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Meta-analysis of root-associated microbial communities of widely distributed native and invasive Poaceae plants in Antarctic

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Abstract

Deschampsia antarctica Desv. and *Poa annua* L. are two Poaceae plants with enough endurance to successfully establish populations in the Antarctic region. Their adaptation to the Antarctic environment is closely linked to root-associated microbial communities. In this study, we obtained 16S rRNA sequencing data of the root-associated microbial communities of these two Poaceae plants from NCBI. Meta-analysis was used to investigate the similarities and differences between the root-endosphere and rhizosphere-dwelling microbial communities in these two Poaceae plants. Here we report that two Poaceae-Poaceae plants' rhizospheric communities were found to be more species diversity than endospheric communities. The species diversity of *P. annua* was higher than that of *D. antarctica* in both endosphere and rhizosphere communities. Seven bacterial families form a core microbiome of two Antarctic Poaceae plants' root endosphere, in which Microbacteriaceae appears to be obligatory root endophytes of the two Antarctic Poaceae plants. The core microbiome of the two Poaceae plants' rhizosphere has six bacterial families. Chitinophagaceae, Burkholderiaceae, and Flavobacteriaceae are most likely to play a crucial role in Poaceae plants' adaptation to cold Antarctic conditions. Sphingobacteriaceae, Caulobacteraceae, Gemmatimonadaceae, and Flavobacteriaceae have a great influence on two Antarctic Poaceae plants.

Keywords: Antarctic bacteria; rhizosphere; endosphere; microbial diversity; invasive species

1. Introduction

The Antarctic ecosystem is one of the most stressful natural habitats, especially for terrestrial vegetation (Convey et al., 2014). Antarctic terrestrial vegetation has no trees or shrubs and consists mainly of cryptogams. There are three species of Poaceae plants in the Antarctic, one of which is native to the continent, *Deschampsia antarctica* Desv. (Antarctic hairgrass). The other two Poaceae plants are *Poa annua* L. (annual bluegrass) and *Poa pratensis* L., which were introduced to the continent accidentally (Galera, et al. 2019; Pertierra, et al. 2013; Teixeira, et al. 2013). The native plants *D. antarctica* are widely distributed in maritime and coastal Antarctica (Znój, et al. 2021a). *P. annua* has successfully survived, reproduced, and spread in the Antarctic region for many years, and it's now also widely distributed in the Antarctic and sub-Antarctic regions (Molina-Montenegro, et al. 2012; Pertierra, et al. 2017; Shaw, et al. 2010). Nevertheless, *P. pratensis* has only occupied a small patch and has not dispersed across the surrounding environment during the 60 years of its presence in the Antarctic, and it has limited endurance in extreme Antarctic environmental conditions (Pertierra, et al. 2017).

To cope with the stress of harsh environments, Antarctic plants have evolved adaptive mechanisms in terms of molecular, cellular, biochemical, and physiological responses, such as stress protein production, accumulation of non-structural proline and carbohydrates, accumulation of compatible solutes and higher levels of antioxidant systems (Gill and Tuteja 2010; Iordachescu and Imai 2008; Lee, et al. 2013; Theocharis, et al. 2012). Extensive studies have found that *D. antarctica* has a conservative tolerance mechanism to environmental stresses. The carbon and nitrogen metabolism, such as the accumulation of amino acids, sucrose and fructose, occurred significant changes in *D. antarctica* under cold conditions (Bocian, et al. 2015; Clemente-Moreno, et al. 2020a; Iordachescu and Imai 2008; Van den Ende 2013). The *D. antarctica* has recrystallization inhibition activity and developed efficient low-temperature-efficient photosynthetic systems (John, et al. 2009; Lee, et al. 2013). The *P. annua* has also developed a range of characteristics that ensure its ecological success, such as high phenotypic variability, compact plant growth habits, and tolerance to a wide range of soil conditions (Galera, et al. 2015; Galera, et al. 2019; Rudak, et al. 2019).

Nowadays, several studies have shown that microorganisms are involved in the tolerance of plants in extreme environments (Berríos, et al. 2013; Gallardo-Cerda, et al. 2018; Zhang, et al. 2020). Several bacteria have been found in association with plant roots, including facilitating the establishment, spread, and/or increasing plant fitness in stressful environments (Bano and Fatima 2009; Hoffman and Arnold 2010; Torres-Diaz, et al. 2016; Turner, et al. 2013). The plant-microbe interactions occur mainly in two distinct rhizocompartments, the root endosphere and the rhizosphere (Turner, et al. 2013). And some studies have shown that the rhizospheric and endospheric microbial communities exhibit different niche characteristics (Beckers, et al. 2017a). Rhizobacteria can directly affect the host plants' roots by secreting phytohormones. Rhizospheric bacteria can also secrete organic acids, siderophores, or cyanide to participate in the dissolution of mineral matrices, thereby indirectly affecting plants. Endophytes have a major contribution to promoting plant growth by providing fixed nitrogen (Znój et al., 2021a; Oses-Pedraza et al., 2020). Endospheric bacteria can also participate in plant stress responses by reducing levels of the plant's internal stress hreformone ethylene through 1-aminocyclopropane-1-carboxylate (ACC) deaminase-mediated hydrolysis (Hayat, et al. 2010).

To better understand Poaceae plants' root-associated microbial communities in Antarctic continent, we collected and analyzed raw data of 16srRNA V3-V4 regions from the rhizospheric and endosphere microbial communities of native and non-native Poaceae plant (*D. antarctica* and *P. annua*) of Antarctica from NCBI. The similarities and differences within the rhizospheric and endosphere microbial communities of *D. antarctica* and *P. annua* of Antarctica were investigated in terms of bacterial phylogenetic diversity and searched for microorganisms that help the Poaceae plant adapt to extreme environments. This is the first study that sheds light on comparing the root-

associated microbiomes associated with native and non-native Poaceae plants of Antarctica. This will provide new insights into the adaptation of plants to extreme environments

2. Materials and methods

2.1. Source of data

We collected two Poaceae plants with root-endosphere and rhizosphere microbial communities from NCBI, including six samples of *D. antarctica* and four samples of *P. annua*. All sample materials were sampled from King George Island, South Shetland Islands, and maritime Antarctica during the austral summer season of 2017–2018 (Fig. 1). All data were obtained by sequencing the V3-V4 region of the prokaryotic 16S rRNA gene by Illumina MiSeq. All data has been published and deposited from PRJNA678861 (Znoj, et al. 2021b) and PRJNA726953 (Znój, et al. 2021a). In addition, we also collected information on the physicochemical properties of the soil (Fig. S1) and the proportion of plants growing on the soil at each sampling site (Table S1) from the literature (Znoj, et al. 2021b) in which the data were published.

Fig. 1 Map showing the five sampling site.

2.2. Data processing

Quality control and analysis of the original sequence samples were carried out by quantitative insights into the microbial ecology version 2 (qiime2) software suite (version 2020.2). This process consists of the upstream phases and downstream phases. The upstream stage includes importing 16S rRNA sequences, ensuring sequence quality control, building feature tables, and generating phylogenetic trees. The downstream stage includes taxonomic, diversity, and abundance analysis (Bai, et al. 2019). The processing of filtering chimeras and cutting off low-quality sequences can be realized through the q2-dada2 plugin. To obtain the difference in the microbial community structure of two Poaceaes' root-associated samples, we use the q2-diversity plugin to calculate several commonly used alpha and beta diversity indices and visualized them using the principal

coordinates analysis (PCoA) plots plugin. Bacterial taxonomies were assigned using the pre-trained 16S rRNA V3-V4 classifier. This classifier artifact is trained on the silva reference database, trimmed to the V3-V4 hypervariable region using primers 5'-ACTCCTACGGGAGGCAGCAG-3' and 5'-GGACTACHVGGGTWTCTAAT-3'. Taxonomy was assigned to amplicon sequence variations (ASVs) using this classifier artifact.

2.3. Random forest

Classification random forest analysis was implemented in R (v.4.1.3) using the randomForest, packages. A Random Forest (RF) classification model was implemented to predict the relationship between different proportions of plants in the soil and nutrients in the soil. The algorithm was optimized via two parameters: tree- the number of trees grown from a bootstrapped sample (ntree = 500); mtry- the number of predictors randomly tested at each node (mtry = 8) (Liaw and Wiener 2002). The influence degree of soil elements on plants was judged according to the Mean Decrease Accuracy index.

2.4. Statistical analysis

A two-sample *t*-test was applied to compare different data sets. Variance within the sets was assessed using the *f*-test beforehand. Linear discriminate analysis (LDA) effect size (LEfSe) was performed on bacterial community family-level abundance using an online analysis website (URL: http://huttenhower.sph.harvard.edu/galaxy/), and families with LDAScore greater than 4 were selected. Correlations between biological and geochemical parameters were calculated using Pearson's correlation coefficient, which was performed via SPSS (version 21.0). Data visualization and statistical analysis have been performed using Image GP (http://www.ehbio.com/ImageGP/) and the R software (R v.4.1.3) and the following packages: ggplot2, pheatmap, UpSetR, corrplot, and magrittr.

3. Results and discussion

3.1. Root-associated microbial community structure of two Poaceae plants

We detected more than 1250 ASVs and the majority of ASVs observed were not shared. The *D. antarctica* shared 288 ASVs and non-shared 623 ASVs and the *P. annua* shared 306 ASVs and non-shared 536 ASVs between the rhizosphere and endosphere. In addition, most of the ASVs observed were not shared between the rhizosphere samples of *D. antarctica* and *P. annua*, and similar phenomena were observed in the endosphere samples. These findings are consistent with studies showing niche differentiation in plants (Beckers, et al. 2017b; Cheng, et al. 2019; Rilling, et al. 2018; Zhang, et al. 2020). Non-shared phenomena were also found in *D. antarctica* and *Colobanthus quitensis* rhizosphere samples by Zhang et al (Zhang, et al. 2020). *D. antarctica* and

C. quitensis are the only two native flowering plants in Antarctica. The occurrence of this phenomenon may be influenced by a combination of different factors, such as plant root secretion and chemical properties of rhizosphere soil. Moreover, Zhang et al. 2020 also found that most of the ASVs observed were not shared between endospheres (leaves and roots) of Antarctic indigenous plants, and this was attributed to the influence of plant genotypes (species) on the bacterial endophytic community in extreme environments (Zhang, et al. 2019).

The alpha diversity index can reflect the species diversity of bacterial communities. Based on the Shanno index (Fig. 2a), it can be seen that the species diversity of the root-associated microbial community of *P. annua* was higher than that of *D. antarctica*. The species diversity of rhizosphere bacteria in two Poaceae plants was significantly higher than those of bacteria in the endosphere, which might be caused by the influence of plants on endosphere bacteria communities (Zhang, et al. 2020). The richness of bacteria communities in *P. annua* was higher than that of *D. antarctica* in both the endosphere and rhizosphere bacteria (Fig. 2b). The opposite was observed in terms of evenness (Fig. 2c). The endophytic bacteria mostly derive from the rhizosphere (Compant, et al. 2010; Compant, et al. 2005; Hardoim, et al. 2008) and the diversity of rhizosphere microorganisms has a direct influence on endophytic bacteria (Dong, et al. 2019; Znoj, et al. 2021b). The beneficial interaction between plants and microbes mainly occurs in the rhizosphere (Bais, et al. 2006; Ho, et al. 2017). Studies of plant-microbial interactions have shown that plants can shape their rhizosphere microbial communities by actively secreting compounds that specifically stimulate or inhibit members of the microbial community (Berendsen, et al. 2012; Doornbos, et al. 2012). In the rhizosphere soil microecosystem, after receiving the "recruitment" effect of plant rhizosphere and forming a stable rhizosphere community, the soil microbial community is still regulated by the material and energy in the system, and constantly changes the ecological characteristics of the community to adapt to the changes of the surrounding environment (Cui, et al. 2018). Rhizosphere microorganisms play an important role in improving plant nutrient absorption, pathogen defense and stress resistance (Huang, et al. 2019; Nascimento, et al. 2020; Suárez-Moreno, et al. 2019). The beta diversity index can reflect the differences between microbial communities. The PCoA analysis plots based on the bray-Curtis distance algorithm showed that the microbial community structure of the two Poaceae plants' root-associated microbial communities were obvious differences (Fig. 3).

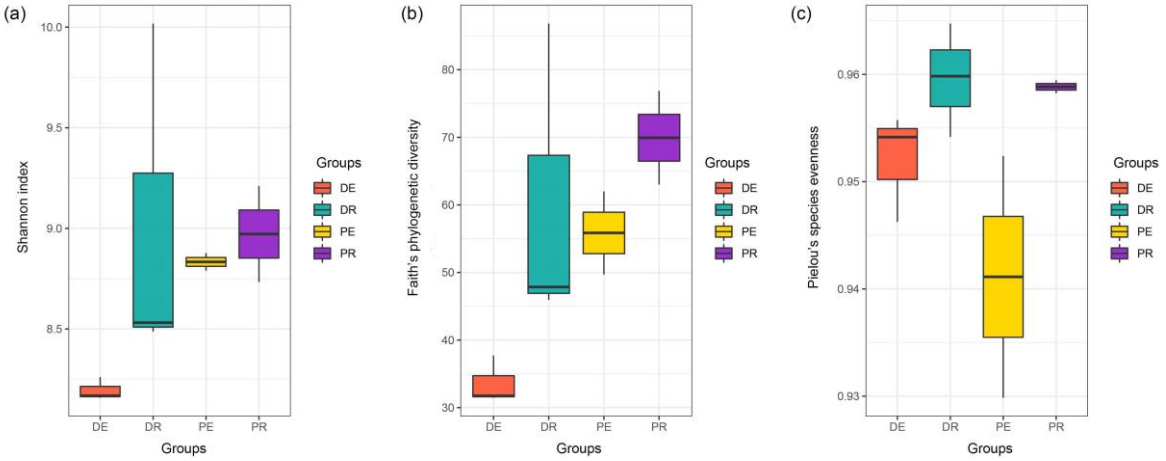

Fig. 2 Statistical comparison of alpha diversity index between two poaceae plants root-associated microbial community samples. (a) Shanno index. (b) Faith's phylogenetic diversity. (c) Pielou's species evenness. DR, *Deschampsia antarctica* rhizospheric soil samples; PR, *Poa annua rhizospheric* soil samples; DE, *Deschampsia antarctica* root samples; PE, *Poa annua* root samples.

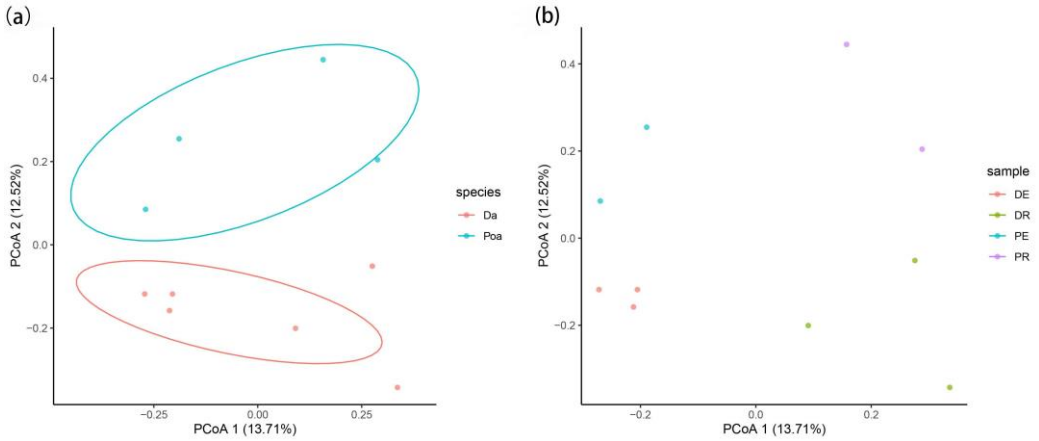

Fig. 3 PCoA analysis plot based on bray-curtis distance algorithm. (a) Da, *Deschampsia antarctica* root-associated samples; Poa, *Poa annua* root-associated samples. (b) DR, *Deschampsia antarctica* rhizospheric soil samples; PR, *Poa annua rhizospheric* soil samples; DE, *Deschampsia antarctica* root samples; PE, *Poa annua* root samples.

3.2. Comparison of root-associated bacterial communities composition between *D. antarctica* and *P. annua*

The rhizosphere bacteria community of two Poaceae plants are most abundant in the following bacterial phyla: Proteobacteria (*D. antarctica*, av. 24.2% and *P. annua*, av. 25.1%), Bacteroidetes (*D. antarctica*, av. 18.0% and *P. annua*, av. 13.9%), Patescibacteria (*D. antarctica*, av. 9.7% and *P. annua*, av. 13.2%), Actinobacteria (*D. antarctica*, av. 14.5% and *P. annua*, av. 9.9%), Verrucomicrobia (*D. antarctica*, av. 7.5% and *P. annua*, av. 8.0%), Acidobacteria (*D. antarctica*, av. 6.0% and *P. annua*, av. 10.4%) (Fig. 4). In addition, Acidobacteria (*D. antarctica*, av. 6.0% and *P. annua*, av. 10.4%) had considerable differences between plant species. Chloroflexi was more enriched in the rhizosphere communities of two Poaceae plants than in the endosphere communities. Some findings suggest that bacteria of the Chloroflexi phylum may play an active biogeochemical

role in cold, anoxic soils (Costello and Schmidt 2006), and the Chloroflexi phylum is a relatively understudied bacterial lineage (Hug, et al. 2013).

The root endosphere of two Poaceae plants is mainly occupied by bacteria from the phylum Proteobacteria (*D. antarctica*, av. 38.4% and *P. annua*, av. 41.3%) and Bacteroidetes (*D. antarctica*, av. 25.4% and *P. annua*, av. 21.3%), but also by Patescibacteria (*D. antarctica*, av. 7.4% and *P. annua*, av. 6.5%) and Actinobacteria (*D. antarctica*, av. 12.8% and *P. annua*, av. 7.4%) (Fig. 4). Moreover, Proteobacteria (*D. antarctica*, av. 38.4% and av. 24.2%; *P. annua*, av. 41.3% and av. 25.1%) and Bacteroidetes (*D. antarctica*, av. 25.4% and av. 18.0%; *P. annua*, av. 21.3% and av. 13.9%) were more enriched in the root endosphere compartment in two Poaceae plants compared to rhizosphere soil communities, and their sequences were the most abundant in the samples investigated. Proteobacteria are well known to respond to labile carbon sources and the Bacteroidetes are often playing a vital role in the degradation of plant-derived organic matter (Naumoff and Dedysh 2012; Spain, et al. 2009). Members of the Proteobacteria are dominant in plant rhizosphere microbial communities and endosphere microbial communities (Lei, et al. 2019; Proenca, et al. 2017; Wang, et al. 2018; Yang, et al. 2017).

Significant differences were noted in the relative abundance of Actinobacteria (*D. antarctica*, av. 12.8% and *P. annua*, av. 7.4%) between the root endosphere of native and non-native Poaceae plants of Antarctica. The role of Actinobacteria as endophytes allows them to effectively promote plant growth through a series of mechanisms, including the production of plant hormones, the acquisition of nutrients, and the direct inhibition of pathogens by antibiosis or competition (Franco, et al. 2007). Related studies have found that endophytic actinomycetes isolated from healthy wheat tissue can inhibit a variety of wheat fungal pathogens both in vitro and in planta (Coombs., et al. 2004). Moreover, they drive nutrient cycling under harsh conditions (Jose, et al. 2021). The proportion of Patescibacteria in the root-associated microbial communities of these two Poaceae plants in Antarctica is much higher than that in other continental soils, for example, its proportion in forest soils is only 0.55% (Herrmann, et al. 2019). Patescibacteria with high relative abundance has also been observed in other studies of Antarctic soils (Ortiz, et al. 2021). The main reason for this phenomenon may be that soils in Antarctica are nutrient-poor and bacteria of the Patescibacteria phylum are adapted to oligotrophic environments (Herrmann, et al. 2019).

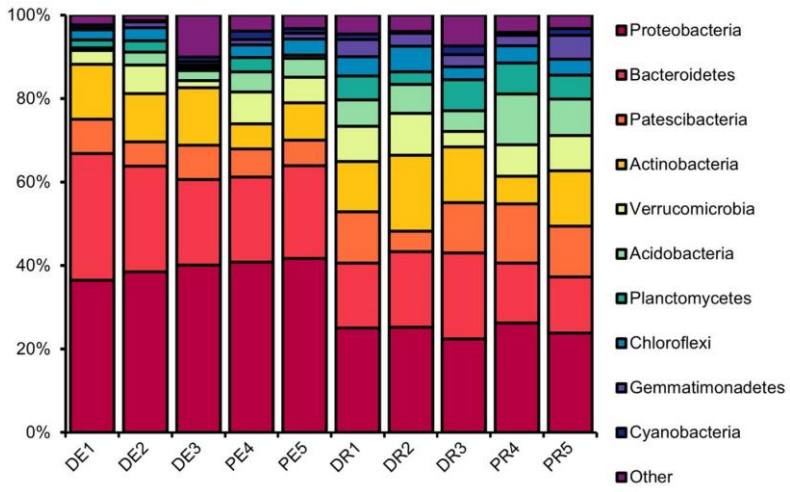

Fig. 4 Relative abundance by percentile contribution of sequences identifed on a phylum-rank taxonomic level. DE, *Deschampsia antarctica* root samples; PE, *Poa annua* root samples; DR, *Deschampsia antarctica* rhizospheric soil samples; PR, *Poa annua rhizospheric* soil samples. 1—5, sampling site numbers.

In the rhizosphere community, some families displayed a comparable average relative abundance in both sample types, most notably the Chitinophagaceae, followed by Burkholderiaceae (Fig. 5). Related studies found that isolates of certain strains of the family Chitinophagaceae showed growth-promoting properties, such as the ability to produce indole-3-acetic acid, solubilize phosphate, and NH_3 production, in addition, these isolates could utilize ACC as a sole source of nitrogen source and possessed the ACC deaminase enzyme (Madhaiyan, et al. 2015). *P. annua* samples had a significantly higher sequence abundance of the family Rhodocyclaceae (p=0.043), Xanthobacteraceae (P=0.016), etc (Fig. 6a). Additionally, the average relative abundance of Flavobacteriaceae in the *P. annua* endosphere and rhizosphere was higher than that of *D. antarctica*. *Flavobacterium* typically possesses a large number of extracellular enzymes that enable them to degrade fungi, bacteria, nematode and insect constituents (Tian and Gao 2014). In addition, certain strains of the genus *Flavobacterium* have displayed ACC deaminase activity.

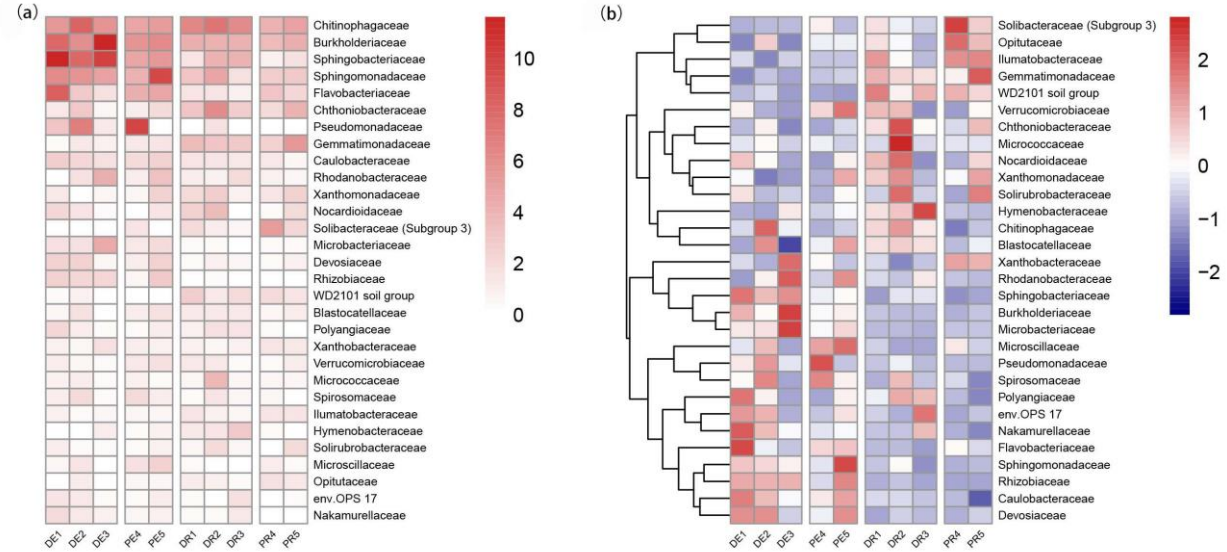

Fig. 5 Relative abundance heatmap of sequences identified on a family-rank taxonomic level. (a) Relative abundance

according to sequence percentage value; color scale—relative abundance (%). (b) Scaling within genus rows across all examined samples; relative abundance above average—red, relative abundance below average—blue. DE, *Deschampsia antarctica* root samples; PE, *Poa annua* root samples; DR, *Deschampsia antarctica* rhizospheric soil samples; PR, *Poa annua rhizospheric* soil samples. 1—5, sampling site numbers.

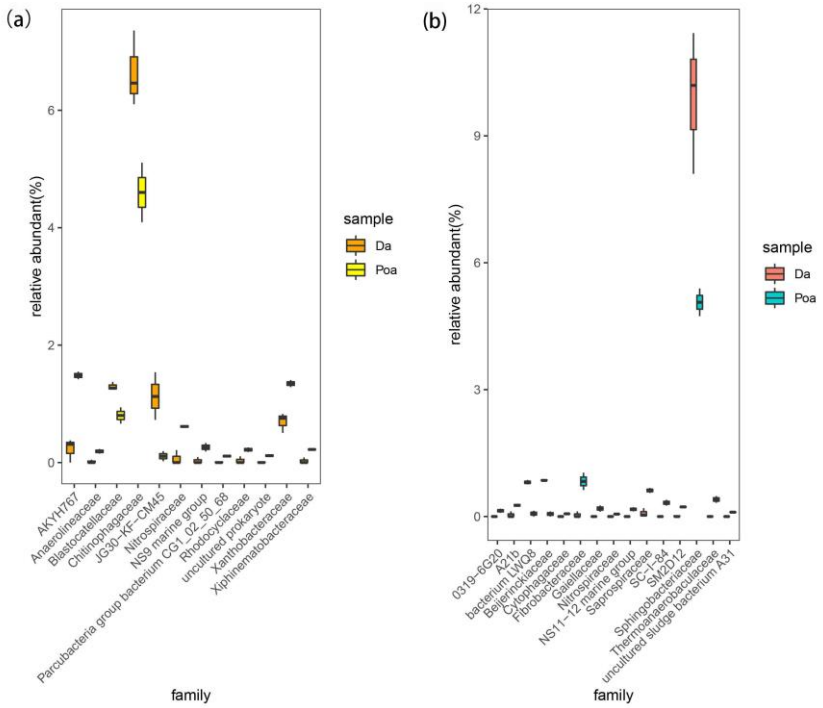

Fig. 6 Statistically signifcant diferences (p<0.05) within two poaceae plants rhizosphere/endosphere communities based on sequence contribution identifed on a family taxonomic level. (a) rhizosphere communities. (b) endosphere communities.

The endosphere community harbored high average relative abundances of the Burkholderiaceae both for the *D. antarctica* and the *P. annua*. Related strains of the Burkholderiaceae family in soil showed significant disease-suppressive activity. Several *Burkholderia spp.* can lower plant ethylene levels through ACC deaminase activity or to produce phytohormones. Furthermore, nitrogen fixation ability has been demonstrated in many *Burkholderia* species associated with different plants (Castanheira, et al. 2016). Sphingobacteriaceae sequences were the most numerous in *D. antarctica* root endosphere samples and Sphingomonadaceae sequences were the most numerous in *P. annua* root endosphere samples (Fig. 5). Among them, the sequence abundance of Sphingobacteriaceae in *D. antarctica* root endosphere materials was significantly (p=0.032) higher than that in *P. annua* root endosphere materials (Fig. 6b), especially at salt-stressed site 1. The extensive literature on Sphingobacteriaceae indicates that some genera of this family have demonstrated great potential as bioremediation and plant growth promoters. For instance, *Mucilaginibacter spp.* and *Sphingobacterium spp.* can induce plant energy metabolism and antioxidant systems allowing them to cope with salinity-induced toxicity (Fan, et al. 2020; Figueiredo, et al. 2022; Vaishnav, et al. 2020).

In polar regions, the mitigation of cold-induced stress is of great importance for plant survival and development. In this regard, studies on bacterial-mediated cold resistance in crops point to the role of ACC deaminase, a microbially produced enzyme that reduces the concentration of the plant stress hormone ethylene and promotes plant growth under cold conditions (Araya, et al. 2020). Certain strains of Chitinophagaceae, Burkholderiaceae, and Flavobacteriaceae families showed ACC deaminase activity. Therefore, Chitinophagaceae, Burkholderiaceae, and Flavobacteriaceae may play a crucial role in widely distributed Poaceae plants' adaptation to cold Antarctic conditions.

3.3. Similarities and differences between the root-associated microbial community in two Poaceae plants at the family level

To further search for families with statistically significant differences between groups, LEfSe analysis was performed. The four taxa were distinguishing the four groups based on LDA scores > 4.0 (Fig. 7). DE, PE, and PR have one, one, and two taxa with significant differences, respectively. Among them, Sphingobacteriaceae in *D. antarctica* endosphere microbial community samples showed the highest significant difference scores. Moreover, the rhizosphere community samples of the invasive Poaceae plant contained more taxa with significant differences than other samples.

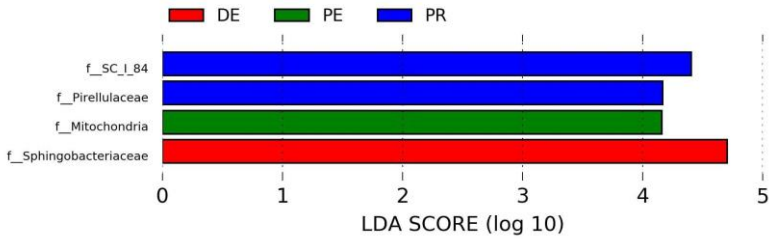

Fig. 7 LEfSe analysis of root-associated microbial community samples at the family level. DE, *Deschampsia antarctica* root samples; PE, *Poa annua* root samples; PR, *Poa annua rhizospheric* soil samples.

Most families were common to the rhizosphere and root-endosphere dwelling microbial community of the two Poaceae plants (Fig. 8). However, four families occur only in the root endosphere of two Poaceae plants, namely Enterobacteriaceae, Dongiaceae, Crocinitomicaceae, and 01D2Z36. Twenty families were found only in rhizosphere soil bacterial communities of two Poaceae plants, including Cryptosporangiaceae, Hyphomicrobiaceae, Gallionellaceae, etc. Ten families appeared both in the root endosphere and in the rhizosphere soil of *P. annua* but were not found in the related samples of *D. antarctica*, including Schlesneriaceae, Mycoplasmataceae, Pseudonocardiaceae, Puniceicoccaceae, Porticoccaceae, Coxiellaceae, uncultured eubacterium WD294, Chlorobi bacterium OLB5 and Parcubacteria group bacterium GW2011_GWF2_40_69. These families may be closely related to *P. annua* and may have an impact on the successful colonization of the invasive Poaceae plant in Antarctica. Eight families occur both in the *D. antarctica* endosphere community and in the *D. antarctica* rhizosphere soil community and were

not found in samples related to *P. annua*, including Acidothermaceae, Thermomicrobiaceae, Frankiaceae, Eubacteriaceae, uncultured gamma proteobacterium, P3OB-42, KD3-10, and uncultured bacterium SBR2013. These families may be closely related to *D. antarctica* and have important implications for the adaptation of native Antarctic plants to the Antarctic environment.

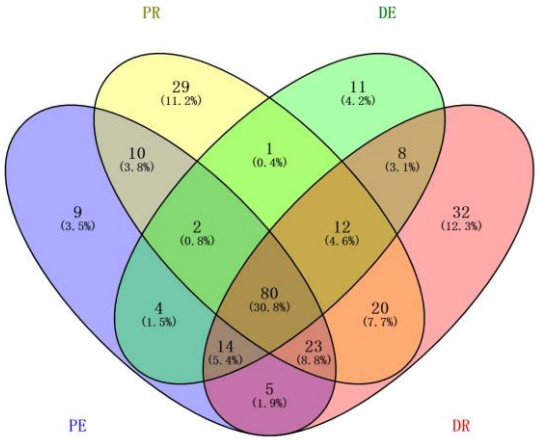

Fig. 8 Number of total families, shared and non-shared families present in the root-associated microbial community of two poaceae plants. DE, *Deschampsia antarctica* root samples; PE, *Poa annua* root samples; DR, *Deschampsia antarctica* rhizospheric soil samples; PR, *Poa annua rhizospheric* soil samples.

3.4. The core microbiome of two Antarctic Poaceae plants

The core community was based on the relative abundance of family-rank groups are shown in Fig. 9. Families that showed a relative abundance of 1% or higher at each site were rated as core community members. Three families were at the sufficient abundance in the rhizosphere and root-endosphere of two Antarctic Poaceae plants: Chitinophagaceae (4.09%-8.18%), Burkholderiaceae (3.55%-11.62%), Sphingomonadaceae (1.82%-9.72%). Three families were above the 1% threshold only in the rhizosphere of two Poaceae samples: Gemmatimonadaceae (2.47%-5.37%), Chthoniobacteraceae (1.95%-6.18%), and WD2101 soil group (1.30%-2.64%). Sphingobacteriaceae (4.74%-11.43%), Flavobacteriaceae (1.71%-8.40%), Caulobacteraceae (1.64%-2.79%), and Microbacteriaceae (1.22%-4.52%) have sufficient relative abundance only in the root-endosphere of two Poaceae samples. Among them, Microbacteriaceae are considered to be widely distributed Antarctica Poaceae plants' obligatory root endophytes, as they were observed in considerable abundance（>1%） in the endosphere at each location of *D. antarctica* and *P. annua*, and they were not observed in considerable abundance in two plants rhizospheric soils at all location. Members of the family Microbacteriaceae are widely distributed in various terrestrial ecosystems and often occur in association with plants as endophytes and pathogens (Tarlachkov, et al. 2020). Jurado et al. found that the Microbacteriaceae family is capable of producing bioactive substances that actively participate in the control of plant pathogens. Moreover, the Microbacterium family

can further stimulate the growth of plants and is an important microbiota with biocontrol potential (Jurado, et al. 2019).

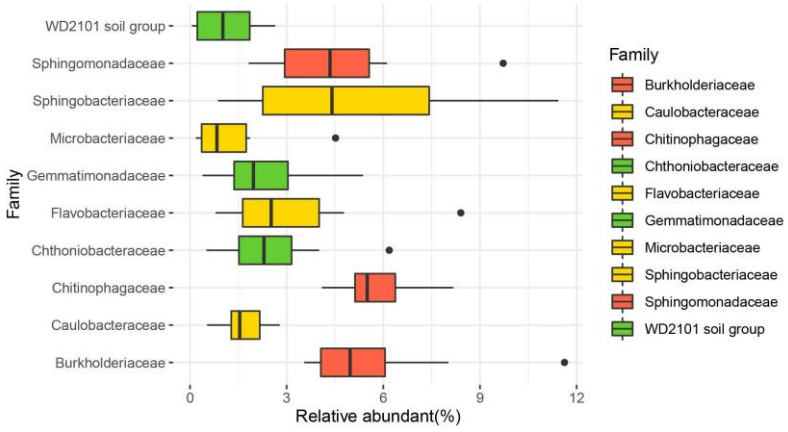

Fig. 9 Core microbiome of two Antarctic poaceae plants root-associated microbial communities based on sequence contribution (>1%) identifed on a family-rank taxonomic level. Red boxplots, bacterial families present in the rhizosphere and root-endosphere of two poaceae plants at>1%; green boxplots, bacterial families present only in the rhizosphere of two poaceae plants at>1%; yellow boxplots, bacterial families present only in the root-endosphere of two poaceae plants at>1%.

3.5. Identification of soil element importance to plants using random forest

Mixed growth of vascular plants is common in Antarctica (Schultz and Rosado 2019), and nutrients in the soil directly affect plant growth. There are many kinds of nutrients needed for plant growth and development, and 16 essential nutrients (carbon, hydrogen, oxygen, nitrogen, phosphorus, sulfur, potassium, calcium, magnesium, iron, manganese, zinc, copper, molybdenum, boron, and chlorine) have been confirmed, among which only carbon, hydrogen and oxygen mainly come from the atmosphere and water, and the rest mainly come from the soil (Wang, et al. 2001). However, excessive concentrations of these elements in the soil can be stressors for plant growth and development (Adamski, et al. 2011; Broadley, et al. 2007; Gupta, et al. 2011).

We use RF modeling to predict the relationship between different proportions of plants in the soil (Table S1) and nutrients in the soil (Fig. S1). The results showed that the soil elements (sodium, manganese, magnesium, zinc, and phosphorus) have a greater impact on both Poaceae ranked by their importance value (Fig. 10). Among them, manganese can promote the hydrolysis of carbohydrates, activate carboxylase and activate many dehydrogenases in plants, which is of great significance to plant respiration. Poaceae crops such as wheat, corn, and rice show yellowing of leaves when they are deficient in manganese. In the soil sample data collected in this study, all the areas where *D. antarctica* was grown had low concentrations of manganese in the soil, while all the areas where *P. annua* was grown had a high concentration of manganese in the soil. *D. antarctica* individuals have mixed pattern leaves of green and yellow (Clemente-Moreno, et al. 2020b). It can be speculated that the manganese concentrations in the soil may have a relationship

with the mixed pattern of green and yellow leaves of *D. antarctica*. However, more studies are required to determine the effect of manganese in soil on the leaves of *D. antarctica*. Zinc plays an important role in the stability and functional integrity of plant root cell membranes and cell structures. Zinc also participates in auxin metabolism in plants and is closely related to protein metabolism. The study found that Zn^{2+} concentration had a significant effect on seed germination, amylase activity, and seedling growth of Poaceae plant wheat (Li et al 2008). Phosphorus plays a significant role in the development of herbaceous roots and in increasing the resistance of herbaceous plants to extreme environments. Previous studies have found that phosphorus application significantly increased the biomass accumulation and distribution of *P. pratensis* and was able to enhance the growth rate of *P. pratensis* (Zhang et al 2021). Magnesium acts as a phosphorus carrier in plants, which is conducive to promoting better growth of plant roots and improving the utilization efficiency of nutrients and water in plants. In addition, magnesium can also promote the absorption of other nutrients by crops, thereby improving the ability of crops to resist drought and cold. The study found that the sugar and starch content of magnesium-deficient Poaceae plant rice decreased significantly.

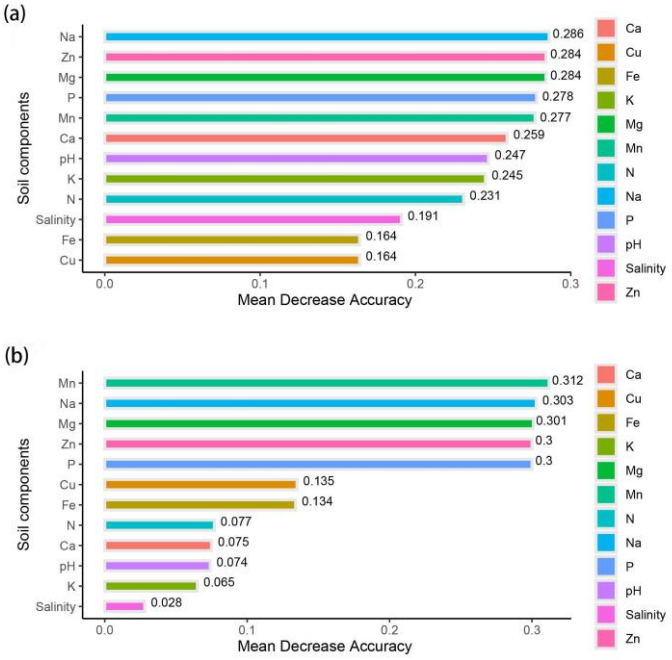

Fig. 10 Bar plots show the importance value of each soil element by the random forest model. Na at sites 4 and 5 takes the value of 150; Zn at sites 4 and 5 takes the value of 50. (a) soil elements associated with *Deschampsia antarctica*; (b) soil elements associated with *Poa annua.*

3.6. Correlations between microorganism and soil components

Pearson's correlation coefficient between the abundance of bacterial families and soil chemical composition revealed significant (p<0.05) correlations (Fig. 11). In the rhizosphere of two Antarctic Poaceae plants, the abundance of the family Sphingobacteriaceae displayed significant negative correlations with manganese concentrations (p=0.011) and zinc concentrations (p=0.008). In the

root endosphere community of two Antarctic Poaceae plants, the abundance of the family Caulobacteraceae was negatively correlated with phosphates concentrations (p=0.042), while it was positively correlated with the concentration of manganese (p=0.039) and magnesium (p=0.022). The abundance of Gemmatimonadaceae showed positive correlations with manganese concentrations (p=0.033) and zinc concentrations (p=0.047). In addition, the abundance of Flavobacteriaceae was negatively correlated with phosphates concentrations (p=0.019) and positively correlated with magnesium concentrations (p=0.011).

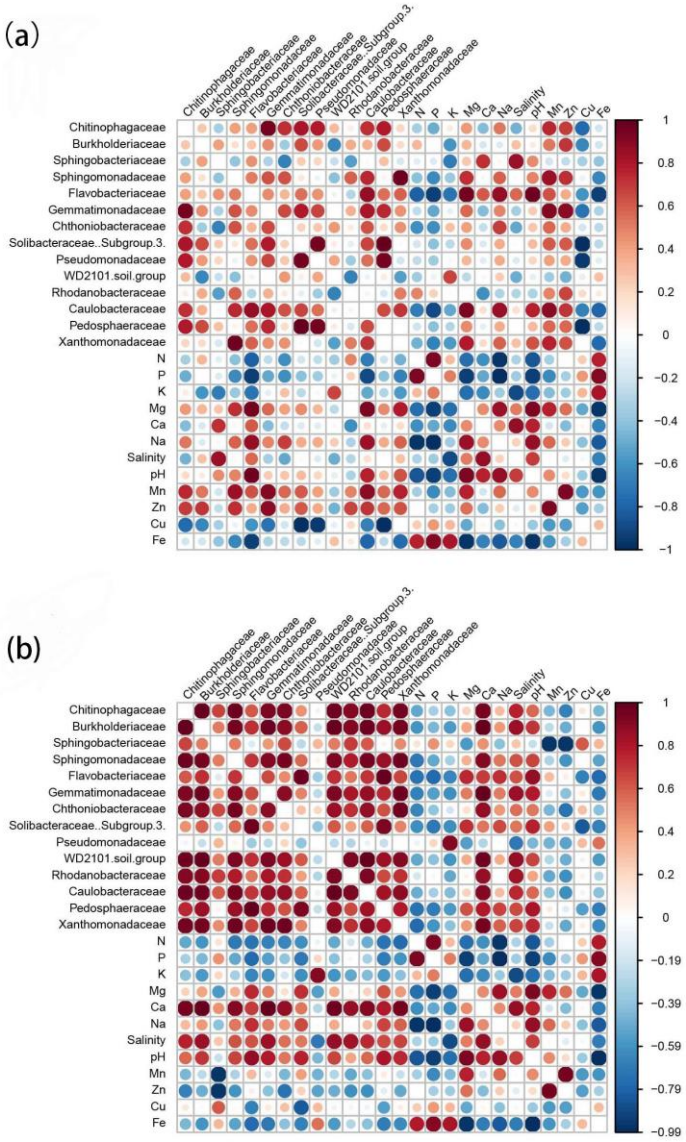

Fig. 11 Correlogram of rhizosphere/endosphere family-rank sequence abundance data and soil chemistry in two poaceae plants. (a) two poaceae plants root endosphere; (b) two poaceae plants rhizospheric. The color scale represents correlation coefficient values: dark red—positive correlation, dark blue—negative correlation.

Studies on root-related microorganisms indicated that the physiological status of the host plant affects the phylogenetic structure of its root-associated microbiome. Meanwhile, this physiological status is dependent on the edaphic and climatic conditions experienced by the plant (Znój, et al. 2021a). Our findings show: It is predicted that two Antarctic Poaceae plants have a strong relationship with manganese, magnesium, sodium, zinc, and phosphorus in soil by random forest

model. Moreover, in the endosphere and rhizosphere of two Antarctic Poaceae plants, Pearson's correlation coefficient showed that these elements were significantly correlated with bacterial family-rank groups: Sphingobacteriaceae, Caulobacteraceae, Gemmatimonadaceae, Flavobacteriaceae.

Therefore, the families that have a great influence on widely distributed Antarctica Poaceae plants include Sphingobacteriaceae, Caulobacteraceae, Gemmatimonadaceae, and Flavobacteriaceae.

4. Conclusion

We found the species diversity of root-associated microbial communities of invasive Poaceae plants is significantly higher than that of non-invasive Poaceae species, and the majority of ASVs observed were not shared between the respective rhizosphere and endosphere of the two Poaceae plants. In addition, Chitinophagaceae, Burkholderiaceae, Sphingomonadaceae, Sphingobacteriaceae, Flavobacteriaceae, Caulobacteraceae, and Microbacteriaceae were recognized in this study to form a core microbiome of two Antarctic Poaceae plants' root endosphere. The core microbiomes of the rhizosphere of the two Poaceae plants are Chitinophagaceae, Burkholderiaceae, Sphingomonadaceae, Gemmatimonadaceae, Chthoniobacteraceae, and WD2101 soil group. Of these, Chitinophagaceae, Burkholderiaceae, and Flavobacteriaceae were more abundant in the root-associated microbial communities of two Poaceae plants and their strains had ACC deaminase activity. Based on random forest and correlation analyses the families that were found to have a great impact on Poaceae plants growing in extreme environments are: Sphingobacteriaceae, Caulobacteraceae, Gemmatimonadaceae, and Flavobacteriaceae.

Competing Interests

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Author Contributions Statement

ZX (Zhikai Xing), XW, YY and JQ conceived and designed the project. YQ, HX, CW, XL and ZX (Zhuoran Xun) analyzed the data. LW, QZ, XT, LX, SW and LJ performed the data visualization. ZX (Zhikai Xing), LZ and YQ drafted and reviewed the manuscript with contributions from other authors.

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