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# 天然高寒草地转变为混播人工草地对土壤微生物群落特征的影响

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**摘要:** 为了研究天然高寒草地转变为混播人工草地对土壤微生物群落的影响, 采用高通量测序技术分析了青海省共和县的天然以及由天然转变为混播人工草地样地土壤中的微生物群落. 结果表明, 天然草地转变为混播人工草地后植被物种多样性和土壤有机质含量显著下降 ( $P < 0.05$ ). 在两块样地共检测到 29 个细菌门和 11 个真菌门的微生物. 天然草地转变为人工草地后, 土壤细菌的多样性显著升高, 细菌的香农指数从 9.51 增加到 9.89; 土壤真菌的多样性降低但差异不显著. 与天然草地相比, 人工草地的土壤细菌与真菌群落结构、组成均发生了明显的变化, 细菌群落结构与总有机质的含量、总氮含量和土壤含水量显著相关, 真菌群落结构与总有机质含量和土壤含水量显著相关. 线性判别分析 (LEfSe) 结果表明, 暗黑菌门细菌 (Atribacteria) 和子囊菌门真菌 (Ascomycota) 可作为天然草地的指示微生物类群, 出芽菌属细菌 (*Gemmata*) 和发菌科真菌 (*Trichocomaceae*) 可作为人工草地的指示微生物类群. 利用 Tax4Fun2 对细菌群落功能的预测发现, 天然草地向人工草地的转变影响了细菌群落对不同碳源的利用潜力.

**关键词:** 高寒草地; 人工草地; 土壤微生物; 群落多样性; 指示微生物

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## Effects of the Transformation from Natural Alpine Grassland to Mixed Artificial Grassland on the Characteristics of Soil Microbial Community

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**Abstract:** This study aimed to analyze the effects of the transformation from natural alpine grassland (NAG) to mixed artificial grassland (MAG) on the characteristics of soil microbial community. We used Illumina Miseq high-throughput sequencing technology to investigate the soil microbial community of natural grassland and mixed artificial grassland. The results showed that plant diversity and the content of soil organic matter decreased significantly from NAG to MAG. In total, 29 and 11 phyla bacteria and fungi were detected, respectively. Compared with that in NAG, the Shannon indexes of the bacterial community increased significantly in MAG (from 9.51 to 9.89), whereas these differences were not significant between the NAG and MAG fungal community. The structure and composition of the soil microbial community showed significant differences between NAG and MAG. In addition, Mantel test results suggested that soil total organic matter, total nitrogen, and soil moisture were significantly correlated with variations in the bacterial community, and soil total organic matter and soil moisture were significantly correlated with variations in fungal community. The results of linear discriminant analysis (LEfSe) indicated that Atribacteria and Ascomycota microorganisms could be considered as the indicator groups for NAG, whereas *Gemmata* and Trichocomaceae microorganisms could be considered as the indicator groups for MAG. Tax4Fun2 results showed that the transition from NAG to MAG affected the utilization of different carbon sources by bacteria.

**Key words:** alpine grassland; artificial grasslands; soil microorganism; community diversity; indicator microorganism

由于青藏高原具有独特的地理环境与气候条件使得该区域的生态系统变得相对脆弱, 对全球气候变化更为敏感<sup>[1]</sup>. 青藏高原高寒草地是世界上海拔最高、面积最大且类型最为独特的草地生态系统, 在保持水土、涵养水源和调节区域气候等方面发挥着重要的作用. 草地土壤微生物是土壤中最活跃和最丰富的生物类群, 是土壤和植物之间的关键纽带, 其数量和多样性较高<sup>[2~4]</sup>, 对维持生态系统的功能至关重要, 微生物群落结构能够影响生态系统过程<sup>[5]</sup>, 不同的微生物类群在元素生物化学循环中有不同的生态功能<sup>[6]</sup>. 土壤细菌和真菌参与凋落物分解和腐殖质形成, 在影响土壤碳排放和改变土壤肥

力方面有重要作用<sup>[7~10]</sup>, 而土壤养分状况往往制约着植物群落演替过程和生态系统对环境变化的响应<sup>[11,12]</sup>.

近些年来, 由于人口的增加和畜牧业的发展, 在青藏高原东北部的青海湖周边, 大面积的天然草地被改建为人工草地<sup>[13,14]</sup>. 土壤利用方式的变化不仅会影响地面植被和土壤理化性质还能进一步影响土

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壤微生物群落<sup>[15]</sup>,进而影响土壤碳循环过程及碳库储量<sup>[16,17]</sup>.郑鑫<sup>[18]</sup>针对藏北高寒地区人工补播的草地进行了生态环境影响与风险评估,其研究结果表明天然草地转变为人工草地植被生物多样性显著下降,地上生物量增多,出现草地退化的现象.邢云飞等<sup>[19]</sup>研究了不同建植年限人工草地植物群落和土壤有机碳氮的特征,发现在0~10 cm土层天然草地的全氮含量显著高于人工草地,且人工草地的全氮含量随着建植年限的增加而减少.陈璐<sup>[20]</sup>的研究表明,多年生人工草地会降低土壤有机质含量,加速土壤碳的流失.耿德洲<sup>[21]</sup>的研究表明,建植超过6 a的人工草地土壤细菌群落多样性下降,土壤微生物食物网和稳定性变差,草地开始退化.由此可见,由天然草地转变为人工草地后植物群落、土壤理化性质都会发生明显变化,而这些变化可能会进一步影响土壤微生物群落,从而影响土壤中营养物质的循环过程,导致土壤碳库的变化.目前关于天然草地转变为人工草地对土壤微生物群落的影响方面的研究较少.土壤微生物在物质循环过程中起重要作用<sup>[22]</sup>,研究群落的特征与功能有助于深入了解微生物群落高寒人工草地营养物质循环过程中的作用,对研究高寒人工草地退化及土壤碳库变化规律有重要意义.本文研究了天然草地和转变为建植20 a的人工草地中土壤细菌和真菌的群落多样性和结构,并结合环境因子分析了影响群落结构的主要因素,最后预测了群落功能的变化规律,以期科学管理高寒草地提供理论依据.

## 1 材料与方法

### 1.1 土壤样品的采集

试验样地位于青海省海南藏族自治州共和县境内的青海湖西岸(37°03'58.6"N, 99°33'19.8"E).该地区海拔为3 270 m,年平均气温为-0.7℃,7月为最热月,平均气温为17.5℃,最冷月为1月,平均气温为-22.6℃,年平均降水量为368.11 mm.本试验选取天然草地和混播人工草地作为研究样地,两块样地相距约4 km,为青海省草原改良试验站管理的同一片草场.草场夏秋季封育,冬春季节放牧,自然环境条件相似.天然草地中主要植物种类有嵩草、早熟禾、冷蒿和委陵菜等.混播人工草地原为天然草地,20年前将其转变为人工补播草地,前茬混播种植苜蓿(*Medicago sativa* L.)和老芒麦(*Siberian wildrye*).本研究在两块样地各设置5个5 m×3 m的重复小区,2个样地共有小区10个,每个小区间均有1.5 m的缓冲带,缓冲带上不做任何处理,在每个小区内随机设置2个2 m×2 m小样方,小样方内

选取0.5 m×0.5 m的范围进行植被调查.在样方内测量植被自然高度、盖度和鲜草产量,然后用土钻按S型在每个小样方内取5钻0~10 cm深度的土壤,将土壤均匀混合成一个土样过2 mm筛,装入已灭菌的袋中,储存在装有干冰和冰袋的泡沫保温箱中,密封后运回实验室.将采集的人工草地土壤样品(R)与天然草地的土壤样品(T)分成两部分,一部分用于土壤理化参数测定,其余部分保存在-20℃冰箱准备提取DNA.

### 1.2 土壤理化参数测定

土壤水分(soil moisture, SM)用便携式土壤三参数仪测定(型号TDR-350, Spectrum, 德国),在样品采集时直接测定;土壤中的总有机质(total organic matter, TOM)采用重铬酸钾-硫酸容量法测定<sup>[23]</sup>;总氮(total nitrogen, TN)按照燃烧法采用Costech ECS4010元素分析仪进行测定.土壤氨氮(NH<sub>4</sub><sup>+</sup>-N)采用KCl浸提-靛酚蓝比色法测定,硝氮(NO<sub>3</sub><sup>-</sup>-N)采用双波长分光光度法测定<sup>[24]</sup>.

### 1.3 DNA提取、PCR扩增以及测序

土壤微生物的DNA采用使用Mobio试剂盒(MOBIO Laboratories, Carlsbad, CA, 美国)提取.按照试剂盒的操作流程提取纯化DNA并检测浓度.将得到的DNA样品用于16S rRNA和ITS rRNA基因的PCR扩增.使用针对原核生物16S rDNA V4区的通用引物(515F/806R) 515F: 5'-GTGCCAGCMGC CGCGGTAA-3'和806R: 5'-GGACTACHVGGGT WTCTAAT-3',以及针对真菌ITS 2区的通用引物gITS-7F/4R(7F: 5'-GTGARTCATCGARTCTTTG-3')和(4R: 5'-TCCTCCGCTTATTGATATGC-3')进行扩增<sup>[25]</sup>,并且在引物双端各添加10bp的barcode序列来区分样本.样品DNA在总体系为50 μL的反应体系中进行扩增,包含1 μL *Taq*聚合酶,1 μL dNTP混合物,1 μL上游引物,1 μL下游引物,1 μL模板DNA,25 μL PCR buffer,20 μL ddH<sub>2</sub>O,配好体系后分别在95℃下预变性5 min,随后95℃变性15 s,52℃退火15 s,72℃延伸45 s,16S循环30次,ITS循环35次,最后72℃延伸5 min.对扩增产物切胶回收,将纯化的扩增产物等量混合构建测序文库之后采用Illumina MiSeq进行高通量测序.

### 1.4 统计分析方法

测序得到的原始数据以FASTQ格式提交到Galaxy平台上(<http://mem.rcees.ac.cn:8080>)进行后续的处理与数据分析<sup>[26]</sup>.使用UPARSE<sup>[27]</sup>对物种进行聚类生成物种分类单元OTU,使用FastTree构建基因的系统发育树.本研究分析了样地中微生物群落的香农指数(Shannon)和群落丰富度参数

Chao1 指数<sup>[28]</sup>; 通过基于 Bray-Curtis 距离矩阵的主坐标分析(PCoA)来研究天然与人工草地中微生物群落结构的差异; 用 Mantel 检验以及典范对应分析(CCA)探讨了植物参数、土壤理化性质和微生物群落之间的关系; 用 LEfSe 做线性判别分析(LDA)<sup>[29]</sup>, 确定人工草地和天然草地的指示微生物; 使用 Tax4Fun2 对 KEGG 数据库中 16S rRNA 基因序列进行计算和预测两种草地上微生物基因的功能通路. 所有统计分析均使用 R 软件(V 4.0.5)进行.

## 2 结果与分析

### 2.1 植被参数和土壤理化性质分析

由表 1 可知, 天然草地植物的物种丰富度显著高于人工草地 ( $P < 0.05$ ), 而人工草地的鲜草产量大于天然草地 ( $P < 0.05$ ). 另外, 人工草地土壤的总有机质(TOM)含量显著低于天然草地, 而两种类型的草地土壤的总氮(TN)含量、氨氮含量、硝氮( $\text{NO}_3^-$ -N)含量和土壤水分(SM)都没有显著差异, 尽管天然草地的总氮含量要大于人工草地.

表 1 天然草地和人工草地的植被特征和土壤理化性质<sup>1)</sup>

Table 1 Vegetation characteristics and soil physicochemical properties of natural grassland and artificial grassland

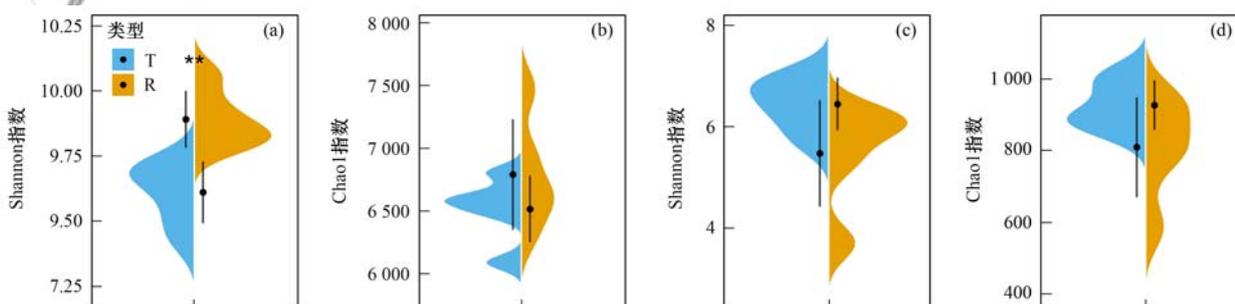
项目	因子	草地类型		P 值
		T	R	
植被特征	物种丰富度/ $\text{m}^2$	$7.62 \pm 1.34$	$5.44 \pm 1.14$	0.023 *
	鲜草产量/ $\text{g} \cdot \text{m}^{-2}$	$52.15 \pm 13.33$	$79.88 \pm 18.52$	0.026 *
	盖度/%	$72.00 \pm 0.22$	$57.00 \pm 0.13$	0.222
土壤性质	$\omega$ (总氮)/ $\text{mg} \cdot \text{kg}^{-1}$	$2059.34 \pm 201.08$	$1673.87 \pm 212.87$	0.225
	$\omega$ (氨氮)/ $\text{mg} \cdot \text{kg}^{-1}$	$4.44 \pm 0.29$	$5.29 \pm 0.56$	0.218
	$\omega$ (硝氮)/ $\text{mg} \cdot \text{kg}^{-1}$	$45.53 \pm 1.38$	$45.30 \pm 2.49$	0.938
	$\omega$ (总有机质)/%	$5.61 \pm 0.35$	$3.06 \pm 0.40$	0.001 **
	土壤含水量/ $\text{mg} \cdot \text{kg}^{-1}$	$9.97 \pm 0.90$	$12.37 \pm 0.82$	0.086

1) 数据为平均值  $\pm$  标准差 ( $n=5$ ); \* 为  $P < 0.05$ , \*\* 为  $P < 0.01$  ( $t$ -test)

### 2.2 土壤微生物多样性分析

本研究选取香农指数(Shannon index)和 Chao1 指数来研究样地土壤中微生物群落的  $\alpha$  多样性. 由图 1 可知, 人工草地土壤细菌的 Shannon 指数显著大于天然草地, 从 9.61 显著

增加到 9.87, 而真菌的 Shannon 指数和 Chao1 指数在两块草地上没有显著差异. 这表明天然草地转变为人工草地后, 土壤细菌群落的  $\alpha$  多样性显著增加, 而土壤真菌的  $\alpha$  多样性未发生显著变化.



(a) 和 (b) 为细菌群落, (c) 和 (d) 为真菌群落; \* 为  $P < 0.05$

图 1 天然草地和人工草地土壤中微生物群落的  $\alpha$  多样性指数

Fig. 1 The  $\alpha$  diversity indices of soil microbial community in artificial grassland and natural grassland

### 2.3 土壤微生物群落组成分析

对土壤细菌群落的组成进行分析发现, 在高寒天然草地和人工草地土壤细菌群落主要来自 29 个菌门, 土壤真菌群落主要来自 11 个菌门. 两个样地土壤中优势细菌类群是变形菌门(Proteobacteria) (31.2% ~ 36.7%)、放线菌门(Actinobacteria) (19.5% ~ 22.7%) 和酸杆菌门(Acidobacteria) (8.7% ~ 10.2%) [图 2(a)]. 经  $t$  检验发现, 在两样地之间土壤细菌的变形菌门和放线菌门的相对丰度

存在显著差异. 天然草地转变为人工草地后变形菌门的相对丰度从 34.92% 显著下降到 31.72% ( $P < 0.05$ ), 放线菌门的相对丰度从 20.71% 显著升高到 22.20% ( $P < 0.05$ ). 高寒草地土壤中优势的真菌类群是子囊菌门(Ascomycota) 和担子菌门(Basidiomycota), 它们共占真菌群落的 93% 以上, [图 2(b)]. 在人工草地样品中的子囊菌门的丰度明显低于天然草地样品, 而人工草地担子菌门的丰度高于天然草地样品.

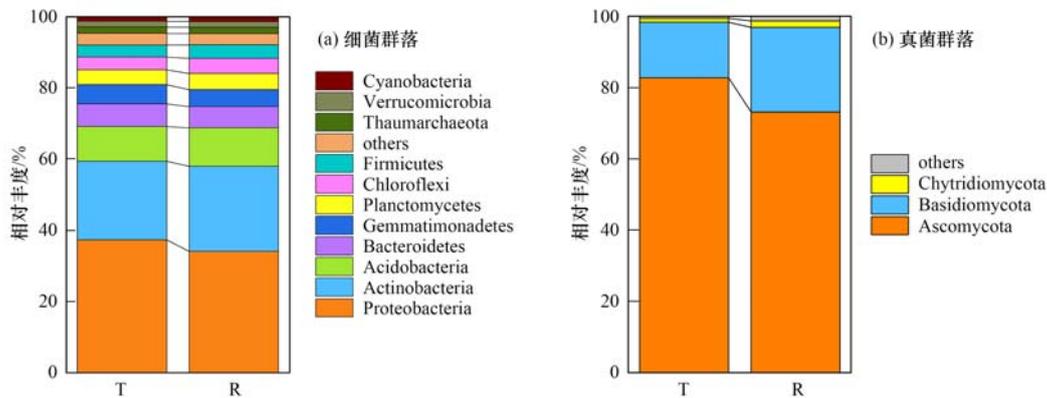


图2 天然与人工草地土壤中微生物群落门水平相对丰度分析

Fig. 2 Analysis of phylum composition of soil microbial community in natural and artificial grassland

为了进一步检验两组样品土壤微生物群落之间的差异,本文做了 MRPP 分析,发现人工草地和天然草地之间土壤的细菌和真菌群落差异显著 ( $P < 0.01$ ),这表明天然草地转变为人工草地后土壤微生物群落的结构发生了显著变化。

#### 2.4 土壤微生物群落与环境因子关系分析

为了研究土壤微生物群落与环境因子之间关系,本研究分别做了环境因子与草地土壤细菌和真菌群落的典范对应分析(CCA).结果如图3所示,天

然和人工草地样品的点分别聚集在一起,而不同草地管理模式的样品点沿第一坐标轴明显分开,这表明两组样品的微生物群落结构存在较大的差异. Mantel 分析结果显示细菌群落与总有机质的含量、总氮含量和土壤水分显著相关;真菌群落与总有机质含量和土壤水分显著相关 ( $P < 0.05$ ).天然草地的土壤细菌群落与土壤总氮、总有机质和植被盖度呈正相关关系,人工草地的土壤细菌群落与土壤氨氮含量和土壤水分呈正相关关系。

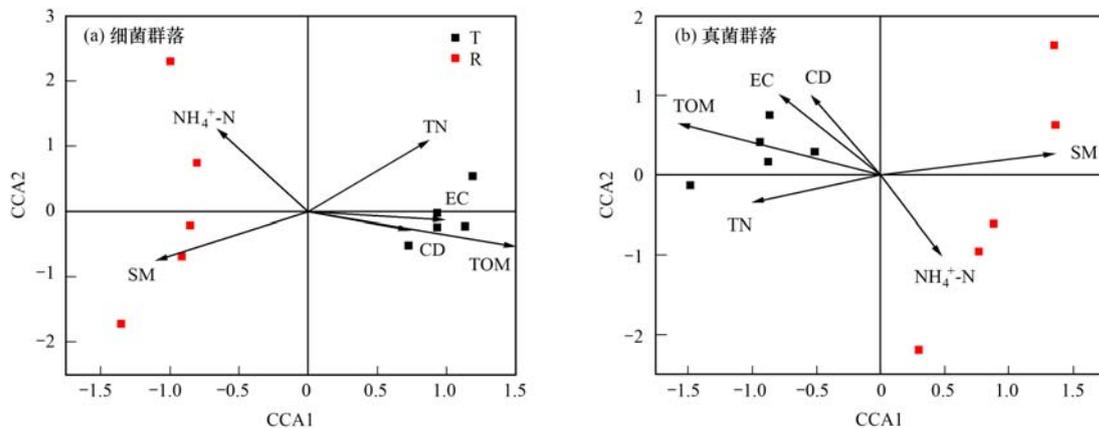


图3 天然与人工草地土壤中微生物群落与环境因子的典范对应分析分析

Fig. 3 Canonical correspondence analysis between soil microbial community and environmental factors in natural and artificial grassland

#### 2.5 高寒草地指示微生物类群分析

本研究采用 LEfSe 分析天然草地和人工草地的指示微生物,选取 2 为 LEfSe 的阈值.图 4 展示了细菌群落和真菌群落中经过筛选后的微生物的 LDA 值,选取 LDA 值最大的微生物作为两种类型高寒草地的指示微生物.作为天然草地的指示细菌类群是暗黑菌门(Atribacteria)细菌,指示真菌类群是子囊菌门(Ascomycota)真菌;作为人工草地的指示细菌类群是出芽菌属(*Gemmata*)细菌,指示真菌类群是发菌科(*Trichocomaceae*)真菌。

#### 2.6 土壤微生物群落功能预测

土壤微生物群落功能直接影响着生态系统的稳

定与功能的发挥.本研究使用 Tax4Fun2 对人工草地和天然草地中细菌群落的功能进行预测.预测结果共得到 375 种功能代谢通路,其中丰度最高的是新陈代谢类群,占 74.3%~75.3%,它主要包括碳水化合物代谢、能量代谢、生物降解和代谢等与生物体基础生命活动密切相关的代谢.碳水化合物代谢包括 TCA 循环、糖酵解和糖质新生和半乳糖代谢等与碳的合成与利用有关的过程;能量代谢包括氮代谢、甲烷代谢、光合作用和氧化磷酸化等与能量产生与转化有关的过程;生物降解和代谢包括多环芳烃降解、甲苯降解、苯甲酸降解和硝基甲苯降解等有机物化合物和污染物的降解过程<sup>[30]</sup>.使用响应比

(response ratio, RR) 分析方法对新陈代谢功能进行深入分析, 结果如图 5 所示. 与天然草地相比, 人工草地土壤细菌群落中辅助因子和维生素代谢、核苷酸代谢和碳水化合物代谢显著减弱, 而生物降解和

代谢、氨基酸代谢、脂质代谢、其他氨基酸的代谢和能量代谢则显著增强 ( $P < 0.05$ ). 这表明, 天然草地转变为人工草地后可能对碳水化合物的利用能力减弱, 但对氨基酸和脂质等物质的代谢能力增强.

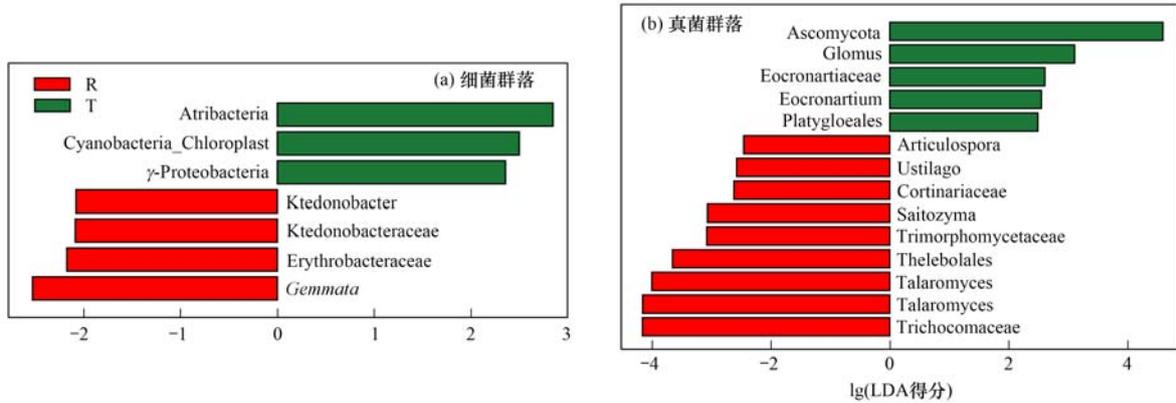
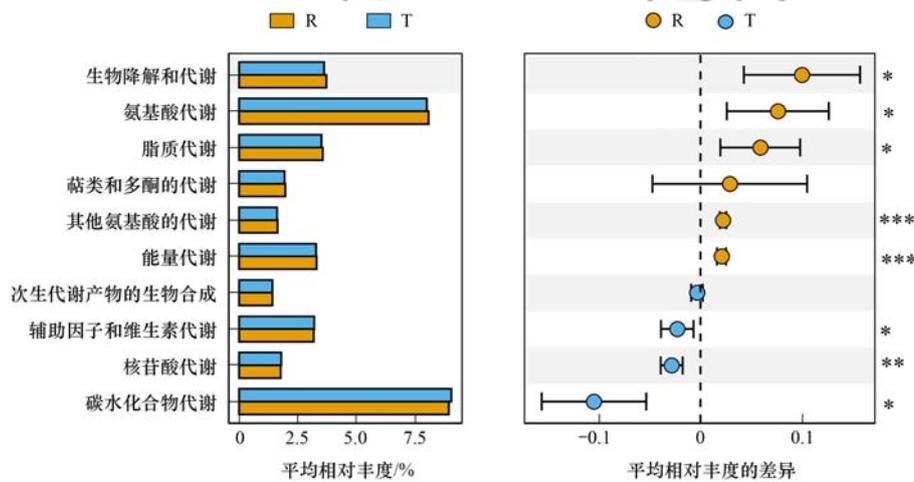


图 4 天然与人工草地土壤中微生物群落的线性判别分析

Fig. 4 LEISe analysis of soil microbial community in natural and artificial grassland



置信区间为 95%; \* 为  $P < 0.05$ , \*\* 为  $P < 0.01$ , \*\*\* 为  $P < 0.001$

图 5 人工和天然草地细菌群落新陈代谢通路

Fig. 5 Metabolic pathways of soil bacterial community in natural and artificial grassland

### 3 讨论

天然草地转变为人工草地后土壤微生物群落多样性发生了显著的变化. 土壤微生物群落的这些变化可能与植被特征和土壤理化性质的改变有关<sup>[31,32]</sup>. 天然草地转变为人工草地必然会引起地面植被特征的变化, 而这些变化能够直接或间接地影响到土壤的理化性质<sup>[33]</sup>. 张超等<sup>[34]</sup>的研究发现阿鲁科尔沁旗草牧场中天然草地与人工草地土壤的含水量、全碳含量和全氮含量均存在明显差异, 这种差异因不同的草地利用方式而不同. 杨锐等<sup>[35]</sup>的研究也发现由天然高寒草地转变为燕麦人工草地后土壤含水量显著增加, 而土壤有机质及总氮的含量显著下降. 微生物群落作为土壤生态系统的重要组成部分, 对外界环境比较敏感, 群落多样性与结构会随

着外界环境的变化而发生改变<sup>[36]</sup>. Chen 等<sup>[37]</sup>的研究发现土壤细菌群落的  $\alpha$  多样性与地面植物的生物量呈显著线性相关, 细菌群落的  $\alpha$  多样性会随地面植物的生物量减少而降低. 本研究中人工草地鲜草的产量显著高于天然草地, 这刺激了土壤中的细菌群落, 使得土壤细菌多样性显著增加<sup>[38]</sup>. 虽然有研究表明真菌对植物类型的变化比细菌更敏感<sup>[39]</sup>, 但随着转变年限的延长, 土壤真菌群落的多样性可能越来越趋于稳定, 与天然草地更接近.

对比天然草地和人工草地发现, 土壤细菌与真菌群落的结构与组成都发生了明显的变化, 这与刘爽等<sup>[40]</sup>和王欣禹<sup>[41]</sup>的研究结果一致. 天然转变成人工草地后地面植被组成、多样性和生物量的较大差异导致土壤环境发生变化<sup>[42]</sup>, 进而导致土壤微生物群落结构与组成有显著变化. Mantel 分析结果进

一步证明这一观点,细菌群落与 TOM、TN 和 SM 显著相关,真菌群落与 TOM 和 SM 显著相关( $P < 0.05$ )。本研究还发现,天然草地转变为人工草地后,变形菌门细菌的丰度显著降低,放线菌门细菌的丰度显著升高,说明转变为人工草地后土壤细菌群落优势种群的丰度发生了变化。放线菌门细菌是有机物的主要降解者,其菌丝体能够降解复杂有机物,在养分循环和改良土壤肥力等方面发挥着重要的作用<sup>[43]</sup>。变形菌门细菌在全球分布较广,与碳的代谢有关<sup>[44]</sup>。天然草地的指示微生物暗黑菌门细菌在自然环境中广泛分布,有较强的分解有机物的能力<sup>[45]</sup>。这些微生物功能类群丰度的变化表明人工草地和天然草地中可被微生物利用的有机质的组分或各组分比例可能发生了变化。

与天然草地相比,人工草地土壤细菌群落的功能也发生了较大的变化。生物降解和代谢、氨基酸代谢、脂质代谢、其他氨基酸的代谢和能量代谢功能显著增强。Weng 等<sup>[46]</sup>的研究发现地面植被的改变导致了土壤碳水化合物和脂类等物质的组成发生变化,进而影响了土壤微生物对碳源的利用模式。本研究中,天然草地转变为人工草地后地面植被发生了明显的变化,植物物种丰富度显著降低,鲜草产量显著增加,优势物种也由原来的嵩草、早熟禾、冷蒿和委陵菜转变成苜蓿和老芒麦。以上变化导致植物凋落物及根系分泌物也相应地发生了较大的变化,植物对土壤输出的营养物质的量及种类也相应地改变,土壤细菌多样性升高,进而影响了土壤微生物的功能<sup>[47]</sup>。微生物生物降解和代谢能力的增强可能进一步加剧了土壤有机质的流失,并影响了土壤碳库的储量<sup>[48]</sup>。Wang 等<sup>[49]</sup>的研究发现采用人工建植的方式对草地边利用边恢复的方法,即使经过 10 a 的时间也无法达到高寒草地土壤功能原始的状态,甚至存在草地进一步退化的风险。因此在改变草地管理方式后应经常检测土壤有机碳的含量及组成,以防止土壤中的碳流失。

#### 4 结论

(1)天然草地转变为人工草地土壤细菌群落  $\alpha$  多样性发生了显著的变化,而真菌群落  $\alpha$  多样性变化不明显。

(2)天然草地转变为人工草地土壤微生物群落组成与结构都发生了明显的变化,这可能是受地上植被与土壤理化性质的影响。暗黑菌门(Atribacteria)细菌和子囊菌门(Ascomycota)真菌可作为天然草地的指示微生物,出芽菌属(*Gemmata*)细菌和发菌科(Trichocomaceae)真菌可作为人工草

地的指示微生物。

(3)天然草地转变为人工草地土壤微生物群落功能发生了明显变化,这些变化可能会影响土壤中有机质的含量,进而影响高寒草地的碳循环和草地生态系统的稳定。

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