

RESEARCH ARTICLE

Drivers and human impacts on topsoil bacterial and fungal community biogeography across Australia

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Abstract

Soil microbial diversity mediates a wide range of key processes and ecosystem services influencing planetary health. Our knowledge of microbial biogeography patterns, spatial drivers and human impacts at the continental scale remains limited. Here, we reveal the drivers of bacterial and fungal community distribution in Australian topsoils using 1384 soil samples from diverse bioregions. Our findings highlight that climate factors, particularly precipitation and temperature, along with soil properties, are the primary drivers of topsoil microbial biogeography. Using random forest machine-learning models, we generated high-resolution maps of soil bacteria and fungi across continental Australia. The maps revealed microbial hotspots, for example, the eastern coast, southeastern coast, and west coast were dominated by Proteobacteria and Acidobacteria. Fungal distribution is strongly influenced by precipitation, with Ascomycota dominating the central region. This study also demonstrated the impact of human modification on the underground microbial community at the continental scale, which significantly increased the relative abundance of Proteobacteria and Ascomycota, but decreased Chloroflexi and Basidiomycota. The variations in microbial phyla could be attributed to distinct responses to altered environmental factors after human modifications. This study provides insights into the biogeography of soil microbiota, valuable for regional soil biodiversity assessments and monitoring microbial responses to global changes.

KEYWORDS

bacterial and fungal distributions, Habitat Condition Assessment System (HCAS), human impacts, land use, microbial biogeography, topsoil

1 | INTRODUCTION

Microorganisms are abundant and diverse in soil, with estimates of up to 10^{10} cells and 10^3 to 10^5 different species in a single gram of soil (Hoorman, 2010; Roesch et al., 2007). Those microbes play

an integral role within the soil ecosystem, serving as linchpins for various critical functions, including nutrient cycling (Yadav et al., 2021), carbon sequestration (Bhattacharyya et al., 2022), and water regulation (Creamer et al., 2022). A comprehensive understanding of microbial assembly contributes to our knowledge

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of soil functions and ecological regulations. However, our comprehension of their spatial distribution and the environmental factors shaping their variation, particularly at the continental scale, remains largely unknown. This limitation comes from a combination of factors, including the high density and diversity of soil microorganisms, as well as the limited availability of sampling and monitoring networks operating at extensive spatial scales (Karimi et al., 2020). Notably, microbial populations do not exhibit uniform distribution in soils, and the composition of microbial communities can exhibit significant variations within just a few centimetres (O'Brien et al., 2016). Moreover, the intricate composition of microbial communities and their interactions with the environment often necessitate the use of multiple and complementary techniques to effectively capture their spatial distribution. The recent development of molecular technologies through DNA fingerprinting has advanced our understanding of soil microbial communities (Orgiazzi et al., 2015). For instance, amplicon sequencing using housekeeping genetic biomarkers is currently widely used for microbial identification and taxonomy (Ishii & Sadowsky, 2009; Park & Won, 2018).

Microbial distribution is not random; rather, it is intricately associated with ecological niches that provide specific environmental conditions favouring the growth and survival of particular microbial taxa (He et al., 2020; Hibbing et al., 2010). Notably, soil properties, including pH (Delgado-Baquerizo et al., 2017; Shi et al., 2018), nutrients and organic carbon contents (Oliverio et al., 2020; Peng et al., 2019; Siciliano et al., 2014), as well as soil texture (Constancias et al., 2015), have emerged as important drivers influencing microbial diversity and abundance across diverse soil types. For example, niche difference of pH was reported to structure the arbuscular mycorrhizal fungal community (Dumbrell et al., 2010). Moreover, environmental factors like climate (Bahram et al., 2018; Qin et al., 2023) and topography (Peng et al., 2019), exert their own distinct regulations on microbial spatial patterns. Additionally, anthropogenic interventions, including agricultural practices, have demonstrated significant alterations to the underground microbial communities (Yang et al., 2021). For example, land use influences on soil microbial communities and their functions are widely reported (Constancias et al., 2015; Xue, Minasny, McBratney, Jiang, & Luo, 2023). The impact of human modification on the heterogeneity of soil microbes at a large geographic scale is still limited.

Recent developments in statistical modelling and machine-learning algorithms have provided compelling evidence linking microbial spatial distributions to various soil and environmental factors (Bissett et al., 2023; Chu et al., 2020; Delgado-Baquerizo & Eldridge, 2019). Bahram et al. (2018) illustrate global niche differentiation among fungi and bacteria, which is significantly related to divergent diversity responses to precipitation and soil pH. Delgado-Baquerizo and Eldridge (2019) estimated the alpha diversity of bacteria across the globe from a dataset encompassing 237 sampling sites. Karimi et al. (2018), conversely, used spatial modelling to understand the distribution of soil bacteria and archaea throughout

France, capitalizing on 2173 soil samples collected from a systematic grid design. Similarly, Mod et al. (2021) undertook spatial modelling of bacterial dynamics in the western Swiss Alps, considering factors such as elevation, slope, and aspect strata. Their studies establish that the environmental variables can serve as niche parameters for microbial biogeography studies (Lee et al., 2020; Lennon et al., 2012; Mahjenabadi et al., 2022). However, the distinct characteristics of microorganisms (e.g., small size, high diversity, sensitive interactions with the environment) had a substantial effect on the accuracy of microbial spatial prediction. Among the challenges encountered in this endeavor, a prominent one lies in assemblage of sample sets that are both sufficiently large and have a spatial coverage that allows a representative analysis (Fierer, 2008).

In this paper, we analyzed microbial community structures at a continental scale using 1384 topsoil samples from diverse regions across Australia, encompassing various land uses and soil types. Statistical modelling and machine-learning algorithms were applied to investigate the factors driving the biogeography of soil bacteria and fungi throughout continental Australia. Based on the key drivers, we build spatial models that account for the diversity of climate and soil types. These models enabled the estimation of the spatial distribution of the dominant bacteria and fungi across Australia. These maps were then combined with the Habitat Condition Assessment System (HCAS) (Harwood et al., 2016) to assess the impacts of human modification on the underground microbial ecosystem. This study can help researchers, policymakers, and land managers make locally informed decisions regarding soil management and environmental conservation, particularly in the face of the challenges posed by climate change and the increasing anthropogenic pressures on soils.

2 | MATERIALS AND METHODS

2.1 | Sequence data and bioinformatics analysis

To capture a diverse range of soil types and land use patterns, we combined data from the Biomes of Australian Soil Environments (BASE) and the National Geochemical Survey of Australia (NGSA) databases. As this study focuses on the topsoil, we subset surface soil information from both databases, encompassing regions across continental Australia and Tasmania. In total, we obtained a dataset of 1384 soil samples containing information on soil properties and soil DNA. Among these, 1095 samples were derived from the BASE project, collected within the 0–15 cm depth interval and spanning over 900 locations across Australia (Bissett et al., 2016). Furthermore, an additional 289 samples were obtained from the NGSA project at the 0–10 cm depth, gathered from sediments at top catchment outlets across the country (de Caritat, 2022; de Caritat & Cooper, 2011). To date, this is Australia's largest and most comprehensive microbial diversity dataset, covering various bioregions and land uses. The distribution of the 1384 sampling points is visually presented in Figure 1.

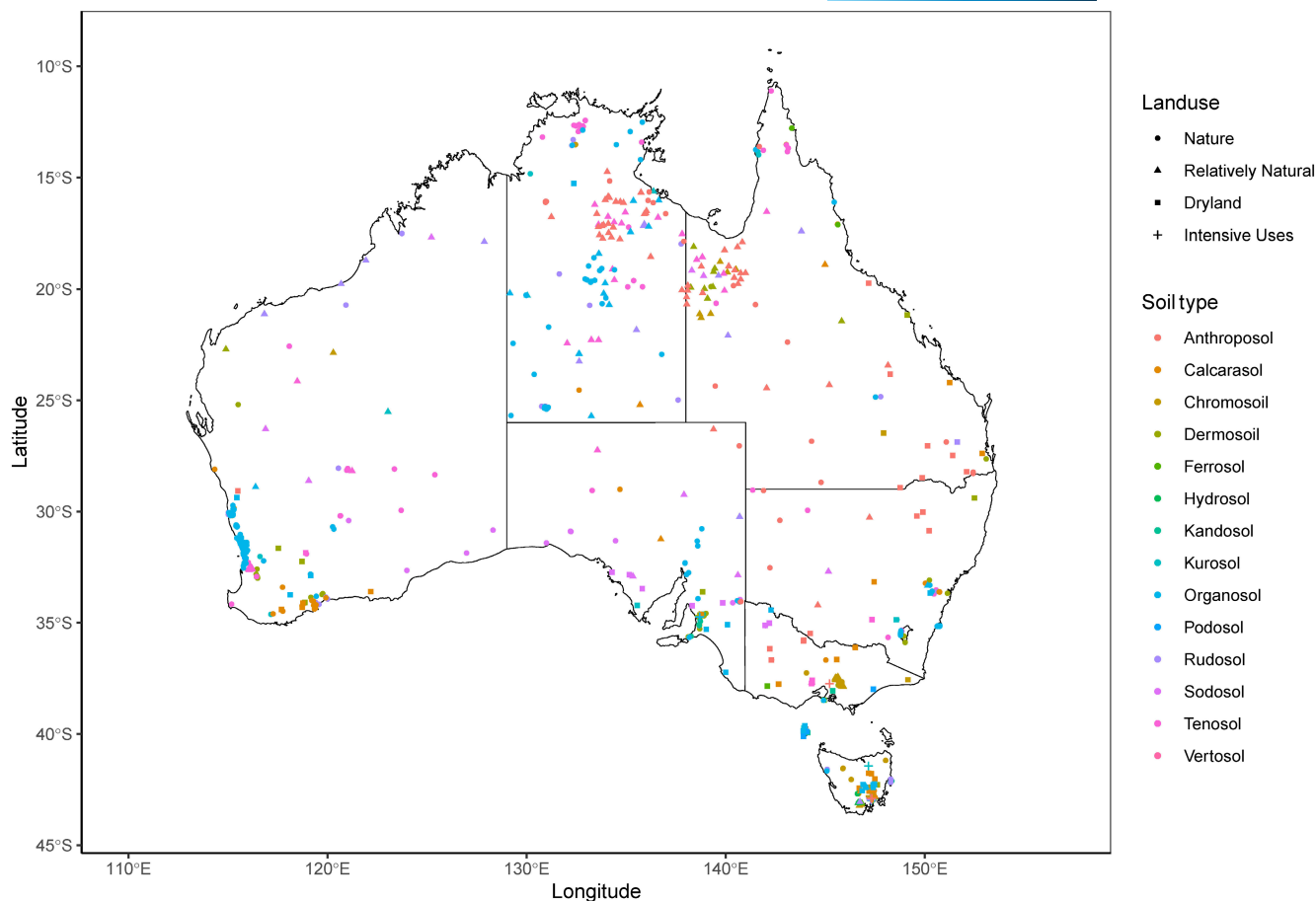


FIGURE 1 The 1384 sampling sites across Australia obtained by combining the Biomes of Australian Soil Environments (BASE) and National Geochemical Survey of Australia (NGSA) datasets on soil microbial diversity.

The amplicon sequencing data was used to characterize soil microbial diversity. Bacterial and fungal diversity was acquired from the 16S rRNA gene (27F-519R) and ITS region (ITS1F-ITS4), respectively. Sequencing data was analysed following Bissett et al. (2016). Briefly, sequencing data were assessed visually using FastQC and then trimmed and merged with FLASH (Magoc & Salzberg, 2011). Operational Taxonomic Units (OTUs) were clustered at 97% sequence similarity using USEARCH (v8.0.1517) (Edgar, 2010). OTUs were then filtered and classified in MOTHUR (v1.34.1) (Schloss et al., 2009). Single OTUs or OTUs with less than 10 copies were filtered. Samples that total sequences less than 10,000 counts were eliminated as well. OTU taxonomy was assigned referring to SILVA 138 database (Quast et al., 2013) for bacteria and UNITE database 8.0 (Nilsson et al., 2018) for fungi with a 60% cut-off value. The OTU table was rarefied before following analysis. The dominant taxa were selected based on the average relative abundances of >0.5% and with a minimum occurrence probability of 60% across all samples. Shannon indexes were calculated for alpha diversity using 'vegan' (Dixon, 2003) in RStudio (v 4.3.1). Principal coordinates analysis (PCoA) was applied to calculate the sample dissimilarity of microbial community composition based on the Bray-Curtis distance (Beals, 1984).

Permutational multivariate analysis of variance (PERMANOVA) was applied to calculate the impacts of land use and soil type on microbial community composition.

2.2 | Soil properties and climate factors

Soil properties like soil organic carbon (SOC), pH, total nitrogen (TN), total phosphorus (TP), total sulphur (S), electric conductivity (EC), cation exchangeable capacity (CEC), and clay content were downloaded from the aforementioned database (Bissett et al., 2016; de Caritat & Cooper, 2011). A total of 14 covariate raster layers representing soil physicochemical properties, land use, soil type, and climate factors were downloaded from the Terrestrial Ecosystems Research Network (TERN) using 'SLGACloud' package in R. All covariates were pre-processed to conform with a grid cell of 1000m×1000m and projected to WGS84 (EPSG:4326). Refer to Table S3 for more information on the list of covariates. The climate variables of the sampling sites were extracted from above rasters based on the coordinates using 'raster' package in R, including mean annual aridity index (Clim_ADM), annual potential evaporation (Clim_EPA), annual daily mean temperature (Clim_meanann), total annual precipitation

(Clim_PTA), short-wave solar radiation (Clim_RSM), and annual temperature range (Clim_TRA).

2.3 | Mapping model fitting, validation, and prediction

We used the random forest model (Biau, 2012; Breiman, 2001) to build a relationship between the environmental covariates and dominant taxa. Relative abundances of the microbial phyla were employed as response variables in random forest models. Land use, soil type, soil properties (i.e., SOC, pH, TN, TP, TS, EC, CEC, and clay content), and climate factors, including Clim_ADM, Clim_EPA, Clim_meanann, Clim_PTA, Clim_RSM, and Clim_TRA, were applied as the covariables. We compared the prediction models using land use, soil type, soil properties, climate factors, and the combination of soil properties and climate factors as environmental covariable sets, respectively.

The performance of the random forest model was evaluated with the 10-fold cross-validation (CV) method. In the 10-fold CV, the dataset was randomly split into 10 approximately equal subsets. Nine subsets were used for model fitting and prediction on the remaining subset. The procedure was repeated 10 times, each time using a different subset for validation. Validation statistics were calculated on the whole dataset. We calculated the mean error, the root mean square error (RMSE), the Pearson's *r* linear correlation coefficient. The contributions of soil and climate factors to dominant phyla were assessed by their importance within the random forest models. To gain deeper insights into how microbial communities responded to these environmental factors, partial dependence analyses (Greenwell, 2017) were conducted for the climate factors and soil properties to each dominant phylum, respectively.

Based on the model performance, we selected the combination of soil properties and climate factors as the covariable sets. Those environmental covariates were further selected based on the importance of random forest models for the continental map prediction. The relative abundance values of dominant phyla for bacteria and fungi were used as response variables for the machine-learning model within a digital soil mapping framework (McBratney et al., 2003; Wadoux et al., 2020). Spatial prediction over Australia was made using a quantile regression forest (QRF) model (Meinshausen & Ridgeway, 2006) fitted on the whole dataset. The three parameters of the QRF models, namely the number of trees, the minimum node size and the number of covariates to randomly subsample at each split (i.e., *mtry*) were set to default values at 250, 5 and to the rounded down square root of the number of covariates, respectively.

2.4 | Other statistics

Differences of microbial alpha diversity were compared between land use categories using the Tukey HSD test after OTU table rarefaction. To evaluate the impact of human on soil microbial distribution,

we used the HCAS that assessed human modification on Australian habitat (Williams et al., 2021). The influences of human modification on microbial distributions were assessed by the relations between microbial phyla abundance and HCAS scores. The continental HCAS map (HCAS version 2.1) was derived from Harwood et al. (2022), which was then stacked with the predicted spatial raster layers of microbial phyla abundance. Human modification was categorized into five categories (e.g., Removed, Replaced, Transformed, Modified, Residual) based on the HCAS condition scores following Williams et al. (2021). For each category, 1000 samples were randomly sampled across the continental Australian map. The relative abundances of microbial phyla and HCAS condition scores were derived from the stacked spatial raster file. The correlation between phyla abundance was then fitted to linear regression. All the statistical and machine learning algorithms mentioned above were implemented using the R software.

3 | RESULTS

3.1 | Ubiquity and dominance of soil microorganisms

After processing amplicon sequencing data, we obtained a dataset comprising 568,189 bacteria OTUs from the observed samples. This diverse array of bacteria was assigned to 53 phyla, and 19 of which were observed in no less than 60% of the samples (Figure S1). Moreover, five phyla, namely Proteobacteria, Actinobacteria, Acidobacteriota, Firmicutes, and Planctomycetota, demonstrated ubiquity by being found in all recorded samples. Furthermore, nine bacterial phyla, (e.g., Chloroflexi, Bacteroidota, Verrucomicrobiota, among others) were prevalent in over 90% of the samples. In contrast, 13 phyla were endemic, appearing in less than 1% of the samples (Figure S1). Across the sample set, Proteobacteria, Actinobacteria, and Acidobacteriota emerged as the dominant communities with mean relative abundances exceeding 10% (Figure S1). They were followed closely by Chloroflexi and Firmicutes, which exhibited relative abundances within 5%–10%. Conversely, the remaining 43 phyla constituted minor contingents, with relative abundances below 1%.

Taking into account both average relative abundance and ubiquity, a dozen bacterial phyla were identified as dominant, as they were consistently recorded in over 60% of our samples, with an average abundance exceeding 0.5%. These dominant phyla collectively constituted a substantial portion of the bacterial community, accounting for a range of 95.6%–99.9% across 90% of the samples (Figure S1).

Regarding fungi, our data filtering efforts yielded a dataset comprising 60,746 fungal OTUs, which were classified into 16 phyla (Figure S2). Notably, Ascomycota and Basidiomycota exhibited ubiquity. These two phyla also emerged as the most dominant fungal representatives, accounting for ~50% and ~37% of the fungal community, respectively. Mortierellomycota and Glomeromycota were discovered in about 90% of samples and ranged between 3%

and 5%. Mucoromycota and Chytridiomycota occurred in more than 80% of our samples. Basidiobolomycota stood as the rarest, found in less than 1% of samples with a relative abundance value around 0.001%. Other fungal phyla were scarcely encountered, with mean relative abundances less than 0.5%.

Considering their relative abundances and wide distributions across the soil samples, it becomes evident that these samples were predominantly characterized by six dominant fungal phyla. These phyla exhibited relative abundances exceeding 0.5% and consistently featured in more than 60% of the samples. Remarkably, on average, these six phyla collectively had a strong influence over the fungal community, accounting for 99.1% of its composition (Figure S2).

3.2 | Regulation by soil types and land uses

Our dataset reveals differences in microbial diversity across various land uses and soil types (Figure 2). First, alpha diversity, for both

bacteria and fungi, was influenced by land use, displaying a significant correlation with land use intensity, as depicted in Figure 2a. Concerning bacteria, our analysis uncovers a significant distinction in Shannon index between soils under native vegetation and agricultural soils. Conversely, for fungi, the intensively used soils showed the most prominent divergence with other land uses, e.g., nature and relatively natural lands. Furthermore, land use effects varied for different phyla. For illustration, Proteobacteria showed higher relative abundances in natural soils, while higher values for Actinobacteria were observed in intensive agricultural lands (Figure S3). The detailed microbial composition differences are illustrated in Figures S3 and S4.

The PERMANOVA result shows that both land use and soil type presented significant regulation on bacterial ($p < .001$) and fungal ($p < .001$) community composition (Figure 2c and 2d). The PCoA results make it evident that soils with similar characteristics tended to exhibit greater similarity in their bacterial and fungal community compositions. To exemplify, the Ferrosol and Vertosol samples consistently clustered closely together in both bacterial and fungal

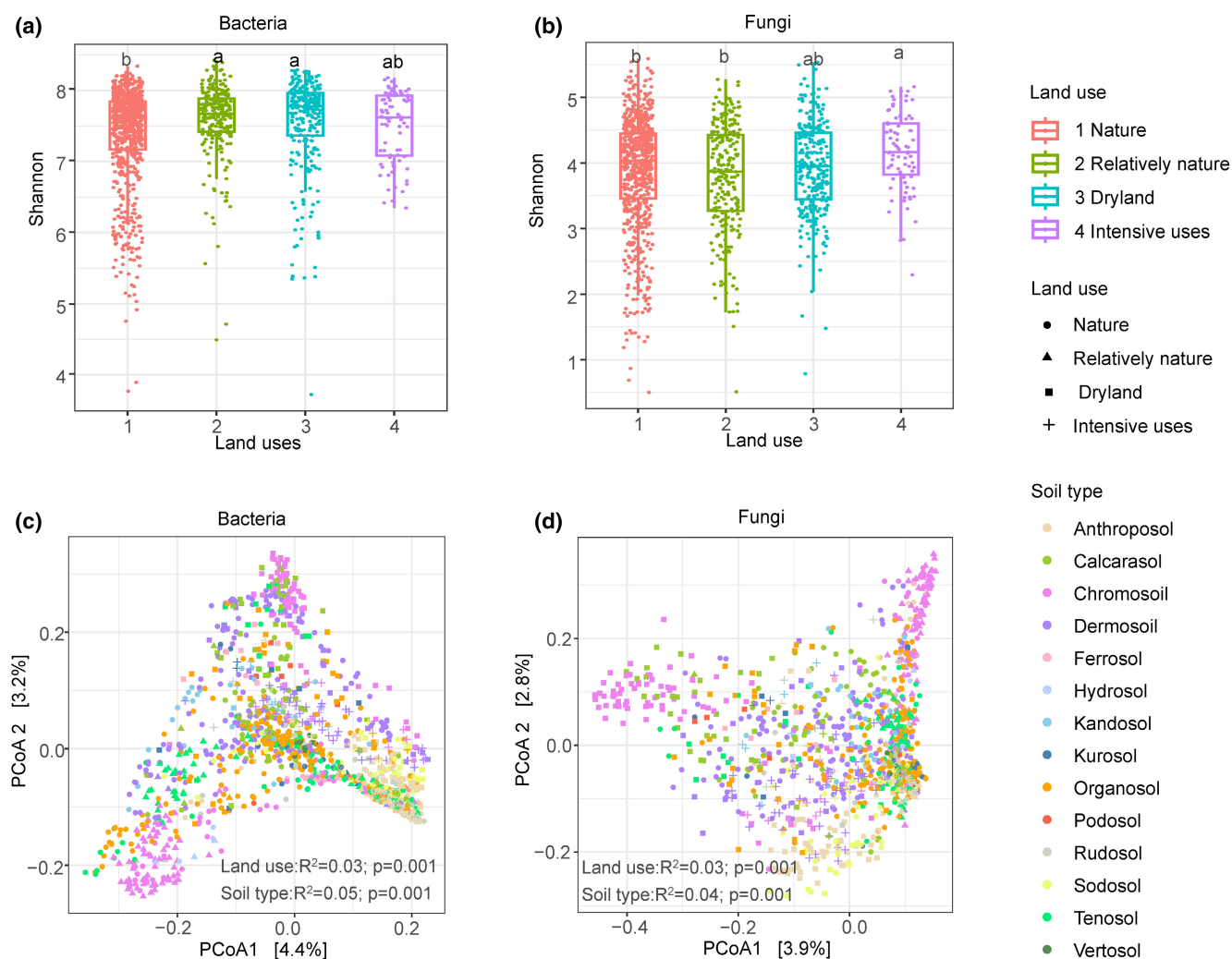


FIGURE 2 Boxplots of Shannon index for soil bacteria (a) and fungi (b) as a function of land uses; PCoA of soil bacteria (c) and fungi (d) for different land uses and soil types. PCoA, principal coordinates analysis.

datasets, underscoring their compositional resemblance. In contrast, samples derived from Chromosols and Dermosols displayed a notably higher degree of dissimilarity when analysed across different geographical regions within the country.

3.3 | Controls of soil microbial biogeography

The data-driven strategy using random forest modelling provided empirical insights into the influential environmental factors shaping the dominant phyla (Figure 3a). We constructed soil microbial models using random forests by incorporating soil types, land uses, soil properties, and climate factors as predictors. The CV results revealed that the fitted models had good predictive capabilities for all sets of factors (Table 1). Soil properties and climate factors individually explained at least 85% of the variation of soil bacterial phyla. When combining the set of soil properties and climate factors, the highest accuracy was obtained (i.e. RMSE=3.67 for bacteria; RMSE=4.19 for fungi). This synergistic approach resulted in R^2 values of .9 and .83 for bacteria and fungi models, respectively (Figure S5). These outcomes underscore the importance of considering both soil properties and climate factors for the spatial prediction of soil microbes.

In general, most bacterial and fungal phyla exhibited a similar pattern, with climate-related factors, particularly precipitation and temperature, standing out prominently (Figure 3a). Specifically, we observed that annual precipitation (PTA) emerged as the most influential driver for Actinobacteria, Basidiomycota, and Ascomycota. Furthermore, the annual temperature range (TRA) displayed remarkable importance, particularly for Proteobacteria and Armatimonadota phyla, closely followed by the annual mean temperature. In the case of Acidobacteriota, pH emerged as the primary driving factor. Moreover, soil pH demonstrated significant contributions to Myxococcota, Gemmatimonadota, and Basidiomycota. Notably, soil texture, specifically clay content, had an effect over Proteobacteria, Chloroflexi, and Actinobacteria.

The partial dependency analysis offered a nuanced perspective, showing the influence of environmental factors on microbial phyla (Figures S6–S10). For instance, Actinobacteria exhibited a decline in relative abundance in ecosystems with PTA less than 1000mm (Figure 3b). Beyond this threshold, Actinobacteria's abundance remained consistently low. Regarding Proteobacteria, our analysis revealed an optimal annual temperature variation of approximately 26°C. Proteobacteria exhibited stability when temperature variations remained below this optimum, but a significant decline was observed when temperature ranges exceeded 26°C. Within acidic soils, we identified a robust negative correlation between Acidobacteria and soil pH, with Acidobacteria maintaining lower levels in neutral and alkaline soils. Additionally, our investigation showed distinct responses of Ascomycota and Basidiomycota to precipitation. Ascomycota exhibited a higher relative abundance in regions with annual rainfall below 1000mm, while its abundance remained low when exceeding 1500mm. In contrast, Basidiomycota displayed a contrasting pattern, with a relatively high proportion

in soil fungal communities in regions where annual precipitation exceeded 1500mm. These findings highlight that the relationship between environmental factors and microbial phyla is context-dependent and highly variable.

3.4 | Biogeography of soil bacteria and fungi

Based on the above results, we integrated soil properties and climate factors as covariates to derive a continental-wide soil microbial biogeographic prediction. Since the importance of soil TS and EC was relatively weak for most phyla (Figure 3a), only SOC, pH, TN, TP, CEC, clay content, clim_ADM, clim_EPA, clim_meanann, clim_PTA, clim_RSM, and clim_TRA were selected as predictors.

The model presented good fitness for dominant phyla (Tables S1 and S2). The resultant maps of dominant microbial phyla (Figure 4; Figure S10) reveal detailed patterns and large variation in Australia among climatic and pedological regions. It shows a changing gradient of abundance between the coastal areas, in particular the eastern coast and the inland areas of the country.

For Proteobacteria, we observed three distinct regions: along the eastern coast, northeastern region, and west coast of Australia (Figure 4; Figure S11). Its abundance ranged between 12% and 49%. It was approximately three times higher in coastal areas than in the rest of Australia, although Western Australia exhibits a relatively low abundance, less than 15%. Acidobacteria, Planctomycetota, Verrocumicrobiota have a similar spatial pattern, but Actinobacteriota, Chloroflexi, and Armatimonadota had an opposite pattern (i.e., less in the coast) (Figure 4). Acidobacteria, for instance, was more abundant in the tropical regions in the north and east coast regions. Firmicutes and Cyanobacteria had local patches of higher abundance, for example, a higher abundance around Lake Torrens in South Australia for Firmicutes. Finally, Bacteroidota had no clear hotspots and an overall low abundance, ranging between an absence in the North of Australia to 7% in the South.

The maps of dominant soil fungi phyla are presented in Figure S13. The spatial pattern was distinct between fungal phyla. The most abundant fungi, Ascomycota (Figure S14), had a low relative abundance in the northern territory (Figure S14b), southwest coast (Figure S14c), and the east coast (Figure S14a). Significant differences in abundance were observed on either side of the Great Dividing Range, with a lower relative abundance in the mountainous regions facing the ocean (Figure S14a). The Basidiomycota, conversely, was more abundant in coastal regions with a relative abundance of around 40%–75% (Figure S15); it represented ~80% of the abundance of the fungal community in the north of Australia (Figure S15b), whereas in west side of the Great Dividing Range, it was lower than 20% (Figure S15a). Mortierellomycota made up 0.1%–16.9% of the fungal community across the country with some hotspots (as high as 15%) scattered in the southeast of the country (Figure S13). Glomeromycota was predicted to constitute 0.1%–21.3% of fungi with higher relative abundances around 20°–30°S, 135°–140°E. Mucoromycota and Rozellomycota are always lower

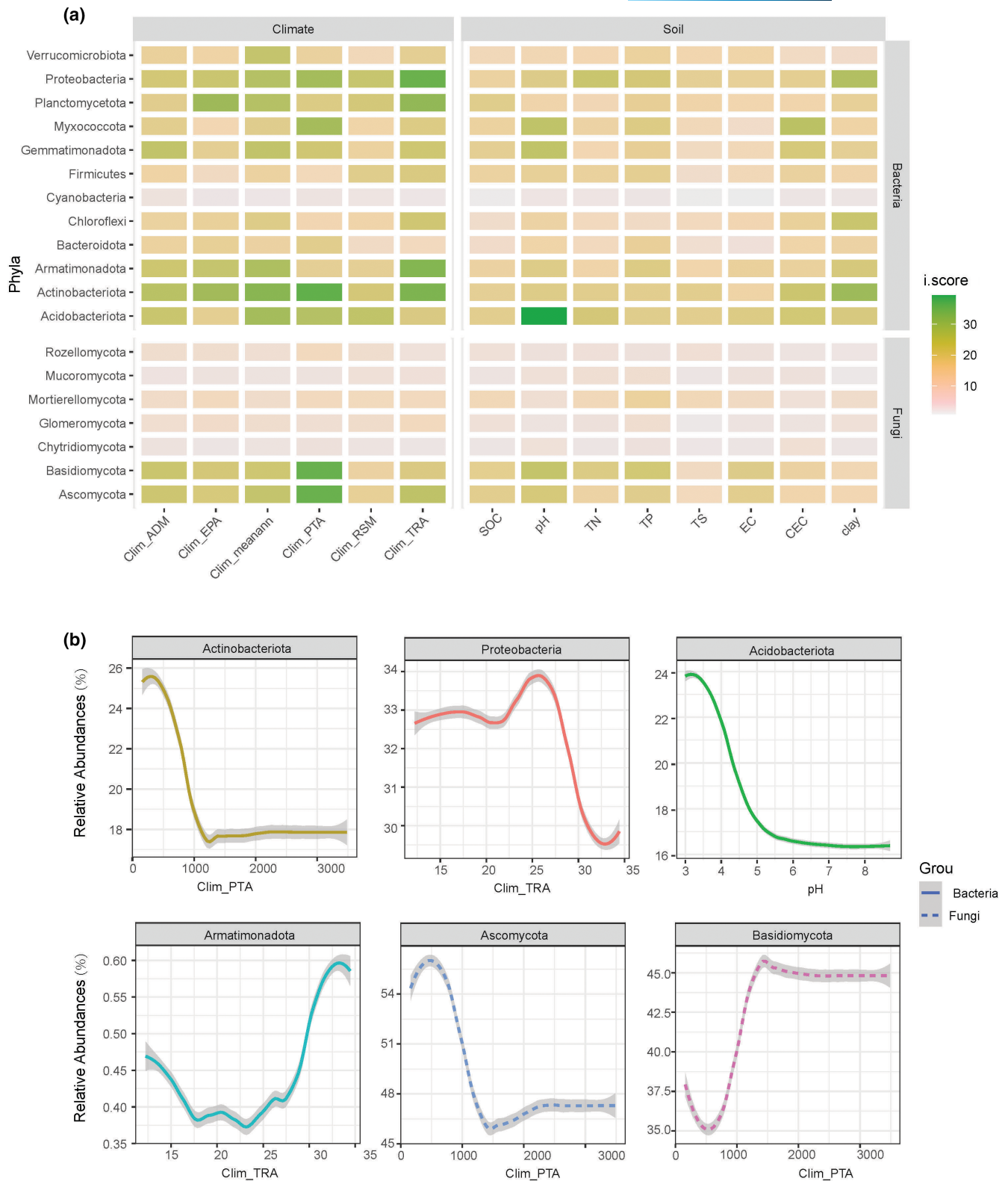


FIGURE 3 (a) Heatmap of the importance of climate factors and soil properties for the dominant bacterial and fungal community. (b) Examples of the partial dependence plot of the environmental factors for the dominant phyla. CEC, cation exchange capacity; Clim_ADM, mean annual aridity index; Clim_EPA, annual potential evaporation; Clim_meanann, annual daily mean temperature; Clim_PTA, annual precipitation; Clim_RSM, short-wave solar radiation; Clim_TRA, annual temperature range; EC, electric conductivity; SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus; TS, total sulphur.

Covariable sets	Bacteria		Fungi	
	R ²	RMSE	R ²	RMSE
Soil type	.68	6.34	.51	7.3
Land use	.77	5.47	.5	7.36
Soil properties	.85	4.6	.74	5.28
Climate	.86	4.17	.78	4.84
Soil and climate	.9	3.67	.83	4.19

TABLE 1 Mean validation statistics (10-fold cross-validation) of random forest models for the dominant bacteria and fungi obtained by different sets of environmental factors.

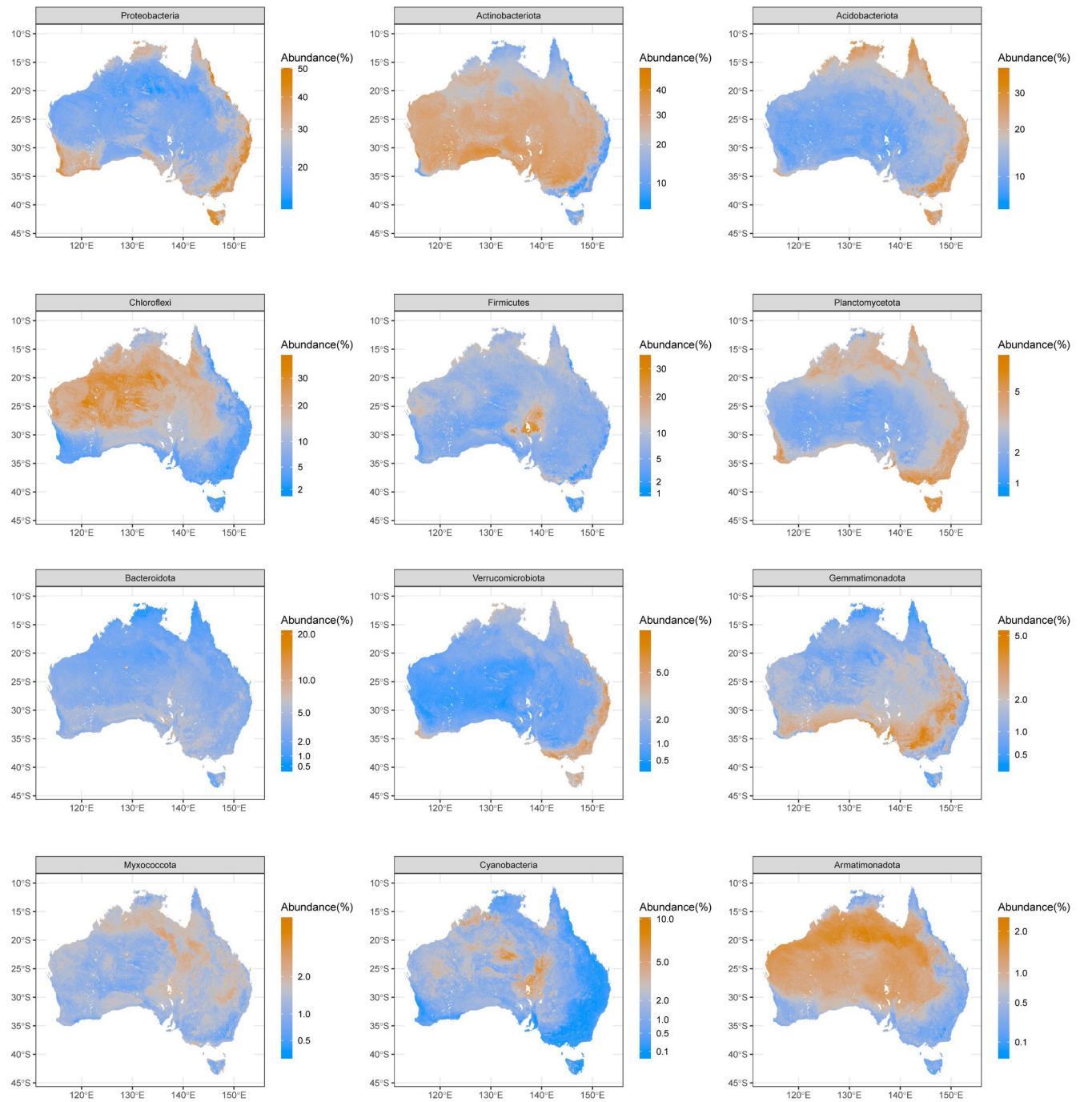


FIGURE 4 Predicted distributions of the domain bacterial phyla across Australia.

than 10% across Australia with higher relative abundances in coastal regions in the southeast (Figure S13).

3.5 | Regulation of human modification

Habitat Condition Assessment System combined with microbial distribution maps revealed significant linear correlations between the human impact on soil and microbial phyla abundances as observed in Figure 5 and Figure S16. The degree of human modification tends to increase the relative abundance of Proteobacteria and highest Proteobacteria abundance was found in soils where their native vegetation had been removed. Similarly, this trend was observed in Planctomycetota, Bacteroidota, Verrucomicrobiota, Gemmatimonadota. In contrast, Chloroflexi, Cyanobacteria, and Armatimonadota were more abundant in the less modified habitat, and the highest values were observed in residual lands.

For fungi, the impact of human modification was even stronger, as significant correlation was found in all the domain fungal phyla

(Figure S16). Ascomycota abundance was negatively correlated with HCAS conditions, with the highest abundance found in removed lands. A similar pattern is observed for Mortierellomycota, Mucoromycota, and Rozellomycota. However, Basidiomycota and Glomeromycota exhibited higher abundance in less disturbed soils.

4 | DISCUSSION

Our spatial models provide strong evidence that the combination of climate and soil is necessary for the understanding of the distribution of soil microbial communities at the continental scale. This finding reconciles the complexity of past studies demonstrating the interaction of climatic, biotic, and edaphic factors on soil microbial communities (Labouyrie et al., 2023; Waldrop et al., 2017). By including soil properties as predictors, the explained microbial spatial variance was increased by 5%–10% (Table 1). This is also found in recent studies where soil physical and chemical properties should be considered along with climate conditions, vegetative

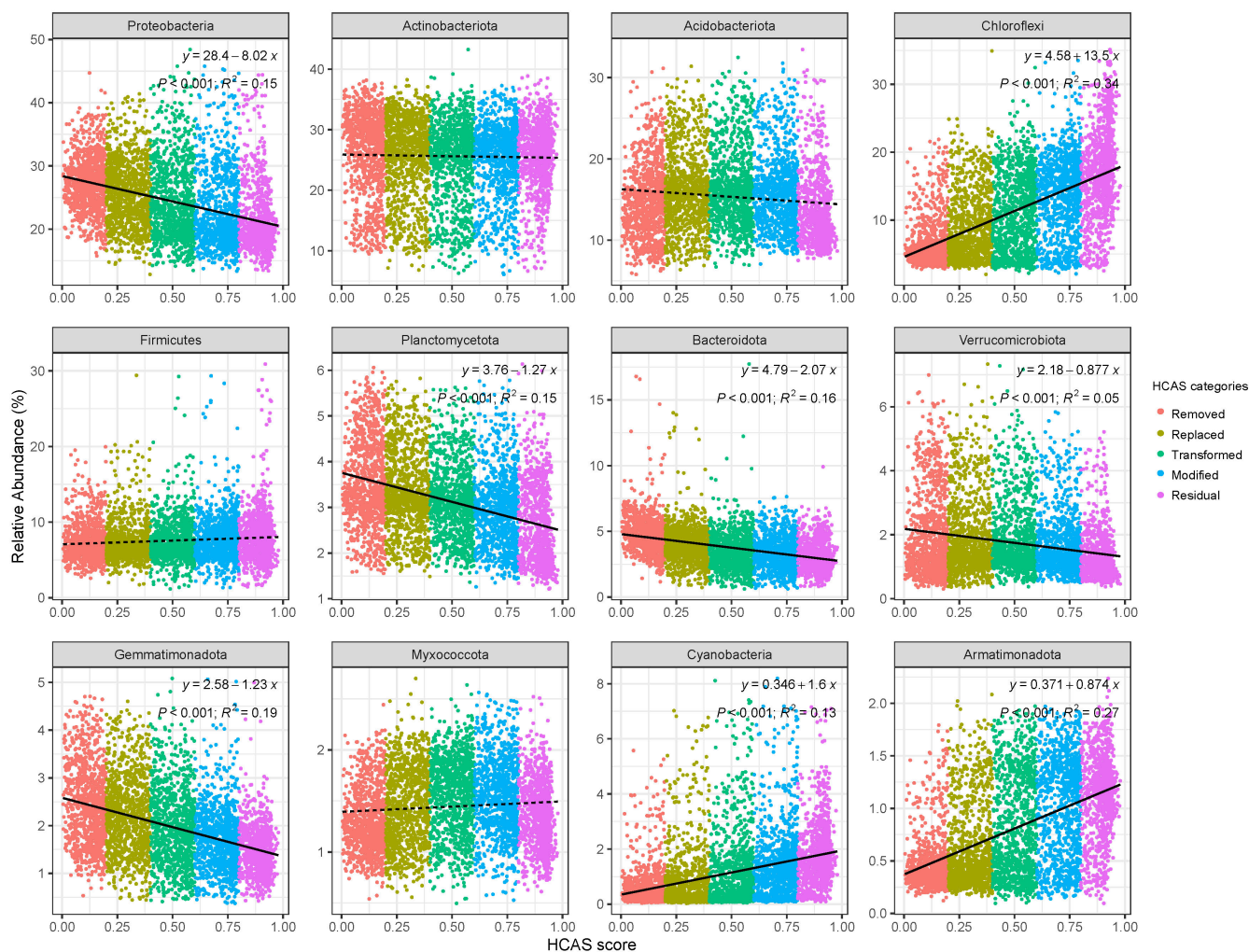


FIGURE 5 The linear correlations fitted between bacterial relative abundance and Habitat Condition Assessment System (HCAS) scores (0 indicates intensive human modification and the original habitats were removed; 1 indicates no or low changes). The dashed line indicates that the line fitting is not statistically significant.

indices, and topographic variables to explain microbial biogeography (Yu et al., 2022).

Many studies revealed the important role of climate factors in shaping the distribution of soil microbial communities at the regional scale (Drenovsky et al., 2010; Qin et al., 2023), in particular temperature and precipitation. Chen et al. (2020) argued that temperature and precipitation changes alter microbial composition and microbial degradation process. Soil microorganisms are highly sensitive to temperature, as temperature regulates their growth and metabolic activity (Jude et al., 2006; Kwon et al., 2017). A study by Nottingham et al. (2018) showed that temperature was the dominant driver of microbial diversity and dissimilarity gradients from the Amazon to the Andes. Precipitation is also an important climate factor that influences soil microbial communities, as it affects soil moisture content, which is essential for microbial growth and activity (Borowik & Wyszowska, 2016). Studies have shown that increased precipitation can lead to increased microbial abundance and activity (Chen et al., 2015).

The importance of soil factors as covariates in the predictive spatial models supports the hypothesis concerning the role of soil properties for microbial spatial distribution, especially for soil pH, clay content and SOC (Figure 3). Soil physical and chemical properties, such as pH, nutrient availability, and soil texture, directly affect microbial growth, metabolism, and community structure. For instance, soil pH influences microbial community composition and activity by controlling microbial metabolisms (Jin & Kirk, 2018) and nutrient availability (Stark et al., 2014). The optimal pH for microorganisms varies for different groups (Figure S6). For instance, most Acidobacteria members exhibit a preference for acidic conditions (pH 3.0–6.5) for optimal growth, particularly those from subdivision 1 (Kalam et al., 2020; Sait et al., 2006). Consequently, this study observed a significant decreasing trend of Acidobacteria with increasing pH (Figure 3b). The enhanced adaptation of Acidobacteria to acidic environments may be attributed to increased cell specialization and enzyme stability at more extreme pH conditions (Kielak et al., 2016). A study by Lauber et al. (2009) also found that soil pH was the main factor influencing soil bacterial community structure. Soil texture was another important soil property that influenced soil microbial communities. Soil texture affects water retention, which in turn impacts microbial growth and activity, and determines the distribution of microhabitats within the soil, controlling microbial diversity and composition (Xia et al., 2020). For example, soils with a high proportion of clay may have more diverse microbial communities due to micro-scale pores providing habitats for diverse microbial taxa (Xia et al., 2020). Additionally, nutrient availability is a critical soil property that impacts soil microbial communities (Miransari, 2013). The availability of nutrients such as nitrogen, phosphorus, and carbon can influence microbial growth and activity, as well as microbial community composition (Dai et al., 2020; Stark & Grellmann, 2002).

Additionally, land use also affected microbial communities. One of the reasons could be attributed to the changes in soil properties

after agricultural practices (Xue, Minasny, McBratney, Wilson, et al., 2023). Additionally, the change of above vegetation also influences the belowground microbial community due to the input forms of soil organic matter and different interactions between the rhizosphere microorganisms and plants (Le Provost et al., 2021; Meena & Rao, 2021; Ramírez et al., 2020). This might be the reason for the higher fungal diversity in intensively used soils in this study (Figure 2a). This study shows that the effects of land use were correlated to land use intensity, consistent with past findings (Le Provost et al., 2021; Romdhane et al., 2022).

Soil management information is difficult to obtain at a large geographic scale but can be an important driver of local-scale heterogeneity of soil microbes. The continental mapping enabled us to evaluate the effect of intensification of human pressures on soil microbial communities. Different microbial phyla may respond uniquely to various environmental stressors and disturbances brought about by human activities. For example, some phyla, such as Proteobacteria, might thrive in disturbed habitats due to their wide adaptability (Spain et al., 2009). Consequently, a negative correlation between Proteobacteria and HCAS scores was observed in this study (Figure 5). However, numerous microbial phyla experienced a significant decrease under human pressure, including Chloroflexi and Basidiomycota. The altered environment may exert a strong filtering effect on certain microbial phyla, leading to population declines due to their specificity in responding to human modifications. This might be caused by habitat disruption (especially for some anaerobic microbes) (Srou et al., 2020), altered soil properties (Xue, Minasny, McBratney, Wilson, et al., 2023), modified microbial interactions (Xue, Minasny, McBratney, Jiang, & Luo, 2023) after human modification. Understanding human changes on microbial community is crucial for preserving biodiversity and ecosystem health. The study of Guerra et al. (2022) identified global regions characterized by high soil microbial species diversity, community variation, and valuable soil-related ecosystem services. Surprisingly, the majority of these biodiversity and service hotspots are situated outside of protected conservation zones and are susceptible to the impacts of global change.

This study used machine learning to reveal the drivers of variation at a continental scale and then to map the dominant microbial distribution patterns. The identification of continental drivers allows us to achieve highly accurate predictions of soil bacterial and fungal distributions. Compared to some recent studies at the national (Griffiths et al., 2016) and global scale (Delgado-Baquerizo et al., 2018, 2020; Egidi et al., 2019; Zheng et al., 2022), this study incorporated a larger and more comprehensive set of soil samples in the predictions models, resulting in a higher prediction accuracy. In addition to providing valuable insights into large-scale microbial biogeography, mapping microbial biodiversity has many implications for direct and indirect users of soils, such as policymakers. This is particularly relevant in the context of climate change, as microbial abundance and spatial distribution is intrinsically linked to soil carbon storage (Fan et al., 2021; Soto-Navarro et al., 2020), global biodiversity (Thakur et al., 2020), and functionality of

terrestrial ecosystems (Delgado-Baquerizo et al., 2016; Singh & Gupta, 2018).

Future research efforts should focus on establishing a connection between soil spatial pattern and its functional aspects, investigating how soil properties respond to human changes, and their impact on biodiversity and specific microbial functions. This research is vital for informing land managers, enabling them to make informed decisions based on specific field conditions such as soil types. By manipulating manageable factors like organic carbon and soil pH, land managers can work towards sustaining or enhancing soil biodiversity within specified ranges, ensuring optimal soil functionality.

5 | CONCLUSIONS

In conclusion, this study represents a contribution to our comprehension of the interactions between topsoil microbes and their environment, such as temperature, precipitation, soil pH, clay content, and SOC. Our findings underscore the strong influence of climate and soil properties on microbial community dynamics at large scales. Notably, we found that the combination of climate factors and soil properties yielded the most accurate predictive models. Further, this study reveals for the first time the spatial pattern of dominant bacterial and fungal communities across Australia. The integration of machine learning facilitated the efficient prediction and enabled empirical estimation of the factors driving soil microbial biogeography patterns at a large spatial scale. The continental mapping enabled us to evaluate the impact of human modification on the underground microbial ecosystem. This research paves the way for a more profound understanding of soil microbial communities which is key to enhancing ecosystem sustainability, improving soil conditions, and supporting food security and human health. It also has implications for defining conservation policies at continental level.

AUTHOR CONTRIBUTIONS

Peipei Xue: Conceptualization; data curation; formal analysis; methodology; validation; visualization; writing – original draft; writing – review and editing. **Budiman Minasny:** Conceptualization; funding acquisition; methodology; supervision; validation; writing – review and editing. **Alexandre M. J.-C. Wadoux:** Conceptualization; data curation; methodology; software; writing – review and editing. **Mercedes Román Dobarco:** Conceptualization; data curation; methodology; writing – review and editing. **Alex McBratney:** Conceptualization; funding acquisition; methodology; project administration; supervision; writing – review and editing. **Andrew Bissett:** Investigation; writing – review and editing. **Patrice de Caritat:** Investigation; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing financial interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the BioPlatforms Australia project's data portal at <http://doi.org/10.4227/71/561c9bc670099> and the Geoscience Australia repository at <https://doi.org/10.11636/Record.2011.020>.

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SUPPORTING INFORMATION

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

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