Effects of *Fusarium solani* inoculation on microbial communities in different compartments of *Angelica sinensis*

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Abstract

This study explored microbial changes in different parts of Angelica sinensis under the intervention of Fusarium solani, with the aim of revealing the microbiome response mechanism of Angelica sinensis to soil-borne diseases and preliminarily screening potential cross-compartment core disease-resistant microbial groups. Angelica sinensis was used as the research object, and a diseased-plant model was established through exogenous addition of Fusarium solani. High-throughput sequencing was employed to analyze changes in the community structures of bacteria and fungi in six different compartments: the leaf surface, leaf interior, root surface, root interior, rhizosphere soil, and non-rhizosphere soil. The results showed that: (1) microbial communities in different compartments of Angelica sinensis exhibited significant spatial specificity, with diversity and evenness showing a gradient decline from belowground to aboveground parts. (2) Under the intervention of Fusarium solani, the bacterial community richness in the rhizosphere soil and root surface, as well as the fungal community richness in the rhizosphere soil and leaf interior, decreased significantly. The bacterial and fungal community structures in belowground compartments tended to become simplified, whereas the number of bacterial genera in the phyllosphere increased abnormally, and the variation pattern of fungal communities was not entirely consistent. (3) Spearman correlation analysis between differential genera and Fusarium in different compartments of healthy and diseased Angelica sinensis showed that bacteria such as Pseudomonas, Bradyrhizobium, Sphingobium, and Devosia were significantly positively correlated with the pathogen in multiple compartments, suggesting that they may be coordinately enriched during the host response to disease. (4) Phenotypic and functional predictions indicated that, alongside the increase in pathogenic bacteria in diseased plants, beneficial microbial groups such as stress-tolerant bacteria, microbes containing mobile genetic elements, and pathotrophic-saprotrophic-symbiotrophic fungi were also synchronously enriched. In summary, microbial communities in different compartments of Angelica sinensis form a natural spatial specificity characterized by a decreasing gradient from belowground to aboveground parts; however, pathogens drive the microbiome toward simplification in belowground compartments and increased complexity in aboveground compartments, triggering aboveground-belowground microbial migration or systemic responses. Resistance of Angelica sinensis to Fusarium solani infection mainly relies on bacteria-mediated microecological regulation strategies. Whether these beneficial bacteria are actively recruited by the host remains to be further verified through inoculation experiments.

Full Text

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Effects of *Fusarium solani* inoculation on microbial communities in different compartments of *Angelica sinensis*

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Abstract: To explore microbial changes in different compartments of *Angelica sinensis* under the intervention of *Fusarium solani* inoculation, reveal the microbial community response mechanisms of *A. sinensis* to soil-borne diseases, and preliminarily screen potential core cross-compartment antagonistic microbiota, this study used *A. sinensis* as the research object. A disease-strain model was established through exogenous addition of *F. solani*. High-throughput sequencing technology was used to analyze structural changes in bacterial and fungal communities in six different compartments: the leaf surface, inside the leaf, root surface, inside the root, rhizosphere soil, and non-rhizosphere soil. The results showed that: (1) Microbial communities in different compartments of *A. sinensis* exhibited significant spatial specificity, and their diversity and evenness showed a gradient decreasing trend from belowground to aboveground. (2) Under the intervention of *F. solani*, the richness of bacterial communities in rhizosphere soil and on the root surface, and the richness of fungal communities in rhizosphere soil and inside leaves, decreased significantly; the structures of bacterial and fungal communities in belowground compartments tended to become simplified, while the number of bacterial genera in the leaf compartment increased abnormally, and the patterns of change in fungal communities were not completely consistent. (3) Spearman correlation analysis between differential genera in different compartments of healthy and diseased *A. sinensis* and the genus *Fusarium* showed that bacteria such as *Pseudomonas*, *Bradyrhizobium*, *Sphingobium*, and *Devosia* were significantly positively correlated with the pathogen in multiple compartments, suggesting that they may be co-enriched during the host response to disease. (4) Phenotypic prediction and functional prediction showed that, while diseased plants had increased pathogens, beneficial groups such as stress-tolerant bacteria, fungi containing mobile genetic elements, and pathotrophic-saprotrophic-symbiotrophic fungi were also synchronously enriched. Overall, the microbial communities in different compartments of *A. sinensis* form a naturally decreasing spatial specificity from belowground to aboveground, but pathogens cause their microbiota to evolve toward simplification in belowground compartments and complexity in aboveground compartments, triggering aboveground–belowground microbial migration or systemic responses. Resistance of *A. sinensis* to *F. solani* infection mainly relies on bacteria-mediated microecological regulatory strategies; whether these are beneficial microbes actively recruited by the host still requires further verification

through inoculation experiments.

Keywords: *Angelica sinensis*; root rot; *Fusarium solani*; bacteria; fungi; multi-compartment microbiome

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Effects of *Fusarium solani* inoculation on microbial community assembly in different compartments of *Angelica sinensis*

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Abstract: Exploring microbial changes in different niches of *Angelica sinensis* under the intervention of *Fusarium solani* to reveal the microbiome response mechanisms of *A. sinensis* against soil-borne diseases and preliminarily screen potential core cross-niche antagonistic microbiota. In this study, *A. sinensis* was used as the research object. A diseased plant model was established by exogenous inoculation with *F. solani*. High-throughput sequencing technology was

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employed to analyze the structural changes in bacterial and fungal communities across six distinct niches: phylloplane, endophyllosphere, rhizoplane, root endosphere, rhizosphere soil, and non-rhizosphere soil. The results were as follows: (1) The microbial communities in different niches of *A. sinensis* exhibited significant spatial specificity, with a gradient decline in diversity and evenness

from belowground to aboveground compartments. (2) Under the intervention of *F. solani*, bacterial species richness in the rhizosphere soil and rhizoplane, as well as fungal species richness in the rhizosphere soil and endophyllosphere, significantly decreased. The bacterial and fungal community structures in belowground niches tended to simplify, while the number of bacterial genera in the phyllosphere increased abnormally; the pattern of change in fungal communities was not entirely consistent. (3) Spearman correlation analysis between differential genera across different niches of healthy and diseased *A. sinensis* and the genus *Fusarium* revealed that bacterial genera such as *Pseudomonas*, *Bradyrhizobium*, *Sphingobium*, and *Devosia* showed significant positive correlations with the pathogen across multiple niches, suggesting their potential co-enrichment in the host' s response to disease. (4) Phenotypic prediction and functional prediction indicated that while pathogenic fungi increased in diseased plants, beneficial genera such as stress-tolerant bacteria, mobile genetic elements, and pathotroph-saprotroph-symbiotroph type fungi were simultaneously enriched. In summary, the microbial communities in different niches of *A. sinensis* exhibit a natural spatial specificity characterized by a bottom-up decreasing gradient. However, pathogen invasion drives a directional shift toward simplification of belowground communities and increased complexity of aboveground communities, triggering an aboveground-belowground microbial migration or systemic response. The resistance of *A. sinensis* to *F. solani* infection primarily relies on bacterial-mediated microecological regulation strategies. Whether these bacteria represent beneficial taxa actively recruited by the host requires further validation through inoculation experiments.

Keywords: *Angelica sinensis*, root rot, *Fusarium solani*, bacteria, fungi, multi-compartment microbiome

Angelica sinensis is a genuine medicinal root herb of Gansu Province. Because it is widely used for its anti-inflammatory, antitumor, antidepressant, and cardiocerebrovascular enhancing functions, it has long been known as the "one of the ten prescriptions, nine contain Angelica" (National Pharmacopoeia Commission, 2025; Zhao Shujie et al., 2024). The *A. sinensis* planting industry is an important economic source for local farmers. At present, however, the frequent occurrence of root rot in *A. sinensis* has severely affected farmers' income. It has been reported that in the Weiyuan region of Gansu alone, the incidence of *A. sinensis* disease can reach 40%–90% (Zhang Ting et al., 2024). Root rot causes decay of the root system, dehydration and curling of leaves, and drooping of the shoot apex; in severe cases, the entire plant withers and dies (Liu Hua et al., 2011). Studies have shown that root rot is mainly caused by pathogenic fungi of the genus *Fusarium* spp., but the pathogen displays significant host specificity (Acosta et al., 2010; Cao Jian et al., 2022) and regional heterogeneity (Chen Yihang et al., 2022; Shen Litao, 2012). Previous studies found that the key pathogen causing root rot of *A. sinensis* in the Weiyuan region of Gansu is *Fusarium solani* (Xie Tianpeng et al., 2025).

Plants and soil can form a close symbiotic system. As a link, microorganisms

have coevolved with plants over long periods and play important roles in nutrient absorption, regulation of growth and development, improvement of disease resistance, and degradation of harmful substances (Acosta et al., 2010; Chaparro et al., 2014; Müller et al., 2016; Tang et al., 2023; Ge Lei et al., 2024). It is generally believed that when plants face biotic or abiotic stress, the balance among plant–soil–microorganisms is disrupted. For example, after infection by pathogens, the microbial community in the rhizosphere soil of plants often changes; abnormal enrichment of pathogens in the rhizosphere leads to a reduction or even disappearance of beneficial bacterial richness, causing the rhizosphere soil bacterial community to shift from a healthy to a subhealthy state (Gao Xiaomei et al., 2021). However, studies have also shown that when biotic stress occurs, plants can recruit beneficial microorganisms by secreting specific signaling substances to alleviate disease. This recruitment process can be achieved in two ways: one is from the soil. For example, after infection by *Pseudomonas syringae* pv. tomato, the malic acid secreted by roots can recruit beneficial 枯草菌 in the rhizosphere soil.

After infection by *Bacillus subtilis*, FB17 (Rudrappa et al., 2008), and cucumber wilt caused by *Fusarium oxysporum*, plants can stimulate the enrichment of beneficial bacteria such as *Bacillus subtilis* SQR9 and *Pseudomonas stutzeri* in the rhizosphere soil by secreting salicylic acid, thereby enhancing plant disease resistance (Liu et al., 2017). On the other hand, other plant tissues can coordinate with the diseased site. For example, under the stress of wilt disease, pepper showed enrichment of microbial community functional genes involved in detoxification, chemotaxis, and biofilm formation, promoting the enrichment of beneficial microbial groups such as *Pseudomonas*, *Streptomyces*, and *Bacillus* in the host (Gao et al., 2021). It can be seen that biological stress can not only shift plant rhizosphere soil toward a sub-healthy state, but can also stimulate the release of signals that attract "reinforcements" to help resist disease. At present, scholars have generally focused on changes in plant rhizosphere microbial communities under biological stress (Gao Xiaomei et al., 2021; Liu et al., 2017). However, plant rhizosphere, endophytic, and phyllosphere microorganisms together constitute a highly diversified plant microbiome (Müller et al., 2016), and these microorganisms colonize the surfaces and interiors of various plant organs. When disease occurs, microbial communities in different plant parts may undergo coordinated changes. For example, after pepper is invaded by root rot disease, beneficial bacteria are enriched in its roots, stems, and fruits, and some beneficial bacteria are identified as core taxa of the microbial community and hub nodes of the interaction network (Gao et al., 2021); in the rhizosphere soil, roots, stems, and leaves of diseased root-rot *Astragalus membranaceus*, the relative abundance of multiple bacterial genera changes significantly compared with healthy *Astragalus membranaceus* (Tang Tao et al., 2022). Therefore, studying changes in microbial communities in different plant parts under disease stress can help provide a more comprehensive understanding of the pathways by which plants recruit potential beneficial bacteria, reveal the interaction mechanisms between plants and microbiomes, and thereby provide

a theoretical basis for targeted regulation of microbial communities to prevent and control plant diseases. Nevertheless, current research on root rot of *Astragalus membranaceus* still mainly focuses on rhizosphere microorganisms, and knowledge of the coordinated changes of multi-site microbiomes remains limited.

Therefore, this study used *Astragalus membranaceus* from Weiyuan County, Gansu Province, as the research object. By exogenously adding *Fusarium solani* to establish a diseased-plant model, and using high-throughput sequencing technology, this study analyzed structural changes in bacterial and fungal communities in six different parts of *Astragalus membranaceus*—the leaf surface, inside leaves, root surface, inside roots, rhizosphere soil, and non-rhizosphere soil—under *Fusarium solani* intervention. The study sought to explore the following questions: (1) What changes occur in the bacterial and fungal community structures of the six different parts of *Astragalus membranaceus* under *Fusarium solani* intervention? (2) What relationship exists between the relative abundance of differential bacterial genera in multiple changed parts of *Astragalus membranaceus* and the relative abundance of *Fusarium*? (3) Are there significant changes in the functions of microbial communities in different parts of healthy and diseased *Astragalus membranaceus*? This study aims to reveal the microbial-community response mechanism of *Astragalus membranaceus* to soil-borne diseases and to preliminarily screen potential cross-site core disease-resistant microbial groups.

1 Materials and Instruments

1.1 Experimental Materials

The tested *Astragalus membranaceus* seedlings were purchased from the agricultural trade market in Weiyuan County, Dingxi City, Gansu Province. The pot-control experiment was completed at the Pharmaceutical Industry Innovation Research Institute, Gansu University of Chinese Medicine. *Fusarium solani* was isolated, purified, and cultured from *Astragalus membranaceus* plants with obvious root rot symptoms in farmland in Weiyuan County, using PDA medium.

1.2 Experimental Methods

1.2.1 Preparation of the Bacterial Suspension

Previously isolated and preserved *Fusarium solani* was taken, and a 0.5 cm × 0.5 cm fungal block was picked with an inoculation needle and placed in the center of PDA medium. It was cultured at 25 °C for 10 d. Subsequently, 20 mL of sterile water was added to the culture dish, and the mycelia were scraped with a sterile glass rod. The suspension was filtered through double-layer sterile gauze to prepare a spore suspension, which was adjusted to a concentration of $3.5 \times 10\hat{}8$ CFU · mL$\hat{}$-1 for later use (Xie Tianpeng et al., 2025).

1.2.2 Establishment of the Diseased-Plant Model

Healthy *Astragalus membranaceus* plants of uniform size (seedling root diameter approximately 0.55 cm) and weight (fresh seedling weight approximately 100 g per 100 seedlings) were selected. The roots of *Astragalus membranaceus* were rinsed with sterile water for 30 min, surface-disinfected with 75% ethanol solution for 30 s, soaked in 5% sodium hypochlorite for 5 min, rinsed several times with sterile water, and then blotted dry with sterile filter paper. Sterilized flowerpots with a diameter of 10 cm and a height of 15 cm were used to hold equal amounts of sterilized soil, and *Astragalus membranaceus* plants were transplanted, one plant per pot. After the transplanted *Astragalus membranaceus* had grown for 30 d, the root-wounding inoculation method was used: a wound area of approximately 0.2 cm × 0.1 cm was made on the root, and 10 mL of the bacterial suspension was inoculated onto the wound site. The control *Astragalus membranaceus* was drenched with an equal amount of sterile water. Each treatment was set up with 30 sample replicates. If the root became rotten and the leaves withered, yellowed, and curled, the diseased-plant model was considered to have been successfully established.

1.2.3 Sample Collection

About 20 d after inoculation with the pathogen suspension, when rotting appeared at the roots and the leaf surface turned yellow and curled, healthy and diseased *Angelica sinensis* samples were collected separately. The non-rhizosphere soil of *A. sinensis* (soil shaken off from the outside), rhizosphere soil (soil attached to the roots at 0–0.5 cm), root surface (roots were placed in centrifuge tubes containing 15 mL sterile PBS solution, shaken at 4 °C and 180 $r \cdot min^{-1}$ for 20 min, removed and then placed in fresh sterile PBS solution and treated under the same conditions for 20 min; the liquids from the two treatments were combined and mixed, and the sediment after centrifugation at 1 000 $r \cdot min^{-1}$ and 4 °C for 10 min was collected), inside the roots (roots were soaked in 70% ethanol for 2 min and in 6% H_2O_2 for 15 min for surface disinfection, rinsed three times with sterile water, plated to verify sterility, and then placed in a sterile mortar with liquid nitrogen and fully ground into powder), leaf surface (leaves were cut with sterilized scissors, sterile water and the surfactant Silwet L-77 were added, and the mixture was shaken at 25 °C and 200 $r \cdot min^{-1}$ for 20 min; the shaking liquid was filtered with a vacuum filtration device, and microorganisms retained on a 0.22 μm pore-size filter membrane were collected), and leaf endosphere samples (after the leaves were further cut and mixed, they were disinfected with 75% ethanol for 1 min, rinsed once with sterile water, disinfected with 5% sodium hypochlorite solution for 5 min, and rinsed three times with sterile water; the final sterile-water rinse was plated to verify sterility) were collected. Each group had 5 replicates, for a total of 60 samples. All samples were stored in an ultra-low-temperature freezer at −80 °C until DNA extraction (Xian Kanghua et al., 2025).

1.3 DNA extraction and sequencing

A reagent-box extraction method was used to extract the total genomic DNA of the different *A. sinensis* samples. For bacteria, the forward primer 341F, 5′-CCTACGGGNGGCWGCAG-3′, and the reverse primer 785R, 5′-GACTACHVGGGTATCTAATCC-3′, were used to amplify the V3–V4 region of the 16S rDNA gene by polymerase chain reaction (PCR). For the fungal ITS region, the forward primer ITS1F, 5′-CTTGGTCATTAGAGGAAGTAA-3′, and the reverse primer ITS2R, 5′-GCTGCGTTCTTCATCGATGC-3′, were used. Each sample was amplified in a 25 μL system. The first-round reaction system included 15 μL 2×Gflex PCR buffer, 0.6 μL Tks Gflex DNA polymerase (1.25 U $\cdot$ μL^{-1}), 1 μL template, and 1 μL each of forward and reverse primers at 5 pmol $\cdot$ μL^{-1}. The PCR reaction system was: 5×TransStart FastPfu buffer 4 μL, 2.5 mmol $\cdot$ L^{-1} dNTPs 2 μL, upstream and downstream primers (5 μmol $\cdot$ L^{-1}) 0.8 μL each, TransStart FastPfu DNA polymerase 0.4 μL, template DNA 10 ng, and double-distilled water added to 20 μL. The amplification program was as follows: pre-denaturation at 95 °C for 5 min; denaturation at 95 °C for 30 s, annealing at 55 °C for 30 s, and extension at 72 °C for 30 s, for a total of 25 cycles; and final stable extension at 72 °C for 5 min (Lei Xianglun et al., 2026; Jiang Haiyang et al., 2025). PCR results were verified by 2% agarose gel electrophoresis. If no band appeared for a negative result, magnetic-bead purification was performed using an AMPure XP kit (BECKMAN COULTER, USA). After purification, the product was diluted to 50 μg $\cdot$ μL^{-1} and used as the PCR template for the second round of amplification. Under the same conditions as the first round of PCR, DNA samples were amplified for 8 cycles. Two microliters of the purified second-round product were taken for 2% agarose gel electrophoresis to determine whether a band was present and whether the band was single. One microliter of the purified second-round product was used for concentration determination with a Nanodrop. After passing sample quality control, the samples were submitted to a sequencing company, where the Illumina Novaseq 6 000 sequencing platform was used for 16S rDNA amplicon sequencing and ITS rDNA amplicon sequencing (Meiji Biotech, Shanghai).

1.4 Data analysis

After paired-end assembly, filtering, and chimera removal, the raw sequencing reads yielded optimized sequences. DADA2 was used for denoising to obtain amplicon sequence variants (ASVs). The 16S representative sequences and ITS representative sequences were aligned against the SILVA database (v138.0) and the Unite database (v8.0), respectively, and ASV taxonomic annotation was performed. The confidence threshold was 70%. ASV sequences aligned to chloroplasts and mitochondria in all samples were removed. Alpha-diversity analysis and principal coordinates analysis (PCoA) were performed using QIIME and the R package vegan 2.5-6, and permutation multivariate analysis of variance (PERMANOVA) was used for testing. SPSS 26 software (SPSS Inc., Chicago, IL) was used for data statistics and analysis; one-way analysis of variance (ANOVA) was

Rarefaction curves of bacterial (A) and fungal (B) communities in *Angelica sinensis* samples from different plant tissues

Figure 1: Rarefaction curves of bacterial (A) and fungal (B) communities in *Angelica sinensis* samples from different plant tissues

used to test significance. The Wilcoxon rank-sum test (Mann–Whitney U test) was used to analyze species differences between healthy and diseased plants. Origin2021 was used to generate volcano plots of differential species, and the 10 species with the most significant differences between healthy and diseased plants were selected. Then, Spearman correlation analysis was performed between the differential bacterial genera that changed in multiple *A. sinensis* compartments and the genus *Fusarium*. The R package psych and Gephi 0.9.2 were used to conduct cross-domain microbial co-occurrence network analysis of bacterial and fungal communities in healthy and diseased plants based on ASV-level SparCC co-occurrence networks. The BugBase and FunGuild databases were used to annotate the phenotypes and functions of bacterial and fungal communities, respectively.

2 Results and analysis

2.1 Sequencing depth and ASV clustering analysis

Microbial sequencing was performed on 60 samples. For bacteria, a total of 4,098,035 high-quality, quality-controlled sequences were obtained, with 1,545,104,101 valid bases; the number of bacterial ASVs in each sample ranged from 374.28 to 378.21. For fungi, a total of 3,913,933 high-quality, quality-controlled sequences were obtained, with 947,362,284 valid bases; the number of fungal ASVs in each sample ranged from 217.06 to 286.35. Taking the randomly extracted sequencing data volume as the horizontal coordinate and the number of ASVs obtained by clustering as the vertical coordinate, rarefaction curves for bacteria and fungi in samples from the six tissue/site categories of healthy and diseased *Angelica sinensis* were constructed. As shown in Fig. 1, the bacterial and fungal ASV rarefaction curves for all six tissue/site categories of healthy and diseased *A. sinensis* tended to be flat. The sequencing coverage of the bacterial database was above 99.72% (Fig. 1A), and that of the fungal database was above 99.98% (Fig. 1B), indicating that the sequencing depth was sufficient to reflect the microbial community structure of the samples.

A gentle curve indicates sufficient sequencing depth. **HG.** Non-rhizosphere soil of healthy *Angelica sinensis*; **HS.** Rhizosphere soil of healthy *A. sinensis*; **HRT.** Rhizoplane of healthy *A. sinensis*; **HRO.** Root endosphere of healthy *A. sinensis*; **HLT.** Phylloplane of healthy *A. sinensis*; **HLO.** Endophyllosphere of healthy *A. sinensis*; **DG.** Non-rhizosphere soil of diseased *A. sinensis*; **DS.** Rhizosphere soil of diseased *A. sinensis*; **DRT.** Rhizoplane of diseased *A. sinensis*;

DRO. Root endosphere of diseased *A. sinensis*; **DLT.** Phylloplane of diseased *A. sinensis*; **DLO.** Endophyllosphere of diseased *A. sinensis*. The same applies below.

Fig. 1 Rarefaction curves of bacterial (**A**) and fungal (**B**) communities in *Angelica sinensis* samples from different plant tissues

2.2 Analysis of Diversity Indices

As shown in Table 1, the Ace index and Chao 1 index of bacterial communities in samples from different tissue/site categories of *A. sinensis* showed a trend of soil > root > leaf, indicating that species richness gradually decreased from belowground to aboveground. Meanwhile, the Shannon index showed a trend of soil > root > leaf, and the Simpson index showed a trend of leaf > root > soil, indicating that species diversity and evenness gradually decreased from belowground to aboveground. In addition, under interference by *Pseudomonas syringae* pv. *angelicae*, the Ace index and Chao 1 index of diseased *A. sinensis* decreased significantly compared with the healthy group in root-zone compartments such as non-rhizosphere soil, rhizosphere soil, rhizoplane, and root endosphere ($P < 0.05$), whereas there was no significant difference between the healthy and diseased groups in the phylloplane and endophyllosphere. This indicates that the pathogen caused a decline in bacterial richness and a reduction in species number in root-zone compartments, but had a relatively minor effect on the phyllosphere. Moreover, the Shannon index of diseased *A. sinensis* decreased significantly only in the rhizoplane and root endosphere ($P < 0.05$), indicating that the pathogen mainly interfered with the evenness of bacterial communities in the root compartments; the Simpson index decreased significantly only in the endophyllosphere ($P < 0.05$), indicating that the relative-abundance distribution of species in the microbial composition of the leaf endosphere became more even. This phenomenon contrasted with the significant response observed in root-zone compartments and may reflect the specificity of the response of the leaf endophytic microecological environment to interference by *Pseudomonas syringae* pv. *angelicae*.

As shown in Table 2, overall, the Ace index and Chao 1 index of fungal communities in samples from different tissue/site categories of *A. sinensis* showed a trend of soil > root > leaf, indicating that species richness was highest in soil, followed by the root endosphere. Meanwhile, the Shannon index showed···

···showed the trend of soil > root > leaf, whereas the Simpson index showed the trend of leaf > root > soil, indicating that species diversity and evenness gradually decreased from bottom to top. Meanwhile, under the interference of *Fusarium solani*, the Ace index and Chao 1 index of diseased *Angelica sinensis* were significantly lower than those of the healthy group in the rhizosphere soil and root endosphere compartments ($P<0.05$), but there were no significant differences between the healthy and diseased groups in non-rhizosphere soil and phyllosphere samples. This indicates that the pathogen mainly caused

decreases in fungal richness and species number in the root endosphere and rhizosphere, while its influence on the phyllosphere and non-rhizosphere was relatively small. In addition, the Shannon index of diseased *Angelica sinensis* decreased significantly in rhizosphere soil, rhizoplane, root endosphere, and phylloplane ($P<0.05$), indicating that the pathogen simultaneously interfered with the evenness of fungal communities in the root zone and phyllosphere; whereas the Simpson index decreased significantly only in the rhizoplane and phylloplane ($P<0.05$), indicating that the pathogen had a significant effect on the dominance distribution of fungal communities on the rhizoplane and phylloplane, but relatively weak interference with the dominant species structure in other compartments.

Table 1 Variations in bacterial community alpha diversity indices across different tissue samples of *Angelica sinensis*

Sample	Sample	Ace index	Chao 1 index	Shannon index	Simpson index
Non-rhizosphere soil	Healthy group HG	2 264.85 ± 201.48a	2 210.39 ± 199.10a	6.82 ± 0.07a	0.00 ± 0.00c
Non-rhizosphere soil	Diseased group DG	2 038.95 ± 86.74bc	1 996.80 ± 82.79bc	6.75 ± 0.05a	0.00 ± 0.00c
Rhizosphere soil	Healthy group HS	2 048.18 ± 151.96bc	1 994.71 ± 143.14bc	6.71 ± 0.08a	0.00 ± 0.00c
Rhizosphere soil	Diseased group DS	1 760.59 ± 122.49b	1 717.89 ± 121.09b	6.31 ± 0.15a	0.00 ± 0.00c
Rhizoplane	Healthy group HRT	922.17 ± 97.56cd	921.75 ± 97.15cd	5.77 ± 0.11a	0.01 ± 0.00c
Rhizoplane	Diseased group DRT	279.33 ± 15.94ef	276.75 ± 15.93ef	3.08 ± 0.11c	0.10 ± 0.01bc
Root endosphere	Healthy group HRO	1 088.83 ± 83.38c	1 076.47 ± 84.65c	5.76 ± 0.08a	0.01 ± 0.00c
Root endosphere	Diseased group DRO	657.53 ± 306.15de	648.14 ± 299.85de	4.23 ± 1.04b	0.07 ± 0.05bc
Phylloplane	Healthy group HLT	141.11 ± 37.95f	139.28 ± 37.83f	3.02 ± 0.25c	0.12 ± 0.06b

Sample	Sample	Ace index	Chao 1 index	Shannon index	Simpson index
Phylloplane	Diseased group DLT	528.79 ± 840.15def	524.88 ± 833.64ef	4.01 ± 1.60bc	0.08 ± 0.08bc
Endophyllosphere	Healthy group HLO	383.91 ± 106.73ef	383.30 ± 107.01ef	3.41 ± 1.47bc	0.23 ± 0.23a
Endophyllosphere	Diseased group DLO	405.58 ± 392.69ef	403.44 ± 393.70ef	3.74 ± 1.27bc	0.07 ± 0.05bc

Note: The data are $\bar{x} \pm s$, and different letters in the same column indicate significant differences (P<0.05). The same below.

Table 2 Variations in fungal community alpha diversity indices across different tissue samples of *Angelica sinensis*

Sample	Ace index	Chao 1 index	Shannon index	Simpson index

Sample compart-ment	Group	Chao1	Observed species	Shannon	Simpson
Non-rhizosphere soil	Healthy group HG	475.55 ± 44.13a	476.04 ± 43.42a	4.46 ± 0.21a	0.03 ± 0.01e
Non-rhizosphere soil	Diseased group DG	466.01 ± 32.98a	464.91 ± 32.91a	4.34 ± 0.31a	0.04 ± 0.02e
Rhizosphere soil	Healthy group HS	483.56 ± 57.41a	483.65 ± 58.44a	4.38 ± 0.17a	0.03 ± 0.01e
Rhizosphere soil	Diseased group DS	381.64 ± 73.76b	379.48 ± 72.91b	3.29 ± 0.67b	0.11 ± 0.09e
Rhizoplane	Healthy group HRT	87.08 ± 13.67e	87.00 ± 13.56e	3.52 ± 0.38b	0.07 ± 0.04e
Rhizoplane	Diseased group DRT	112.64 ± 11.94de	113.20 ± 11.99de	2.05 ± 0.14c	0.41 ± 0.04b

Fig. 2 Principal coordinate analysis (PCoA) of bacterial (A) and fungal (B) communities in different tissue compartments of healthy and diseased Angelica sinensis

Figure 2: Fig. 2 Principal coordinate analysis (PCoA) of bacterial (A) and fungal (B) communities in different tissue compartments of healthy and diseased Angelica sinensis

Sample compartment	Group	Chao1	Observed species	Shannon	Simpson
Root endosphere	Healthy group HRO	210.00 ± 29.69c	211.65 ± 32.81c	3.17 ± 0.37b	0.13 ± 0.08de
Root endosphere	Diseased group DRO	112.87 ± 32.85de	112.17 ± 33.13de	2.20 ± 0.49c	0.23 ± 0.10cd
Phylloplane	Healthy group HLT	91.80 ± 21.00e	91.80 ± 21.00e	1.19 ± 0.21d	0.63 ± 0.07a
Phylloplane	Diseased group DLT	114.82 ± 17.61de	114.75 ± 17.74de	2.05 ± 0.13c	0.38 ± 0.04b
Endophyllosphere	Healthy group HLO	129.15 ± 20.18de	128.94 ± 20.37de	2.40 ± 0.68c	0.22 ± 0.20cd
Endophyllosphere	Diseased group DLO	154.85 ± 16.80d	154.18 ± 16.94d	2.16 ± 0.31c	0.33 ± 0.08bc

Principal coordinate analysis (PCoA) was performed by calculating the Bray-Curtis distance matrix. As shown in Fig. 2, under the intervention of the root-rot pathogen, samples from the healthy and diseased groups within the same corresponding compartment all separated along the coordinate axes, indicating that the pathogen had a relatively large effect on the community structures of bacteria (Fig. 2: A) and fungi (Fig. 2: B) in different corresponding compartments. At the same time, regardless of whether exogenous interference was present, samples from different compartments within *Angelica sinensis* individuals were clearly separated along the coordinate axes, further verifying that the community structures in different compartments of *A. sinensis* exhibit significant spatial heterogeneity.

Fig. 2 Principal coordinate analysis (PCoA) of bacterial (A) and fungal (B) communities in different tissue compartments of healthy and diseased *Angelica sinensis*

Fig. 3A-B

Figure 3: Fig. 3A-B

2.3 Composition of bacterial community structures in different compartments

As shown in Fig. 3: A, the composition of the dominant bacterial phyla in different compartments of *A. sinensis* was basically consistent. The major bacterial phyla consisted of 12 phyla, including Proteobacteria, Actinobacteriota, and Firmicutes, accounting for 98.56%-99.84% of the total relative abundance. At the genus level (Fig. 3: B), the bacterial microbial communities in different compartments were mainly composed of 19 genera, including *Pseudomonas*, *Pantoea*, Unclassified__f__Comamonadaceae, *Sphingomonas*, and *Massilia*, accounting for 12.86%-82.35% of the total relative abundance.

In addition, the relative abundances of the dominant bacterial phyla in samples from different compartments of *A. sinensis* were disturbed to varying degrees by the root-rot pathogen, indicating that pathogen infection reshaped the bacterial community structures in different compartments of *A. sinensis*. In the diseased group, the relative abundances of Proteobacteria and Actinobacteriota increased significantly in the rhizoplane, root endosphere, and phylloplane; Firmicutes decreased significantly in the rhizoplane and phylloplane; whereas the relative abundances of Bacteroidota, Verrucomicrobiota, Chloroflexi, Acidobacteriota, Gemmatimonadota, and Nitrospirota, among others, did not change significantly in the interleaf compartment,

The main manifestation was a significant decrease in non-rhizosphere soil, rhizosphere soil, root surface, and root interior. In particular, the relative abundance of dominant bacterial phyla in rhizosphere soil decreased significantly in all six cases, followed by the root surface, where the relative abundance of dominant bacterial phyla decreased significantly in three cases. This indicates that rhizosphere soil and the root surface are extremely sensitive to the interference of *Fusarium solani* and may be core sites of changes in bacterial community structure.

Fig. 3 The composition of bacterial communities in different parts samples of *Angelica sinensis* at phylum level (**A**) and genus level (**B**)

As shown in Fig. 4, the proportions of shared bacterial genera between the diseased group and the healthy group of *Angelica sinensis* in non-rhizosphere soil (Fig. 4: A), rhizosphere soil (Fig. 4: B), root surface (Fig. 4: C), root interior (Fig. 4: D), leaf surface (Fig. 4: E), and leaf interior (Fig. 4: F) were 69.63%, 65.60%, 32.19%, 57.47%, 26.68%, and 50.81%, respectively. Among them, the proportion of shared bacterial genera on the root surface and leaf surface was the smallest, indicating that the pathogen caused the most severe disturbance to the bacterial genus structure in these parts. Meanwhile, it was found that the number of bacterial genera in diseased *Angelica sinensis* decreased signif-

Fig. 4A-F

Figure 4: Fig. 4A-F

Fig. 5 Volcano plot of differentially bacterial genera in different tissue compartments of healthy and diseased Angelica sinensis

Figure 5: Fig. 5 Volcano plot of differentially bacterial genera in different tissue compartments of healthy and diseased Angelica sinensis

icantly in soil and root parts, but increased significantly on the leaf surface, indicating that different parts respond differently in their bacterial communities to pathogen interference. Further analysis of the shared bacterial genera in different parts of healthy and diseased *Angelica sinensis*, as shown in Fig. 5, showed that in non-rhizosphere soil (Fig. 5: A), rhizosphere soil (Fig. 5: B), root surface (Fig. 5: C), root interior (Fig. 5: D), leaf surface (Fig. 5: E), and leaf interior (Fig. 5: F), there were respectively 43, 137, 106, 112, 11, and 28 bacterial genera with significant differences ($P<0.05$), indicating that the pathogen had the strongest effect on the relative abundance of bacterial genera in rhizosphere soil, root surface, and root interior, and that diseased *Angelica sinensis* had more bacterial genera with reduced relative abundance in the above three parts.

A. Non-rhizosphere soil samples of *Angelica sinensis*; **B.** rhizosphere soil samples of *Angelica sinensis*; **C.** root-surface samples of *Angelica sinensis*; **D.** root-interior samples of *Angelica sinensis*; **E.** leaf-surface samples of *Angelica sinensis*; **F.** leaf-interior samples of *Angelica sinensis*. Same below.

A. Non-rhizosphere soil samples of *A. sinensis*; **B.** Rhizosphere soil samples of *A. sinensis*; **C.** Rhizoplane samples of *A. sinensis*; **D.** Root endosphere samples of *A. sinensis*; **E.** Phylloplane samples of *A. sinensis*; **F.** Endophyllosphere samples of *A. sinensis*. The same below.

Fig. 4 Venn diagram of bacterial genera in different tissue compartments of healthy and diseased *Angelica sinensis*

Fig. 5 Volcano plot of differentially bacterial genera in different tissue compartments of healthy and diseased *Angelica sinensis*

The 10 bacterial genera with the most significant differences among different compartments of *A. sinensis* between the healthy group and the diseased group were analyzed. As shown in Supplementary Table 1, the diseased group and the healthy group each had distinct differential bacterial genera in all six compartments. However, *Pseudomonas*, *Bradyrhizobium*, *Sphingobium*, *Allorhizobium-Neorhizobium-Pararhizobium-Rhizobium*, *Devosia*, and other genera showed significant differences in multiple compartments. Among them, *Pseudomonas* appeared simultaneously in rhizosphere soil, rhizoplane, root endosphere, phylloplane, and leaf endosphere; except in the phylloplane, it showed a significant in-

creasing trend in the other compartments. *Bradyrhizobium* appeared simultaneously in non-rhizosphere soil, rhizoplane, root endosphere, and phylloplane; except in non-rhizosphere soil, it showed a significant decreasing trend in the other compartments. *Sphingobium* and *Allorhizobium-Neorhizobium-Pararhizobium-Rhizobium* appeared simultaneously in rhizosphere soil, rhizoplane, and root endosphere, and both increased significantly. *Devosia* appeared simultaneously in rhizosphere soil, rhizoplane, and leaf endosphere; it increased significantly in rhizosphere soil and decreased significantly in rhizoplane and leaf endosphere. These genera, which exhibit specific dynamic changes across different compartments under pathogen disturbance, may be key microbial taxa affecting the health status of *A. sinensis*.

2.4 Structural composition of fungal communities in different compartments

As shown in Fig. 6A, the composition of the dominant fungal phyla differed among different compartments of *A. sinensis*. Among them, the dominant fungal phyla in non-rhizosphere soil, rhizosphere soil, rhizoplane, and root endosphere were mainly Ascomycota, Basidiomycota, Fungi_phy_Incertae_sedis, Mortierellomycota, Chytridiomycota, Unclassified_fungi, and Kickxellomycota, seven phyla in total, accounting for 99.15%–100% of the total relative abundance. In contrast, the phylloplane and leaf endosphere were mainly composed of Ascomycota, Basidiomycota, Fungi_phy_Incertae_sedis, and Unclassified_fungi, four phyla in total, accounting for 99.99%–100% of the total relative abundance. At the genus level (Fig. 6B), the fungal microbial communities in different compartments of *A. sinensis* were mainly composed of *Filobasidium*, [[unclear: text continues on next page]]

Plectosphaerella, *Erysiphe*, *Fusarium*, Fungi_gen_Incertae_sedis, and other 15 genera, accounting for 58.10%–91.72% of the total relative abundance.

In addition, the relative abundance of the dominant fungal phyla in samples from different parts of *Angelica sinensis* was disturbed to varying degrees by *Fusarium solani*, indicating that pathogen invasion reshaped the fungal community structure in different parts of *Angelica sinensis*. In the diseased group, the relative abundance of Ascomycota increased significantly in rhizosphere soil and root surface, and decreased significantly in leaf surface; the relative abundance of Basidiomycota increased significantly on the leaf surface and inside leaves; the relative abundance of Fungi_phy_Incertae_sedis decreased significantly inside leaves; the relative abundance of Mortierellomycota decreased significantly in rhizosphere soil; the relative abundance of Chytridiomycota increased significantly in non-rhizosphere soil and decreased significantly in rhizosphere soil; the relative abundance of unclassified fungi decreased significantly in rhizosphere soil and inside leaves; the relative abundance of Glomeromycota decreased significantly in rhizosphere soil, root surface, and inside roots; the relative abundance of Kickxellomycota decreased significantly in non-rhizosphere soil; the relative abundance of Zoopagomycota increased significantly in non-rhizosphere

Fig. 6. The composition of fungal communities in different parts samples of Angelica sinensis at phylum level (A) and genus level (B)

Figure 6: Fig. 6. The composition of fungal communities in different parts samples of Angelica sinensis at phylum level (A) and genus level (B)

Fig. 7 Venn diagram of fungal genera in different tissue compartments of healthy and diseased *Angelica sinensis*

Figure 7: Fig. 7 Venn diagram of fungal genera in different tissue compartments of healthy and diseased *Angelica sinensis*

soil; and the relative abundance of Olpidiomycota decreased significantly inside roots. Among them, the relative abundance of five fungal phyla changed significantly in rhizosphere soil, and that of three changed significantly inside leaves, indicating that rhizosphere soil and leaf interior were extremely sensitive to disturbance by *Fusarium solani* and may be the core sites of changes in fungal community structure.

Fig. 6 The composition of fungal communities in different parts samples of *Angelica sinensis* at phylum level (A) and genus level (B)

As shown in Fig. 7, under *Fusarium solani* interference, the proportions of shared fungal genera between the healthy and diseased groups of *Angelica sinensis* in non-rhizosphere soil (Fig. 7: A), rhizosphere soil (Fig. 7: B), root surface (Fig. 7: C), root interior (Fig. 7: D), leaf surface (Fig. 7: E), and leaf interior (Fig. 7: F) were 24.99%, 20.92%, 14.67%, 14.98%, 19.07%, and 18.20%, respectively. Among them, the proportions of shared fungal genera on the root surface and inside roots were relatively the lowest, indicating that pathogen disturbance of the fungal genus structure in these parts was the most intense. It was also found that the number of fungal genera in diseased *Angelica sinensis* decreased markedly in rhizosphere soil, root surface, and root interior, further indicating that the response of root-associated parts to pathogen disturbance was relatively strong.

Through further analysis of the shared fungal genera in different parts of healthy and diseased *Angelica sinensis*, as shown in Fig. 8, there were 20, 46, 10, 22, 15, and 23 fungal genera with significant differences ($P<0.05$) between the diseased and healthy groups in non-rhizosphere soil (Fig. 8: A), rhizosphere soil (Fig. 8: B), root surface (Fig. 8: C), root interior (Fig. 8: D), leaf surface (Fig. 8: E), and leaf interior (Fig. 8: F), respectively. This indicates that the pathogen had the most pronounced effect on the relative abundance of fungal genera in rhizosphere soil, and that the relative abundance of most fungal genera decreased.

Fig. 7 Venn diagram of fungal genera in different tissue compartments of healthy and diseased *Angelica sinensis*

Fig. 8 Volcano plot of differentially fungal genera in different tissue compartments of healthy and diseased Angelica sinensis

Figure 8: Fig. 8 Volcano plot of differentially fungal genera in different tissue compartments of healthy and diseased Angelica sinensis

Fig. 8 Volcano plot of differentially fungal genera in different tissue compartments of healthy and diseased *Angelica sinensis*

The 10 fungal genera with the most significant differences among different tissue compartments of healthy and diseased *Angelica sinensis* were analyzed. As shown in Supplementary Table 2, the diseased group and the healthy group each had distinct differential fungal genera in all 6 compartments. However, the genus *Erysiphe* showed significant differences; it occurred simultaneously in the root surface, root interior, leaf surface, and leaf interior, and, except in the root interior, showed a significant decreasing trend in all of these compartments. The genus *Plectosphaerella* occurred simultaneously in rhizosphere soil, the root surface, and the root interior, and all showed a significant increasing trend. The genus Fungi_gen_Incertae_sedis occurred simultaneously in rhizosphere soil, the leaf surface, and the leaf interior; it showed a significant decreasing trend in rhizosphere soil and on the leaf surface, and a significant increasing trend inside the leaf. The genus *Filobasidium* occurred simultaneously in the root interior, leaf surface, and leaf interior, and decreased significantly in the root interior while increasing significantly on the leaf surface and in the leaf interior.

2.5 Correlations between differential bacterial genera that varied across multiple compartments and *Fusarium* genera

Spearman correlation analysis was performed between differential bacterial genera that varied across multiple compartments of *Angelica sinensis* and *Fusarium* genera. As shown in Table 3, the differential fungal genera showed no significant correlation with *Fusarium* genera, whereas differential bacterial genera exhibited varying degrees of correlation with *Fusarium* genera in different compartments. Among them, *Pseudomonas* was significantly positively correlated with *Fusarium* in rhizosphere soil; *Bradyrhizobium* was significantly positively correlated with *Fusarium* in the root interior and on the leaf surface; *Sphingobium*

In the rhizosphere soil, rhizoplane, and root endosphere, it was significantly positively correlated with *Pseudomonas*; *Devosia* was significantly positively correlated with *Pseudomonas* in the rhizosphere soil and endophyllosphere.

Table 3 Correlation analysis between key bacterial/fungal genera and *Fusarium* across *Angelica sinensis* tissue compartments

Figure 9: Visualized networks of microbial co-occurrence patterns across healthy and diseased *Angelica sinensis* tissue compartments

Figure 9: Figure 9: Visualized networks of microbial co-occurrence patterns across healthy and diseased *Angelica sinensis* tissue compartments

Bacterial and fungal genus	Non-rhizosphere soil	Rhizosphere soil	Rhizoplane	Root endosphere	Phylloplane	Endophyllosphere
Pseudomonas	—	0.782**	-0.600	0.610	0.550	-0.150
Bradyrhizobium	-0.260*	—	0.479	0.670*	0.650*	—
Sphingobium	—	0.661*	0.661*	0.800*	—	—
Allorhizobium-Neorhizobium-Pararhizobium-Rhizobium	—	-0.697*	-0.600	0.600	—	—
Devosia	—	0.636*	0.200	—	—	0.770**
Erysiphe	—	—	0.370	-0.480	0.600	0.330
Plectosphaerella	—	-0.500	-0.570	0.040	—	—
Fungi_gen_Incertae_sedis	0.610	—	—	0.410	-0.140	
Filobasidium	—	—	—	-0.490	-0.600	-0.095

Note: * and ** indicate significantly correlated at the levels of $P<0.05$ and $P<0.01$, respectively.

2.6 Microbial co-occurrence network analysis

To clarify the effects of Angelica root rot on interspecific interactions among microorganisms, a cross-kingdom bacterial–fungal co-occurrence network was constructed at the ASV level. As shown in Figure 9 and Supplementary Table 3, after the occurrence of Angelica root rot, the rhizoplane and root endosphere exhibited simpler network patterns, with fewer network nodes than healthy plants; in contrast, the microbial networks in the phylloplane and endophyllosphere became more complex after disease occurrence, with both the number of network nodes and the number of network edges exceeding those in healthy plants, while there were no substantial changes in non-rhizosphere soil and rhizosphere soil. Except for the rhizoplane, among network nodes in all other compartments, the proportion of bacteria showed an upward trend, whereas the proportion of fungi showed a downward trend. This indicates that root rot altered the complexity and composition of microbial co-occurrence networks in different compartments of *A. sinensis*, and that its effects were compartment-specific.

The pink and blue dots represent bacteria and fungi, respectively, and the red and green edges indicate positive and negative correlations, respectively.

Fig. 9 Visualized networks of microbial co-occurrence patterns in across healthy and diseased *Angelica sinensis* tissue compartments

2.7 Microbial Phenotypes and Functional Prediction in Different Compartments

To further understand the proportions and characteristics of different phenotypic microorganisms in each compartment of *A. sinensis* under dry-rot-pathogen stress, BugBase was used to predict nine bacterial phenotypes, as shown in Fig. 10A. Except for the leaf endosphere compartment, the proportions of bacterial phenotypes in the other compartments differed significantly between groups. Among them, in the non-rhizosphere soil diseased group, the proportions of aerobic bacteria ($P = 0.038$) and Gram-positive bacteria ($P = 0.032$) were significantly lower than those in the healthy group, whereas the proportions of anaerobic bacteria ($P = 0.022$), facultatively anaerobic bacteria ($P = 0.036$), and Gram-negative bacteria ($P = 0.032$) were significantly higher. In the rhizosphere soil diseased group, the proportions of mobile-element-containing taxa ($P = 0.05$), facultatively anaerobic bacteria ($P < 0.001$), potential pathogens ($P = 0.04$), and stress-tolerant bacteria ($P = 0.028$) were significantly higher than those in the healthy group. In the root epidermis diseased group, the proportions of aerobic bacteria ($P = 0.022$), anaerobic bacteria ($P = 0.003$), and Gram-positive bacteria ($P = 0.045$) were significantly lower than those in the healthy group, whereas the proportions of Gram-negative bacteria ($P = 0.045$), potential pathogens ($P = 0.02$), and stress-tolerant bacteria ($P = 0.017$) were significantly higher. In the root endosphere diseased group, the proportion of anaerobic bacteria ($P < 0.001$) was significantly lower than that in the healthy group, whereas the proportion of mobile-element-containing taxa ($P = 0.022$) was significantly higher. In the leaf epidermis diseased group, the proportions of mobile-element-containing taxa ($P = 0.003$), Gram-negative bacteria ($P < 0.001$), potential pathogens ($P = 0.003$), stress-tolerant bacteria ($P = 0.003$), and Gram-positive bacteria ($P < 0.001$) were significantly lower than those in the healthy group.

FUNGuild was used to perform functional prediction of 10 guilds for the fungal community, as shown in Fig. 10B. In the non-rhizosphere soil diseased group, the proportion of pathogen-saprotroph guilds ($P = 0.004$) was significantly lower than that in the healthy group. In the rhizosphere soil diseased group, the proportions of saprotroph-symbiotroph guilds ($P = 0.014$) and pathogen-saprotroph-symbiotroph guilds ($P = 0.006$) were significantly lower than those in the healthy group, whereas the proportion of pathogen guilds ($P = 0.023$) was significantly higher. In the root epidermis diseased group, the proportions of saprotroph guilds ($P = 0.007$) and pathogen-saprotroph-symbiotroph guilds ($P = 0.018$) were significantly lower than those in the healthy group, whereas the proportions of pathogen-symbiotroph guilds ($P < 0.001$) and pathogen guilds ($P < 0.001$) were significantly higher. In the root endosphere diseased group, the proportion of saprotroph-symbiotroph guilds ($P = 0.020$) was significantly

Figure 10A-B: stacked bar charts of BugBase phenotypic prediction and FUNGuild functional prediction

Figure 10: Figure 10A-B: stacked bar charts of BugBase phenotypic prediction and FUNGuild functional prediction

lower than that in the healthy group. In the leaf epidermis diseased group, saprotroph-symbiotroph guilds ($P = 0.003$) and pathogen guilds in the leaf endosphere diseased group ($P = 0.001$) were significantly lower than those in the healthy group.

decreased significantly, whereas the saprotroph trophic type ($P = 0.001$), pathotroph-saprotroph-symbiotroph trophic type ($P = 0.003$), and pathotroph-saprotroph trophic type ($P = 0.016$) increased significantly.

Fig. 10 BugBase phenotypic prediction of bacterial communities (A) and FUNGuild functional prediction of fungal communities (B) across healthy and diseased *Angelica sinensis* tissue compartments

Fig.10 BugBase phenotypic prediction of bacterial communities (A) and FUNGuild functional prediction of fungal communities(B)across healthy and diseased *Angelica sinensis* tissue compartments

3 Discussion

3.1 Changes in microbial communities in different compartments of *Angelica sinensis* under *Fusarium solani* intervention

PCoA analysis showed that, regardless of whether there was pathogen intervention, the bacterial and fungal communities in different compartments of *Angelica sinensis* were clearly separated in the coordinate system. Meanwhile, the Alpha diversity indices indicated that the species diversity and evenness of microorganisms in different compartments of *Angelica sinensis* exhibited a gradual decline from belowground to aboveground. This suggests that significant spatial heterogeneity exists among different compartments of *Angelica sinensis*, and that different compartments exert directional selectivity on microbial taxa (Chaparro et al., 2014). This phenomenon may occur because soil provides microorganisms with a more complex nutrient structure and microhabitats, supporting more diversified colonization by microbial communities, whereas the phyllosphere is affected by light exposure, humidity fluctuations, and plant defense systems, resulting in a relatively high threshold for microbial colonization (Nwachukwu et al., 2021).

Under *Fusarium solani* intervention, the relative abundance of most bacterial phyla decreased significantly in the rhizosphere soil and root surface of *Angelica*

sinensis, and the relative abundance of most fungal phyla decreased significantly in the rhizosphere soil and leaves of *Angelica sinensis*. This indicates that pathogen invasion exerted strong competitive or inhibitory effects on the bacterial communities of the rhizosphere and root surface, as well as on the fungal communities in leaves, possibly due to differences in resistance among the various compartments. Similar situations have also been reported for root rot infection in *Lycium barbarum* in Ningxia (Jia Chenbo, 2021) and angular leaf spot infection in tobacco (Wu Xiaojun et al., 2023). Compared with the healthy group, the proportion of shared bacterial genera in the root surface and leaf surface of diseased *Angelica sinensis* was the lowest (32.19% and 26.68%, respectively), and the proportion of shared fungal genera in the root surface and root interior was the lowest (14.67% and 14.98%), suggesting that pathogens most markedly disturbed the microbial community structure in these compartments. At the same time, the numbers of bacterial genera and fungal genera in the soil and root compartments of diseased *Angelica sinensis* decreased significantly, whereas the number of bacterial genera in the phyllosphere increased significantly. This phenomenon—where pathogen intervention led to simplification of belowground microbial communities and increased complexity of aboveground microbial communities—may reflect differential effects of disease on the microenvironments of plant compartments, as well as potential microbial migration or systemic responses (Ling et al., 2022).

In addition, Venn analysis and volcano plots of differential genera showed that, among the shared bacterial genera in different compartments, the rhizosphere soil, root surface, and root interior contained the greatest number of genera with significant differences; among the shared fungal genera, the rhizosphere soil contained the greatest number of genera with significant differences and

The abundance of most bacterial genera decreased, indicating that pathogens exerted a broad inhibitory effect on the local underground microbial community, possibly damaging the core functional microbial groups that maintain root health and disrupting the original stable structure of the microbial community in this region (Wang Baoying, 2022). Moreover, studies of microbial network interactions under *Fusarium* root-rot interference in *Angelica sinensis* also confirmed that root rot altered the complexity and composition of microbial networks in different parts of *A. sinensis*. Overall, pathogens had a much greater impact on the underground microbial community of *A. sinensis* than on the aboveground community, and caused greater fluctuations in bacterial communities. Therefore, early prevention and control of root rot should focus on the stability of underground microbial communities.

3.2 Co-occurrence relationships between differentially abundant genera and pathogens in *Angelica sinensis* under interference by *Fusarium oxysporum*

Although, under pathogen interference, the bacterial and fungal genera showing the most significant differences between diseased and healthy *A. sinensis*

differed among different plant parts, bacterial genera such as *Pseudomonas*, *Bradyrhizobium*, *Azohydromonas*, and Devosiaceae, among others, showed significant differences in multiple parts of *A. sinensis*; fungal genera such as *Erysiphe*, *Plectosphaerella*, *Fungi_gen_Incertae_sedis*, and *Filobasidium* also showed significant differences in multiple parts of *A. sinensis*. These genera that differed significantly across multiple plant parts are likely to play key roles in the physiological response of *A. sinensis* to pathogen interference.

Spearman correlation analysis showed that bacterial genera such as *Pseudomonas*, *Bradyrhizobium*, *Azohydromonas*, and Devosiaceae were significantly positively correlated with *Fusarium* in multiple parts of *A. sinensis*. This suggests that they were co-enriched during the disease process, but this correlation cannot directly demonstrate active host recruitment. Existing studies have shown that multiple members of the above genera possess disease-resistance, growth-promoting, or detoxification functions: *Pseudomonas* can control pathogens by producing antibiotics and inducing systemic resistance (Yang Yalin et al., 2024; Qessaoui et al., 2019); *Azohydromonas* can enhance plant tolerance to abiotic stress and secrete growth-promoting hormones (Boss et al., 2022); *Bradyrhizobium* has nitrogen-fixation capacity (Tao et al., 2021); and Devosiaceae can degrade fungal toxins (Liu et al., 2024; Sun Jing et al., 2022). These functional traits indicate that the above genera may be potential beneficial bacteria co-enriched during the response of *A. sinensis* to disease, but their specific functional roles still require further verification through inoculation experiments and metabolomic analysis.

3.3 Functional changes in microbial communities in different parts of *Angelica sinensis* under interference by *Fusarium oxysporum*

BugBase bacterial phenotype prediction showed that, under interference by *Fusarium oxysporum*, the abundance of mobile elements that negatively affect plant growth and pathogenic-potential bacteria increased significantly in the rhizosphere soil, root surface, and root interior, but decreased in leaves; meanwhile, stress-tolerant bacteria that positively affect plant growth also increased significantly in the corresponding parts and decreased in leaves. This seems to indicate that among the genera increasing or decreasing synchronously with *Fusarium*, some potential beneficial bacteria recruited by the plant may exist. In the early stage of pathogen invasion, plants may actively restructure their microbial communities, recruiting and accumulating beneficial bacteria to enhance resistance and delay disease progression. This is consistent with the findings of Carrión et al. (2019), who found that endophytic bacteria induced by pathogens suppress fungal diseases by activating specific biosynthetic gene clusters. Gao et al. (2025) reported that in the early stage of root rot in *Ligusticum chuanxiong*, bacterial communities showed the potential to suppress disease and beneficial groups increased, such as *Microbacterium* and *Variovorax*.

FUNGuild fungal functional prediction showed that saprotrophic nutritional types and saprotrophic–symbiotrophic nutritional types of fungi beneficial to

plant growth decreased significantly in the rhizosphere soil, root surface, root interior, and leaves, whereas pathotrophic nutritional types increased significantly, revealing from a functional perspective the microbiological mechanism underlying the occurrence of root rot. Gao et al. (2021) showed that, under the stress of Fusarium wilt, the fungal communities in pepper rhizosphere organs such as roots and stems exhibited "disordered changes" rather than "functional recruitment"—the abundance of beneficial saprotrophic and symbiotrophic fungi decreased, the proportion of pathogenic fungi increased, and functionally compensatory beneficial fungi were not enriched. This is consistent with the results of the present study, indicating that fungi are not the main recruitment targets of *A. sinensis* in response to disease, and also provides ideas for field control of soil-borne diseases: targeted regulation of the community structure of saprotrophic fungi can serve as a key approach for preventing and controlling soil-borne diseases. For example, compound probiotic agents with both colonization capacity and antagonistic activity may be developed, and measures such as seed coating, root irrigation at the seedling stage, or inoculation with organic-fertilizer carriers may be used to strengthen the colonization advantage of saprotrophic fungi and suppress the proliferation of pathotrophic fungi by occupying ecological niches and secreting antimicrobial metabolites. It is worth noting that, although saprotrophic–symbiotrophic fungi decreased significantly and pathotrophic fungi increased, correlation analysis showed that these fungal genera with significant differences across multiple parts were not significantly correlated with *Fusarium*. This suggests that their changes may not be directly driven by *Fusarium* abundance, but instead may be influenced by overall microecological imbalance.

It can therefore be seen that, under interference by *Fusarium oxysporum*, the fungal community of *A. sinensis* developed in a subhealthy direction, but this did not induce its recruit···

fungi with disease-suppressive or growth-promoting potential, and bacteria are the principal microbial taxa collaboratively enriched during the disease-response process of *Codonopsis pilosula*. This result is consistent with the findings of He Xiaobing et al. (He Xiaobing et al., 2025), who found that tobacco wilt root rot caused changes in the richness and community diversity of rhizosphere soil fungal taxa, while beneficial *Bacillus* increased; the pattern of bacterial response was likewise consistent.

4 Conclusion

This study revealed that the microbial communities in different parts of *Codonopsis pilosula* exhibit significant spatial heterogeneity, with both diversity and uniformity showing a gradient of decline from belowground to aboveground. Invasion by *Fusarium solani* reshaped the microbial communities in different parts of *C. pilosula*: on the one hand, the pathogen significantly reduced the abundance of bacterial communities in rhizosphere soil and root surfaces, and the abundance of fungal communities in rhizosphere soil and

within leaves, and led to simplification of bacterial and fungal community structures in belowground parts, potentially disrupting the core microbiota associated with root health; on the other hand, the number of bacterial genera in leaves increased abnormally, suggesting that disease may trigger migration of bacterial communities from aboveground to belowground parts or a systemic response, whereas the patterns of change in fungal communities were not entirely consistent. Notably, through differential recruitment of potentially beneficial bacteria in response to stress, *C. pilosula* showed significant positive correlations with the pathogen in multiple tissues for bacteria such as *Pseudomonas*, *Bradyrhizobium*, *Azospirillum*, and *Devosia*, suggesting that they may be collaboratively enriched during the disease process; their disease-resistance, growth-promoting, or detoxification functions require further verification. Fungal communities, however, did not exhibit a similar pattern of positive enrichment. Overall, when *C. pilosula* resists infection by *Fusarium solani*, it mainly relies on microecological regulation strategies mediated by bacteria. This finding provides a theoretical basis for the further development and utilization of targeted probiotics to control soil-borne diseases. Future studies may combine probiotic inoculation experiments to verify the control effects of single-strain and composite inoculations of bacterial genera such as *Pseudomonas*, *Bradyrhizobium*, *Azospirillum*, and *Devosia* against root rot of *C. pilosula*, and explore their interaction mechanisms with host metabolites and immune responses.

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Supplementary Table 1. Changes in the most significantly differentially abundant bacterial genera between diseased and healthy groups across *Angelica sinensis* tissue compartments

Non-rhizosphere soil: Bacterial genera	Non-rhizosphere soil: Diseased	Non-rhizosphere soil: Healthy		Rhizosphere soil: Bacterial genera	Rhizosphere soil: Diseased	Rhizosphere soil: Healthy		Rhizoplane: Bacterial genera	Rhizoplane: Diseased	Rhizoplane: Healthy		Root endosphere: Bacterial genera	Root endosphere: Diseased	Root endosphere: Healthy		Phylloplane: Bacterial genera	Phylloplane: Diseased	Phylloplane: Healthy		Endophyllosphere: Bacterial genera	Endophyllosphere: Diseased	Endophyllosphere: Healthy	
MB-A2-108	0.75 ± 0.11	1.16 ± 0.11	***	Cellvibrio	2.44 ± 0.47	6.16 ± 0.22	***	Pseudomonas	61.92 ± 3.56	25.83 ± 0.79	***	Bradyrhizobium	0.67 ± 0.59	4.01 ± 0.64	**	Bradyrhizobium	0.95 ± 0.09	2.09 ± 0.18	**	Massilia	2.12 ± 0.65	6.12 ± 0.11	***
0319-7L14	4.17 ± 0.21	2.31 ± 0.45	***	Sphingomonas	2.80 ± 0.33	5.36 ± 0.51	***	Stenotrophomonas	8.70 ± 0.67	0.22 ± 0.1	***	Allorhizobium-Neorhizobium-Pararhizobium-Rhizobium	3.32 ± 0.62	0.83 ± 0.17	**	Exiguobacterium	0.27 ± 0.26	6.28 ± 2.24	*	Pseudomonas	10.85 ± 4.81	0.95 ± 0.83	***
TK1066	2.18 ± 0.2	2.18 ± 0.23	***	Phyllobacterium	2.40 ± 0.6	0.61 ± 0.15	***	Devosia	0.23 ± 0.05	2.48 ± 0.22	***	Streptomyces	0.83 ± 0.89	3.98 ± 0.37	**	Arthrobacter	10.3 ± 5.32	0.38 ± 0.33	*	Massilia	32.53 ± 21.79	0.61 ± 0.98	**

Taxon 1	Value 1	Value 2	Taxon 2	Value 3	Value 4	Taxon 3	Value 5	Value 6	Taxon 4	Value 7	Value 8	Taxon 5	Value 9	Value 10	Taxon 6	Value 11	Value 12
Genus *Sphingomonas***	7.08 (±)17	5.16 (±)11	Genus *Pseudomonas***	3.52 (±)1.13	0.54 (±)0.41	Genus *Chryseobacterium***	5.38 (±)2	0.11 (±)0.02	Genus *Actinoplanes***	0.37 (±)0.14	5.06 (±)1.53	Genus *Massilia***	0.64 (±)0.2	0.12 (±)0.14	Genus *Exiguobacterium*	1.83 (±)1.33	0.16 (±)0.19
Genus *Blastococcus***	1.89 (±)0.94	1.1 (±)1.28	Genus *Sphingobium***	3.08 (±)1.12	0.38 (±)0.2	Genus *Bacillus***	0.11 (±)0.05	2.72 (±)0.37	Genus *Sphingobium***	11.1 (±)8.04	1.58 (±)0.86	Genus *Sutterella*	3.05 (±)2.07	0.17 (±)0.25	*Mitochondria*	0.31 (±)0.15	0.66 (±)0.24
Bryobacter	0.82 (±)0.3	0.60 (±)0.17	Genus *Devosia***	4.03 (±)1.11	1.42 (±)0.21	Genus *Exiguobacterium***	0.08 (±)0.01	2.92 (±)0.47	Genus *Pseudomonas***	26.5 (±)14.76	0.26 (±)0.1	Genus *Pseudomonas*	5.37 (±)3.55	11.69 (±)3.4	Genus *Kineococcus*	0.57 (±)0.46	0.02 (±)0.02
bacterium	0.42 (±)0	2.51 (±)0.17	Genus *Mesorhizobium***	1.15 (±)0.15	1.79 (±)0.25	Genus *Bradyrhizobium***	0.04 (±)0.01	2.7 (±)0.56	Genus *Promicromonospora*	5.01 (±)3.8	0.52 (±)0.25	Genus *Modestobacter*	8.79 (±)2	1.3 (±)5.2	Genus *Mesorhizobium*	0.13 (±)0.29	0.74 (±)0.48
Genus *Bradyrhizobium*	1.30 (±)0.4	0.76 (±)0.17	Genus *Flavobacterium***	3.53 (±)1.05	1.45 (±)0.83	*Allorhizobium-Neorhizobium-Pararhizobium-Rhizobium***	2.39 (±)0.12	1.12 (±)0.2	Genus *Phyllobacterium*	11.7 (±)7.94	0.22 (±)0.14	Genus *Brigantibacter*	1.02 (±)0.8	0.00 (±)0.00	Genus *Staphylococcus*	0.07 (±)0.13	0.71 (±)0.59
Family *Gemmatimonadaceae*	1.7 (±)0.12	2.30 (±)0.53	*Allorhizobium-Neorhizobium-Pararhizobium-Rhizobium***	2.56 (±)0.53	1.63 (±)0.57	Genus *Sphingobium***	3.04 (±)0.36	0.86 (±)0.24	*Sandaracinaceae*	0.16 (±)0.07	4.33 (±)3.1	Genus *Delftia*	3.83 (±)2.32	23.44 (±)17.21	*P3OB-42*	0.67 (±)0.58	0.05 (±)0.11

Col. 1	Col. 2	Col. 3	Col. 4	Col. 5	Col. 6	Col. 7	Col. 8	Col. 9	Col. 10	Col. 11	Col. 12	Col. 13	Col. 14	Col. 15	Col. 16	Col. 17	Col. 18
Microbacterium	3.57 (±)1.29	2.13 (±)0.34	*Microbacterium*	1.10 (±)0.18	3.02 (±)1.72**	*Microbacterium*	2.17 (±)0.31	0.71 (±)0.62	*Nocardioides*	1.97 (±)1.46	3.58 (±)0.39	*Paracoccus*	0.54 (±)0.38	0.09 (±)0.14	*Devosia*	0.37 (±)0.69	1.87 (±)1.27

Note: , , indicate significantly correlated at the levels of $P<0.05$, $P<0.01$ and $P<0.001$, respectively. The same below.

Supplementary Table 2 Changes in the most significantly differentially abundant fungal genera between diseased and healthy groups across *Angelica sinensis* tissue compartments

Non-rhizosphere soil Fungi genera	Non-rhizosphere soil Diseased	Non-rhizosphere soil Healthy	Rhizosphere Fungi genera	Rhizosphere Diseased	Rhizosphere Healthy	Rhizoplane Fungi genera	Rhizoplane Diseased	Rhizoplane Healthy	Root endosphere Fungi genera	Root endosphere Diseased	Root endosphere Healthy	Phylloplane Fungi genera	Phylloplane Diseased	Phylloplane Healthy	Endophyllosphere Fungi genera	Endophyllosphere Diseased	Endophyllosphere Healthy
Paraphoma	2.33±1.26	5.15±3.26	*Plectosphaerella*	28.55±6.85	10.11±3.83	*Plectosphaerella*	67.74±2.59	2.61±1.72	*Fusarium*	19.06±18.39	0.68±0.4	*Erysiphe*	0.65±0.28	79.3±4.55	*Filobasidium*	57.02±8.13	23.63±8.52
Didymella	1.06±0.39	8.83±3.14	*Mortierella*	3.9±2.22	17.25±5.69	*Titaea*	1.37±0.32	10.47±12.96	*Plectosphaerella*	17.81±20.31	1.2±0.76	*Filobasidium*	67.31±3.44	2.62±0.77	Fungi_gen_Incertae_sedis*	0.38±0.55	0.01±0.02
[[unclear: Chinese genus name]]	3.5±[illegible]	0.46	*Fusarium*	4.36±[illegible]	9.12±	*[[unclear: Chinese genus name]]*	0.28±	1.34	*[[unclear: Chinese genus name]]*	0.92±	3.01	*[[unclear: Chinese genus name]]*	12.2	5.32	*[[unclear: Chinese genus name]]*	0.50±	0.37±

Taxon	Value 1	Value 2	Taxon	Value 1	Value 2	Taxon	Value 1	Value 2	Taxon	Value 1	Value 2	Taxon	Value 1	Value 2	Taxon	Value 1	Value 2	Taxon	Value 1	Value 2
Beauveria *	2.43(±)0.15	2.14 3.88	*Erysiphe* *	0.37(±)3.93	[illegible]	*Mortierella* *	0.79(±)0.72	[illegible]	*Vishniacozyma* *	(±)1.57	[illegible]	*Erysiphe* *	0.82	2.23						
Hair-shell fungus genus *Chaetomium* *	0.55±0.22	2.00±1.24	Fungi_gen_Incertae_sedis*	1.01±0.4	3.97±1.69	*Cladosporium* *	0.23±0.19	3.59±7.24	[illegible] *	0.09±0.01	3.27±2.77	*Ampelomyces* *	0.72±0.19	3.08±0.86	*Alternaria*	8.36±2.8	10.15±4.5			
Spiromyces *	0.1±0.08	1.19±1.56	*Acrostalagmus* *	4.4±2.82	0.12±0.05	*Alternaria* *	0.14±0.06	6.96±10.46	[illegible] *	0.06±0.005	0.23±0.565	[illegible] *	3.19±0.9	0.23±0.19	[illegible]	7.2±2.02	10.29±8.2			
Linnemannia *	0.13±0.11	1.13±0.84	Genus *Fusariella* **	2.61±2.76	0.00±0.01	*Paraphoma* *	3.95±0.76	1.10±1.29	*Filobasidium* *	0.07±0.03	1.73±0.96	*Buckleyzyma* *	2.7±0.19	0.31±0.13	*Symmetrospora*	3.33±0.58	1.37±0.7			
Phialophora *	0.77±0.71	0.09±0.08	*Titaea* *	0.75±0.37	1.63±0.88	Tetracladium **	3.28±0.85	1.36±0.59	[illegible] *	0.0[illegible]±0.00	1.7[illegible]±2.76	[illegible]	2.2±0.58	0.15±0.11	Genus *Didymella* *	0.43±0.33	0.20±0.1			

Taxon	Value 1	Value 2	Taxon	Value 1	Value 2	Taxon	Value 1	Value 2	Taxon	Value 1	Value 2	Taxon	Value 1	Value 2	Taxon	Value 1	Value 2	Taxon	Value 1	Value 2
Genus *Volutella* *	0.40±0.37	0.08±0.06	*Mortierella*	[illegible]±0.06	0.05±0.03	*Aspergillus* *	0.32±0.2	2.10±2.19	[illegible] *	1.50±0.61	0.01±0.01	[illegible]_sedis *	0.87±0.41	0.14±0.08	*Erythrobasidium* *	0.15±0.05	0.05±0.05			
Sampaiozyma *	0.1±0.08	0.32±0.12	*Pyr*[illegible]	0.00±0.00	1.59±2.89	*Bra*[illegible]	0.00±0.00	2.86±2.27	*Dio*[illegible] *	0.28±0.47	1.35±1.08	[illegible]_sedis *	0.50±0.25	0.08±0.1	Genus *Epicoccum* **	0.6±0.16	1.48±0.81			
Thel[illegible] *	0.39±0.46	0.01±0.02	*Paly*[illegible] *	0.02±0.02	1.25±0.91	[illegible] **	0.01±0.03	1.94±1.17	Powdery mildew genus *Erysiphe* *	0.01±1.00	1.74±0.49	Fungi_gen_[illegible]	0.06±0.05	0.49±0.35	*Sep*[illegible]_sedis*	0.46±0.05				

Supplementary Table 3 Topological properties of microbial networks

Network	Non-rhizosphere soil DG	Non-rhizosphere soil HG	Rhizosphere soil DS	Rhizosphere soil HS	Rhizoplane DRT	Rhizoplane HRT	Root endosphere DRO	Root endosphere HRO	Phyllosphere DLT	Phyllosphere HLT	Endophyllosphere DLO	Endophyllosphere HLO
Number of nodes	1 044	1 041	1 002	1 122	290	851	558	815	779	192	581	542
Number of edges	8 380	7 776	9 267	8 628	1 657	1 2267	10 804	8 844	152 267	1 132	57 919	9 189
Positive edge ratio (%)	86.62	84.10	91.99	87.00	96.32	98.44	99.07	94.22	99.90	98.67	99.81	99.74
Negative edge ratio (%)	13.38	15.90	8.01	13.00	3.68	1.56	0.93	5.78	0.10	1.33	0.19	0.26

Network	Non-rhizosphere soil DC	Non-rhizosphere soil HG	Rhizosphere soil DS	Rhizosphere soil HS	Rhizosphere DRT	Rhizosphere HRT	Root endosphere DRO	Root endosphere HRO	Phyllosphere DLT	Phyllosphere HLT	Phyllosphere DLO	Phyllosphere HLO
Bacterial node ratio (%)	70.21	68.01	70.86	69.52	57.24	82.37	75.45	71.53	87.55	59.90	85.71	81.18
Fungal node ratio (%)	29.79	31.99	29.14	30.48	42.76	17.63	24.55	28.47	12.45	40.10	14.29	18.82
Average degree	16.05	14.94	18.50	15.38	11.43	28.83	38.72	21.70	390.93	11.79	199.38	33.91
Network diameter	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	3.84	1.00	3.84	1.00
Network density	0.02	0.01	0.02	0.01	0.04	0.03	0.07	0.03	0.50	0.06	0.34	0.06
Modularity	4.23	4.34	4.47	4.18	2.59	5.73	4.72	4.97	0.05	2.24	0.38	5.56
Average clustering coefficient	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	0.98	1.00
Number of clusters	125	128	129	132	59	116	63	108	39	42	40	72
Degree centralization	0.04	0.03	0.05	0.04	0.07	0.07	0.13	0.05	0.20	0.11	0.24	0.11