Microbiology in Extreme Environments 极端环境微生物

微生物对低温极端环境适应性的研究进展

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摘　要：嗜冷微生物是地球寒冷环境中最主要的生物类群，并且是驱动全球生物地球化学循环的关键环节。嗜冷微生物在适应策略上显示出应对多种极端环境因素的巨大潜力，研究其适应和进化机制有助于更好地理解微生物与环境之间相互作用过程，并有效利用极端环境微生物资源。近年来，随着分子生物学和基因组学技术的高速发展，对微生物适应寒冷环境的机制及嗜冷微生物在指示气候变化和工农业应用方面均有一系列的突破。在此，本文将从基因组的 GC 含量、蛋白质稳定性、转录翻译调控、细胞膜流动性、渗透压调节、抗氧化损失和基因组适应性进化等方面总结当前在微生物适应低温环境机制上所取得的进展，并展望低温环境微生物在指示气候变化和工农业应用中的前景。

关键词：嗜冷微生物；低温环境；适应机制；微生物资源

Progress in research on the adaptability of microorganisms to extremely cold environments

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Abstract: Psychrophilic microorganisms are a major life form in cold environments of the Earth and

drive critical global biogeochemical cycles. The survival strategies of these microorganisms have demonstrated great potential in overcoming the extreme environmental factors. Deciphering their adaptation and evolutionary mechanisms will improve our understanding of the interaction between microorganisms and the environment and facilitate the effective use of microbial resources from extreme environments. With the rapid development of molecular biology and genome sequencing in recent years, researchers have made great breakthroughs in research on the adaptation mechanisms of microorganisms to cold environments and application of these psychrophiles in climate change prediction, industry, and agriculture. In this review, we summarize the progress of research on microbial adaptation to cold environment in terms of genomic GC content, protein stability, transcriptional and translational regulation, cell membrane fluidity, osmotic pressure regulation, oxidation resistance, and genome adaptive evolution.

Keywords: psychrophiles; cold environment; adaptation mechanism; microbial resources

温度常年低于 5 ℃ 的环境一般被认为是永久寒冷环境，地球上 75%的生物圈处于永久寒冷环境中(南极、北极、高山地区、深海、冰洞和大气层上层等)[1]。被大型地理屏障所隔离的南极、北极以及青藏高原冰川和冻土环境的温度常年低于 0 ℃，是地球上的极端寒冷环境。本文主要总结关于极端寒冷环境微生物适应性的研究进展[2-4]。通过与全球尺度微生物群落组成对比，可发现在大的分类单元上，极端寒冷环境中的微生物群落与其他环境存在一些明显差别[5-6]。如在冰川环境中以 β-变形菌纲(Betaproteobacteria)为主，在海冰中以 黄 杆 菌 纲 (Flavobacteriia) 和 γ- 变 形 菌 纲 (Gammaproteobacteria)为主，在冻土以放线菌门(Actinobacteria)为主[5]。从低温代谢(尤其是温度低于 0 ℃)能力的角度看，极地和山地高寒环境中微生物的活性显著高于其他非寒冷环境中的近缘物种[7-10]。嗜冷微生物(嗜冷菌的定义在下文中讨论)是驱动广阔寒冷环境中关键的生物地球化学循环的重要生物因素，并且对气候环境变化十分敏感[11-13]。例如，气候变暖可能会促进冰川微生物介导的有机碳转化，而形成微生物来源的有机碳释放增加-反照率下降-冰川消融加速等反馈机制[14]。

气候变暖还可能导致冰川环境特有的嗜冷微生物类群(specialist taxa)丧失竞争优势，而被广布类群(generalist taxa)或者中温类群替代[10,15]。极端低温环境中的微生物不仅可以指示气候变化，其良好的低温活性也预示着嗜冷菌在工业节能减排和山地高寒农田增收中有着广阔的应用前景[16-17]。

1　最适和最高生长温度特征定义嗜冷菌的局限性

嗜冷菌通常被定义为最适生长温度接近或者低于 15 ℃，最高生长温度低于 20 ℃，最低生长温度为 0 ℃ 或者更低的微生物。在 4 ℃ 或者以下能够生长，最高生长温度高于 20 ℃ 则被认为是耐冷微生物[18-20]。但基于生长温度特征定义的嗜冷菌和耐冷菌的概念很难准确描述一个细菌适应寒冷环境的能力及其在寒冷环境中生态功能的强弱[9,21]。因为当温度上升时，酶的活性通常也将上升，细菌的生长速率随之上升，一直到受某个温度的限制。因此，最高生长温度仅仅定义了微生物能耐受的最高温度，而不能衡量其低温适应能力。实际上大部分从寒冷环境分离的细菌都能够在高于它们分离环

境的温度中生长良好。如一个嗜冷菌可以耐受 30 °C 以上的生长温度,这株菌就应该被定义成嗜中温菌,这不符合实际情况[21]。基于这个逻辑,就出现了一个问题:这些含义不清晰的名词嗜冷菌、耐冷菌和兼性嗜冷菌为什么会被经常用到?自 1967 年 Farrell 和 Rose 提出嗜冷菌概念以来,微生物学家在如何准确定义和使用嗜冷菌这个问题上难以达成一致[21–22]。直到 2016 年 Cavicchioli 在已有的研究基础上通过对比分析,认为只要细菌能够在寒冷环境中自然生长并发挥生态功能,即可认为它们是适应寒冷环境的,并建议将这些能够适应寒冷环境的细菌统称为嗜冷菌[21–23];如这些嗜冷菌能够在系统发育树上形成(可操作)单系类群,则可称之为低温环境特有类群[10]。实际上,即使在–1 °C 或者 0 °C 生长良好的细菌,仍然可在 20 °C 以上的温度生长,但这并不意味着这类微生物不是嗜冷菌或者低温环境特有类群[8,10,24–25]。

到目前为止,微生物生长温度的下限还没有明确的概念,但有研究认为,微生物繁殖的温度下限为–12 °C,维持细胞代谢的温度下限约为–40 °C[7,26]。嗜冷菌在低温(–8 °C)的生长曲线往往不呈指数形,而是表现为线性或者是逐渐下降的曲线[27]。利用稳定同位素标记分析发现,在北极冻土中的微生物可在–16 °C 保持群落水平的代谢活性,涵盖了 9 个门,10 个科。这项研究还发现 *Melioribacteriaceae*、疣微菌科(*Verrucomicrobiaceae*) 和 *Candidatus Saccharibacteria* (TM7)中的一些分类单元与来自其他低温环境相似类群形成了可在零下保持活性的群簇[28]。低温对细胞会产生一系列的物理化学限制,如影响细胞完整性、水的粘滞性、溶质的融化速率、细胞膜流动性、酶活性和大分子之间的相互作用[29–30]。有证据表明,微生物在低温下(–40 °C)有活性,那微生物必定会有相应的适应性策略来应对低温环境

造成的不利影响。因此,嗜冷菌进化出了相应的机制从而使它们成功地在寒冷环境中存活[31–32]。围绕微生物如何适应寒冷环境,已开展了大量的研究,包括生理学和近些年发展起来的组学研究。通过组学和生理学相结合的方法,在微生物适应寒冷环境的机制方面取得了丰富的成果。

2 低温微生物的适应机制

2.1 基因组 GC 含量、RNA 二级结构与低温适应性

微生物(细菌和古菌)的基因组由环状或线性的双链 DNA 组成[33],在双链 DNA 序列中,GC 碱基对比 AT 碱基对之间多一个氢键,GC 含量的改变被认为会影响 DNA 双链的稳定性,从而与微生物的生长温度相关[34]。但是在嗜冷、嗜热和中温菌之间,全基因组 GC 含量与最适生长温度之间缺乏统一的显著相关性[34–35]。不过最近有研究发现,最适生长温度较低的冷杆菌属(*Cryobacterium*)菌株,其基因组第三位密码子 GC 含量要低于同属最适生长温度较高的菌株[36];节细菌属(*Arhtrobacter*)的极地和山地环境嗜冷类群(polar and alpine psychrophilic lineage)全基因组 GC 含量要显著低于同属其他非极地环境的中温菌株[10],这些显著相关性只局限在一些类群中,不具有普适性[35,37]。虽然全基因组 GC 含量与最适生长温度之间缺乏普遍的相关性,但是在大部分微生物类群中,RNA 的二级结构(rRNA 茎环结构中的茎,tRNA 的三叶草结构中的茎)与 GC 含量之间显著正相关,嗜冷微生物 RNA 的 GC 含量要低于中温菌和嗜热菌[38]。对于含有多拷贝 16S rRNA 基因的微生物,在较低的生长温度条件下,倾向于表达 GC 含量低的 16S rRNA 基因,这进一步支持了 RNA 的 GC 含量与生长温度密切相关[39]。

2.2　蛋白质氨基酸组成的调整以获得低温下活性

　　恒温动物可在寒冷中保持合适的体温，其细胞内的代谢活动在一个大致恒定的温度中进行。而微生物与其环境则处于完全热平衡状态，嗜冷菌细胞的所有组成部分都必须适应低温，从整体上实现维持生长和生存的细胞功能[40]。作为生命的物质基础，蛋白质是生命活动的主要承担者。蛋白质如何保持低温下的活性，是微生物在低温环境下实现生长和发挥功能所要解决的首要问题[29,41]。通过比较基因组学和蛋白质结构分析的方法研究发现，改变特定氨基酸的比例可改变蛋白质的热稳定性和底物亲和力，从而维持低温下的活性。如降低精氨酸(arginine)和脯氨酸(proline)含量，可减少氢键和盐桥，增强蛋白质构象的柔性，提高酶在低温下的活性；相应地，赖氨酸(lysine)、异亮氨酸(isoleucine)和谷氨酰胺(glutamine)的含量会增加。从氨基酸性质上看，整体表现为极性氨基酸比例的增加，酸性氨基酸比例的减少，而疏水性氨基酸在不同蛋白质中的变化趋势并不完全一致[42]。用精氨酸代替赖氨酸使得嗜冷 α-淀粉酶构象更稳定、活性更低，表现出嗜中温酶的特征，这为赖氨酸残基在促进酶冷适应中的重要性提供了实验支持[43]。上述趋势也在嗜冷酶[白三烯 A4 水解酶, leukotriene A₄ hydrolase；C β-内酰胺酶, C β-lactamase]中得到了验证[44-45]。通过增加带有疏水侧链氨基酸在溶质接触区域的含量，减少疏水残基在酶核心区域的含量来提高低温下酶的催化效率则在嗜冷白三烯 A4 水解酶中得到了验证[44]。增长外部环状结构的长度，减少脯氨酸的含量从而降低蛋白质稳定性，可增加嗜冷蛋白质的折叠活性和运动性，此现象在嗜冷酶[异三烯 A4 水解酶(alleuotriene

A₄ hydrolasehe)和纤维素酶(cellulase)]上也得到了验证[46-47]。上述蛋白质序列和构象的改变，可使底物更容易接近酶的活性中心，从而降低活化能，保证微生物在低温下足够的代谢活性[48-49]。高分辨率的嗜冷蛋白质结构研究发现，其表面的空穴(cavity)的数量与大小都高于同源的中温蛋白[50]。蛋白质表面空穴可保存大量的亲水基团，结合更多的水分子，通过加强内部溶解性从而增加酶的折叠活性[50]。比如来自菌株解脂酸发光杆菌(Photobacterium lipolyticum)的嗜冷 M37 脂肪酶就含有表面空 穴[51]。降低蛋白质表面空穴的稳定性，可提高蛋白质螺旋的柔性，提高代谢底物向酶的结合位点移动的效率。通过比较嗜冷 M37 脂肪酶和来自嗜中温菌米黑根毛霉(Rhizomucor miehei)的同源脂肪酶也发现了嗜冷酶有着更宽的含氧的阴离子穴(oxy anion hole)，此类修饰可使 M37 脂肪酶结合更多的水分子，有助于降低酶在作用过程中需要的能量，从而降低最适生长温度[51]。

　　上述研究主要是针对单一蛋白质或者单个菌株进行的分析，这些规律是否适用于多菌株甚至群落水平呢？最近，Shen 等[10]对 Arthrobacter 中由 9 个来自南北极和青藏高原的菌株形成的低温环境单系分支进行了整体的蛋白质稳定性分析。结果显示，寒冷环境单系类群的 δ 吉布斯自由能(ΔG)在温度低于 0 ℃时要显著高于对照组的中温菌株。较高的 δ 吉布斯自由能对应较高的构象柔性和更低的热稳定性，通过蛋白质热稳定性曲线预测证实了寒冷环境特有类群的菌株通过氨基酸序列的改变增强了低温活性，但是降低了高温耐受性。这项结果表明，基于单一蛋白质或者单个菌株分析获得的结论也可能是适用于多个菌株甚至整个群落。随着人工智能技术的进步，如 AlphaFold 的出现，蛋白质结构组学领域正在经历一场变革。不依

赖模板的高精度、高通量建模将会给环境微生物学领域带来新的发现[52]。

2.3 DNA 结合蛋白维持低温下的转录和翻译

冷休克反应是指突然暴露在低温环境下，微生物会上调或者下调一些基因的表达量的过程[53]。冷休克过程可以分为适应期和低温生长期，在适应期，低温诱导蛋白的表达量达到峰值，非低温诱导蛋白的表达量受到抑制；适应期之后开始进入低温适应性生长期，这时低温诱导蛋白的表达量开始下降并逐渐趋于平稳，微生物所表达的全部蛋白质会调整到一个新的低温适应性模式[54]。对比嗜冷甲烷叶菌(*Methanolobus psychrophilus*)在 4 ℃ 和 18 ℃ 条件下基因表达特征，发现总共有 1 295 个基因的表达量发生了明显的改变，约占细菌全部基因的 40%[55]。菌株奥奈达希瓦氏菌(*Shewanella oneidensis*)在 8 ℃ 和 15 ℃ 条件下分别有 785 和 546 个基因的表达量发生了明显的变化[56]。这种冷休克反应通常能在很短的时间内发生，如恶臭假单胞菌(*Pseudomonas putida*)在温度从 30 ℃ 降低到 10 ℃ 后，2 h 内就有 2 337 个基因的表达量发生了改变[57]。低温下高表达的主要是编码冷休克蛋白相关的基因，冷休克蛋白主要是一类单链 DNA 结合蛋白，可调控一系列的细胞过程，包括转录、翻译、蛋白质折叠和细胞膜流动性[23,58]。另外一些在低温下高表达的基因与 RNA 解旋酶以及核糖体的加工与成熟相关。其中，RNA 解旋酶可以降低 DNA 和 RNA 二级结构的稳定性，有利于启动基因的转录。核糖体结合因子 A (RbfA)的高表达有助于低温下核糖体的加工和成熟，RbfA 的过度表达可以将冷休克反应后的滞后时间缩短一半，从而使微生物更快地适应低温并促进蛋白质合成[59]。研究发现，翻译起始因子 IF2 (initiation factor 2)在冷休克细胞的核糖体组装和成熟中也发挥重要作用[60]。

2.4 维持低温下细胞膜的流动性

低温对微生物的另一个显著影响是降低细胞膜的流动性，而细胞膜的流动性是保持细胞功能的关键因素。相应地，嗜冷菌进化出了低温下调整细胞膜流动性的能力[61-62]。这些策略包括增加多不饱和脂肪酸含量、改变脂肪酸组成类型、降低脂肪酸的极性以及反式异构向顺式异构转变[61-63]。实验发现，在较低的生长温度下，伯顿嗜甲基甲烷拟球菌(*Methanococcoides burtonii*)细胞中不饱和脂肪酸的比例显著提高[64]。转录组和生理实验的研究发现，低温可以引起细胞膜合成相关基因(如脂肪酸、磷脂脂肪酸、肽聚糖和糖基转移酶)的快速上调表达，在嗜冷菌深海发光杆菌(*P. profundum*) SS9 中也发现了细胞膜合成相关基因的富集现象[65]。蛋白质组的研究发现，膜运输蛋白在低温下的表达量上调，以应对低温导致的细胞膜溶解率降低的不利因素[66-67]。如膜运输转运载体可通过加强对营养物质、相容性溶质和膜多肽的吸收从而应对低温和高渗透压的环境压力[66-68]。

色素在保持低温下细胞膜的流动性中也有重要的作用，是极地和高山地区微生物应对环境压力的重要策略之一[69]。极性和非极性的色素在许多南极和青藏高原的细菌中都能产生，色素被认为是细胞膜流动性的缓冲剂，可以帮助细胞膜在面对温度波动时保持粘性；色素还可以通过直接吸收紫外辐射来起到保护作用，随机突变实验表明，产色素缺陷型菌株对紫外线更加敏感[29,70-72]。

2.5 低温下的渗透压调节

低温导致的细胞质中的水分形成冰晶，将直接损伤细胞并引起渗透压失衡[70]。嗜冷菌通过吸收甘氨酸、甜菜碱和蔗糖等相容性溶质降

低细胞内的凝固点，同时还可以抵御脱水和高渗透压从而获得低温下保持活性的能力[58,70]。实验发现，大肠杆菌(*Escherichia coli*)在低温下通过上调海藻糖合成量来抵抗低温带来的损伤，此过程对于 *E. coli* 在低温下生存十分关键[73]，进一步通过转录组实验发现，海藻糖合成基因 *otsA* 和 *otsB* 可在低温下被诱导表达[74]。一些嗜冷菌可产生抗冻蛋白或者冰结合蛋白，此类蛋白质可结合并限制冰晶的生长，起到降低细胞质冰点的作用[75]。另外，冰核蛋白可通过促进冰晶的形成从而阻止过冷水的产生[76]。

胞外多糖(exopolysaccharides，EPS)也是一种低温保护剂，嗜冷菌在低温下可以产生大量的 EPS[77–81]。EPS 可降低水的凝固点和冰核形成的温度，锁住水分、营养物质、离子并且提高细胞表面粘度，促进细胞聚集和生物膜的形成，还可保护胞外酶[78–80]。实验发现，添加 EPS 可促进冷红科尔韦尔氏菌(*Colwellia psychrerythraea*) 34H 在–1− –20 °C 的代谢速率[82]。实验还发现，由硅藻北极直链藻(*Melosira arctica*)，圆柱拟脆杆藻(*Fragilariopsis cylindrus*)和嗜冷菌 *C. psychrerythraea* 产生的 EPS 可阻止脱盐过程并破坏生长中冰晶的微结构，从而避免微生物细胞在结冰的过程中受到损伤[83–85]。因此，EPS 通过改变冰的渗透性，锁住冰中的盐分，通过提高盐分而阻止冰的生长，从而为低温环境中的微生物创造有利的生存环境[79–80]。

2.6 低温下的氧化损伤

由于低温下氧气的溶解度增加，导致活性氧(reactive oxygen species，ROS)浓度的增加，从而使细胞在寒冷环境的胁迫下容易发生氧化损伤。ROS 为含有氧的化学反应分子，包括超氧自由基(O_2^-)和羟自由基(HO^-)等[86]。ROS 可对细胞结构造成严重的损害，如造成脂质过氧化破坏细胞流动性、引起蛋白质氧化、导致

DNA 碱基修饰和键断裂等[87–89]。因此，防止氧化损伤对于微生物在低温下生存尤为重要。

嗜冷菌有多种克服在寒冷环境下造成的氧化损伤的策略。研究表明，编码 ROS 解毒的基因在冷应激下上调，如过氧化氢酶(catalase)、2 种超氧化物歧化酶(SodA 和 SodC)，硫醇过氧化物酶(Bcp)以及硫氧还蛋白和硫氧还蛋白还原酶(TrxA 和 TrxB)等，这些酶具有强大的抗氧化活性，能抵抗氧化应激。超氧化物歧化酶催化超氧阴离子转化为过氧化氢，再通过过氧化氢酶和过氧化物酶催化发生歧化反应[90–91]。TrxA 和 TrxB 在保持细胞内硫醇-二硫化物平衡的同时，也清除 ROS[92]。通过对嗜盐浮游假交替单胞菌(*Pseudoalteromonas haloplanktis*) TAC125 基因组序列的分析发现，其含有编码 H_2O_2 和超氧化物酶具有活性的基因，且该生物对 H_2O_2 具有明显抗性，在抵抗 ROS 损伤中发挥重要作用[93]。耐压希瓦氏菌(*S. piezotolerans*) WP3 在低温和 H_2O_2 的胁迫下表现出良好的耐受性，基于基因组学分析，其有关编码 H_2O_2 清除的基因 *ccpA2* 和 *gpx* 分别上调了 1.6 倍和 2.6 倍[94]。除过氧化氢和超氧化歧化酶外，红球菌 (*Rhodococcus* sp.) CNS16 在低温下表现出过氧化氢酶和超氧化物歧化酶活性的丧失，并利用硫氧还蛋白依赖性的过氧化物酶来参与清除细菌中的 ROS[95]。涅斯特连科氏菌(*Nesterenkonia* sp.) AN1 与 *Nesterenkonia* sp. PF2B19 中均发现了编码与 ROS 解毒相关的基因，如过氧化氢酶、超氧化物歧化酶，硫醇过氧化物酶以及硫氧还蛋白和硫氧还蛋白还原酶[96–97]。亚精胺和腐胺是最常见的细胞保护多胺，通过作用于核酸和中和 ROS 来增强分子功能[98]。多胺氨基丙基转移酶 SpeE2 仅在冷胁迫下表达，冷胁迫催化丙胺基团从氨基供体 S-腺苷甲硫氨酸不可逆地转移到腐胺以产生亚精胺。反之，腐胺由鸟氨酸或

精氨酸分别通过鸟氨酸脱羧酶或精氨酸脱羧酶产生[99]。近期研究发现，在冷胁迫下的嗜冷菌萨拉曼卡假单胞菌(*P. helmanticensis*)除了过氧化物酶和超氧化物歧化酶上调外，2-酮精氨酸脱羧酶上调了 35.51 倍，表明产生了保护性多胺的亚精胺和腐胺，从而来抵抗氧化应激[100]。此外，还有一些嗜冷菌可能通过缩短代谢途径，不产生或者是较少产生 ROS，从源头上减少氧自由基的来源[101]。

2.7　微生物对低温环境的适应性进化

　　Cryobacterium 是一类高度适应了低温环境的放线菌，其绝大部分成员分离自南北极和青藏高原等寒冷环境。对 78 株 *Cryobacterium* 的最适生长温度特征和基因组进行联合比较分析发现，它们之间的最适生长温度存在梯度差异，并且与系统发育分支的聚类密切相关。有着相对较低最适生长温度的菌株其基因组更加偏好于 A/U 结尾的同义密码子，表现为密码子第三位的 GC 含量显著降低。由自然选择所导致的较低的 GC 含量使相应 DNA 具有更高的柔韧性，进而确保 DNA 在低温下以合适的分子动态正常行使功能。而这个自然选择压力可能主要来自冰川环境的胁迫[36]。

　　嗜冷菌基因组的可塑性促进了其对低温极端环境的适应性进化[102]，为了探索细菌的基因组功能、基因含量和动力学变化是否受冰川环境胁迫因素驱动，Liu 等[103]对 21 个嗜冷性冷杆菌 *Cryobacterium* 菌株的基因组进行了比较基因组学分析，发现嗜冷低温细菌的基因组含量发生了更多的动态变化，并且它们的基因组中涉及应激反应，运动性和趋化性的基因数量显著多于嗜温性低温细菌。基于多基因串联系统发育树的 birth-and-death 模型分析，发现在中温菌株嗜中温冷杆菌(*C. mesophilum*)分化后，嗜冷 *Cryobacterium* 的最近共同祖先基因组经历了一个快速扩增的过程(通过 1 168 个基因获得了最多的基因)。基因组的扩增带来了关键基因，这些基因主要和辅酶、维生素和色素、碳水化合物和膜运输等功能相关。嗜冷 *Cryobacterium* 菌株的氨基酸取代率比嗜中温菌株低两个数量级。然而，在嗜冷的 *Cryobacterium* 菌株中并未发现明显更多的冷休克基因，这表明，尽管冷休克基因对于嗜冷菌是必不可少的，但多拷贝并不是微杆菌科(*Microbacteriaceae*)冷适应的关键因素。由冰川环境胁迫因素驱动的广泛的基因水平转移可能是嗜冷细菌抵抗冰川上的低温、寡营养和高紫外线辐射的策略。此项研究结果与泛基因组分析所发现的关键推论一致，原核生物的关键进化过程不是点突变，而是通过基因水平转移和基因丢失造成的基因替换[104]。

3　展望

　　低温环境中的微生物类群丰富，在复杂类群中判断哪些类群在该生态系统中发挥关键作用还十分困难。很大一部分从低温环境中分离的菌株最低生长温度在 4 ℃ 左右，这个温度显然要高于其生存环境大部分时间的温度，判断这些类群是否能在原位环境发挥生态功能是一项具有挑战性的工作[13,105-106]。那些在实验室中没有表现出 0 ℃ 及以下温度活性的类群，可能仅仅是因为低温被保存下来的外源中温微生物，也可能是在实验条件下无法完全模拟其原位生存条件，如物种间群体感应条件的缺失。还可能是脱离相互作用的物种和微环境之后，这些微生物无法在 0 ℃ 及以下温度表现出显著的生长迹象[107]。但是如 *Arthrobacter*、*Cryobacterium*、微小杆菌属 (*Exiguobacterium*)、黄杆菌属 (*Flavobacterium*)和极单胞菌属(*Polaromonas*)等属中能够形成低温环境(可操作)单系分支，并且

在 0 ℃ 及以下温度具有较高生长活性的类别，可以优先作为研究微生物对低温环境适应性的模式物种[10,27,108]。而随着基因组数据(包括来自纯培养菌株的全基因组、单细胞测序全基因组和宏基因组组装的全基因组)的持续增加，结合不同温度条件下的生长控制实验，将会有更多的低温环境单系类群被发现。这些类群的基因组和生理特征更能代表微生物对特定环境的适应性[109]。那些在基因组和生理特征上与中温菌区分开的低温环境类群，将可能在指示气候变化、节能减排和农业生产中发挥重要作用。

由于人类的活动，全球气候与环境发生着剧烈的变化。冰冻圈是气候系统最敏感的圈层，气候变暖对冰川生态系统的影响要比其他区域更为深刻和敏感[110-111]。气候变化可以直接或者间接影响微生物的群落及其功能，在冰川环境中可表现为低温特有类群竞争优势的丧失，被广布类群所替代，导致微生物群落结构改变；在永久冻土中，参与好氧和厌氧碳分解、氨氧化以及产甲烷相关的功能基因丰度在短期变暖过程中显著增加，从而促进二氧化碳和甲烷等温室气体的排放，对气候变暖形成正反馈[10-11,112-116]。因此，了解低温环境类群对于冰川和冻土等生态系统的气候变化的响应将有助于人们了解气候变化的趋势，但目前有关冰川的增温研究还非常少，需要积累长期的观测数据。

在工业生产中，冷适应酶因其在较低的温度下就可以发挥很高的催化活性，而在降低能耗、减少碳排放中有着广泛的应用前景[117]。研究表明，在工业洗涤领域，反应体系温度每降低 10 ℃ 就可减少 30% 的用电量，即相当于每次洗涤减少 0.1 kg 的 CO_2 排放[64,118]。从喜马拉雅冰川土壤中分离出来的嗜麦芽寡养单胞菌(*Stenotrophomonas maltophilia*) MTCC 7528 和短小芽孢杆菌(*Bacillus pumilus*) BO1 产生的嗜冷蛋白酶将来可能会在上述领域发挥重要作用[119-121]。除了在应用于洗涤行业，冷适应酶在食品、纺织等行业中也发挥着重要的应用[122]。如在食品加工过程中使用冷适应酶可以避免高温处理步骤，有助于保留风味、提高营养价值[123]。

世界上有很大一部分可耕作土地处在高寒环境中，利用能在寒冷环境中生长的低温环境类群可能会成为促进丘陵和山地等高海拔寒冷地带农业生产力的重要方法[16,124]。已有研究表明，某些低温环境类群具有促进植物生长(如在低温下合成植物生长激素吲哚乙酸、促进溶磷作用等)以及缓解植物的生物胁迫的特性[125]。从南极、喜马拉雅山脉和其它高海拔地区分离的假单胞菌(*Pseudomonas* spp.)，芽孢杆菌(*Bacillus* spp.)，链霉菌(*Streptomyces* sp.) 5 和小单孢菌(*Micromonospora* sp.) 18 在低温下能够促进植物种子的萌发与生长；而 *Pseudomonas* spp.、*Streptomyces* sp. 5 和 *Micromonospora* sp. 18 还可以抑制尖孢镰孢菌(*Fusarium oxysporum*)和晚疫病病菌(*Phytophtora infestans*)等植物致病菌，从而缓解植物病害[126-130]。冷适应植物生长促进微生物可以作为在寒冷环境中有效的生物肥料和生物防治剂，这为极端寒冷环境微生物资源在农业领域的应用打开了新的大门[16]。

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