



Bacteriome diversity in leaf and root of the resurrection species *Selaginella convoluta* and *S. sellowii* in the Brazilian Cerrado

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Abstract

Plants have developed adaptive strategies to combat dehydration, including forming associations with microbes, which help plants cope with drought by altering hormone levels, enhancing antioxidants, or improving water uptake. *Selaginella* species, the resurrection plants, can endure desiccation and revive with rehydration. Here, we investigated the bacteriome of leaves and roots of *S. convoluta* and *S. sellowii* inhabiting rocky outcrops. We analyzed 16 S rRNA bacterial sequences from 38 leaves samples and 36 from roots. *Actinobacteriota*, *Chloroflexi*, *Proteobacteria*, and *Acidobacteriota* were the dominant phyla, with *Methylobacteriaceae*, *Pseudonocardiaceae*, and *Sphingomonadaceae* being the most prevalent bacterial families. The roots and leaves exhibited an increased relative abundance of the phyla *Actinobacteriota* and *Proteobacteria*, whereas *Chloroflexi* and *Acidobacteriota* were also common in the roots. The families identified in the leaves are commonly associated with soil, likely reflecting the plant structure and their close contact with the ground; root samples displayed higher diversity indices than leaves. The functional diversity analysis showed no significant differences between the species' roots, though some samples displayed increased photoautotrophic reactions. *Selaginella sellowii* exhibited enhanced aerobic ammonia oxidation, photoautotrophy, and denitrification, while *S. convoluta* showed increased methanol oxidation and methylotrophy, with *Methylopila* as the main contributor. The identified bacterial families were beneficial for nutrient acquisition, growth, and fungal regulation at the root interface, contributing to plant health in nutrient-poor, shallow, and acidic soils characteristic of the Brazilian Cerrado. This study highlights the importance of understanding plant–microbiome interactions in harsh environments, such as the Cerrado biome, using *Selaginella* as a model for drought tolerance.

Keywords 16S rRNA · Abiotic stress · Drought tolerance · Metabarcoding · Resurrection plant

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Introduction

Plants of *Selaginella* (Selaginellaceae, spike mosses) biosynthesize rare and specialized secondary metabolites, including selaginellins, bioflavonoids, and high-molecular-weight phenylpropanoid derivatives, which exhibit a wide range of biological effects (Queiroz et al. 2016; Li et al. 2021). In this way, several *Selaginella* species are used in traditional medicine to treat various conditions such as inflammation, dysmenorrhea, chronic hepatitis, and hyperglycemia (Yang et al. 2012; Nguyen et al. 2015; Le et al. 2017; Zhang et al. 2017; Li et al. 2021). The genus exhibits its highest species diversity within tropical and subtropical forest regions, often thriving on shaded slopes. Notably, some species can withstand environments that are permanently or temporarily subject to severe drought (Mickel et

al. 2004). *Selaginella convoluta* is widely distributed across the Americas, including from the Greater Antilles and Central America to South America, encompassing northwestern Argentina, Bolivia, Brazil, French Guiana, and Paraguay (Lellinger 1983). It occupies biomes with varying degrees of seasonality in Brazil, particularly the Cerrado (Brazilian Savanna) and the Caatinga (Ambrósio and Melo 2001; Maris 2005). In its most severe dehydrated state, *S. convoluta* exhibits tightly curled microphylls that resemble compact spheres, which can fully recover upon rehydration (Reginaldo et al. 2021). Another desiccation-tolerant lycophyte in tropical America is *S. sellowii*, which occurs in Argentina, Bolivia, Brazil, Colombia, Cuba, Ecuador, Mexico, Paraguay, Peru, Uruguay, and Venezuela. This species occurs on rocky outcrops throughout the Brazilian Cerrado, and its spirally arranged acicular leaves distinguish it, each tipped with a whitish apical bristle that sometimes detaches (Barfels 2005; Heringer et al. 2016).

The Cerrado ecosystem is highly diverse, with a significant degree of endemism and pronounced seasonality (Gamarra et al. 2021). The rainy season extends from November to March, whereas the dry season, characterized by arid conditions and elevated temperatures, lasts from April to October (Nascimento and Novais 2020). This seasonality creates a dynamic and challenging environment for the species inhabiting the Cerrado, demonstrating their resilience and the necessity to adapt to contrasting and adverse conditions throughout the year. Desiccation tolerance is a trait that enables plants to endure cycles of severe dehydration and rehydration without losing viability, earning them the designation of resurrection plants (Porembski et al. 2021). Several *Selaginella* species can rapidly restore metabolic function and resume growth after prolonged desiccation (Zhou et al. 2015). Some *Selaginella* genes have been associated with desiccation tolerance, including ROS scavenger genes and genes related to abscisic acid synthesis, both of which are overexpressed during desiccation (Xu et al. 2018). Furthermore, metabolic profiling studies have shown that *Selaginella* species maintain elevated levels of amino acids, sugar alcohols, and polysaccharides under drought conditions, which may contribute to their robust desiccation tolerance (Yobi et al. 2012).

In addition to metabolic adaptation, plants can employ other survival mechanisms under drought conditions, such as leveraging their microbiome in the phyllosphere, rhizosphere, and roots (endosphere; Trivedi et al. 2020). This plant-microbiome interaction is pivotal for various plant development stages, aiding in seed germination and vigor, cell development, stress tolerance, nutrient uptake, productivity enhancement, and regulation of plant metabolism (Schlaeppli and Bulgarelli 2015; Compant et al. 2021; Singh et al. 2020). A particularly important group within the plant

microbiome is endophytic bacteria, which colonize internal tissues without showing external signs of infection or exerting negative effects on their host (Schulz and Boyle 2005), being an ubiquitous presence in most higher plants (Lodewyckx et al. 2002). The interaction is highly specific, as plant-associated microbial communities demonstrate structured organization and exhibit a defined phylogenetic arrangement during community assembly (Li et al. 2023).

Complex interactions between the environment and plant hosts shape plant-microbiome associations. The phyla *Proteobacteria* and *Firmicutes* are highly represented in endophytic communities, whereas *Bacteroidetes*, *Firmicutes*, *Actinomycetes*, and *Proteobacteria* are more abundant in phyllosphere communities (Carlström et al. 2019; Trivedi et al. 2020). Notably, *Proteobacteria* comprise approximately 50% of the phyllosphere community (Trivedi et al. 2020). Although most *Proteobacteria* are free-living, certain members, such as rhizobia, form symbiotic relationships with specific leguminous plants to fix nitrogen. These bacteria perform various plant-related functions, including enhancing soil fertility, nitrogen fixation, acting as biopesticides, and promoting plant growth by the direct or indirect action of their genes (Bruto et al. 2014; Orellana et al. 2022).

Considering resurrection plants such as *Oreocharis mileensis* (WTWang) Mich.Möller & A.Weber, *Myrothamnus flabellifolia* Welw., *Boea hygrometrica* (Bunge) R.Br., and species of *Ramonda* Rich., it has been reported that they actively filter and maintain microbial communities to support survival under extreme desiccation (Sun et al. 2024; Tebele et al. 2024; Asatulloev et al. 2025). In these plants, the plant-soil compartment (bulk soil, rhizosphere, and endosphere) acts as a strong, plant-driven ecological filter for microbial diversity, which consistently declines from the bulk soil toward the root endosphere (Sun et al. 2024; Tebele et al. 2024; Asatulloev et al. 2025). In addition, in *Ramonda serbica* and *R. nathaliae*, high similarity in bacterial composition despite geographic distance indicates that host genotype and specific root exudates precisely define the microbiome structure (Lozo et al. 2023). Moreover, drought conditions promote the enrichment of stress-tolerant taxa. For instance, *Actinobacteriota* often increase under drought; their thick peptidoglycan cell walls and ability to produce antimicrobial compounds enhance their survival (Asatulloev et al. 2025; Tebele et al. 2025).

In this context, the present study investigated bacteriome diversity during the dry season in *S. convoluta* and *S. sellowii*, two desiccation-tolerant species (resurrection plants) commonly found in the Brazilian Cerrado. We tested the hypothesis that these species exhibit similarities in the bacteriomes of their leaves (phyllosphere) and roots (rhizosphere and endosphere). Although considerable knowledge exists regarding the metabolic adaptations of certain

Selaginella species to drought conditions, the bacteriomes of *S. convoluta* and *S. sellowii* remain unexplored. This knowledge may enhance our understanding of bacteriome diversity and composition associated with *S. convoluta* and *S. sellowii*, particularly regarding the severe seasonal droughts characteristic of Cerrado ecosystems.

Materials and methods

Studied area and species

Selaginella convoluta and *S. sellowii* coexist along rocky outcrops within the Cerrado vegetation in Midwest Brazil (Fig. 1a). Samples were collected in Mato Grosso do Sul state (-20.339703/-54.695883, approximately 410 m a.s.l.), in August 2021, following 35 days of rainfall shortage, in the middle of the dry season. The plants, preferably in pairs

of species (Fig. 1b), were at least 4 m from each other, totaling 16 specimens from *S. convoluta* (Fig. 1c) and 22 from *S. sellowii* (Fig. 1d). Voucher specimens were deposited in the CGMS Herbarium at the Federal University of Mato Grosso do Sul, Brazil, and the project is registered in the National Genetic Heritage Management System (SisGen) under the number A63DB37. Each plant compartment samples, leaf and root, were stored in separated falcon tubes using sterilized tweezers. The samples were kept in ice during the transport to the laboratory, washed with ultrapure sterilized water (DNA-free) on the same day, and then stored at -80 °C.

DNA extraction and 16S rRNA sequencing

The DNA was extracted with MagMax™ Microbiome Ultra Nucleic Acid Isolation (Thermo Fisher Scientific, Waltham, MA), using 0.25 g of each sample, according to the manufacturer's instructions. The 16 S rRNA region was amplified

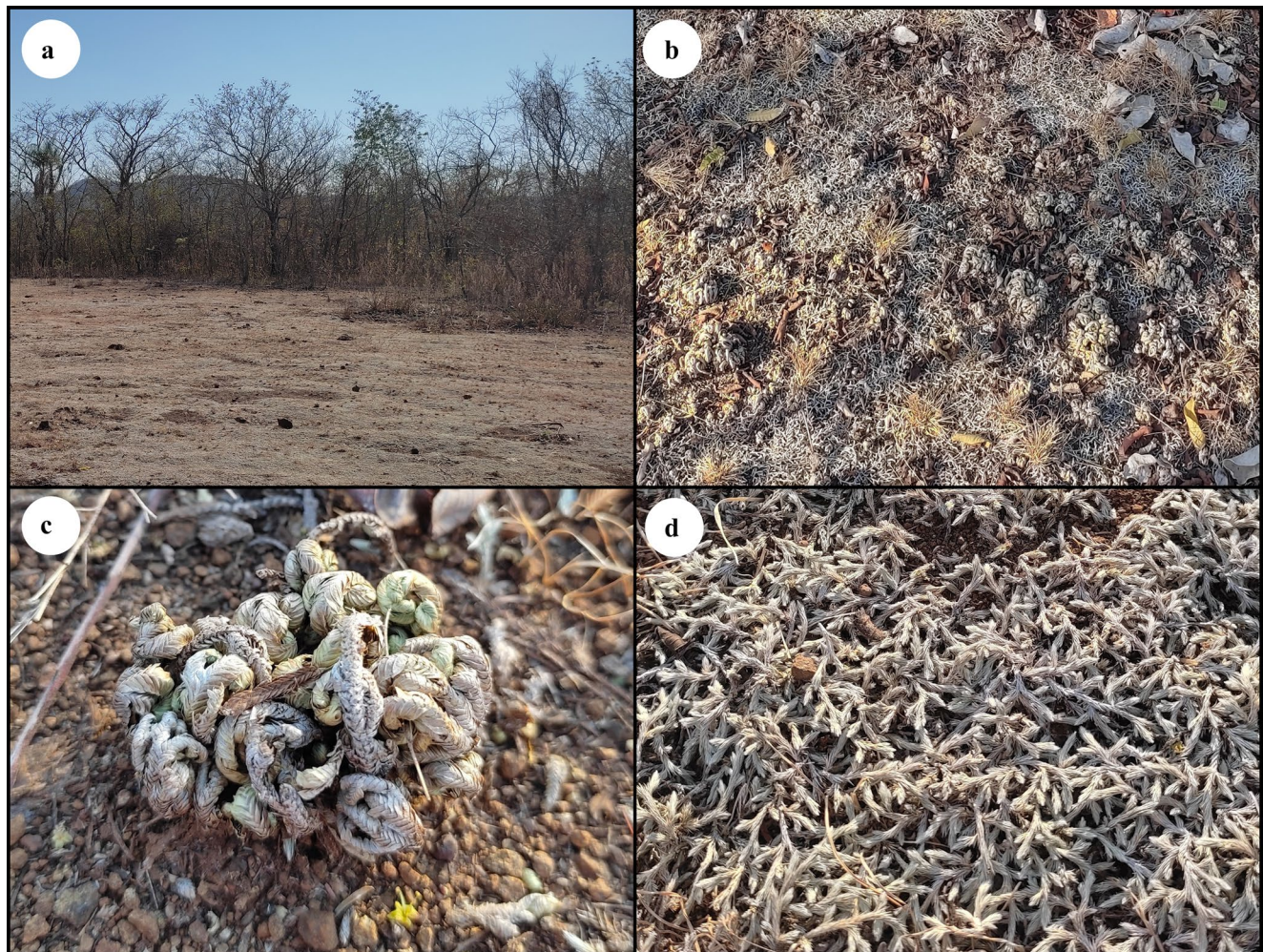


Fig. 1 (a) Overview of the *Selaginella* population sampling area during the dry season, August 2021, Morro do Ernesto, Campo Grande (MS). (b) Cooccurring natural populations of *Selaginella convoluta*

and *S. sellowii*. (c) Detail of a *Selaginella convoluta* individual. (d) Detail of *Selaginella sellowii* individuals

in triplicate, using the primer pair 515 F (GTGCCAGC-MGCCGCGGTAA) and 806R (GGACTACHVGGGT-WTCTAAT) (Caporaso et al. 2011) to target the V4 region. The PCR mix consisted of 22.5 µL of Platinum PCR Super-Mix High Fidelity (Invitrogen™), 2 µL of genomic DNA, and 0.5 µL of 10 µM primer. The initial step of PCR was 94 °C for 3 min, followed by 40 cycles of denaturation at 94 °C for 30 s, primers' annealing at 60 °C for 30 s, and extension at 68 °C for 1 min. The triplicates were united and purified in two rounds using the AMPure® XP reagent (Beckman Coulter, Indianapolis, IN, USA). The samples were quantified in a Qubit® instrument and then diluted to 40pM. The amplicon pool was loaded onto the Ion Chef™ System (Thermo Fisher Scientific) for emulsion PCR, enrichment, and loading onto an Ion S5 530 chip. Following templating and chip loading, samples were sequenced using 850 flows in the Ion GeneStudio S5 System, following the manufacturer's instructions (Life Technologies).

Sequences treatment and diversity analyses

Bioinformatic analyses were performed with QIIME 2 2023.7 (Bolyen et al. 2019) (R Core Team 2024, <https://www.R-project.org/>). Raw sequence data were quality filtered using the q2-demux plugin, followed by denoising with DADA2 (Callahan et al. 2016). All amplicon sequence variants (ASVs) were aligned with MAFFT (Katoh et al. 2002) and used to construct a phylogeny with FastTree 2 (Price et al. 2010). Taxonomy was assigned to ASVs using the classify-sklearn naïve Bayes taxonomy classifier (Bokulich et al. 2018a, b) against the Greengenes 13_8 99% OTUs reference sequences (McDonald et al. 2011). We filtered all samples to exclude sequences: (1) with less than ten copies; (2) from mitochondria and chloroplast; (3) identified only at the phylum level. The processed sequences have been deposited in the NCBI database under BioSample accession numbers SAMN48454655 to SAMN48454730.

Alpha-diversity metrics (observed amplicon sequence variants – ASVs) and Faith's Phylogenetic Diversity (Faith 1992), beta-diversity metrics weighted UniFrac (Lozupone et al. 2007), unweighted UniFrac (Lozupone and Knight 2005), Jaccard distance, Bray-Curtis dissimilarity, and Principle Coordinate Analysis (PcoA) were estimated after rarefaction of 8,000 sequences per sample. The Kruskal-Wallis test compared alpha diversity metrics of plant compartments and species. PERMANOVA (Anderson 2017) analysis on beta diversity metrics using 999 permutations was used to compare group distances. The fractions of shared and exclusive variants at the family level were visualized using Venn diagrams in the InteractiVenn web platform (<http://www.interactivenn.net/>; Heberle et al. 2015).

Differential abundance was assessed using QIIME 2 2025.10.1 (Bolyen et al. 2019) with the ANCOM-BC method (Lin and Peddada 2020) based on genus-level collapsed tables. Comparisons between *S. convoluta* and *S. sellowii* were performed separately for each plant compartment, while their comparisons were conducted within each species; additionally, an integrated analysis was performed using the combined species_plant compartment variable. Visualizations were generated using the da-barplot package, considering statistical significance at $p < 0.05$. At the family level, differential abundance was evaluated using Random Forest (Breiman 2001), with families treated as target variables. The 40 most important families were selected and visualized through heatmaps for leaves and roots, with samples grouped by category in a sample-classifier heatmap format, a complementary approach for testing if and how samples are different from one another, using machine-learning methods to determine how predictive microbiome composition is, implemented in Qiime2 software (version 2024.10). The resulting tables were exported for plot generation in R using the ggplot2 package (Wickham 2011). For the functional diversity analysis, the FAPROTAX pipeline was used to relate microbial diversity to the functions performed by each taxa (Louca et al. 2016).

Results

Bacteriome composition

After filtering, we obtained 1,765,957 sequences from 74 samples, including 16 leaves of *S. convoluta*, 22 leaves of *S. sellowii*, 16 roots of *S. convoluta*, and 20 roots of *S. sellowii*. We identified 8,487 and 9,404 ASVs for *S. convoluta* and *S. sellowii*, respectively, spanning 34 bacterial phyla. For both *Selaginella* species, the dominant phyla were *Actinobacteriota*, *Chloroflexi*, *Proteobacteria*, and *Acidobacteriota*. Comparing leaf and root bacteriome composition, both presented *Actinobacteriota* and *Proteobacteria* as the main phyla; however, there was an increase in the relative abundance of *Acidobacteriota* and *Chloroflexi* in the roots, while *Bacteroidetes* and *Planctomycetes* were the second more frequent in the leaves (Fig. 2).

Alpha rarefaction plotting revealed no differences in the maximum values of the Shannon index when comparing species (Online Resource). However, a comparison of plant compartments showed that the lines approached a zero slope at different Shannon index values for root and leaf samples (approximately 8 and 6, respectively; Online Resource), suggesting greater heterogeneity in root samples as the Shannon index accounts for relative abundance. No significant differences were observed in the alpha diversity

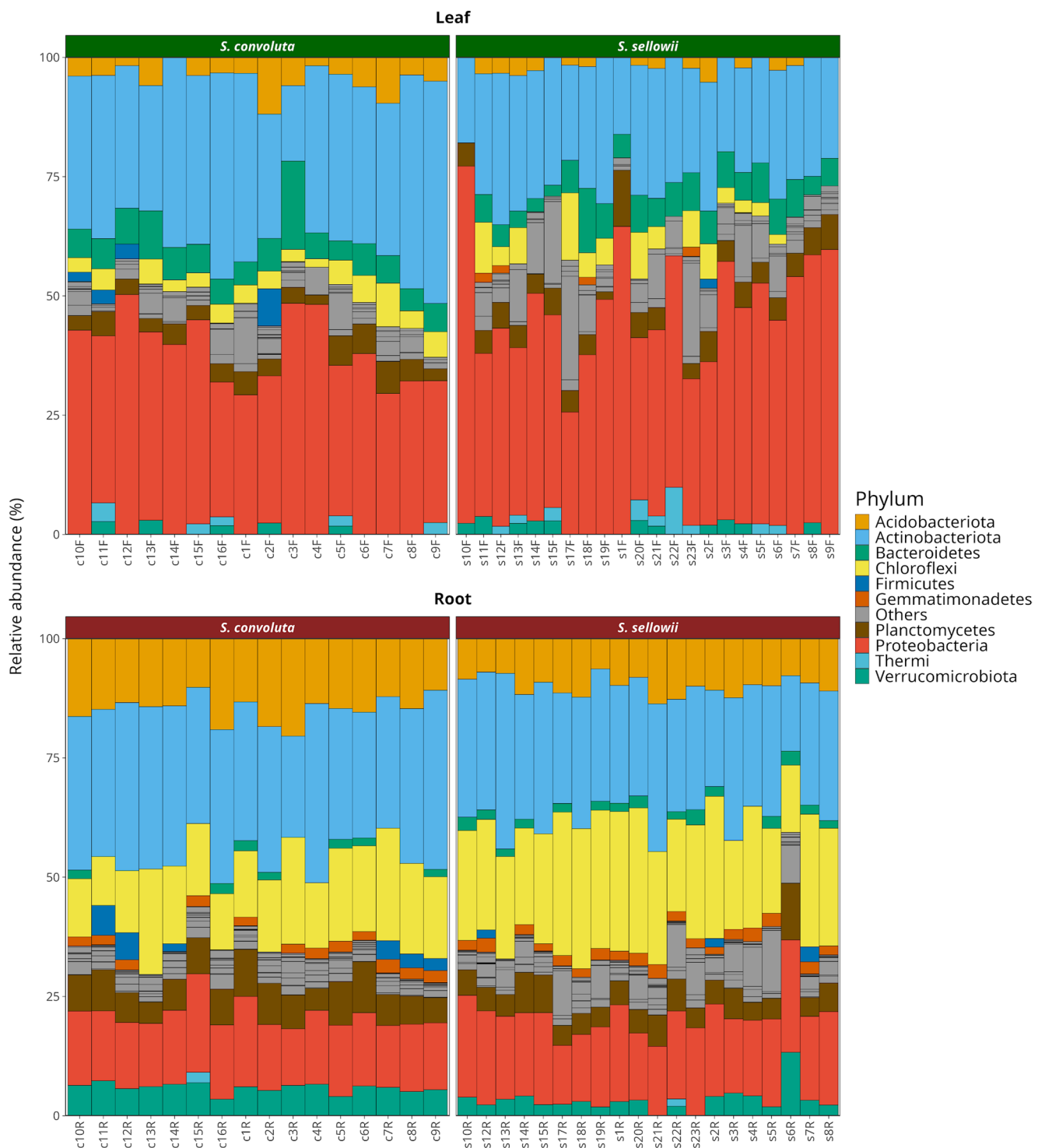


Fig. 2 Bar-plot of the bacteriome diversity composition at bacterium phylum level identified by Qiime2. Data are presented for the leaf and the root of *Selaginella convoluta* and *S. sellowii*

metrics of species samples ($p > 0.05$). In contrast, significant differences were noted in all alpha diversity metrics (observed ASVs, Shannon index, Faith's phylogenetic diversity, and Pielou's evenness) between plant compartments, with root samples consistently exhibiting higher levels (data not shown).

Taxon exclusivity and sharing patterns

The PCoA plots for beta diversity metric revealed the clustering of plant compartments for both species. Leaf and root samples were differentiated along Axis 1, whereas species samples were slightly distinguished along Axis 2, considering the leaf (Fig. 3; Online Resource; test statistic = 1.83832; $p = 0.001$). We compared samples from the same plant compartment and species collected at different points (plants were collected in pairs) and detected no statistical differences in microbiome composition (data not shown; $p > 0.05$). This finding underscores that the influence of plant compartments and species on the bacterial community composition is more pronounced than spatial proximity (Online Resource).

The Venn diagram, derived from barplot data, illustrates the number of unique and shared bacterial taxa at the family level among the sampled species and plant compartments (Fig. 4). The results indicate that *S. convoluta* and *S. sellowii* shared 12.9% of bacterial taxa (117 out of 902; Fig. 4). In contrast, 3.8% were specific to *S. convoluta*, and 4.1% were specific to *S. sellowii*. The roots exhibited the

highest number of unique taxa at 5.4%, whereas the leaves contained only 1.3%. *Selaginella convoluta* and *S. sellowii* shared only one bacteria taxa in the leaves; the bacteriome specific to the *S. convoluta* leaf was 0.99%, and for *S. sellowii*, it was a mere 0.33%. Finally, the species share 7.4% of bacterial taxa at roots. The exclusive taxa of each species and plant compartments can be observed in the Online Resource.

Bacteriome differential abundance

The ANCOM-BC results for the bacteriome of leaves and roots indicated significantly different ASV abundances between *S. convoluta* and *S. sellowii* (Fig. 5). For the top 20 taxa presented in Fig. 5, seven families appeared in both leaf species, *Cytophagaceae*, *Geodermatophilaceae*, *Microbacteriaceae*, *Methylobacteriaceae*, *Methylocystaceae*, *Pseudomonadaceae*, and *Scytonemataceae*, corresponding to 31.8% of all families observed in the leaf for both species. In *S. convoluta*, additional 13 families exhibited high differential abundance, with emphasis on *Nakamurellaceae*, *Pseudanabaenaceae*, and *Aurantimonadaceae* (Fig. 5a). For *S. sellowii*, two other families exhibited high differential abundance, *Kineosporiaceae* and *Acidobacteriaceae* (Fig. 5b). Regarding roots, eleven taxa appeared in both species, the families *Chthoniobacteraceae*, *Conexibacteraceae*, *Gaiellaceae*, *Haliangiaceae*, *Hyphomicrobiaceae*, *Nitrososphaeraceae*, *Pirellulaceae*, and *Sinobacteraceae*, and the taxa identified as Dolo 23, S47, and FFCH4570,

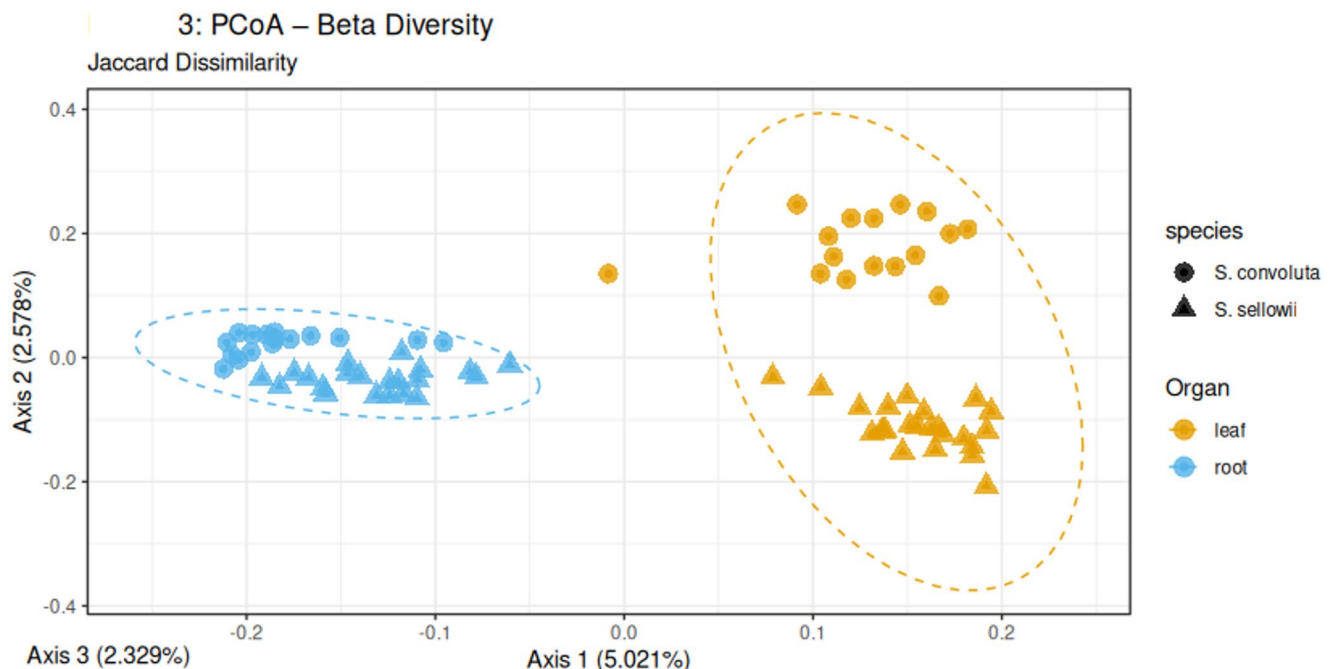


Fig. 3 Beta diversity of bacterial communities from the leaf (yellow) and root (blue) of *Selaginella convoluta* (circle) and *Selaginella sellowii* (triangle). The similarities were calculated by Jaccard distance (statistic test = 1.83832; $p = 0.001$), using the RStudio software (version 4.3.3)

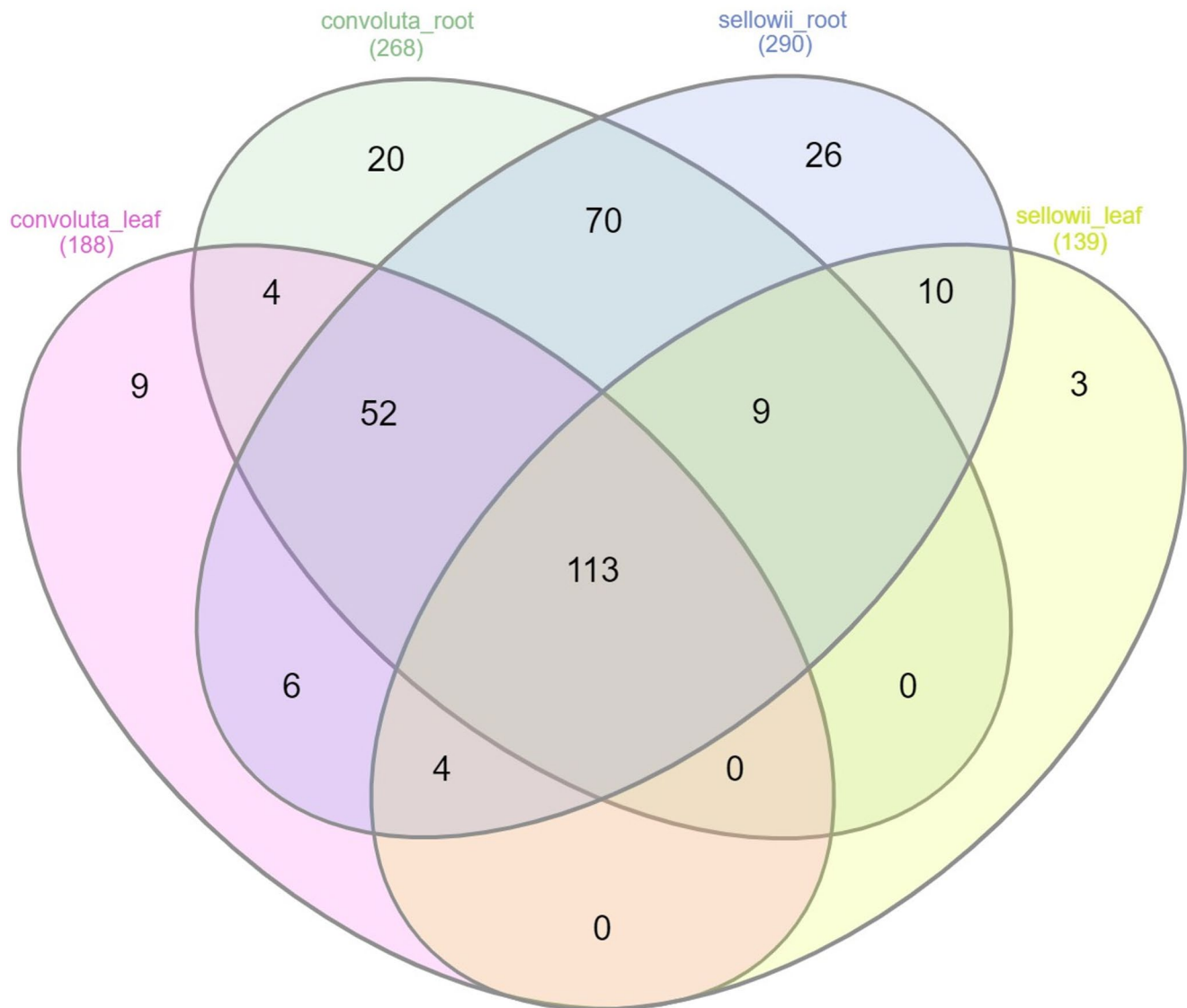


Fig. 4 Venn diagrams for each species and organ of *Selaginella*. Together with the name of the subgroup, the total number of variants represented is indicated in parentheses. The number of variants that are shared between the subgroups is shown at the intersections of the sets

corresponding to 37.9% of all taxa observed in the top 20 most abundant in the root for both species.

In *S. convoluta*, additional 9 taxa exhibited high differential abundance, with emphasis on *Opitutaceae*, *Streptosporangiaceae*, *Ktedonobacteraceae*, and *Anaeroplasmataceae* (Fig. 5a). For *S. sellowii*, nine other families exhibited high differential abundance too, standing out *Kouleothrixaceae*, *Streptomycetaceae*, *Bradyrhizobiaceae*, and *Micromonosporaceae* (Fig. 5b).

The heatmap analysis depicted the 40 ASVs (rows) common to each sample and the frequency of their occurrence (Fig. 6). In the leaf samples, the predictive microbiome composition revealed the family *Nakamurellaceae* as predictive of *S. convoluta* leaves, as it only appears in this species. Other 12 families (32.5%) can be considered predictive

of leaf for both species, especially *Methylobacteriaceae* and *Microbacteriaceae*. In the root samples, the predictive microbiome composition revealed the family *Methylobacteriaceae* as predictive of *S. sellowii* roots, although it also appears in the leaf for both species. Another 14 taxa (35%) can be considered predictive to root for both species, especially *Gaiellaceae*, *Kouleothrixaceae*, and *Pseudonocardiaceae*. Based on the results of the analysis, we can say that there is a difference in the microbial communities among plant compartments regardless of the species. Therefore, we found that the organ is the primary driver of alpha diversity.

The heatmap of functional diversity analysis did not reveal significant differences between the species when the root-associated communities were compared, although some samples showed an increase in photoautotrophic

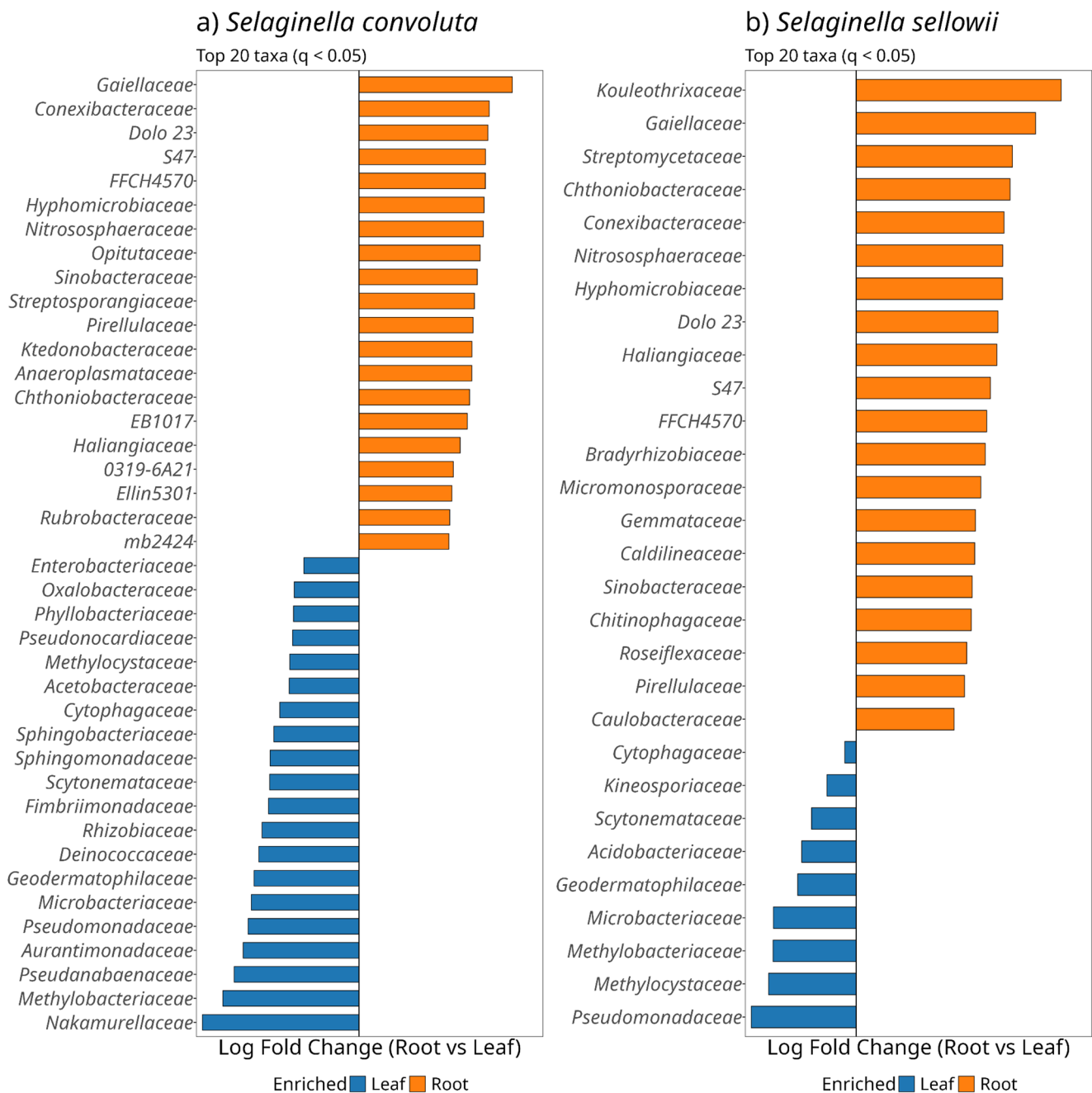


Fig. 5 Differential abundance analysis using ANCOM-BC on Qiime2 software (version 2024.10), comparing leaf and root within species (**a**) *Selaginella convoluta* and (**b**) *S. sellowii*

functions (Fig. 7a). In the roots (Fig. 7b), *S. sellowii* exhibited increased taxa related to aerobic ammonia oxidation, photoautotrophy, and denitrification, the latter being associated with a higher abundance of the genus *Rhodoplanes*. In *S. convoluta*, an increase in methanol oxidation was observed, mediated by the families *Nostocophycidae* and *Oscillatoriohaptophycidae*, as well as methylophagy activity, predominantly driven by the genus *Methylophaga*.

Discussion

Plants maintain a close relationship with microbial communities capable of forming complex and dynamic interactions that generate mutual benefits. Influenced by the environment and the host genotype, these interactions can enhance plant resilience to biotic and abiotic factors such as diseases, drought, life cycle phenology, and environmental stresses (Trivedi et al. 2021). Plants have evolved a multi-layered

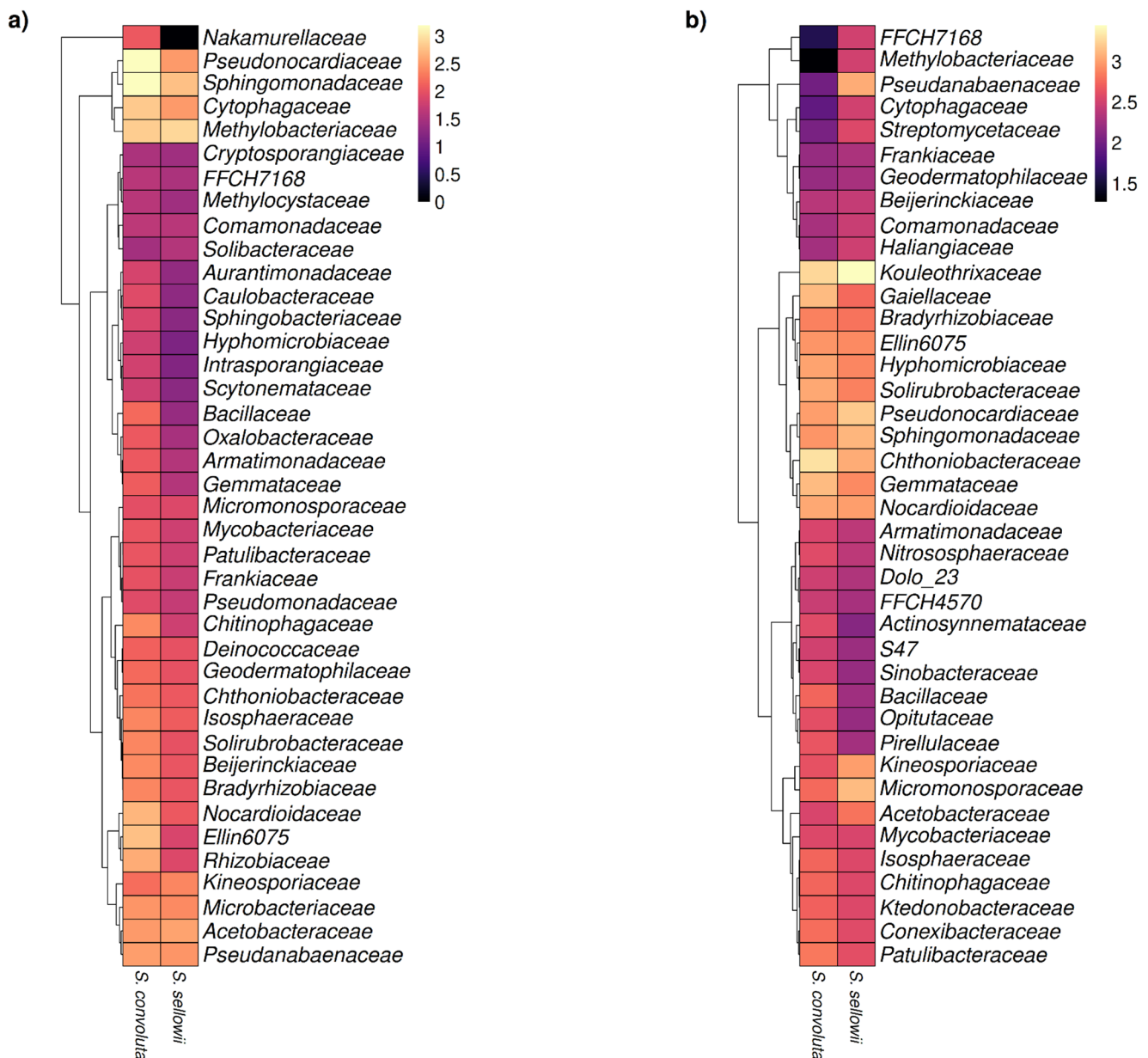


Fig. 6 Heatmap based on the 40 most important bacteria taxa of the *S. convoluta* and *S. sellowii* plant compartments, generated using Qiime2 software (version 2024.10). Annotations on bottom of the heatmap show the species considering **a)** leaf and **b)** root samples

microbial management system to incorporate the most beneficial microbes (Teixeira et al. 2019). When comparing the leaves and roots of the two species, *S. convoluta* and *S. sellowii*, variations in the bacterial communities associated with each compartment were observed, revealing a higher bacterial richness in the roots. These variations suggest a significant selective force within plant compartments, shaping the bacterial communities associated with plants, including epiphytes and endophytes (Morella et al. 2019).

Some Cerrado plants lose all or part of their leaves during the dry season, consequently increasing soil biomass and biogeochemical processes during the rainy season (Klink

and Solbrig 1996). This suggests that the low abundance of bacterial groups in the leaves may be related to the lack of environmental humidity. On the other hand, the presence of bacterial groups in the roots is associated with the protection offered by the soil to this plant structure, allowing bacteria to survive in the long term by regulating the balance of microorganisms in the root environment, promoting the health and survival of both (Hayat et al. 2010). Notably, the leaf bacteriome was relatively consistent at the phylum level; however, notable differences were evident at the family level. This demonstrates that the microbial community profile reveals significant differences even among plants of

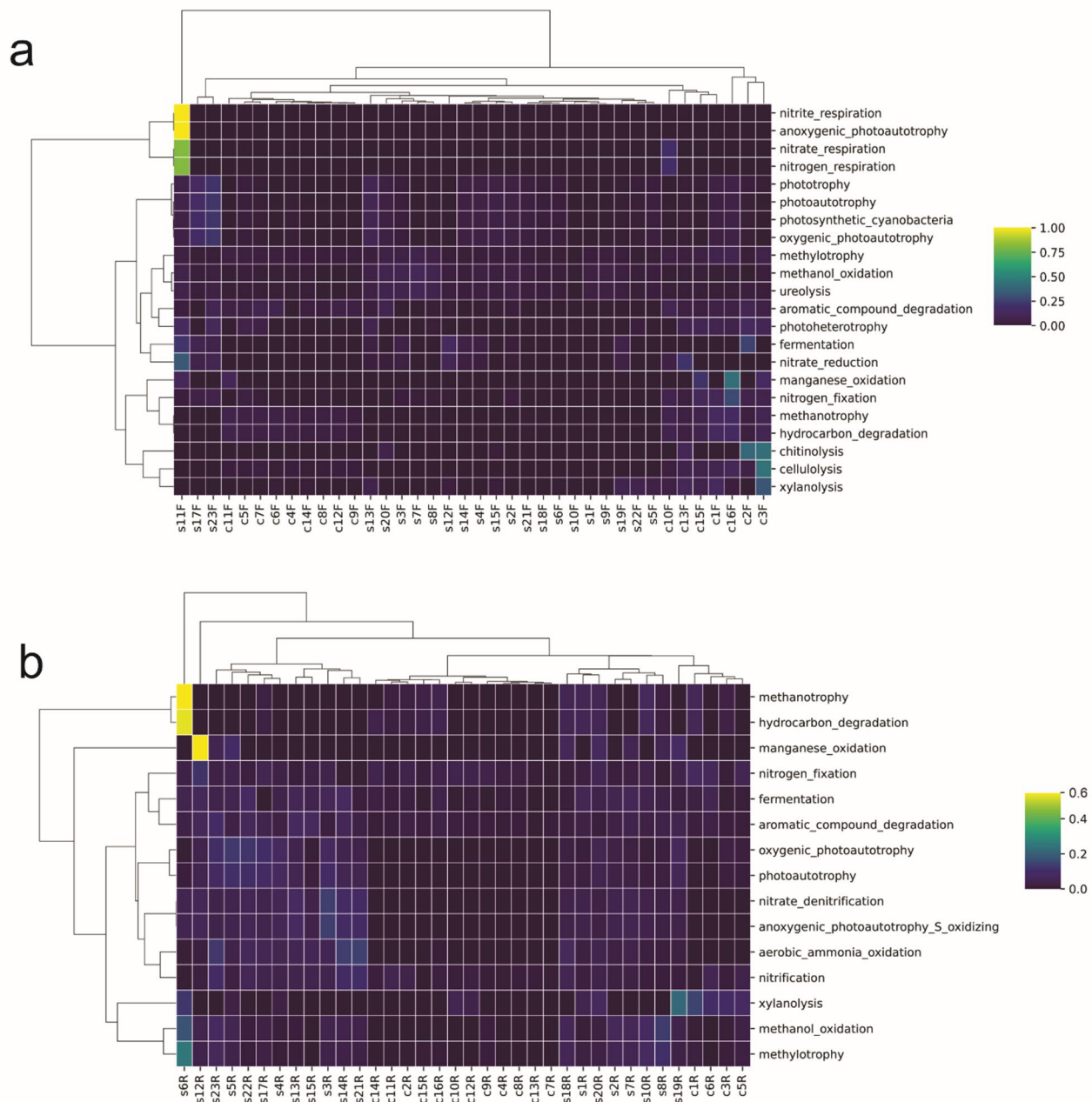


Fig. 7 Heatmap of bacterial metabolic functions of the bacteriome from (a) leaf and (b) root. Data were obtained from ASVs with functions identified using FAPROTAX, based on samples of *Selaginella convoluta* and *S. sellowii*

different species growing near each other (Kim and Price 2011).

Considering the phylum level, the bacterial community composition in *Selaginella* species showed the predominance of *Actinobacteriota*, *Proteobacteria*, *Acidobacteriota*, and *Chloroflexi*. Different studies have reported a shift toward stress-tolerant lineages in the bacterial communities associated with resurrection plants (such as *Oreocharis mileensis*, *Boea hygrometrica*, and *Myrothamnus flabellifolia*) during

periods of drought. Consistently with our results for the *Selaginella* species, drought-stressed microbiome are dominated by a few key phyla, *Actinobacteriota*, *Proteobacteria*, *Chloroflexi*, *Acidobacteriota*, *Firmicutes*, and *Cyanobacteria* (Sun et al. 2024; Asatulloev et al. 2025; Liu et al. 2025; Tebele et al. 2025). *Actinobacteriota* may increase in abundance due to their thick peptidoglycan cell walls, which provide physical resistance to desiccation. They play critical roles in producing antimicrobial compounds, osmolytes

like trehalose, and secondary metabolites that support host resilience (Tebele et al. 2025). In some systems, *Proteobacteria* dominance is maintained in the endosphere even under stress, though rehydration typically triggers a further surge in this phylum (Asatulloev et al. 2025; Tebele et al. 2025). *Acidobacteriota* is consistently identified as a core component of the resurrection plant microbiome. According to Tebele et al. (2024), in *M. flabellifolia*, *Acidobacteriota* show high enrichment in the root endosphere specifically during extreme environmental stress. Similarly, *Chloroflexi* are identified as core members across diverse populations and are particularly abundant in the bulk soil of resurrection plants during desiccation (Tebele et al. 2024, 2025; Asatulloev et al. 2025).

The bacterial community composition at the family level in *Selaginella* showed *Sphingomonadaceae*, *Methylobacteriaceae*, and *Pseudonocardiaceae* as the most abundant. This may be attributed to these bacteria's ability to produce siderophores (compounds that help plants acquire iron from the soil), their ability to grow under specific soil conditions, such as rocky outcrops, and their capacity to regulate the abundance and diversity of fungi at the root interface, thus ensuring overall plant health (Macey et al. 2020; Camargo et al. 2022).

ANCOM-BC showed that *Pseudonocardiaceae* exhibited a compartment-specific distribution between the two species, being enriched in the leaves of *S. convoluta* and in the roots of *S. sellowii*, suggesting that host identity modulates the preferential niche of this family within *Selaginella*. *Nakamurellaceae*, in turn, was the family most strongly enriched in the leaves of *S. convoluta*, indicating a preferential association with the phyllosphere in this species. The families identified in the leaves of *Selaginella* are commonly associated with soil, suggesting that their presence in the leaves is linked to the plant's structural characteristics. As a ground-covering plant, its leaves are in constant contact with the soil, promoting interactions between bacteria associated with the leaves and the soil. Additionally, *Gaiellaceae* was significantly enriched in the roots of both species according to the ANCOM-BC analysis. This family is associated with oligotrophic soil communities and has been linked to carbon and nitrogen cycling processes, being consistently more prevalent in soils with high bacterial diversity and low disturbance (Hermans et al. 2017; Lozo et al. 2023).

The root microbiota of *S. convoluta* showed increased abundance of *Streptosporangiaceae* and *Anaeroplasmataceae*. These bacteria are crucial for maintaining plant health and fitness as they promote growth, enhance stress resistance, and facilitate nutrient mobilization, transport, and absorption (Grossi et al. 2020; Macey et al. 2020). *Micromonosporaceae* is enriched in the roots of *S. sellowii*, and members of this family are recognized as important

producers of bioactive secondary metabolites, including antibiotics and antifungal compounds, as well as for playing a key role in the degradation of chitin, cellulose, lignin, and pectin, contributing to the turnover of plant organic matter (Trujillo et al. 2014; Matsumoto and Takahashi 2017). The presence of these bacteria may be linked to the climatic conditions of the Brazilian Cerrado and the nutrient-poor, shallow, acidic soils of rocky outcrops (van der Heijden et al. 2008). Additionally, members of *Actinobacteriota*, found abundantly in the roots in this study, significantly increased during the dry season (Bonatelli et al. 2021). Thus, plant adaptations include associations with endophytic bacteria that can positively influence plant nutritional status, protect against pathogens and pests, and improve stress tolerance by modulating plant development (Hannula et al. 2021).

In the roots of *S. sellowii*, the presence of the genus *Rhodoplanes*, associated with increased denitrification, a process that transforms nitrites and nitrates into gaseous nitrogen compounds, probably contributes to the balance of the global nitrogen cycle and reduces eutrophication (Knowles 1982; Hiraishi and Ueda 1994). Moreover, cyanobacteria of the subclasses *Nostocophycidae*, which increase photosynthetic efficiency by fixing CO₂ into organic compounds (Norena-Caro and Benton 2018), and *Oscillatorophycidae*, which sustain fragile ecosystems by providing energy and demonstrating high resistance to extreme variations in salinity and temperature (Sandzewickz et al. 2023), were highlighted. In the roots of *S. convoluta*, taxa related to methanol oxidation, such as *Methylobacterium*, were found, efficiently oxidizing methanol under lanthanide-dependent conditions using the XoxF1 enzyme with cofactors such as lanthanum (La³⁺). This process generates formaldehyde for specific metabolic pathways, and the regulation of genes like *XoxF* and *ExaF* improves toxin tolerance and metabolic efficiency (Good et al. 2019). The genus *Methylopila*, composed of facultative methylotrophic bacteria, plays an important role in carbon cycling, using methanol as a carbon and energy source in soils and aquatic environments (Doronina et al. 2013). Its ability to oxidize methanol and related compounds contributes to pollution mitigation by transforming toxic substances into less harmful products (Doronina et al. 2013). No predominant functions were observed in the leaves when comparing the two species, although photoautotrophic taxa were abundant in both. Nevertheless, studies on resurrection plant species indicate that the microbiome can be critical for post-drought recovery and may have potential agricultural applications. For example, Sun et al. (2024) reported that *Boea hygrometrica* recruits *Sphingosinicella* and *Plectosphaerella* during desiccation, taxa associated with nutrient supply and auxin regulation. During drought, *Microlunatus* (enriched in *O. mileensis* and *R. heldreichii*) may release stored phosphate to support host nutrition (Dhakar et al.

2024; Asatulloev et al. 2025). Additionally, *Cyanobacteria* associated with *B. hygrometrica* and *M. flabellifolia* likely contribute to nitrogen fixation and soil stabilization in their rocky habitats (Sun et al. 2024; Tebele et al. 2025).

The plant-bacteria relationship is crucial for nutritional adaptations in environments such as the Cerrado. The average monthly precipitation exhibits marked seasonality, peaking in spring and summer (October to March), corresponding to the rainy season. However, from May to September, monthly precipitation levels decrease significantly, potentially reaching zero (Marcuzzo and Melo 2012). These relationships play essential roles in influencing host responses to biotic and abiotic stresses and modulating the plant's phenotypic plasticity (Hoyos et al. 2021; Selari et al. 2021; Silva et al. 2021). This study highlights the importance of bacteria in supporting *Selaginella*'s growth, maintenance, and survival. It also emphasizes that plants should not be studied in isolation but as units comprising hosts and their associated microbiota.

Additional initiatives are needed to gain deep and potentially predictive insights into plant-microbiome interactions, as these dynamics and biodiversity remain underexplored. Understanding these relationships is crucial for predicting how beneficial plant-microbiome interactions will respond to environmental stresses. Leveraging this knowledge will facilitate predictions of the impacts of climate change on plant-associated microbiomes, creating opportunities for new research that deepens our understanding of plant-microbiome interactions and improves the climate resilience of plant communities.

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Data availability The 16 S rRNA data are available in the NCBI

Sequence Read Archive (SRA) under the accession number PRJNA1063726. Metadata are available upon request.

Declarations

Competing interests The authors declare no competing interests.

Supporting Information Additional supporting information can be found in the Online Resource.

Conflict of Interests The authors declare no conflicts of interest.

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