

围栏管理对柠条锦鸡儿种子内生微生物群落组成和多样性的影响

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摘要: 【目的】种子内生菌作为植物微生物组的重要组成部分, 其群落结构组成和多样性易受环境变化的影响。研究围栏和放牧不同管理方式对柠条锦鸡儿(*Caragana korshinskii*, 俗名柠条)种子内生微生物群落的影响, 对于揭示植物、土壤和微生物之间的相互作用具有重要意义, 也可为干旱区荒漠草地的生态恢复提供一定的理论依据。【方法】以内蒙古鄂托克前旗柠条灌丛为研究对象, 利用高通量测序技术分析围栏和放牧管理下土壤理化性质的差异, 以及其种子内生微生物群落结构组成和多样性的变化。【结果】围栏管理降低了土壤 pH 值, 增加了土壤含水量、总碳、总氮和总磷含量; 放牧管理增加了种子内生真菌的丰富度指数(abundance-based coverage estimator, ACE)。围栏管理增加了种子内生细菌中假单胞菌门(*Pseudomonadota*)的相对丰度, 降低了芽孢杆菌门(*Bacillota*)的相对丰度; 并增加了泛菌属(*Pantoea*)的相对丰度。在种子内生真菌群落中, 链格孢菌属(*Alternaria*)在围栏管理下是优势菌属, 而木霉属(*Trichoderma*)在放牧管理下具有较大的占比。此外, 放牧管理增加了种子内生细菌-真菌网络的模块数量和复杂性。【结论】荒漠草原围栏和放牧不同管理方式改变了土壤环境, 进一步塑造了柠条种子内生细菌和真菌群落的多样性及群落结构。本研究揭示了不同管理措施对荒漠草原植物-微生物互作的影响, 为相关研究提供了理论支持。

关键词: 围栏管理; 柠条锦鸡儿种子; 内生微生物; 群落结构; 网络关系

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Effects of fencing management on the composition and diversity of endophytic microbial communities in *Caragana korshinskii* seeds

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Abstract: [Objective] Seed endophytes are key components of the plant microbiome, and their community structure and diversity are highly susceptible to environmental changes. Revealing the effects of fencing versus grazing management on the endophytic microbial communities of *Caragana korshinskii* seeds is essential for elucidating the dynamic interactions among plants, soil, and microorganisms. This study also provides a theoretical foundation for ecological restoration in arid and semi-arid grasslands. [Methods] The study was conducted in Otog Front Banner, Inner Mongolia, focusing on *C. korshinskii* under two management practices: fencing and grazing. The physicochemical properties of soil were analyzed by high-throughput sequencing of seed endophytic microbial communities to assess shifts in their structural composition and diversity under these contrasting regimes. [Results] Fencing management decreased soil pH while increasing moisture content, total carbon, total nitrogen, and total phosphorus of soil. Grazing management increased the abundance-based coverage estimator (ACE) index of seed endophytic fungi. Fencing increased the relative abundance of *Pseudomonadota* and decreased the relative abundance of *Bacillota* in seed endophytic bacteria, while promoting the relative abundance of *Pantoea*. In seed endophytic fungi community, *Alternaria* dominated under fencing management, while *Trichoderma* dominated under grazing management. Additionally, grazing management increased the number of modules and complexity in seed endophytic bacterial-fungal networks. [Conclusion] The contrasting management practices of fencing and grazing in desert steppes alters soil environment, thereby shaping the diversity and community structure of both bacterial and fungal endophytes in *C. korshinskii* seeds. This study reveals the impact of different management measures on plant-microbe interactions in desert steppes, providing theoretical support for related research.

Keywords: fencing management; *Caragana korshinskii* seed; endophytic microorganism; community structure; network relationship

围栏管理作为我国北方荒漠草原常见的生态管理措施, 通过限制牲畜对植被的采食与践踏, 对生态系统的平衡和稳定具有积极影响^[1-2]。围栏管理有助于植物多样性的恢复, 并提高草地生产力^[3-4]; 同时, 还会增强土壤团聚体的稳

定性, 降低水土流失^[5], 有利于土壤有机碳的固存^[6]。已有研究表明, 围栏管理通过改变植物群落结构(增加优势种比例和物种多样性)来提高微生物的营养利用效率, 进而影响微生物种群的聚集过程和功能基因表达^[7-8]。更多研究表明,

土壤环境异质性改变了植物根际微生物的营养获取策略和功能, 进一步影响植物内生微生物群落的多样性和群落结构的变化^[9]。鉴于此, 围栏管理下植物-土壤-微生物之间的相互关系仍需深入研究。

植物内生菌指生活在植物组织内部(细胞间或细胞内)的微生物, 主要由细菌和真菌组成^[10]。这些微生物定殖于植物各器官中, 如根、茎、叶、花、果实和种子等, 与宿主植物建立起复杂的互惠关系^[11-15]。内生菌不仅能够帮助植物提高养分获取能力, 还能够协助宿主植物抵御各种生物胁迫^[16-17]。例如, 内生菌通过竞争生态位和分泌抗菌化合物(如抗生素、细胞壁降解酶)降低病原体对宿主植物的伤害^[18]; 还通过诱导系统抗性增强植物自身的防御能力^[19]。此外, 植物内生菌的结构和功能的变化积极响应非生物胁迫^[20]。例如, 在盐胁迫下, 耐盐内生菌通过富集优势菌群和分泌渗透调节物质提高植株盐耐受性^[21]; 干旱胁迫下, 内生菌通过合成植物激素和胞外多糖(extracellular polymeric substances, EPS)提高植物抗旱能力^[22]。尽管上述研究揭示了内生菌在植物应对生物、非生物胁迫中的关键作用, 但其响应机理及其功能变化仍值得深入探讨。

种子内生菌作为植物微生物群落的重要组成部分, 能够在植物生命周期中继代传播^[23-24]。研究表明种子内生菌与宿主植物之间的互利共生, 不仅有助于提高植物幼苗的成活率, 还会提高植株养分获取能力^[25]。此外, 种子内生菌在促进植物生长和防御方面发挥着关键作用^[24]。Lobato 等^[26]发现低驯化大麻(*Cannabis sativa*)种子内含特定内生细菌, 接种这些菌株能够明显增强植物生长并提高其抗逆恢复能力; Radhakrishnan 等^[27]发现大豆(*Glycine max*)种子经内生真菌预处理后能有效促进盐胁迫下植株的生长; Ishida 等^[28]还检测到鸡蛋果(*Passiflora edulis*)种子内生菌能够产生白藜芦醇和白皮杉醇等次级代谢产物, 提高植株抵御生物胁迫的能力。综上所述, 研究围栏管理下种子内生菌的

群落组成及其动态变化, 可进一步为种子内生微生物生态功能的相关研究提供科学依据。

柠条锦鸡儿(*Caragana korshinskii*, 俗名柠条)作为我国北方干旱区典型防风固沙灌木, 凭借其深根系、强耐旱性和抗风蚀等适应性特征, 在生态恢复中发挥了关键作用^[29-30]。围栏管理对柠条灌丛的相关研究已被广泛报道, 徐苗苗等^[31]研究发现, 围栏管理能提高柠条根系对水分和养分的吸收; 余轩等^[32]和 Pan 等^[33]进一步研究发现, 围栏管理提高了柠条灌丛物种多样性和生物量, 在提高土壤有机碳固存的同时, 改变了土壤微生物多样性和群落结构。鉴于研究围栏管理下柠条灌丛-土壤-微生物相互作用的积极意义, 探讨柠条种子内生菌的多样性和群落组成在围栏和放牧不同管理下的生态功能变化, 可为荒漠草原生态恢复和微生物资源利用提供更多理论依据。

1 材料与方法

1.1 研究区域概况及样品采集

研究区域位于中国内蒙古自治区鄂托克前旗地区(107°21′-107°38′E, 37°43′-37°55′N), 该地处于内蒙古、陕西和宁夏交界处, 属于鄂尔多斯高原向毛乌素沙地的过渡地带, 以荒漠草原为主, 气候类型为典型温带大陆性气候^[34]。由于其极端自然条件, 该地区以柠条、红砂(*Reaumuria songarica*)、苦豆子(*Sophora alopecuroides*)、牧马豆(*Thermopsis lanceolata*)和短花针茅(*Stipa breviflora*)等耐旱植物为主。

样品采集于2021年6月下旬, 在围栏和放牧2种管理样地各设置5个5 m×5 m的采样点, 每个采样点间距至少150 m。采用对角线取样法在每个采样点中选择10株健康、无虫害且长势相似的柠条植株, 将同一采样点的种子合并成一个样品。分别装入标记的保鲜袋中, 置于低温收纳箱后带回实验室。土壤样本通过五点采样法采集, 取样时清除地表垃圾并避开植物根

系^[35], 取样深度为 10–20 cm。将每个样方的 5 个土壤样本混合, 定义为 1 个样方的土壤样品。所有土壤样本低温保存后带回实验室^[36]。

1.2 土壤理化特性测定

根据土与水体积比 1:5, 测定土壤样品 pH 值; 土壤含水率在烘箱 105 °C 下采用称重法进行测定^[35]。将土壤样品烘干后采用元素分析仪测定土壤总碳和总氮含量, 总磷通过使用碱性过硫酸钾消解法进行测定^[37]。使用 SPSS v25.0 软件对柠条样地土壤理化性质进行单因素方差分析(analysis of variance, ANOVA), 以 Duncan's 多范围检验($P < 0.05$)确定均值间的显著差异, 数据以均值±标准误差($n=9$)表示。

1.3 DNA 提取、扩增和测序

采用 Guo 等^[38]的方法进行种子表面灭菌。使用 70% 乙醇浸泡种子 5 min 以去除表面附着杂质, 使用 10% 氯化钠溶液进行表面消毒, 浸泡时间为 10 min。然后使用无菌水冲洗 3 次, 以去除消毒剂残留, 确保种子表面干净。完成表面消毒后, 将种子放置于无菌环境中晾干。采用十六烷基三甲基溴化铵(cetyltrimethylammonium bromide, CTAB)法提取种子中内生微生物总 DNA, 随后进行 PCR 扩增。细菌的 16S rRNA 基因使用引物 V5 (5'-AGAGTTTGATCCTGGC TCAG-3') 和 V7 (5'-TACGGCTACCTTGTTAC GACTT-3') 扩增, 真菌 ITS 序列采用引物 ITS1 (5'-CTGGTCATTTAGAGGAAGTAA-3') 和 ITS2 (5'-GLGCTGCGTTCTTCATCGATGC-3') 扩增^[35]。PCR 反应体系: 10×Buffer 2 μL, dNTPs (2.5 mmol/L) 2 μL, 正、反向引物(10 μmol/L)各 0.8 μL, Phusion DNA 聚合酶(2 U/μL) 0.2 μL, DNA 模板 1 μL, ddH₂O 补足 20 μL。PCR 反应条件: 98 °C 1 min; 98 °C 10s, 50 °C 30 s, 72 °C 30 s, 30 个循环; 72 °C 5 min^[39]。

1.4 柠条内生微生物多样性分析

使用 FLASH v1.2.7 对下机数据进行拼接^[39], 去除嵌合体后以≥97% 相似度获得可操作

分类单元(operational taxonomic unit, OTU)^[40]。使用核糖体数据库项目(ribosomal database project, RDP)分类器对每个序列进行物种分类标注, 其中细菌 16S rRNA 基因序列基于 Silva 数据库(SSU128)进行对比^[41], 真菌 ITS 序列采用 UNITE 数据库(v9.0)进行注释^[42]。本研究获得的 16S rRNA 基因和 ITS 序列已提交至 NCBI SRA 数据库(<https://www.ncbi.nlm.nih.gov/sra>), 序列号分别为 PRJNA1026058 和 PRJNA1026303。

使用 QIIME v1.9.1 软件对获得的柠条种子内生微生物数据进行 OTU、Shannon、Simpson、Chao1、丰富度指数(abundance-based coverage estimator, ACE)和 PD 指数计算, 并用 R 软件(v4.1.0)进行 α 多样性分析; 使用 R 的“vegan 包”进行非度量多维尺度(non-metric multidimensional scaling, NMDS)分析柠条种子内生微生物群落的 β 多样性; 利用“ggalluvial 包”和“ggplot2 包”描述柠条内生微生物群落变化; 通过 LEfSe 软件(LDA score>3.3)进行线性判别分析(linear discriminant analysis, LDA); 使用“ggClusterNet 包”和“ggplot2 包”进行 Zi-Pi 分析; 为进一步分析围栏管理对柠条种子中内生细菌和真菌群落生态位的影响, 计算所有种子中内生细菌和真菌 OTU 之间所有可能的 Spearman's 相关系数($R > |0.9|$ 和 $P < 0.01$), 并在 Cytoscape 软件(v3.7.1)中对其进行可视化^[42]。

2 结果与分析

2.1 柠条土壤理化性质差异

围栏和放牧管理下土壤理化性质如表 1 所示。围栏管理降低了荒漠草原土壤 pH 值, 增加了土壤含水量(soil water content, SWC), 围栏样地中的总碳(total carbon, TC)、总氮(total nitrogen, TN)和总磷(total phosphorus, TP)含量也显著高于放牧样地。其中, 围栏管理使土壤 TC 含量较放牧地提高了 2.2 倍, TN 和 TP 分别增加了 42.9% 和 83.3%。

表1 土壤理化性质分析

Table 1 Analysis of soil physical and chemical properties

土壤理化性质 Soil physicochemical characterization	放牧地 Pasturage	围栏地 Fencedly
含水量SWC (%)	13.87±0.56a	14.41±0.64a
pH	8.84±0.02a	8.65±0.01b
总碳 Total carbon (g/kg)	4.23±0.220b	9.31±0.50a
总氮 Total nitrogen (g/kg)	0.28±0.01b	0.40±0.03a
总磷 Total phosphorus (g/kg)	0.12±0.01b	0.22±0.01a

SWC: 土壤含水量。不同小写字母表示组间差异显著。

SWC: Soil water content. Different lowercase letters indicate significant differences between groups.

2.2 柠条种子内生微生物群落多样性变化

如图 1 所示, 在围栏和放牧管理下, 柠条

种子内生真菌群落表现出明显差异。其中, 放牧管理下 ACE 和 PD 指数明显高于围栏管理, 然而, 内生真菌 Simpson 指数则正好相反, 放牧管理明显低于围栏管理 ($P < 0.05$), OTU、Chao1 指数和 Shannon 指数则未表现出明显差异。基于 Bray-Curtis 分析发现, 围栏和放牧管理下柠条种子内生细菌和真菌群落 β 多样性均存在一定组间差异(细菌: Stress=0.124 9, 真菌: Stress=0.113 2) (图 2)。

2.3 柠条种子内生微生物群落结构变化

如图 3 所示, 假单胞菌门(*Pseudomonadota*)和芽孢杆菌门(*Bacillota*)是柠条种子内生细菌的优势菌门; 而子囊菌门(*Ascomycota*)则是种子内生真菌的优势菌门。围栏管理增加了 *Pseudomonadota* 的相对丰度, 而降低了 *Bacillota* 的相对丰度。2 种管理方式下柠条种子内生细菌属水平上除了具有更高的泛菌属(*Pantoea*)外, 未出现明显的变

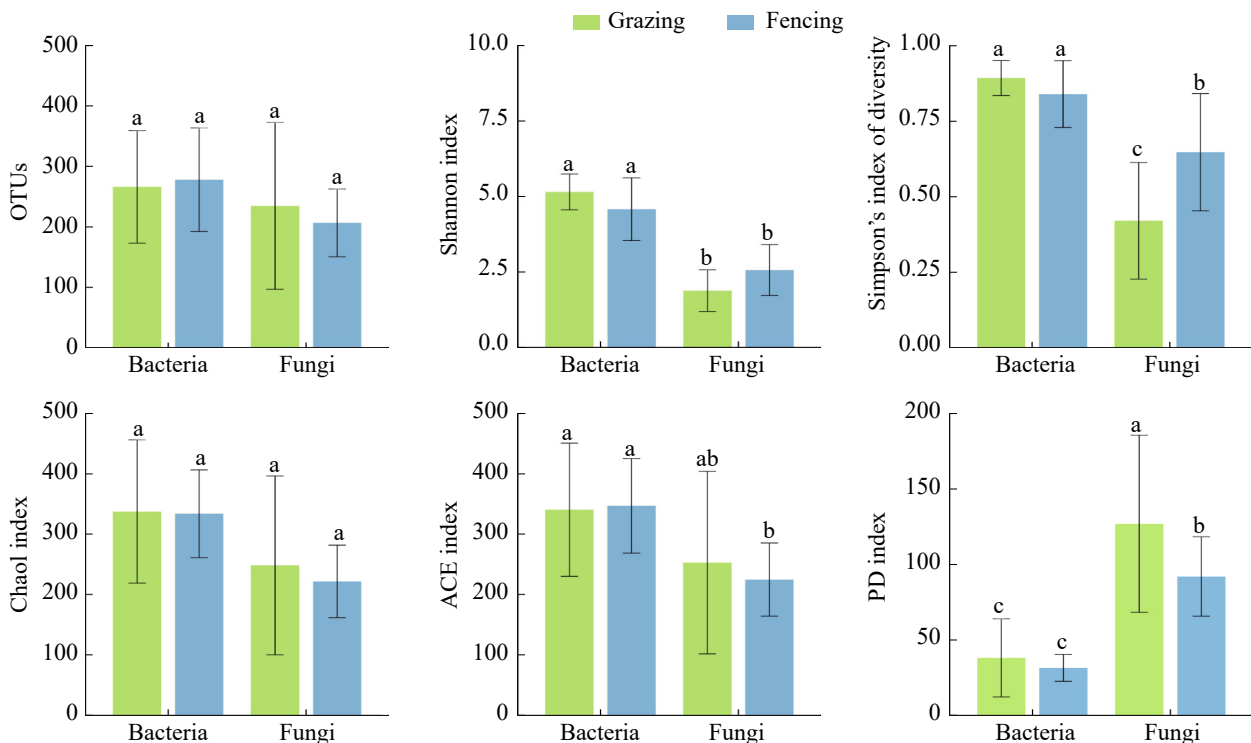
图1 柠条种子内生真菌和细菌 α 多样性分析

Figure 1 Analysis of alpha diversity of endophytic fungi and bacteria in *Caragana korshinskii* seeds. Different lowercase letters indicate significant differences.

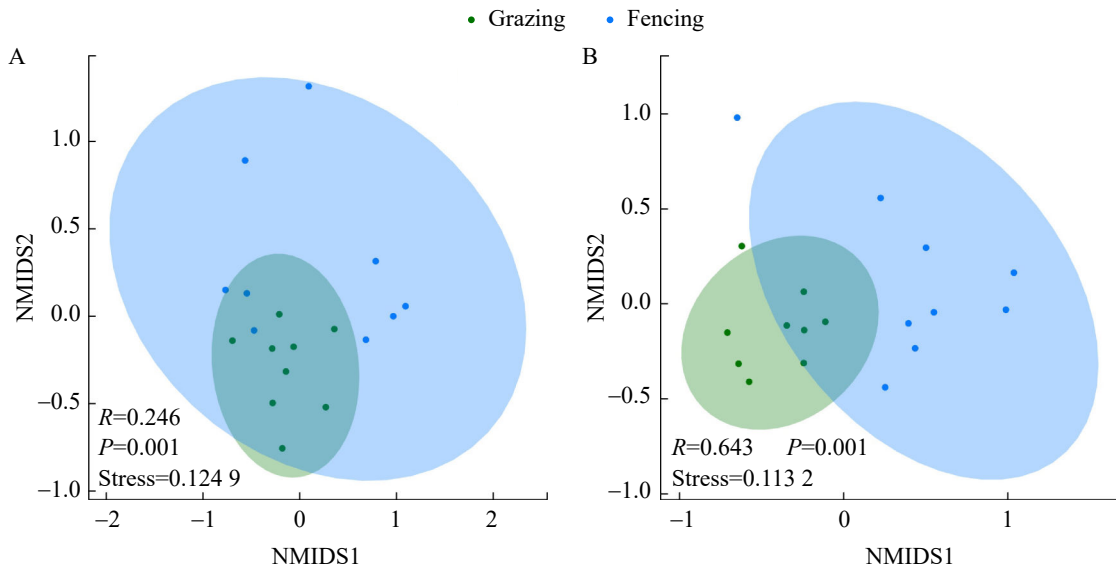


图2 柠条内生细菌(A)和真菌(B) NMDS分析

Figure 2 NMDS analysis of endophytic bacteria (A) and fungi (B) in *Caragana korshinskii*.

化, 但 2 种不同管理下柠条种子中未识别的菌属所占的比值在逐渐上升。相较于内生细菌属水平上的变化, 内生真菌属水平上的变化则比较明显, 围栏管理降低了木霉属(*Trichoderma*)的相对丰度, 同时, 增加了链格孢菌属(*Alternaria*)的相对丰度(图 3)。

如图 4A 所示, 在种子内生细菌中, 围栏和放牧管理下有 254 个共有 OTUs, 其中围栏管理下有 100 个特有 OTUs, 放牧管理下有 96 个特有 OTUs; 而在种子内生真菌中, 围栏管理下有 57 个特有 OTUs, 放牧管理相较于围栏管理其特有 OTUs 有明显增加(121 个), 两者共有 154 个 OTUs (图 4B)。进一步对不同管理下柠条种子内生细菌和真菌进行 LDA 分析发现, 种子内生细菌中放牧管理下 *Pseudomonadota*、欧文氏菌科(*Erwiniaceae*)、蛭弧菌门(*Bdellovibrionota*)和微球菌目(*Micrococcales*)等菌属为特有类群, 围栏管理下主要是 *Bacillota*、梭菌纲(*Clostridia*)、难养杆菌属(*Mogibacterium*)和假交替单胞菌属(*Pseudoalteromonas*)等为特有类群(图 4C)。种子内生真菌中, 放牧管理下主要是座囊菌纲(*Dothideomycetes*)、*Alternaria*、葡萄座腔菌属

(*Botryosphaeia*)和毛孢子菌属(*Trichosporon*)等为特有类群, 围栏管理下则主要是 *Trichoderma*、瑞恩氏酵母菌属(*Ruinenia*)以及伞型束梗孢菌纲(*Agaricostilbomycetes*)等为特有类群(图 4D)。

2.4 柠条种子内生菌共现网络

基于柠条种子内生细菌-真菌共现网络分析, 放牧管理下内生菌网络有 14 个模块, 而围栏管理下的柠条种子内生菌中有 11 个模块。围栏样地网络的复杂性和连通性均高于放牧样地, 且网络中 OTUs 以真菌为主(图 5)。

如图 6 所示, 在放牧管理下种子中有 8 个核心 OTU, 分别是未鉴定的子囊菌(unidentified *Ascomycota*)、短梗霉菌属(*Aureobasidium*)、巴塔利亚菌属(*Bartalinia*)、丝孢酵母菌属(*Trichosporon*)、枝孢菌属(*Cladosporium*)、德沃斯氏菌属(*Devosia*)、鞘氨醇杆菌属(*Sphingobacterium*)和寡养单胞菌属(*Stenotrophomonas*)。围栏管理下种子中盾壳霉菌属(*Coniothyrium*)、有益杆状菌属(*Agathobacter*)、布劳特氏菌属(*Blautia*)、双歧杆菌属(*Bifidobacterium*)、毛螺菌属(*Lachnospiraceae* ND3007 group)、鞘氨醇单胞菌

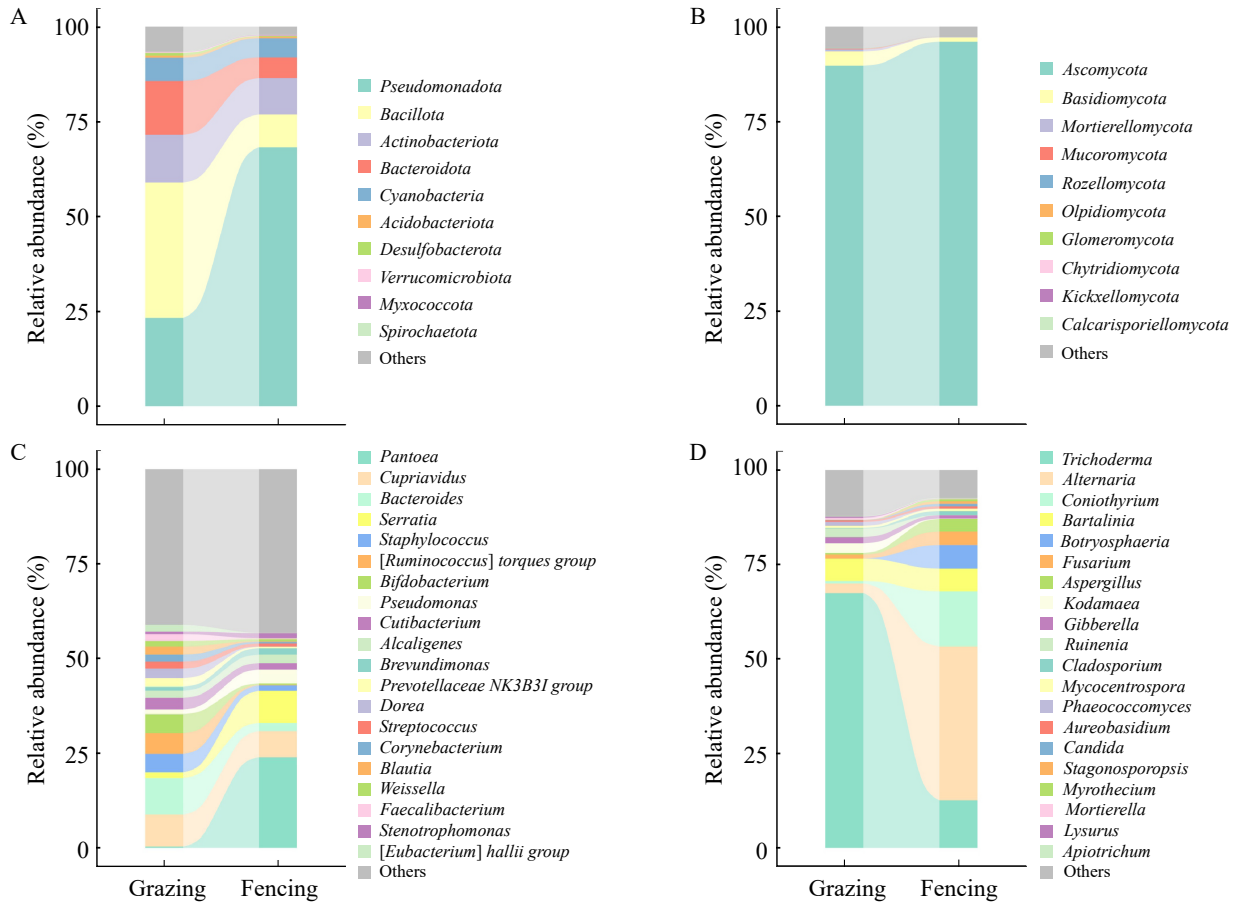


图3 柠条种子内生细菌和真菌群落组成。A: 柠条种子内生细菌门水平上群落组成; B: 柠条种子内生真菌门水平上群落组成; C: 柠条种子内生细菌属水平上群落组成; D: 柠条种子内生真菌属水平上群落组成。

Figure 3 Community composition of endophytic bacteria and fungi in *Caragana korshinskii* seeds. A: Community composition at the phylum level of endophytic bacteria in *C. korshinskii* seeds; B: Community composition at the phylum level of endophytic fungi in *C. korshinskii* seeds; C: Community composition at the genus level of endophytic bacteria in *C. korshinskii* seeds; D: Community composition at the genus level of endophytic fungi in *C. korshinskii* seeds.

属 (*Sphingomonas*)、凸腹真杆菌 (*Eubacterium ventriosum*) 和代尔夫特菌属 (*Delftia*) 为核心 OTU (图 6)。

3 讨论与结论

3.1 围栏管理改变了荒漠草原土壤理化特性

围栏管理通过调控凋落物输入量和根系分泌物组成促进土壤养分积累, 改变了土壤理化

性质^[9,43]。本研究发现围栏管理下土壤 pH 值略低于放牧管理(从 pH 8.84 降至 pH 8.65), 这一结果与 Zhou 等^[44]在内蒙古草原的研究结论一致。pH 值降低这一现象很可能与围栏管理下植物凋落物积累增加有关, 凋落物分解过程中释放的有机酸进一步降低了土壤 pH^[44]; 同时, 放牧管理下家畜排泄物的输入也可能局部提升了土壤 pH 值^[45]。本研究中, 围栏管理下 SWC 的含量增加, 这或许是植物群落盖度增加对土壤持水

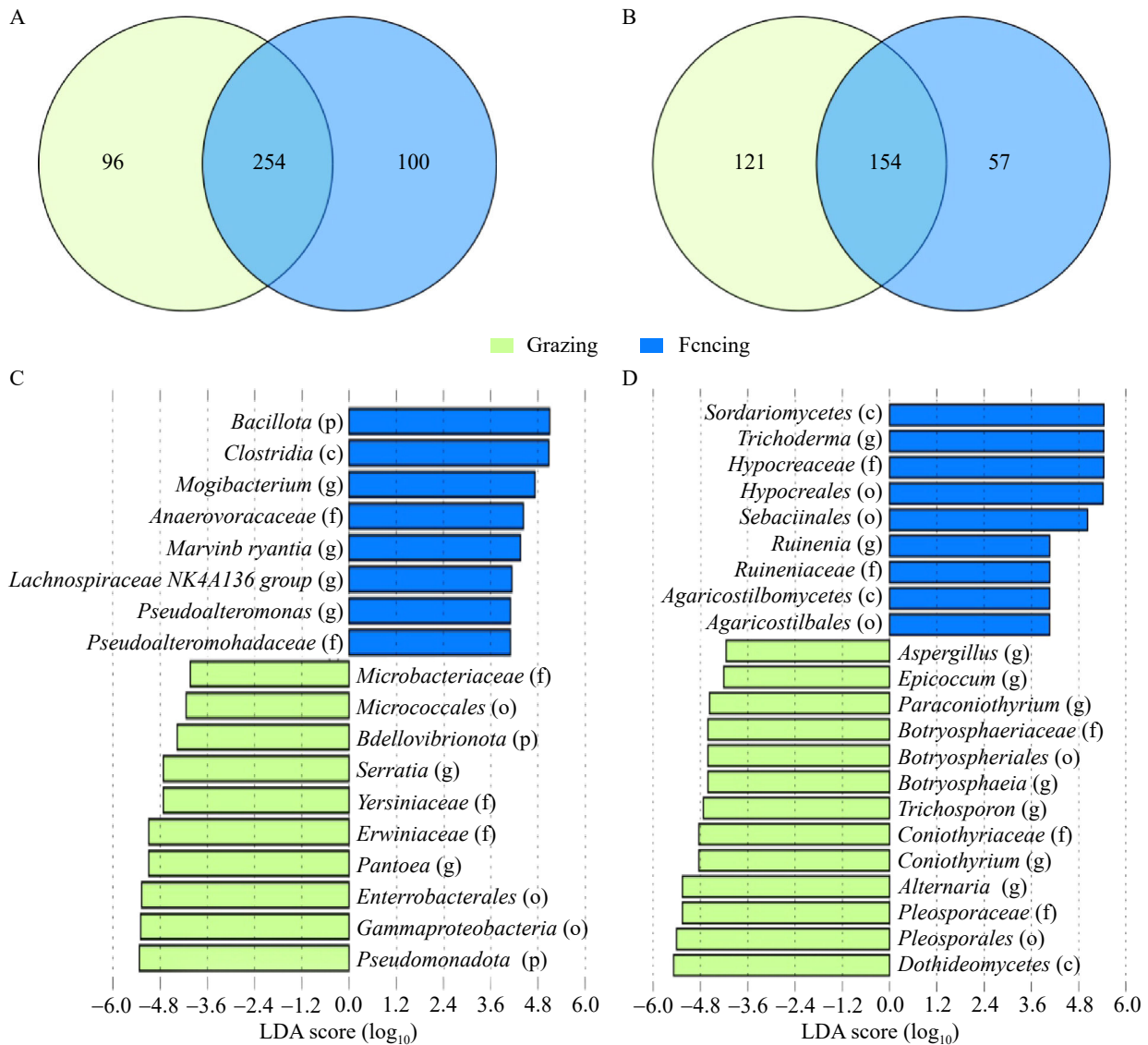


图4 柠条种子内生细菌和真菌Venn图和LDA图。A: 内生细菌共有和特有OTU数量; B: 内生真菌共有和特有OTU数量; C: 柠条内生细菌LDA分析; D: 柠条内生真菌LDA分析。

Figure 4 Venn diagram and LDA diagram of endophytic bacteria and fungi in *Caragana korshinskii* seeds. A: The number of common and unique OTU of endophytic bacteria; B: Number of common and endemic OTUs of endophytic fungi; C: LDA analysis of endophytic bacteria in *C. korshinskii*; D: LDA analysis of endophytic fungi in *C. korshinskii*.

能力的提升有关。围栏样地土壤 TC 和 TP 含量均高于放牧管理(表 1), 鉴于围栏对植物多样性和生物量的积极影响, 这可以进一步提升土壤有机质的积累, 这在诸多研究中已得到证实^[46-47]。此外, Wang 等^[48]的研究也指出, 围栏

管理能够提高中国北部干旱和半干旱地区草原的 TP 含量, 与放牧管理措施相比围栏管理下土壤总磷增加了 14.2%。这些发现共同证明, 围栏管理不仅是碳固存的有效措施, 更是实现荒漠草原生态系统多功能性恢复的关键策略。

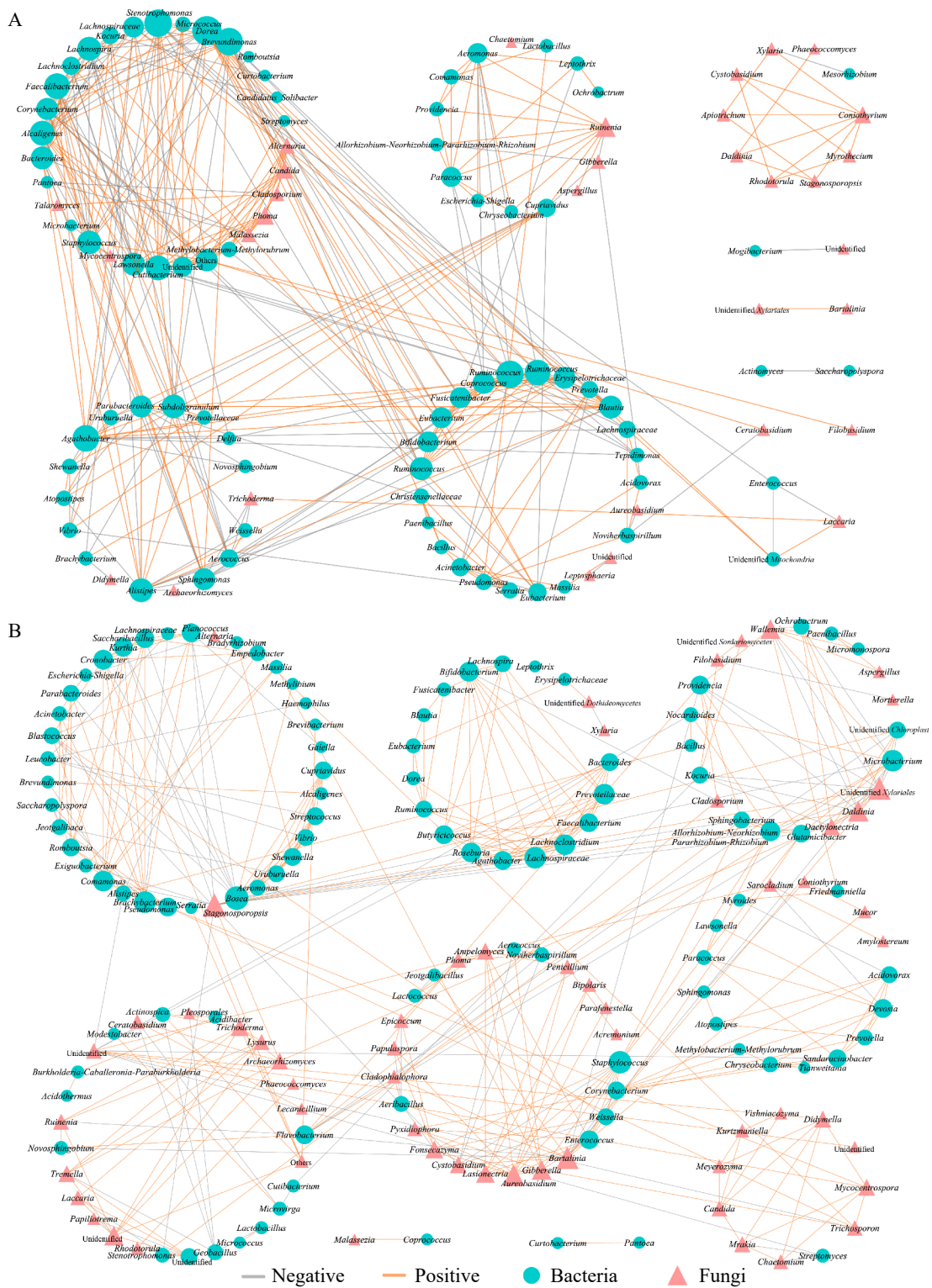


图5 放牧(A)和围栏(B)样地中柠条种子内生细菌、真菌的共现网络

Figure 5 Correlation networks of endophytic bacteria and fungi in *Caragana korshinskii* seeds in grazing (A) and fencing (B) plots.

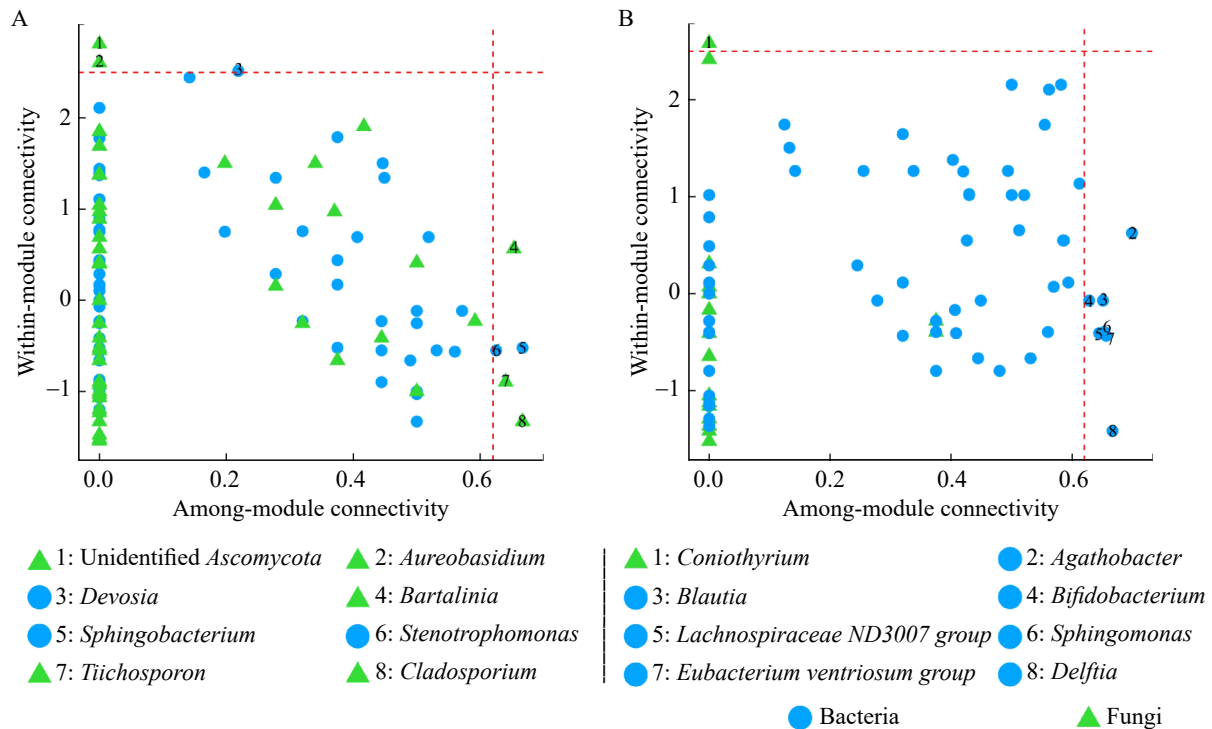


图6 Zi-Pi图分析。A: 放牧; B: 围栏。

Figure 6 Zi-Pi diagram analysis. A: Grazing; B: Fencing.

3.2 柠条种子内生菌群落变化对围栏管理作出积极响应

种子内蕴藏着丰富的微生物, 并具有复杂的群落结构, 其组成受环境因素和宿主基因型的共同影响^[49-52]。在本研究中, 柠条种子内生细菌和真菌 α 多样性指数在围栏和放牧管理下存在差异, 尤其是真菌的差异性更为明显, 放牧管理下内生真菌 ACE 和 PD 指数明显高于围栏管理(图 1)。 β 多样性分析进一步表明, 2 种管理方式下柠条种子内生真菌群落结构同样存在明显差异(图 2B)。这些差异表明, 管理方式(围栏/放牧)通过改变土壤特性, 为内生微生物创造更适宜的微生境, 进而驱动了种子内生微生物的多样性和丰富度的增加。Klaedtke 等^[50]研究指出生境差异对种子内生微生物群落组成有明显影响, 该研究还强调土壤环境被认为是影响种子内生微生物群落组成的主要因素。值得注意的是, 本研究发现管理措施对种子内生真菌

群落的影响要大于内生细菌, 与 Guo 等^[38]在青藏高原对不同区域垂穗披碱草(*Elymus nutans*)种子内生菌的研究结果一致, 该研究发现 4 个采样点的种子内生真菌分类群存在明显差异, 而种子内生细菌分类群则均无明显差异。Chartrel 等^[53]采集 3 个国家的豌豆(*Pisum sativum*)种子, 研究发现不同地区种子内生真菌群落结构的差异性要高于细菌群落, 这一特征也在不同区域土壤下的葫芦(*Lagenaria siceraria*)^[54]和葡萄(*Vitis vinifera*)^[55]的种子内生微生物群落中均有体现。这些证据共同表明, 围栏管理通过影响土壤环境来改变种子内生微生物群落的组成且对内生真菌群落的影响更为明显。

植物内生微生物大多数与宿主互惠共生, 其群落组成呈动态变化规律^[56]。这一变化受植物群落和土壤环境的双重调控, 其中寄主植物与区域环境因素的协同作用尤为关键^[57]。种子内最常见细菌群通常有假单胞菌门、放线菌门

(*Actinobacteria*)和芽孢杆菌门组成^[58]；本研究同样发现柠条种子内生细菌主要由假单胞菌门和芽孢杆菌门组成。在围栏管理下，假单胞菌门相对丰度明显增加，而芽孢杆菌门则明显减少。有研究发现，假单胞菌门能在有机质丰富的环境中具备竞争优势，能分解复杂的有机物质(如纤维素和木质素)释放植物可利用的营养物质^[59-60]，因此推测围栏管理可能通过提高土壤养分含量促进假单胞菌门的竞争优势。相反，芽孢杆菌门更适应贫瘠或干旱环境，放牧管理下的胁迫条件有利于其形成内生孢子并影响微生物群落组成^[61-62]。

属水平上，*Pantoea* 在不同管理下表现出明显变化，已在水稻(*Oryza sativa*)、玉米(*Zea mays*)和桉树(*Eucalyptus robusta*)种子中被报道^[63-65]，通过调节植物激素、表现出促进固氮酶活性和铁载体分泌等功能来影响植物生长并增强其抗病能力^[63-66]。在种子内生真菌属水平中也有类似的变化，在围栏管理形成的稳定环境中，*Alternaria* 表现出明显竞争优势，这种优势可能是源于其双重功能机制，一方面通过有效利用可用养分促进植物生长，另一方面通过合成乙烯等植物激素调控宿主的成熟与衰老进程，从而在围栏管理下成为优势菌属^[67-68]。在放牧管理下，*Trichoderma* 则具有更高的相对丰度。这一生态位转变主要归因于 *Trichoderma* 特有的适应性策略，首先，该菌属能够合成植物激素促进宿主生长；其次，它通过激活水杨酸、乙烯和茉莉酸等关键防御信号通路增强对植物病原体(如线虫和真菌)的耐受性^[69]。因此，可以推测土壤作为关键环境因子影响种子内生微生物的群落组成和功能。

3.3 围栏管理提高了柠条种子内生细菌-真菌共现网络的复杂性

种子内生菌通过调控核心微生物种群的结构和组成，帮助植物应对生物与非生物胁迫^[70-72]。Walitang 等^[73]研究发现，水稻在盐胁迫

下能招募耐盐菌群，这些菌群往往占据优势或主导地位以提高宿主植物的逆境适生能力。本研究中，柠条种子中 *Sphingomonas* 和 *Delftia* 属于核心微生物组成员，它们通过分泌胞外多糖(EPS)形成保护性生物膜^[74]，合成超氧化物歧化酶(superoxide dismutase, SOD)等抗氧化酶缓解氧化损伤，从而协助宿主植物应对干旱环境^[75]。此外，本研究发现 *Coniothyrium* 是围栏管理下特有且关键的核心真菌 OTU，*Coniothyrium* 是一类具有生物防治潜力的真菌，能分泌抗菌活性物质抑制植物病原菌的生长^[76]。已有研究表明，在油菜(*Brassica napus*)上喷施 *Coniothyrium* 菌剂后，不仅改变了其根际土壤微生物群落结构，还能有效降低病原菌类群的相对丰度^[77]。放牧管理下，柠条种子内生菌群落 OTU 以真菌为主(如 *Aureobasidium*、*Cladosporium* 和 *Trichosporon*)，核心细菌 OTU 以 *Devosia*、*Sphingobacterium* 和 *Stenotrophomonas* 为主。大量研究证实，上述菌群均具有合成抗氧化酶的能力，并展现出生物防治的潜力^[78-81]。

微生物共现网络有助于揭示微生物群落间的相互关系^[36]。共现网络分析表明，与放牧管理相比，围栏管理下细菌-真菌节点数量增加且连接更加密集，显示出更复杂的网络关系，展现出更强的网络稳定性。这可能与围栏管理下较为稳定的环境和丰富的养分资源有关^[82]，同时意味着内生微生物能在养分转化以及病原体抑制等关键生态过程中发挥着更加重要的作用^[83]，相比之下，放牧管理下微生物群落的共现网络虽然较为简单，但其可能对环境变化更为敏感。例如，放牧管理导致了土壤扰动和养分流失，从而限制了微生物多样性，降低了群落对环境胁迫的适应能力^[84]。

综上所述，种子内生菌作为植物微生物组的重要组成部分，其群落组成和多样性易受到环境变化的影响^[70,85]。本研究发现，围栏管理通过限制放牧活动明显增加了土壤含水量，促进了土壤有机质和氮磷养分积累，这些土壤环境

的改变进一步影响了柠条种子内生细菌和真菌群落组成及多样性。围栏管理下土壤养分条件的改善进一步改变了种子内生菌群落结构以及网络关系。本研究为理解植物-微生物互作在荒漠生态系统中的作用提供了新的视角, 同时为北方荒漠草地恢复提供了一定科学依据。

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姬秋博: 论文撰写和修改; 庄蝉瑜: 数据分析; 艾孜买提江·艾热提: 采样和数据分析; 潘雅清: 研究方案设计和数据分析; 刘建利: 执行调研; 雷茜: 基金获取; 康鹏: 论文指导与修改。

作者利益冲突公开声明

作者声明不存在任何可能会影响本文所报告工作的已知经济利益或个人关系。

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