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# 稀有微生物群落研究进展

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**摘要:**微生物对人类生活和全球生物地球化学循环存在深刻影响,其中稀有微生物群落是评价微生物多样性的因素,是微生物遗传和功能多样性的存储库,具有驱动地球化学循环、指示环境变化、降解污染物、稳定群落结构等重要功能。介绍了稀有微生物群落的相关概念、类型、研究方法、存在机制及功能作用,为进一步研究微生物的生物地理学、探索微生物基因组等提供参考。

**关键词:**稀有微生物;群落;稀有性;类型;功能

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## Research progress on rare microbial community

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**Abstract:** Microbes have a profound impact on people's lives and they also affect the global biogeochemical cycle. A rare microbial community has an important ecological role, in evaluating microbial diversity, a repository with genetic and functional diversity, and serves severe important functions, such as driving the geochemical cycle, responding to environmental changes, degrading pollutants, and stabilizing the community structure. The concept, types, research methods, existing mechanism and function of rare microbial community were introduced, which could provide reference for further study of microbial biogeography and exploration of microbial genome.

**Key words:** rare microorganism; community; rarity; type; function

环境中具有典型的物种丰度分布偏斜特征,表现为相对高丰度的少量优势物种与相对低丰度的大量稀有物种共存<sup>[1]</sup>。稀有种群作为地球生态系统中至关重要但又脆弱的组成部分,在生物地球化学循环中扮演着重要的角色,是微生物群落功能的一个潜在驱动力<sup>[2]</sup>。虽然现阶段对稀有微生物群落的关注与日俱增,但大部分研究仍以优势物种为基础<sup>[3]</sup>。主要是由于优势微生物的丰度变化往往会掩盖低丰度类群的种群动态,导致其被忽视。但随着科学技术的发展,低丰度微生物群落的进一步测定分析成为可能,继而发现稀有微生物圈物种也可以作为关键物种,对生态系统做出重要贡献<sup>[4-7]</sup>。有研究表

明,稀有微生物群落虽然所占丰度比例较低,却是 $\alpha$ 多样性和 $\beta$ 多样性的重要贡献者<sup>[8]</sup>,物种多样性能够影响群落的稳定性和恢复能力,这意味着低丰度群落在维持生态系统健康方面具有重要作用和意义<sup>[3,9,10]</sup>。此外,稀有微生物群落的丰度还可以反映环境的选择<sup>[11,12]</sup>,也可以代表一种特殊的生物地理学环境<sup>[13-16]</sup>,它们的存在与独特的丰度分布和系统发育组成有关<sup>[17]</sup>,当稀有微生物作为关键物种存在时,其对生态系统能够产生巨大的影响<sup>[18-20]</sup>。

## 1 稀有微生物群落的定义

稀有性可能是随机过程<sup>[21]</sup>、生命史策略的内在

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权衡<sup>[22]</sup>以及生物与非生物相互作用<sup>[23,24]</sup>的结果。稀有性可以通过多种方式来定义,如局部丰富度、栖息地特异性、地理分布等<sup>[25]</sup>,在微生物生态学中,局部丰富度(Local abundance)是衡量物种稀有性最简单、最常用的指标<sup>[2]</sup>。高通量测序技术(HTS)分辨率的不断提高,为微生物多样性的研究提供了新的支持<sup>[26]</sup>。核糖体 RNA 小亚基序列(SSU-rRNA)基因测序<sup>[27]</sup>开发的几种 HTS 方法揭示了大量的低丰度微生物类群的存在。在这些数据中定义稀有微生物群落使用的方法包括相对丰度截止值( $<0.1\%$ <sup>[28,29]</sup>或 $<0.01\%$ <sup>[17]</sup>)、生成数据集的序列计数(如每个样本 2 个序列<sup>[30]</sup>)和经验阈值<sup>[31,32]</sup>。无论用于定义稀有性的阈值如何选择,基于标记基因测定的微生物群落丰度分布通常显示出低相对丰度操作分类单元(OTUs)的长“尾巴”,这条“尾巴”即为稀有微生物群落,它的长度和形状取决于样品群落的多样性和基本物种的丰度分布<sup>[33-35]</sup>。不同的样品中稀有微生物相对应的长尾的大小存在差异,一般高多样性微生物的样本“尾巴”更长<sup>[3]</sup>。

## 2 稀有微生物群落分类及存在机制

根据相对丰度的周期性变化,Lynch 等<sup>[3]</sup>将稀有微生物群落分为 5 类(图 1)。第一类属于 r-策略者,该类群微生物的丰富度可以在丰富和稀有之间进行周期性的变换,这种变换取决于周期性的环境调节,如温度、季节等。第二类属永久稀有类群,虽然表现出周期性的丰度变化,但却始终以低相对丰度存在,并且相对丰度能够对 k-选择变化作出反应,该类群占据狭窄生态位。第三类同样属于 r-策略者,但与第一类的区别在于该类群只是偶尔以相对罕见的高丰度持续存在,归因于对偶尔或随机的环境变化做出反应,如降水、压力等。第四类同样属于永久稀有类群,包括可能的关键物种,表现出持久的丰度变化不明显的低丰度分布,占据狭窄生态位。第五类属于暂时类群,只是偶尔出现,但相对丰度在稀有范围内,其存在的持久性取决于合适的繁殖和生存条件。稀有性生物圈中周期性或偶发性出现的类群可以被认为是条件的稀有分类群。

稀有性可能是随机过程,简单地通过随机的种群波动而出现,不存在任何特定的生理特征<sup>[21]</sup>;也可能是物种在进入新群落时,由于数量上的差异表现出来的稀有;同时外在的非生物和生物因素在物种稀有性中起着关键作用。Jousset 等<sup>[2]</sup>认为导致微生物局部稀有的可能潜在机制主要包括 4 个方面:狭窄的生态位(图 2a)、高度的种间竞争(图 2b)、低竞争能力(图 2c)和捕食频率(图 2d)。功能高度专一化的物种只有在特定的适宜环境下才能大量存在,而在大多数环境中以稀有形式存在,生态位狭窄(图 2a)。生物相互作用在解释稀有性方面也有重要意义,对于那些竞争能力弱、无法构建生物膜等保护性结构或无法利用关键资源的微生物而言,随着竞争对手的增加,其丰富度下降(图 2b)。一个对于资源没有竞争力的物种可能经常保持稀有而不灭绝状态(图 2c)。许多微生物在大多数情况下通常都是不活跃的,丰度很低,只有在更有利的条件出现时才逐渐占优势(图 2d),例如某些物种过度地捕食其他物种为稀有物种留下生存的空间,导致稀有物种相对丰度的增加。

## 3 稀有微生物群落的研究方法

复杂的微生物群落包含大量的低丰度物种且低丰度物种占有相当大的比例。研究表明稀有微生物圈包含关键物种,并充当基因组多样性的储存库以促进群落的适应能力。所以说稀有微生物圈在一定程度上控制着微生物群落,并占据重要的生态位。如表 1 所示,传统的纯培养技术在研究高度多样化环境(如土壤)中的微生物时具有重要价值<sup>[36,37]</sup>,因为在培养中获取的稀有物种能够进行特定的生理生化试验,结合单细胞基因组学和重建基因组学可以深入了解它们的功能作用,然而传统培养技术却也在一定程度上限制了人类对稀有微生物群落的理解。高通量测序技术的发明和改进使得微生物群落结构的深入分析成为可能<sup>[38-42]</sup>。但测序显示的是特定时间地点存在的物种,提供有关特定物种或群落潜在功能的有用信息仍需通过试验来验证完成;并且测序数据分析过程中的人为处理导致细菌群落中

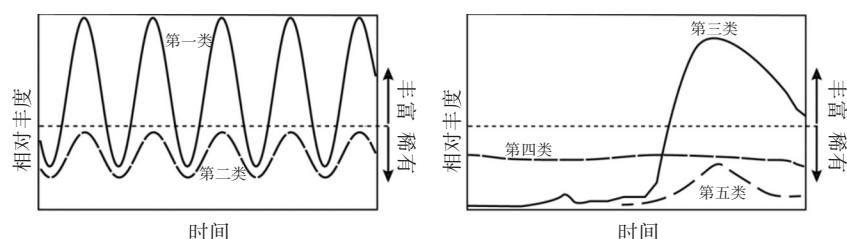


图 1 稀有微生物群落分类<sup>[3]</sup>

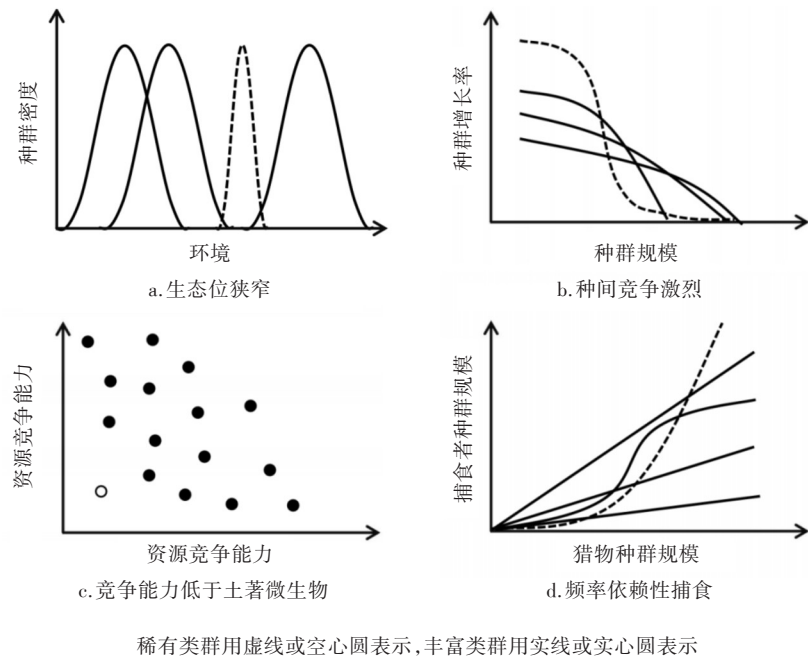


图2 可能导致局部稀有的潜在机制<sup>[2]</sup>

表 1 稀有微生物群落研究方法

稀有微生物来源	检测方法	结果	参考文献
土壤样品	显微镜观察法	细胞平均大小与可培养性有关,细胞越小越不容易培养,相对丰度越低	[36]
土壤样品	纯培养	土壤细菌的生长速率和基质利用率并不是决定其丰富度的主要因素	[37]
水体样品	16S rDNA 扩增序列分析	优势菌门的稀有 OTUs 在维持群落多样性方面发挥了重要作用	[38]
水库表层水体	16S rDNA 扩增序列分析	稀有浮游生物类群更容易受到 DNA 提取过程的影响	[39]
大肠杆菌	焦磷酸测序	去除未解析碱基和异常读取数,增加了多样性的不准确性的	[40]
农田土壤样品	SARD rRNA 扩增序列分析	SARD 可以提供一种方法,定性和定量稀有微生物群落的生态作用	[41]
深海沉积物样品	高通量微流控制平台	该方法能高效率地揭示环境稀有微生物群落,特别是对生长缓慢的物种	[42]
农田土壤样品	纯培养+流式细胞术	培养时间不影响可培养稀有物种,但可以改变其系统发育组成	[43]
农田土壤样品	纯培养+焦磷酸测序	传统的培养条件能够发现稀有微生物群落	[44]
地中海水体样品	纯培养+高通量测序	纯培养仍然是揭示海洋细菌多样性的有用手段	[45]
太平洋水体样品	核酸标记+焦磷酸测序	稀有微生物是微生物群落功能生态系统的重要组成部分	[46]
土壤样品	荧光原位杂交+流式细胞术+基因组扩增测序	该方法可以快速定向获取复杂微生物群落中低丰度物种基因组	[47]

大量先前未被发现的稀有物种消失,使得稀有群落各种生态系统中的功能的重要性无法探知。因此,将传统培养方法与现代测序技术相结合,比单独采用一种方法更能够描述稀有微生物群落的多样性<sup>[43-47]</sup>,再加上细胞分离、基因组恢复、多重置换扩增、稳定同位素探测、功能性亚基因组学、稀有类群的靶向扩增和培养、共生网络和指示物种分析等技术手段,可以更全面地了解稀有微生物圈在微生物群落中的分布和作用<sup>[3]</sup>。

4 稀有微生物群落的功能作用

稀有物种可以驱动地球化学循环的关键过程,能够响应并适应环境的变化,是温室气体产生与消

耗、污染物降解的参与者。它们可以通过阻止新物种的入侵来影响群落的聚集,并在波动的环境中稳定群落。此外,稀有微生物能够阻止病原菌群落的建立和刺激宿主发生免疫反应,是动植物宿主相关微生物群的重要组成部分。

4.1 驱动地球化学循环

微生物是驱动地球生物地球化学循环的重要引擎<sup>[48]</sup>,物质循环过程中,稀有微生物种属能够产生巨大影响。研究发现,高活性的稀有关键物种 *Chromatium okenii* 属(约占细胞总数的 0.3%)贡献了系统中 40% 以上的铵和 70% 以上的碳的吸收量,对环境介质中氮和碳的吸收至关重要<sup>[49]</sup>。Zhang 等<sup>[50]</sup>研究发现土壤稀有微生物(细菌和真菌)在调节土壤



有效氮含量方面作用明显。反硝化菌的减少导致土壤中潜在的反硝化活性显著降低<sup>[51]</sup>。稀有微生物还能够还原硫酸盐,进而抑制甲烷的排放。在缺氧环境中,亚硫酸盐和硫酸盐还原微生物(SRM)能够将硫和碳的循环联系在一起,Vignerón 等<sup>[52]</sup>对 14 个生态系统样品中的 SRM 研究发现,环境变化导致 SRM 分布不断扩大,其中 96% 以上可被视为稀有生物圈的 SRM。泥炭地硫酸盐的减少可以大大减少甲烷的排放。Hausmann 等<sup>[53]</sup>对泥炭地中异养硫酸盐还原研究发现,低丰度 OTUs (<1% 的基因组丰度)对硫酸盐的添加有显著反应。这些 OTUs 包括已知的硫酸盐还原类群,如脱硫孢子菌、脱硫弧菌等,也包括未知硫酸盐还原剂或其代谢相互作用类群。Pester 等<sup>[54]</sup>在泥炭地长期试验场中同样发现,一种仅占微生物群落 16S rRNA 基因总数 0.006% 的脱硫孢子菌是一种重要的硫酸盐还原剂,能够转化碳流,改变它们对全球变暖的影响。

#### 4.2 指示环境变化

稀有微生物群落对环境变化敏感<sup>[24]</sup>。目前与人类活动有关的环境变化,如全球气候变化、土地集约利用等,均能够对稀有生物圈和相关的生态系统功能产生影响<sup>[55]</sup>。监测稀有微生物群落相对丰度或活性的变化可以作为环境变化的早期预警<sup>[56]</sup>。在水环境介质中,研究发现短时间内环境的变化能够改变盐沼上覆水体中稀有类群(<1% 总丰度)的群落结构<sup>[57]</sup>,水体理化性质的变化能够改变稀有浮游细菌群落结构,总磷、铵态氮和叶绿素是制约水环境中稀有类群变异的主要环境因子<sup>[58]</sup>。Wang 等<sup>[59]</sup>研究发现稀有类群有助于微生物群落对水体里的有机污染物做出反应。在土壤环境介质中温度改变后,能够使稀有细菌群落进行重新组合<sup>[60]</sup>。Bartram 等<sup>[61]</sup>对苏格兰克雷布斯通实验农场土壤中的微生物研究发现,传统分析方法无法识别的 OTUs 与不同的 pH 具有相关性。因此,稀有类群有助于提高微生物群落对环境扰动的响应,加强稀有微生物的研究,对于更好地理解微生物多样性的价值具有重要意义。

稀有微生物群落还可以提供一个长期支持生态系统稳定的生物库,响应干扰并适应干扰。干扰改变微生物群落组成,影响生态系统潜在过程。生态系统适应环境扰动的能力取决于干扰持续的时间和强度以及系统整体的生物多样性<sup>[62]</sup>。Gomez-alvarez 等<sup>[63]</sup>研究显示稀有类群在模拟饮用水分配系统中受到干扰(消毒、改变运行参数、生物膜阶段)时,结构发生变化,但却能够恢复到稳定状态。而 Sjöstedt 等<sup>[64]</sup>研究表明干扰(盐度变化)能够对浮游

细菌群落组成造成影响,稀有类群在受到干扰后变得更加丰富,而这些稀有浮游细菌在维持生态系统功能过程中具有重要作用。

#### 4.3 参与温室气体甲烷的产生与消耗

Yang 等<sup>[65]</sup>以 *mcrA* 基因为靶点对环境中的稀有产甲烷古菌进行研究发现,在考虑稀有类群的情况下, $\alpha$  多样性与甲烷的产生呈正相关,条件稀有产甲烷类群在很大程度上解释了稀有微生物圈的整体群落动态,并可能在有利的环境条件下转化为优势群落。Sierocinski 等<sup>[66]</sup>研究发现天然群落的初始组成与甲烷产量之间没有相关性,但在实验室条件下进行生态选择后,稀有物种在甲烷生成群落中起着重要作用,与甲烷产量之间呈现正相关关系;认为产甲烷菌群几乎没有功能上的冗余,因此,在厌氧消化过程中,繁殖条件变化造成的多样性损失都有可能减少甲烷的产生。而 Wagner 等<sup>[67]</sup>对北极阿拉斯加土壤中产甲烷微生物进行研究,结果与 Sierocinski 等<sup>[66]</sup>不同,认为产甲烷菌可能存在高度的功能冗余,稀有物种丰度可能是微生物群之间的驱动力,影响北极甲烷产量。而 Bodelier 等<sup>[68]</sup>在研究微生物群落结构组成在调节河漫滩甲烷排放中的作用时发现,河岸湿地甲烷消耗的动态和强度与甲烷氧化菌(MOB)相对丰度和活性有关,MOB 作为该生态系统中微生物群落的次要组成部分,其多样性参数与体外甲烷消耗量呈线性关系。

#### 4.4 降解污染物

微生物多样性的减少会降低污染物的降解<sup>[69]</sup>。Wei 等<sup>[70]</sup>应用培养技术和 16S rRNA 测序技术对污泥中胆固醇厌氧降解途径的研究过程中发现,胆固醇的降解能力为某些稀有微生物种群所保留。稀有物种可能是提供了催化复杂降解过程所需的基因库,即污染物通常是由原始样品中低于检测限的物种完成降解<sup>[71]</sup>。这种解释得到了 Fuentes 等<sup>[72]</sup>的验证,其研究土壤微生物群落在石油烃污染及不同生物修复处理下短期动态变化过程中发现,试验中受柴油污染的土壤中都观察到一种天然的  $\gamma$ -蛋白杆菌迅速而显著增长的情况,该操作分类单元在试验初期相对丰度仅占 0.1%,但在 6 周后竟高达 60% 以上。这种从稀有到丰富的丰度的转变,说明了稀有微生物群落在面对环境干扰时的潜在作用。

#### 4.5 保障机体/环境健康

小麦根际致病菌铜绿假单胞菌的入侵会随着微生物多样性的降低而增加,入侵程度与微生物多样性成反比<sup>[73]</sup>,高多样性的土壤微生物群落是防止李斯特菌入侵的生物屏障<sup>[74]</sup>。Gera Hol 等<sup>[75]</sup>在量化稀有种群在生态系统中作用的过程中发现,土壤稀有

微生物群落能够增加植物的防御能力,在作物保护中发挥作用。低丰度菌群在植物根际代谢活跃,是植物根际细菌群落组成的主要驱动因子<sup>[76]</sup>,在一定程度上稀有菌群有助于植物叶面积和根长等性状的表达<sup>[77]</sup>;稀有物种的丧失会影响植物的生产力<sup>[78]</sup>。综上所述,稀有微生物群落在控制有害微生物的入侵、保障机体/环境健康等方面起到了至关重要的作用<sup>[79,80]</sup>,分析原因可能是由于其占据了关键生态位,减缓了入侵物种群落的建立<sup>[81]</sup>。

## 5 总结和展望

近年来,稀有微生物群落的生态学意义和潜在的进化学意义受到越来越多的关注,以下几方面问题亟需解决。①稀有微生物群落在分类上存在盲点,识别和解决这些盲点将有助于发现新的系统发育谱系。②随着测试手段的不断创新,数以百万甚至千万的低丰度序列会被发现,测试结果中大部分 OTUs 属于稀有微生物部分,且很大一部分基因序列未被分类。如何科学有效地处理和分析这些数据,这些基因序列对应着怎样的功能,如何使这些基因序列为人类所用,都值得研究。③不同环境中稀有微生物种群究竟以怎样的存在方式发挥作用,是否存在功能上的冗余;对于全球气候的变化稀有微生物群落又起到怎样的作用。现阶段人类可能只触及稀有微生物的表面,稀有微生物很可能包含比迄今为止所发现的更多的多样性。因此,有关稀有微生物的分类学、基因组学和生态学还需进一步探究。

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