

## RESEARCH ARTICLE OPEN ACCESS

# The Biogeography of Soil Bacteria in Australia Exhibits Greater Resistance to Climate Change Than Fungi

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## ABSTRACT

Soil microorganisms are crucial to ecosystem health, and their composition and distribution are shaped by a range of environmental factors. However, the effects of accelerating climate change on soil microbiomes remain under-explored. This study examines the continental-scale factors controlling soil microbiomes and evaluates their responses to climate change. We applied machine learning algorithms to analyze the distribution patterns of bacteria and fungi in 1300 Australian topsoil samples. Our results indicate that bacterial distributions align closely with the soil class map, highlighting the dominant impact of soil properties. In contrast, fungal distributions are more strongly associated with temperature gradients, emphasizing the critical role of climate. Climate projections for 2040 suggest a notable southward shift in both bacterial and fungal patterns, particularly around latitude 25°S. Moreover, our findings suggest that fungal biogeography is likely to undergo more pronounced changes, with approximately 24% of Australian topsoils expected to experience significant shifts in fungal community structure, compared to about 19% for bacteria, which appear more resistant. This study emphasizes the diverse vulnerabilities of soil microbial communities and stresses the need to account for microbial dynamics in future land use and management practices.

## 1 | Introduction

Soil microorganisms are essential drivers of terrestrial biogeochemical processes, facilitating element cycling across diverse biomes (Sokol et al. 2022). They play key roles in litter decomposition, carbon turnover (Bhattacharyya et al. 2022), nutrient dynamics (Yadav et al. 2021), water regulation (Creamer et al. 2022), and soil-borne disease control (Jayaraman et al. 2021), among other essential ecosystem functions (Evangelista et al. 2023). Among these microorganisms, bacteria and fungi are key components of the soil microbial community. Bacteria are the most

abundant microorganisms in soil, serving as primary decomposers and playing a critical role in nutrient cycling (Paul and Frey 2023). On the other hand, fungi also dominate soil ecosystems, acting as important decomposers of complex organic matter, contributing to the formation of stable soil organic matter and maintaining soil structure (Romani et al. 2006). Studies demonstrate the close cooperation between bacteria and fungi in decomposing diverse substrates, with their activities spanning various spatial scales (You et al. 2014; Zhu et al. 2022). Soil bacteria and fungi coexist, compete, and collaborate within

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various soil environments (Schimel et al. 2007). However, their distinct ecological niches at large scales remain underexplored.

At large scales, soil microbial communities are shaped by the interaction of soil properties and climatic variables (Jing et al. 2020; Tajik et al. 2020; Xue et al. 2024). Due to their distinct evolutionary adaptations and physiological acclimation mechanisms, bacteria and fungi respond differently to these environmental factors, leading to divergent biogeographical patterns. Bacteria, with simpler cellular structures and faster metabolic rates, can rapidly adapt to fluctuating environmental conditions, enabling them to dominate dynamic ecosystems (Nguyen et al. 2021). In contrast, fungi, with their more complex structures and slower growth rates, tend to adapt better in stable environments (Mickan et al. 2019; Samanta 2015). Previous studies have highlighted that soil pH, moisture, organic matter content, and temperature are key determinants of microbial community structure and functions (Greaves and Carter 1920; Kaiser et al. 2016; Xue, Minasny, McBratney, Pino, et al. 2023). However, the relative importance of these factors can vary significantly for different microbial communities. For instance, Mod et al. (2021) found that soil bacterial communities are more strongly influenced by pH than by other edaphic and climatic factors. In contrast, fungi can tolerate a wider pH range, although certain fungal species may have specific optimal pH preferences (Davison et al. 2021; Rousk et al. 2010). Additionally, bacteria and fungi respond differently to temperature variations. As temperatures exceed 30°C, the decrease in growth rate and activity is more drastic in fungi than in bacteria, while the opposite trend occurs at temperatures below 25°C (Pietikäinen et al. 2005). The fundamental differences in the physiology and life histories of bacteria and fungi explain their differing responses to environmental changes and management practices, suggesting variations in their biogeographical patterns (Yu et al. 2022). Malard et al. (2022) reported that microorganisms have well-defined niches for different communities in a study along environmental gradients in the Alps. Understanding the differing responses of soil microbial groups to environmental factors is crucial for microbial biogeography and soil functions, for example, carbon decomposition and soil organic matter formation. Additionally, the strong influence of climate on soil microorganisms suggests that climate change will significantly impact belowground microbial ecosystems. Several studies have cautioned that the impacts of rising global temperatures and shifting precipitation patterns on microbial abundance, diversity, and activity remain understudied (Jain et al. 2020). Therefore, further research on microbial responses to global climate change is necessary.

Our previous study predicted the relative abundances of the dominant bacteria and fungi across Australia (Xue et al. 2024). However, the biogeographical differences between bacteria and fungi, as well as their responses to climate change, have not been well investigated. This study aims to elucidate the patterns of soil bacteria and fungi at the continental scale, characterized by a wide range of soil types and climatic zones. By analyzing soil DNA sequences of 1,300 samples, we assess the impact of various environmental factors on soil bacteria and fungi across Australia. Incorporating the projected climate for 2040, we forecast the future distributions of bacteria and fungi across Australia. We hypothesize that (1) bacteria are primarily influenced by soil types and properties, whereas fungi are

more significantly regulated by vegetation and climatic conditions, and (2) the biogeographical patterns of soil bacteria will exhibit greater resistance to climate change, while the distribution patterns of fungi are likely to experience more pronounced alterations. By advancing our understanding of the distinct distribution patterns of bacterial and fungal communities, this research offers insights for predicting and managing the effects of environmental change on microbial functions and overall ecosystem stability.

## 2 | Materials and Methods

### 2.1 | Data Source

We analyzed the soil microbiome data in Xue et al. (2024), which integrates the Biomes of Australian Soil Environments (BASE) database (Bissett et al. 2016) with microbial data from the National Geochemical Survey of Australia (NGSA) (de Caritat 2022; de Caritat and Cooper 2011). The topsoil samples (0–15 cm) with both bacterial and fungal DNA information were selected. A total of 1300 samples were included in this study, with 1037 from the BASE database and 263 from the NGSA database (Figure S1A). These samples encompass all regions across Australia, covering a range of land uses (Figure S1B) and all soil classes in Australia (Figure S1C). The composition of soil bacteria and fungi was characterized by the Operational Taxonomic Units (OTUs) table and taxonomy table in Xue et al. (2024), following the amplicon sequencing process developed by Bissett et al. (2016). Single OTUs and OTUs that had fewer than 10 reads were filtered out. Samples with fewer than 10,000 total sequence reads were also excluded (see the rarefaction curves in Figure S2).

Raster layers of Australian soil, topography, and climate variables were obtained from the Terrestrial Ecosystems Research Network (TERN) using the “SLGACloud” package in R (O'Brien and Searle 2019). These map layers included soil organic carbon (SOC), pH, total phosphorus (P), cation exchange capacity (CEC), clay and sand content, mean annual aridity index (ADM), annual daily mean temperature (Temp), annual temperature range (TRA), total annual precipitation (PTA), elevation, and slope (Figure S20). The land use map was retrieved from the Australian Bureau of Agricultural and Resource Economics and Sciences (ABARES) website, following the Australian Land Use and Management Classification system (ABARES 2016). The Australian soil class map was obtained from Searle (2021), and the phytogeographic zone map was based on the phytogeographic regions in Brundrett (2017).

Future climate projection layers (i.e., Temp, TRA, and PTA) were downloaded from CMIP6 (Fick and Hijmans 2017) using the Google Earth Engine platform. We selected the future climate projections under the SSP3-7.0 scenario, which represents the upper-middle range of possible outcomes, characterized by a doubling of CO<sub>2</sub> emissions by 2100 and an estimated global warming of 2.1°C (Tebaldi et al. 2021). Temp, TRA, and PTA data for 2040 were obtained by averaging projections from simulations of ACCESS-CM2, BCC-CSM2-MR, CMCC-ESM2, EC-Earth3-Veg, GFDL-ESM4, GISS-E2-1-G, INM-CM5-0,

IPSL-CM6A-LR, MIROC6, MPI-ESM1-2-HR, MRI-ESM2-0, and UKESM1-0-LL (Eyring et al. 2016).

Soil properties, including SOC, pH, total P, EC, CEC, clay, and sand content, for the 1300 samples were obtained from the databases mentioned above, with measurement details reported previously (Bissett et al. 2016; de Caritat and Cooper 2011). Additionally, environmental variables at those sites were also extracted from the above raster layers using the “raster” package (Hijmans et al. 2015) for the following spatial model training. These variables included soil properties (i.e., SOC, pH, total P, CEC, clay, and sand content), climate variables (i.e., Temp, TRA, and PTA), and topography information (i.e., elevation and slope).

## 2.2 | Beta-Diversity and Environmental Influences

Microbial beta-diversity was calculated by the Bray–Curtis dissimilarity metric (Beals 1984) using the “vegan” package (Oksanen et al. 2007) in R. The nonmetric multidimensional scaling (NMDS) (Kenkel and Orlóci 1986) was applied to ordinate sample dissimilarity, representing variations in microbial community composition. NMDS components reflect beta diversity by capturing variations in microbial community composition across samples, allowing for visualizing and comparing differences driven by environmental factors and spatial distribution. We used the three components of their corresponding NMDS results for both bacteria and fungi to represent their community composition variations.

To examine the environmental controls on microbial communities, we assessed the relationships between NMDS components and the environmental variables using the 1300 samples described above. The NMDS components served as response variables, while measured soil properties, climate, and topography values acted as predictor variables. We assessed the importance of environmental factors for microbial distributions by employing SHAP values (Lundberg 2017). They were calculated from regression models with squared loss using “xgboost” package (Chen et al. 2015) in R. The SHAP value represents the importance of the predictor variable relative to the mean of the prediction and is expressed in the unit of the target variable. The key environmental variables with higher importance were selected for the subsequent prediction models. The distance-based redundancy analysis (db-RDA) was also employed to assess the influences of key environmental variables on microbial community composition. To examine how microbial community composition responds to environmental factors, partial dependence analysis (Greenwell 2017) was applied to the NMDS components derived from the Random Forest model.

## 2.3 | Modelling and Prediction

A range of machine learning (ML) models was employed to establish relationships between key environmental variables and microbial communities, including Random Forest (RF), Extreme Gradient Boosting (XGBoost), Support Vector Machines (SVM), Multiple Linear Regression (MLR), Recursive Partitioning and Regression Trees (RPART), Neural Networks (NN), and k-Nearest Neighbors (kNN). Model performance

was assessed using 10-fold cross-validation (CV) (Fushiki 2011; Wadoux et al. 2021). The root mean square error (RMSE) and the coefficient of determination ( $R^2$ ) were calculated to assess the model accuracy. RMSE measures the average magnitude of errors between predicted and actual values, with a lower RMSE indicating better model performance. The  $R^2$  was calculated as  $1 - \text{RSS}/\text{TSS}$ , where RSS is the residual sum of squares and TSS is the total sum of squares (Wadoux et al. 2022). It quantifies the proportion of variance in the dependent variable explained by the model's predictions and can be negative if the root mean square error exceeds the standard deviation of the observations. A higher  $R^2$  (i.e., close to 1) indicates better model performance. We also compared the prediction models using soil properties, climate factors, and the combination of both.

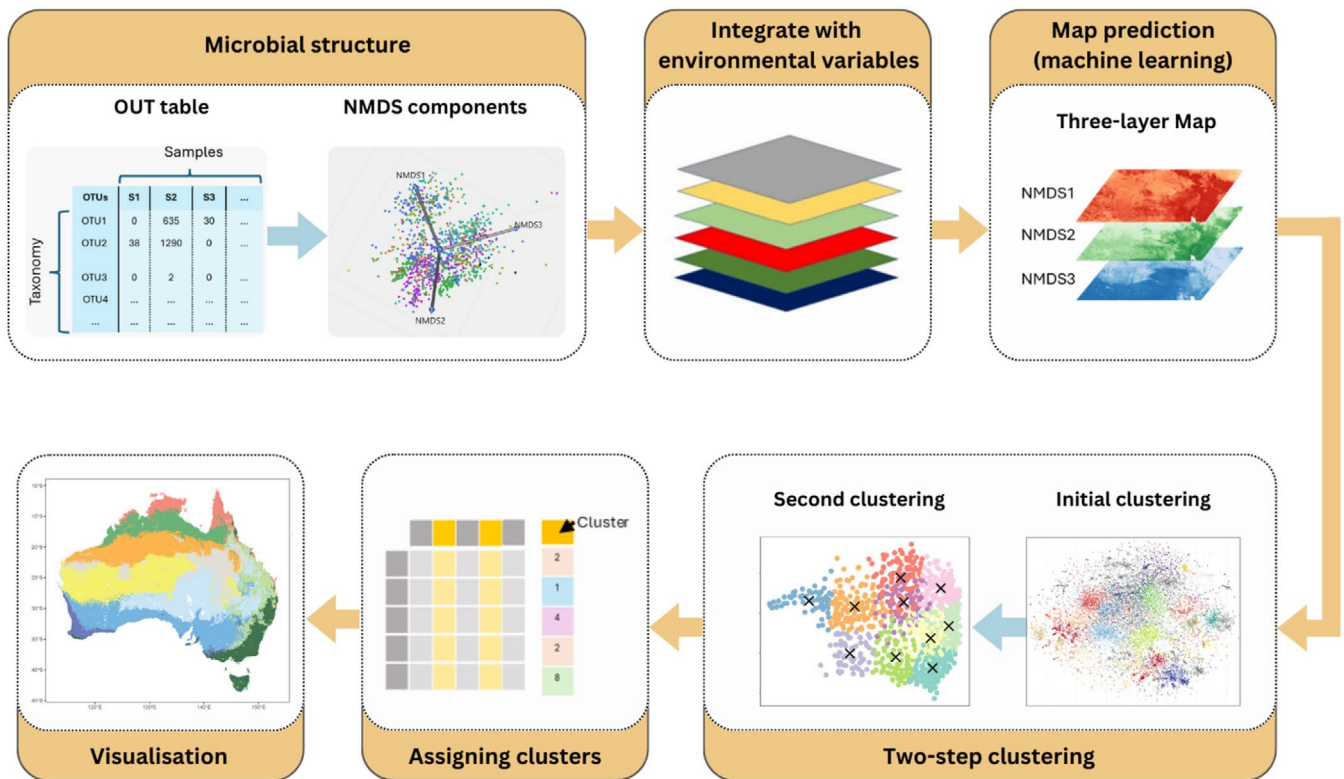
Based on model performances (Figure S8), we selected the best ML model (Random Forest) to upscale the observations to the continental-scale biogeography of bacteria and fungi using soil properties and climate factors as covariates (Biau 2012; Breiman 2001). The covariates include SOC, soil pH, soil P, CEC, clay and sand contents, as well as Temp, PTA, and TRA (extracted from the corresponding rasters). The three components of the NMDS of bacteria and fungi were the response variables modeled using the digital soil mapping framework (Ma et al. 2019; McBratney et al. 2003; Wadoux et al. 2020). The three parameters of the RF 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 of 250, 5, and to the rounded down square root of the number of covariates, respectively.

Once the models were trained, they were projected across Australia, as in our previous study's approach (Xue et al. 2024). The resolution of the predicted map is  $0.01^\circ$  (approximately  $1.11 \times 1.11$  km near the equator). The predicted NMDS layers for bacteria and fungi were stacked and visualized using “plotRGB” in “raster” R package with NMDS1 for the red layer, NMDS2 for the green layer, and NMDS3 for the blue layer. Using soil properties and predicted climate rasters for 2040, we projected the future potential distributions of bacteria and fungi by applying the trained machine-learning models.

## 2.4 | Unsupervised Classification With k-Means

To compare the distribution patterns of bacteria and fungi effectively, we grouped the NMDS maps into different spatial regions, as outlined in Styc et al. (2025). We applied non-hierarchical clustering to the biogeography maps of bacteria and fungi, specifically the three-layer maps representing the three NMDS components.

The following procedure was applied separately for bacteria and fungi (Figure 1): First, the raster of the three-layer maps was converted into a dataframe. Next, 1000 initial centroids were generated from the dataframe using the “ClusterR” package (Mouselimis et al. 2019) with the “kmeans++” option. The optimal number of clusters for the initial centroids, ranging from 5 to 50, was then determined using the “NbClust” package (Charrad et al. 2014), and the most suitable number was selected based on the elbow method. Subsequently, k-means clustering with this



**FIGURE 1** | Workflow of soil microbial distribution mapping and clustering.

optimal number of samples was performed on the initial centroids to determine the final centroids. The distances between the clusters were visualized in a dendrogram of the final centroids. For each pixel, the three NMDS values were compared to the established centroids and assigned to a cluster based on the closest Euclidean distance. The resulting map visually represents the spatial clusters of microbial composition for bacteria or fungi.

To assess the impact of climate change on microbial community structure, the projected 2040 maps of the three NMDS components were assigned to clusters using the final centroids previously established for the bacteria and fungi groups. We then evaluated each pixel on the map to determine whether cluster assignments changed or remained consistent between 2020 and 2040. Subsequently, we calculated the area change for each cluster.

## 2.5 | Other Statistical Analyses

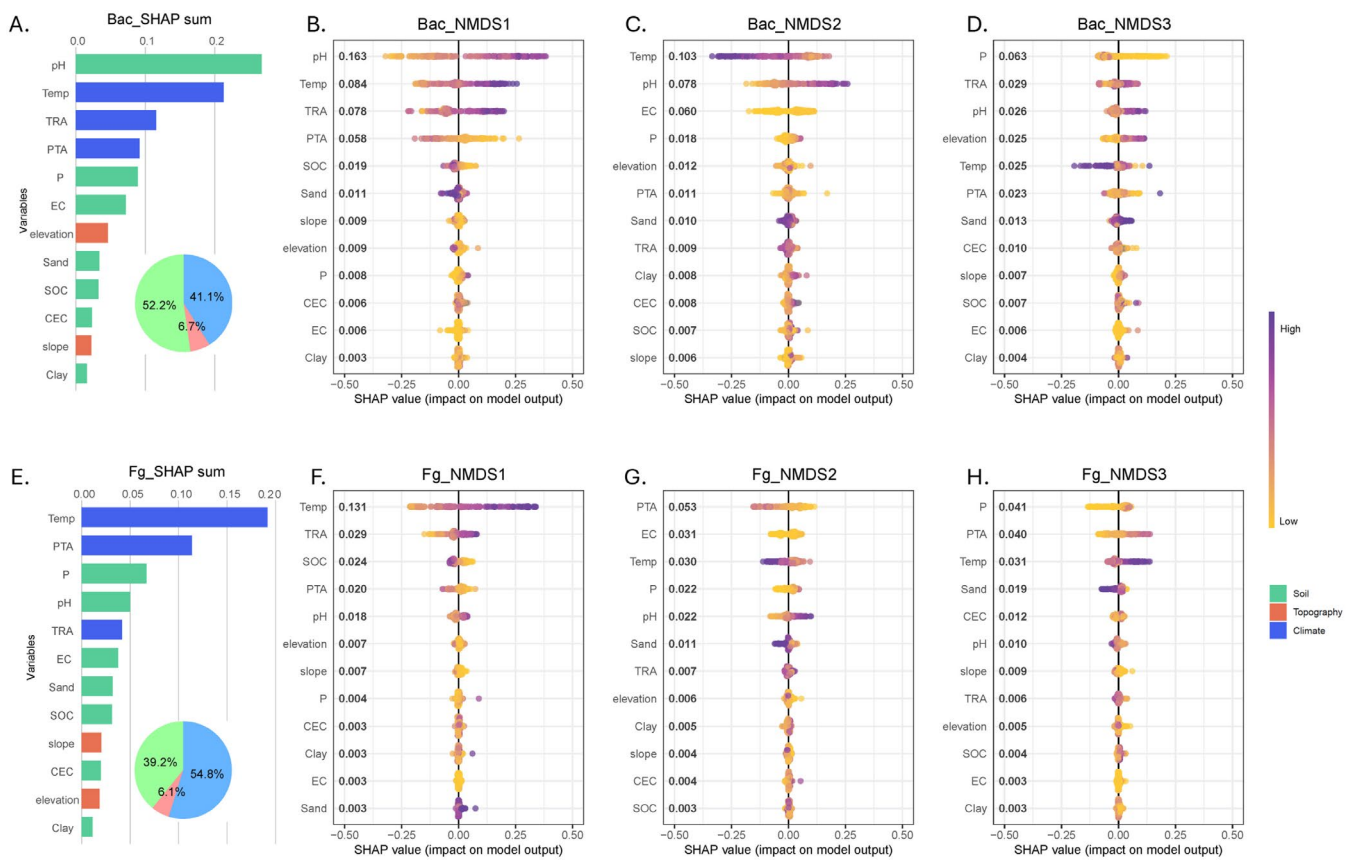
Density plots were further generated to view bacterial and fungal distributions for different soil types and different phyto-geographic zones. To explore the ecological significance of the NMDS components, we randomly sampled 500 samples from each cluster and examined the relationships between microbial abundances and NMDS values using “loess” and “lm” regression models in R. Additionally, the importance of each environmental factor for the clustered regions was assessed using *i.scores* from the Random Forest model. Other remaining figure visualizations were plotted in R using “ggplot2” (Wickham 2011).

## 3 | Results

### 3.1 | Different Drivers of Soil Bacteria and Fungi

The variations in community composition for bacteria and fungi were presented through NMDS analysis (Figure S3). Using SHAP values, we found that soil pH emerged as the primary driver for the variation in bacterial community composition, followed by annual mean temperature (Temp) and annual mean temperature range (TRA) (Figure 2A). Bacterial NMDS1 was primarily influenced by pH, followed by mean temperature and annual temperature range (TRA) (Figure 2B). For NMDS2, the primary drivers were annual mean temperature, soil pH, and EC (Figure 2C). Variable contributions to NMDS3 were weaker than those to the other two components, but soil total phosphorous concentration (P) and annual temperature range (TRA) were the major contributors (Figure 2D). In total, soil factors contributed the most to the variation in bacterial community composition, accounting for ~52%, while climate explained ~41% (Figure 2A). We further used db-RDA to calculate the overall influence of soil and climate factors on the bacterial community composition. The db-RDA confirmed the significant regulation by pH and temperature (Figure S4A). The db-RDA results also indicate that soil organic carbon (SOC) significantly impacted bacterial community composition.

For fungal composition, the primary driver appeared to be temperature range (TRA), followed by annual total precipitation (PTA) and soil P (Figure 2E). Specifically, the main driver for fungal NMDS1 was annual mean temperature; the second driver was TRA, but its contribution was around five times smaller. For NMDS2 of the fungal community, PTA had the greatest



**FIGURE 2** | Importance of environmental factors in shaping bacterial and fungal communities, assessed using SHAP values from regression models with squared loss. (A) Sum of absolute mean SHAP values for each factor across the three NMDS components for bacteria, with total contributions from soil, climate, and topography. (B–D) Variable importance for bacteria in NMDS1, NMDS2, and NMDS3, respectively. (E) Sum of absolute mean SHAP values for fungi, with total contributions from soil, climate, and topography. (F–H) Variable importance for fungi in NMDS1, NMDS2, and NMDS3, respectively. “Bac” indicates bacteria; “Fg” indicates fungi. Dot colors in panels B–D and F–H show standardized predictor values.

influence. Similar to bacteria, soil P and PTA were primary drivers for NMDS3 of fungi, although their SHAP values were relatively low. Overall, climate factors explained most of the variation in fungal community composition (~54%), followed by soil factors (~39%) (Figure 2E). Additionally, db-RDA indicated significant influences of SOC and pH on variations in the fungal community composition (Figure S4B).

Partial dependence analyses further illustrated the distinct responses of bacteria and fungi to environmental factors, as shown in Figures S6 and S7. Significant differences were observed for most variables, particularly for soil pH and TRA. For example, changes in NMDS1 were more pronounced for bacteria than fungi as pH increased from acidic to neutral ( $3 < \text{pH} < 7$ ) (Figure S6). When pH exceeded 7, NMDS1 and NMDS2 remained relatively stable for both bacteria and fungi. In alkaline soils, bacterial NMDS3 increased significantly, while fungal NMDS3 initially declined before rebounding as the pH exceeded 8. For TRA, its variation had a more significant effect on bacteria in NMDS1, while bacteria and fungi exhibited opposite trends in NMDS2 and NMDS3 (Figure S7). Additionally, NMDS2 variation was more pronounced for fungi as PTA changed from approximately 100 to 1000 mm. NMDS3 of bacteria and fungi showed differing responses to annual mean temperature (below 15°C), PTA (less than 500 mm), and P (below 30 mg/kg).

### 3.2 | Spatial Variances of Bacteria and Fungi

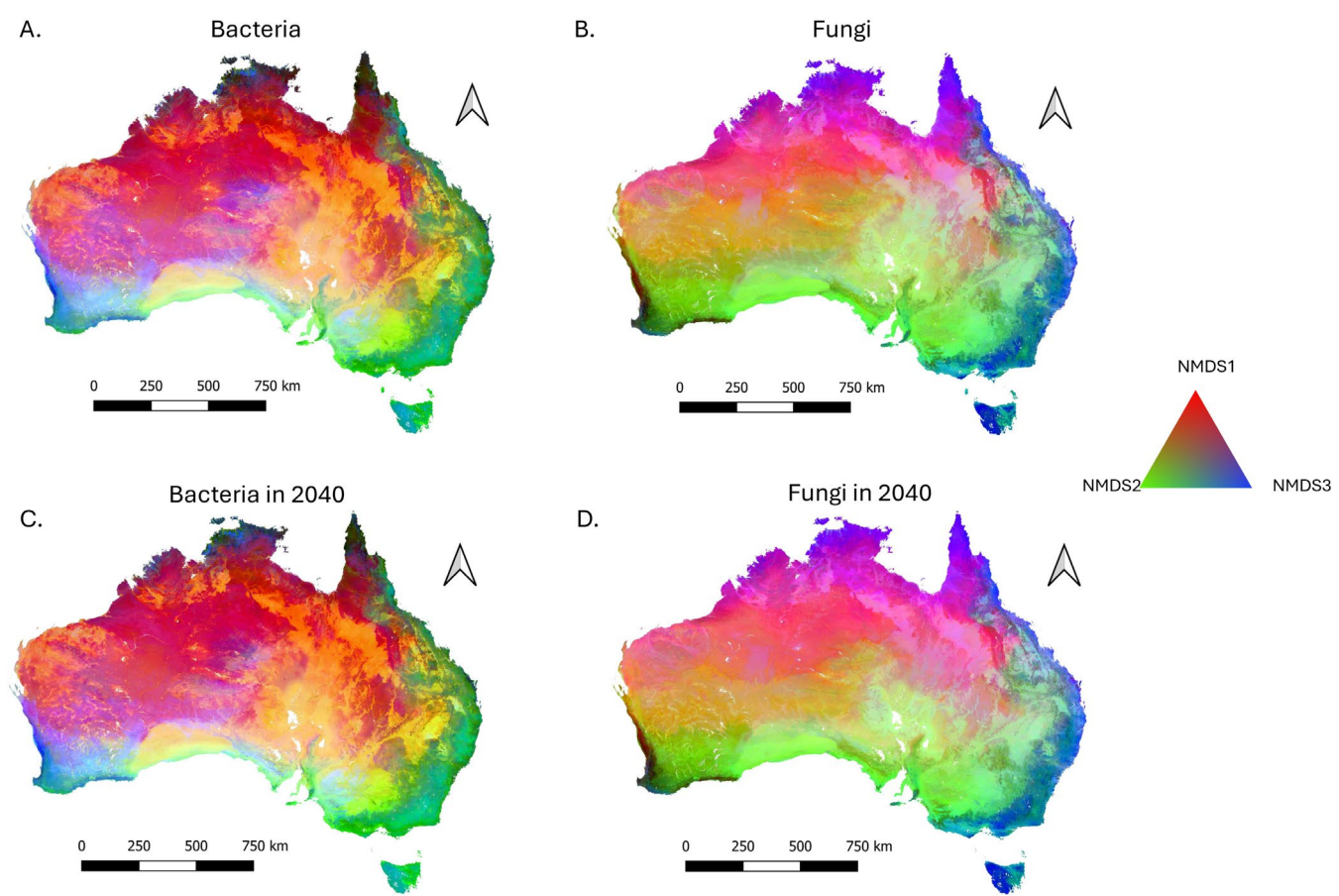
Continental-scale relationships between the environmental factors and microbial communities in the soil samples were derived using Random Forest models. Cross-validation results revealed that the fitted models had the best predictive capabilities when combining soil and climate factors (Table 1). Using soil factors only, the models explained more variability for the bacterial community (NMDS1,  $R^2=0.82$  and NMDS2,  $R^2=0.63$ ) than for the fungi community (NMDS1,  $R^2=0.78$  and NMDS2,  $R^2=0.61$ ). Using climate factors only,  $R^2$  was generally higher for fungi in NMDS1 (bacteria,  $R^2=0.86$ ; fungi  $R^2=0.89$ ) and NMDS3 (bacteria,  $R^2=0.72$ ; fungi  $R^2=0.74$ ). Incorporating both soil properties and climate factors showed the highest explanatory power for both bacteria and fungi. Since the topographic variables had minimal influence on the models (Table 1), the final predictions only used soil and climate variables as predictors.

Applying the calibrated models to Australian soil and climate rasters, we generated bacterial and fungal biogeography maps for 2020, represented by NMDS1, NMDS2, and NMDS3 layers. As shown in Figure 3, distinct spatial patterns were observed between bacteria (Figure 3A) and fungi (Figure 3B). The changes from north to south were more evident for fungi. Generally, variation was more pronounced for bacteria in the inland regions.

**TABLE 1** | Validation statistics (10-fold cross-validation) of the random forest models for bacterial and fungal beta diversity obtained by different environmental factors.

|           | Soil |                | Climate |                | Soil + Climate |                | Soil + Climate + topography |                |
|-----------|------|----------------|---------|----------------|----------------|----------------|-----------------------------|----------------|
|           | RMSE | R <sup>2</sup> | RMSE    | R <sup>2</sup> | RMSE           | R <sup>2</sup> | RMSE                        | R <sup>2</sup> |
| Bac_NMDS1 | 0.19 | 0.82           | 0.17    | 0.86           | 0.15           | 0.89           | 0.15                        | 0.89           |
| Bac_NMDS2 | 0.19 | 0.63           | 0.17    | 0.69           | 0.14           | 0.79           | 0.14                        | 0.79           |
| Bac_NMDS3 | 0.16 | 0.55           | 0.13    | 0.72           | 0.13           | 0.71           | 0.13                        | 0.71           |
| Fg_NMDS1  | 0.13 | 0.78           | 0.09    | 0.89           | 0.08           | 0.9            | 0.08                        | 0.9            |
| Fg_NMDS2  | 0.11 | 0.61           | 0.1     | 0.69           | 0.09           | 0.78           | 0.09                        | 0.78           |
| Fg_NMDS3  | 0.1  | 0.64           | 0.09    | 0.74           | 0.08           | 0.78           | 0.08                        | 0.78           |

Abbreviations: Bac, for bacteria; Fg, fungi.

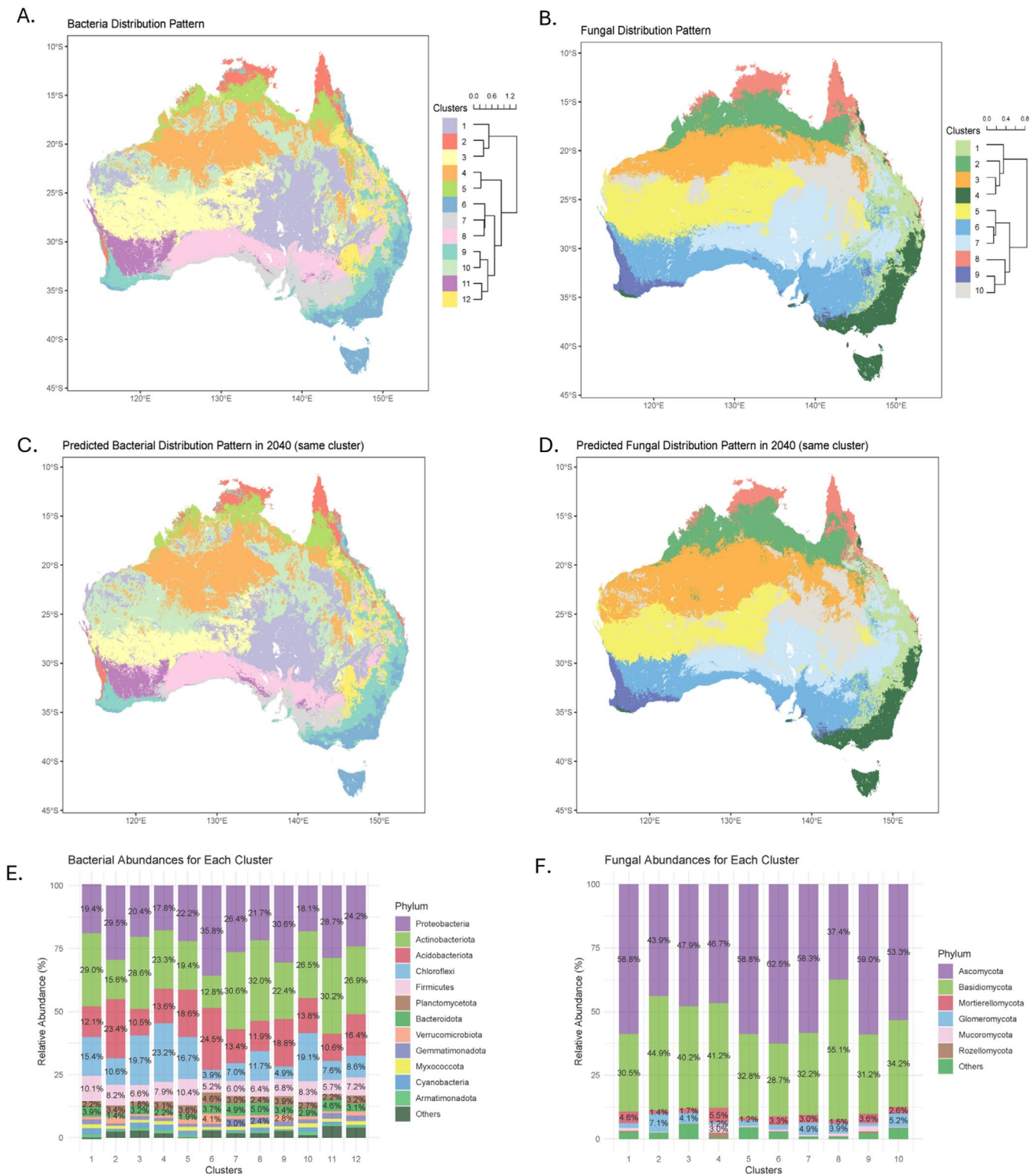


**FIGURE 3** | Predicted distribution patterns of bacterial and fungal communities across Australia based on NMDS components. (A) Current bacterial distribution. (B) Current fungal distribution. (C) Projected bacterial distribution in 2040. (D) Projected fungal distribution in 2040. Maps are shown using an RGB color scheme, with NMDS1 mapped to red, NMDS2 to green, and NMDS3 to blue, representing gradients in community composition across regions. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

Significant differences between coastal regions and inland areas were apparent for both bacteria and fungi, especially for the east and southwest coasts.

To understand the spatial assembly patterns of soil microbes, the NMDS maps were classified into distinct groups using the k-means unsupervised clustering method (Figure 4). For bacteria, the optimal number of clusters was 12, while the optimal

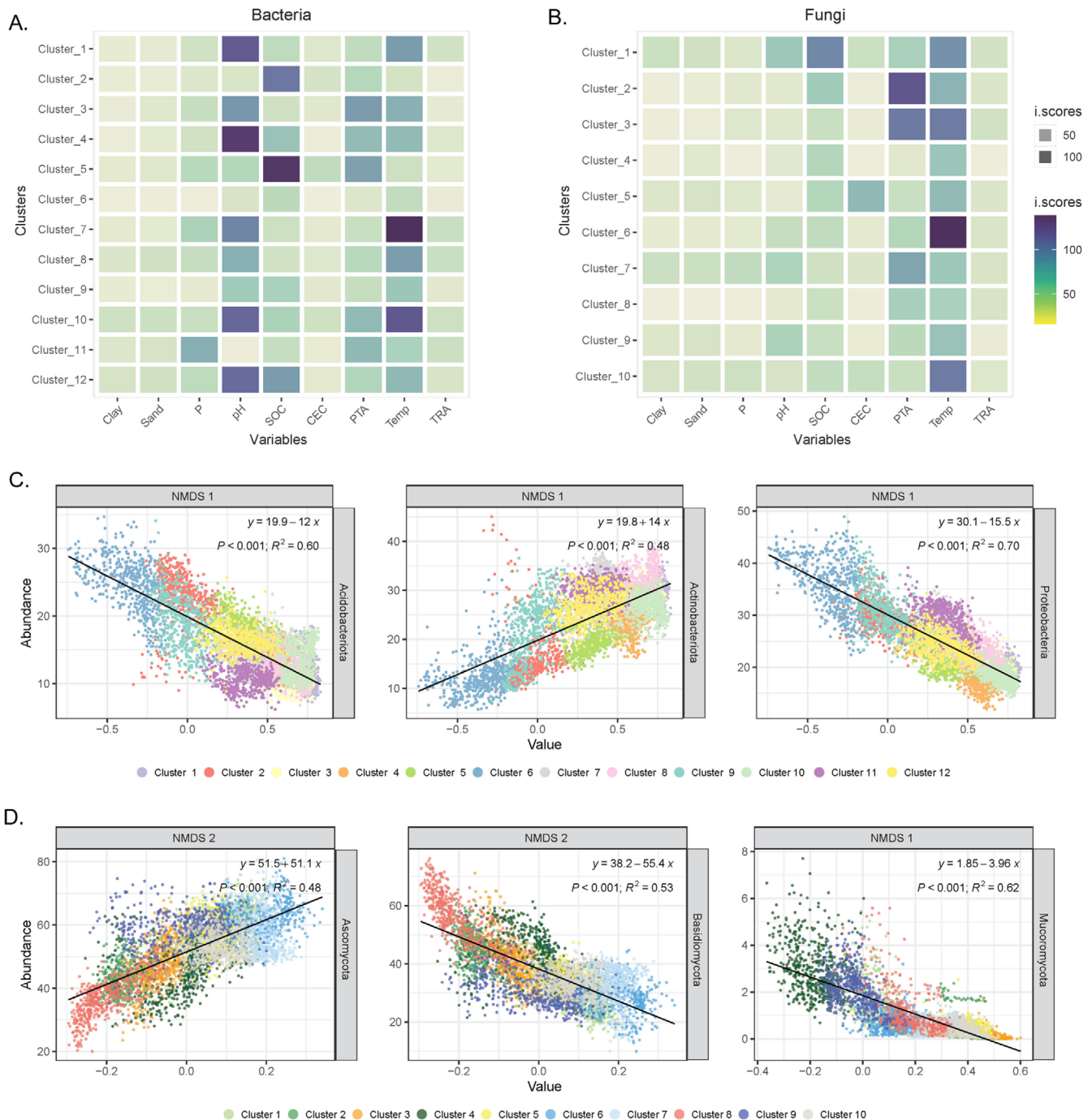
number of clusters for fungi was 10 (Figure S9). The northern coastal region of Australia was characterized by the bacterial community predominantly composed of Proteobacteria (~30%) and Acidobacteriota (~23%), with a low abundance of Actinobacteriota (~16%) (Cluster 2 in Figure 4E). The fungal community in this region showed the highest abundance of Basidiomycota (Cluster 8 in Figure 4F). In the inland regions, bacteria were distributed across five clusters (Clusters 1, 3, 4, 5,



**FIGURE 4** | Current and projected distribution patterns of bacterial and fungal communities across Australia, grouped by K-means clustering. (A, B) Current distribution patterns of bacterial and fungal communities, respectively. (C, D) Projected distribution patterns for bacteria and fungi in 2040. (E, F) Mean community composition at the phylum level for bacteria (E) and fungi (F) within each cluster. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

and 10). Notably, Clusters 1 and 3 comprised relatively high proportions of Actinobacteriota (around 28%–29%), while Clusters 4 and 10 generally exhibited lower abundances of Proteobacteria (around 17%–18%) compared to other clusters. Bacteria distributions exhibited greater complexity in eastern Australia,

particularly in the coastal regions of Queensland and New South Wales. In contrast, fungal communities displayed more defined north-to-south transitions in west Australia, with Cluster 2 transitioning to Cluster 3 and then Cluster 5. Clusters 2 and 3 showed similar composition patterns with Ascomycota abundance



**FIGURE 5** | Importance of key environmental variables for each cluster in bacterial (A) and fungal (B) communities. (C, D) Examples of significant correlations between NMDS values and bacterial (C) or fungal (D) phyla, fitted by linear regression and displayed by cluster.

around 43%–48% and Basidiomycota about 40%–45%, while Cluster 5 showed a marked increase in Ascomycota abundance (~59%). The bacterial community composition in the southern coastal region was divided into five clusters, while fungi were clustered into two distinct classes: the southwest coast (Cluster 9, where Ascomycota accounted for ~59% and Basidiomycota for ~31%) and the south-central coast (Cluster 6, where Ascomycota made up ~62% and Basidiomycota constituted ~28%).

As the bacterial and fungal distribution patterns were divided into distinct regions (clusters), the variable importance varied across these regions (Figure 5). For bacteria, pH was the

dominant controlling factor in Clusters 1, 4, 10, and 12, located in the central region of Australia (Figure 5A). In the northern coastal areas, such as Clusters 2 and 5, SOC was the most influential factor. Cluster 7, situated on the southern coast, was primarily shaped by the mean temperature.

For fungal distributions, the most significant factors were PTA and temperature. Clusters 2 and 3 were most strongly influenced by PTA, suggesting that precipitation plays a key role in the northern regions (Figure 5B). Temperature emerged as the primary driver in Cluster 6, emphasizing the critical role of temperature along the southern coast.

The correlations between the NMDS values and microbial abundance further illustrate the spatial variations in bacterial (Figure S11) and fungal (Figure S12) community compositions, as grouped by the clustered regions. For example, bacterial NMDS1 showed a significant negative linear relationship with Acidobacteriota and Proteobacteria. In contrast, a positive linear relationship was found between NMDS1 and Actinobacteria (Figure 5C). Consequently, with the lowest NMDS1 values in the southern coastal region, this area (Cluster 6) exhibited the highest proportions of Actinobacteria and Proteobacteria. For fungi, significant linear relationships were observed between NMDS2 and Ascomycota, as well as NMDS2 and Basidiomycota (Figure 5D). Accordingly, the relative abundance of Ascomycota increased, while Basidiomycota decreased from the northern coastline toward the inland region (from Cluster 8 to 2), corresponding to lower NMDS2 values. Additionally, higher proportions of Mucoromycota were observed along the southeast coast (Cluster 4) and southwest coast (Cluster 9), where NMDS1 values were lower. The detailed spatial variations for the environmental drivers were compared by cluster regions in Figures S18 and S19.

To understand the dominant controls of microbial distributions, we compared the spatial patterns of bacteria and fungi with established environmental maps. The bacterial distribution map closely mirrors the Australian soil class map (Figure S10A), suggesting that soil properties are the primary drivers of bacterial community patterns. In contrast, the fungal distribution map aligns more with the Australian climate zone map, and more specifically, the phytogeographic map (Figure S10B)—indicating that fungal communities are more strongly influenced by climatic conditions. The significant differences between bacterial and fungal communities across soil classes and phytogeographic regions were further illustrated by different peaks in the density diagrams in Figures S13 and S14, highlighting the distinct environmental drivers shaping each microbial group.

### 3.3 | Changes in Microbiomes Between 2020 and 2040

To assess the impact of climate change on microbial communities, we projected the potential future distributions of bacteria and fungi for the year 2040, as shown in Figure 3C,D. Changes in each NMDS component for bacteria (Figure S15) and fungi (Figure S16) were quantified pixel by pixel to understand the dynamics at a granular level. Generally, significant shifts were observed in the distribution patterns of both bacteria and fungi, with more pronounced changes for fungi as depicted in Figure 3. This trend is further supported by the microbiome cluster maps (Figure 4C,D), which illustrate regions expected to undergo changes in 2040, as highlighted in Figure 6.

Projections for 2040 indicate that the total area experiencing shifts in microbial clusters is substantially larger for fungi, with approximately 24% of the region (~1,800,000 km<sup>2</sup>) anticipated to undergo changes (Figure 6B). This contrasts with about 19% for bacteria (~1,400,000 km<sup>2</sup>), as shown in Figure 6A. Furthermore, a greater number of fungal clusters are predicted to experience changes (Figure S17).

In bacterial communities, two clusters (Clusters 4 and 10) are projected to expand significantly, with increases of 13.75% (~521,213 km<sup>2</sup>) and 57.09% (~159,303 km<sup>2</sup>), respectively (Figure 6C, Figure S17). These clusters are predominantly located between latitudes 15°S and 25°S and are characterized by a higher abundance of Chloroflexi (23%–27%). Both clusters are expected to shift southward (Figure 6A). In contrast, three clusters (Clusters 3, 6, and 7) are anticipated to shrink substantially, with area reductions of 36.67%, 26.68%, and 42.77%, respectively (Figure 6C).

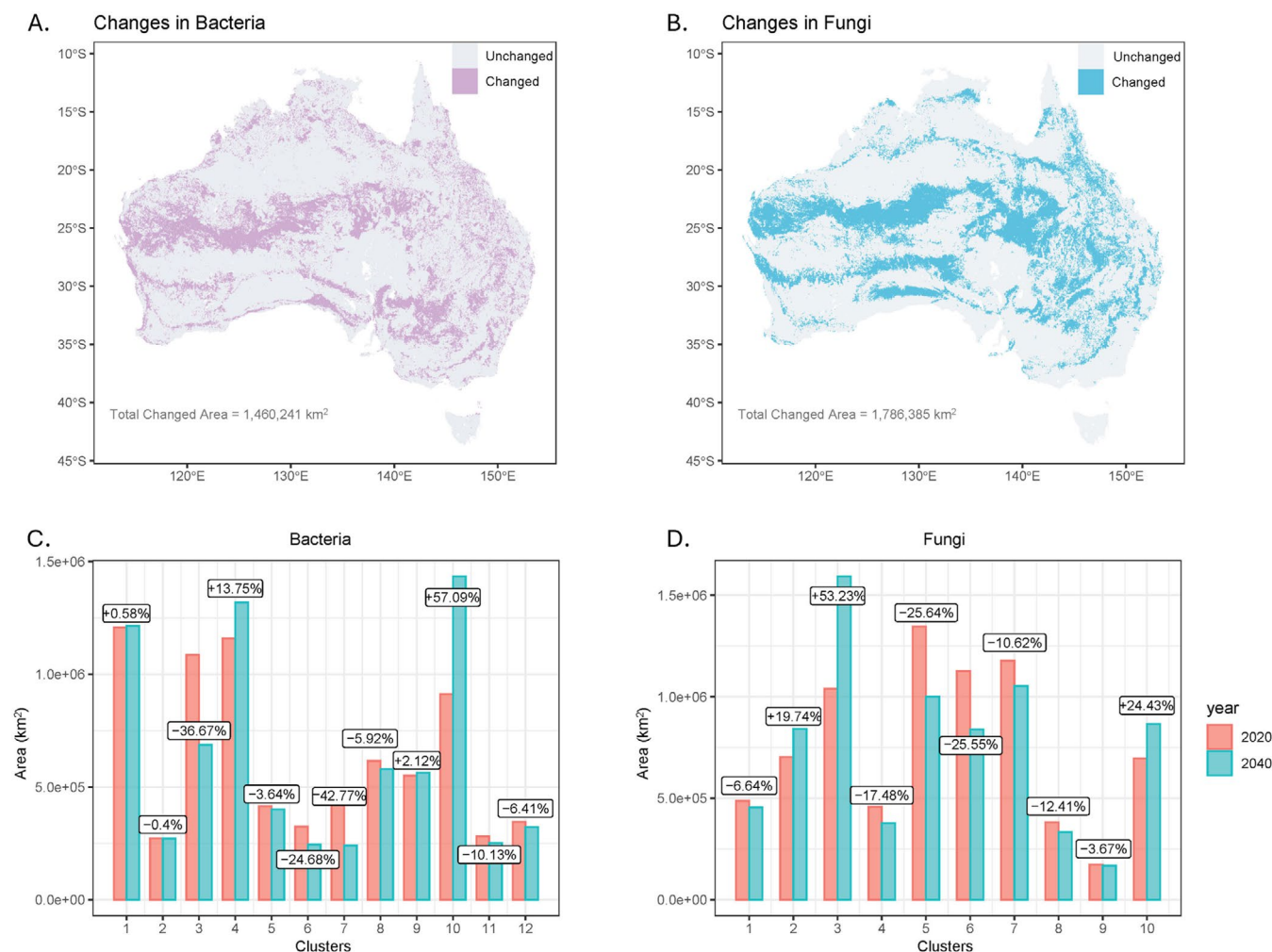
For fungi, three of the 10 clusters (Clusters 2, 3, and 10) are projected to expand significantly, while four clusters (Clusters 4, 5, 6, and 7) are expected to contract (Figure 6D). The areas of Clusters 2, 3, and 10 are predicted to increase by approximately 20%, 53%, and 24%, respectively. In contrast, Clusters 4 through 7 are anticipated to shrink by 10%–25%. The most pronounced expansion is projected for Cluster 3, centered around latitude 20°S, which is dominated by Ascomycota (~47%) and Basidiomycota (~40%). Notably, the greatest spatial changes for both bacteria (Figure 6A) and fungi (Figure 6B) are concentrated around latitude 25°S. Overall, fungal distribution patterns are projected to undergo more substantial shifts than bacterial ones by 2040, suggesting that fungi may be more affected by climate change.

## 4 | Discussion

### 4.1 | Different Responses of Bacteria and Fungi to Environmental Factors

Our data revealed distinct distribution patterns for bacteria and fungi at the continental scale. This divergence reflects the inherent ecological strategies and resistance of these microbial groups to pedoclimatic factors and environmental stresses, such as soil pH and temperature.

The critical role of pH in shaping soil microbial communities has been widely reported at local, regional (Ni et al. 2021; Xue, Minasny, McBratney, Wilson, et al. 2023), and continental scales (Labouyrie et al. 2023). Soil pH influences microbial growth and metabolic activity. Most bacteria have optimal pH ranges for growth and enzyme activity. However, the impact of pH on soil fungi is less pronounced. The differing pH tolerances of bacteria and fungi can be attributed to their distinct cell wall compositions and metabolic activities. Bacteria are encased in a peptidoglycan cell wall, which is susceptible to acidic conditions, making them more sensitive to pH changes (Mueller and Levin 2020). In contrast, fungal cell walls are composed of chitin, providing more resistance across varying pH levels, which may increase fungal tolerance to environmental pH fluctuations (Brown et al. 2020). Moreover, bacteria typically have faster metabolic processes, enabling rapid responses to environmental changes, while fungi, with their more complex cell walls and slower metabolic rates (Lapiere and Richard 2022), exhibit higher tolerance to pH variations. Additionally, the ability of fungi to form mycelium networks enhances their capacity for nutrient absorption, which may help buffer the negative impacts of pH fluctuations (Naranjo-Ortiz and Gabaldón 2020). The predominant role of pH in influencing bacterial community composition but not fungi was also reported by Lauber et al. (2008).



**FIGURE 6** | Changes in clusters from the present to 2040 for bacteria (A) and fungi (B). (C) Area of each cluster and the proportion of change between 2020 and 2040 for bacteria. (D) Area of each cluster and the proportion of change between 2020 and 2040 for fungi. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

The experiment conducted by Rousk et al. (2010) further reported that the composition of the bacterial communities was closely defined by soil pH, while the composition of fungal communities was less affected by pH, with fungal diversity showing only a weak correlation to pH. This finding is consistent with our observation that fungi were less responsive to pH variations than bacteria (Figure S6).

Bacteria and fungi exhibit distinct responses to temperature, with the influence of temperature being more pronounced for fungi than bacteria. This difference can be attributed to their unique physiological and ecological characteristics. Bacteria, known for their rapid growth rates and metabolic versatility, typically display a broader range of temperature adaptability. This might be due to their relatively simple cellular structure and the presence of heat-shock proteins that aid in managing thermal stress (Madigan and Martinko 2006). For example, Frey et al. (2013) reported that bacterial biomass and activity increased significantly with temperature, while fungi exhibited a peak activity at more moderate temperatures. Additionally, a significant shift in fungal community structure was observed in a closed-top greenhouse experiment, with a decreased relative abundance of a Thelephoroid fungus and an increased relative

abundance of Ascomycetes and Zygomycetes in response to warming (Allison and Treseder 2008). Fungi generally exhibit more defined temperature optima, with some species being particularly sensitive to temperature extremes. This heightened sensitivity is partly attributed to their complex cell wall structure and their reliance on specific temperature ranges for optimal enzyme function (Pietikäinen et al. 2005). Thus, temperature regulation was more significant in the biogeography of fungi than bacteria in this continental study.

The different influences on bacteria and fungi were also evident for other factors such as soil texture, EC, P, and precipitation (Figures S7 and S8). For instance, precipitation also contributes to the different biogeography patterns between bacteria and fungi. In the short term, fungi may exhibit higher drought resistance than bacteria due to their ability to redistribute water through mycelial networks (Guhr et al. 2015). However, bacterial communities may recover after rewetting, allowing them to remain conserved at the phylum level over the long term (Barnard et al. 2013).

Generally, we found that soil properties exert a greater influence on soil bacteria; accordingly, bacterial distribution patterns

closely resembled soil class maps. Conversely, climate factors play a more significant role in shaping fungal distributions, aligning them with temperature zones. These distinct responses to environmental factors mean that soil heterogeneity and climate variations shape the community structures of bacteria and fungi differently at the continental scale. This is in contrast with the finding of Labouyrie et al. (2023) in Europe, who reported that soil properties, particularly soil pH, were the most important indicators explaining both bacterial and fungal  $\beta$ -diversity. This discrepancy might be due to the more significant climate variation in Australia.

## 4.2 | The Biogeography of Soil Bacteria Exhibits More Resistance Than Fungi

The 2040 climate projections of Australia show a mean temperature increase of approximately 2°C, with precipitation becoming more variable, shifting from 138–4058 to 85–4145 mm. These changes are expected to have significant impacts on the soil microbiome. Microbial resistance refers to the degree to which microbial composition remains unchanged in response to a disturbance (Allison and Martiny 2008; Hawkes and Keitt 2015). Our results indicate that the composition of soil bacterial communities in 2040 is projected to undergo fewer changes than that of fungi, suggesting that bacterial biogeography is more resistant to climate change than fungal biogeography. This could be attributed to several factors. First, the less significant changes in the bacterial community compared to fungi may be due to the higher richness of bacterial communities in soil habitats (Xue, Minasny, McBratney, Jiang, et al. 2023). The higher diversity indicates a broader tolerance of bacteria to temperature and moisture variations, ensuring wider adaptations under fluctuating climatic conditions. Studies have shown that bacterial communities can maintain functional stability across a broader range of temperatures than fungi (Boer et al. 2005; Pietikäinen et al. 2005). Secondly, bacteria's ability to utilize diverse substrates and rapidly acquire new genetic traits through horizontal gene transfer allows them to adapt quickly to changing environmental conditions. Soil bacteria are known for their metabolic versatility, allowing them to exploit a wide range of substrates and survive in diverse environmental conditions (Arnold et al. 2022; Fierer et al. 2007). In contrast, fungi generally have more specialized ecological niches and relatively slower metabolic rates (Naranjo-Ortiz and Gabaldón 2020), which can limit their adaptability to rapid climate changes. Thirdly, the rapid reproductive rates of bacteria enable them to quickly adjust their population structure and genetic composition in response to environmental changes, enhancing their resistance to climate stressors. Bacteria reproduce asexually through binary fission, leading to rapid population growth and the potential for quick genetic diversification (Lenski and Travisano 1994). This high reproductive rate allows bacterial communities to quickly adapt to new environmental conditions. Fungi, conversely, reproduce both sexually and asexually, but their growth and reproduction rates are generally slower than those of bacteria (Dighton 2018). This slower rate of adaptation can make fungi more vulnerable to climate change. Thus, fungal communities are more sensitive to future climate change than bacteria (Fu et al. 2024).

Under the climate change scenario, a significant southward shift was observed for both bacteria and fungi in 2040. This result indicates that the temperature increase might lead to a general southward movement in the distribution of soil microbial communities. It is worth mentioning that the most significant changes were predicted to be around latitude 25°S (around the tropic of Capricorn). This trend may be attributed to rising temperatures, which are causing the influence of tropical climates to extend further south within Australia. The tropical expansion has been widely reported, and it has widened about 0.5° of latitude per decade since 1979 (Madigan and Martinko 2006). Thus, bacterial and fungal community patterns around latitude 20°S are projected to extend southward to latitude 25°S in 2040, while patterns south of latitude 25°S are expected to shrink accordingly (Figure 4).

Microbes play a crucial role in biogeochemical cycling, with shifts in soil microbial communities directly impacting microbial activities and soil processes. Influenced by climate and land use changes, alterations in microbial communities can, in turn, modify soil properties, creating a feedback loop that intensifies soil changes over time. For example, bacterial and fungal communities in tropical regions are characterized by higher abundance and activity, which leads to a greater turnover rate of soil carbon (Raiesi and Beheshti 2014). Additionally, microbial metabolites and necromass play a crucial role in SOC stabilization and formation (Liang et al. 2019). As bacterial and fungal distributions shift southward, soil carbon stocks in those regions may change. While the exact impact—whether positive or negative—remains uncertain, such changes could, in turn, alter the belowground microbial community. Singh et al. (2010) provided evidence that microbial feedback responses contribute to global warming, such as by increasing CO<sub>2</sub> and CH<sub>4</sub> fluxes. Additionally, shifts in microbial composition could disrupt nitrogen cycling, affecting soil fertility and structure, which, in turn, would influence microbial diversity (Xu et al. 2011). Given the critical role of microbes in sustaining soil functions, it is essential to understand these bidirectional interactions. The distinct changes observed in soil bacteria and fungi suggest potential shifts in microbial functions and soil processes, highlighting the importance of considering microbial dynamics in future agricultural practices and implementing tailored strategies for different microbial groups. To further enhance our understanding and predictive capabilities, future work should focus on developing and refining process-based machine learning models that incorporate microbial dynamics, enabling more accurate forecasts of soil responses to environmental changes and guiding effective soil management practices (Minasny et al. 2024; Sun et al. 2023).

We recognize the limitations and assumptions of our models; in particular, the stable soil properties (pH and SOC) by 2040 might lead to an underestimation of the changes in soil microbial communities, particularly for bacteria. On one hand, we currently lack reliable and comprehensive predictions of soil properties for 2040. On the other hand, changes in soil properties over a 20-year period may be minimal if land use and management practices remain consistent despite climate variations. Soil changes are primarily driven by a combination of climatic factors and human activities, with land use change and land management playing a more prominent role in altering soil

properties (Beillouin et al. 2022; Jang et al. 2023). In this study, we only modelled climate change and assumed constant land management and land use. Although some underestimation may occur, the projections still provide valuable insights.

## 5 | Conclusions

This study investigated the distribution patterns of bacteria and fungi across Australia, discovering that soil bacteria distribution closely aligns with the soil class map, while the fungal distribution is more closely associated with temperature zones. The distinct biogeographic patterns between soil bacteria and fungi can be attributed to their differing responses to environmental factors. This study highlights that bacterial biogeography is primarily influenced by soil properties, especially pH, while fungal biogeography is significantly shaped by climatic factors such as temperature and precipitation. These insights can be integrated into process-based models to enhance their accuracy and specificity in forecasting microbial responses to environmental changes. Projections for 2040 indicate that fungi may undergo more substantial changes due to climate change than bacteria, which appear to be more resistant to such variations. While bacterial community composition was more influenced by soil properties, human influence on soil through land use and management could disrupt the bacterial community. These findings suggest that soil management practices in climatically variable regions should be tailored to enhance microbial functions, focusing on soil amendments for bacteria and climate-adaptive strategies for fungi to maintain ecosystem health and productivity. This study emphasizes the diverse vulnerabilities of soil microbial communities and stresses the need to account for microbial dynamics in future land use and land management practices.

## Author Contributions

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

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## Conflicts of Interest

The authors declare no conflicts of interest.

## Data Availability Statement

The code and data that support the findings of this study are openly available in Zenodo at <https://doi.org/10.5281/zenodo.15428619> and <https://doi.org/10.5281/zenodo.15428651>. The original sequencing data 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.