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Global analysis of soil bacterial genera and diversity in response to pH

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ABSTRACT

Soil pH stands as a decisive factor in shaping bacterial diversity and community composition, yet predicting the pH preferences and traits of individual bacterial taxa is still incomplete. We surveyed 942 samples from seven biomes worldwide to unravel the responses of individual bacterial genus to soil pH. Our findings indicate that soil pH surpasses the influences of spatial and climatic factors (biomes) in affecting bacterial composition and diversity. We observed that a comparable proportion of genera had low pH optima (21%), high pH optima (18%), and neutral pH optima (18%). However, apart from genera with optima groups, only a small percentage of genera were low pH tolerant (0.8%) compared to those that were high pH tolerant (21%). This suggests that a greater number of non-extremophiles genera can tolerate alkaline conditions compared to acidic conditions. Bacterial richness forms unimodal relationship with soil pH, consistently increasing from acidic levels to neutral across all biomes. However, the decline in richness when pH rises beyond neutral was less pronounced. This can be attributed to the higher number of alkaline-tolerant genera compared to acidic-tolerant genera. As expected, genera with acidic optima are more prevalent in humid climates, such as tropical forests, arctic tundra, and boreal forests, whereas genera with alkaline optima are generally dominant in arid grasslands and drylands. Collectively, our results indicate that the probability of existence of at least 75% of genera in specific soil pH conditions can be predicted, irrespective of biome. The identification of the actual niche spaces occupied by individual soil bacterial genera forms the foundation for developing comprehensive hypotheses regarding the response of soil communities to changing soil conditions worldwide.

1. Introduction

A central aim in ecology is to predict the environmental preferences of organisms. Understanding the conditions that allow a particular taxon to thrive enables us to better predict its biogeographical distribution (Delgado-Baquerizo et al., 2018). Bacteria, recognized as the most diverse and widespread organisms on Earth (Hug et al., 2016), actively shape soil biogeochemistry (Falkowski et al., 2008). Their rapid reproduction and adaptability, driven by high rates of mutation and genetic recombination, enable them to thrive in diverse environments (Roszakt and Colwell, 1987). However, this extensive diversity and adaptability present challenges in predicting bacterial community dynamics across spatial and temporal scales.

Soil properties, climate, and biotic factors impact bacterial diversity and community composition (Sul et al., 2013; Yashiro et al., 2016), with soil pH being a primary and consistent influence, explaining more variation than other environmental factors (Lauber et al., 2009; Rousk et al., 2010; Rath et al., 2019; Mod et al., 2021). Different bacterial taxa exhibit distinct pH preferences; for example, Acidobacteriota (synonym Acidobacteria) decreases with increasing soil pH, while Actinomycetota (synonym Actinobacteria) and Bacteroidota (synonym Bacteroidetes) show a positive correlation (Lauber et al., 2009). However, within the Acidobacteriota phylum, responses vary among subgroups, with subgroups 1, 2, and 3 increasing in abundance with soil pH while with subgroups 3, 4, and 6 decrease (Jones et al., 2009; Rousk et al., 2010). This suggests nuanced responses to soil pH within bacterial taxa of the same phylum. Most studies, however, are limited to investigating pH effects at the phylum or subgroup level (Tripathi et al., 2012; Mod et al., 2021). A more straightforward assessment of pH responses was conducted at the operational taxonomic unit (OTU) level (Delgado-Baquerizo et al., 2018; Jones et al., 2021), highlighting the significance of pH on individual taxa. However, to ensure comparability

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with other studies and to achieve a comprehensive understanding of community assembly and its impacts on ecosystem functions, the genus level will be used as the appropriate taxonomic level in the current study.

Bacteria must maintain a stable cytoplasmic pH to ensure the optimal functional and structural integrity of cytoplasmic proteins that essential for growth (Baker-Austin and Dopson, 2007). Some yeast and bacteria maintain a relatively stable and neutral intracellular pH, even with a rapid drop in extracellular pH (Siegumfeldt et al., 2000). The extreme alkaliphile, *Bacillus pseudofirmus* OF4, can respond to a sudden and significant alkaline shift from pH 8.5 to 10.5 (Takami and Krulwich, 2000). Most bacteria that are not extremophiles can grow across a wide range of external pH values (5.5–9.0) while keeping their internal pH within a narrow range (7.4–7.8) (Booth, 1985). Conversely, some bacteria are unable to do this due to their lack of active H+ extrusion or uptake system necessary for pH homeostasis, such as *Caloramator fervidus* (Collins et al., 1994). However, cultivating most microorganisms in vitro is challenging, making it difficult to measure their environmental preferences directly. Even if they can be cultivated, the conditions created in vitro may not accurately reflect those in their natural environments due to interplay of multiple environmental factors. Therefore, direct field data is crucial for predicting microbial distributions across space and time (Delgado-Baquerizo et al., 2018; Jones et al., 2021; Ramoneda et al., 2023).

The impact of soil pH on bacterial richness extends across various terrestrial environments. Acidic and alkaline soils typically exhibit lower bacterial richness compared to near neutral counterparts (Fierer and Jackson, 2006), attributed to growth constraints and metabolic activity limitations for microorganisms involved in processes such as nitrogen, sulphur, and phosphorus (P) mineralization (Robson and Abbott, 1989). Similarly, bacterial richness in alkaline soils may decrease due to reduced solubility of certain nutrients, such as P and Fe (Nautiyal et al., 2000). As a result, microbial richness tends to be highest in neutral soils and lower in acidic and alkaline soils (Fierer and Jackson, 2006; Malard et al., 2019).

Soil pH is subject to influence from regional and local factors, including vegetation (Thomson et al., 2010), soil development stage (Ren et al., 2019), and local temperature and precipitation (i.e., precipitation-evaporation rates) (Slessarev et al., 2016). These factors contribute to the diverse pH conditions observed in soils across different climates. In boreal soils, the presence of coniferous trees (e.g., spruce and pine) and mosses can foster the development of acidic conditions, as coniferous litter tends to be more acidic (Růžek et al., 2021). In tropical forests, the warm and humid conditions intensify plant growth and organic matter decomposition, producing organic acids and causing soil acidification (Fujii, 2014). The heightened nitrification process in tropical areas also contribute to acidity (Binkley and Richter, 1987). Unlike tropical soils, which are assumed to have experienced long-term acidity due to continuous weathering, acidity in boreal and arctic soils, particularly podzol and peat, has developed relatively recently after Pleistocene glaciation (Sanchez and Buol, 1975). As a result, dominant taxa exhibit significant variation across different biomes (Yang et al., 2020). Given the uncertainties and diverse bacterial distribution patterns across biomes, it is crucial to independently examine how bacterial community composition and richness responds to soil pH in these environments.

In this study, we surveyed a global 16S rRNA metabarcoding dataset of 942 samples to determine the optimal pH range for the presence of bacteria taxa at the genus level, aiming to identify patterns that are consistent across different environmental biomes. We categorised genera with either low pH optima, low pH tolerant, high pH optima, high pH tolerant, neutral pH optima, or no trend with soil pH gradient using Huisman-Olff-Fresco (HOF) models and compared their composition within each phylum and across different biomes. HOF models are widely used in hypothetical testing of ecological response shapes of species distribution across environmental gradients (Jansen and Oksanen, 2013). In this study, we distinguish between alkaline/acidic optima and tolerance of bacterial genera. Tolerant genera are distributed across a broad range of pH levels, while genera with distinct optima are specifically adapted to either acidic or alkaline conditions. We note that pH niche used here refers to the realized ecological space occupied by a species and quantified as probability of occurrence based on presence-absence data. Due to interactions with other environmental factors, the pH niche of a given taxon in nature can differ from growth response under controlled conditions. We further assessed bacterial richness and community composition across soil pH levels and biomes; and examined the global distribution of bacterial genera based on pH niche characteristics, providing insights into the global control of soil bacterial diversity by soil pH. Overall, our findings emphasise the role of soil pH in shaping bacterial diversity and global bacterial community composition at the genus level.

2. Materials and methods

2.1. Soil metabarcoding data collection

To investigate the impact of soil pH on bacterial genera distribution, we compiled data from 11 studies comprising 1001 global soil metabarcoding data (screened to 942 samples after rarefaction; Fig. 1A; Table S1). Our inclusion criterion required studies to publish both 16S rRNA barcoding raw sequence data of natural soils and corresponding soil pH information. The data cover studies from the globe scale (n = 236) (Delgado-Baquerizo et al., 2018), and regional scales, including the Arctic regions (n = 192) (Malard et al., 2019), Europe (n = 70) (Sun et al., 2016; Ma et al., 2019), Asia (including Japan (Cho et al., 2019), n = 47; China (Xia et al., 2016), n = 115; Japan and Malaysia (Ito et al., 2017), n = 29), Africa (n = 235) (Cowan et al., 2022), and Canada (n = 77) (Whitman et al., 2019; Zhou et al., 2020). Given the large sample size (n = 810), African data were randomly selected from the overall sample pool (Cowan et al., 2022).

Global data was categorised into distinct biomes using site information provided from cited articles. The classification aligned with the functional classification of world ecosystems (Keith et al., 2022), resulting in seven biomes: arctic tundra, boreal forests, grasslands, drylands, subtropical forests, temperate forests, and tropical forests (Fig. 1A). Adjustments were made to match the new biome system, such as categorizing ‘cold forests’ and ‘boreal’ annotated in Delgado et al. (2018) as boreal forests, and ‘dry grasslands’, ‘dry forests’, and ‘shrublands’ were collectively classified as drylands. An exception was made for the African study lacking ecosystem types (Cowan et al., 2022). The biomes were classified using aridity class and vegetation coverage. The detailed biome information is listed in Table S1.

Detailed information and accession numbers of the raw sequence data are available in Supplementary Material Table S1. Mean annual soil and air temperature, soil moisture and precipitation from 2000 to 2022 were collected and aggregated from the ERA5-Land dataset by using Google Earth Engine (Gorelick et al., 2017). The dataset offers high temporal resolution (hourly) and spatial resolution (0.1°) for multi-environmental variables, making it widely employed in land surface modelling, hydrology, agriculture, and ecology research (Muñoz Sabater, 2019).

2.2. Sequence processing

Amplicons from diverse studies, targeting different 16S rRNA regions (Table S1), were separately analysed using mothur 1.48.0 pipeline following the standard operating procedure (Schloss et al., 2009). In total of 72,844,532 raw reads were obtained from 1001 soil samples. Raw 16S rRNA reads' quality was assessed using FastQC and MultiQC software. Pre-processing involved filtering low-quality reads based on length criteria (V4 region <275 bases; V3–V4 region <475 bases; V1–V3 region <575 bases), ambiguity (removing reads with N and

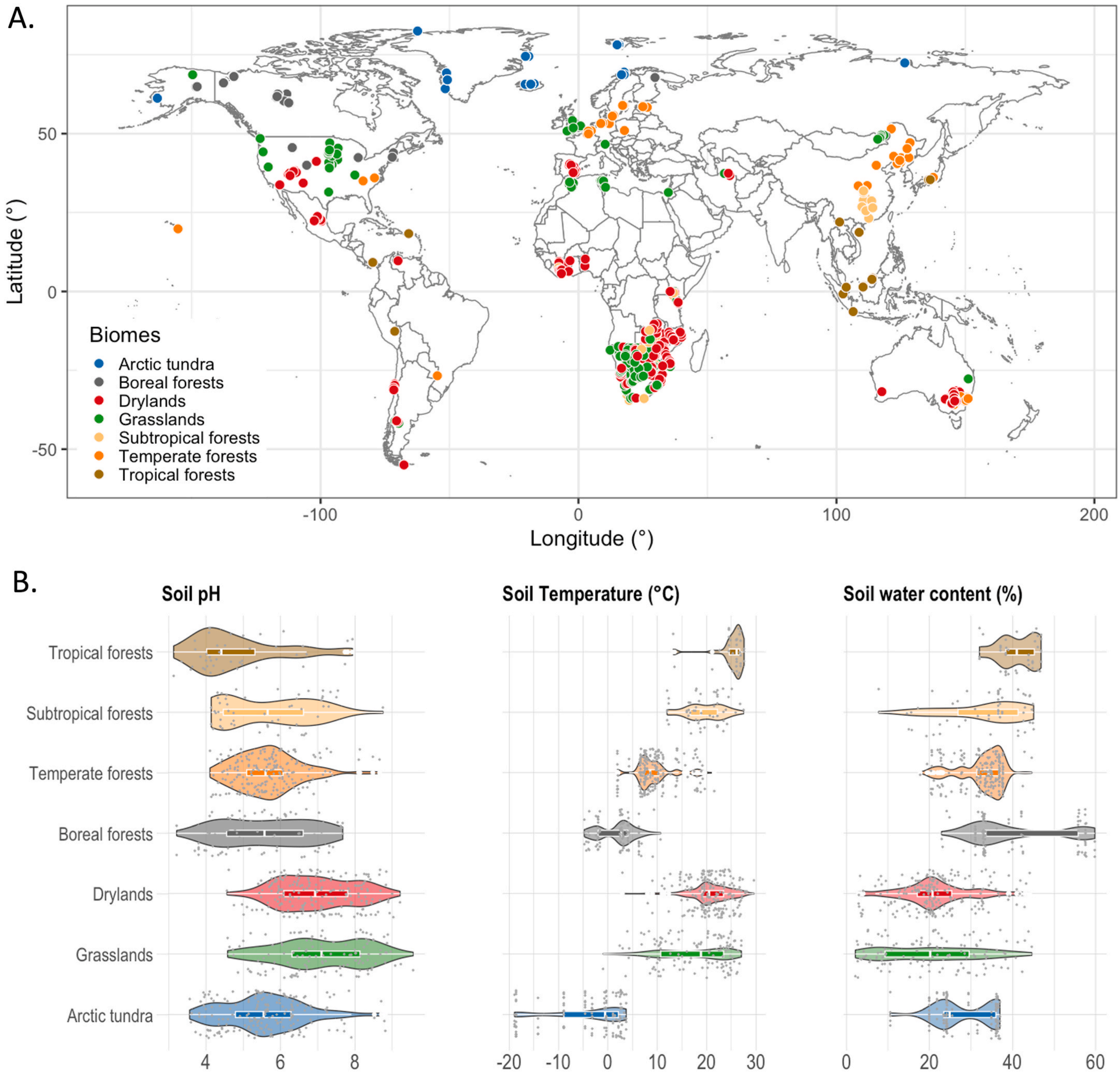

Fig. 1. Sampling sites and biome types of the sampling sites collected from 16S sequencing database. (A) Locations of 942 sites collected from 11 studies across the world, where soil pH and soil bacterial communities were determined. Different colours indicate the biome types categorised based on local environmental conditions. (B) The range of soil pH, annual mean soil temperature and soil water content of each biome.

homopolymers of >8 consecutive bases), and chimeras (PCR errors). Reads were aligned into operational taxonomic units (OTUs) using SILVA database (release 138.1) (Quast et al., 2013) with a 97% similarity threshold. Eukaryotic and archaea classifications, as well as those unclassified at the super kingdom taxonomic rank, were removed from taxonomic profiles. The final sequencing depth, after these steps, ranged from 2000 to 102,006 reads per sample.

The high-quality reads for each sample were rarefied to 3304 reads per sample through random selection to prevent biased community comparisons (Fig. S1). This resulted in 942 (removed 59 from 1001 samples) soil samples for subsequent analyses, comprising a total of 29,137,800 reads.

2.3. Statistical analysis

All statistical analyses were conducted using R Statistical Software (v4.3.2; R Core Team, 2023) OTU counts were uploaded to R and pre-processed using the *phyloseq* package (Callahan et al., 2016). To avoid extremely rare taxa among samples, OTUs present in less than 5% of the total samples per study were removed. Then OTUs from each study were joined into a single phyloseq file, encompassing a total of 83, 230 unique OTUs. These OTUs were then grouped into 969 genera. However, to prevent biased results stemming from extensive scarcity (i.e. excessive zeros), genera not present in at least 1% of all samples were further removed. This led to the retention of 849 genera for the subsequent statistical analyses. As the sequence reads were collected from various studies sequenced with different sequencing regions of 16S rRNA gene and different sequencing depths, the raw OTU counts are not comparable. Instead, the presence-absence (1-0) data and relative abundance of those OTUs were selected for the subsequent analyses below.

Bacterial richness was estimated at both OTU and genus level using the default command in phyloseq package in R. As the difference is minimal, we present bacterial richness at genus level for comparability with the rest of the results. Beta-diversity of bacterial communities of all samples was evaluated using non-metric multidimensional scaling (NMDS) ordination. This analysis, conducted with the ordinate function in the *phyloseq* package in R (Callahan et al., 2016), utilized relative abundance data converted into a Bray-Curtis dissimilarity matrix, three dimensions, and 100 independent runs, allowing visual assessment of differences among different biomes.

The basic HOF models were used to estimate the pH preference of a bacterial genus using presence-absence data collected globally. It predicts the probability of the genus being present along soil pH gradients.

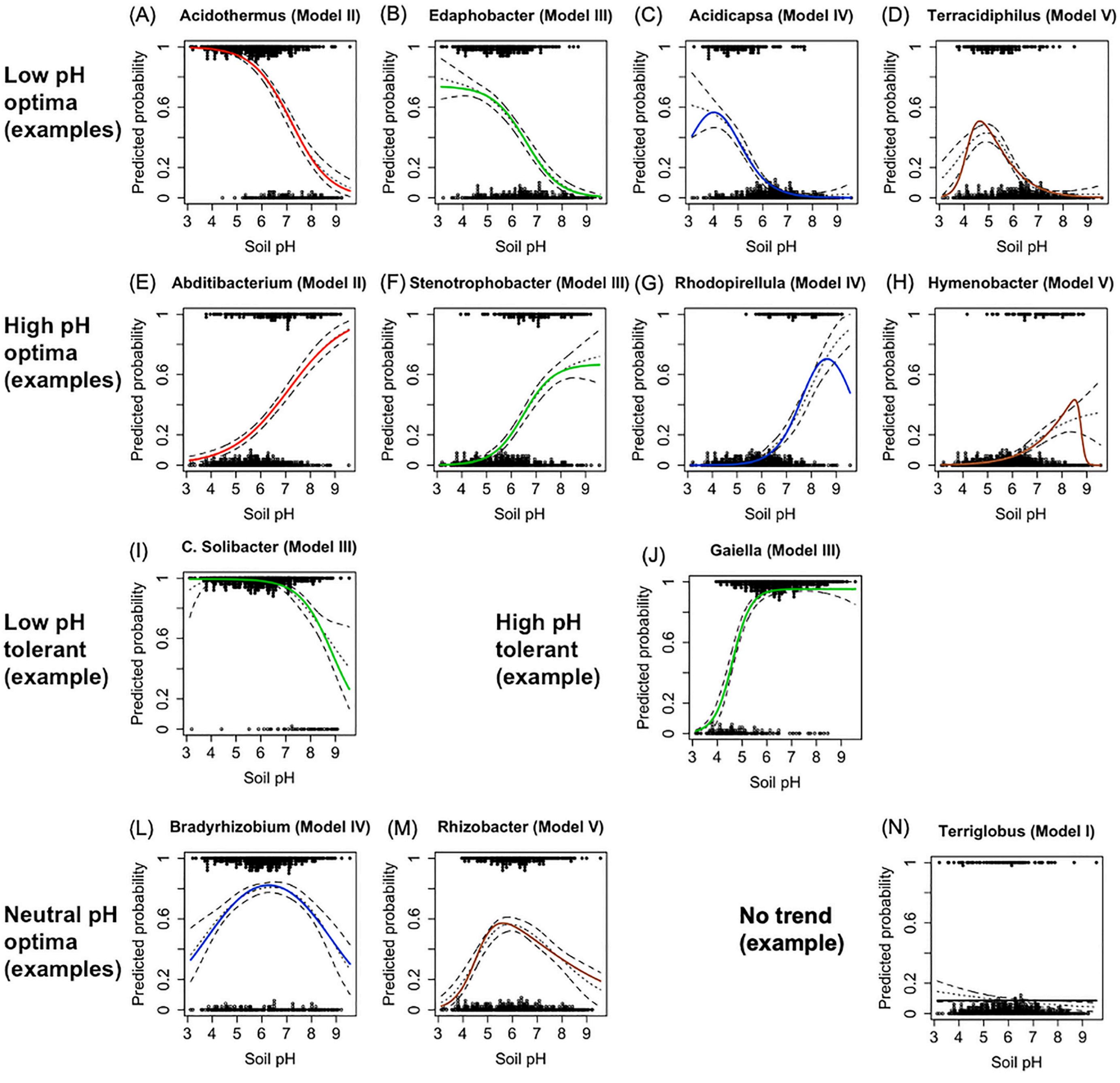

Fig. 2. The pH preference of genera classified using HOF models (type I to V). The HOF-model curves are fitted on binomial data and represent the genus response as probability of occurrence along the pH gradient. Solid lines are response curves fitted using HOF models, including (N) no response (Model I; grey line), (A & E) monotone (Model II, red lines), (B, F, I & J) plateau (Model III, green), (C, G & L) symmetric unimodal (Model IV, blue), and (D, H, and M) skewed unimodal (Model V, brown). Genera fitted with HOF models displaying patterns A-D are classified as having low pH optima, while those with patterns E-H are classified as having high pH optima. Genera with HOF model type III, where pH optima plateau from neutral to acidic (I) and neutral to alkaline (J), are classified as low pH tolerant and high pH tolerant, respectively. Genera with unimodal or skewed patterns and pH optima between 5.5 and 7.5 (L & M) are classified as having neutral pH optima. Genera fitted with Model I are considered to show no trend in relation to soil pH. Dotted lines mark the generalised Additive models (GAM), fitted to the data using cubic regression splines as smoothing basis. Dashed lines define the 95% confidence intervals of these GAM models.

The equations of HOF models are listed in Table S3. Five models were fitted for each genus, and the best models were initially chosen based on Akaike information criterion (AIC) values. The best model was then compared to the null model (Model I) or more parsimonious models using the likelihood ratio test (chi-square distribution). If the p-value was greater than 0.05, the best model was replaced with the more parsimonious one to minimize the risk of overfitting while still adequately explaining the data variability. Parsimonious models that significantly differed from the null model ($p < 0.0001$) were selected for further classification. Models that did not significantly differ from the null model ($p > 0.0001$) were considered to show no trend. Here, a p-value threshold of <0.0001 is chosen to uphold stringent statistical significance amidst the large dataset of the current study. This approach guards against overfitting by ensuring only highly robust relationships are deemed significant, thus prioritizing meaningful results over potentially false relationships (Type I error).

The HOF models fitting to example genera that classified to six pH preference groups are shown in Fig. 2. Genera with parsimonious models of Model II-V with $b > 0$ (only applies to Model II-III; see Tables S2 and S3) and with optima pH (or maximum optima pH) < 5.5 were classified as having low pH optima (e.g. Fig. 2A–D), while those with $b < 0$ and with optima pH (or minimum optima pH) > 7.5 were classified as having high pH optima (e.g. Fig. 2E–H). Genera fitted using Model III with maximum optima pH > 5.5 are classified as low pH tolerant (Fig. 2I), while those fitted with Model III with minimum optima pH < 7.5 are classified as high pH tolerant (Fig. 2J). Genera with unimodal/skewed models (Model IV and V) with pH optima between 5.5 and 7.5 were classified as having neutral pH optima (e.g. Fig. 2L and M). Genera fitted with Model I that showed no specific trend with soil pH were classified as no trend group (Fig. 2N).

2.4. Mapping

The global distribution of genera with low pH optima/tolerant, high pH optima/tolerant, neutral pH optima, and no trend with soil pH was generated utilizing freely available layers. Representative points were thoroughly selected for a comprehensive perspective. Zoomed maps were specifically tailored for North America, Europe, Africa, Asia, and Australia and were shown in Fig. S3. The predictive distribution map for pH measured in water was obtained from the global digital soil mapping products SoilGrids (version 2.0) (Poggio et al., 2021), powered by ISRIC using the Web Map Service server (WMS). The maps were created using Esri (2023) ArcGIS Pro [3.1.0] from Redlands, CA: Environmental Systems Research Institute.

3. Results

3.1. Soil and climatic gradients in bacterial distributions across the globe

Overall, 942 samples spanning a pH range from 3.1 to 9.6 were retained for the downstream analysis (Fig. 1A). Mean annual air temperature (°C), precipitation (mm), soil temperature (°C), and soil water content (%) from 2000 to 2022 were collected based on provided site coordinates. The collected sites were categorised into seven biomes based on climate information and vegetation types provided in cited articles. Arctic tundra had relatively low annual soil temperature (−20 to 5 °C) and high soil water contents (10–40%) compared with grasslands and drylands (Fig. 1B). Among forest ecosystems, the annual temperature of boreal forests (−5 to 10 °C), temperate forests (0–20 °C), subtropical forests (12–28 °C), and tropical forests (20–30 °C) ranked from low to high (Fig. 1B). Soil moisture was highest in boreal forests (20–60%), followed by temperate forests (20–40%), subtropical forests (15–45%), and tropical forests (30–45%; Fig. 1B).

Each biome exhibited a wide range of soil pH (Fig. 1B). In arctic tundra, soil pH ranged from 3.5 to 8.5 with a median pH around 5.5, while in grasslands and drylands, it ranged from 4.5 to over 9 with a median pH around 7. The median pH in boreal forests, temperate forests, subtropical forests was all around 5.5, whilst in tropical forests it was around 4.5 (Fig. 1B).

3.2. Dominance and ubiquity of bacterial genera across the globe

Aligned with SILVA database, taxonomic assignment of the global dataset revealed 37 bacterial phyla and 849 genera. Based on the average relative abundance of each phylum, the 37 phyla were separated into major [>5%, Pseudomonadota (synonym Proteobacteria), Actinobacteriota, Acidobacteriota, Verrucomicrobiota, Planctomycetota, Chloroflexota (synonym Chloroflexi), and Bacteroidota)], medium (<5% and >0.5%, Myxococcota, Bacillota (synonym Firmicutes), Gemmatimonadota, etc.), minor (<0.5% and >0.01%), and rare phyla (<0.01%, Fig. S2A)]. All major phyla were present in over 99% of all sites, with average relative abundances ranging from 5% to 24%. Medium phyla, despite the lower abundance (0.5%–2%) covered over 60%–99% of all sites (Fig. S2A). Although minor phyla had low abundances (<0.05%), most phyla were found in over 25% of all sites (Fig. S2A). Rare phyla were neither abundant nor ubiquitous across all sites (Fig. S2A).

Out of the 849 detected genera, 193 genera exhibited an average relative abundance greater than 0.1% (Fig. S2; unclassified genera were not shown). These 193 genera span 26 phyla. The most abundant genus was *Candidatus* Udaeobacter (Verrucomicrobiota), with an average relative abundance of 5.4%, following with *RB41* (4.0%, Acidobacteriota), *Acidothermus* (3.1%, Actinobacteriota), and *Bryobacter* (2.1%, Acidobacteriota) (Fig. S2B).

The prevalence of these genera varied from 18% (*Geobacter*) to 99% (*Bryobacter*) across all sites (Fig. S2B). The top five prevalent genera, which were found in over 95% of all sites, included *Bryobacter* (Acidobacteriota), *Chthoniobacter* and *Candidatus* Udaeobacter (Verrucomicrobiota), *Haliangium* (Mycococcota), and *Acidibacter* (Pseudomonadota). Their mean relative abundance ranged from 0.7% to 4.8%, highlighting that the most ubiquitous genera are not necessarily the most abundant across the globe (Fig. S2B).

3.3. Bacterial genera in response to soil pH

Based on the response of genera (presence/absence data) to soil pH, determined through HOF models with a binomial distribution, all genera were classified into six groups: low pH optima (Fig. 2A–D), low pH tolerant (Fig. 2I), high pH optima (Fig. 2E–H), high pH tolerant (Fig. 2J), neutral pH optima (Fig. 2L and M), and genera showed no trend with soil pH (Fig. 2N). The differences between optima and tolerant groups depend on the range of their pH preferences. A genus that can persist across a wide pH range, from neutral to highly acidic or highly alkaline, is considered tolerant of low or high pH. However, a genus that thrives only in acidic ($pH < 5.5$) or alkaline ($pH > 7.5$) conditions is considered to have low pH or high pH optima.

Out of the 849 genera, 181 (21%) were classified as having low pH optima, and 7 (0.8%) as having low pH tolerant (Table 1). In contrast, 134 genera (18%) were identified as having high pH optima, and 177 (21%) as having high pH tolerant. Neutral pH optima were found in 150 genera (18%). Additionally, 200 genera (26%) showed no trend with soil pH (Table 1).

Among low pH optima, Acidobacteriota had highest average relative abundance at approximately 5.5%, followed by Actinobacteriota (3.8%), Gammaproteobacteria (3.6%) and Alphaproteobacteria (3.2%). Verrucomicrobiota constituted 2.4%, Chloroflexota 1.5%, Planctomycetota (1.1%) and Bacteroidota <1% (Fig. 3A). At the genus level, prominent representatives having low pH optima included *Acidothermus* (2.8%), Acidibacter (1%), *Candidatus* Xiphinematobacter (*C.* Xiphinematobacter; 0.9%), *Roseiarcus* (0.6%) *Granulicella* (0.6%), *Burkholderia* (0.6%), and Puia (0.5%) (Fig. 3A).

Among high pH optima, Actinobacteriota had the highest abundance

Table 1

Percentage and criteria of 849 genera classified to different pH preference groups based on HOF model results.

pH preferences	Model fit	Criteria	Percentage of global survey genera
Low pH optima	Model II - V	b > 0; $p < 0.0001$; $pH_{opt} < 5.5$	21 %
Low pH tolerant	Model III	pH_{opt}: pH_{min} to pH > 5.5	0.8 %
High pH optima	Model II - V	b < 0; $p < 0.0001$; $pH_{opt} > 7.5$	18 %
High pH tolerant	Model III	pH_{opt}: pH < 7.5 to pH_{max}	21 %
Neutral pH optima	Model IV & V	$5.5 < pH_{opt} < 7.5$	18 %
No trend	Model I	No trend	24 %

Each genus was fitted to one of the five HOF model types in response to soil pH. The criteria labels are based on equation listed in Table S3 in supplementary materials. pH_{min} in current study is 3.13 and pH_{max} is 9.49.

(6%), followed by Bacteroidota (1.3%), Alphaproteobacteria (1.2%), Bacillota (0.6%), and Chloroflexota (0.6%) (Fig. 3B). At the genus level, the most abundant genus having high pH optima was *Rubrobacter* (Actinobacteriota), representing approximately 1.3% of the total. This was followed by *Flavisolibacter* (0.7%), *Bacillus* (0.5%), and *Geodermatophilus* (0.4%) (Fig. 3B).

Among phyla having neutral pH optima, Alpha- and Gammaproteobacteria were the most prevalent phyla, constituting 2.3% and 2.2% of the total, respectively. Following Pseudomonadota, Actinobacteriota accounted for 1.8%, Acidobacteriota 1.5%, Bacteroidota 1.4%, and Planctomycetota 0.6%. At the genus level, *Bradyrhizobium* (0.7%, Acidobactiota) was the most abundant genus among genera with neutral pH optima (Fig. 3C).

When comparing the number of genera within different pH preference groups across each phylum, we anticipated that most genera would prefer neutral pH conditions, but this was not the case. We found that only a few phyla consistently exhibit a specific pH preference. Most phyla contain genera with either, acidic, alkaline, or neutral pH optima

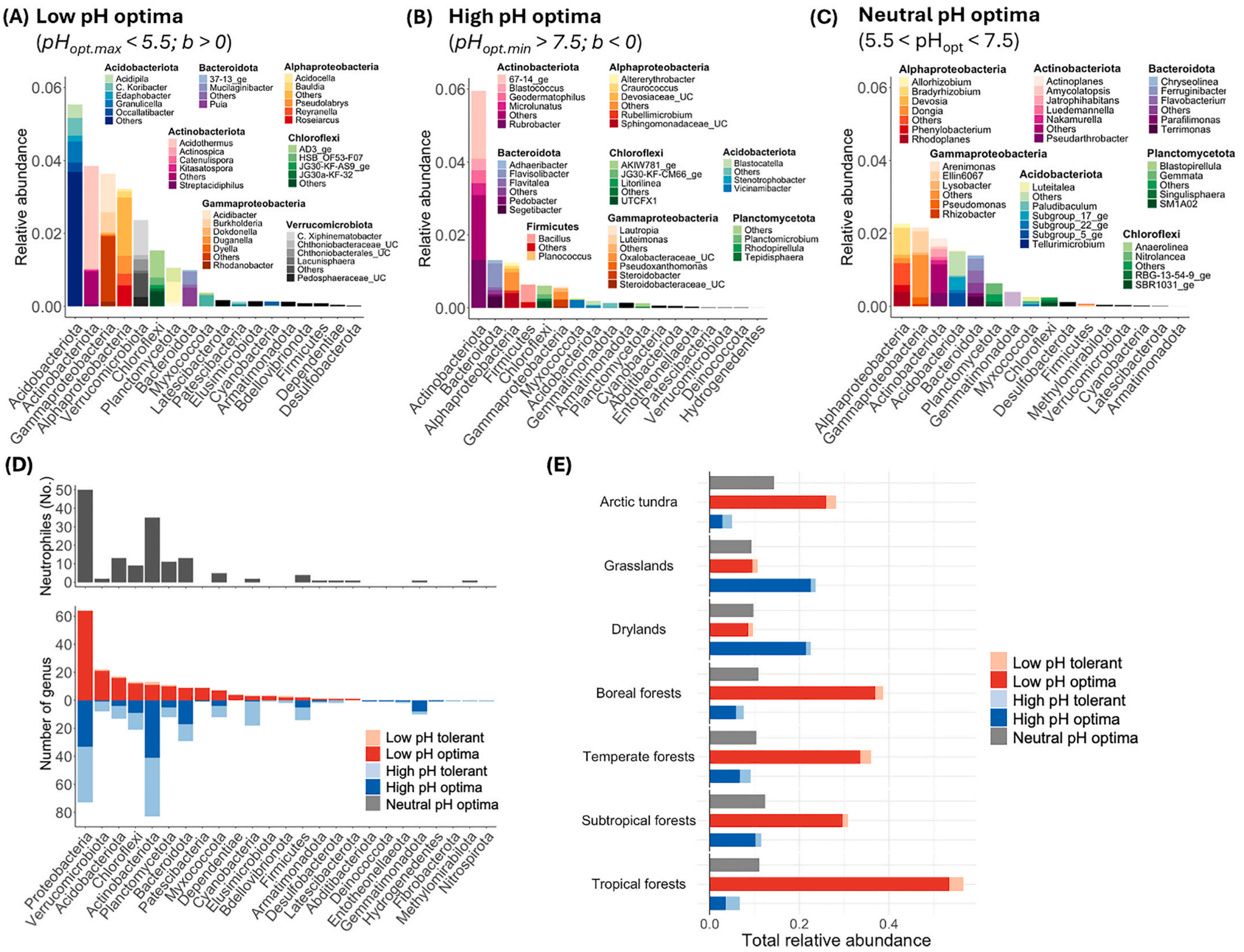

Fig. 3. Average relative abundance of genera with low pH optima, high pH optima, and neutral pH optima within each phylum (A–C) and within each biome (E), as well as the number of genera classified to each phylum (D). The relative abundance of genera with low pH optima (A), high pH optima (B), and neutral pH optima (C) that classified using HOF models are shown in stacked barchart. Details on the classification of genera within different pH preference groups are listed in Table S3. Briefly, genera fitted with models II -V with optima pH < 5.5 were classified as low pH optima, while those with optima pH > 7.5 were classified as high pH optima. Genera with optima between 5.5 and 7.5 were classified as neutral pH optima. Two hundred genera exhibited no response with soil pH (model I, data not shown). (D) Number of genera with low pH optima/tolerant (red/pink), high pH optima/tolerant (blue/light blue), and neutral pH optima (grey) within each phylum. (E) Comparison of total relative abundance of low pH optima/tolerant, high pH optima/tolerant, and neutral pH optima across different biomes. Note: In the main text, the phyla Proteobacteria and Firmicutes are referred to by their synonyms, Pseudomonadota and Bacillota, respectively.

(Fig. 3D). For example, most genera in Verrucomicrobiota, Patescibacteria, and Dependentiae have low pH optima, while more than half of the genera in Actinobacteriota, Bacteroidota, Cyanobacteria, Bacillota, and Gemmatimonadota prefer or have a high tolerance for high pH. In contrast, Pseudomonadota has a roughly equal number of genera with low pH optima/tolerance, neutral pH optima, and high pH optima/tolerance. Although Acidobacteriota has many genera with low pH optima, it also contains many genera preferring neutral pH and alkaline conditions (Fig. 3D).

When comparing the relative abundances of genera with high or low pH optima/tolerant across different biomes, we found that tropical, boreal, temperate, and subtropical forests, as well as arctic tundra had significantly higher abundance of genera with low pH optima compared to those with high pH optima. In contrast, grasslands and drylands show quite the opposite, with significantly higher abundance of genera preferring high pH conditions (Fig. 3E). Across all biomes, the relative abundance of genera with neutral pH optima was consistent. Notably, soils in grasslands and drylands have higher pH than soils in other biomes, while soils in tropical forests exhibit lower pH ranges (Fig. 1B).

3.4. Alpha- and beta-diversities of bacterial communities along soil pH

Bacterial richness estimated at the genus level exhibit a positive correlation with soil pH on a global scale, plateaued at pH around 6.5 (Fig. 4A). When examining correlations within individual biomes, most relationships showed a unimodal pattern, peaking in soils with near-neutral pH and experiencing a slight decline, roughly 20% lower than the peak richness, under alkaline conditions (Fig. 4A). An exception was observed in tropical forest, where bacterial richness decreased under alkaline conditions to a level comparable to that under acidic conditions. In grasslands and drylands, bacterial richness also showed a unimodal relationship with soil pH, but the decline in richness at pH levels above 6 was not pronounced (Fig. 4A). In temperate and subtropical forests, however, bacterial richness plateaued when soil pH exceeded 6.5 (Fig. 4A).

To explore the reason behind the varying responses of bacterial richness to soil pH across different biomes, we examined the richness between different pH preference groups under near-neutral conditions (pH between 5.5 and 7.5) within each biome, and how this composition changed as pH levels shifted. When comparing genera at near-neutral conditions across different biomes, the Arctic tundra, boreal forests,

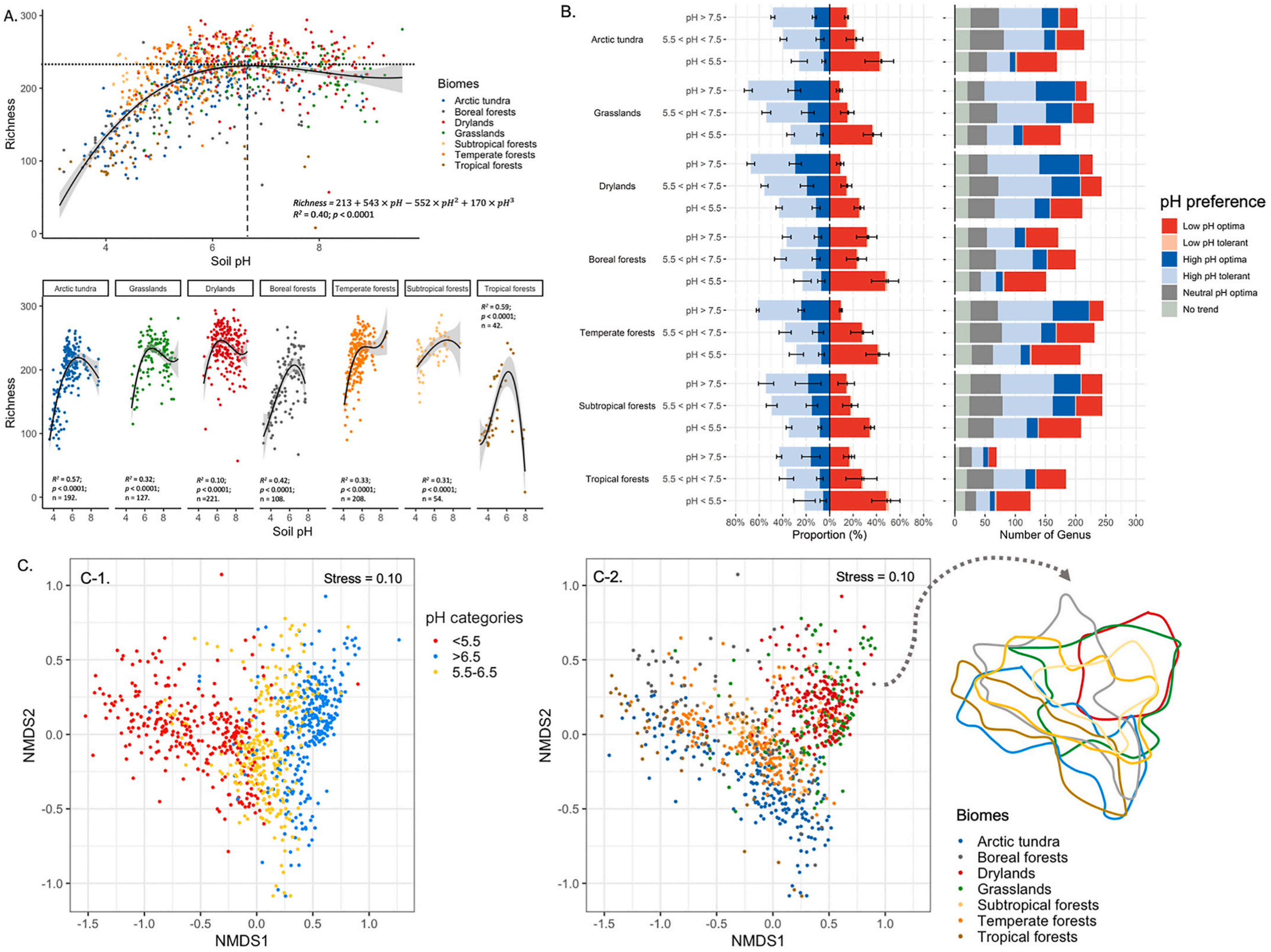

Fig. 4. Alpha- and beta-diversity of bacterial communities across soil pH levels and biomes. (A) Relationships between bacterial richness and soil pH at global scale (upper) and across biomes (below). Bacterial richness is defined as the number of unique genera. Different colours represent diverse biome types. (B) The proportion or the number of genera with low pH optima/tolerant, high pH optima/tolerant, neutral pH optima, and genera showing no trend with soil pH across different biomes; and (C) Non-metric multidimensional scaling (NMDS) ordination plots with Bray-Curtis dissimilarities for bacterial communities at genus level. Samples were coloured based on pH categories (left) and biome types (right). Circles with different colours roughly represent the bacterial communities from different biomes.

temperate forests, and tropical forests contained over three times more genera with acidic optima than those with alkaline optima. In contrast, grasslands, drylands, and subtropical forests contains similar proportion of genera with alkaline optima than with acidic optima (Fig. 4B).

Interestingly, only a few genera are classified as acidic tolerant (Fig. 3D, Table S2), preferring optimal pH ranging from pH > 5.5 down to very acidic soils (Fig. 2I). In contrast, many genera are classified as alkaline tolerant Fig. 3D, Table S2), favoring optimal pH ranging from <7.5 up to very alkaline soils (Fig. 2J). The prevalence of alkaline-tolerant genera across all biomes was notably higher, exceeding two to three times the proportion of genera with alkaline optima (Fig. 4B). This disparity elucidates the pronounced reduction in bacterial richness observed in acidic soils, contrasting with the relatively modest decrease observed in alkaline soils.

NMDS ordinations, conducted using Bray-Curtis dissimilarities, unveiled variations of bacterial community structure among samples with diverse soil pH levels (Figs. 4C–1). However, distinctions among samples from different biomes were not readily apparent (Figs. 4C–2). Although bacterial communities in drylands and grasslands were separated from other biomes, there was no clear separation between boreal forests, temperate forests, and tropical forests (Figs. 4C–2). Notably, drylands and grasslands predominantly featured alkaline soils compared to other biomes (Fig. 1B). This emphasises that bacterial communities exhibit clearer separation based on pH levels rather than biome distinctions.

A higher proportion of genera with acidic optima was found in Northern Europe, along the coast of Greenland, Alaska and Northern America, and South-eastern Asia (Fig. 5). In contrast, the genera with alkaline optima and alkaline tolerant were more prevalent in arid regions, including Southern America, Southern Europe, Africa, Mid-east Asia, and Australia (Fig. 5).

4. Discussion

Our research provides a comprehensive global perspective on how bacterial richness and community compositions at the genus level differ in response to soil pH across different biomes. We identified a comparable number of genera favouring alkaline soils (18%) compared to those favouring acidic soils (21%), with approximately 18% of genera favouring neutral pH. However, a significantly greater number of genera was classified as alkaline-tolerant (21%) compared to those classified as acidic-tolerant (0.8%). Here, we distinguish alkaline/acidic optima from tolerance because tolerant genera survive across a broader pH range, unlike optima groups adapted specifically to acidic or alkaline conditions. Bacterial richness consistently increased with pH from acidic (around pH 4) to neutral (pH 6–7) across all biomes, but the decrease in richness was much less pronounced as soil pH continued to rise. This can be attributed to the greater number of alkaline-tolerant genera compared to acidic-tolerant genera (Fig. 4B), leading to a smaller decline in richness as soil pH increases to alkaline levels (Fig. 4A). Most genera in Verrucomicrobiota, Acidobacteriota, and Patescibacteria

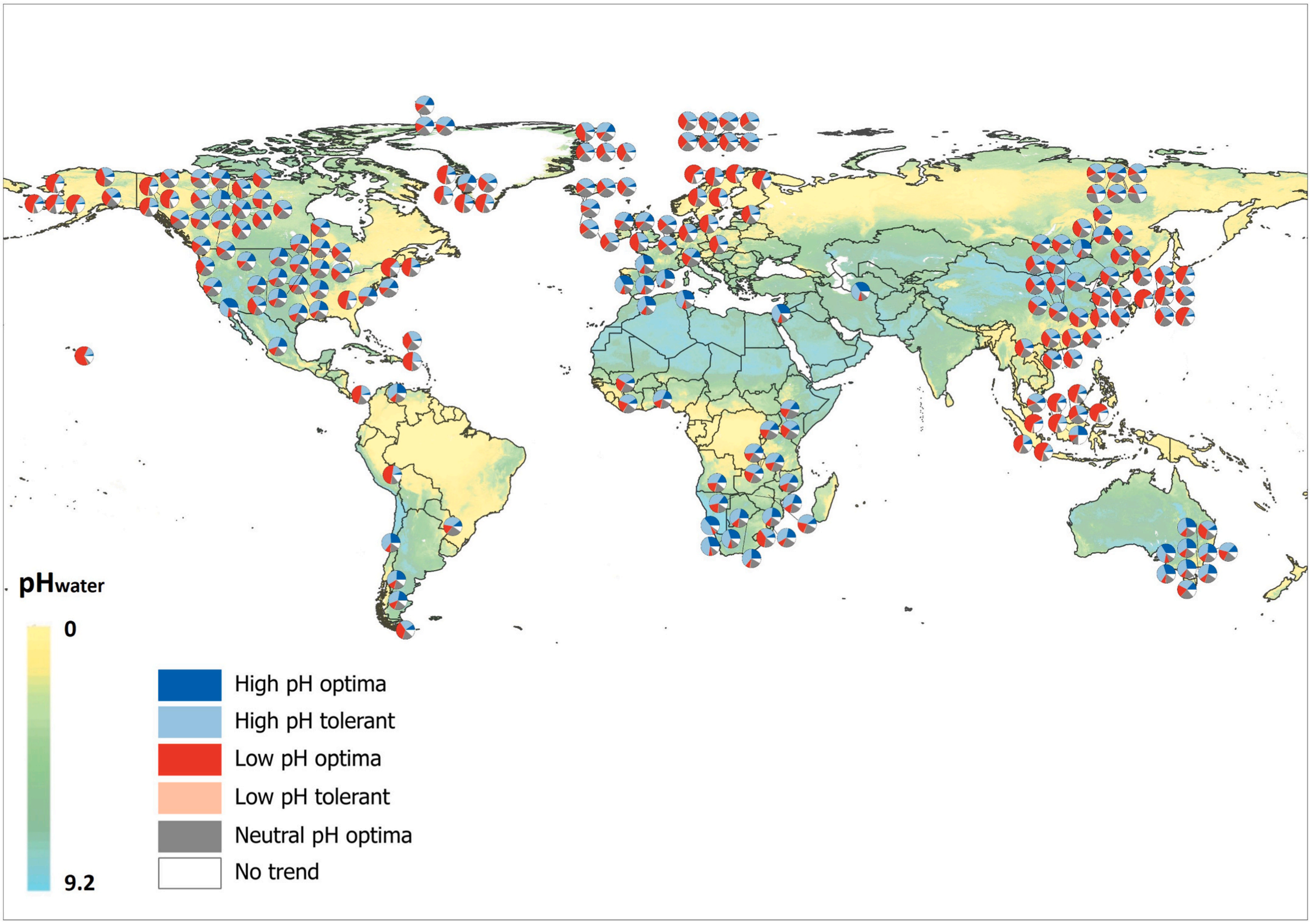

Fig. 5. The global distribution of genera with different pH preferences. Representative sites were selected to provide a more comprehensive view. Genera with low pH optima and tolerant are represented as red and pink, respectively, and genera with high pH optima and tolerant are as blue and light blue. Genera with neutral pH optima are in grey and genera showing no trend with soil pH are leave as empty (white). The base map is coloured by soil pH data predicted by Poggio et al. (2021). Detailed map with all sites is shown in Fig. S3.

exhibited low pH optima, while most genera in Actinobacteriota, Bacillota, and Gemmatimonadota had high pH optima (Fig. 3D). Among different biomes, genera with low pH optima were much more abundant were prominent in wetter climates like arctic tundra, boreal forests, and tropical forests (Figs. 3E and 5). In contrast, genera with high pH optima were more abundant in arid environments like grasslands and drylands (Fig. 3E).

In this study, despite finding a comparable number of genera having acidic and alkaline niche optima, genera that can tolerate high pH were significantly outnumbered by those that can tolerate low pH (21% versus 0.8%; Table 1). This prompts the question of whether acidic pH poses greater challenges to bacteria than alkaline pH. Bacteria maintain intracellular pH within a narrow range around neutral, regardless of external pH (Slonczewski et al., 2009). They employ various mechanisms, such as cation flux, metabolic acids/bases, and less permeable cell membranes, to regulate intracellular pH (Booth, 1985). While conclusive evidence on whether bacteria struggle more with acidic conditions than alkaline conditions is lacking, studies indicate that acidic conditions can have more damaging effects on cell membranes, enzymes, and DNA than alkaline conditions (Cotter and Hill, 2003; Chu-Ky et al., 2005). This aligns with the widespread use of weak acid environments in food preservation to prevent microbial spoilage (Beales, 2004). In contrast, the impact of alkaline pH on bacterial growth is primarily related to nutrient availability, as essential nutrients become less soluble at high pH values (Bolan et al., 2011). Consistent with our results, bacterial species that tolerate alkaline conditions often thrive in a broader pH range, covering both neutral and alkaline conditions (Horikoshi, 2004). However, most genera preferring acidic soils cover only a narrow pH range, suggesting they have strategies specifically for coping with acidic conditions rather than neutral or high pH conditions.

Acidobacteriota, Pseudomonadota, Actinobacteriota, Verrucomicrobiota, Bacteroidota, and Chloroflexota consistently emerged as the most abundant phyla (Fig. S2A), aligning with previous findings on soil microbial communities (Janssen, 2006). Acidobacteriota notably showed heightened abundance among genera with low pH optima (Figs. 3A–1), in line with the common association of Acidobacteriota with acidic soils (Lauber et al., 2008; Rousk et al., 2010). However, the relative abundance of Acidobacteriota among neutral pH optima is also high (Fig. 3C), which again confirming the assumption that Acidobacteriota is not always predominant in acidic soils (Jones et al., 2009; Rousk et al., 2010; Naether et al., 2012). Compared to Acidobacteriota, Verrucomicrobiota and Patescibacteria contain a majority of genera with low pH optima, thus more accurately representing low pH preferences (Fig. 3D). In contrast, most genera in Actinobacteriota, Bacteroidetes, and Bacillota are high pH optima or tolerant (Fig. 3D), explaining the consistent increasing trend of these phyla with soil pH (Lauber et al., 2009; Rousk et al., 2010).

Among the genera with high pH optima, *Blastocatella* prefer high pH (Fig. 3B), but its optimal growth occurs at pH 6–6.5 under culture (Foesel et al., 2013). The pH optima for *Aridibacter*, ranging between 7 and 9 as determined in the current study (Table S2), does not align with its optimal growth conditions in culture, recorded at pH 6.5–7 (Huber et al., 2014). Previous studies have shown that *Rubrobacter*, *Sphingomonas*, *Microvirga*, and *Solirubrobacter* are more abundant in high pH soils (Chen et al., 2019), consistent with their classification to high pH optima/tolerant identified in current study (Fig. 3B and Table S3). Consistent with genera classified as with low pH optima (Fig. 3A; Table S2), *Edaphobacter*, *Granulicella*, *Occallatibacter*, and *Acidothermus* were also found to grow between pH 3.4 to 7.0 in culture conditions (Mohagheghi et al., 1986; Foesel et al., 2016; Belova et al., 2018; Oshkin et al., 2019). *Candidatus* Udaeobacter showed a preference for acidic pH (Fig. 3A; Table S2), with its abundance peaking at pH 4.7–5.2 (Willms et al., 2021). Conversely, field data from the current study show that *C.* Udaeobacter has a broad pH optimum ranging from 4.5 to 9 (Table S2). It demonstrates its extensive tolerance to soil pH, particularly to alkaline levels. These varying results from culture experiments and field sampling further suggest that the pH tolerance of one species can vary due to interactions with other factors in natural environments.

Bacterial richness and differences in community composition across the globe consistently highlight soil pH as the primary factor influencing bacterial community composition (Fig. 4C). Within each biome, bacterial richness exhibited a consistent increase with soil pH when pH is below 7 and decreased when pH continues to rise (Fig. 4A), aligning seamlessly with previous findings (Fierer and Jackson, 2006). However, the pattern of this decrease varied between biomes. To understand this variation, we compared the pH preferences of bacterial genera across biomes at near-neutral conditions. In tropical, boreal, and temperate forests, as well as arctic tundra, the proportion of genera with acidic optima were nearly three times more than those with alkaline optima (Fig. 4B). In contrast, in grasslands and drylands, the proportion of genera with alkaline optima was similar to those with acidic optima (Fig. 4B). These distinct compositions at near-neutral pH suggest that soils with more genera having acidic optima are more sensitive to alkaline conditions, while soils with more genera having alkaline optima are more sensitive to acidic conditions (Fig. 4A). This also explains the clear decreasing pattern of richness at pH > 7 in Arctic tundra, boreal forests, and tropical forests ($R^2 > 0.42$). In grasslands and drylands, where soils contained more genera having alkaline optima and alkaline tolerant, the changes of richness are less pronounced ($R^2 < 0.32$; Figs. 5A–2). Moreover, the higher number of genera tolerant to high pH compared to those tolerant to low pH (Table 1, Fig. 4B) suggests that bacterial richness overall exhibits less sensitivity to alkaline soils compared to acidic soils.

Patterns from tropical forests and drylands indicate that changes in bacterial richness are driven by the pH preference of genera specific to each biome. In tropical forests, bacterial richness plummets at both highly alkaline and highly acidic soils (Fig. 4A). This is due to the predominant adaptation of species to acidic soils in tropical forests, resulting in a higher proportion of genera with low pH optima (Figs. 3E and 4B). Consequently, even a small increase in pH reduces the number of species that prefer low pH conditions, leading to decreased richness in alkaline soils. However, we should note that subtropical and tropical forests had lower sampling sizes than other biomes, warranting caution in interpreting findings from these regions. In contrast, bacterial richness in drylands exhibited slight changes with soil pH ($R^2 = 0.1$; Fig. 4A), as most genera in drylands were with alkaline optima or alkaline tolerant compared to those in other biomes (Fig. 4B). This parallels a global observation in drylands, where bacterial diversity appears unaffected by soil pH (Maestre et al., 2015). These observations may link to the alkaline nature of arid areas, as drylands typically accumulate alkalinity in the soil when there is insufficient water flow, leading to soluble salt leaching (Slessarev et al., 2016). The adaptability of many genera to alkaline environments suggests that the rise in soil pH above 7 may exert a diminished impact on bacterial richness. When aggregating the global data, bacterial richness displayed an increase with soil pH with a plateau around 6.5 (Fig. 4A). In contrast to the unimodal trends observed within individual biomes, this result underscores that diverse patterns of bacterial richness in response to soil pH in alkaline conditions can become blurred when data from different biomes are combined.

Previous studies on other phyla have failed to demonstrate consistent patterns with soil pH. For example, Alphaproteobacteria exhibited a negative correlation, while Beta-, Gamma-, and Delta-proteobacteria showed a positive correlation with soil pH in some studies (Rousk et al., 2010; Shen et al., 2013), while Lauber et al. (2008) observed no relationship. However, our results showed that both Alphaproteobacteria and Gammaproteobacteria had a higher relative abundance of genera having low pH optima compared to those with high pH optima (Fig. 3A and B), not to mention the high abundance of genera with neutral pH optima (Fig. 3C). The number of genera in Pseudomonadota with acidic optima/tolerant, alkaline optima/tolerant, and neutral pH optima were relatively similar (Fig. 3D). Acidobacteria displayed a similar case, with most genera having low pH optima, but also including genera that prefer neutral or high pH optima. This indicates that analysing pH preference at the phylum level is not accurate, which has led other studies to seek method for determining taxa pH preference using functional gene approaches (Ramoneda et al., 2023). Despite this, genera within some phyla showed relative consistency. For example, in Verrucomicrobiota, most genera had low pH optima and were much more abundant than those with high or neutral pH optima (Fig. 3A–C). In this study, many genera within the same phylum exhibited different responses to soil pH, emphasizing the importance of studying bacteria at the genus or species level for a comprehensive understanding of how different taxa respond to changing environments. Such insights are essential for predicting microbial function in various ecosystems.

The total relative abundance of low pH and high pH optima varied significantly between biomes, with that of genera with neutral pH optima relatively stable. In grasslands and drylands, genera with high pH optima were notably more abundant than those with low pH optima (Fig. 3E), reflecting the higher mean soil pH in these biomes. Conversely, tropical, boreal, temperate, and subtropical forests, as well as arctic tundra, genera with low pH optima predominated due to the typically acidic nature of their soils. When comparing bacterial richness across biomes, the richness of both types of genera increased when the pH conditions are suitable (Fig. 4B). However, with long development of soil towards either more acidic or alkaline conditions, different biomes have their own dominant pH conditions, which harbours unique bacterial communities. Under near neutral conditions (5.5–7.5), the proportion of genera with acidic optima is comparable with genera with alkaline optima and alkaline tolerant combined in tropical, boreal, and temperate forests, as well as arctic tundra (Fig. 4B). However, the proportion of genera with alkaline optima/tolerant in drylands and grasslands surpass those with acidic optima at near neutral pH (Fig. 4B). As pH increases, the disparity between alkaline optima and acidic optima expanded further in drylands and grasslands compared to other biomes. Similar patterns were observed in tropical, boreal, and arctic areas, where the diversity gap between acidic optima and alkaline optima widened as soil pH decreased (Fig. 4B). These findings suggest that different climates provide distinct pH niches conductive to the survival of specific bacterial genus.

In nature, acidic soils cover up to 26% of the global ice-free surface land area, with 31% North America and about 43% of European surface soils being acidic (Moniz, 1997). Alkaline soils prevail in subhumid, semiarid, and arid climates, particularly in regions of west central and Mideastern Asia, North Africa, and Australia (Poggio et al., 2021). Given the significant variability in soil pH worldwide, we have identified only a handful of bacterial genera, such as *Bryobacter, Chthoniobacter, Candidatus* Udaeobacter*, Acidibacter*, as generalists present in over 90% of all sites. This finding aligns with a global study of bacterial communities, revealing that merely 2% of bacterial phylotypes are ubiquitous, being found in half of the soil bacterial community worldwide (Delgado-Baquerizo et al., 2018).

5. Conclusion

In conclusion, even across the global scale, soil pH, dominating over the spatial and climatic effects, emerges as the main driver in shaping bacterial communities. Analysing the pH niche of each genus, we found that soil pH explained the distribution of at least 75% of global bacterial genera, with distinct preferences for acidic, alkaline, or neutral pH conditions. Notably, our study highlights a comparable number of genera favouring high pH (18%) and low pH (21%), while there is a greater prevalence of genera tolerant of alkaline soils (21%) compared to acidic soils (0.8%). This significant difference in the number of alkaline-tolerant genera explains why the decline in bacterial richness at alkaline levels is less pronounced than at acidic levels. Over 1/3 of genera within Actinobacteriota, Pseudomonadota, Bacteroidota, and Gemmatimonadota exhibited high pH niche optima. Conversely, most genera in Verrucomicrobiota had low pH niche optima. Globally, genera with high pH optima are predominant in arid environmental conditions, such as Mideastern Asia, Africa, South America, and Australia, while genera with low pH optima show a greater affinity for wetter climates, including in North Europe, South-eastern Asia, and North America.

The current study uncovers a global distribution of bacterial genera in relation to soil pH, yet it also raises additional questions that warrant further investigation. Why more genera appear to tolerant in alkaline than acidic conditions? What are the primary environmental factors that drive the changes of bacterial richness when soil pH is above neutral? Is there evidence of geographical isolation in microbial communities? Addressing these questions is crucial for deepening our understanding of the complex interactions between soil pH and microbial community.

CRediT authorship contribution statement

Xuan Zhou: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Conceptualization. **Teemu Tahvanainen:** Writing – review & editing, Methodology, Conceptualization. **Lucie Malard:** Writing – review & editing, Methodology. **Liang Chen:** Writing – review & editing, Visualization, Investigation. **Juliana Pérez-Pérez:** Writing – review & editing, Visualization. **Frank Berninger:** Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data utilized in this study has been included in the supplementary materials accompanying this publication.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2024.109552.

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