selection and ecological processes (Karimi et al., 2018). It is now recognised that specific high-level bacterial taxa, such as phyla or subphyla, exhibit shared ecological traits, respond predictably to environmental variables (Philippot et al., 2010). For example, species within the same phyla may collaborate in response to ecologically relevant traits, such as drought or wet conditions, signifying that similar environments initiate corresponding assembly processes (Amend et al., 2016). Therefore, comprehending the distinctive species within a specific ecosystem and their influencing factors is crucial for discerning their specific roles in the ecological system. This understanding also provides valuable insights for predicting potential distribution changes in response to ongoing global change.

At the global scale, studies suggest that only a small proportion of soil bacteria is shared between any pair of soil samples across regions, highlighting the geographical influence and heterogeneity in bacterial community composition (Fierer et al., 2012b; Maestre et al., 2015). This diversity can be attributed to the wide-ranging adaptability of some bacterial taxa to diverse environmental conditions, while others are specialised, thriving in more restricted and specific environments (Karimi et al., 2018). For example, *Bradyrhizobium* has been identified as a predominant genus in forest soils across North America (VanInsberghe et al., 2015). Additionally, a lineage within the class *Thermoleophilia* has been recognised as highly abundant in high-temperature environments (Foesel et al., 2016). Particularly, closely related taxa also exhibit distinct environmental preferences. For instance, some *Acidobacteria*, are generally more prevalent in low-pH soils, although this trend does not apply to all subgroups within the phylum (Ramoneda et al., 2023).

The unique biogeographical patterns of microbes are contingent upon multiple factors, including the spatial scale of the research area, the prevailing environmental conditions, and the specific taxonomic groups. Consequently, understanding the living strategies and ecological attributes of these taxa is important for anticipating their probable variations in changing environments (Griffiths et al., 2011). To date, most regional studies have typically involved limited numbers of soil samples collected from relatively restricted areas or have focused on specific environmental contexts. In contrast, larger-scale studies conducted at the global scale often compromise on sample density or environmental resolution, emphasising coarse-scale variables that may overlook critical local interactions. To bridge these gaps, a systematic transect design integrating diverse soil types, climatic regimes, and paired land uses is necessary. Such an approach enables simultaneous examination of fine-scale environmental drivers and maintains relevance at continental scales.

We conducted a large-scale survey along a transect with contrasting land use types in New South Wales (NSW), Australia, to disentangle the interactions between land use management and soil factors on bacterial communities. This comprehensive survey captured significant gradients in annual precipitation (from 230 mm to 1340 mm) and soil types with three land uses.

The key hypotheses of this study are: 1) Soil bacterial communities exhibit distinct distribution patterns along the 1400 km transect; 2) Certain bacterial taxa show clear regional enrichment associated with specific environmental conditions; 3) Increased land-use intensity significantly reduces bacterial diversity and promotes the dominance of specific taxa; and 4) Pedo-climatic variables (including soil type, moisture, temperature, and organic matter content) have stronger impacts on regional bacterial community composition compared to land-use intensity alone. This study seeks to uncover bacterial ecological preferences in relation to pedo-climatic factors and anthropogenic disturbances on a large scale, ultimately providing insights into how bacterial ecosystems respond to changing environments.

2 Material and methods

2.1 Study area

The study area was designed along a transect extending approximately 1400 km from the east coast to the western border of New South Wales (NSW), Australia, within a latitude range of 30°S−31°S. The transect spans from longitude 153°E to 141°E, capturing a significant variation in precipitation (Fig. 1). The mean annual precipitation and mean annual temperature along the transect ranged from 200 to 1300 mm and 10° to 20 °C, respectively.

The transect within latitude 30°S−31°S was subdivided into 19 sampling zones, each approximately 20 km wide, with a 50 km interval between adjacent zones. Within each zone, a sampling buffer with a 10 km radius was established, focusing on the predominant soil class indicated by the soil or pedogenon map of Román Dobarco et al. (2021). To facilitate meaningful comparisons across land-use types while minimizing climatic variability, paired sampling sites within each buffer were selected from identical soil classes. These included natural ecosystems, such as woodlands and forests, as well as managed agricultural lands used for grazing or cropping. Sampling sites within each buffer were positioned within 1–5 km of one another to ensure consistency in environmental conditions.

Given the spatial distribution of cropping areas, predominantly concentrated within the central region of the transect and observed discrepancies between the mapped soil classes and actual field conditions, we adjusted our sampling strategy accordingly. Finally, we obtained a total of 47 sample sites: soil samples under natural vegetation from all 19 sampling buffers, under grazing from 18 buffers (excluding buffer 14, which is entirely within a national park), and cropping soil samples from 10 buffers (ranging from buffer 4 to buffer 13).

At each sampling site, three replicates of topsoil samples (0−10 cm) were collected within a 1 m × 1 m square area, resulting in 141 soil samples (57 natural soils, 54 grazing soils, and 30 cropping soils). Sampling was conducted from October to November 2022, and the geographic coordinates of each sampling site were recorded using a portable GPS. After collection, each sample was divided into two sub-samples: one sub-sample was stored at −20 °C for DNA extraction, while the other was kept at room temperature for physical and chemical analyses.

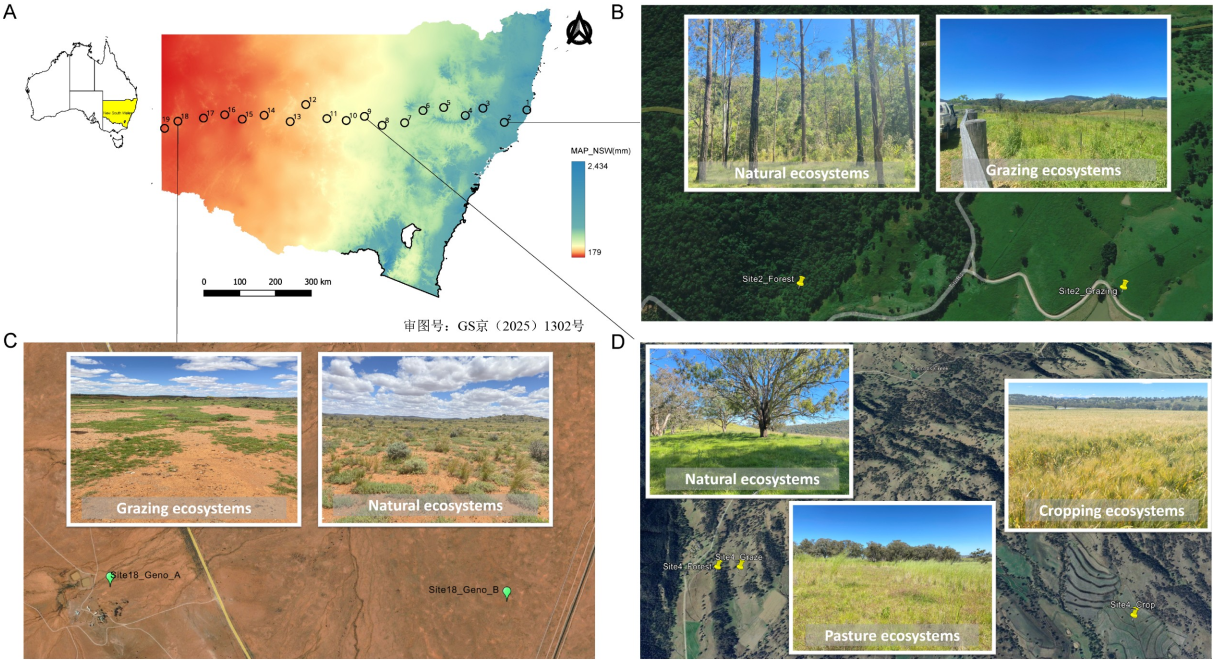

Fig. 1 Sampling design. (A) Sampling buffers along the transect (within latitude 30°S−31°S) in NSW following the different mean annual precipitation gradient from east to west. Examples of the sampling sites: photos and satellite images compared between land uses in the eastern (B), western (C) and central (D) regions.

2.2 Soil DNA sequencing and analysis

Soil DNA was extracted from 0.25 g soil using the Qiagen DNeasy PowerSoil Pro Kit following the manufacturer's protocol. The bacterial community was characterised via targeted sequencing of the bacteria 16S rRNA gene. Amplification was performed using the primer set Pro341F (CCTACGGGNBGCASCAG) and Pro805R (GACTACNVGGGTATCTAATCC) which specifically targets the V3-V4 region of the 16S rRNA gene in bacteria (Amend et al., 2016). Subsequently, the resulting amplicons were then purified using SPRI beads and sequenced by the IMB Sequencing Facility using the Illumina MiSeq (2 × 300 bp) platform.

Raw sequencing data were processed using the 'DADA 2' package in R following Callahan et al. (2016). Low-quality sequencing reads were filtered out with the expected errors exceeding 2 for the forward reads or 3 for the reverse reads. The identification and removal of chimaeras were finished using the "consensus" method of the "removeBimeraDenovo" function. The amplicon sequence variant (ASV) table was generated after denoising and chimaera removal. Taxonomic assignment for the ASVs up to genus level was conducted using the naïve Bayesian Classifier with version 138 of the Silva reference database (Quast et al., 2012).

2.3 Soil properties and climate data

Soil pH was measured by electrochemical sensors with a 1:5 soil to deionized water. Soil texture was analysed using the hydrometer method (Gee and Bauder, 1986). Other soil properties, including total carbon (TC), total nitrogen (TN), total soil phosphorus (TP), and total soil sulphur (TS), were measured by a commercial lab using standard methods (Rayment and Lyons, 2011).

Climate data, including mean annual precipitation (MAP), and mean annual temperature (MAT), were downloaded from the Terrestrial Ecosystems Research Network (TERN) (O'Brien and Searle, 2019) and extracted based on the site coordinates using the 'raster' package (Hijmans et al., 2015) in R.

Based on principal component analysis (PCA) of physicochemical characteristics, the east-to-west transect exhibited pronounced regional patterns: East (Buffer 1 to 3), Centre (Buffer 4 to 13), and West (Buffer 14 to 19) (Fig. 2). The Eastern region (from Port Macquarie to Niangala) was characterised by higher annual precipitation (more than 900 mm) with the highest soil carbon content ranging from 1.7% to 6.9%. The primary soil type in this region was Dermosol according to the Australian Soil Classification (Luvisol, or Cambisol in World Reference Base classification, WRB), and the predominant vegetation consists of Eucalyptus open forests. The Central region (between Willow Tree and Sandy Creek) was Vertosol-dominated (Vertisol in WRB), with woodlands as the prevailing plant community and a concentration of farming. This area had MAP ranging from 900 mm to 300 mm, displaying a neutral pH level and higher CEC and soil clay content. In the Western area (between Noona and Cockburn), which experienced a deficit of annual precipitation (less than 300 mm), the dominant features included the highest pH levels, ranging from 6.25 to 8.7. The soils in this region are primarily Kandosol (Acrisol or Lixisol in WRB) and the vegetation is dominated by shrublands (Román Dobarco et al., 2021).

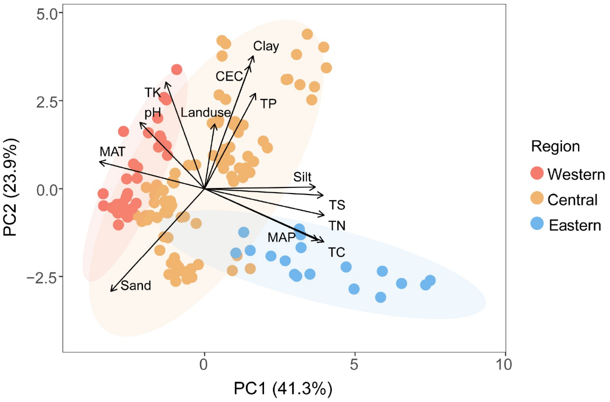

Fig. 2 Principal component analysis (PCA) biplot of soil properties and environmental factors, clustered by three regions (n = 141).

2.4 Data analysis

To visualise regional soil properties and climate characteristics, we performed Principal Component Analysis (PCA) using the 'FactoMineR' package (Lê et al., 2008). The ASV table, taxonomy table, and sample metadata were integrated using the 'phyloseq' package (Quast et al., 2012) in R studio (R 4.3.1). Initially, we filtered out ASVs with fewer than 10 reads across all samples and those that were present in only a single sample. Subsequently, ASV reads were rarefied to the minimum read count (9200). The 'microeco' package (Liu et al., 2021) was employed to compute bacterial community alpha diversity. Statistical significance in observed richness among the three regions was determined using the *t*-test.

To elucidate the effects of region and land use types on bacterial beta diversity, we applied the 'vegdist' function in the 'vegan' package based on Bray−Curtis dissimilarity (Oksanen et al., 2013). Differences in diversity patterns due to regional and land use type effects were assessed using Permutational Multivariate Analysis of Variance (PERMANOVA) via the 'adonis2' function. The distribution of the bacterial community was depicted by the mean relative abundance of bacterial phyla in relation to regional patterns and land use impacts. To better illustrate the variation in bacterial diversity across different sampling ranges, we grouped the ASVs within each range (from 25 km^2 to 1587600 km^2) and then calculated the total species pool and Shannon diversity index. We analysed the bacteria network for three land use types within three regions using the ‘microeco’ package (Liu et al., 2021). Thus, each network was based on at least 9 communities. Only ASVs with relative abundance >0.05% were used in this analysis, and we set the cutoff ($p < 0.01$, $\rho > 0.7$) based on Spearman correlation. The network visualization was performed using Gephi (Bastian et al., 2009). To identify regional unique patterns from the species pool, we first calculated the variation in regional species pool size (total ASV richness). Then, the frequency of each ASV occurring across all sites was calculated for each region, respectively. ASVs with two or more occurrences were classified as regionally unique.

Environmental factors influencing regional bacterial distribution were analysed using Distance-based Redundancy Analysis (db-RDA) based on Bray−Curtis dissimilarity with the ‘microeco’ package (Liu et al., 2021). MAT, MAP, sand, silt, clay, contents, pH, TC, TN, TP, TS, and CEC were calculated as environmental variables. Correlations among bacterial alpha, beta diversity, and environmental factors were evaluated using the Mantel test via the ‘linkET’ package (Huang, 2021). To identify the most significant environmental factors affecting bacterial diversity, we employed the XGBoost machine learning algorithm to evaluate the SHAP value through regression with squared loss, using the ‘SHAPforxgboost’ package (Liu and Just, 2019).

To identify the differences in the bacterial community composition at different regions, we conducted a Linear Discriminant Analysis Effect Size (LefSe) using the ‘microeco’ package (Liu et al., 2021). The LefSe results are illustrated using ‘ComplexHeatmap’ package (Gu et al., 2016). Additional data visualisations were generated in R using ‘ggplot2’ (Sall and Lehman, 2001).

3 Results

3.1 Pedo-climatic factors and bacterial diversity along the transect

Across the longitudinal transect, we observed a pronounced rainfall gradient from east to west, with mean annual precipitation (MAP) ranging from 1340 mm to 230 mm (Fig. 3). As MAP decreased, soil pH increased substantially, exceeding values of 8.7 in the western regions. This gradient also corresponded to a decrease in soil carbon content from 6.9% in the eastern to 0.2% in the western. Concurrently, soil DNA yield also exhibited a substantial reduction from 663.6 μg L^{-1} in eastern sites to 3.7 μg L^{-1} in western sites. Regarding bacterial diversity, the observed ASVs was higher in the central region (Buffer 4 to 13) of the transect. Additionally, the first axis of the Principal Coordinates Analysis (PCoA1) exhibited a clear west-to-east gradient along the transect.

3.2 Regional distribution of soil bacteria along the transect

Along the transect, soil bacteria communities exhibited significant regional clustering consistent with distinct soil regions along the transect (Fig. 4). The Bray-Curtis-based PCoA results revealed significant dissimilarities in bacterial

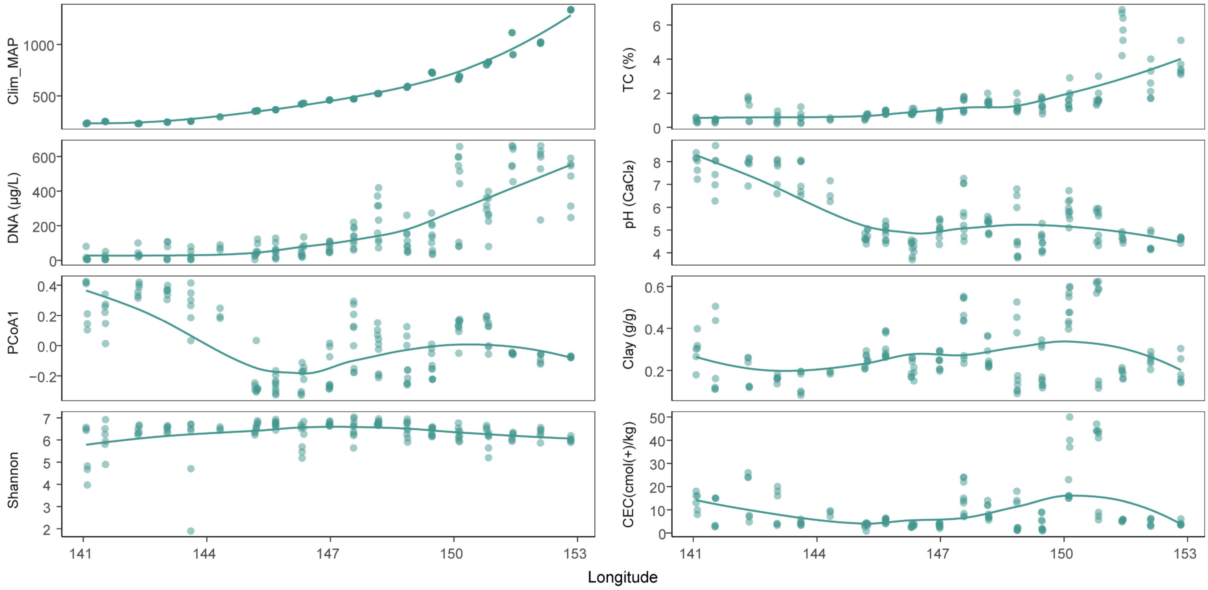

Fig. 3 Soil properties, climate conditions and bacterial diversity along the transect (n = 141). CEC, cation exchange capacity; MAP, mean annual precipitation; TC, soil total carbon; PCoA 1, the first axes of the PCoA result based on the Bray–Curtis distance.

community composition among the three soil regions, with the first two axes explaining 12.37% and 9.89% of the total variance (Fig. 4A). Regarding alpha diversity, the central region displayed the highest mean richness, with a mean value of 1335 (Fig. 4B). Although the observed richness in the western region was slightly higher than the eastern region, the discrepancy was not statistically significant.

Across the transect, 25 bacterial phyla were identified from 141 topsoil samples. Generally, *Actinobacteria* and *Proteobacteria* were the most abundant and diverse phyla (Fig. 4C). In the western region, *Actinobacteria* was the most prevalent phylum, with a relative abundance of around 50.7%. It was followed by *Proteobacteria* at 21.7% and *Acidobacteria* at 5.17%. In the central region, *Actinobacteria* remained the dominant phylum with a relative abundance of 42.4%, while *Proteobacteria* made up 19.9%. In contrast to other regions, the eastern area was dominated by *Proteobacteria* with a relative abundance of 33.7%, whereas *Actinobacteria* accounted for 23.4%.

Notably, *Actinobacteria* and *Gemmatimonadetes* exhibited an increasing relative abundance gradient from east to west, whereas *Acidobacteria* and *Verrucomicrobia* notably declined, with *Verrucomicrobia* decreasing sharply from 12.7% in the eastern to 0.8% in the western. For the *Chloroflexi* phyla, the relative abundance was higher in the central. The *Proteobacteria* and *Firmicutes* exhibited contrasting regional distribution, with *Proteobacteria* predominantly found in the terminal regions while *Chloroflexi* was more prevalent in the central region.

3.3 Regional unique and site species taxa

The three regions demonstrated distinct bacterial taxa pool sizes, with 1496 unique ASVs in the western region, 4878 in the central region, and 704 in the eastern region (Fig. 5). The central region exhibited the largest proportion of unique ASVs (32.6%), while the western and eastern regions accounted for 10% and 4.7%, respectively. 11.5% of ASVs were common across all three regions.

Regional unique taxa, defined as ASVs occurring at multiple sites within a region, showed clear regional differences (Fig. S1). We obtained 448 regional unique ASVs in the eastern region, 4168 in the central region and 1297 in the western region. The relative abundance of these unique

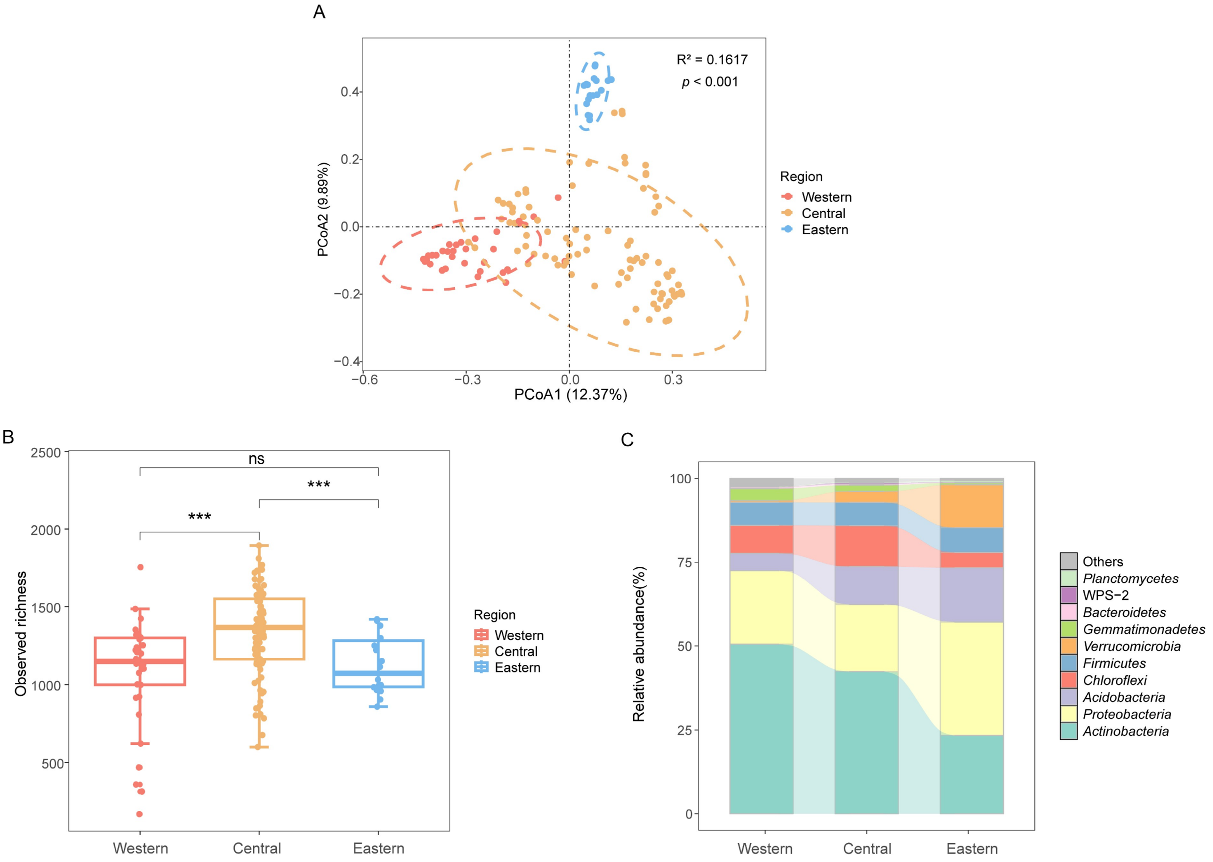

Fig. 4 Bacterial diversity and composition in three regions (n = 141). (A) Principal coordinate analysis (PCoA) of bacterial communities based on the Bray−Curtis distance, clustered by three regions. (B) Observed richness richness of soil bacteria compared across three regions. (C) Relative abundances of soil bacterial community at the phylum level compared across three regions. CEC, cation exchange capacity; MAT, mean annual temperature; MAP, annual precipitation; EC, electric conductivity; TC, soil total carbon; TN, total nitrogen; TP, total phosphorus; TS, total sulphur; TK, total potassium.

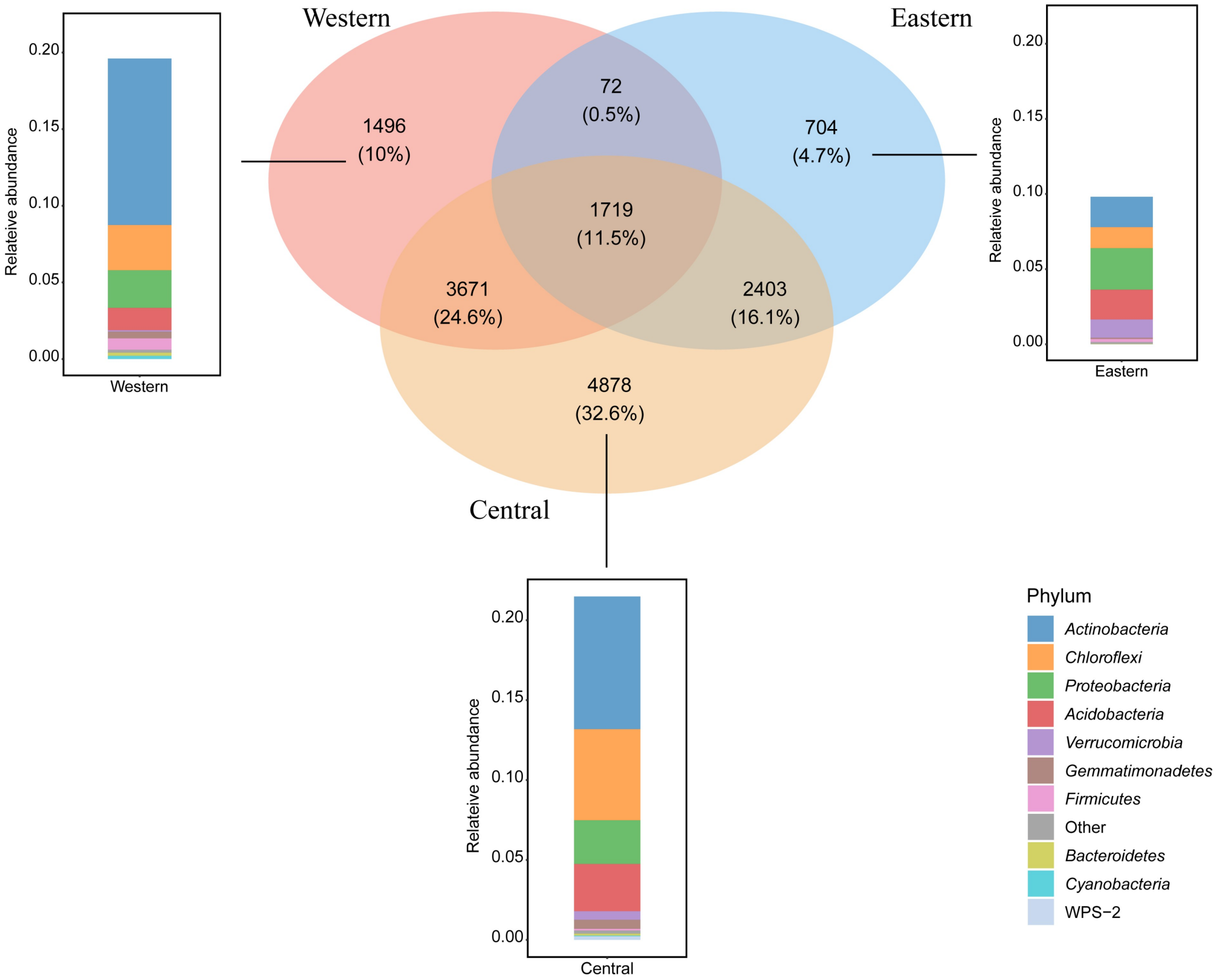

Fig. 5 Venn diagram of bacteria ASVs across three regions, and the relative abundances of the regional unique bacteria at the phylum level for the three regions, respectively (n = 141).

taxa was generally modest, highest in the central region (21.5%), followed by the western (19.6%) and eastern regions (9.8%). For those regional unique taxa, *Actinobacteria*, *Chloroflexi*, and *Proteobacteria* emerged as the dominant phyla exhibiting significant regional patterns (Fig. 5). *Actinobacteria* was the most abundant phyla in both the western and central regions, while *Proteobacteria* accounted for the largest proportion in the western region. However, the diversity of bacteria within each phylum varied by region. The phylogenetic distribution of the *Chloroflexi* group further highlights the regional selection of its phylogenetic lineages (Fig. S2).

Location-specific taxa (present in only one sampling buffer) comprised approximately 4.66% of ASVs in the eastern, decreasing to 1.25% in the western (Fig. S3). The eastern region displayed the highest percentage of shared ASVs across regions, at approximately 36.5%.

3.4 Land use effect on bacterial community

Species richness and Shannon diversity increased according to a power-law relationship with the expansion of the study area (Fig. 6A). This trend was consistent across land uses, including grazing and natural areas. Initially, cropping areas exhibited slightly higher diversity; however, with increasing spatial scales, this increment slowed and eventually fell below levels observed in natural and grazing areas.

Land use significantly modulated microbial diversity and composition within each region (Fig. 6). Across all regions, increased land use intensity was associated with increased bacterial similarities (Fig. 6B), particularly in the central region. This trend reflected the changes in soil properties, with cropping significantly affecting topsoil texture, pH, total carbon (TC), and total phosphorus (TP), unlike grazing, which had negligible impacts (Table 1). Grazing reduced bacterial dissimilarity significantly in both eastern and western regions. Natural areas exhibited higher relative abundances of *Verrucomicrobia* and *Proteobacteria*, whereas *Firmicutes* were more prevalent in grazing areas (Fig. 6C). In the central region, land-use intensity correlated positively with the abundance of *Actinobacteria*. In the western region, natural areas showed higher abundances of *Proteobacteria*

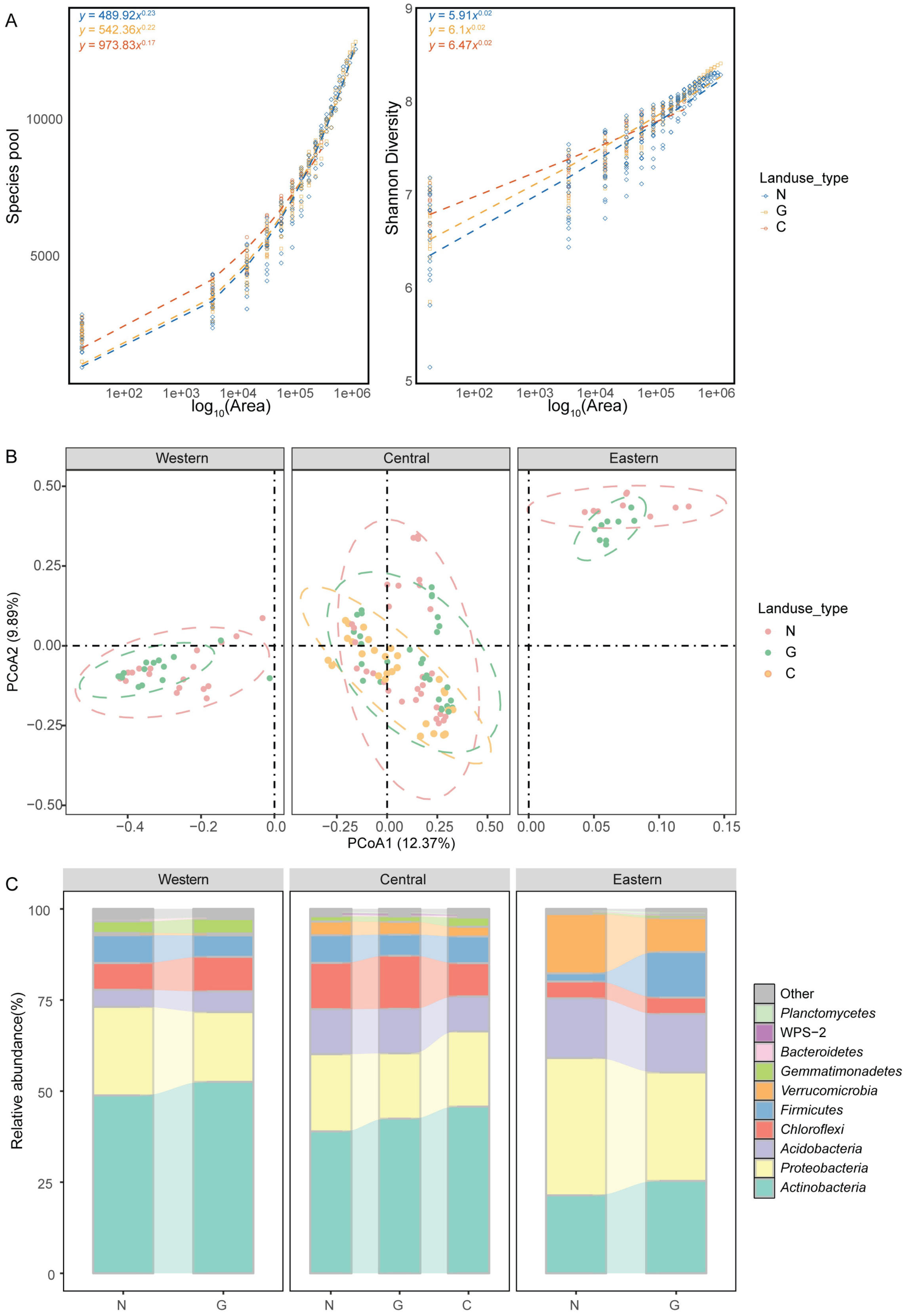

Fig. 6 Land use effects on soil bacterial diversity and composition (n = 141). (A) A power-scaling species-area relationship of species pool and Shannon diversity in the study areas. (B) Principal coordinate analysis (PCoA) of bacterial communities compared by land uses for the three regions. (C) Regional relative abundances of soil bacterial communities compared by land uses at the phylum level. N, natural soils; G, grazing soils; C, cropping soils.

Table 1 Mean soil physicochemical properties of different land use within three regions along the transect.

	Eastern		Central			Western	
	Nature	Grazing	Nature	Grazing	Cropping	Nature	Grazing
Clay (g/g)	0.23 ± 0.01 a	0.20 ± 0.02 a	0.26 ± 0.02 a	0.30 ± 0.03 ab	0.36 ± 0.03 b	0.19 ± 0.02 a	0.22 ± 0.03 a
Silt (g/g)	0.30 ± 0.03 a	0.25 ± 0.02 a	0.13 ± 0.02 a	0.12 ± 0.01 a	0.12 ± 0.01 a	0.06 ± 0.01 a	0.07 ± 0.01 a
Sand (g/g)	0.47 ± 0.03 a	0.55 ± 0.02 b	0.62 ± 0.03 b	0.58 ± 0.03 ab	0.51 ± 0.03 a	0.75 ± 0.02 a	0.71 ± 0.04 a
pH	4.51 ± 0.10 a	4.62 ± 0.08 a	4.88 ± 0.12 b	4.83 ± 0.12 b	5.42 ± 0.16 a	7.31 ± 0.16 a	7.87 ± 0.15 b
CEC	4.32 ± 0.30 a	5.13 ± 0.44 a	9.11 ± 2.16 a	9.89 ± 2.27 a	12.89 ± 2.32 a	8.74 ± 1.26 a	12.54 ± 2.16 a
Total C (%)	3.80 ± 0.62 a	4.22 ± 0.49 a	1.36 ± 0.12 a	1.09 ± 0.07 b	1.12 ± 0.08 ab	0.53 ± 0.06 a	0.70 ± 0.15 a
Total N (%)	0.21 ± 0.04 a	0.25 ± 0.03 a	0.09 ± 0.01 a	0.09 ± 0.01 a	0.09 ± 0.01 a	0.05 ± 0.01 a	0.05 ± 0.01 a
Total P (%)	6.36 ± 1.27 a	9.34 ± 1.60 a	22.57 ± 5.07 b	17.28 ± 2.93 b	38.77 ± 5.77 a	9.27 ± 1.18 a	10.37 ± 1.09 a
Total K (%)	0.13 ± 0.03 a	0.09 ± 0.02 a	0.26 ± 0.03 a	0.27 ± 0.03 a	0.34 ± 0.03 a	0.41 ± 0.03 a	0.49 ± 0.05 a
Total S (%)	0.02 ± 0.00 a	0.02 ± 0.00 a	0.01 ± 0.00 a	0.01 ± 0.00 a	0.01 ± 0.00 a	0.01 ± 0.00 a	0.01 ± 0.00 a

Note: the data are means ± standard error (SE), different letters suggest significant levels ($P < 0.05$).

and *Firmicutes*, with a slight decline in *Chloroflexi*.

Network analysis further revealed distinct bacterial co-occurrence patterns (Fig. S4). The western and central regions exhibited more extensive co-occurrence networks, characterized by higher numbers of nodes and edges compared to the eastern region (Table S1). Regarding land use, the bacterial co-occurrence networks in the central and eastern regions exhibited similar structures. However, significant differences were observed in the central region under different land use intensities. Specifically, in the central region, increasing land-use intensity decreased modularity and average path length, while increasing average degree, density, and centralization, indicating more interconnected but less clustered bacterial networks.

3.5 Soil and environmental factors influencing the bacterial community

The distance-based Redundancy Analysis (db-RDA) revealed significant relationships between ASVs and climatic and edaphic physicochemical factors (Fig. 7A), with the first two axis explaining 51.4% of the total variation. Soil pH and MAP were the strongest explanatory factors, correlating predominantly with the western and eastern regions, respectively. The MAP was significantly related to soil nutrients, including carbon (TC), nitrogen (TN), potassium (TK), pH, and soil texture (Fig. 7B). The specific impacts of environmental conditions and soil properties on bacterial diversity were further assessed. PCoA 1 was primarily related to soil pH (R^2=0.7), while PCoA 2 was influenced by MAP (R^2=0.71) (Fig. S5). Optimal bacterial richness occurred within a soil pH range of 5.5–7, and beta diversity exhibited distinct patterns across varying pH levels (Fig. 7C).

We obtained 226 bacterial genera showing significant differences (p<0.05) between regions by the LefSe analysis (Fig. 8A). *Acidobacteria*, *Verrucomicrobia*, and *Proteobacteria* were significantly enriched in the eastern region, while *Chloroflexi* and *Actinobacteria* dominated the central and western regions, respectively. Clear regional shifts in bacterial genera distribution were observed, particularly between the eastern and western regions (Fig. 8B).

The distribution of the top ten bacterial genera further revealed regional specificity (Fig. 8C). While *Bacillus* can be found in all regions, each region was dominated by specific genera. *Candidatus_Udaeobacter, Candidatus_solibacter*, and *Acidothermus* were mainly found in the eastern region, but their relative abundance decreased as we moved to the west. The central region had a more even distribution of bacteria genera compared to the other regions and was dominated by *Conexibacter. Rubrobacter* and *Solirubrobacter* were more enriched in the western region. Significant linear correlation coefficients were observed between the enriched bacterial genera and environmental factors (Fig. 8D). For instance, the *Rubrobacter* genus showed a positive correlation with higher pH.

4 Discussion

Our megametre east-to-west transect study has demonstrated that similar environmental conditions lead to comparable bacterial distribution patterns, underscoring the critical role of pedo-climatic factors in shaping bacterial community composition on a large scale. Soil bacteria display specific regional preferences even at higher taxonomic levels, highlighting the combined influence of environmental selection and neutral processes. Although pedo-climatic factors are the primary drivers of bacterial distribution on a large scale, our study also emphasises the important role of agricultural activities in influencing bacterial diversity at a local scale.

Similar to previous studies across the USA (Fierer and Jackson, 2006), north China (Liu et al., 2014), and Canada

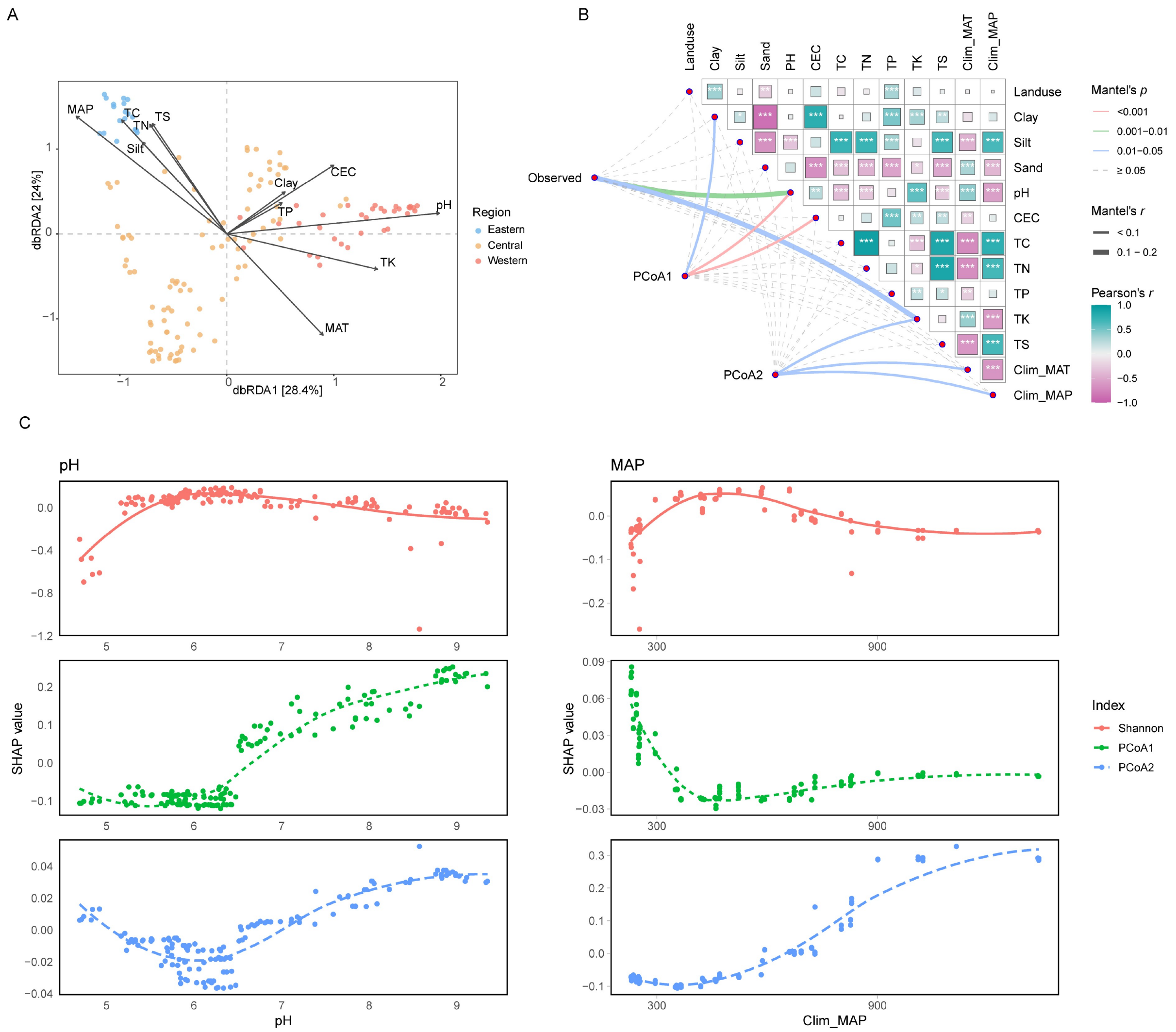

Fig. 7 Relationships between bacterial community composition and environmental factors (n = 141). (A) db-RDA plot based on ASV level showed the variation with respect to different regions. (B) Pearson correlation coefficients indicate the relationship between environmental factors. Mantel tests were used to assess the relationship between bacteria diversity and each environmental factor. Observed, observed richness; PCoA1, the first axis of Principal coordinate analysis; PCoA2, the second axis of Principal coordinate analysis. (C) SHAP values of soil pH and MAP to bacterial diversity were evaluated using regression with squared loss. CEC, cation exchange capacity; MAT, mean annual temperature; MAP, mean annual precipitation; EC, electric conductivity; TC, soil total carbon; TN, total nitrogen, TP, total phosphorus, TS, total sulphur, TK, total potassium. *p <0.05, **p <0.01, ***p <0.001.

(Banerjee et al., 2016), our study also found that *Actinobacteria*, *Proteobacteria*, and *Acidobacteria* are the dominant phyla in Southeastern Australia. However, we place greater emphasis on regional differences within the transect. Overall, bacterial distribution is influenced by a combination of pedo-climatic and land use patterns. Our findings offer valuable insights for microbial researchers, indicating specific regions where targeted microbes are abundant and their optimal habitat.

4.1 Unique habitats of soil bacteria along the transect

Across the transect, three distinct regions were identified based on pedo-climatic factors from east to west. The significant and unique geographic and climatic patterns across the transect are primarily attributed to the Great Dividing Range across the NSW. The north-south orientation of the Great Dividing Range creates a division between the expansive low-elevation arid regions (the central and western regions) and the coastal areas (the eastern region). This division results in stark contrasts in vegetation, soil types, and land use practices. For instance, the eastern region, with its abundant rainfall, supports lush forests, while the central region is characterised by its mixed farming systems, and the western region is dominated by rangelands.

In the eastern region, characterised by high precipitation and carbon content, *Acidobacteria*, *Proteobacteria*, and *Verrucomicrobia* prevailed. These bacterial phyla thrive in

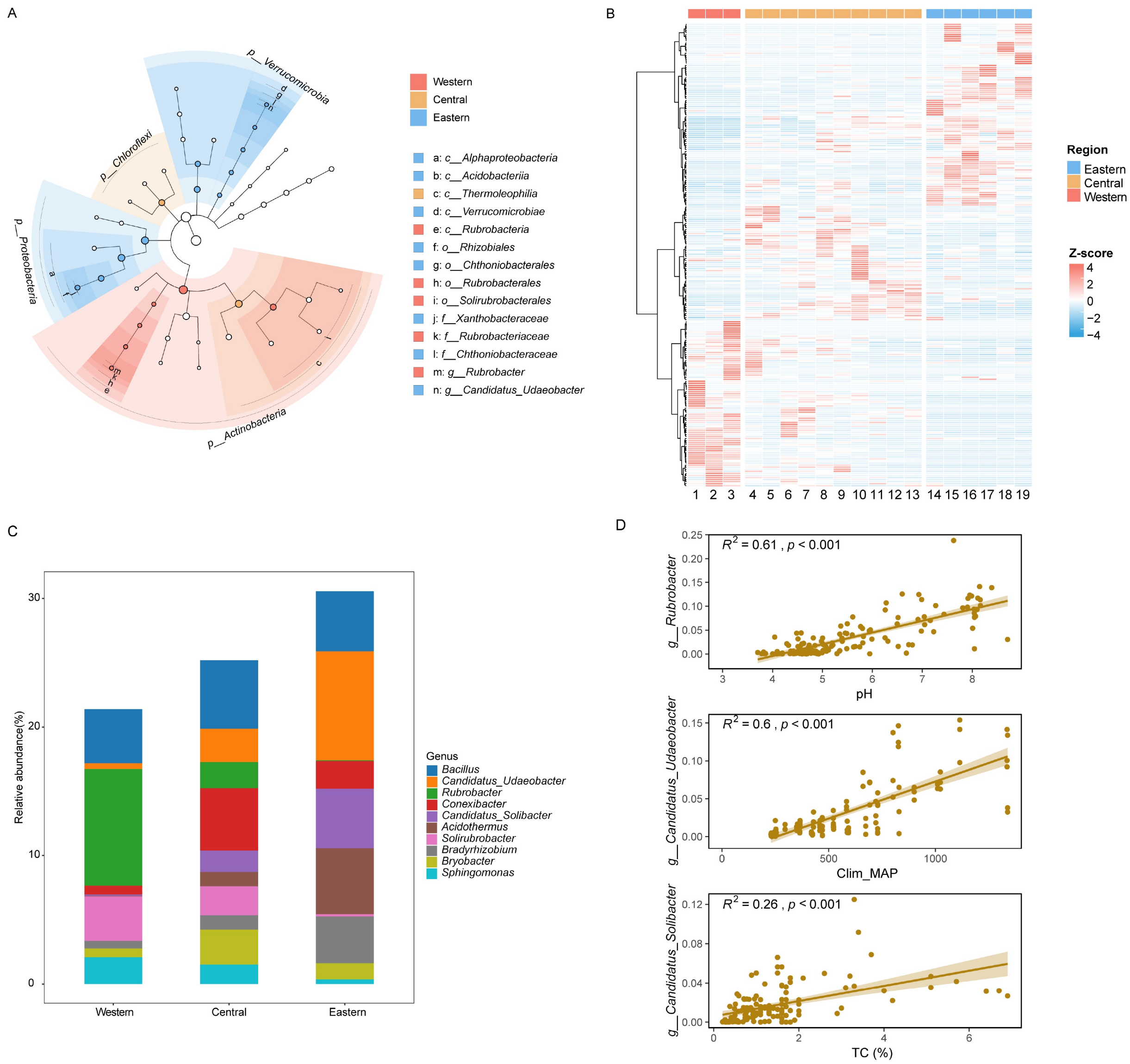

Fig. 8 Enriched bacteria communities and the pedo-environmental drivers (n=141). (A) LEfSe analysis of major enriched bacterial communities (with an LDA score higher than 4.5). (B) Hierarchically clustered heatmap illustrating the Z-score normalized abundance of 226 bacterial genera identified through LEfSe analysis across different regions. (C) Top 10 bacterial general distribution in three regions. (D) Examples of the relationships between enriched bacteria genera and environmental factors. MAP, mean annual precipitation.

nutrient-rich environments, as higher carbon and nitrogen availabilities trigger rapid growth (Fierer et al., 2012a). For example, the main *Acidobacteria* genera, *Candidatus Koribacter* and *Candidatus Solibacter* might increase with substrates, degrading cellulose and participating in nitrogen cycling (Fierer et al., 2012a). Additionally, acidic conditions are more suitable for the optimal growth of most *Acidobacteria* (Qin et al., 2023). This preference for acidic environments may be linked to greater cell specialisation and enhanced enzyme stability under extreme pH conditions (Kielak et al., 2016). *Verrucomicrobia* has been reported to correlate positively with soil moisture (Buckley and Schmidt, 2001), consistent with previous findings (Xia et al., 2020).

The genus *Candidatus Udaeobacter* (within *Verrucomicrobia*), was often regarded to be prevalent in soils (Willms et al., 2020). However, our results show that this genus was prevalent in eastern areas with 8.4% relative abundance but occupied less than 2.6% of the most fertile soil in the central region and only 0.4% in the western region. This notable decrease along the transect (Fig. S6) suggested a distinct regional distribution pattern for *Candidatus Udaeobacter*.

The central region, characterised by the most fertile soils, exhibited the highest richness along the transect. The increased richness may be attributed to the more neutral pH compared to the western and eastern areas, as high and low pH inhibits microbial growth and even lyse bacterial cells (Fierer and Jackson, 2006). The *Chloroflexi* phyla were more enriched in these regions and displayed the strongest regional distribution pattern, consistent with previous findings of its remarkable patchy distribution (Karimi et al., 2018). *Chloroflexi* was also reported to have a positive relationship with clay content (Karimi et al., 2018; Xia et al., 2020). Soils with higher clay content may cause a more diverse microbial community since the micro-scale pores can provide the habitat for *Chloroflexi* to live (Seaton et al., 2020; Xia et al., 2020). Interestingly, *Actinobacteria* were enriched in the western region, while *Thermoleophilia* were significantly enriched in the central region. This discrepancy suggests that understanding at phylum or class levels may not suffice to identify them. More detailed research at finer taxonomic resolutions is needed to better understand bacterial adaptations to changing environments.

The dry, alkaline western region was dominated by the *Actinobacteria* phylum. Recent studies have revealed that some *Actinobacteria* can form resistant physiological stages and alleviate salt and water stress, then enabling them to survive in dry regions (Ramadoss et al., 2013). The genus *Rubrobacter*, within *Actinobacteria*, was one the most enriched groups in this region, positively correlating with pH. The *Gemmatimonadetes* also displayed a decreasing pattern from west to east, supporting previous findings that this phylum prefers higher pH soils and may adapt to low soil moisture conditions (DeBruyn et al., 2011). Interestingly, most laboratory incubation studies reported that the optimal pH environment for the genus *Conexibacter* (belonging to *Actinobacteria*) is between 7 and 9 (Foesel et al., 2016; Vieira et al., 2022). Meanwhile, research conducted in the Atacama Desert, with pH levels ranging from 7.8 to 8.6, identified *Conexibacter* as the second most frequent genus (Miralles et al., 2023). However, in our survey, we found a significant negative correlation with pH, with *Conexibacter* evidently being more enriched in soils with a pH lower than 4.5. This contradiction between the preferences observed *in vitro* and *in situ* suggests that each bacterial species may have an optimal and specific niche influenced by covarying pedo-chemical factors. Additionally, a hierarchical structure may exist among environmental drivers in that specific niche.

4.2 The impact of land use intensity on soil bacteria

Here, we compared bacterial diversity under three different land uses. Within each habitat, microbial communities were more similar in less disturbed areas compared to more managed areas. Additionally, the relative abundance of the bacterial phyla responded uniquely among the natural, grazing, and cropping soils. For example, the bacterial phyla *Proteobacteria* and *Verrucomicrobia* experienced a notable decline under cropping, while *Actinobacteria* increased. These contrasting bacterial responses may be due to their specificity in responding to anthropogenic activities. Continuous plant residues are added to natural soil, whereas these residues are reduced in agricultural systems, which may also trigger bacterial responses. Changes in crop species resulting from agricultural practices can introduce new microbial communities to the soil, leading to increased microbial diversity in local areas. However, the diversity of these microbial communities is constrained by the limited variety of crops used in agriculture. The introduction of new microbial species can intensify competition with native soil microbes, potentially causing a decrease in the abundance and diversity of indigenous species (Wang et al., 2021). Consequently, bacterial communities in the topsoil become more homogenised and species-poor due to intensive agricultural practices (He et al., 2012). This change is especially notable when considering the effects of land use over large areas.

Network analysis shows that human activities altered microbial interactions in the central regions. For example, compared to natural soil, grazing and cropping soils exhibited higher microbial network complexity and evenness. This change, responding to the decrease in diversity, indicates that cropping leads to a more homogenised microbial community while enhancing bacterial connectivity. However, despite the observed decrease in diversity, the western and eastern regions did not show increased connectivity with higher land use intensity. This discrepancy indicates the importance of investigating both microbial diversity and interrelationships, as univariate diversity metrics alone may not capture the critical dimensions of community organization (Griffiths et al., 2011). One possible explanation for the significant changes observed in the central region is that this area is the primary hub for agricultural activities and has experienced more intensive land use change (Xue et al., 2022). The alteration of soil properties could be another important reason. It might be caused by habitat disturbance, which leads to changes in bacterial community composition, especially for some anaerobic microbes (Srour et al., 2020). Different land use types significantly change the pH, which can have major consequences for soil bacterial diversity and composition at landscape scales (Griffiths et al., 2011). In our survey, the cropping activity significantly improved the pH to neutral, which may contribute to a high bacterial richness and evenness. Foremost, soil carbon content tended to be lower in agricultural systems compared to natural sites (Peyraud et al., 2014). In addition, tillage could change the soil texture via soil mixing or erosion.

Understanding the human-drive disturbance in microbial diversity and community variation is important for preserving biodiversity and maintaining ecosystem health. A global standardised survey first revealed specific regions characterised by high soil biodiversity, community variation, and valuable soil-related ecosystem service (Guerra et al., 2022). However, no land use management can protect all these ecological dimensions, calling for a commonly sustainable method to preserve global biodiversity.

5 Conclusion

This study revealed the distinct regional distribution patterns of soil bacteria along a ~1,400 km transect in NSW, Australia. We found three distinct bacteria habitats influenced by covarying pedo-climatic characteristics from the eastern coast to the western outback. The regional unique taxa further proved the environmental selection of the underground soil microbial communities. In addition, land use modified bacterial composition within each habitat, with intensive agricultural activities leading to more homogenised and interconnected microbial communities. The diversity of the bacteria can be explained mostly by soil pH, annual precipitation and soil organic carbon. These findings will help researchers understand bacterial ecological preferences and spatial distributions, thereby enhancing our ability to predict shifts in community structure in response to environmental perturbations. We also note that interactions between community members and functioning are still challenging. Identifying and integrating these biotic and abiotic interactions on a large scale remains incomplete and needs to be the focus of future work in soil microbial ecology.

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References

Amend, A.S., Martiny, A.C., Allison, S.D., Berlemont, R., Goulden, M.L., Lu, Y., Treseder, K.K., Weihe, C., Martiny, J.B.H., 2016. Microbial response to simulated global change is phylogenetically conserved and linked with functional potential. The ISME Journal 10, 109–118.

Baas Becking, L.G.M., 1934. Geobiologie of Inleiding Tot De Milieukunde. W.P. Van Stockum & Zoon, The Hague.

Banerjee, S., Baah-Acheamfour, M., Carlyle, C.N., Bissett, A., Richardson, A.E., Siddique, T., Bork, E.W., Chang, S.X., 2016. Determinants of bacterial communities in Canadian agroforestry systems. Environmental Microbiology 18, 1805–1816.

Bastian, M., Heymann, S., Jacomy, M., 2009. Gephi: an open source software for exploring and manipulating networks. In: Proceedings of the 3rd International AAAI Conference on Weblogs and Social Media. San Jose, 361–362.

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. Science of the Total Environment 815, 152928.

Buckley, D.H., Schmidt, T.M., 2001. Environmental factors influencing the distribution of rRNA from Verrucomicrobia in soil. FEMS Microbiology Ecology 35, 105–112.

Callahan, B.J., McMurdie, P.J., Rosen, M.J., Han, A.W., Johnson, A.J.A., Holmes, S.P., 2016. DADA2: high-resolution sample inference from illumina amplicon data. Nature Methods 13, 581–583.

DeBruyn, J.M., Nixon, L.T., Fawaz, M.N., Johnson, A.M., Radosevich, M., 2011. Global biogeography and quantitative seasonal dynamics of Gemmatimonadetes in soil. Applied and Environmental Microbiology 77, 6295–6300.

Delgado-Baquerizo, M., Maestre, F.T., Reich, P.B., Trivedi, P., Osanai, Y., Liu, Y.R., Hamonts, K., Jeffries, T.C., Singh, B.K., 2016. Carbon content and climate variability drive global soil bacterial diversity patterns. Ecological Monographs 86, 373–390.

Delgado-Baquerizo, M., Oliverio, A.M., Brewer, T.E., Benavent-González, A., Eldridge, D.J., Bardgett, R.D., Maestre, F.T., Singh, B.K., Fierer, N., 2018. A global atlas of the dominant bacteria found in soil. Science 359, 320–325.

Evangelista, S.J., Field, D.J., McBratney, A.B., Minasny, B., Ng, W., Padarian, J., Román Dobarco, M., Wadoux, A.M.J.C., 2024. Soil security—strategizing a sustainable future for soil. Advances in Agronomy 183, 1–70.

Fierer, N., 2017. Embracing the unknown: disentangling the complexities of the soil microbiome. Nature Reviews Microbiology 15, 579–590.

Fierer, N., Jackson, R.B., 2006. The diversity and biogeography of soil bacterial communities. Proceedings of the National Academy of Sciences of the United States of America 103, 626–631.

Fierer, N., Lauber, C.L., Ramirez, K.S., Zaneveld, J., Bradford, M.A., Knight, R., 2012a. Comparative metagenomic, phylogenetic and physiological analyses of soil microbial communities across nitrogen gradients. The ISME Journal 6, 1007–1017.

Fierer, N., Leff, J.W., Adams, B.J., Nielsen, U.N., Bates, S.T., Lauber, C.L., Owens, S., Gilbert, J.A., Wall, D.H., Caporaso, J.G., 2012b. Cross-biome metagenomic analyses of soil microbial communities and their functional attributes. Proceedings of the National Academy of Sciences of the United States of America 109, 21390–21395.

Foesel, B.U., Geppert, A., Rohde, M., Overmann, J., 2016. *Parviterribacter kavangonensis* gen. nov., sp. nov. and *Parviterribacter multiflagellatus* sp. nov., novel members of *Parviterribacteraceae* fam. nov. within the order *Solirubrobacterales*, and emended descriptions of the classes *Thermoleophilia* and *Rubrobacteria* and their orders and families. International Journal of Systematic and Evolutionary Microbiology 66, 652–665.

Fondi, M., Karkman, A., Tamminen, M.V., Bosi, E., Virta, M., Fani, R., Alm, E., McInerney, J.O., 2016. “Every gene is everywhere but the environment selects”: global geolocalization of gene sharing in environmental samples through network analysis. Genome Biology and Evolution 8, 1388–1400.

Gee, G.W., Bauder, J.W., 1986. Particle-size analysis. In: Klute, M., ed. Methods of Soil Analysis: Part 1 Physical and Mineralogical Methods. 2nd ed. American Society of Agronomy, 383–411.

Griffiths, R.I., Thomson, B.C., James, P., Bell, T., Bailey, M., Whiteley, A.S., 2011. The bacterial biogeography of British soils. Environmental Microbiology 13, 1642–1654.

Griffiths, R.I., Thomson, B.C., Plassart, P., Gweon, H.S., Stone, D., Creamer, R.E., Lemanceau, P., Bailey, M.J., 2016. Mapping and validating predictions of soil bacterial biodiversity using European and national scale datasets. Applied Soil Ecology 97, 61–68.

Gu, Z.G., Eils, R., Schlesner, M., 2016. Complex heatmaps reveal patterns and correlations in multidimensional genomic data. Bioinformatics 32, 2847–2849.

Guerra, C.A., Berdugo, M., Eldridge, D.J., Eisenhauer, N., Singh, B.K., Cui, H.Y., Abades, S., Alfaro, F.D., Bamigboye, A.R., Bastida, F., Blanco-Pastor, J.L., de los Ríos, A., Durán, J., Grebenc, T., Illán, J.G., Liu, Y.R., Makhalanyane, T.P., Mamet, S., Molina-Montenegro, M.A., Moreno, J.L., Mukherjee, A., Nahberger, T.U., Peñaloza-Bojacá, G.F., Plaza, C., Picó, S., Verma, J.P., Rey, A., Rodríguez, A., Tedersoo, L., Teixido, A.L., Torres-Díaz, C., Trivedi, P., Wang, J.T., Wang, L., Wang, J.Y., Zaady, E., Zhou, X.B., Zhou, X.Q., Delgado-Baquerizo, M., 2022. Global hotspots for soil nature conservation. Nature 610, 693–698.

He, Z.L., Piceno, Y., Deng, Y., Xu, M.Y., Lu, Z.M., DeSantis, T., Andersen, G., Hobbie, S.E., Reich, P.B., Zhou, J.Z., 2012. The phylogenetic composition and structure of soil microbial communities shifts in response to elevated carbon dioxide. The ISME Journal 6, 259–272.

Hijmans, R.J., Van Etten, J., Cheng, J., Mattiuzzi, M., Sumner, M., Greenberg, J.A., Lamigueiro, O.P., Bevan, A., Racine, E.B., Shortridge, A.J.R., 2015. Package ‘raster’. R Package 734, 473.

Huang, H., 2021. LinkET: everything is linkable. R package version, 0.03.

Karimi, B., Terrat, S., Dequiedt, S., Saby, N.P.A., Horrigue, W., Lelièvre, M., Nowak, V., Jolivet, C., Arrouays, D., Wincker, P., Cruaud, C., Bispo, A., Maron, P.A., Bouré, N.C.P., Ranjard, L., 2018. Biogeography of soil bacteria and archaea across France. Science Advances 4, eaat1808.

Kielak, A.M., Barreto, C.C., Kowalchuk, G.A., Van Veen, J.A., Kuramae, E.E., 2016. The ecology of Acidobacteria: moving beyond genes and genomes. Frontiers in Microbiology 7, 744.

Lê, S., Josse, J., Husson, F., 2008. FactoMineR: an R package for multivariate analysis. Journal of Statistical Software 25, 1–18.

Liu, C., Cui, Y.M., Li, X.Z., Yao, M.J., 2021. *microeco*: an R package for data mining in microbial community ecology. FEMS Microbiology Ecology 97, fiaa255.

Liu, J.J., Sui, Y., Yu, Z.H., Shi, Y., Chu, H.Y., Jin, J., Liu, X.B., Wang, G.H., 2014. High throughput sequencing analysis of biogeographical distribution of bacterial communities in the black soils of northeast China. Soil Biology and Biochemistry 70, 113–122.

Liu, Y., Just, A., 2019. SHAPforxgboost: SHAP plots for'XGBoost'. CRAN: Contributed Packages.

Maestre, F.T., Delgado-Baquerizo, M., Jeffries, T.C., Eldridge, D.J., Ochoa, V., Gozalo, B., Quero, J.L., García-Gómez, M., Gallardo, A., Ulrich, W., Bowker, M.A., Arredondo, T., Barraza-Zepeda, C., Bran, D., Florentino, A., Gaitán, J., Gutiérrez, J.R., Huber-Sannwald, E., Jankju, M., Mau, R.L., Miriti, M., Naseri, K., Ospina, A., Stavi, I., Wang, D.L., Woods, N.N., Yuan, X., Zaady, E., Singh, B.K., 2015. Increasing aridity reduces soil microbial diversity and abundance in global drylands. Proceedings of the National Academy of Sciences of the United States of America 112, 15684–15689.

Miralles, I., Ortega, R., del Carmen Montero-Calasanz, M., 2023. Functional and biotechnological potential of microbiome associated with soils colonised by cyanobacteria in drylands. Applied Soil Ecology 192, 105076.

O'Brien, L., Searle, R., 2019. slga: data access tools for the soil and landscape grid of Australia. R package version, 1.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O’Hara, R., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2013. Package ‘vegan’. Community Ecology Package, Version, 2, 1–295.

Peyraud, J.L., Taboada, M., Delaby, L., 2014. Integrated crop and livestock systems in western Europe and South America: a review. European Journal of Agronomy 57, 31–42.

Philippot, L., Andersson, S.G.E., Battin, T.J., Prosser, J.I., Schimel, J.P., Whitman, W.B., Hallin, S., 2010. The ecological coherence of high bacterial taxonomic ranks. Nature Reviews Microbiology 8, 523–529.

Pino, V., McBratney, A., Fajardo, M., Wilson, N., Deaker, R., 2019. Understanding soil biodiversity using two orthogonal 1000km transects across New South Wales, Australia. Geoderma 354, 113860.

Qin, C., Pellitier, P.T., Van Nuland, M.E., Peay, K.G., Zhu, K., 2023. Niche modelling predicts that soil fungi occupy a precarious climate in boreal forests. Global Ecology and Biogeography 32, 1127–1139.

Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., Peplies, J., Glöckner, F.O., 2012. The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. Nucleic Acids Research 41, D590–D596.

Ramadoss, D., Lakkineni, V.K., Bose, P., Ali, S., Annapurna, K., 2013. Mitigation of salt stress in wheat seedlings by halotolerant bacteria isolated from saline habitats. SpringerPlus 2, 6.

Ramoneda, J., Stallard-Olivera, E., Hoffert, M., Winfrey, C.C., Stadler, M., Niño-García, J.P., Fierer, N., 2023. Building a genome-based understanding of bacterial pH preferences. Science Advances 9, eadf8998.

Rayment, G.E., Lyons, D.J., 2011. Soil Chemical Methods-Australasia. CSIRO Publishing: Collingwood.

Román Dobarco, M., McBratney, A., Minasny, B., Malone, B., 2021. A modelling framework for pedogenon mapping. Geoderma 393, 115012.

Rout, M.E., Callaway, R.M., 2012. Interactions between exotic invasive plants and soil microbes in the rhizosphere suggest that 'everything is *not* everywhere'. Annals of Botany 110, 213–222.

Sall, J., Lehman, A., 2001. JMP Start Statistics: A Guide to Statistics and Data Analysis Using JMP and JMP IN Software. Duxbury Press: Pacific Grove.

Seaton, F.M., George, P.B.L., Lebron, I., Jones, D.L., Creer, S., Robinson, D.A., 2020. Soil textural heterogeneity impacts bacterial but not fungal diversity. Soil Biology and Biochemistry 144, 107766.

Srour, A.Y., Ammar, H.A., Subedi, A., Pimentel, M., Cook, R.L., Bond, J., Fakhoury, A.M., 2020. Microbial communities associated with long-term tillage and fertility treatments in a corn-soybean cropping system. Frontiers in Microbiology 11, 1363.

VanInsberghe, D., Maas, K.R., Cardenas, E., Strachan, C.R., Hallam, S.J., Mohn, W.W., 2015. Non-symbiotic *Bradyrhizobium* ecotypes dominate North American forest soils. The ISME Journal 9, 2435–2441.

Vieira, S., Huber, K.J., Geppert, A., Wolf, J., Neumann-Schaal, M., Luckner, M., Wanner, G., Müsken, M., Overmann, J., 2022. *Capillimicrobium parvum* gen. nov., sp. nov., a novel representative of *Capillimicrobiaceae* fam. nov. within the order *Solirubrobacterales*, isolated from a grassland soil. International Journal of Systematic and Evolutionary Microbiology 72, 005508.

Wang, Z.K., Chen, Z.Y., Kowalchuk, G.A., Xu, Z.H., Fu, X.X., Kuramae, E.E., 2021. Succession of the resident soil microbial community in response to periodic inoculations. Applied and Environmental Microbiology 87, e00046.

Willms, I.M., Rudolph, A.Y., Göschel, I., Bolz, S.H., Schneider, D., Penone, C., Poehlein, A., Schöning, I., Nacke, H., 2020. Globally abundant "*Candidatus* Udaeobacter" benefits from release of antibiotics in soil and potentially performs trace gas scavenging. mSphere 5.

Xia, Q., Rufty, T., Shi, W., 2020. Soil microbial diversity and composition: links to soil texture and associated properties. Soil Biology and Biochemistry 149, 107953.

Xue, P.P., Carrillo, Y., Pino, V., Minasny, B., McBratney, A.B., 2018. Soil properties drive microbial community structure in a large scale transect in South eastern Australia. Scientific Reports 8, 11725.

Xue, P.P., Minasny, B., McBratney, A.B., 2022. Land-use affects soil microbial co-occurrence networks and their putative functions. Applied Soil Ecology 169, 104184.

Xue, P.P., Minasny, B., Wadoux, A.M.J.C., Dobarco, M.R., McBratney, A., Bissett, A., de Caritat, P., 2024. Drivers and human impacts on topsoil bacterial and fungal community biogeography across Australia. Global Change Biology 30, e17216.