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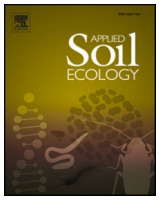

Enhanced complexity of interkingdom co-occurrence networks in blueberry rhizosphere microbial communities under soil pH stress

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ABSTRACT

Blueberry prefers acidic soils, resulting in its growth and development being limited by soil pH across various habitats. However, the effect of soil pH stress on the structure and interactions within its root-associated microbiome remains unclear. In this study, we investigated how varying soil pH conditions affect the composition, assembly processes, network complexity, and stability of blueberry root-associated bacterial and fungal communities. The results showed soil pH affected both bacterial and fungal community structures, with community assembly predominantly governed by stochastic processes. Notably, fungal communities were more influenced by stochastic drift than bacterial communities. Higher network complexity (nodes, edges, and average degree) and lower network stability were observed in the rhizosphere under low and high pH conditions compared to optimum pH conditions. A total of 24 and 29 keystone taxa were identified in the rhizosphere and endosphere, respectively. Collectively, these findings suggested that soil pH stress modulates the blueberry root-associated microbiome by reshaping community composition and enhancing interkingdom network complexity, though accompanied by reduced network stability. This study shed insights into changes in microbial interaction networks within the root-associated microbiome of host plants under abiotic stresses and lay essential groundwork for leveraging keystone microbes to improve plant health and resilience.

1. Introduction

Blueberry (*Vaccinium* spp.) is a perennial deciduous or evergreen shrub whose fruits offer numerous human health benefits and have been increasingly cultivated worldwide in recent years (Silva et al., 2020; Yang et al., 2022). The optimum soil pH range for blueberry is 4.0–5.5. If the soil pH falls outside of this range, the blueberry may suffer from stunted growth and reduced fruit yield and quality (Caspersen et al., 2016; Jiang et al., 2019). Plant root-associated microorganisms, as an essential component of the holobiont, are intimately linked to plant health and fitness (Choi et al., 2021; Trivedi et al., 2020). Recent studies have demonstrated that ericoid mycorrhizal (ErM) fungi can establish a symbiotic relationship with blueberry roots, enhancing the plant's adaptation to nutrient-deprived acidic soils by improving nutrient uptake efficiency for growth (Wei et al., 2022). In addition, studies have also revealed the important beneficial effects of bacteria in promoting blueberry plant growth and blueberry fruit yield and quality (Lee et al., 2021; Wang et al., 2022; Yu et al., 2020).

Plant root-associated microorganisms play a critical role in agroecosystems by enhancing host plants resistance to various environmental stresses (Hartmann and Six, 2023). These beneficial effects are mediated by root exudates, which recruit plant-growth-promoting microorganisms to colonize the root system (Compant et al., 2019). Previous studies indicated that the colonization of *Arabidopsis* roots by *Bacillus subtilis* FB17 was significant increased when the aboveground tissues were exposed to pathogen infection (Berendsen et al., 2012). This “cry for help” response pattern has been found not only under biotic stress but also under abiotic stress conditions, where it can be activated

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by altering the immune response of the plant and root exudates (Liu et al., 2024). It has been shown that under drought or salt stress, plants can recruit beneficial microorganisms to colonize the rhizosphere or endosphere, such as *Streptomyces*, *Bacillus* and *Pseudomonas* (Oppenheimer-Shaanan et al., 2022; Santos-Medellín et al., 2021). The structure of root-associated microbiome may suffer alterations in response to environmental stresses faced by the plant, thereby affecting the complex relationships and stability of the microbial community, which in turn exerts beneficial effects (Kang et al., 2024; Qu et al., 2020). Therefore, harnessing beneficial root-associated microorganisms to mitigate abiotic stresses and enhance blueberry growth and development is an effective strategy.

Environmental stresses can alter not only the compositional structure but also the interaction networks of microbial communities, thereby affecting their functional profiles (Banerjee et al., 2019). These changes can be revealed by co-occurrence network analyses, which enhance our understanding of how microbe-microbe associations shift in response to environmental variation (Barberán et al., 2012; Guo et al., 2022; Zhong et al., 2022). Studies have demonstrated that drought stimulated destabilizing properties in bacterial co-occurrence networks, such as increased connectivity and centrality, along with decreased modularity (de Vries et al., 2018). In contrast, studies have demonstrated that microbial networks in rhizoplane communities exhibit greater stability, characterized by high modularity and negative associations, which may enhance microbial community resilience under elevated stress conditions (Zhong et al., 2022). The increased species numbers within microbial networks likely reflects alterations in interactions among coexisting microorganisms, consequently influencing community stability (Coyte et al., 2015). The higher the modularity, the lower the positive correlation between taxa, and the higher the negative correlation between taxa in a microbial network, the greater its stability and resistance to environmental disturbances (Hernandez et al., 2021). In particular, modularity allows for the division of taxa into functionally distinct groups, which limits to some extent the expansion of the effects of the disappearance of a taxa to perturbations of other modules and prevents the overall destabilization of the network (Stouffer and Bascompte, 2011; Zhang et al., 2018). Positive and negative correlations reflect ecological niche overlap or differentiation between taxa, respectively (Mougi and Kondoh, 2012). Positive interactions create positive feedback loops to support mutual fitness, however, when the abundance of one taxon in a positive feedback loop decline, it can cascade down to affect the fitness of other taxa that rely on the services of that loop, ultimately affecting community stability (Coyte et al., 2015; Herren and McMahon, 2017).

In addition, co-occurrence network analyses can be used to identify keystone species, which interact directly or through microbial communities to regulate the growth and diversity of other microbes. These species are promising targets for enhancing plant resilience through promoting beneficial microorganisms or suppressing pathogens, thereby providing benefits for agroecosystem sustainability (Agler et al., 2016). Host plants can leverage keystone species through root exudate release, which serves various ecological functions that facilitate belowground nutrient cycling and plant growth (Yue et al., 2023). Although keystone taxa are fewer in number, they exhibit higher connectivity within microbial networks, and their impacts on community structure and composition can be quantified (Herren and McMahon, 2018). Abiotic factors and host genotypes have been shown to cascade their effects to regulate plant microbial communities by influencing keystone species (Agler et al., 2016; Jia et al., 2022). For blueberry plants, soil pH in the majority of fields is not compatible with their growth, which becomes a major abiotic factor limiting their growth and development. Consequently, it is imperative to elucidate the dynamics of key microbial taxa in blueberry plants under abiotic stress conditions, providing a foundation for enhancing stress resilience through targeted manipulation of these keystone taxa to optimize microbial community functions.

In this study, we investigated the composition, assembly processes, and interkingdom co-occurrence networks of blueberry root-associated microbial communities under three soil pH conditions. Our objectives were to: (1) reveal variations in the composition of blueberry root-associated microbiome in response to soil pH stress; (2) elucidate variations in the topological characteristics and stability of bacterial and fungal interaction networks when blueberry plants are exposed to soil pH stress; and (3) identify beneficial keystone taxa under different soil pH conditions. We hypothesize that soil pH stress alters the structures of blueberry root-associated microbial communities, enhances bacterial-fungal interactions, and enables the identification of keystone taxa with beneficial functions under stress conditions.

2. Materials and methods

2.1. Experimental design and microbiome sampling

The greenhouse experiment was performed in Lishui, Nanjing, Jiangsu Province (31°60′ N, 119°20′ E). The two-year-old rabbiteye blueberry (*Vaccinium ashei* Reade) "Brightwell" cultivar was selected. Blueberry roots were rinsed with water to remove soil adherents and pruned to retain a length of approximately 3 cm, then transplanted into the pots with 0.5 kg soil. The soil (pH = 4.2–4.9) consisted of the plantation soil, peat, and perlite with a volume ratio of 3:1:0.5, where the plantation soil and peat were sieved through a 0.8–1 cm sieve. Three different soil pH treatments were set up, low (pH = 3.3–3.6), optimum (pH = 4.2–4.9), and high (pH = 5.8–6.4) levels, where $C_6H_8O_7{\cdot}H_2O$ and $CaCO_3$ were added into the low and high treatment soils, respectively. Each pot with tray of 17 cm diameter was planted with a single seedling. There were a total of 25 pots in each treatment, 20 of which were planted with seedlings and the remaining 5 pots served as bulk soil. All treatments were maintained under uniform greenhouse conditions throughout the two-year cultivation period from January 11, 2022, with controlled irrigation, regulated sunlight exposure, and periodic manual weeding. Throughout the experiment, each planted pot and bulk soil pot received weekly irrigation with 500 ml of nutrient solution at consistent concentration. The applied NPK fertilizer was diluted at a 1:1000 ratio, containing 20 % nitrogen, 20 % phosphorus, and 20 % potassium. All the soil samples and roots were collected on July 17, 2023. A multipoint sampling approach was employed for each treatment. For bulk soil, five subsamples were collected from each pot and homogenized into one composite sample per pot. For rhizosphere soil and root endosphere samples, five subsamples were taken from each of four pots and combined into a one composite sample. Ultimately, there were five composite samples of each treatment for each ecological niche, for a total of 45 samples collected. For bulk soil sampling, a sterilized spade was used to obtain composite samples from unplanted pots after discarding the topsoil layer. Rhizosphere soil was collected by brushing adherent soil from the roots using sterilized brush. All soil samples and root samples were immediately placed on ice during transport to the laboratory. Soil samples were then sieved (2-mm sieve) to remove impurities. Root samples were rinsed with sterilized water and processed in a sterile 50 ml centrifuge tube for rhizoplane microorganism removal via ultrasonic treatment (60 Hz, 30 s sonication followed by 30 s breaks, repeated for 3 cycles) (Che et al., 2023). Individual composite soil samples and root samples were stored at −80 °C for microbiome analysis, and all soil samples were stored at −20 °C for soil physiochemical analysis.

2.2. Soil physicochemical properties and blueberry growth parameters measurement

Bulk soil samples and rhizosphere soil samples were collected for soil physiochemical analysis (Table S1), and the analytical methods were consistent with previous studies (Che et al., 2022). Specifically, soil pH was measured with a glass electrode in a soil-water solution (*w/v*) (Liu et al., 2018). Moisture content was determined by oven-drying for 48 h at 105 °C (Huang et al., 2019). Soil organic matter (SOM) was analyzed

via potassium dichromate oxidation (Yu et al., 2020). Total nitrogen (TN) and total carbon (TC) were quantified using an automatic elemental analyzer (PerkinElmer 2400 Series II, USA) (Tan et al., 2023). Nitrate and ammonium were measured by ultraviolet spectrophotometer (Shimadzu UVmini-1285, Japan) (Huang et al., 2019). Total phosphorus (TP) and total potassium (TK) were digested with HNO_3-HF-$HClO_4$, while available phosphorus (AP) and available potassium (AK) were extracted with HCl-H_2SO_4 and ammonium acetate, respectively. TP and AP were analyzed by atomic absorption spectrometer (PerkinElmer PinAAcle 900 T, USA), whereas TK and AK were determined using ultraviolet spectrophotometer, respectively (Jiang et al., 2017).

The height and basal diameter of blueberry plants were determined by using a tape measure along with digital Vernier calipers, and leaf chlorophyll content was evaluated utilizing a portable chlorophyll meter (SPAD-502 plus, Minolta, Japan) (Yang et al., 2022).

2.3. Microbiome analyses and Illumina sequencing

Extraction of total DNA from 0.5 g of soil and root samples was performed using the FastDNA SPIN Kits (MP Biomedicals, Santa Ana, CA, USA) following the instruction provided by the manufacturer. The V5-V7 region of the bacterial 16S rRNA was amplified using primers specific for 799F (5'-AACMGGATTAGATACCCKG-3′) and 1193R (5'-ACGTCATCCCCACCTTCC-3′). And the ITS1 region of the fungal rRNA was amplified using primers specific for ITS1F (5'-CTTGGTCATTTAGAGGAAGTAA-3′) and ITS2R (5'-GCTGCGTTCTTCATCGATGC-3′), which have been widely used to analyze fungal communities associated with blueberry plants (Cai et al., 2021; Dong et al., 2022; Gomes et al., 2023; Ye et al., 2023; Zhou et al., 2022). Sequencing was then performed by using Illumina MiSeq PE300 platform (Illumina, San Diego, USA). The raw sequences were filtered and merged by using fastp (v0.20.0, https://github.com/OpenGene/fastp) and FLASH (v1.2.7, http://www.cbcb.umd.edu/software/flash) software, respectively (Chen et al., 2018; Magoč and Salzberg, 2011). DADA2 was then used to denoise and remove chimeras, ultimately obtaining amplicon sequence variants (ASVs) (Callahan et al., 2016). The taxonomy of bacterial and fungal ASVs was based on the SILVA (v13.8, http://www.arb-silva.de) and UNITE (v8.0, http://unite.ut.ee/index.php) databases, respectively. After quality filtering, 3,798,160 and 4,253,853 sequence reads were obtained for bacteria and fungi, respectively, with an average of 84,403 and 94,530 sequence reads per sample, respectively. Finally, a total of 66,406 bacterial ASVs and 4,621 fungal ASVs were taxonomically identified.

2.4. Statistical analysis

Mantel correlation analysis was conducted to explore the relationships among plant growth parameters and microbial communities using "*linkET*" in R (https://github.com/Hy4m/linkET) (Kong et al., 2023). Beta diversity was evaluated using QIIME software (v1.9.1) based on Bray-Curtis distance by nonmetric multidimensional scaling (NMDS), and differences among treatments in various niches were evaluated by analysis of similarity (ANOSIM) (Voges et al., 2019). A null-model based β-nearest taxon index (βNTI) and Bray–Curtis-based Raup–Crick (RC_{bray}) index was used to characterize the assembly processes of microbial community (Stegen et al., 2012, 2013). βNTI and RC_{bray} were calculated by using the R package "*iCAMP*" (Zhou and Ning, 2017), where the $|\beta NTI| \geq 2$ was expected to the deterministic processes and $|\beta NTI| < 2$ was expected to the stochastic processes. Deterministic and stochastic processes are composed of five ecological processes, homogeneous selection ($\beta NTI < -2$), heterogeneous selection ($\beta NTI > 2$), dispersal limitation ($|\beta NTI| < 2$ and $RC_{bray} > 0.95$), homogenizing dispersal ($|\beta NTI| < 2$ and $RC_{bray} < -0.95$), and drift process ($|\beta NTI| < 2$ and $|RC_{bray}| < 0.95$) (Stegen et al., 2012). The neutral community model was applied to evaluate the contribution of stochastic processes in microbial community assembly (Sloan et al., 2006). R^2 is used to assess the accuracy and fit of model, with higher values indicating a greater influence of stochastic processes, and m parameter value is used to estimate the migration rate, with lower values indicating a greater dispersal limitation of the microbial community. ASVs with over 50 sequences per ASV in each sample were used to perform the bacterial-fungal interkingdom co-occurrence network analysis (Bazany et al., 2022; Pérez-Jaramillo et al., 2019). The SparCC correlations were calculated via the "*SpiecEasi*" package in R (Friedman and Alm, 2012; Kurtz et al., 2015), and statistically significant correlations (p) < 0.05 with absolute coefficient values (r) > 0.3 were considered valid co-occurrence correlations (Mendes et al., 2018). The co-occurrence networks were then constructed by using the R package "*igraph*" (Gabor and Nepusz, 2006; Frank E. Harrell, 2008) and visualized in Gephi software (*v0.10.1*). Network complexity was quantified as the number of associations among taxa, with higher average degree values indicating greater complexity (Wagg et al., 2019; Xiong et al., 2021). Graph density was calculated as the ratio of observed edges to the maximum possible edges between all node pairs, with higher values indicating stronger species interactions and greater network connectivity (Monchka et al., 2022). To determine the stability of the networks, we performed a cohesion analysis based on the significant positive and negative correlations (absolute SparCC's $r > 0.3$ and $p < 0.05$) between ASVs. The positive and negative cohesion values for each sample were calculated by summing the correlations between ASVs weighted with relative abundance, with larger negative cohesion values resulting in greater network stability (Herren and McMahon, 2017). Meanwhile, we use the ratio of the absolute values of negative cohesion to positive cohesion to assess network stability, which facilitates evaluation of negative association drivers potentially attributable to competition interactions or niche differentiation (Gao et al., 2023; Hernandez et al., 2021; Li et al., 2024). In the co-occurrence network, topological roles of each ASV were categorized by using their within-module connectivity (Zi) and among-module connectivity (Pi) scores (Guimerà and Amal, 2005), and divided into four subcategories. Network hubs (Zi >2.5, Pi >0.62) are nodes with high connectivity within or among modules, module hubs (Zi > 2.5, Pi <0.62) are nodes with high connectivity within a module, connectors (Zi < 2.5 and Pi >0.62), nodes with high connectivity among modules, and peripheral nodes (Zi < 2.5, Pi <0.62), nodes with less connectivity within or among modules (Ling et al., 2022).

3. Results

3.1. Growth phenotypes and microbial community structure of blueberry in response to soil pH variation

The growth of blueberry plants was inhibited under both low and high pH conditions (Fig. 1A). Growth parameters, including root, shoot, and leaf biomass, stem diameter, and crown width, were significantly reduced under soil pH stress. Leaf morphology characteristics and chlorophyll (SPAD value) contents were also significantly affected by soil pH stress. In particular, blueberry biomass, leaf width and thickness, and chlorophyll contents were significantly correlated with the community structure of rhizosphere and endosphere bacterial communities as well as rhizosphere fungal communities (Fig. 1B).

Nine dominant bacterial phyla and twelve major fungal classes, each with a relative abundance >1 %, exhibited shifts in their relative abundance under different soil pH conditions (Fig. 2A and B). NMDS analysis based on the Bray-Curtis distance suggested significant differences for bacterial ($R^2 = 0.992$, $p = 0.001$) and fungal ($R^2 = 0.938$, $p = 0.001$) community composition under various soil pH conditions in different niches (Fig. 2C and D). Furthermore, the relative abundance of order *Helotiales* (4.6 %) and order *Chaetothyriales* (27.9 %) in the root endosphere was higher under optimum pH conditions compared to low pH conditions (*Helotiales*: 1.1 % and *Chaetothyriales*: 26.9 %) and high pH conditions (*Helotiales*: 2.1 % and *Chaetothyriales*: 18.5 %) (Fig. S1).

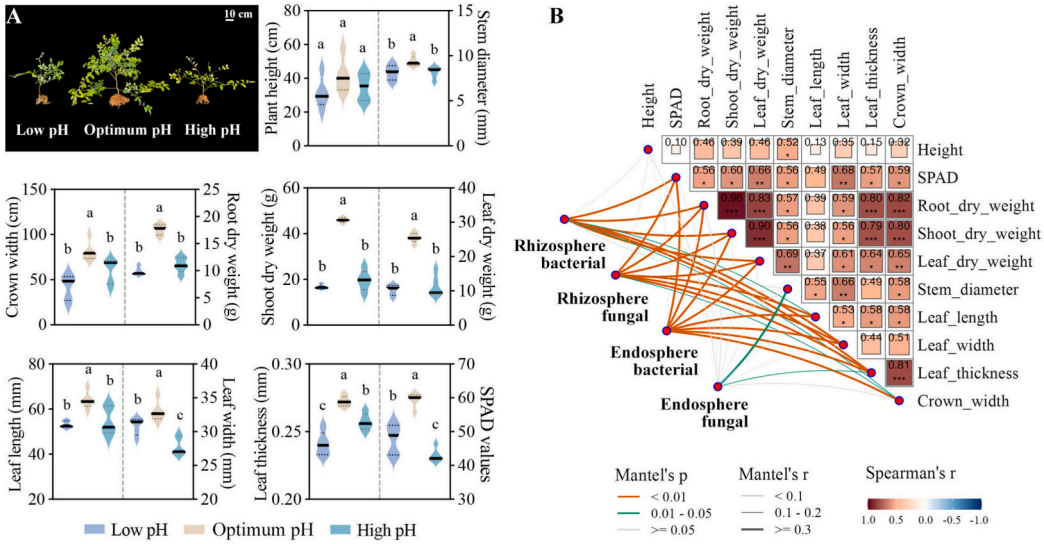

Fig. 1. Growth characteristics of blueberry under different soil pH conditions (A). The different letters indicate significant ($p < 0.05$) differences based on Duncan's multiple range test. Spearman's correlation of pairwise comparisons of blueberry growth characteristics and the relation between community composition with each growth characteristic by Mantel tests (B). Edge width corresponds to the Mantel's r statistic for the corresponding distance correlations, and edge colour denotes the statistical significance based on 999 permutations.

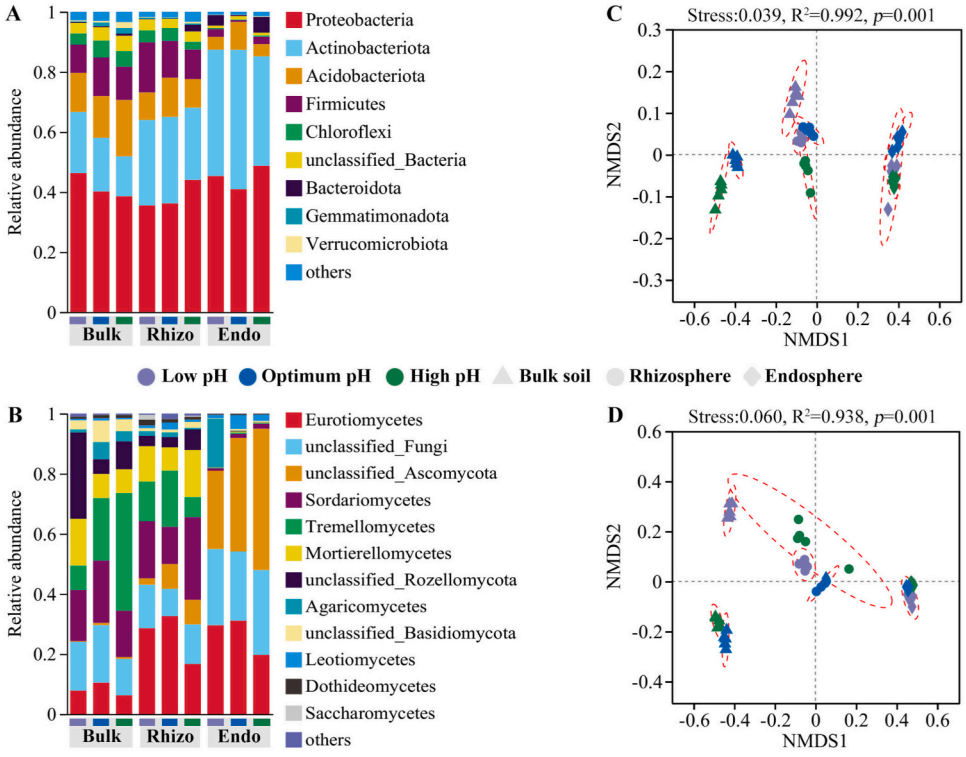

Fig. 2. Taxonomic composition of bacterial (A) and fungal (B) communities in various niches of blueberry under different soil pH. Nonmetric multidimensional scaling (NMDS) analysis of bacterial (C) and fungal (D) communities based on Bray-Curtis distance.

3.2. Microbial community assembly processes under different soil pH conditions

Stochastic processes dominated both bacterial and fungal communities under the low, optimum, and high soil pH conditions. The relative proportions of stochastic processes in the bacterial community were 83.11 %, 88.45 %, and 56.44 %, respectively, while in the fungal community they were 85.78 %, 89.33 %, and 89.33 %, respectively (Fig. 3A and Table S2). Although stochastic processes predominated in all niches, deterministic processes accounted for a higher proportion in the endosphere bacterial communities compared to those in the rhizosphere and bulk soil (Fig. S2). Homogeneous selection showed an increasing trend with increasing soil pH in the bacterial community, while the opposite trend was found in the fungal community. Heterogeneous selection contributed the least to the microbial community under optimum soil pH, compared to the low and high soil pH conditions. Interestingly, stochastic drift played a particularly important role in shaping fungal communities under different soil pH conditions,

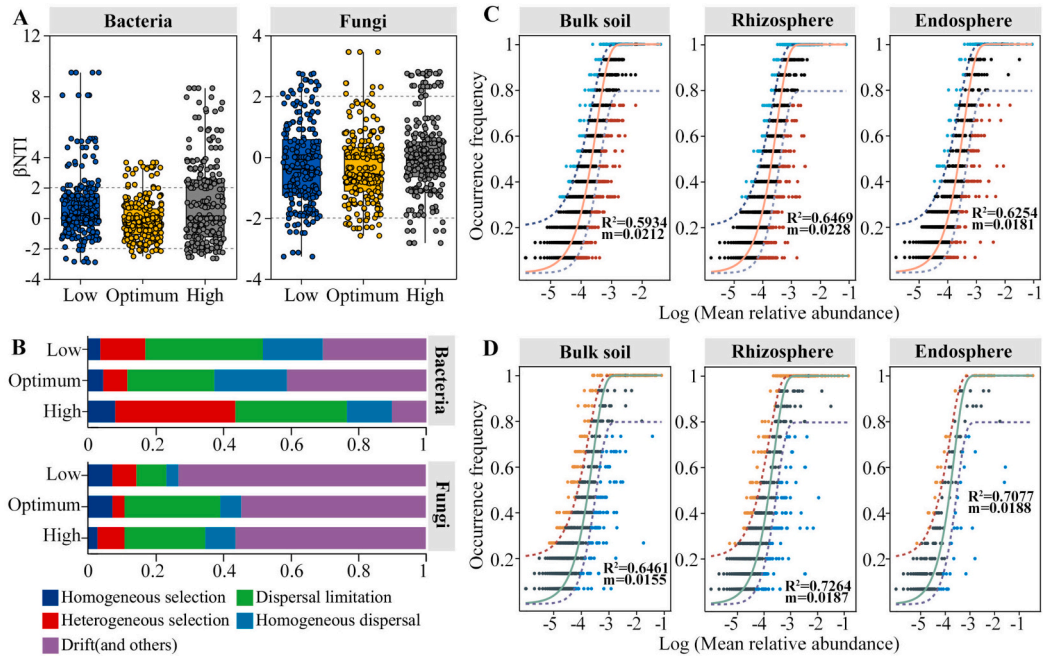

Fig. 3. Null model analysis of assembly processes influencing microbial community structure (A) and relative importance of five ecological processes (B). Sloan's neutral model for characterizing assembly processes in bacterial (C) and fungal (D) community. The solid line represents the fit of the neutral model and the upper and lower dashed lines represent the 95 % confidence level of the model predictions. R^2 and m value indicates the fit to the neutral model and the estimated migration rate, respectively.

compared to bacterial communities. We therefore using the neutral model to characterize the assembly processes of bacterial and fungal communities. In each ecological niche, the neutral model fit the fungal community better than the bacterial community, indicating that stochastic processes play a more significant role in shaping the fungal community structure (Fig. 3C and D). Bacterial communities had much

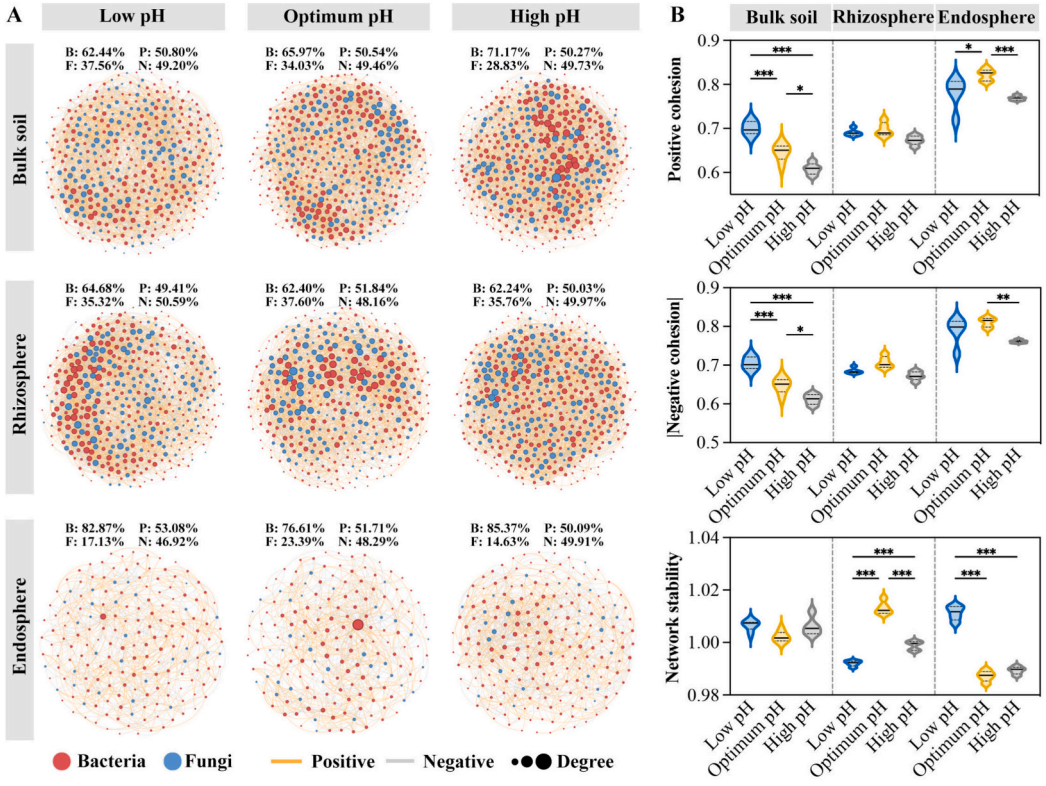

Fig. 4. Co-occurrence networks of bacterial and fungal communities under different soil pH conditions based on SparCC correlations (A). Yellow or gray connecting lines were used to represent significant correlations ($p < 0.05$), including positive (SparCC's $r > 0.3$) or negative (SparCC's $r < -0.3$) correlations. Network stability of microbial co-occurrence networks based on the positive and negative cohesion values (B). The values of network stability were assessed as the ratio of the absolute value of negative cohesion to the positive cohesion.

higher migration rates than fungal communities in bulk soil and rhizosphere, suggesting that their migration limitations are lower than those of fungal communities. However, bacterial and fungal communities in the endosphere exhibit comparable levels of dispersal limitation.

3.3. Microbial interkingdom co-occurrence network structures

The topological characteristics of microbial co-occurrence networks revealed a higher proportion of bacterial nodes in root endosphere networks under both low and high pH conditions, with bacterial node proportions of 82.87 %, 76.61 %, and 85.37 % under low, optimal, and high pH conditions, respectively (Fig. 4A). Higher numbers of nodes and edges in the rhizosphere and endosphere co-occurrence networks were observed under both low and high pH conditions compared to optimum pH conditions (Fig. 4A and Table S3). However, the average clustering coefficients was observed lower for the rhizosphere and root endosphere co-occurrence networks under both low and high pH conditions (Table S3). In addition, contrasting trends were observed in the average degree of rhizosphere and endosphere networks. The rhizosphere network had a higher average degree under low and high pH conditions, whereas the endosphere network exhibited a higher average degree under high pH conditions. The modularity of rhizosphere co-occurrence networks was also higher under low (0.492) and high (0.517) pH conditions compared to optimum (0.465) pH conditions. Therefore, the relationships between bacteria and fungi in the rhizosphere co-occurrence networks were more complex under low and high pH conditions, although these associations were less dense than under optimum pH conditions.

The positive and negative cohesion of the rhizosphere and the root endosphere showed different trends (Fig. 4B). Positive cohesion of the root endosphere was significantly higher under optimum pH condition than under low and high pH conditions, while negative cohesion was significantly higher under optimum pH condition compared to high pH condition. The stability of bacterial and fungal communities in the rhizosphere was significantly reduced under low and high pH conditions, whereas the stability of microbial communities in the endosphere was significantly higher under low pH conditions.

3.4. Keystone taxa in the interkingdom co-occurrence networks

We then identified the keystone taxa within each root niche across different soil pH conditions. The topological features of co-occurrence network indicated the highest number of nodes and edges in the rhizosphere (Fig. 5A and Table S4). The average degree and clustering coefficient were highest in the bulk soil, gradually decreased from the rhizosphere to the endosphere. As the proportion of bacterial nodes increased, the proportion of fungal nodes gradually decreased across the soil-root continuum. Furthermore, the potential topological role of ASVs in the co-occurrence networks was evaluated based on Zi-Pi values (Fig. 5B). In the bulk soil network, 17 bacterial ASVs and 11 fungal ASVs were identified as connectors, respectively (Table S6). In the rhizosphere network, two ASVs were identified as module hub belonging to the bacterial class *Gammaproteobacteria* and fungal genus *Solicoccozyma* (Table S5). 17 bacterial ASVs and 6 fungal ASVs were identified as connectors in the rhizosphere network (Table S7). Among these connectors, the relative abundance was higher for the bacterial genus *Bradyrhizobium* and the fungal genus *Trichoderma*, *Byssochlamys*, and *Chaetomium* (Fig. 6A and B). For the root endosphere network, one ASV belonging to *Conexibacter* was identified as the module hub (Table S5). A total of 26 bacterial ASVs and 2 fungal ASVs identified as connectors in the root endosphere network (Table S8), with higher relative abundance of bacterial ASVs belonging to the genus *Chujaibacter*, *Acidibacter*, *Bradyrhizobium*, and *Granulicella* and fungal ASVs belonging to the family *Chaetothyriaceae* (Fig. 6A and B).

Among these module hubs, *Solicoccozyma* in the rhizosphere and endosphere showed significant positive correlations with blueberry

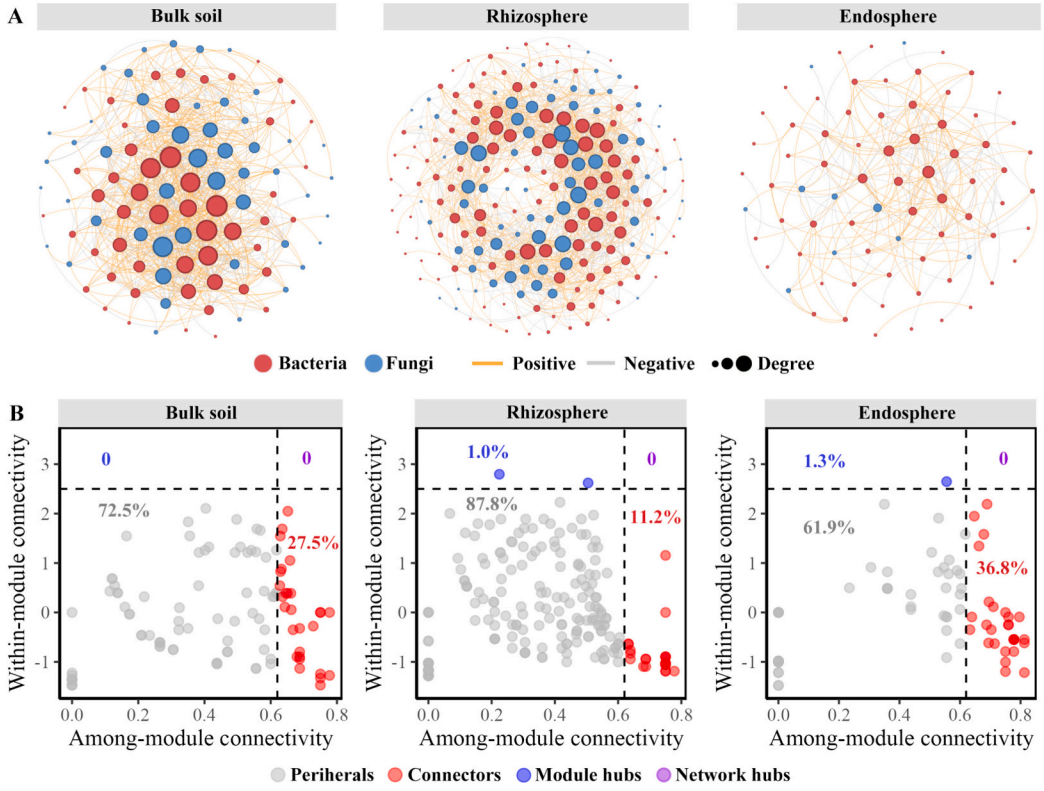

Fig. 5. Co-occurrence network patterns of each niche under different soil pH conditions based on SparCC correlations (A). Yellow or gray connecting lines were used to represent significant correlations ($p < 0.05$), including positive (SparCC's $r > 0.3$) or negative (SparCC's $r < -0.3$) correlations. Within-module connectivity (Zi) and among-module connectivity (Pi) plot demonstrating the distribution of ASVs based on topological characteristics in the co-occurrence networks (B).

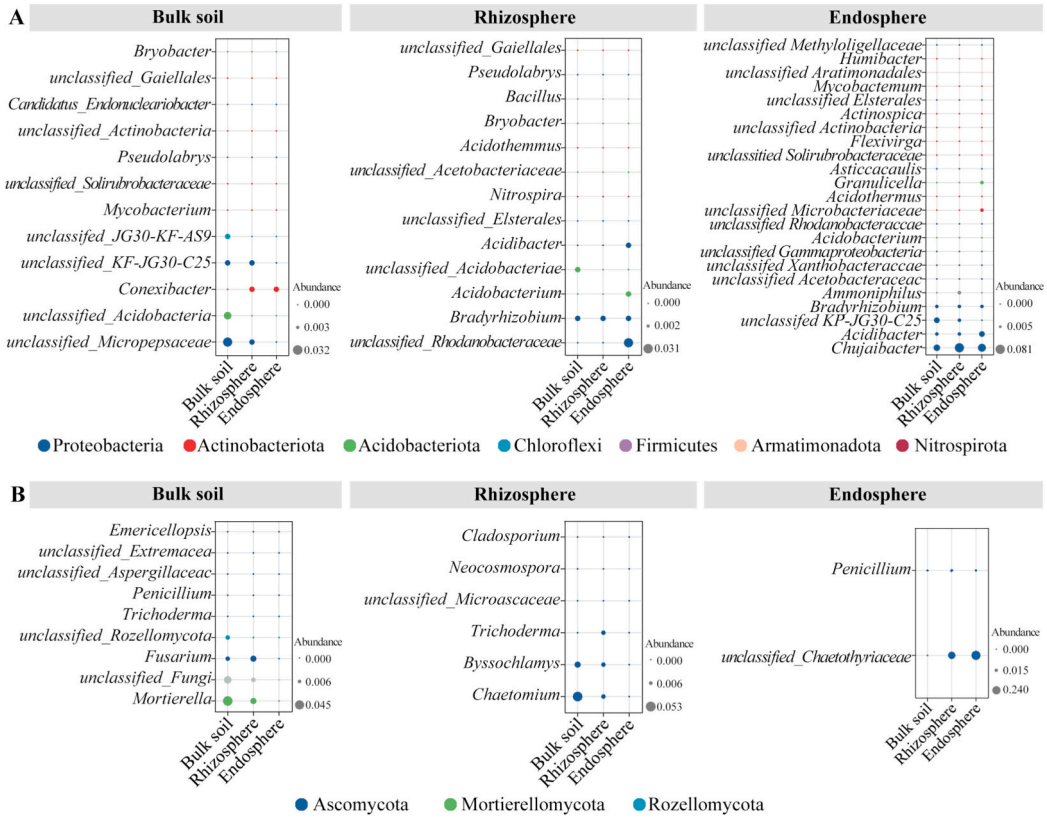

Fig. 6. Relative abundance of bacterial connectors (A) and fungal connectors (B) based on topological characteristics of bulk soil, rhizosphere, and endosphere co-occurrence networks.

plant growth parameters, such as biomass and leaf morphology, while *Conexibacter* in the rhizosphere was positively correlated with these growth parameters (Fig. S3). For bacterial connectors, *Granulicella* and *Actinospica* in the rhizosphere and endosphere showed significant positive correlations with the growth parameters of blueberry plant, and *Asticcacaulis* and *Humibacter* in the endosphere were also positive correlated with blueberry plant growth parameters (Fig. S3A and B). For fungal connectors, *Chaetothyriaceae* in both the rhizosphere and endosphere showed significant positive correlations with blueberry plant growth parameters. Additionally, *Byssochlamys* in the rhizosphere and *Penicillium* in the endosphere were significantly positively correlated with these growth parameters (Fig. S3C and D). Overall, the relatively high abundance of *Granulicella* in the endosphere, along with *Chaetothyriaceae* in both the rhizosphere and endosphere, was positively associated with blueberry plant growth.

4. Discussion

4.1. Community structure of the root-associated microbiome in relation to soil pH

Soil pH stress induces nutritional imbalance in blueberry plants, leading to damage in leaf membrane integrity and antioxidant defense systems, reduced photosynthetic efficiency, and ultimately diminished dry matter accumulation (Jiang et al., 2019; Yang et al., 2022). Soil pH is recognized as a key environmental factor influencing microbial communities across various habitats, including agricultural fields and grasslands (Lammel et al., 2018; Liu et al., 2018; Zhalnina et al., 2015). Our study found that microbial community composition was affected under different soil pH conditions. As the dominant phylum, the relative abundance of Proteobacteria gradually increased with increasing soil pH in the rhizosphere, from 35.5 % to 36.2 % and then to 44.0 % (Fig. 1A). This is in line with previous findings where the abundance of Proteobacteria in arable soils increases significantly as the soil pH is increased (Rousk et al., 2010). Moreover, soil pH was found to primarily determine bacterial community composition in natural mountain forests, with Actinobacteria positively correlated with soil pH and Acidobacteria negatively correlated with soil pH (Ni et al., 2021). However, different results were found in our study, where the relative abundance of Actinobacteria and Acidobacteria was higher in both the rhizosphere and the endosphere under optimum soil pH conditions. Blueberry is a plant adapted to acidic soils with a suitable pH of 4.0–5.5, and soil pH values above 5.5 can adversely affect blueberry growth and development (Yang et al., 2022). Therefore, this inconsistency may result from the more constrained pH range in our study (maximum 6.4) compared to natural mountain forests (pH above 8.0), potentially limiting comprehensive assessment (Rousk et al., 2010).

Additionally, we observed that fungal community composition varied under different soil pH conditions. Previous studies have demonstrated that fungal community composition exhibits stronger correlations with the taxonomic and phylogenetic structure of the aboveground plant assemblages than bacterial communities (Barberán et al., 2015), highlighting their close association with plant hosts. Blueberry plants exhibited optimal phenotypic performance in soils with pH 4.0–5.5. As integral components of a holobiont, plant fitness may shape their associated microbial communities (Vandenkoornhuyse et al., 2015). The healthy growth of blueberry plants under optimal pH conditions may explain the observed variations in fungal community composition. Notably, higher relative abundances of *Helotiales* and *Chaetothyriales* were observed in the root endosphere under optimum pH conditions, both of which include confirmed and putative ericoid mycorrhizal fungi, respectively (Leopold, 2016). This likely reflects enhanced mutualistic symbiosis between these fungal taxa and blueberry plants under favorable soil conditions.

Furthermore, our study demonstrated that soil pH influenced not only the rhizosphere microbial community structure but also altered the root endosphere microbial community composition. Root endophytic microbes are primarily acquired through two pathways: vertical transmission via seed-borne and recruitment from rhizosphere and rhizoplane microbial communities (Bulgarelli et al., 2013). The successful colonization of rhizosphere-derived microbes in roots is regulated by the plant immune system (Edwards et al., 2015). Consequently, as a subset of the rhizosphere microbial community, the root endosphere microbial community is influenced through cascading effects of environmental factors on the rhizosphere microbiome. Previous studies have demonstrated that transplanting plants into different soils leads to rhizosphere bacterial community reassembly, driven by recruitment from both the bulk soil and the plant's endosphere microbiota (Ren et al., 2020). This supports the notion of a bidirectional exchange between rhizosphere and endosphere microbial communities. Collectively, our results indicate that changes in soil pH, by altering the rhizosphere microbial community, may indirectly influence the composition of the root endosphere microbiome.

4.2. Microbial community assembly processes and co-occurrence network structure under various soil pH conditions

Our results showed that stochastic processes dominated both bacterial and fungal community assembly under differed soil pH conditions. Consistent with our findings, previous studies on forest restoration in nutrient-limited systems have demonstrated that microbial community assembly is largely governed by stochastic processes, regardless of environmental conditions (Kang et al., 2024). Contrary to traditional ecological niche-based processes, which assumes microbiome structure is shaped by deterministic processes, neutral theory hypothesizes that microbiome assembly occurs independently of species characteristics and is dominated by stochastic processes (Chase and Myers, 2011; Stegen et al., 2013; Zhou and Ning, 2017). Soil pH is a crucial environmental factor in shaping the structure of bacterial and fungal communities (Li et al., 2021), and it has been shown to affect the microbiome assembly processes in agricultural and forest soils (Fan et al., 2018; Ni et al., 2021). However, in our study, the soil pH range was comparatively narrow and did not range from acidic to neutral to alkaline. Thus, the reduction in environmental pressure and the weakening of environmental filtering may have contributed to the predominance of stochastic over deterministic processes. Furthermore, stochastic drift, a central concept in community ecology, becomes more significant when selection pressures are weak and local communities are small in size, as it can alter community structure and biogeographic patterns regardless of selection effects (Chase and Myers, 2011; Zhou and Ning, 2017). In our study, fungal communities were more dominated by stochastic drift than bacterial communities, potentially due to the relatively weaker impact of soil pH on fungal communities compared to bacterial communities (Rousk et al., 2010). Conversely, our findings indicated that bacterial communities were more governed by deterministic processes than fungal communities. Neutral community model suggested that bacterial communities have higher migration rates in bulk and rhizosphere soils, which may enhance their responsiveness to environmental changes and contribute to the greater role of deterministic processes (Kang et al., 2024).

We observed that the numbers of nodes, edges, and average degrees were higher in the rhizosphere co-occurrence networks under both low and high pH soil conditions. Similar patterns have been reported in previous studies, where co-occurrence interactions between bacterial and fungal communities were facilitated under weak nutrient-limited conditions (Kang et al., 2024). The interactions within microbial communities—whether competitive or cooperative—is influenced by resource availability (Dai et al., 2022; Ghoul and Mitri, 2016). Environmental changes have been shown to reshape ecological networks, resulting in increased network complexity and a decline in microbial diversity over successive plant growth seasons (Shi et al., 2016). Notably, complex networks with greater connectivity tend to exhibit higher resilience to environmental disturbances compared to simpler networks with lower connectivity (Guo et al., 2022; Santolini and Barabási, 2018). Therefore, increased microbial network complexity may enhance the community's capacity to withstand environmental stress. Furthermore, negative cohesion quantifies the extent of competitive association among microorganisms, whereas positive cohesion indicates cooperative mutualistic relationships (Hernandez et al., 2021; Herren and McMahon, 2017). The balance between competitive and cooperative relationships influences the stability of the network, with higher competitive interactions leading to higher stability (Kang et al., 2024). In our study microbial network stability declined under low and high soil pH conditions. Previous studies demonstrates that within positive feedback loops mediated by positive interactions, a decline in the abundance of a single taxon can propagate cascading fitness effects throughout the entire community, negatively impacting all dependent taxa (Coyte et al., 2015; Hernandez et al., 2021). This implies that network destabilization may arise from a higher effect of positive interactions or a lower proportion of negative interactions. Consequently, the observed decrease in network stability in the rhizosphere microbial communities could reflect a shift towards stronger microbe-microbe mutualisms, with competitive interactions being weakened under environmental stresses.

4.3. Abundant keystone taxa across various soil pH conditions

In this study, we identified several bacterial and fungal keystone taxa as module hub in the rhizosphere and endosphere, including the bacterial taxa belonging to *Gammaproteobacteria* and *Conexibacter*, as well as fungal taxa belonging to *Solicoccozyma*. Although *Gammaproteobacteria* showed no positive correlation with blueberry growth, its role as a network hub aligns with previous findings in the rhizosphere microbial community of rabbiteye blueberry (Jiang et al., 2017). Members of *Gammaproteobacteria* are known to be fast-growing *r*-strategist bacteria that can utilize a widespread rhizodeposits (Peiffer et al., 2013). The diversity of *Gammaproteobacteria*, along with the abundance of *Pseudomonas* and *Stenotrophomonas*, have been identified as potential health indicators with beneficial effects on host plants (Köberl et al., 2017). In addition, both *Solicoccozyma* and *Conexibacter* were found to be significantly positively correlated with the growth of blueberry plants. *Solicoccozyma* was identified as a core member of the rhizosphere microbiome in wild blueberry (*Vaccinium angustifolium*) (Morvan et al., 2020). It was revealed that a *Solicoccozyma* strain YCPUC79 exhibited IAA synthesis and ACC deaminase activities, promoting root growth and reducing root ethylene synthesis (Carvajal et al., 2024). Though *Conexibacter* has been reported as a biomarker of unhealthy orchard plants and considered as a pathogen (Obieze et al., 2023; Wen et al., 2022), some studies suggest that *Conexibacter* improves ecotoxicity resistance and microbial community stability under heavy metal stress (Chen et al., 2022). Additionally, *Conexibacter* was also found to be significantly and positively correlated with plant growth under arsenic-contaminated conditions (Wang et al., 2024). Its beneficial effects in such conditions may be attributed to its ability to reduce nitrate to nitrite (Chen et al., 2022), potentially influencing nitrogen cycling in the soil-plant system.

In addition, bacterial taxa of *Granulicella*, *Actinospica*, *Asticcacaulis*, and *Humibacter*, as well as fungal taxa of *Chaetothyriaceae*, *Byssochlamys*, and *Penicillium*, were found significantly positively correlated with blueberry plant growth. Previous studies have shown that strains belonging to the genera *Granulicella* and *Actinospica* are capable of producing the phytohormone IAA, which improves the biomass of roots and shoots of host plants (Kalam et al., 2020; Kielak et al., 2016). While strains of the genus *Asticcacaulis* have been reported as plant growth-inhibiting bacteria, reducing the productivity of duckweed (*Lemna minor*), they have also been identified as plant growth-promoting bacteria that can enhance the growth of sugar beet (*Beta vulgaris* L.)

(Ishizawa et al., 2018; Okazaki et al., 2021). This suggests that microbial colonization can have differential effects on various host plants. *Humibacter*, while recognized as a keystone taxon in microbial networks, still lacks sufficient research on its direct interactions with host plants (Wang et al., 2023; Zhao et al., 2023). Among fungal taxa, members of the *Chaetothyriaceae* family are recognized as sooty molds that obtain nutrients from sugar exudates, with their ascomata appressed to leaf and stem surfaces, demonstrating a plant-associated life cycle (Huang et al., 2023; Tian et al., 2021). Despite the lack of reports on the *Chaetothyriaceae* family, the order *Chaetothyriales* has been recognized as putative ErM (Leopold, 2016) and has been found in the roots of a variety of blueberry plants (Kariman et al., 2018; Li et al., 2020; Morvan et al., 2020, 2022). Some species of *Byssochlamys* have been reported to exhibit antagonistic activity against a range of plant pathogens, suggesting they could function as biological control agents with beneficial effects on plant health (Linkies et al., 2021; Rodrigo et al., 2017). Furthermore, *Penicillium* has been reported to promote plant growth by inducing systemic resistance to pathogen infection (Murali and Amruthesh, 2015).

Moreover, the higher relative abundance of keystone taxa such as *Bradyrhizobium*, *Chujaibacter*, *Acidibacter*, and *Trichoderma* may positively contribute to plant growth and health. Members of the genus *Bradyrhizobium* are known to facilitate nitrogen uptake and utilization by forming nitrogen-fixing nodules with legumes (Morvan et al., 2020; Zhang et al., 2014). *Chujaibacter* has been reported positively correlated with cucumber growth at the fruiting stage (Zhang et al., 2023), while *Acidibacter* can colonize various plant species and is associated with soil nutrient and iron cycling, plant blights, and soil contamination control (Li et al., 2023a). *Trichoderma* are capable of producing IAA as well as both volatile and nonvolatile secondary metabolites, which are widely recognized as plant growth stimulants (Li et al., 2023b). Taken together, these keystone taxa likely play pivotal roles in supporting plant health and resilience, especially under variable soil pH conditions. Their presence and positive associations with blueberry growth suggest strong potential for future application in microbiome-based strategies to enhance blueberry cultivation and stress tolerance.

5. Conclusions

When blueberry plants are exposed to soil pH stress, the composition and structure of their root-associated microbiome was affected. In particular, the relative abundance of *Helotiales*, an endophytic beneficial taxon including ericoid mycorrhiza fungi specific to blueberry roots, was higher in the root endosphere under optimum soil pH conditions than under low and high soil pH conditions. Stochastic processes predominated bacterial and fungal communities under different pH conditions, and stochastic drift was apparently particularly relevant for fungal communities in all soil pH groups compared to bacterial communities. Rhizosphere interkingdom co-occurrence networks exhibited increased complexity—characterized by higher numbers of nodes, edges, and average degree—yet lower stability under both low and high soil pH conditions compared to optimal soil pH. The beneficial keystone taxa were identified within each root niche across various soil pH habitats. Of these, the bacterial keystone taxa *Conexibacter*, *Granulicella*, *Actinospica*, and *Asticcacaulis*, as well as the fungal keystone taxa *Solicoccozyma*, *Chaetothyriaceae*, *Byssochlamys*, and *Penicillium* were positively correlated with the growth of blueberry plants. These keystone taxa may contribute to enhancing blueberry plant resilience under soil pH stress, thereby supporting their growth and productivity. However, further research is needed to elucidate the specific functions and underlying mechanisms by which these beneficial microorganisms confer abiotic stress resistance in blueberry plants.

CRediT authorship contribution statement

Jilu Che: Writing – original draft, Visualization, Investigation, Data curation, Conceptualization. **Yaqiong Wu:** Writing – review & editing, Supervision, Conceptualization. **Hao Yang:** Writing – review & editing, Investigation, Data curation. **Ying Chang:** Writing – review & editing, Investigation, Data curation. **Wenlong Wu:** Investigation, Data curation. **Lianfei Lyu:** Investigation, Data curation. **Xiaomin Wang:** Investigation, Data curation. **Fuliang Cao:** Writing – review & editing, Supervision, Conceptualization. **Weilin Li:** Writing – review & editing, Supervision, Conceptualization.

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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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2025.106191.

Data availability

No data was used for the research described in the article.

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