Endophytic bacterial and fungal community compositions in different organs of ginseng (*Panax ginseng*)

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Abstract

*Panax ginseng* (*Panax ginseng* C. A. Mey) is a perennial herb of the genus ginseng, which is used as medicine with dried roots and rhizomes. With the deepening of research on ginseng, the chemical components and pharmacological effects of ginseng have gradually been discovered. Endophytes are beneficial to host plants. However, the composition of endophytes in different organs from ginseng is poorly elucidated. The report of ginsenoside production by endophytic microbes isolated from *Panax* sp., motivated us to explore the endophytic microbial diversity related to the roots, stems, and leaves. In this study, the V5–V7 variable region of endophytic bacteria 16S rRNA gene and V1 variable region of endophytic fungi ITS gene in different organs were analyzed by high-throughput sequencing. The diversity and abundance of endophytic microbes in the three organs are different and are affected by the organs. For example, the most abundant endophytic bacterial genus in roots was *Mycobacterium*, while, the stems and leaves were *Ochrobactrum*. Similarly, the fungal endophytes, *Coniothyrium* and *Cladosporium*, were also found in high abundance in stems, in comparison to roots and leaves. The Shannon index shows that the diversity of endophytic bacteria in roots is the highest, and the richness of endophytic bacterial was root > stem (*p* < 0.05). Principal coordinate analysis showed that there were obvious microbial differences among the three groups, and the endophytic bacterial composition of the leaves was closer to that of the roots. This study provides an important reference for the study of endophytic microorganisms in ginseng.

Keywords Endophyte · High-throughput sequencing · Endophytic microbial community composition · *Panax ginseng* C. A. Mey

Introduction

*Panax ginseng* is a perennial herb of the genus ginseng that is used as medicine with dried roots and rhizomes (Lee et al. 2019). It is mainly produced in Northeast China and rarely distributed in Japan, North Korea, and other places (Singh et al., 2016). Ginseng contains ginsenosides, polysaccharides, vitamins, sterols, and other effective ingredients, which have pharmacological effects such as anti-tumor, antibacterial, immune regulation, and treatment of liver fibrosis (Yang et al. 2017; Han and Kim 2020; Yuan et al. 2021). Ginsenosides were distributed in different parts of ginseng, and their composition and content were different (Pang et al. 2015). After ginseng was approved as a new resource food and circulated in the market in 2012, its demand soared (Xu et al. 2018). However, ginseng has a long growth cycle and often suffers from diseases, which restricts the crop and quality of ginseng. Although there have been reports on the ginseng genome (Hu et al. 2019; Xu et al. 2017; Liao et al. 2021), different microbiomes of rusted
and healthy ginseng roots (Liu et al. 2019a), and the effect of ginseng cultivation on the soil microbiome (Tong et al. 2021), the diversity of endophytes and ginseng-related microorganisms is still in its infancy and needs further research.

Endophytes are microorganisms that live in the internal tissues of living plants, usually bacteria or fungi (Pimente et al. 2011; Gouda et al. 2016). Some endophytes have benefits to host plants, including promotion of plant growth and resistance to plant diseases (Roodi et al. 2021). Endophytes can be used as a promising alternative to obtain bioactive compounds since the report of Taxol production by the endophytic fungus (Taxomyces andreanae) separating from Taxus brevifolia (Andrea et al. 1993). As a new microbial resource, endophytes have received widespread attention, and their diversity has become a vital factor affecting plant productivity and health, which have a wide range of application potential. It has been shown that distinct groupings of microbial communities were related to different plant organs (Ottesen et al. 2013). At present, a variety of endophytes such as Bacillus, Pantoea, Serratia, Enterobacter, Yersinia, and Pseudomonas, have been separated from plants (Mashiane et al. 2018). The distribution of endophytes is related to plant genotypes, types, organs, and growth stages. The number and types of endophytes vary due to these factors (Huang 2019; Liu et al. 2019c). At present, the research on the diversity of endophytes in ginseng is mainly through traditional isolation methods (Cao et al. 2021), and it is relatively rare to use high-throughput sequencing technology to study the diversity of endophytes in ginseng. To compare the diversity of endophytes in different organs of ginseng, this study used amplicon-sequencing technology to analyze the diversity and structure of endophytic microbial communities in the organs. The aim is to obtain more comprehensive and accurate information on the diversity of ginseng endophytes, and lay a theoretical foundation for the future development and utilization of ginseng endophytes, a beneficial biocontrol resource.

In this study, ginseng samples were used as the research object, and high-throughput sequencing technology was used to study the diversity of endophytic microbial communities related to roots, stems, and leaves. The purpose of this research is to analyze the composition, diversity, and potential functions of endophytes in three different organs of ginseng, and provide new ideas for in-depth study of endophytes in ginseng.

### Materials and methods

#### Plant materials

We collected fresh 5-year-old ginseng from Baishan Lin-cun Medicine Development Co., Ltd. in Jingyu County of Jilin Province, China (N42°21’18.85", E126°45’44.94") in September 2019. A total of 21 5-year-old samples were collected for sequencing. The experiment set up 3 groups (roots, stems, and leaves) of sample processing, each group of samples 7 repeated processing. These ginseng plants were cultivated in the planting base which managed according to the WHO guidelines on good agricultural and collection practices for medicinal plants. The soil for ginseng planting is loam with high organic matter content, and the relative soil humidity is maintained at 35% to 50%. The annual average temperature is −2.10 ~ 14.00 °C, the annual average sunshine range is 113.0 ~ 158.6 W/m².

#### Surface sterilization of plant samples and genomic DNA isolation

To obtain endophytes, the sample was washed with tap water and disinfected with 70% ethanol for 1 min and 12% sodium hypochlorite for 3 min, followed by five rinses with sterile water. The successful removal of epiphytes by this disinfection method was confirmed by the absence of colonies in a culture of the final rinse water. These samples were frozen in liquid nitrogen. OMEGA Soil DNA Kit (D5625-01) (Omega Bio-Tek, Norcross, GA, USA) was used to extract total genomic DNA samples, following the manufacturer’s instructions, and kept at −20 °C before additional analysis.

#### PCR amplification

The forward primer 799F (5’-AAMMGAGTGGATACCC CGK-3’) and the reverse primer 1193R (5’-ACGTCACTCC CACCTTCC-3’) were used to obtain amplified fragments representing the V5–V7 variable region of the 16S rRNA gene. The PCR components contained 0.25 μl of Fast pfu DNA Polymerase (5 U/μl), 1 μl of each (10 μM) Forward and Reverse primer, 5 μl of buffer (5×), 2 μl (2.5 mM) of dNTPs, 1 μl of Template DNA, and 14.75 μl of ddH2O. The forward primer ITS1F (5’-CTTGGTCATTTAGAG GAAGTAA-3’) and the reverse primer ITS2R (5’-GCT GCGGTCTTCATCGATGC-3’) were used to obtain amplified fragments representing the V1 variable region of the ITS gene. The PCR components contained 0.25 μl of Fast pfu DNA Polymerase (5 U/μl), 5 μl of buffer (5×), 2 μl (2.5 mM) of dNTPs, 1 μl of Template DNA, 1 μl of each (10 μM) Forward and Reverse primer and 14.75 μl of ddH2O. PCR amplicons were purified with Vazyme VAHTSTM DNA Clean Beads (Vazyme, Nanjing, China) and quantified using the Quant-iT PicoGreen dsDNA Assay Kit (Invitrogen, Carlsbad, CA, USA).
Illumina MiSeq sequencing

After the individual quantification step, the purified amplifiers were equally pooled, and paired-end 2 × 250 bp sequencing was performed at Shanghai Personal Biotechnology Co., Ltd. (Shanghai, China) using the Illumina MiSeq platform and MiSeq Reagent Kit v3.

Data processing and statistical analysis

Microbiome bioinformatics were implemented with QIIME2 2019.4 (Bolyen et al. 2019) with slight modification according to the official tutorials (https://docs.qiime2.org/2019.4/tutorials/). Briefly, raw sequence data were demultiplexed using the demux plugin followed by primers cutting with the cutadapt plugin. Sequences were then quality filtered, denoised, merged and chimera removed using the DADA2 plugin (Callahan et al. 2016). Taxonomy was assigned to amplicon sequence variants (ASVs) using the classify-sklearn naive Bayes taxonomy classifier in the feature-classifier plugin (Bokulich et al. 2013). Taxonomy was assigned to amplicon sequence variants (ASVs) using the classify-sklearn naive Bayes taxonomy classifier in the feature-classifier plugin (Bokulich et al. 2013) against the SILVA Release 132/UNITE Release 8.0 Database. Using the method of rarefaction, by randomly extracting a certain number of sequences from each sample to reach a uniform depth, the observed ASVs and their relative abundance of each sample at the sequencing depth can be predicted to ensure that each sample was analyzed at the same sequencing depth level (Heck et al. 1975; Kemp and Aller, 2004). QIIME2 and R package (v3.2.0) were used for sequence data analysis. During the analysis process, non-bacterial and fungal sequences have been removed to avoid the contamination of host plant chloroplasts and mitochondria. ASV-level alpha diversity estimators (Chao1, Shannon, and Good’s coverage) were calculated using the ASV table in QIIME2 and visualized as box plots. The ASV files generated in sequencing analysis were used in PICRUSt2 (Douglas and Langille 2019) algorithm to predict the biological function(s) associated with endophytes communities of P. ginseng. The ITS and 16S rRNA functional genes were identified from MetaCyc (https://metacyc.org/) databases.

Results

Statistics of endophyte sequences in ginseng samples

After quality control and chimera sequences removal, a total of 1,003,042 effective sequences and 8552 ASVs were obtained of bacterial 16S rRNA genes. The average number of the obtained bacterial sequence was 34,449, and the average length was about 376 bp. Similarly, a total of 8,06,544 effective sequences and 210 ASVs were obtained of fungal ITS regions after quality control and chimera sequences removal. The average length of the obtained fungal sequence was 243 bp. Interestingly, for both root and leaf samples, the amount of ASVs in 16S rRNA gene sequencing analysis was > 28 times more than the ASVs in ITS analysis (Supplementary Table 1). When searched in the SILVA database, these bacterial ASVs corresponded to 3458 ASVs in roots, 2142 ASVs in stems, and 2952 ASVs in leaves. These fungal ASVs corresponded to 52 ASVs from roots, 95 ASVs from stems, and 63 ASVs from leaves were identified using the UNITE database (Fig. 1).

Alpha diversity of bacterial and fungal communities

The richness and diversity of endophytes in three different organs were statistically analyzed by the Kruskal–Wallis test and Dunn post hoc tests. The alpha diversity indexes of different ginseng organs were different (Fig. 2). The coverage of each sample was greater than 84.5%, indicating that the possibility of not detecting the sequence was small, and there were enough sequences for endophyte diversity analysis. We found that roots had the highest Shannon diversity index, which indicated that the root had the highest endophytic bacterial community diversity. The index of Chao1 indicated that roots had the highest endophytic bacterial community richness. Further analysis revealed that the Shannon index of endophytic bacteria of the root was significantly higher than the stem (p < 0.05) (Fig. 2b). The endophytic fungal community diversity in the ginseng roots, stems, and leaves was less affected by the organ and showed no marked change in the diversity.

Beta diversity of bacterial and fungal communities

Principal coordinate (PCoA) analysis and non-metric multidimensional scaling (NMDS) analysis were carried out to evaluate three different organs’ complexity. The results showed differences in microbial communities among the three groups. PCoA was achieved to determine the overall resemblance of endophytic microbial community structure among organs; it showed considerably different community compositions of endophytic bacteria (R = 0.6459, p = 0.001) and endophytic fungi (R = 0.6803, p = 0.001) in different organs (Fig. 3a, b). PCoA analysis showed that the abscissa was the main coordinate component that caused differences in the composition of the endophytic microbial community in different organ samples. In terms of ASV, PC1 contributed 36.1% and 28.6% to the differences in community composition of endophytic bacteria and fungi, respectively (Fig. 3a, b). The NMDS map showed that the microbial community structure of the three organs was different (bacteria: R = 0.6459, p = 0.001, fungus: R = 0.6803, p = 0.001) (Fig. 3c, d).
Relative microbial abundances

The main bacterial phyla detected in different organs of ginseng were Proteobacteria, Bacteroidetes, and Actinobacteria (Fig. 4a). In the root, the main phyla were Proteobacteria (63.74%), Bacteroidetes (8.58%), and Actinobacteria (17.77%). The main phylum in stems and leaves were Proteobacteria (81.80% and 66.57%, respectively). From the composition of endophytic bacteria at the genus level of ginseng roots, stems, and leaves (Fig. 4b), the main genera observed in roots were Ochrobactrum (7.07%), Cupriavidus (6.14%), and Mycobacterium (7.77%). Ochrobactrum was the main genus of stems and leaves (15.91% and 13.12%, respectively). Both phylum and genus account for more than 1%.

Fungal ASVs primarily consisted of phyla Basidiomycota, Ascomycota, and Mortierellomycota. Ascomycota was the most abundant in ginseng roots, stems, and leaves (Fig. 5a). In the root, the main phyla were Ascomycota (80.95%), Basidiomycota (18.99%), and Mortierellomycota that did not exist in the leaf. From the composition of endophytic fungi at the genus level of ginseng roots, stems, and leaves (Fig. 5b), the main genera observed in roots were Aspergillus (15.48%), Cadophora (13.40%), Tetracladium (7.2%). The main genera of stems were Umbilicaria (10.56%), Simplicillium (7.46%), and Monilinia (6.80%). Monilinia (33.52%) was the main genus of leaves.

LEfSe analysis of the endogenous microbiome

To further clarify the possible interactions between the identified endophytic microbes’ dependencies in ginseng organ samples, linear discriminant effect size (LEfSe) was used to quantitatively analyze the biomarkers of different organs. We detected significant differences in biomarker abundance of endophytic bacteria from different groups, and identified a total of 9 biomarkers from all organ samples, as shown in the branch diagram (Fig. 6b). In the root, the significantly highest number of ASVs in the root was 3458. From c and d (fungi), the ASVs shared by the three organs were 9, and the highest number of ASVs in the stem was 95. This indicates that there are great differences in the composition of the endophytic community in different organs of ginseng.
abundant taxa were the family Mycobacteriaceae, genus Mycobacterium and Devosia. In the stem, the significant taxa belonged to the class Gammaproteobacteria, orders Betaproteobacteriales, Sphingomonadales, family Burkholderiaceae, Sphingomonadaceae, and genus Sphingomonas, which were all abundant.

Similarly, a total of 6 biomarkers have been identified for endophytic fungi in different organs, as shown in the branch diagram (Fig. 6d). The significant taxa in the leaves were affiliated with different phylogenetic groups, including the order Capnodiales, family Sclerotiniaceae, and genus Monilinia. In the stem, the significant taxa belonged to the class Sordariomycetes, class Saccharomycetes, and order Saccharomycetales, which were all abundant.

**Functional characteristics of the endophytic microbiome**

The Phylogenetic Investigation of Communities by Reconstruction of Unobserved States (PICRUSt) was used to predict the potential metabolic functions of endophyte communities based on marker gene sequence abundance in samples (Douglas et al. 2020). According to the function prediction results based on 16S rRNA analysis, we found that the microbiota of three organ-associated endophytic bacteria had relatively similar functions in 60 MetaCyc functions. The predicted pathways included metabolic clusters such as L-glutamate and L-glutamine biosynthesis and super pathway of L-aspartate and L-asparagine biosynthesis. Microbiota showed significantly higher metabolic potential for biosynthesis, represented specifically by pathways such as amino acid biosynthesis, cofactor, prosthetic group, electron carrier, and vitamin biosynthesis, nucleoside and nucleotide biosynthesis, fatty acid and lipid biosynthesis, and many more. According to the function prediction results based on ITS analysis, we found that the microbiota of three organ-associated endophytic fungal also had relatively similar functions in 29 MetaCyc functions. The predicted pathways included biosynthesis, generation of precursor metabolite and energy, glycan pathways, metabolic clusters. Mainly enriched in the nucleoside and nucleotide biosynthesis; electron transfer, respiration; etc. It indicated that ginseng endophytes were mainly involved in biosynthetic and metabolic pathways.
Fig. 3 Principal coordinate analysis (PCoA) of endophytic bacteria (a) and endophytic fungi (b) in different organs of ginseng. The contribution rates of PC1 to the differences in the composition of endophytic bacterial and fungal communities were 36.1% and 28.6%, respectively. It indicated that the community composition of endophytic bacteria and endophytic fungi in different organs was quite different. Non-metric multidimensional scaling (NMDS) of endophytic bacteria (c) and endophytic fungi (d) in different organs of ginseng. The closer the distance between the two points, the smaller the difference in the microbial communities in the two samples. Analyses were done using Bray–Curtis distances.

Fig. 4 Relative abundance of endophytic bacterial communities classified at phylum (a) and genus (b) level in different organs. Proteobacteria was the main phylum in the roots, stems, and leaves of ginseng. The most abundant genus in ginseng roots, stems, and leaves were Ochrobactrum.
Discussion

Endophytes are important microbial resources that can interact beneficially with plants (Ahmad et al. 2021; Wu et al. 2021). In this study, the composition of the microbial communities in the roots, stems, and leaves of ginseng was collected to determine the invisible majority of these endophytic microbial communities and to gain an in-depth understanding of these endophytic microbial communities. The Venn diagram preliminarily revealed the differences in ASVs of endophytes among the three organs (Fig. 1). Bacterial communities appear to be much more abundant than fungal communities in the plant endosphere. Consistent with the sequencing reads obtained from 16S rRNA and ITS sequencing analysis.

In this study, we found that roots had the highest Shannon diversity index (7.60), followed by leaves (7.30), and the lowest in stems (6.08). The Chaol and Shannon diversity indexes of endophytic bacterial communities in roots were significantly higher than stems, and there was no significant difference between roots and leaves (Fig. 2a). PCoA and NMDS analysis showed that there were differences in the microbial communities between the three organs. The bacterial composition of roots and leaves were similar (Fig. 3). This is similar to the research results of wild ginseng: the bacterial composition of the leaves closer to the root rather than the stem (Khan et al. 2017). The diversity of endophytic microbial communities in plants will be affected by plants, age, tissue type, etc. (Harold et al. 2015; Ryan et al. 2008). Compared with stems, root endophytic bacteria have a higher diversity (Fig. 2), probably because most endophytic bacteria originate from rhizosphere soil (Wang et al. 2016). However, we also found that the leaf endophyte had high alpha diversity, which suggested that endophyte might enter the ginseng endosphere through other important ways, such as ginseng seeds (Khan et al. 2017).

The main bacterial phyla in the three different organs of ginseng were Proteobacteria, Bacteroidetes, and Actinobacteria. The relative abundance of these species varied between the different organs of ginseng, which is consistent with the results of most studies (Singha et al. 2021; Hong et al. 2018; Gouda et al. 2016). Previous studies have shown that Actinobacteria, and Proteobacteria were common phyla in plant tissues, they play a key role in participating in host metabolism and maintaining the stability of the endophytic microflora (Bashir et al. 2020; Müller et al. 2015). Actinobacteria are widely found in plants and have antibacterial activity (Conn and Franco 2004). The relative abundance of Actinobacteria in roots (17.77%) is about 5 times that in stems (3.17%) and about 2 times that in leaves (9.45%); it may be the result of selective enrichment of roots that need to inhibit certain pathogenic bacteria.

The results show that Ochrobactrum was dominant in all three organs at the endophytic bacteria community abundance on genus level. Mycobacterium and Lactobacillus were more common in the root. Previous studies have shown that Mycobacterium and Sphingomonas bacteria isolated from the roots of Dendrobium moschatum could significantly increase the germination rate of D. moschatum seed (Tsavkelova et al. 2007). Pseudomonas was found in ginseng roots (0.93%), stems (2.37%), and leaves (1.79%). Studies have found that siderophore-producing Pseudomonas has the potential to promote plant growth (Sharma and Johri 2003). In comparison to stem samples, the root samples of P. ginseng contain a more than the five-fold higher abundance of Actinobacteria. Actinobacteria have been reported to produce a variety of microbe-derived secondary metabolites, which have a wide range of applications in agriculture, industry, and medicine (Mishra et al. 2021). Our results indicate that Nocardioidees are present in three ginseng organ samples. Literature search shows that Nocardioidees have been isolated as endophytes from numerous medicinal
plants (Liu et al. 2019b; Qin et al. 2012) and testified to produce economically vital metabolites such as Artemisinin and Actinomycin (Mishra et al. 2021; El-Refai et al. 2011). In this study, the composition and diversity of endophytic microbial communities related to the three organs of ginseng were compared. However, it is necessary to link the physiological characteristics and physiological indicators of the three organs with the conclusion of endophytes diversity.

The ITS analysis performed in this experiment showed that *Periconia* is only present in the leaves. Kim et al. proved that *Periconia* sp. has the ability to produce Periconicins, a diterpene compound with antibacterial activity (Kim et al. 2004). *Cladosporium*, another endophytic fungus, was about 10 times more abundant in stems in this study. Earlier, it was reported to produce Brefeldin A, cardiac glycosides, and Taxol (Khan et al. 2016). It was reported in the literature that the endophytic fungi isolated from ginseng are *Aspergillus*, *Penicillium*, etc. (Wu et al. 2013). In this study, they were also found by high-throughput sequencing analysis. In addition, *Monilinia*, *Simplicillium*, and *Cadophora* were also abundant. The results of this study enriched the types and resources of ginseng endophytic fungi.

Endophytes present in medicinal plants are considered to be potential sources for producing various secondary

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**Fig. 6** Differences between plant organs were assessed using linear discriminant analysis (LDA) of effect size and Kruskal–Wallis and Wilcoxon rank–abundance tests. The taxonomic cladogram shows the taxonomic hierarchies of the main taxa from phylum to genus (from inner circle to outer circle) in the sample community. The histogram of the LDA score calculates the differently abundant microbe among different organs, with a threshold of 4.0. The ordinate is the taxa with significant differences between groups, and the abscissa is a bar chart to visually display the LDA analysis logarithmic score value of each taxon (a, b—bacteria; c, d—fungi). Biomarkers of endophytic bacteria and endophytic fungi in different organs were identified 9 and 6, respectively.
metabolites, which can reduce disease symptoms caused by plant pathogens (Passari et al. 2017). The function prediction indicated that the metabolic functions of the microbial groups in the roots, stems, and leaves of ginseng were similar. The functional classification “Amino Acid Biosynthesis and Carbohydrate Biosynthesis” was significantly abundant in all three organs. Carbohydrate catabolism can provide energy for the growth of mycelium and provide a carbon skeleton for another metabolism (Deveau et al. 2008). According to the definition proposed by Hardoim et al. (Hardoim et al. 2015), endophytes should be defined in terms of habitat rather than function. The differences in the composition of endophytes in roots, stems, and leaves can be explained by differences in physiological structure and nutritional components. It is speculated that the selection preference of endophytes may be related to the secondary metabolites secreted by the host. In addition, external environmental factors also play a significant role in regulating plant growth. For example, humidity, environmental temperature, soil structure, etc., are also related to the function of root endophytes (You et al. 2016).

There are two main methods for studying the plant microflora: (1) culture-dependent methods, which are developed by developing appropriate nutrient media and/or under appropriate culture conditions; (2) culture-free methods (e.g., next-generation sequencing), which are culture-independent methods that involve sequencing microbial DNA directly from the target microorganism (Oita et al. 2021). Culture-dependent analysis of microbial community diversity reveals only a small fraction of the actual microbial population. Studies have shown that ~99% of microorganisms are unculturable (Schloss and Handelsman 2005). Recently, metagenomics has gained a lot of attention in the research of plant endophytes, which can help identify different microorganisms in the environment. The diversity and abundance of microorganisms can be estimated through amplification and sequence analysis of specific marker genes like the 16S ribosomal RNA (rRNA) gene for bacteria and ITS regions for fungi (Fadiji and Babalola, 2020a). This method can also help to identify different microorganisms (nonculture and culturable) present in the environment (Fadiji and Babalola, 2020b). It has been reported that high-throughput sequencing data can supplement the prediction of fungal diversity based on traditional mycology methods, and improve our understanding of fungal diversity (Baldrian et al. 2021).

In summary, this study used high-throughput sequencing technology to analyze the composition, diversity, and differences of microbial communities in the three organs of ginseng. Similar to many studies, Proteobacteria was the most abundant endophytic bacterial phyla and Ascomycota was the most abundant endophytic fungal phyla of all samples. In addition, this study also revealed the compositions of the endophytic microbial communities. The diversity of endophytic bacterial communities in ginseng roots was significantly higher than that in stems (p < 0.05). Ginseng organs are one of the important factors affecting the diversity of endophytic microbial communities, and the soil characteristics can provide an essential contribution to the understanding of their effects on the endophytic microbial communities associated with P. ginseng roots. This research helps fill in the lack of scientific understanding of ginseng endophytic microbial communities. However, in-depth research on plant–endophyte symbiosis is needed in the future.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00203-022-02815-y.

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Data availability Raw amplicon sequence data related to this study were deposited in the NCBI Sequence Read Archive (NCBI SRA) under Bioprojects PRJNA766834.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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