

鲍婧婷,孙靖尧,王进.生物土壤结皮中微生物群落特征综述[J].中国沙漠,2022,42(6):33-43.

生物土壤结皮中微生物群落特征综述

鲍婧婷^{1,2,3},孙靖尧³,王进³

(1.西安文理学院 生物与环境工程学院,陕西 西安 710065; 2.兰州理工大学 生命科学与工程学院,甘肃 兰州 730050; 3.中国科学院西北生态环境资源研究院 沙坡头沙漠研究试验站,甘肃 兰州 730000)

摘要:生物土壤结皮(也称生物结皮)是联结荒漠区地表生物成分与非生物成分的纽带,它不仅是荒漠区生物多样性的“热点”,也是退化生态系统修复的“工程师”。生物结皮的拓殖不仅能稳定地表,影响土壤水文过程,对土壤形成起着重要作用,还对荒漠区土壤碳氮循环等产生重要影响。蓝藻、细菌、真菌和古菌等微生物在生物结皮形成和发挥生态功能过程中发挥重要作用。本文系统总结了全球寒漠、冷漠和热漠生物结皮中微生物的组成和群落特征,厘清了主要生物气候区不同演替阶段的生物结皮中主要微生物物种,对相关微生物的研究进展和存在问题进行了分析,最后从微生物相互作用角度为明确关键枢纽微生物种提出了建议,以期对筛选潜在高效固沙菌种、培育人工结皮促进受损生态系统恢复提供参考。

关键词:生物气候区;生物土壤结皮;微生物群落特征;全球变化

文章编号: 1000-694X(2022)06-033-11

DOI: 10.7522/j.issn.1000-694X.2021.00137

中图分类号: Q938.1

文献标志码: A

0 引言

生物土壤结皮(也称生物结皮, biological soil crusts, BSC)是由生活在土壤表层中的蓝藻(蓝细菌)、细菌、古菌、微真菌、微藻、地衣和藓类等利用菌丝体、假根和分泌物“胶结”形成的团聚结构^[1-3]。从能量来源和营养方式划分, BSC群落生物体的组成主要包括自养生物体(autotrophic organism)和异养生物体(heterotrophic organism)。蓝藻、绿藻、硅藻、地衣和苔藓等是BSC中的初级生产者,它们是BSC群落生产力的主要贡献者,属于BSC中的自养生物;而在BSC中起分解和代谢作用的细菌、微小真菌、原生生物(protist)和无脊椎动物(invertebrate)等属于BSC中的异养生物^[4]。

在不利于维管束植物生长的干旱区、半干旱区、极地和高山环境,以及植被盖度暂时或永久性减少的温带地区, BSC是当地常见的地表景观^[5],据模型评估, BSC覆盖了陆地面积的12%左右^[6]。BSC不仅是生物多样性的“热点”,也是退化生态系统修复的“工程师”^[7-8],在干旱半干旱生态系统中发

挥关键作用,它能够通过产生土壤团聚体保护土壤免受侵蚀、影响土壤水文过程、固定大气中的碳和氮增强土壤肥力等,因此BSC与全球生态健康息息相关^[9-10]。

根据BSC发展过程中主要优势隐花植物的替代特点,其演替可以明显区分为3个结皮类型阶段。先锋种阶段或演替的初级阶段,主要优势种是蓝藻;其次是能够抵抗较大干扰的演替阶段,主要表现为蓝藻-地衣混合结皮和地衣结皮;最后为演替的后期或相对稳定阶段,地衣-藓混合结皮,在降水较多或局部湿度相对较高的地区则形成以苔藓为优势的结皮类型^[4, 11-13]。微生物是BSC中的主要生物组成部分,也是BSC发挥生态功能的重要生物载体,其重要性日益得到重视,近年来在不同生物气候区如寒漠(cold desert,通常位于高纬度地区,年平均气温接近于零度的沙漠)、冷漠(cool desert,通常位于中高纬度地区,年平均气温低于18℃的沙漠)和热漠(hot desert,通常位于中低纬度地区,年平均气温高于18℃,夏季炎热,白天温度经常超过

收稿日期:2021-09-04; 改回日期:2021-10-29

资助项目:国家自然科学基金项目(41661016,41201250);兰州市科技计划项目(2021-1-22)

作者简介:鲍婧婷(1980—),女,甘肃兰州人,博士,主要从事恢复生态学研究。E-mail: jingtingbao@126.com

通信作者:王进(E-mail: wangjin@lzb.ac.cn)

30 °C, 冬季气候温和, 降雨集中于夏季的沙漠, 三大类型的沙漠划分主要见网页 www.britannica.com) 等荒漠生态系统广泛开展了不同演替阶段的 BSC 中微生物组成和群落结构研究, 本文对各大生物气候区 BSC 中的蓝藻、细菌和真菌的组成特征进行了系统总结, 将有助于厘清主要生物气候区不同演替阶段 BSC 中的主要微生物物种, 对我们筛选潜在高效固沙菌种、培育人工结皮促进受损生态系统恢复具有重要的实践指导意义。

1 蓝藻

蓝藻是 BSC 中已知的最古老的光合自养组分, 26 亿年前的 BSC 化石土壤结构表明, 它很可能是由蓝藻组成的^[5]。近年来关于 BSC 蓝藻的研究在寒漠集中在美洲科罗拉多高原 (the Colorado Plateau) 的寒冷沙漠地区 (犹他州南部、亚利桑那州北部和科罗拉多州西部) 和极地 (Arctic) 地区等^[14-15]。冷漠的研究集中于亚洲的古尔班通古特沙漠 (Gurbantunggut Desert)、腾格里沙漠 (Tenger Desert) 和克孜勒库姆沙漠 (Kyzyl kum Desert), 西欧的塔韦纳斯沙漠 (Tabernas Desert) 等^[16-18]。对热漠的研究集中于美洲的奇瓦瓦沙漠 (Chihuahuan Desert), 南美洲的阿塔卡马沙漠 (Atacama Desert) 和蒙特沙漠 (Monte Desert)、以色列的内盖夫沙漠 (Negev Desert)、非洲的纳米布沙漠 (Namib Desert) 等^[19-23]。

从功能的角度来看, BSC 中的蓝藻可分为三类: ①丝状蓝藻, 如微鞘藻属 (*Microcoleus*), 细胞外多糖基质可将土壤颗粒粘在一起稳定土壤, 从而形成土壤团聚体, 这些蓝藻不仅负责 BSC 的形成, 也是 BSC 中最丰富的蓝藻种类, 丝状蓝藻是 BSC 能够在不稳定环境中定居所必需的, 并在生物稳定过程中成功地起到先锋作用; ②倾向于生活在 BSC 中的蓝藻, 这些蓝藻通过它们对 C 和 N 循环的贡献来增强 BSC 的生态作用。如单细胞的 *Chroococcidiopsis*、丝状 *Scytonema* 和 *Stigonema*; ③仅随机出现在 BSC 中的蓝藻, 这些蓝藻可能起源于水生环境或地衣共生体等其他生境, 如 *Chroococcus*、*Gleocapsa*、*Gleocapsopsis*、*Cylindrospermum*、*Phormidium*、*Tolypothrix* 属等^[5]。

目前已经在 BSC 中鉴定出了 70 个属 320 种蓝藻, 但是仅有少数蓝藻参与 BSC 形成, 参与 BSC 形成的蓝藻主要有具鞘微鞘藻 (*Microcoleus*)、念珠藻 (*Nostoc*)、伪枝藻 (*Scytonema*) 和真枝藻 (*Stigonema*)

等^[5]。在全球范围内, *Microcoleus* 属是绝大多数干旱半干旱地区 BSC 中的优势种^[5,17], 研究发现 *Microcoleus* 属的两个常见种 *M. vaginatus* 和 *M. steenstrupii* 对温度具有不同的适应性, 在较冷的环境中 *M. vaginatus* 相对丰度较高, 而 *M. steenstrupii* 在更温暖的环境中占据优势^[24]。念珠藻目也在全球范围内广泛分布, 念珠藻目中的 *Scytonema* 和 *Nostoc* 属和颤藻目中的 *Phormidium* sp. 广泛报道于水分受制约的干旱和半干旱区^[18]。在西欧和极地的生物结皮中, *Leptolyngbyaceae* 科占优势^[15,18], 色球藻目 (*Chroococcales*) 中的 *Chroococcus* sp. 和 *Cyanothece* sp. 常见于寒漠 BSC 中, 如极地 BSC, 科罗拉多高原的寒漠和大盆地沙漠^[25-26], 不同蓝藻对水分的响应也有明显的不同, 如 Fernandes 等^[19] 研究发现, *Scytonema* sp. 对降水最敏感, 而 *M. vaginatus* 对干旱的适应能力更强, 优势种蓝藻在不同气候区及各个演替阶段 BSC 中的主要分布情况见表 1。

2 细菌

目前, 在全球范围内对 BSC 中细菌群落组成结构开展了广泛研究, 如在科罗拉多高原、极地、奇瓦瓦沙漠、阿曼苏丹国沙漠、非洲的卡鲁沙漠 (Karoo Desert)、莫哈韦沙漠 (Mojave Desert)、索诺拉沙漠、塔韦纳斯沙漠、黄土高原、古尔班通古特沙漠和腾格里沙漠等地区。在全球尺度上, 放线菌门 (*Actinobacteria*)、蓝细菌门 (*Cyanobacteria*)、变形菌门 (*Proteobacteria*)、厚壁菌门 (*Firmicutes*)、绿弯菌门 (*Chloroflexi*)、拟杆菌门 (*Bacteroidetes*)、酸杆菌门 (*Acidobacteria*)、疣微菌门 (*Verrucomicrobia*)、芽单胞菌门 (*Gemmatimonadetes*)、浮霉菌门 (*Planctomycetes*)、装甲菌门 (*Armatimonadetes*) 和异常球菌-栖热菌门 (*Deinococcus-Thermus*) 被证实为 BSC 细菌群落中的常见菌门^[27-33]。

在蓝藻结皮中往往以蓝藻占据绝对优势, 变形杆菌门、放线菌门和酸杆菌门是最常见的细菌^[14], 以地衣为主的 BSC 细菌群落中, 变形杆菌门、放线菌门和拟杆菌门为主要的优势种, 如西班牙塔韦纳斯沙漠^[31], 但是 Nagy 等^[27]、Gundlapally 等^[14] 分别在索诺拉沙漠和科罗拉多高原的研究中发现, Alpha 变形杆菌 (*Alpha-Proteobacteria*) 和放线菌是优势菌门, Alpha 变形杆菌中的 *Sphingomonadales* 目和 *Rhizobiales* 目是最主要的优势种。而在苔藓占优势的结皮细菌群落中, 拟杆菌门、酸杆菌门和变形杆菌

表 1 不同生物气候区 BSC 中蓝藻优势种分布概况 (表格中“—”代表目前未见报道)

Table 1 The distribution of dominant cyanobacteria in biocrusts of different bioclimatic regions ("—" in the table represents no report at present)

演替阶段	气候区		
	寒漠	冷漠	热漠
藻结皮	<i>Microcoleus vaginatus</i> 和 <i>M. steenstrupii</i> (科罗拉多高原的寒漠, 犹他州) ^[14] Synechococcales (<i>Leptolyngbya antarctica</i>) Oscillatoriales, Nostocales, Gloeobacterales, Chroococcidiopsidales (北极的 <i>Petunia</i> 湾) ^[15]	<i>Microcoleus vaginatus</i> , <i>Microcoleus steenstrupii</i> , <i>Chroococcidiopsis</i> , <i>Nostoc</i> , <i>Scytonema</i> (古尔班通古特沙漠) ^[16] <i>Microcoleus</i> , <i>Mastigocladopsis</i> , <i>Wilmottia</i> , <i>Chroococcidiopsis</i> (腾格里沙漠) ^[17] <i>Microcoleus</i> , <i>Tolypothrix</i> , <i>Wilmottia</i> , <i>Scytonema</i> (克孜勒库姆沙漠) ^[17] <i>Microcoleus</i> , <i>Vaginatus</i> , <i>Chroococcidiopsis</i> , <i>M. steenstrupii</i> , <i>Leptolyngbya</i> , <i>Scytonema</i> , <i>Tolypothrix</i> 和 <i>Nostoc</i> (东伊比利亚半岛) ^[10]	<i>Microcoleus vaginatus</i> , <i>M. steenstrupii</i> , <i>Leptolyngbya</i> spp. 和 <i>Phormidium</i> spp. (浅色结皮); <i>M. vaginatus</i> , <i>M. steenstrupii</i> , <i>Nostoc</i> spp. 和 <i>Scytonema</i> spp. (深色结皮) (奇瓦瓦沙漠) ^[19] ; <i>Chroococcidiopsis</i> sp., <i>Pseudanabaena</i> spp., <i>Phormidium</i> spp., <i>Leptolyngbya</i> spp., <i>Microcoleus paludosus</i> , 和 <i>Nostoc</i> spp. (纳米布沙漠) ^[20] ; Synechococcophycidae, Oscillatorio- phycidae, Nostocophycidae (阿塔卡马沙漠) ^[22] ; <i>Microcoleus</i> like, <i>Leptolyngbya</i> , <i>Chroococcidiopsis</i> , <i>Nostoc</i> , <i>Scytonema</i> , <i>Trichocoleus</i> (内盖夫沙漠) ^[21]
地衣结皮	Synechococcales, Oscillatoriales (<i>Phormidium</i> sp.), Nostocales, Chroococcidiopsidales, Gloeobacterales, Chroococcales (北极的 <i>Petunia</i> 湾) ^[15]	<i>Microcoleus vaginatus</i> , <i>Microcoleus steenstrupii</i> , <i>Chroococcidiopsis</i> , <i>Nostoc</i> , <i>Scytonema</i> (古尔班通古特沙漠) ^[16]	Oscillatoriales (<i>Microcoleus</i> , <i>Lyngbya</i> , <i>Phormidium</i> , <i>Oscillatoria</i>) 和 Nostocales (<i>Nostoc</i> , <i>Scytonema</i> , <i>Tolypothrix</i>) (蒙特沙漠) ^[23]
藻-地衣结皮	Synechococcales (<i>Leptolyngbya</i> sp. 和 <i>Leptolyngbya antarctica</i>), Oscillatoriales, Nostocales, Gloeobacterales, Chroococcidiopsidales (北极的 <i>Petunia</i> 湾) ^[15]	<i>Microcoleus vaginatus</i> , <i>Microcoleus steenstrupii</i> , <i>Chroococcidiopsis</i> , <i>Nostoc</i> , <i>Scytonema</i> (古尔班通古特沙漠) ^[16]	<i>Scytonema</i> 和 <i>Microcoleus steenstrupii</i> (索诺拉沙漠) ^[27] ; <i>Chroococcidiopsis</i> , <i>Pseudoanabaena</i> , <i>Phormidium</i> , <i>Leptolyngbya</i> , <i>Microcoleus</i> 和 <i>Nostoc</i> (非洲的卡鲁沙漠) ^[23]
地衣-藓结皮	<i>Pseudanabaenaceae</i> (filamentous species without heterocytes) 和 <i>Nostoc</i> (heterocytous) (北极苔原土壤) ^[28]	Nostocales (<i>Scytonema</i> and <i>Nostoc</i>) 和 <i>Pseudanabaenaceae</i> (西班牙塔韦纳斯沙漠) ^[18] ; <i>Microcoleus vaginatus</i> , <i>Microcoleus steenstrupii</i> , <i>Chroococcidiopsis</i> 和 <i>Scytonema</i> (古尔班通古特沙漠) ^[16] ; <i>Microcoleus</i> , <i>Mastigocladopsis</i> , <i>Wilmottia</i> , uncultured_Nostocales, uncultured_Coleofasciculaceae, <i>Nostoc</i> (腾格里沙漠) ^[17] ; <i>Microcoleus</i> , <i>Mastigocladopsis</i> , <i>Tolypothrix</i> , <i>Wilmottia</i> , <i>Phormidium</i> , uncultured_Nostocales (克孜勒库姆沙漠) ^[17]	—
藓结皮	—	<i>Microcoleus</i> , <i>Mastigocladopsis</i> , <i>Wilmottia</i> , uncultured_Coleofasciculaceae, uncultured_Nostocales, <i>Nostoc</i> (腾格里沙漠) ^[17] <i>Microcoleus</i> , <i>Wilmottia</i> , <i>Mastigocladopsis</i> , <i>Tolypothrix</i> , uncultured_Nostocales, uncultured_Coleofasciculaceae (克孜勒库姆沙漠) ^[17]	—

门为主要的优势种^[34]。

然而,由于地理位置、地貌、气候因素和土壤特性等的影响,上述细菌群落中优势种的分布特征及相对丰度存在较大差异,比如在非洲的纳米布沙漠的卡哈尼沙丘(Kahani dune)开展的研究发现,栖息地过滤(habitat-filtration)是影响沙丘细菌群落组成的决定因素,在变形杆菌占优势的沙丘样品(即顶部、斜坡和底部)中,变形杆菌相对丰度从42%升至49%,而在沙丘间生境中,放线菌相对丰度占51%。绿弯菌门、厚壁菌门、 α 、 γ 和 δ 变形杆菌的相对丰度从沙丘顶部到沙丘间呈现出减少趋势,而酸杆菌门和 β -变形杆菌则呈现升高的趋势^[35]。而在腾格里荒漠不同演替序列的BSC中^[36],厚壁菌门在无BSC的荒漠表层土壤中相对丰度最高,随着BSC的演替,其相对丰度逐渐下降。蓝细菌门在藻类结皮中相对丰度最高,BSC演替过程中逐渐下降。除此之外,放线菌门、变形菌门、绿弯菌门、酸杆菌门、芽单胞菌门、拟杆菌门、浮霉菌门、疣微菌门和奇异球菌-栖热菌门随着BSC的演替,它们的相对丰度逐渐增加^[37-38]。值得注意的是,即使是同一地区同一类型的结皮中,比如不同种的地衣结皮中细菌组成可能也会有很大的不同^[39]。

细菌群落在BSC碳氮循环过程中发挥重要作用,例如,Zhao等^[40]在腾格里沙漠东南缘BSC中的研究发现细菌群落的碳循环功能基因是BSC碳循环功能基因的主要组成(占总丰度的84.78%),说明参与碳循环的相关功能基因主要来源于细菌群落,而且,细菌氮循环功能基因占BSC氮循环功能基因总丰度的95.12%,表明BSC微生物氮循环主要是细菌群落在发挥功能^[41]。在腾格里沙漠东南缘的研究还发现蓝细菌门为BSC中的优势固氮微生物^[42],而在美国科罗拉多高原寒漠BSC中变形杆菌为固氮作用的优势菌门,氨氧化细菌为氨氧化作用的主要物种^[43],变形杆菌也是阿曼苏丹国热漠藻结皮和地衣结皮中氨氧化作用的主要物种^[44]。此外,BSC细菌群落的组成结构与土壤黏粉粒和养分含量呈正相关关系,与土壤pH值呈负相关关系,说明细菌群落可能影响着BSC系统的稳定性^[36]。优势种细菌在全球不同气候区及BSC中各个演替阶段的主要分布见表2^[14,27,29,31-34,39,45-54]。

3 真菌

BSC中的真菌分为非共生的真菌(free-living

fungi)和共生的真菌,BSC为非共生的真菌提供了适宜的生态位,它们能经受干燥胁迫,在干旱地区,这些真菌在介导BSC和植物之间的养分交换中起着关键作用,这被称为真菌环假说^[55]。而共生的真菌如地衣真菌包括生活在地衣内或地衣上的所有物种,截至目前已发现大约1800种地衣真菌。大多数地衣真菌对寄主(即地衣化真菌物种)具有高度的特异性,它们通过局部菌丝定殖,最终形成有性结构。共生的地衣型真菌主要分布于子囊菌门(Ascomycota)^[56]、子囊菌门的石果衣属(*Endocarpon*)、瓶口衣属(*Verrucaria*)和饼干衣属(*Rinodina*)为全球地衣型真菌的优势属,地衣型真菌在全球的分布是高度变异的,干旱度、土壤pH值和植被覆盖度是影响其全球分布的最重要因素^[57-59],但是也有研究表明,少量的凋落物可能通过缓冲环境压力(如干旱和高温)对地衣型真菌有利,而且植物覆盖也在维持土壤稳定性和肥力方面发挥作用,从而对地衣型真菌的分布和发展具有积极影响^[7,58]。

迄今为止,BSC中的真菌主要分布于子囊菌门(Ascomycota)、担子菌门(Basidiomycota)、接合菌门(Zygomycota)、毛霉门(Mucoromycota)和壶菌门(Chytridiomycota)5个真菌门^[37,50,60],其中子囊菌门是BSC中的主要优势真菌门,而毛霉门和壶菌门在BSC中相对丰度非常低,在空间尺度上变化较明显。Ascomycota门中常见纲及目包括Dothideomycetes纲(Botryosphaerales、Capnodiales、Dothideales、Pleosporales目),Eurotiomycetes纲(Chaetothyriales、Eurotiales、Onygenales、Verrucariales目),Lecanoromycetes纲(Lecanorales目),Leotiomycetes纲(Helotiales、Rhytismatales、Thelebolales目),Pezizomycetes纲(Pezizales目),Saccharomycetes纲(Saccharomycetales目)和Sordariomycetes纲(Coniochaetales、Hypocreales、Microascales、Sordariales、Trichosphaeriales目),子囊菌门中的Dothideomycetes, Eurotiomycetes和Lecanoromycetes在全球BSC中都是优势真菌纲^[27,33,37,60-66]。

真菌多样性随BSC的年龄和类型而变化,在演替后期,真菌多样性高于演替早期结皮^[61],如在腾格里荒漠BSC中发现真菌群落超过275个属,分属3个门,包括子囊菌门、担子菌门和壶菌门,而且BSC真菌群落组成结构随地理位置和季节的改变明显不同。BSC演替过程中,真菌群落在门水平上

表 2 不同生物气候区 BSC 中细菌优势种分布概况 (表格中“—”代表目前未见报道)

Table 2 The distribution of dominant bacteria in biocrusts of different bioclimatic regions ("—" in the table represents no report at present)

演替阶段	气候区		
	寒漠	冷漠	热漠
藻结藻结皮	Actinobacteria, β -Proteobacteria, Bacteroidetes, Low-GC Gram-positives (<i>Bacilli</i>), α -Proteobacteria, Acidobacteria 和 Thermomicrobiales (科罗拉多高原的寒漠, 犹他州) ^[14]	Actinobacteria, Proteobacteria, Firmicutes, Chloroflexi, Acidobacteria, Cyanobacteria, Gemmatimonadetes, Bacteroidetes (腾格里沙漠) ^[45] ; Cyanobacteria, Bacteroidetes, Proteobacteria, unclassified bacteria, Actinobacteria (古尔班通古特沙漠) ^[46] ; <i>Leptolyngbya</i> (Cyanobacteria), <i>Rubrobacter</i> , <i>Solirubrobacter</i> , <i>Geodermatophilus</i> (Actinomycetes) (塔韦纳斯沙漠) ^[39]	Rhizobiales (phylum Proteobacteria), Chroococcales, Nostocophycidae (Cyanobacteria) (西澳) ^[47] ; Cyanobacteria, Alphaproteobacteria, Bacteroidetes, Chloroflexi, Actinobacteria, Acidobacteria (阿曼) ^[29] ; Cyanobacteria, Proteobacteria, Bacteroidetes, Acidobacteria (莫哈韦沙漠) ^[48]
地衣结皮	Actinobacteria, Proteobacteria, Acidobacteria, Firmicutes, Armatimonadetes Cyanobacteria, Bacteroidetes 和 Planctomycetes (南极洲大陆维多利亚岛) ^[49]	Proteobacteria, Actinobacteria, Chloroflexi, Cyanobacteria, Bacteroidetes, Planctomycetes, Acidobacteria, Armatimonadetes (腾格里沙漠) ^[50] ; Cyanobacteria, Proteobacteria, Bacteroidetes, unclassified bacteria, Acidobacteria, Actinobacteria, Verrucomicrobia (古尔班通古特沙漠) ^[46] ; Proteobacteria, Actinobacteria, Bacteroidetes, Acidobacteria, Cyanobacteria and Verrucomicrobia (西班牙塔韦纳斯沙漠) ^[31]	Acidobacteriales (phylum Acidobacteria), Rhodospirillales (Proteobacteria), Actinomycetales (Actinobacteria) 和 unclassified Proteobacteria (西澳) ^[47] ; Cyanobacteria, Bacteroidetes, Acidobacteria, Alphaproteobacteria, Actinobacteria, Chloroflexi (阿曼) ^[29]
藻-地衣结皮	—	Nostocales, Chroococcidiopsaceae, Coleofasciculaceae (Cyanobacteria) (塔韦纳斯沙漠) ^[39]	Cyanobacteria (<i>Scytonema</i> and <i>Microcoleus steenstrupii</i>), Proteobacteria (β -Proteobacteria), Actinobacteria, Bacteroidetes, 和 Chloroflexi (索诺拉沙漠) ^[27] ; Cyanobacteria, Proteobacteria, Bacteroidetes, Chloroflexi, Armatimonadetes (莫哈韦沙漠) ^[48] ; Bacteroidetes, Proteobacteria, Actinobacteria, Cyanobacteria, Acidobacteria, Chloroflexi, Verrucomicrobia 和 Planctomycetes (非洲的卡鲁沙漠) ^[32]
地衣-藓结皮	Cyanobacteria, Bacteroidetes, Proteobacteria, Actinobacteria, Chloroflexi, Acidobacteria (美国峡谷国家公园) ^[51] ; Actinobacteria, Bacteroidetes, Proteobacteria, Cyanobacteria, Firmicutes, Verrucomicrobia, Acidobacteria, Chloroflexi (美国西部山间寒漠) ^[52] ; Cyanobacteria, Actinobacteria, Bacteroidetes, Chloroflexi 和 Proteobacteria (科罗拉多高原的寒漠) ^[53]	Actinobacteria, Proteobacteria, Chloroflexi, Cyanobacteria, Acidobacteria, Firmicutes, Bacteroidetes (腾格里沙漠) ^[45]	Cyanobacteria, Proteobacteria, Bacteroidetes, Actinobacteria 和 Acidobacteria (奇瓦瓦沙漠的 Actopan 和 Atexcac 地区) ^[54]
藓结皮	—	Proteobacteria, Bacteroidetes, unclassified bacteria, Actinobacteria, Cyanobacteria, Acidobacteria, Verrucomicrobia (古尔班通古特沙漠) ^[46] ; Bacteroidetes, Acidobacteria 和 Proteobacteria (新墨西哥桑迪亚山脉) ^[34] ; Acidobacteria, Proteobacteria, Chloroflexi, Actinobacteria (黄土高原) ^[33]	Proteobacteria, Actinobacteria, Acidobacteria, Chloroflexi, Bacteroidetes, Cyanobacteria, Deinococcus-Thermus, Planctomycetes (莫哈韦沙漠) ^[48] ; Bacteroidetes, Proteobacteria, Actinobacteria, Cyanobacteria, Acidobacteria, Chloroflexi, Verrucomicrobia 和 Planctomycetes (非洲卡鲁沙漠) ^[32]

的物种组成变化不显著,裸地中壶菌门相对丰度较低,BSC中子囊菌门的相对丰度最高,不同演替阶段均超过60%。真菌丰富度在BSC演替过程中持续增加,群落 α 多样性分析和核糖体RNA的ITS区定量PCR结果显示其物种多样性和生物量均随BSC演替阶段的推进而持续增加^[36];而在阿曼苏丹国沙区,Abed等^[29]对BSC真菌群落物种组成的研究表明,大部分真菌序列属于子囊菌门、担子菌门和壶菌门,且子囊菌门的相对丰度在裸地和BSC中无

显著差异,而壶菌门的相对丰度在裸地中比在BSC中更为普遍。迄今为止,除了在阿曼苏丹国和奇瓦瓦沙漠发现少量的壶菌门类群外,其他地区对于BSC真菌群落组成结构的研究均未发现该物种,表明在BSC真菌群落中,壶菌门可能并不具有全球范围的普遍优势性,其在裸地中的优势表明其在BSC发育早期阶段对极端环境具有强耐受性^[67]。真菌在全球不同气候区及BSC中各个演替阶段的主要分布见表3。

表3 不同生物气候区BSC中真菌优势种分布概况(表格中“—”代表目前未见报道)

Table 3 The distribution of dominant fungi in biocrusts of different bioclimatic regions (“—” in the table represents no report at present)

演替阶段	气候区		
	寒漠	冷漠	热漠
藻结皮	Ascomycota, Sordariomycetes, Pezizomycetes 和 Basidiomycota (科罗拉多高原的寒漠, 犹他州) ^[61-62]	Ascomycota, unclassified_Fungi, Basidiomycota, Chytridiomycota 和 Zygomycota (腾格里沙漠) ^[45] ; Dothideomycetes, Eurotiomycetes, Lecanoromycetes (古尔班通古特沙漠) ^[37]	Ascomycota (Dothideomycetes, Eurotiomycetes), Basidiomycota 和 Chytridiomycota (阿曼) ^[29,68] ; Ascomycota (莫哈韦沙漠) ^[48]
地衣结皮	Ascomycota, Pezizomycetes, Basidiomycota, Sordariomycetes, Tremellomycetes 和 Leotiomycetes (科罗拉多高原的寒漠, 犹他州) ^[61]	Ascomycota, no_rank_Fungi, unclassified_Fungi, Basidiomycota, Chytridiomycota 和 Zygomycota (腾格里沙漠) ^[50] ; Eurotiomycetes, Lecanoromycetes 和 unidentified Ascomycota (古尔班通古特沙漠) ^[37]	Ascomycota (Dothideomycetes, Eurotiomycetes), Basidiomycota 和 Chytridiomycota (阿曼) ^[29,68] ; Ascomycota, Pezizomycetes, Basidiomycota 和 Eurotiomycetes (奇瓦瓦沙漠) ^[61] ; Sordariomycetes, Ascomycota, Lichinomycetes, Pezizomycetes 和 Basidiomycota (索诺拉沙漠) ^[61]
藻-地衣结皮	—	—	Ascomycota, Sordariomycetes, Pezizomycetes 和 Eurotiomycetes (奇瓦瓦沙漠) ^[61]
藓结皮	—	Ascomycota, Basidiomycota, unclassified_Fungi, Chytridiomycota 和 Zygomycota (腾格里沙漠) ^[45] ; <i>Penicillium</i> 和 <i>Alternaria</i> (可培养真菌), Unidentified Ascomycota, Eurotiomycetes 和 Dothideomycetes (不可培养真菌) (古尔班通古特沙漠) ^[37,69] ; Ascomycota 和 Basidiomycota (黄土高原) ^[33]	Ascomycota (莫哈韦沙漠) ^[48]

4 古菌

古菌是地球上最古老的生命体,由于能够适应各种极端环境条件(如高酸、高热、高盐 and 高压等)而存活下来^[70]。目前,BSC微生物群落中对细菌和真菌的研究较多,对古菌群落组成结构及其影响因素的相关研究较少,近几年才有涉及。现有研究仅证实了泉古菌门(Crenarchaeota)在毛乌素沙地、塔韦纳斯沙漠和北美干旱区BSC古菌群落组成结构

中的优势性^[31,66,71],以及奇古菌门(Thaumarchaeota)在浑善达克沙地和腾格里沙漠BSC古菌群落组成结构中的优势性^[41,72]。

关于古菌群落组成结构影响因素的研究目前还没有达成共识,Soule等^[71]和赵宇龙^[66]的研究表明BSC古菌群落在不同BSC类型、地理位置和季节中保持相对稳定;而杜颖等^[72]的研究表明古菌群落的组成结构随季节变化而发生较大的改变。除此之外,BSC古菌群落的组成结构还与土壤碳氮输入和

土壤碳氮比密切相关^[41,60],在腾格里沙漠开展的研究表明,BSC古菌群落组成结构单一,仅有奇古菌门、广古菌门(Euryarchaeota)和另一个暂时无法确定命名的门。古菌群落的演替趋势明显,随着BSC的发育,三者中奇古菌和广古菌的相对丰度逐渐下

降,而不确定门的相对丰度逐渐增加,古菌群落的丰富度和古菌16S rRNA基因的拷贝数在BSC演替初期增加,5—7年后逐渐下降,BSC演替后期古菌数量显著减少^[36,41]。古菌在全球不同气候区及BSC中各个演替阶段的主要分布见表4。

表4 不同生物气候区BSC中古菌优势种分布概况(表格中“—”代表目前未见报道)

Table 4 The distribution of dominant archaea in biocrusts of different bioclimatic regions (“—” in the table represents no report at present)

演替阶段	气候区		
	寒漠	冷漠	热漠
藻结皮	—	Thaumarchaeota, unclassified norank Archaea 和 Euryarchaeota (腾格里沙漠) ^[41] ; Thaumarchaeota (浑善达克沙地) ^[72]	Crenarchaeota (索诺拉沙漠和奇瓦瓦沙漠) ^[71]
藓结皮	—	Thaumarchaeota, unclassified norank Archaea 和 Euryarchaeota (腾格里沙漠) ^[41]	—
地衣结皮	—	Crenarchaeota (毛乌素沙地) ^[66] ; Crenarchaeota (西班牙塔韦纳斯沙漠) ^[31]	—

5 结论与展望

自养微生物和异养微生物都是生物结皮中的重要生物组成部分,真核微藻、地衣和藓类等是生物结皮中重要的光合组分^[4,73],生物结皮中的微小动物如原生动物和线虫等也是荒漠生态系统中重要的食物链组成部分^[74-75],但限于篇幅,本文仅对生物结皮中的蓝藻、细菌、真菌和古菌进行了总结。本文主要分析了全球范围内结皮层土壤样本,这使得我们能够在全球尺度上了解不同生物气候区生物结皮中微生物群落组成和分布特征,对科学筛选适合当地环境的潜在高效菌种、人工培育结皮进而恢复生境、促进生态系统再生具有重要的实践指导意义。例如,在中纬度荒漠腾格里沙漠和克孜勒库姆沙漠开展的对比研究表明,相比演替初期的蓝藻结皮,演替后期的藓类结皮和地衣-藓类混生结皮具有更高的碳底物含量,从而支持更高的蓝藻多样性,由于蓝藻是自养光合微生物,也是结皮中的先锋固沙种,可以为其他异养微生物提供光合碳底物,蓝藻丰度在演替初期结皮中显著高于演替后期的结皮,随着演替的推进,先锋种逐步减少也为其他微生物的繁殖提供了适宜的生态位。在群落组成上的研究表明,丝状无异形胞蓝藻 *Microcoleus vaginatus* 和 *Wilmottia* spp., 以及具异形胞的蓝藻 *Mastigocladopsis* sp. 和 *Chroococidiopsis* spp. 可能是两大温带沙漠结皮中的核心蓝藻种^[17],这将有助

于筛选容易生存的本地种进行接种,诱导形成人工结皮稳定沙面从而抵御沙区的风蚀危害。

事实上,土壤中的微生物往往不是孤立存在的,土壤微生物之间以及微生物与环境之间必然存在着相互作用,比如共生、拮抗或者寄生等相互关系。微生物间的相互关系往往是基于经典的平板对峙培养和共培养来确定的^[76-77],对难以培养的微生物群落间的相互作用常常通过构建微生物共生生态网络的方法来实现^[78],微生物共生生态网络分析能提供关键枢纽微生物种。因此,可以基于生态网络分析进一步明确生物结皮形成过程中的微生物关键种,指导人工培育结皮的防沙治沙实践工作。另外,尽管生物结皮中微生物群落结构和生态功能研究已经取得了很大的进展,然而到目前为止,大部分的相关研究都集中于结皮层微生物,不同类型结皮的下层土壤中微生物如何随着演替年限发生变化,尤其在全球变化背景下,例如降雨格局和温度变化导致微生物在土壤中的垂直分布变化对土壤碳氮循环等生态功能的潜在影响亟需开展深入研究。

参考文献:

- [1] West N E. Structure and function of microphytic soil crusts in wildland ecosystems of arid to semiarid regions [J]. *Advances in Ecological Research*, 1990, 20: 179-223.
- [2] Belnap J, Lange O L. *Biological Soil Crusts: Structure, Function, and Management* [M]. Berlin-Heidelberg, Germany:

- Springer-Verlag, 2003:461.
- [3] 李新荣,张元明,赵允格.生物土壤结皮研究:进展、前沿与展望[J].地球科学进展,2009,24:11-24.
- [4] 李新荣.荒漠生物土壤结皮生态与水文学研究[M].北京:高等教育出版社,2012.
- [5] Büdel B, Dulić T, Darienko T, et al. Cyanobacteria and algae of biological soil crusts[M]//Weber B, Büdel B, Belnap J. Biological Soil Crusts: An Organizing Principle in Drylands. Switzerland: Springer, 2016:55-80.
- [6] Rodriguez-Caballero E, Belnap J, Büdel B, et al. Dryland photoautotrophic soil surface communities endangered by global change[J]. Nature Geoscience, 2018, 11:185-189.
- [7] Belnap J, Weber B, Büdel B. Biological Soil Crusts as an Organizing Principle in Drylands[M]. Switzerland: Springer, 2016:3-13.
- [8] Bowker M A. Biological soil crust rehabilitation in theory and practice: an underexploited opportunity[J]. Restoration Ecology, 2007, 15:13-23.
- [9] Li X R, Tian F, Jia R L, et al. Do biological soil crusts determine vegetation changes in sandy deserts? Implication for managing artificial vegetation[J]. Hydrological Processes, 2010, 24:3621-3630.
- [10] Muñoz-Martín M Á, Becerra-Absalon I, Perona E, et al. Cyanobacterial biocrust diversity in Mediterranean ecosystems along a latitudinal and climatic gradient[J]. New Phytologist, 2019, 221:123-141.
- [11] Belnap J, Phillips S L, Miller M E. Response of desert biological soil crusts to alterations in precipitation frequency[J]. Oecologia, 2004, 141:306-316.
- [12] Lan S, Wu L, Zhang D, et al. Successional stages of biological soil crusts and their microstructure variability in Shapotou region (China) [J]. Environmental Earth Sciences, 2012, 65:77-88.
- [13] Viles H A. Understanding dryland and landscape dynamics: do biological crusts hold the key? [J] Geography Compass, 2008, 2:899-919.
- [14] Gundlapally S R, Garcia-Pichel F. The community and phylogenetic diversity of biological soil crusts in the Colorado Plateau studied by molecular fingerprinting and intensive cultivation [J]. Microbial Ecology, 2006, 52:345-357.
- [15] Pushkareva E, Pessi I S, Wilmotte A, et al. Cyanobacterial community composition in Arctic soil crusts at different stages of development[J]. FEMS Microbiology Ecology, 2015, 91:143.
- [16] Zhang B, Li R, Xiao P, et al. Cyanobacterial composition and spatial distribution based on pyrosequencing data in the Gurbantunggut Desert, Northwestern China [J]. Journal of Basic Microbiology, 2016, 56:308-320.
- [17] Wang J, Zhang P, Bao J T, et al. Comparison of cyanobacterial communities in temperate deserts: a cue for artificial inoculation of biological soil crusts[J]. Science of the Total Environment, 2020, 745:140970.
- [18] Williams L, Loewen-Schneider K, Maier S, et al. Cyanobacterial diversity of western European biological soil crusts along a latitudinal gradient[J]. FEMS Microbiology Ecology, 2016, 92:fiw157.
- [19] Fernandes V M C, de Lima N M M, Roush D, et al. Exposure to predicted precipitation patterns decreases population size and alters community structure of cyanobacteria in biological soil crusts from the Chihuahuan Desert[J]. Environmental Microbiology, 2018, 20:259-269.
- [20] Büdel B, Darienko T, Deuschewitz K, et al. Southern African biological soil crusts are ubiquitous and highly diverse in drylands, being restricted by rainfall frequency[J]. Microbial Ecology, 2009, 57:229-247.
- [21] Hagemann M, Henneberg M, Felde V J M N L, et al. Cyanobacterial diversity in biological soil crusts along a precipitation gradient, northwest Negev Desert, Israel [J]. Microbial Ecology, 2015, 70:219-230.
- [22] Patzelt D J, Hodač L, Friedl T. Biodiversity of soil cyanobacteria in the hyper-arid Atacama Desert, Chile [J]. Journal of Phycology, 2014, 50:698-710.
- [23] María E C V, Taboada M A, Aranibar J N. Diversity of cyanobacteria in biological soil crusts of Monte Central ecoregion (Mendoza, Argentina) [J]. Lilloa, 2018, 55:30-46.
- [24] Garcia-Pichel F, Loza V, Marusenko Y, et al. Temperature drives the continental-scale distribution of key microbes in topsoil communities[J]. Science, 2013, 340:1574-1577.
- [25] Rosentreter R, Belnap J. Biological soil crusts of North America [M]//Belnap J, Lange O L. Biological Soil Crusts: Structure, Function, and Management. New York, USA: Springer-Verlag, 2001:31-50.
- [26] Komárek J, Elster J, Komárek O. Diversity of the cyanobacterial microflora of the northern part of James Ross Island, NW Weddell Sea, Antarctica [J]. Polar Biology, 2008, 31:853-865.
- [27] Nagy M L, Pérez A, Garcia-Pichel F. The prokaryotic diversity of biological soil crusts in the Sonoran Desert (Organ Pipe Cactus National Monument, AZ) [J]. FEMS Microbiology Ecology, 2005, 54:233-245.
- [28] Komárek J, Kováčik L, Elster J, et al. Cyanobacterial diversity of Petuniabukta, Billefjorden, central Spitsbergen [J]. Polish Polar Research, 2012, 33:347-368.
- [29] Abed R M M, Tamm A, Hassenrueck C, et al. Habitat-dependent composition of bacterial and fungal communities in biological soil crusts from Oman [J]. Scientific Reports, 2019, 9:6468.
- [30] Fisher K, Jefferson J S, Vaishampayan P. Bacterial communities of Mojave desert biological soil crusts are shaped by dominant photoautotrophs and the presence of hypolithic niches [J]. Frontiers in Ecology and Evolution, 2020, 7:518.
- [31] Maier S, Schmidt T S B, Zheng L, et al. Analyses of dryland biological soil crusts highlight lichens as an important regulator of microbial communities [J]. Biodiversity and Conservation, 2014, 23:1735-1755.

- [32] Maier S, Tamm A, Wu D, et al. Photoautotrophic organisms control microbial abundance, diversity, and physiology in different types of biological soil crusts[J]. *The ISME Journal*, 2018, 12: 1032–1046.
- [33] Xiao B, Veste M. Moss-dominated biocrusts increase soil microbial abundance and community diversity and improve soil fertility in semi-arid climates on the Loess Plateau of China[J]. *Applied Soil Ecology*, 2017, 117–118: 165–177.
- [34] Moquin S A, Garcia J R, Brantley S L, et al. Bacterial diversity of bryophyte-dominant biological soil crusts and associated mites[J]. *Journal of Arid Environments*, 2012, 87: 110–117.
- [35] Ronca S, Ramond J B, Jones B E, et al. Namib Desert dune/interdune transects exhibit habitat-specific edaphic bacterial communities[J]. *Frontiers in Microbiology*, 2015, 6: 845.
- [36] 刘玉冰, 王增如, 高天鹏. 温带荒漠生物土壤结皮微生物群落结构与功能演替研究综述[J]. *微生物学通报*, 2020, 47(9): 2947–2983.
- [37] Zhang B, Zhang Y, Li X, et al. Successional changes of fungal communities along the biocrust development stages[J]. *Biology and Fertility of Soils*, 2018, 54: 285–294.
- [38] Liu L C, Liu Y B, Zhang P, et al. Development of bacterial communities in biological soil crusts along a revegetation chronosequence in the Tengger Desert, northwest China[J]. *Biogeosciences*, 2017, 14: 3801–3814.
- [39] Miralles I, Lázaro R, Sánchez-Marañón M, et al. Biocrust cover and successional stages influence soil bacterial composition and diversity in semiarid ecosystems[J]. *Science of the Total Environment*, 2020, 709: 134654.
- [40] Zhao L N, Liu Y B, Wang Z R, et al. Bacteria and fungi differentially contribute to carbon and nitrogen cycles during biological soil crust succession in arid ecosystems[J]. *Plant and Soil*, 2020, 447: 379–392.
- [41] Zhao L N, Liu Y B, Yuan S W, et al. Development of archaeal communities in biological soil crusts along a revegetation chronosequence in the Tengger Desert, north central China[J]. *Soil and Tillage Research*, 2020, 196: 104443.
- [42] Wang J, Bao J T, Li X R, et al. Molecular ecology of *nifH* genes and transcripts along a chronosequence in revegetated areas of the Tengger Desert[J]. *Microbial Ecology*, 2016, 71: 150–163.
- [43] Yeager C M, Kuske C R, Carney T D, et al. Response of biological soil crust diazotrophs to season, altered summer precipitation, and year-round increased temperature in an arid grassland of the Colorado Plateau, USA[J]. *Frontiers in Microbiology*, 2012, 3: 358.
- [44] Abed R M M, Lam P, de Beer D, et al. High rates of denitrification and nitrous oxide emission in arid biological soil crusts from the Sultanate of Oman[J]. *The ISME Journal*, 2013, 7: 1862–1875.
- [45] Liu L, Liu Y, Hui R, et al. Recovery of microbial community structure of biological soil crusts in successional stages of Shapotou desert revegetation, northwest China[J]. *Soil Biology and Biochemistry*, 2017, 107: 125–128.
- [46] Zhang B, Kong W, Wu N, et al. Bacterial diversity and community along the succession of biological soil crusts in the Gurbantunggut Desert, Northern China[J]. *Journal of Basic Microbiology*, 2016, 56: 670–679.
- [47] Moreira-Grez B, Tam K, Cross A T, et al. The bacterial microbiome associated with arid biocrusts and the biogeochemical influence of biocrusts upon the underlying soil[J]. *Frontiers in Microbiology*, 2019, 10: 2143.
- [48] Pombubpa N, Pietrasiak N, Ley P D, et al. Insights into dryland biocrust microbiome: geography, soil depth and crust type affect biocrust microbial communities and networks in Mojave Desert, USA[J]. *FEMS Microbiology Ecology*, 2020, 96: 125.
- [49] Coleine C, Stajich J E, Pombubpa N, et al. Altitude and fungal diversity influence the structure of Antarctic cryptoendolithic bacteria communities[J]. *Environmental Microbiology Reports*, 2019, 11: 718–726.
- [50] Wang J, Bao J, Su J, et al. Impact of inorganic nitrogen additions on microbes in biological soil crusts[J]. *Soil Biology and Biochemistry*, 2015, 88: 303–313.
- [51] Kuske C R, Yeager C M, Johnson S, et al. Response and resilience of soil biocrust bacterial communities to chronic physical disturbance in arid shrublands[J]. *The ISME Journal*, 2012, 6: 886–897.
- [52] Blay E S, Schwabedissen S G, Magnuson T S, et al. Variation in biological soil crust bacterial abundance and diversity as a function of climate in Cold Steppe ecosystems in the Intermountain West, USA[J]. *Microbial Ecology*, 2017, 74: 691–700.
- [53] Johnson S L, Kuske C R, Carney T D, et al. Increased temperature and altered summer precipitation have differential effects on biological soil crusts in a dryland ecosystem[J]. *Global Change Biology*, 2012, 18: 2583–2593.
- [54] Becerra-Absalón I, Muñoz-Martín M Á, Montejano G, et al. Differences in the cyanobacterial community composition of biocrusts from the drylands of Central Mexico. Are there endemic species?[J]. *Frontiers in Microbiology*, 2019, 10: 937.
- [55] Green L E, Porras-Alfaro A, Sinsabaugh R L. Translocation of nitrogen and carbon integrates biotic crust and grass production in desert grassland[J]. *Journal of Ecology*, 2008, 96: 1076–1085.
- [56] Egidí E, Delgado-Baquerizo M, Plett J M, et al. A few Ascomycota taxa dominate soil fungal communities worldwide[J]. *Nature Communications*, 2019, 10: 2369.
- [57] Liu Y R, Eldridge D J, Zeng X M, et al. Global diversity and ecological drivers of lichenised soil fungi[J]. *New Phytologist*, 2021, 231: 1210–1219.
- [58] Bowker M A, Belnap J, Büdel B, et al. Controls on distribution patterns of biological soil crusts at micro-to global scales[M]// Weber B, Büdel B, Belnap J. *Biological Soil Crusts: An Organizing Principle in Drylands*. Switzerland: Springer, 2016: 173–197.

- [59] Ding J, Eldridge D J. Biotic and abiotic effects on biocrust cover vary with microsite along an extensive aridity gradient [J]. *Plant and Soil*, 2010, 270: 429–441.
- [60] Bates S T, Nash T H I, Sweat K G, et al. Fungal communities of lichendominated biological soil crusts: diversity, relative microbial biomass, and their relationship to disturbance and crust cover [J]. *Journal of Arid Environments*, 2010, 74: 1192–1199.
- [61] Bates S T, Nash III T H, Garcia-Pichel F. Patterns of diversity for fungal assemblages of biological soil crusts from the southwestern United States [J]. *Mycologia*, 2012, 104: 353–361.
- [62] Bates S T, Garcia-Pichel F. A culture-independent study of free-living fungi in biological soil crusts of the Colorado Plateau: their diversity and relative contribution to microbial biomass [J]. *Environmental Microbiology*, 2009, 11: 56–67.
- [63] Steven B, Gallegos-Graves LV, Belnap J, et al. Dryland soil microbial communities display spatial biogeographic patterns associated with soil depth and soil parent material [J]. *FEMS Microbiology Ecology*, 2013, 86: 101–113.
- [64] Steven B, Lionard M, Kuske C R, et al. High bacterial diversity of biological soil crusts in water tracks over permafrost in the high Arctic Polar Desert [J]. *PloS One*, 2013, 8: e71489.
- [65] Wang Z, Liu Y, Zhao L, et al. Development of fungal community is a potential indicator for evaluating the stability of biological soil crusts in temperate desert revegetation [J]. *Applied Soil Ecology*, 2020, 147: 103404.
- [66] 赵宇龙. 内蒙古荒漠生物土壤结皮中微生物多样性分析 [D]. 呼和浩特: 内蒙古农业大学, 2011.
- [67] 赵丽娜. 沙坡头固沙植被区生物土壤结皮微生物群落演替及其对碳氮循环的调控 [D]. 北京: 中国科学院大学, 2020.
- [68] Abed R M M, Al-Sadi A M, Al-Shehi M, et al. Diversity of free-living and lichenized fungal communities in biological soil crusts of the Sultanate of Oman and their role in improving soil properties [J]. *Soil Biology and Biochemistry*, 2013, 57: 695–705.
- [69] 韩彩霞, 张丙昌, 张元明, 等. 古尔班通古特沙漠南缘苔藓结皮中可培养真菌的多样性 [J]. *中国沙漠*, 2016, 36(4): 1050–1055.
- [70] Offire P, Kerou M, Spang A, et al. Variability of the transporter gene complement in ammonia-oxidizing archaea [J]. *Trends in Microbiology*, 2014, 22: 665–675.
- [71] Soule T, Anderson I J, Johnson S L, et al. Archaeal populations in biological soil crusts from arid lands in North America [J]. *Soil Biology and Biochemistry*, 2009, 41: 2069–2074.
- [72] 杜颖, 赵宇龙, 赵吉睿, 等. 浑善达克沙地夏冬季浅色型生物土壤结皮中古菌的系统发育多样性 [J]. *微生物学通报*, 2014, 41(10): 1976–1984.
- [73] Concostrina-Zubiri L, Martínez I, Escudero A. Lichen-biocrust diversity in a fragmented dryland: fine scale factors are better predictors than landscape structure [J]. *Science of the Total Environment*, 2018, 628: 882–892.
- [74] Liu Y, Li X, Jia R, et al. Effects of biological soil crusts on soil nematode communities following dune stabilization in the Tengger Desert, Northern China [J]. *Applied Soil Ecology*, 2011, 49: 118–124.
- [75] 刘艳梅, 李新荣, 赵昕, 等. 生物土壤结皮对荒漠土壤线虫群落的影响 [J]. *生态学报*, 2013, 33(9): 2816–2824.
- [76] Gause G F. *The Struggle for Existence* [M]. Williams & Wilkins, 1934.
- [77] 信文娟. 不同磷水平下菌根真菌与解磷菌、根瘤菌对紫云英生长影响及其相互作用 [D]. 武汉: 华中农业大学, 2009.
- [78] Li H, Huo D, Wang W, et al. Multifunctionality of biocrusts is positively predicted by network topologies consistent with interspecies facilitation [J]. *Molecular Ecology*, 2020, 29: 1560–1573.

A review on microbial community assembly in biological soil crusts

Bao Jingting^{1,2,3}, Sun Jingyao³, Wang Jin³

(1.School of Biological and Environmental Engineering, Xi'an University, Xi'an 710065, China; 2.School of Life Science and Engineering, Lanzhou University of Technology, Lanzhou 730050, China; 3.Shapotou Desert Research and Experiment Station, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, Lanzhou 730000, China)

Abstract: Biological soil crusts (also known as biocrusts) are the link structures between surface biotic components and abiotic components in deserts. Biocrusts are not only the "hot spots" of biodiversity in deserts, but also the "engineers" for the restoration of degraded ecosystems. The colonization of biocrusts not only can stabilize the surface, affect soil hydrological process and play an important role in pedogenesis, but also can affect soil carbon and nitrogen cycles in deserts. As microorganisms (cyanobacteria, bacteria, fungi, archaea, etc.) play an important role in the formation and ecological function of biocrusts, this paper systematically summarized the composition and community assembly of microorganisms in biocrusts in cold deserts, cool deserts and hot deserts, and clarified the main microbial species at different succession stages of biocrusts in different bioclimatic regions at global scale. The existing problems were also discussed. Finally, the authors suggested to focus on microbial interactions and identify the key hub microbial species by co-occurrence ecological network analysis, which will help select potential efficient inoculums for cultivating artificial biocrusts and promoting the restoration of degraded ecosystems.

Key words: bioclimatic regions; biological soil crusts; microbial community assembly; global change