

# 全球草地土壤细菌新种发掘及潜在生态功能研究进展

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**摘要:** 草地土壤微生物(grassland soil microorganisms)在维持生态系统健康与稳定性方面发挥着关键作用。然而, 目前针对草地细菌新种的多样性、地理分布、资源挖掘技术以及功能潜力所开展的系统性研究仍较为匮乏。本研究检索了2004–2025年间全球19个国家草地生态系统的74篇新种文献, 涉及104株细菌新种, 并开展荟萃(meta)分析。结合全基因组信息对其功能进行预测, 同时与草地土壤细菌背景群落进行对比。研究结果发现, 草地土壤细菌新种以放线菌门和假单胞菌门为核心优势类群, 其发现频率与土壤背景微生物丰度高度契合。在地理分布上呈现出纬度地带性特征, 高纬度区域富集休眠体类群, 以适应极端环境。对功能潜力的解析表明, 这些新种不仅实现了对“微生物暗物质”的生理实证, 在驱动关键生态功能方面更展现出不可替代的优势。例如, 土壤河小杆菌(*Amnibacterium soli*)等通过高效水解酶系驱动碳氮循环; 灰白色草地土杆菌(*Chthonobacter albigriseus*)介导甲烷氧化, 有助于缓解温室效应; 草地新草小螺菌(*Noviherbaspirillum agri*)等具备固氮促生或盐碱适应能力; 子午岭链霉菌(*Streptomyces ziwulingensis*)可构建生化防御体系。这些研究结果证实了草地核心微生物具有重要的资源价值。未来将整合多学科和多技术手段, 解析叶际-根际新种功能与演化, 实现序列到功能的突破, 为草原生产力提升与生态稳态维持提供微生物学理论支撑。

**关键词:** 草地生态系统; 细菌新种资源; 微生物功能预测; 微生物地理分布

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# Research progress in novel bacterial species and their potential ecological functions in global grassland soils

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**Abstract:** Grassland soil microorganisms play a pivotal role in maintaining the health and stability of grassland ecosystems. However, systematic studies on the diversity, geographical distribution, isolation techniques, and functional potential of novel bacterial taxa in grassland soils remain limited. Here, we conducted a meta-analysis of 104 novel bacterial taxa described in 74 studies from grassland ecosystems across 19 countries between 2004 and 2025. We further predicted their functions *via* whole-genome data and compared them with background soil bacterial communities in grassland soils. Our results showed that novel bacterial taxa in grassland soils were mainly affiliated with the phyla *Actinomycetota* and *Pseudomonadota*, and their discovery frequency closely matched the abundance of background soil microorganisms. Their geographical distribution exhibited clear latitudinal zonation, with high-latitude regions being enriched with dormant taxa adaptive to harsh environments. Functional potential analysis suggested that these novel species not only provide the physiological verification of microbial dark matter, but may also play important roles in key ecosystem processes. Several representative taxa showed distinct ecological functional potential. *Amnibacterium soli* contributes to carbon and nitrogen cycling through efficient hydrolase systems; *Chthonobacter albigriseus* mediates methane oxidation to mitigate the greenhouse effect; *Noviherbaspirillum agri* possesses nitrogen-fixing, plant growth-promoting, and salt-alkali adaptation capabilities; and *Streptomyces ziwulingensis* can contribute to microbial defenses through secondary metabolite production. Together, these findings highlight the ecological and biotechnological potential of core grassland microbial taxa. Future studies integrating multidisciplinary approaches are needed to elucidate the functions and evolution of novel phyllosphere and rhizosphere taxa and bridge the gap between genomic sequences and ecological functions, thus providing microbiological support for improving the productivity and maintaining the ecosystem stability of grassland.

**Keywords:** grassland ecosystems; novel bacterial taxa; microbial function prediction; microbial biogeography

草地作为覆盖全球约 52.5 亿  $\text{hm}^2$ 、占陆地总面积约 40% 的关键生态系统，不仅是畜牧业的重要基础，更在碳氮循环、水土保持以及生

物多样性维持等方面发挥着不可替代的作用<sup>[1]</sup>。土壤微生物作为草地生态系统的重要组成部分，其群落结构与功能直接关系到生态系统的健康

与稳定。全球尺度下的土壤微生物组调查显示, 草地生态系统主要由放线菌门(*Actinomycetota*)、假单胞菌门(*Pseudomonadota*)和酸杆菌门(*Acidobacteriota*)等类群主导<sup>[2-5]</sup>。假单胞菌门是变形菌门(*Proteobacteria*)的最新分类命名, 依据最新细菌分类标准修订后, 其核心类群的系统发育地位及演化关系未发生本质改变<sup>[6]</sup>。本文后续均采用该最新命名体系, 其中放线菌门和假单胞菌门在群落丰度中占据核心地位。然而, 目前对草地土壤细菌新种的多样性、地理分布和功能潜力的研究仍相对匮乏, 尤其是在如何高效挖掘与利用这些资源, 以及现有新种发掘工作与自然界真实的丰度背景之间是否存在明显脱节等方面仍存在诸多挑战。虽然假单胞菌门因其较高的物种分化速率及易于培养的特性贡献了目前绝大多数的草地细菌新种, 但相比之下, 在全球草地背景中丰度极高的酸杆菌门和疣微菌门(*Verrucomicrobiota*), 由于生理需求苛刻且生长缓慢, 仍处于发掘盲区, 被视为典型的“微生物暗物质”<sup>[7-9]</sup>。因此, 聚焦兼具潜在优势性与功能性的细菌新种挖掘, 不仅有助于完善微生物多样性研究, 还能为草地生态修复提供宝贵的种质资源。

当前, 草地土壤细菌新种研究的局限性主要体现在以下几个维度。(1) 对地理分布规律的认识不足。由于不同草地类型, 如高寒、温带、热带稀树草原的土壤性质差异显著, 现有局部区域的新种发现难以界定其演化特异性, 从而限制了靶向筛选的效率<sup>[10]</sup>。(2) 菌种资源挖掘技术存在局限。传统培养法难以突破难培养类群的生长限制, 导致从宏基因组序列信息向纯培养实物资源的转化效率低下, 无法通过纯培养物进行功能验证<sup>[11]</sup>。(3) 对生态功能的认识不足。多数新种研究仅停留在 16S rRNA 基因同源性 与 平均核苷酸相似度 (average nucleotide identity, ANI) 值等分类学鉴定层面, 对其在碳氮循环、促牧草生长及退化草地修复中的功能缺乏系统梳理<sup>[12]</sup>。鉴于此, 本文通过荟萃(meta)分

析, 系统梳理全球已正式发表的可培养草地土壤细菌新种的分布特征与功能潜力, 旨在为定向发掘功能菌株、优化高效培养技术提供理论支撑。同时, 通过对比新种资源与草地土壤背景群落的关联特征, 揭示当前草地微生物资源挖掘的偏好性问题, 并明确其未被开发的潜在价值。

## 1 草地土壤细菌新种多样性与地理分布

为探索草原生态系统中细菌新种的多样性及其地理分布格局, 对 2004–2025 年间已发表的现有细菌新种文献进行了系统性检索。文献来源于 Scopus 数据库和 Web of Science 数据库中的 *International Journal of Systematic and Evolutionary Microbiology*、*Antonie van Leeuwenhoek*、*Current Microbiology*、*Archives of Microbiology*、*The Journal of Microbiology*、*Systematic and Applied Microbiology*、*Anais da Academia Brasileira de Ciências*、*Frontiers in Microbiology*、*Applied and Environmental Microbiology*。以“Grassland” “Grass” “Meadow” “Steppe” “Prairie” “Pasture” “Savanna” “Rangeland” “New species” “Novel micro\* resources” “New bacte\* species” AND “sp. nov.” OR “gen. nov.” 为关键词进行检索, 筛选到 137 篇相关英文文献。对种属信息整理后, 剔除了非草地的干扰样本, 包括海洋、农田、沙漠、植物组织、根瘤以及重复种属的文献, 最终选取了 74 篇参考文献, 并按照样点数量和国家进行排序。这些参考文献覆盖中国、韩国、德国、荷兰、纳米比亚、美国、法国、澳大利亚、英国、尼泊尔、巴西、俄罗斯等 19 个国家, 共计 81 个样点。这些全球样点分布于稀树草原、温带草原、天然草原和草甸草原等土壤样品中, 从中分离并已正式发表的细菌新种有 104 株, 隶属于 103 个分类单元, 涉及 54 个不

同属。细菌新种的核酸序列通过美国国家生物技术信息中心(National Center for Biotechnology Information, NCBI)数据库(<https://www.ncbi.nlm.nih.gov/>)进行检索, 下载新种 16S rRNA 基因序列。随后使用 MEGA X 软件, 采用多序列比对 (Muscle) 对齐方法, 并通过邻接 (neighbor-joining) 法对所有序列信息进行种的系统发育分析, 模型选择 Kimura 2-parameter, Bootstrap 重复 1 000 次, 最终通过 iTOL 在线工具 (<https://itol.embl.de/>) 绘制了系统发育树(图 1)。另外, 将 104 株分离新种与全球及区域性草地土壤细菌背景数据进行了对比分析。背景数据整合自包括 *Science*、*Nature Microbiology*、*The International Society for Microbial Ecology Journal* 以及 *Frontiers in Microbiology* 等高影响力研究期刊, 涵盖了从全球尺度到青藏高原的典型草地土壤细菌组成<sup>[2-4,6-8]</sup>。通过这一多源数据构建的“背景基准”, 能够分析新种挖掘在类群分布上的偏好性, 并量化其对草地微生物资源库的贡献(图 2)。

对全球 19 个国家的 104 株已发表土壤细菌新种进行系统分析发现, 在门水平上, 放线菌门(*Actinomycetota*)共有 38 株, 优势属为链霉菌属 (*Streptomyces*, 14 株); 假单胞菌门 (*Pseudomonadota*)有 32 株, 优势属为假单胞菌属 (*Pseudomonas*, 5 株); 芽孢杆菌门 (*Bacillota*)有 16 株, 优势属为芽孢杆菌属 (*Bacillus*, 14 株); 酸杆菌门 (*Acidobacteriota*)有 10 株, 优势属为 *Brevitalea* 属(2 株)和 *Aridibacter* 属(2 株); 拟杆菌门 (*Bacteroidota*)有 7 株, 优势属为 *Hymenobacter* 属(3 株); 而疣微菌门 (*Verrucomicrobiota*) 仅 1 株。基于 16S rRNA 基因序列构建的系统发育树进一步揭示了这些新种在演化谱系上的高度多样性, 其发育树拓扑结构呈现的深层分类学分化及显著分支深度, 证明草地土壤中存在大量未被发掘的深层谱系。各门类分支内部显著的属级分化特征不仅涵盖了极宽的演化距离, 更体现了当前挖掘的新种资源在遗传背景与分

类范畴上具有广泛的生态代表性。与全球草地土壤细菌背景值的对比分析显示, 新种发现频率的宏观趋势契合自然群落的丰度分布规律, 放线菌门和假单胞菌门的发现占比与其背景丰度占比均保持较高且匹配的水平, 证实了二者在分类学与资源开发中的核心地位。这一结果的取得正是依托针对性的选择性培养策略实现的, 包括利用几丁质琼脂、淀粉酪蛋白培养基富集链霉菌属 (*Streptomyces*), 以及通过无氮苹果酸培养基或特定 *O*-去甲基化底物筛选固氮、降解型假单胞菌属 (*Pseudomonas*) 等优势类群<sup>[10-13]</sup>。然而, 芽孢杆菌门 (*Bacillota*) 的新种比例显著高于其背景均值, 呈现出明显的非对称性富集特征; 这一技术层面的偏倚主要源于选择性抑制与热处理的联用策略<sup>[14]</sup>。通过醋酸钠抑制非目标菌, 并结合高温杀灭非芽孢型微生物, 可将目标芽孢杆菌的分离率提升至 20%–96%, 直观体现了传统分离手段对易培养类群的选择偏向性<sup>[15]</sup>。酸杆菌门新种占比与背景值基本持平, 反映出高稀释度“稀释至消灭法”结合 12 周以上长周期、低浓度有机碳的培养策略, 已有效弥补其丰度与可培养性的差距, 使生长缓慢的酸杆菌避开速生菌干扰形成菌落, 完成对草地“微生物暗物质”的初步发掘<sup>[16-21]</sup>。疣微菌门等类群极低的新种发现率则预示着高丰度难培养菌群依然是未来微生物多样性挖掘的研究瓶颈<sup>[22]</sup>。

在地理尺度上, 上述类群随纬度梯度呈现出规律性演替, 其分布特征体现了微生物对地带性气候的适应性响应。全球草原低中纬度区 (0°–50° N/S) 以放线菌门和假单胞菌门为优势类群<sup>[2]</sup>, 高度的环境异质性驱动了新种的生态位特化, 宏基因组研究表明, 该区域典型草地生境中的微生物在碳源代谢通路周转上具有高度的遗传分化<sup>[7]</sup>, 且蕴含着丰富的次级代谢基因簇 (biosynthetic gene clusters, BGCs) 等专性代谢潜能<sup>[15]</sup>。链霉菌属 (*Streptomyces*) 新种的高频率出现以及假单胞菌属 (*Pseudomonas*) 对物理梯度的

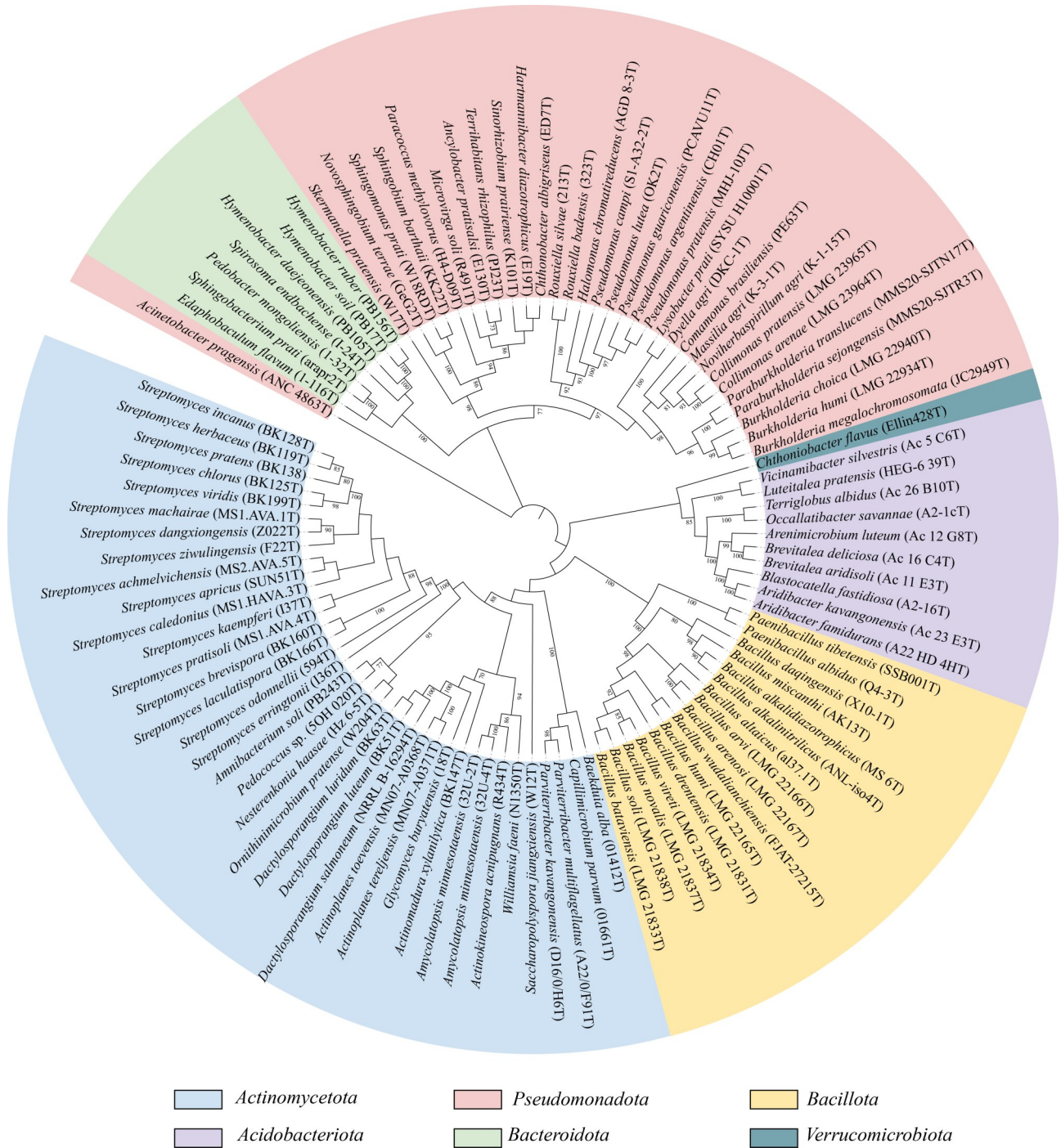


图1 基于16S rRNA基因序列构建的系统发育树

Figure 1 Neighbor-joining phylogenetic tree based on 16S rRNA gene sequences. Different colors represent different bacterial phyla; Color coding: Colored sectors correspond to bacterial phyla; Node support: Numbers at nodes denote bootstrap support values for phylogenetic clade confidence; Labels: The genus and species names of novel taxa; Numbers in parentheses: Overseas culture collection numbers.

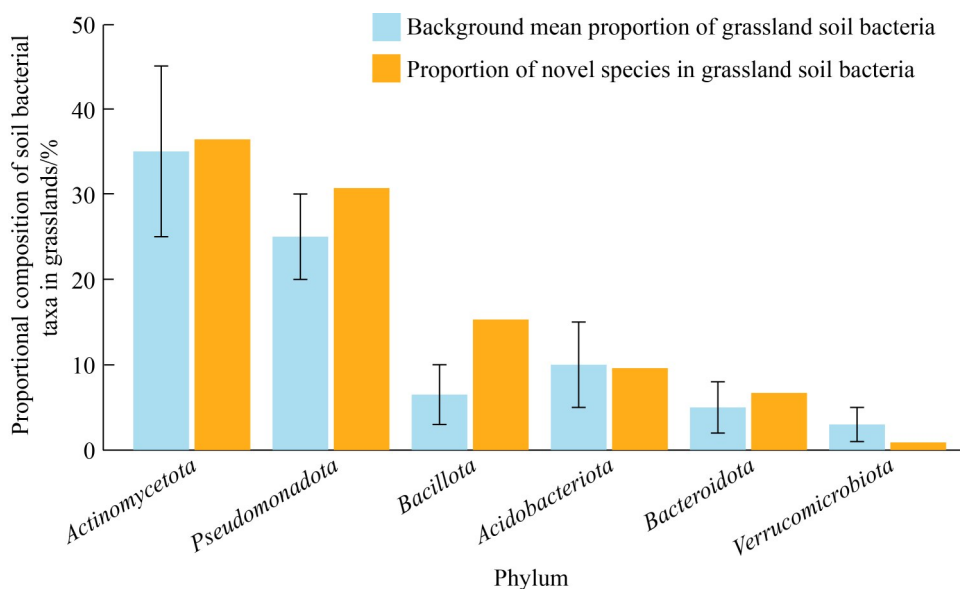


图2 全球草地土壤细菌背景丰度与新种发掘占比对比分析

Figure 2 Comparative analysis of background abundance and novel bacteria species discovery proportion of global grassland soil.

代谢适应，证明了该区域极高的化学生态位竞争与功能潜力<sup>[23-24]</sup>；而副伯克霍尔德氏菌属 (*Paraburkholderia*)与植物的功能互作也对应了中纬度地区较高的宿主依赖型微生物多样性<sup>[25]</sup>。在较高纬度区(50°–60° N/S)，优势类群为放线菌门、假单胞菌门和芽孢杆菌门，在属水平上发生显著特化。链霉菌属与芽孢杆菌属主要通过形成休眠体结构应对极寒胁迫<sup>[23,26]</sup>，而伯克霍尔德氏菌属 (*Burkholderia*)新种则在酸性土壤中具有竞争优势及对顽固性有机质的降解潜力<sup>[27-28]</sup>，从生理水平解释了高通量数据中观测到的胞外多糖合成与复杂碳源利用的功能富集现象。尽管这种纬度分异格局受环境选择与空间过程共同驱动，但当前揭示的格局在很大程度上仍受限于培养依赖型方法的内在偏见与地理采样的不均衡性。综上所述，本研究获得的新种资源实现了从组学视图到生理实证的衔接，为解析草原生态系统微生物多样性的形成机制提供了科学依据。

## 2 草地生态系统土壤细菌新种功能预测

本研究以已正式发表的草地土壤细菌新种为研究对象，通过严格的文献筛选与数据整合，采用系统发育分箱(phylogenomic binning)技术构建新种基因组的系统发育框架。同时结合文献中已报道的新种生理生化特征，以及基于抗生素及次级代谢产物分析系统 (antibiotics and secondary metabolite analysis shell, antiSMASH)的次级代谢产物预测，与基于京都基因与基因组百科全书(Kyoto encyclopedia of genes and genomes, KEGG)的功能通路解析，进行整合分析揭示了草地土壤细菌新种在驱动有机质分解与养分循环、介导细菌-真菌互作及植物促生抗逆、发挥病原菌拮抗与生物防治作用等方面的核心生态功能。这些发现不仅丰富了全球土壤核心菌群的功能谱系，更在功能群水平揭示了草地土壤细菌新种显著的生态位专一性特征；其在复杂底物降解、极端环境适应等低冗余功

能上展现出的不可替代性,修正了单纯依赖宏观环境因子的群落分布预测体系,为高分辨率解析草地细菌群落的功能维度分布格局提供了关键微观证据。

## 2.1 参与有机质分解和养分循环相关功能特性

在碳周转维度,草地土壤细菌新种表现出极强的基质降解广度及生境适应性[数据存储于国家微生物科学数据中心(<http://nmdec.cn>),编号为 NMDCX 31253.11]。分析图谱索引酶谱系统(analytical profile index zymogram, API ZYM)检测证实,土壤河小杆菌(*A. soli*)具备酯酶(C4和C8)及多种糖苷酶活性,能够水解纤维素与半纤维素,从而显著提升土壤有效碳含量<sup>[29]</sup>。与此同时,草地鞘氨醇杆菌(*Sphingobacterium prati*)携带丰富的多糖活性酶(CAZymes),可降解木质纤维素生物质<sup>[30]</sup>;而苍黄指孢囊菌(*Dactylosporangium luridum*)、橙色指孢囊菌(*D. luteum*)及鲑色指孢囊菌(*D. salmonium*)等新种展现了对木聚糖、纤维素及几丁质等大分子底物的高效矿化能力<sup>[31]</sup>。白色类芽孢杆菌(*Paenibacillus albidus*)与西藏类芽孢杆菌(*P. tibetensis*)分别通过产生木聚糖酶及降解复杂多糖<sup>[32-33]</sup>,协同草地戴氏菌(*Dyella agri*)与草原马赛菌(*Massilia agri*)对羧甲基纤维素及酪氨酸的分解作用,加速了草原植物残体的矿化过程<sup>[34-35]</sup>。针对脂质与复杂底物代谢,地卡瓦列罗菌(*Caballeronia choica*)与白色长白山菌(*Baekduia alba*)展现了显著的脂肪酶与酯酶活性<sup>[36-37]</sup>;而巴西北里氏孢菌(*Kitasatospora brasiliensis*)通过水解淀粉、明胶及DNA进一步拓宽了有机物降解谱<sup>[38]</sup>。在养分循环与元素转化方面,明尼苏达拟无枝酸菌(*Amycolatopsis minnesotensis*)与草地斯克曼氏菌(*Skermanella pratensis*)具备硝酸盐还原能力<sup>[39-40]</sup>,协同草地土假单胞菌(*Pseudomonas campii*)的硝酸盐还原基因(*nasA*、*nirBD*)以及嗜甲基假单胞菌

(*Paracoccus methylovorus*)的全套反硝化基因簇,共同调控土壤氮通量并减少温室气体排放<sup>[41-42]</sup>。干草威廉氏菌(*Williamsia faeni*)通过水解尿素及尿囊素<sup>[43]</sup>,与草地金黄纤丝菌(*Luteitalea pratensis*)的有机营养利用机制相配合,为植物生长提供了关键的养分补给<sup>[44]</sup>。此外,草地溶杆菌(*Lysobacter prati*)合成具有生物活性的次级代谢产物<sup>[45]</sup>;黄色土壤棒菌(*Edaphobaculum flavum*)通过产生柔红素样色素在有机质分解竞争中占据优势<sup>[46]</sup>;而巴西丛毛单胞菌(*Comamonas brasiliensis*)利用聚羟基脂肪酸酯(polyhydroxyalkanoates microspheres, PHA)途径实现能量的跨季节锁定<sup>[47]</sup>。荻芽孢杆菌(*Bacillus miscanthi*)及大庆芽孢杆菌(*B. daqingensis*)则通过诱导碳酸钙沉淀或解离复杂有机质,主动调控土壤碱性与养分转化速率<sup>[48-49]</sup>。这些隶属于假单胞菌门、放线菌门及芽孢杆菌门的新种微生物,在全球尺度上构成了驱动生物地球化学循环的基础骨架。草地新种揭示的特定代谢机制表明其分布并非仅受限于环境因子的简单过滤,土地球菌(*Pedococcus* sp.)基因组中包含的复杂碳水化合物降解基因系及灰白色草地土杆状菌(*Chthonobacter albigriseus*)的专性甲烷氧化功能,体现了新种在极端生境下突破代谢瓶颈的独特能力<sup>[50-51]</sup>。这种低冗余核心功能节点的发现,修正了以往基于属水平丰度预测生态功能的偏差,证明了草地细菌群落在功能基因簇维度上具有极高的生态位特异性,为草原生态系统在动态波动下维持碳氮稳态提供了关键的微观证据。

## 2.2 参与细菌-真菌互作及其植物促生潜力与抗逆适应

草地土壤细菌新种在草原植物促生与抗逆中具有显著潜力(编号为 NMDCX 31253.11)。在根际养分直接供给维度,草地新草小螺菌(*N. agri*)经<sup>15</sup>N同位素示踪验证,可通过固氮作用提升土壤氮素回收率并触发根际级联效应<sup>[52]</sup>;

嗜碱固氮芽孢杆菌(*Bacillus alkalidiazotrophicus*)、食二氮哈特曼杆菌(*Hartmannibacter diazotrophicus*)及携带 *nifH* 基因的盐渍草地屈曲杆菌(*Ancylobacter pratisalsi*)均展现出明确的固氮潜力<sup>[53-55]</sup>, 而草原中华根瘤菌(*Sinorhizobium prairiense*)通过 *nodABC* 基因构建了共生体系<sup>[56]</sup>。针对磷素利用, 大染色体卡瓦列罗菌(*C. megalochromosomata*)与藤黄假单胞菌(*Pseudomonas lutea*)通过释放有机酸或水解有机磷增强植物对磷素的吸收与利用效率<sup>[57-58]</sup>, 固氮假单胞菌(*H. diazotrophicus*)则利用高活性磷酸酶协同驱动磷循环。在种间互作关系中, 透明副伯克霍尔德里氏菌(*Paraburkholderia translucens*)分泌吲哚乙酸(indole-3-acetic acid, IAA)及铁载体直接促生<sup>[59]</sup>; 砂土山冈单胞菌(*Collimonas arenae*)则调节真菌-细菌互作<sup>[60]</sup>。针对环境胁迫, 阿根廷假单胞菌(*Pseudomonas argentinensis*)利用黄色色素(442 nm 吸光峰)抵御紫外线<sup>[61]</sup>; 牧场鸟氨酸微生物(*Ornithinimicrobium pratense*)通过独特的磷脂酰胆碱(phosphatidylcholine, PC)结构维持膜稳态<sup>[62]</sup>。在强化宿主抗逆性方面, 黑龙江农科院涅斯捷连科氏菌(*Nesterenkonia haasae*)通过降解胞壁多糖释放半乳糖以协助植物适应盐碱<sup>[63]</sup>; 嗜根际栖土菌(*Terrihabitans rhizophilus*)则利用 83 个 CAZymes 基因家族强化宿主对多糖的利用<sup>[64]</sup>。与 Delgado-Baquerizo 等<sup>[2]</sup>提出的“环境因子驱动植物生产力与微生物多样性关联”的观点相吻合, 本研究中的新种不仅是草原生境中的高频分布类群, 更是植物-微生物反馈回路的具体调节者。*Burkholderia* 作为根瘤菌与特定植被类型共生, 体现出与宿主植物类型具有一定的系统发育关联性<sup>[65]</sup>。在细菌功能群的可替代性方面, 固氮与有机磷水解等促生功能表现出较高的生态位重叠<sup>[66]</sup>。然而, 在干旱、盐碱等极端或多重胁迫环境中, 微生物群落整体虽表现出一定功能冗余, 但部分与渗透调节和抗逆代谢相关的通路通常由少数关键类群承担, 作为网络中的低冗余核心功能节

点<sup>[67]</sup>。值得注意的是, 在盐碱胁迫下由新种 *N. haasae* 介导的半乳糖渗透调节途径呈现生态位专一性<sup>[63]</sup>。该功能特性使其在草地盐碱微生境中形成了不可替代的生态功能位, 成为调控宿主及周边微生物适应盐碱胁迫的关键功能通路, 也进一步证明了草地细菌新种在环境胁迫响应中的生态位分化特征。

### 2.3 病原菌拮抗与生物防治功能

草地土壤细菌新种在病原拮抗方面具有核心潜能(编号为 NMDCX 31253.11)。子午岭链霉菌(*S. ziwulingensis*)对金黄色葡萄球菌及破坏柱果孢具有广谱抗菌活性, 在新型生物源农药制剂的研发中具有重要的应用前景<sup>[68]</sup>; 抗痤疮放线动孢菌(*Actinokineospora acnipugnans*)则通过抑制酪氨酸酶与弹性酶活性干扰病原代谢<sup>[69]</sup>。恩德巴赫螺状菌(*Spirosoma endbachense*)利用 I 型和 III 型聚酮合酶(T1PKS、T3PKS)产生萜烯及聚酮类次级代谢产物构建生化防御体系<sup>[70]</sup>。在资源竞争层面, 小毛状微菌(*Capillimicrobium parvum*)利用高效磷酸 ABC 转运体限制病原菌发育, 并能降解芳香酮类化合物<sup>[71]</sup>。*Bacillus* 属新种中, 田间芽孢杆菌(*B. arvi*)和土地芽孢杆菌(*B. humi*)通过分泌抗菌代谢物诱导植物系统抗性(induced systemic resistance, ISR)<sup>[72]</sup>。抗逆机制进一步支撑了防效稳定性, 如牧场鸟氨酸微生物(*O. pratense*)编码的热休克蛋白与 242 个次级代谢合成基因确保了其在高温下的代谢活性<sup>[62]</sup>; 森林土嗜邻聚杆菌(*Vicinamibacter silvestris*)与草地鞘氨醇单胞菌(*Sphingomonas prati*)分别通过过氧化氢酶和亚精胺调节对抗氧化应激<sup>[73-74]</sup>。针对受污染生境, 嗜盐碱铬还原菌(*Halomonas chromatireducens*)具备 Cr(VI)还原能力<sup>[75]</sup>, 而神户糖多孢菌(*Saccharopolyspora kobensis*)则表现出多重耐药演化优势<sup>[76]</sup>。全球土壤研究主要聚焦于碳、氮、磷转化菌群, 而对涉及病原拮抗的次级代谢产物合成基因簇的空间分布研究较少<sup>[3]</sup>。草地新种携带的多样化 BGCs 不仅赋予了其高度特异的病原拮抗功能, 更构成了草地土

壤在分子水平上抵御生物胁迫的防御性基因库<sup>[77]</sup>。从功能群维度分析,基础养分竞争功能在群落中具有较高的冗余度,而针对特定真菌病原的生化拮抗功能则表现出显著的功能独特性,且该特异性防御功能通常由子午岭糖多孢菌(*S. ziwulingensis*)等少数特定的演化支系所介导<sup>[77]</sup>。这种功能的高度专一化意味着草原生态系统的生物防御能力并非由群落整体均匀分担,而是由特定的关键物种驱动<sup>[78]</sup>。这些新种在拮抗环境中的演化优势决定了其在草地细菌群落中的生态占位。这一发现修正了草原土壤功能主要由广谱优势菌主导的传统认知,通过阐明专性防御功能群在群落维度分布与演替过程中的核心制约作用,为开发针对草原生态退化的精准生物防治方案提供了坚实的理论支撑。

### 3 总结与展望

本研究通过对全球 19 个国家 73 个草地样点的 104 株可培养细菌新种进行系统梳理,解析了其在门、属水平上的分类多样性、地理分布格局及潜在生态功能。研究表明,放线菌门(*Actinomycetota*)与假单胞菌门(*Pseudomonadota*)构成了全球草地新种资源的核心主体,并呈现出显著的纬度地带性演替规律。在不同纬度草地新种组成表现出明显的属级特化特征,链霉菌属与芽孢杆菌属等类群通过形成休眠结构实现对极寒生境的生理适应。这种分布特征不仅受土壤 pH 等局部环境过滤因子的调控,更体现了空间扩散过程对群落构建的深刻影响。功能预测显示,这些新种通过驱动生物地球化学循环、介导植物促生响应、增强宿主抗逆性及构建生物防御体系,协同维持着草原生态系统的稳态。

尽管在草地细菌新种发掘方面取得了阶段性进展,但该领域仍面临显著的现实困境,未来需通过整合前沿技术实现从随机挖掘向目标导向挖掘的范式转变。(1) 资源获取的深度受限于传统培养技术的选择性偏好,导致大量

处于可培养边缘的低丰度类群依然难以获取纯株,应利用培养组学、微流控原位培养技术以及模拟根际与叶际微环境的仿生培养系统(biomimetic cultivation systems),实现对高丰度难培养类群如酸杆菌和疣微菌的定向捕捉。(2) 新种在自然生境中驱动生物地球化学循环的实际贡献率缺乏精准量化,导致基因预测功能与原位代谢速率之间存在认知偏差。未来可结合稳定同位素探针技术、空间代谢组学以及针对叶际新种微生物(phylosphere novel species)的原位活性监测,在分子层面直接关联新种与其在碳氮循环及植物表面定殖中的实际活性,实现对 *N. agri* 等固氮新种根际级联效应的生理实证。(3) 新种之间以及新种与土著群落之间的互作网络逻辑尚不清晰,难以从系统层面解析复杂群落的演替规律与稳态维持机制。引入单细胞转录组学与原位互作成像技术解析 *C. arenae* 等在细菌-真菌互作中的代谢交换特征,有助于从群落维度深度揭示新种不可替代的生态位功能。(4) 草地新种在应对全球气候变化时的表型可塑性与遗传适应潜能仍不明确。通过利用合成生物学平台(synthetic biology platforms)和高通量反向遗传学,利用规律成簇的间隔短回文重复序列系统及相关蛋白(clustered regularly interspaced short palindromic repeats, CRISPR-associated 9, CRISPR-Cas9)基因编辑对 *S. ziwulingensis* 等携带的防御基因簇进行定向激活,并结合环境 DNA 动态监测技术,能够实时评估新种对草原生态系统生产力的长期贡献。(5) 现有研究大多聚焦于静态功能潜力的描述,缺乏在动态环境压力下新种次级代谢产物合成基因簇的原位激活机制及演化速率监测。通过整合前沿技术的跨学科手段将实现对草地微生物“暗物质”从序列信息到生理实证的跨越,为定向改良草原生产力提供核心生物资源支撑。(6) 草地新种的演化轨迹及其对全球变暖的反馈效应仍缺乏宏观尺度的系统评估。利用比较基因组学与分子进化时钟分析,可以追溯如 *C. albigriseus* 等功能

类群的演化历史，评估其功能基因在数千年来如何响应气候波动，并结合全球尺度采样分析，预测在未来增温情景下新种分布范围的迁移趋势，为草原生态系统的长期稳定性预警提供重要参考。

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## 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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