DOI: 10.11766/trxb202511230558 CSTR: 32215.14.trxb202511230558
易彧为，吴一超，张铭，戴珂，高春辉，渠晨晨，黄巧云，蔡鹏. 微生物胞外聚合物（EPS）驱动土壤有机碳稳定的研究进展与展望[J]. 土壤学报，2026，
YI Yuwei, WU Yichao, ZHANG Ming, DAI Ke, GAO Chunhui, QU Chenchen, HUANG Qiaoyun, CAI Peng[J]. Acta Pedologica Sinica, 2026,

微生物胞外聚合物（EPS）驱动土壤有机碳稳定的研究进展与展望*

易彧为[1]，吴一超[1]，张 铭[1]，戴 珂[1]，高春辉[1]，渠晨晨[1]，黄巧云[1,2,3]，蔡 鹏[1,2,3†]

（1. 农业微生物资源发掘与利用全国重点实验室，华中农业大学资源与环境学院，武汉 430070；2. 农业农村部华中耕地修复技术重点实验室，武汉 430206；3. 土壤环境与污染修复湖北省重点实验室，武汉 430070）

摘 要：胞外聚合物（Extracellular polymeric substances, EPS）是微生物在同化作用中合成并分泌的生物大分子。虽然现有土壤有机碳（Soil organic carbon, SOC）循环理论强调微生物细胞残体是 SOC 形成的主要贡献者，但新近研究表明，EPS 在土壤中广泛存在，其产生速率往往与细胞生物量相当甚至更高，构成了微生物向土壤输入碳的重要途径。本综述系统梳理了当前研究进展，重点阐释了 EPS 在土壤碳固持中的独特贡献。我们归纳了 EPS 促进 SOC 稳定的四种关键机制：形成矿物结合态有机质、参与地质聚合反应、驱动土壤团聚体形成以及调控孔隙结构，揭示了其通过直接与间接双重作用实现碳固存的作用路径。最后，本文展望了未来研究方向，指出亟需建立可靠的 EPS 提取与定量技术，将 EPS 动态纳入 SOC 模型，并深入解析环境因子与微生物过程对 EPS 产生与降解的调控机制。填补上述研究空白将有助于深化对微生物参与全球碳循环过程的认识，并为提升土壤碳汇功能提供科学依据。

关键词：胞外聚合物；土壤有机碳固存；矿物结合态有机质；土壤碳库；土壤微生物碳泵

中图分类号：S154.2 **文献标志码**：A

Advances and Perspectives on the Role of Microbial Extracellular Polymeric Substances (EPS) in Soil Organic Carbon Stabilization

YI Yuwei[1], WU Yichao[1], ZHANG Ming[1], DAI Ke[1], GAO Chunhui[1], QU Chenchen[1], HUANG Qiaoyun[1,2,3], CAI Peng[1,2,3†]

(1. *National Key Laboratory of Agricultural Microbiology*, *College of Resources and Environment*, *Huazhong Agricultural University*, *Wuhan* 430070, *China*; 2. *Key Laboratory of Arable Soil Remediation Technology (Central China)*, *Ministry of Agriculture and Rural Affairs*, *Wuhan* 430206, *China*; 3. *Hubei Key Laboratory of Soil Environment and Pollution Remediation*, *Wuhan* 430070, *China*)

Abstract: Extracellular polymeric substances (EPS), as a key component of soil organic carbon (SOC) sequestration, have long been overlooked. Although the prevalent theories emphasize microbial cell residues as the dominant

* 国家自然科学基金项目（42225706）和湖北省自然科学基金创新群体项目（2023AFA009、2024CSA060）资助 Supported by the National Natural Science Foundation of China (No.42225706) and Innovative Research Group Project of Hubei Provincial Natural Science Foundation (Nos.2023AFA009, 2024CSA060).

† 通讯作者 Corresponding author，E-mail：cp@mail.hzau.edu.cn
作者简介：易彧为（2001-），男，湖南岳阳人，硕士研究生，研究方向为土壤生物膜与环境健康。E-mail: 1281414163@qq.com

收稿日期：2025-11-23；收到修改稿日期：2026-05-19；网络首发日期（www.cnki.net）：

contributor to SOC formation, emerging evidence indicates that EPS is widely present in soils and is produced at rates comparable to or even higher than cellular biomass, representing a major pathway of microbially derived carbon input into soils. This review systematically synthesizes current knowledge, with a focus on the distinctive role of EPS in soil carbon stabilization. We summarized four key mechanisms through which EPS promote soil organic carbon stability: the formation of mineral-associated organic matter, participation in geopolymerization reactions, driving the formation of soil aggregates, and regulating pore structure. This reveals the pathway for achieving carbon sequestration through both direct and indirect effects. Following our findings, we outline future research priorities, emphasizing the need to develop reliable extraction and quantification methods, incorporate EPS dynamics into SOC models, and elucidate the environmental and microbial factors regulating EPS production and degradation. Addressing these gaps will significantly advance our understanding of microbial roles in the global carbon cycle and inform strategies for enhancing soil carbon sequestration.

Key words: Extracellular polymeric substances (EPS); Soil organic carbon stabilization; Mineral-associated organic matter; Soil carbon storage; Soil microbial carbon pump

土壤有机碳库是陆地生态系统最大的碳库，在调控全球气候和维持农业生产力方面发挥着重要作用[1]。土壤微生物是土壤有机碳（Soil organic carbon, SOC）转化和稳定的主要驱动力，其不仅通过异化作用分解土壤有机质，还通过同化作用将外源有机质转化为微生物源有机质[2]。这些土壤微生物源的有机质通过在矿物表面吸附或被土壤团聚体包埋而受到保护，形成土壤稳定的有机碳。该过程被视为 SOC 固存的主要途径[3-4]。微生物源有机质由细胞组分与胞外有机质构成。其中，胞外聚合物（Extracellular polymeric substances, EPS）是微生物生长代谢过程中分泌至周围环境的生物大分子聚集体，包括多糖、蛋白质、脂质和核酸等[5-6]。前期研究表明，微生物合成分泌的 EPS 干重可达其自身细胞干重的 10 倍以上，尤其当微生物附着于固相表面形成生物膜[5, 7-8]。这表明 EPS 是土壤中一类产量可观、分布广泛且不可忽视的微生物源有机质。

EPS 在 SOC 固存方面同样具有巨大潜力。已有研究指出，EPS 富含羧基、羟基与磷酸基等多种官能团，且具有黏滞特性[9-11]。这使其对土壤矿物具有强亲和力，可通过静电吸引、配体交换等作用直接形成矿物结合态有机质（Mineral associated organic matter, MAOM）。近期对 MAOM 的表征也发现，这些矿物结合态有机质中存在大量的多糖、蛋白质等生物大分子，说明 EPS 可能是 MAOM 的重要来源[12-14]。EPS 吸附在矿物表面后还能通过静电屏蔽、桥接作用等促进土壤微团聚体形成，包埋其自身与其他土壤有机质。前人研究发现少量 EPS 能够显著降低矿物颗粒的表面电势，从而介导颗粒间的强烈团聚[15]。基于实际土壤调查，发现土壤 EPS 含量与水稳性团聚体数量呈显著正相关，并且胞外蛋白质含量是影响土壤团聚体平均直径的重要因素[16]。这提示 EPS 可以通过多个途径提高 SOC 稳定性。

尽管 EPS 是土壤中含量丰富、分布广泛且具有高度稳定潜力的微生物源有机质[17-18]，但其对 SOC 固存的具体贡献迄今仍未得到系统研究。这主要归因于表征方法的局限与传统观念的影响。现有基于氨基糖生物标识物的定量方法主要用于追踪和量化微生物细胞残体，难以有效捕捉胞外产物。在 EPS 量化表征方面，常用的阳离子交换树脂（Cation exchange resin, CER）等提取方法仅能获取土壤中部分 EPS 组分，且极易混杂非微生物源有机质，导致土壤 EPS 的真实储量至今仍难以准确定量。在认知层面上，由于 EPS 富含多糖和蛋白质等易被微生物降解利用的有机大分子[18]，传统观点认为土壤 EPS 属于活性高、周转快的少量不稳定有机质[19-20]。这种对土壤 EPS 的系统性忽视导致微生物在土壤碳循环中的贡献被整体低估。本综述聚焦 EPS 在 SOC 固存中的关键作用。首先整合现有证据阐明 EPS 是微生物向土壤输入碳的关键通路；进而剖析 EPS 通过直接与间接作用促进 SOC 长期稳定的四大机制；最后提出未来研究的优先方向，为优化碳循环模型和全球气候变化背景下的土壤碳增

汇策略提供科学依据。

1 EPS 是土壤微生物合成的重要有机质

合成分泌 EPS 是土壤微生物普遍具备的生理特征[21]。尽管不同微生物类群在 EPS 合成能力上存在差异，例如部分黑曲霉、气单胞菌、假单胞菌分离株的 EPS 产量相对较低，但分泌 EPS 依然是微生物应对逆境的核心适应策略[8, 22]。EPS 基质能够为微生物提供保护，抵御干旱、捕食、重金属、噬菌体侵染和氧化损伤等多种环境胁迫[8, 18]。前期研究也证实了缺乏 EPS 的微生物在逆境土壤环境中通常表现出较差的存活能力[23-25]。在非根际土壤环境中，大部分微生物属于寡营养型，仅少部分微生物处于活跃繁殖状态[22, 26-27]。寡营养型细菌（如放线菌和厚壁菌门）将更多同化碳和能量分配于 EPS 合成，而非细胞生长[28-29]。活跃生长的富营养型细菌则将同化碳主要用于生物量合成，导致其 EPS 合成速率可能低于生物量积累速率[30]。因此，在养分贫乏、干旱、寒冷等不利于微生物生长的土壤环境中，微生物合成的有机质以寡营养型细菌分泌的 EPS 为主；而在养分充足条件下，微生物群落向富营养型生长策略转变，更多碳被分配至生物量合成与呼吸消耗，导致新合成的土壤微生物源有机质中 EPS 占比下降[31-33]。

除了为微生物提供生存庇护外，EPS 作为微生物与土壤环境互作的核心界面，在介导微生物对土壤有机质的转化过程中也发挥重要作用。胞外代谢过程是限制土壤生态系统中颗粒和溶解性有机物矿化和循环的关键步骤[34]。EPS 作为微生物胞外分泌物的聚集体，是胞外酶的主要载体，也是胞外代谢的活性反应中心。早期研究在真菌 EPS 中发现了多种参与木质纤维素降解的功能酶[35]。EPS 中的多糖通过为这些功能酶提供固定位点，提高其在环境中的活性与稳定性。例如，曲霉（*Aspergillus*）和木霉（*Trichoderma*）等真菌分泌的 β-葡萄糖苷酶与自身或其他真菌物种分泌的 EPS 结合后可显著提升酶活性及其对酸碱、温度和变性剂等不利因素的耐受性[34, 36]。显微红外光谱分析发现外生菌根真菌（*Paxillus involutus*）的木质素酶与 EPS 紧密结合，而不分泌 EPS 的菌丝不具备木质素降解能力[37-38]。微量热滴定实验和分子模型模拟表明，脂肪酶 LipA 中带正电荷的氨基酸与 EPS 中多聚糖链的负电荷基团通过静电作用相互吸引，形成稳定的复合体[39]。这种结合可以防止胞外酶在环境中流失，并且保证酶的催化活性中心始终暴露在溶液中，从而高效催化降解有机底物。因此，EPS 为胞外代谢提供了稳定的催化环境，是土壤有机质胞外转化的活性中心，在促进土壤微生物对有机质的分解、转化及再合成过程中发挥关键作用。

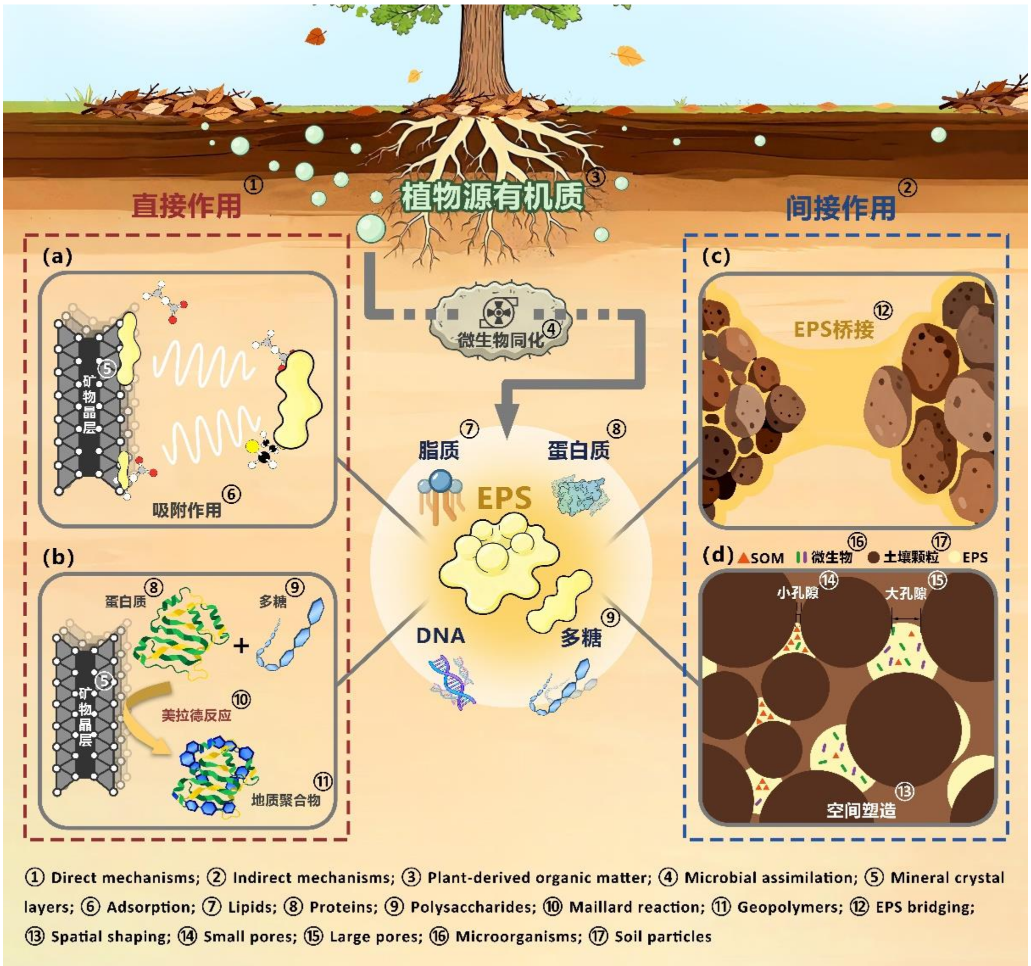
鉴于土壤 EPS 的普遍存在与重要功能，研究者已尝试对其碳含量进行定量分析。基于 CER 的提取方法目前被广泛应用于提取微生物-土壤界面的 EPS[40-42]。部分研究将 CER 提取的有机碳定义为 EPS 碳[43-44]。据估算，CER 可提取的 EPS 碳约占 SOC 的 2%~5%，与微生物生物量碳的比例基本相当。然而，这些量化方法存在明显局限：CER 主要提取通过二价阳离子吸附于固相表面的 EPS，而相当一部分 EPS 通过三价离子键合、共沉淀等机制与土壤矿物紧密结合，无法利用该方法有效提取[41]。此外，CER 提取物中还混杂腐殖质、植物根系黏液等非微生物来源的有机质[45]。由于这些物质在理化性质上与 EPS 相近，难以有效区分，从而对 EPS 的准确定量产生极大干扰[41]。

尽管土壤 EPS 总碳含量的直接测定仍面临困难，但已有多项间接证据表明其在土壤中产量可观。近期一项荟萃分析对比了土壤微生物碳积累效率（Carbon accumulation efficiency, CAE）与碳利用效率（Carbon use efficiency, CUE）的差异。CAE 涵盖了微生物合成的细胞与胞外全部有机质，其定义为微生物合成的有机质碳总量与外源添加葡萄糖碳量的比值；而 CUE 仅考虑微生物细胞碳含量，定义为细胞碳含量与细胞碳含量和呼吸碳之和的比值[46]。

若假设葡萄糖碳经微生物代谢后在呼吸、细胞和胞外产物三部分之间进行分配，该研究显示胞外产物的合成效率约为胞内产物的 1.8 倍[46]。另一项研究表明，与传统模型相比，纳入部分 EPS 组分（如胞外酶）会提升 CUE 数值 1 倍以上；而忽略 EPS 的贡献会导致 SOC 的预测值被低估多达 34%[47]。这些结果一致证明，微生物胞外产物的合成通量显著高于细胞生物量，印证了 EPS 在土壤有机碳库中不可忽视的重要地位。因此，在 CUE 评估及相关模型构建中纳入 EPS 有助于更全面地表征土壤微生物代谢过程中有机质的转化及有机产物的合成，从而提高 CUE 估算的准确性，并降低土壤有机碳库模型预测的不确定性。

2 EPS 介导的 SOC 稳定机制

EPS 丰富的官能团与较强的黏滞性使其具备直接形成稳定 SOC 和间接提高 SOC 稳定性的双重潜能（图 1）。其中，直接作用主要包括 EPS 在矿物表面的吸附及其潜在参与的地质聚合反应，间接作用则包括促进土壤团聚体形成以及调控土壤孔隙结构。这一分类框架有助于从多维度揭示 EPS 在土壤碳固存中的潜在作用方式。



注：红色虚线框表示直接作用机制，蓝色虚线框表示间接作用机制。直接作用包括：（a）在矿物表面吸附并形成矿物结合态有机质；（b）作为地质聚合作用的前体物质。间接作用包括：（c）EPS 驱动的土壤团聚体形成；（d）改变土壤孔隙结构及其连通性。图中箭头表示植物源有机质经微生物同化后分泌 EPS 过程。Note: Red dashed boxes indicate direct mechanisms, whereas blue dashed boxes indicate indirect mechanisms. Direct mechanisms include: (a) adsorption onto mineral surfaces and formation of mineral-associated organic matter, and (b) serving as precursors for geopolymerization. Indirect mechanisms include: (c) EPS-driven soil aggregation, and (d) modification of soil pore structure and connectivity. Arrows indicate the transformation of plant-derived organic matter through microbial assimilation into EPS-associated SOC stabilization processes.

图 1 胞外聚合物（EPS）介导土壤有机碳（SOC）稳定的 4 个关键机制。（以彩图发表）

Fig. 1 Four key mechanisms of soil organic carbon (SOC) stabilization mediated by extracellular polymeric substances (EPS)

2.1 直接途径：吸附于矿物表面形成 MAOM

MAOM 是土壤中受矿物保护的稳定碳库。由于矿物表面的吸附作用降低了其生物可利用性，MAOM 在土壤中表现出显著的持久性[48]。多项研究结果表明，MAOM 主要由微生物来源的生物大分子构成[12-14, 49-53]。基于热解-气相色谱/质谱（Py-GC/MS）、核磁共振（NMR）和傅里叶变换红外光谱（FTIR）等多种分析技术，已明确多糖和蛋白质是 MAOM 的主要成分，其含量分别约占 20%~85%和 10%~30%。在来源判别方面，常采用半乳糖与甘露糖之和与阿拉伯糖与木糖之和的比值（galactose + mannose to arabinose + xylose, GM/AX）来分析 MAOM 中多糖的来源。通常认为，GM/AX < 0.5 主要指示植物来源，> 2 则倾向于指示微生物来源[54-55]。已有研究发现，MAOM 中该比值通常处于 1.5~4.1[50, 56-57]，表明其中多糖具有显著的微生物来源特征。Ludwig 等[57]还通过计算 C_4 至 C_{26} 脂肪酸（通常代表微生物来源）的离子强度总和与 C_{26} 至 C_{38} 脂肪酸（代表植物来源）的离子强度总和来判断微生物源有机质的贡献。结果显示，颗粒有机质（Particulate organic matter, POM）中短链脂肪酸与长链脂肪酸的比值为 5.8~12.4，而在 MAOM 中则高达 240，进一步支持了 MAOM 中微生物来源组分占优势的结论[58]。值得注意的是，基于单糖和脂肪酸指标区分植物与微生物来源仍存在一定局限性。例如，植物源有机质包括其组织及分泌物同样含有半乳糖和甘露糖[59]。此外，植物亦可直接产生短链脂肪酸，而微生物对植物源物质的胞外分解作用也可能将长链脂肪酸转化为短链[60-61]，从而干扰有机质来源判别。综合来看，多糖与蛋白质可占 MAOM 总量的 30%~90%，而微生物细胞残体的占比通常不足 40%[62]。尽管现有数据无法直接定量评估 MAOM 中 EPS 的含量，但这一显著差距表明，除植物来源有机质与微生物胞内的蛋白质与多糖外，微生物胞外代谢产物 EPS 可能是 MAOM 中生物大分子的重要来源。

EPS 对矿物表面具有极强的亲和力，其分子结构中富含羧基、磷酸基、酰胺基、氨基和羟基等多种官能团，能够通过配体交换、静电作用等机制强烈吸附于矿物表面，形成稳定的有机-矿物复合体[9, 63]。有研究发现，当 EPS 通过配体交换与三水铝石形成稳定复合物后，约 99%的吸附态 EPS 可抵抗微生物降解[64]。吸附强度受 EPS 组成、孔隙水化学性质、矿物类型等因素共同影响。例如，EPS 中的蛋白质倾向于通过静电与疏水作用吸附于蒙脱石、高岭石等层状硅酸盐，而核酸等含磷组分更容易与针铁矿等铁氧化物结合[63, 65]。土壤孔隙水化学条件包括 pH 和离子强度可通过调控氢键、配体交换和静电相互作用影响吸附行为。在低离子强度下，EPS 中的羧基和磷酸基团优先吸附在针铁矿表面；而在高离子强度下，酰胺基作用增强，从而提升 EPS 的整体吸附能力[66-67]。EPS 还可作为微生物细胞及其残体的黏附媒介，通过增强黏附力并减弱静电排斥，促进其在矿物表面的附着[68]。研究表明，去除表面 EPS 会降低细菌在矿物上的黏附效率与稳定性[69]。鉴于 EPS 在土壤中产量丰富且对矿物表面具有强亲和力，它被视为 MAOM 形成的关键前体与天然黏合剂。然而，现有关于 EPS 与矿物互作的研究大多基于实验室模拟体系，EPS 在土壤中参与 MAOM 形成的过程及其稳定性还缺乏有效表征与定量认识。

2.2 直接途径：作为地质聚合反应的潜在前体

近期研究提出，地质聚合作用是土壤有机质稳定化的关键机制之一[70-71]。该过程通过美拉德型反应，使含氨基化合物与还原糖发生缩合，形成分子量大于 1 000 $g \cdot mol^{-1}$ 的芳香族类大分子。由于此类地质聚合物质分子量高、结构复杂，能够有效抵抗微生物代谢和胞外酶水

解，从而在土壤中稳定存在。尽管美拉德型反应通常需要在火烧过程等高温条件（>100°C）下进行[72-73]，但近期研究表明，铁锰矿物（如水钠锰矿）和黏土矿物可以在土壤常温（25~45°C）下催化该反应[74-75]，促进类腐殖质物质的生成，其性质与自然土壤中广泛存在的腐殖质高度相似。

EPS 富含可提供氨基与还原糖的蛋白质与多糖组分，并具有较强的矿物表面吸附能力，满足美拉德型聚合反应发生的基本条件。已有研究表明，在温度高于 120 °C 的污泥水热处理过程中，EPS 生物大分子之间可发生美拉德反应[76-77]。除大分子间的直接反应外，EPS 水解产生的单糖、寡肽等小分子物质也可进一步聚合，形成更大分子量的化合物[78-79]。虽然 EPS 是土壤中发生美拉德型聚合反应的理想底物，但目前仍缺乏直接证据证实 EPS 在常温土壤环境中能够在矿物表面发生此类聚合反应。

2.3 间接途径：EPS 驱动的土壤团聚作用

土壤团聚体通过物理闭塞作用，将有机碳封存于致密的矿物-有机复合体中。在未受扰动的天然土壤中，团聚体中 SOC 的周转时间可达 200 至 320 年[80-81]。EPS 作为团聚体形成的关键调节因子，其含量与土壤团聚程度密切相关。田间研究显示，EPS 蛋白质和多糖含量与团聚体粒径、水稳定性等多个土壤团聚指标均呈显著正相关[16, 43, 82-88]。机理分析进一步揭示了 EPS 主要通过静电屏蔽、桥接与胶结的多重作用机制驱动土壤团聚体的形成[89]。EPS 吸附于矿物表面可改变界面性质。前期研究发现，即使微量 EPS 吸附于赤铁矿表面，也能使其表面电位降至接近零，有效消除矿物颗粒间的静电排斥，诱发颗粒发生强烈团聚[15]。在此基础上，EPS 组分的高分子量特性通过聚合物桥接作用，促进土壤颗粒团聚[90]。此外，EPS 还通过物理包裹作用在团聚体内部形成有机桥接结构，增强其对外力扰动和侵蚀作用的抵抗能力[91]。

在动态环境扰动下，EPS 的团聚功能尤为显著。例如，在干湿交替过程中，EPS 多糖可作为瞬时黏合剂，通过干燥时产生的液桥效应驱动颗粒聚集，且该团聚过程对颗粒表面电荷特性及孔隙水化学性质（如 pH、电导率）的依赖性相对较弱[89]。这一特性在实验中得到验证：即使在存在静电排斥的情况下，当动态水合作用等外力缩短接触距离时，EPS 包裹的微生物细胞仍能牢固黏附于带同种电荷的矿物表面，且黏附强度随接触时间延长而增强，并呈现对 pH 依赖性减弱的趋势[91-92]。干旱区生物土壤结皮是体现上述 EPS 团聚功能的典型实例。微生物分泌的 EPS 将矿物与尘埃颗粒团聚成致密表层结皮，与下层松散颗粒形成鲜明对比[93]。尽管 EPS 在促进土壤团聚体形成及提升结构稳定性方面的作用已得到广泛认可，但其介导的 SOC 闭蓄保护效应仍缺乏系统性的定量表征，有待进一步深入研究。

2.4 间接途径：土壤孔隙结构与连通性的修饰

微生物、胞外酶和 SOC 在土壤中的分布表现出显著的空间异质性，该特性通过限制微生物与底物间的相互作用来增强 SOC 的持久性[94]。作为重要的生物胶结剂，EPS 可通过调节土壤孔隙结构与孔隙度，进一步强化这种空间异质性。例如，EPS 介导的团聚过程会显著影响孔隙度、孔隙数量及孔径分布[95]，导致孔隙通道缩窄，限制底物扩散，并形成物理隔离的空间分区。已有研究表明，孔径尺寸是调控 SOC 转化的关键因素之一。当通道直径<10 μm 的小孔隙时会限制氧气扩散且降低微生物多样性，从而抑制矿化作用[96-97]。30~60 μm 范围内的大孔隙则有利于微生物活动，加速 SOC 的分解[98-99]。近期研究还发现，较大的孔隙空间能够缓解微生境空间限制，提升土壤生物膜的系统发育与功能多样性[100]。

EPS 独特的水凝胶性质使其还具有直接堵塞孔隙空间的作用[43, 101-102]。EPS 基质的渗透性远低于土壤矿物基质。例如，在玻璃珠柱体系中添加 1%的 EPS，即可将水力传导率从 1.5×10^{-5} m·s^{-1} 急剧降低至 5.4×10^{-10} m·s^{-1}，接近纯 EPS 自身的低渗透水平[103]。此外，EPS 的积累还可促进土壤生物膜形成，引发生物堵塞效应。土壤生物膜形成会占据原有的孔隙空间，不仅降低了可供液体流动的有效孔隙度，还削弱了土壤的水文连通性。已有研究表明，EPS

合成细菌能够显著降低多孔介质的渗透性并减少有效孔隙度，从而限制 POM、EPS 或微生物细胞等物质的迁移[103-105]。这一过程通过强化空间隔离与封闭效应，为 SOC 的长期保存提供了关键物理屏障。然而，现有研究主要关注 EPS 对地下孔隙环境的改造作用，针对 EPS 在实际土壤体系中对孔隙结构影响的定量表征仍然不足，由此引发的固碳效应亦缺乏系统评估。

3 展 望

基于现有研究，本文提出 EPS 是土壤 SOC 循环中重要但长期被忽视的微生物源有机质。其合成速率与土壤微生物细胞生物量相当，并在矿物表面和土壤团聚体内表现出较强的稳定潜力。这些多重特征表明，EPS 不仅是土壤微生物碳泵（Microbial carbon pump, MCP）框架中不可忽视的关键产物，也为深化对微生物驱动的土壤碳生物地球化学循环的理解提供了全新视角。尽管 EPS 在 SOC 固存中的重要性正逐渐得到认识，但在其提取方法、定量手段以及对土壤碳库贡献评估等方面仍存在重要知识空白。为系统梳理未来研究的关键科学问题与发展路径，本文构建了土壤 EPS 驱动 SOC 稳定的未来研究概念框架（如图 2），并建议围绕以下三个方向展开深入探索：

（1）EPS 的提取、定量与表征技术。

有效提取并准确定量土壤 EPS 是深入解析其生态功能的前提。当前广泛采用的 CER 提取方法主要针对通过二价阳离子结合的 EPS 组分，仅能获取土壤部分 EPS，并且共提取土壤非微生物来源有机质，从而引入较大不确定性[41-42]。鉴于开发能够无污染分离全部土壤 EPS 的提取方法仍面临较大挑战，未来研究应致力于筛选可用于 EPS 定量的特异性生物标志物，类似于以氨基糖作为微生物残体标志物的研究思路。在此基础上，还需建立能够追踪新合成 EPS 的技术路径，例如利用 ^{18}O-H_2O 或 ^{13}C 标记有机物，动态监测微生物对 EPS 的合成过程。尽管近期研究表明忽略 EPS 合成会导致微生物 CUE 被严重低估[46-47]，但土壤中 EPS 的实际合成速率仍缺乏直接的实验数据。相关方法的发展将有助于提高 CUE 估算的准确性，并减少由 CUE 偏差导致的 SOC 预测的不确定性[106]。除了 EPS 储量特征外，其组成也值得深入研究。EPS 的化学组成对其在土壤中的生态功能具有决定性影响。例如，其官能团类型直接调控了其与矿物的吸附亲和力[107]。然而，由于 EPS 组分复杂，现有研究多依赖于破坏性提取后进行光谱官能团分析或通过水解后测定其单糖与氨基酸组成[9, 108]。未来研究亟需发展原位、无损的表征技术，以实现对土壤基质中 EPS 动态变化过程的精细刻画与定量解析。

（2）EPS 在 SOC 稳定和模拟中的作用。

除地质聚合作用仍有待更多的实证支持外，EPS 通过矿物吸附、团聚体形成及孔隙调控等途径对 SOC 的稳定作用已在实验室条件下得到验证。然而，这些机制在真实土壤环境中的相对贡献与耦合效应仍不明确。未来研究中需结合 EPS 量化表征与同位素示踪技术，阐明其与受保护碳组分（如 MAOM、团聚体包埋碳）的关联强度与贡献程度。研究视角还应拓展至 EPS 介导的间接保护作用，例如，在矿物表面和团聚体内对微生物细胞残体与 POM 等其他有机质组分的稳定作用。近期证据显示，EPS 含量与 SOC 积累的相关性强于细胞残体[109-110]，这暗示 EPS 可能是土壤碳汇形成的关键驱动因子[109-110]。因此，将 EPS 过程纳入 SOC 周转模型对提升 SOC 动态预测能力具有重要意义。然而，目前关于 EPS 在土壤中周转动态的研究仍十分匮乏。已有研究通过比较污泥来源的 DOM 与 EPS 在土壤中的降解过程发现，EPS 具有更高的稳定性，其在土壤中的半衰期约为 10 至 30 天[20]。基于 ^{13}C 标记 EPS 与 DNA-SIP 技术的研究表明[111-112]，加入土壤的 EPS 主要被浮霉菌门（Planctomycetes）、疣

微菌门（Verrucomicrobia）、子囊菌门（Ascomycota）和担子菌门（Basidiomycota）等微生物类群同化，并且这些微生物类群中富集了淀粉酶和内切葡聚糖酶等与 EPS 降解相关的功能基因。由于动力学参数的缺乏，现有模型可借鉴污水处理等领域中关于 EPS 动态的研究成果进行类比估算。通过在模型中纳入微生物胞外产物的生成与转化路径，有望显著降低当前 SOC 模型在模拟长期碳动态时的不确定性。在此基础上，进一步开展不同气候情景下 EPS 动态的系统研究，以定量评估其对 SOC 库的长期贡献，将为制定科学有效的气候变化缓解策略提供重要理论支撑。

（3）土壤 EPS 的环境和微生物驱动机制。

明确调控土壤 EPS 含量与组成的关键因素是预测并管理其动态过程的基础。合成分泌 EPS 是微生物响应环境的关键适应性策略。在污水处理体系与纯培养研究中已证实，微生物种类、底物类型、碳氮比、干旱胁迫及矿物等因素均能显著影响 EPS 的产量与组成[113-115]。然而，在更为复杂的土壤生态系统中，关于 EPS 合成的环境驱动机制研究仍较为匮乏。土壤 EPS 合成与分泌受环境因素调控，同时 EPS 通过增强土壤持水性、团聚体稳定性和微生物抗逆性，对土壤理化特性及微生物过程产生反馈作用。然而，目前对这一闭环反馈机制的认识尚不充分。例如，在干旱胁迫下，EPS 组成变化将如何影响土壤水分动态与微生物活性？这些变化又如何进一步反馈于 EPS 合成与 SOC 积累？阐明上述反馈效应，对于提升气候变化背景下土壤碳动态预测的准确性具有关键意义。此外，未来研究亟需整合宏基因组学、宏转录组学、代谢组学与 DNA 稳定性同位素探针（DNA-SIP）等多组学技术，系统识别不同陆地生态系统中参与 EPS 合成的关键微生物类群、代谢途径及其调控机制。深入解析上述驱动机制，不仅能完善 SOC 形成与稳定理论，也有助于构建更精准的土壤碳循环模型，还将为提升土壤增汇潜力、优化碳管理策略及应对全球气候变化提供科学依据[116-117]。

注：蓝色、橙色和绿色模块分别代表方法验证与技术优化、定量贡献与模型整合以及环境驱动与调控机制三个研究方向。箭头表示 EPS、微生物过程、环境因子与 SOC 稳定之间潜在的调控路径与反馈关系。下部生态系统示意图表示 EPS 介导 SOC 稳定在提升碳循环预测能力、促进土壤碳库稳定与增汇、支持可持续土壤管理以及应对气候变化与生态安全中的生态意义。Note: Blue, orange, and green panels represent methodological validation and technical optimization, quantitative contribution and model integration, and environmental driving and regulatory mechanisms, respectively. Arrows indicate potential regulatory pathways and feedback relationships among EPS, microbial processes, environmental factors, and SOC stabilization. The lower ecosystem schematic illustrates the ecological implications of EPS-mediated SOC stabilization, including improved carbon-cycle prediction, soil carbon sequestration and stabilization, sustainable soil management, and responses to climate change and ecological security.

图 2 土壤 EPS 驱动 SOC 稳定的未来研究概念框架。（以彩图发表）

Fig. 2 Conceptual framework for future research on soil EPS-driven SOC stabilization

参考文献（References）

[1] Lal R. Soil carbon sequestration impacts on global climate change and food security[J]. Science, 2004, 304(5677): 1623-1627.

[2] Liang C. Soil microbial carbon pump: Mechanism and appraisal[J]. Soil Ecology Letters, 2020, 2(4): 241-254.

[3] Zhu X, Jackson R D, DeLucia E H, et al. The soil microbial carbon pump: From conceptual insights to empirical assessments[J]. Global Change Biology, 2020, 26(11): 6032-6039.

[4] Liang C, Schimel J P, Jastrow J D. The importance of anabolism in microbial control over soil carbon storage[J]. Nature Microbiology, 2017, 2(8): 1-6.

[5] Flemming H-C, Wingender J. The biofilm matrix[J]. Nature Reviews Microbiology, 2010, 8(9): 623-633.

[6] Tourney J, Ngwenya B T. The role of bacterial extracellular polymeric substances in geomicrobiology[J]. Chemical Geology, 2014, 386: 115-132.

[7] More T, Yadav J S S, Yan S, et al. Extracellular polymeric substances of bacteria and their potential environmental applications[J]. Journal of Environmental Management, 2014, 144: 1-25.

[8] Flemming H-C, van Hullebusch E D, Little B J, et al. Microbial extracellular polymeric substances in the environment, technology and medicine[J]. Nature Reviews Microbiology, 2025, 23(2): 87-105.

[9] Zhang M, Xu Y, Xiao K-Q, et al. Characterising soil extracellular polymeric substances (EPS) by application of spectral-chemometrics and deconstruction of the extraction process[J]. Chemical Geology, 2023, 618: 121271.

[10] Ye L, Wu J, Huang M, et al. The role of suspended extracellular polymeric substance (EPS) on equilibrium flocculation of clay minerals in high salinity water[J]. Water Research, 2023, 244: 120451.

[11] Ren L, Hong Z, Qian W, et al. Adsorption mechanism of extracellular polymeric substances from two bacteria on Ultisol and Alfisol[J]. Environmental Pollution, 2018, 237: 39-49.

[12] Almeida L F, Souza I F, Hurtarte L C, et al. Forest litter constraints on the pathways controlling soil organic matter formation[J]. Soil Biology & Biochemistry, 2021, 163: 108447.

[13] Marchal L, Garcia‐Franco N, Gateuille D, et al. Polycyclic aromatic hydrocarbon contents in soil organic matter fractions along an elevation gradient in the French Alps[J]. European Journal of Soil Science, 2025, 76(1): e70059.

[14] Angst G, Mueller K E, Kögel-Knabner I, et al. Aggregation controls the stability of lignin and lipids in clay-sized particulate and mineral associated organic matter[J]. Biogeochemistry, 2017, 132(3): 307-324.

[15] Narvekar S P, Ritschel T, Totsche K U. Colloidal stability and mobility of extracellular polymeric substance amended hematite nanoparticles[J]. Vadose Zone Journal, 2017, 16(8): 1-10.

[16] Redmile-Gordon M, Gregory A, White R, et al. Soil organic carbon, extracellular polymeric substances (EPS), and soil structural stability as affected by previous and current land-use[J]. Geoderma, 2020, 363: 114143.

[17] Zhang M, Wu Y, Qu C, et al. Microbial extracellular polymeric substances (EPS) in soil: From interfacial behaviour to ecological multifunctionality[J]. Geo-Bio Interfaces, 2024, 1: e4.

[18] Costa O Y, Raaijmakers J M, Kuramae E E. Microbial extracellular polymeric substances: ecological function and impact on soil aggregation[J]. Frontiers in Microbiology, 2018, 9: 1636.

[19] Rossi F, Mugnai G, De Philippis R. Complex role of the polymeric matrix in biological soil crusts[J]. Plant and Soil, 2018, 429(1): 19-34.

[20] Zhou L, Zhou S, Zhan X. Sorption and biodegradability of sludge bacterial extracellular polymers in soil and

their influence on soil copper behavior[J]. Journal of Environmental Quality, 2004, 33(1): 154-162.
[21] Wingender J, Neu T R, Flemming H-C. Microbial extracellular polymeric substances: characterization, structure, and function[M]. Berlin, Heidelberg: Springer, 1999.
[22] McDonald M D, Owusu-Ansah C, Ellenbogen J B, et al. What is microbial dormancy[J]. Trends in Microbiology, 2024, 32(2): 142-150.
[23] Ma W T, Peng D H, Walker S L, et al. Bacillus subtilis biofilm development in the presence of soil clay minerals and iron oxides[J]. npj Biofilms and Microbiomes, 2017, 3: 4.
[24] Krause L, Biesgen D, Treder A, et al. Initial microaggregate formation: Association of microorganisms to montmorillonite-goethite aggregates under wetting and drying cycles[J]. Geoderma, 2019, 351: 250-260.
[25] Gorbushina A A. Life on the rocks[J]. Environmental Microbiology, 2007, 9(7): 1613-1631.
[26] Blagodatskaya E, Kuzyakov Y. Active microorganisms in soil: Critical review of estimation criteria and approaches[J]. Soil Biology & Biochemistry, 2013, 67: 192-211.
[27] Joergensen R G, Wichern F. Alive and kicking: Why dormant soil microorganisms matter[J]. Soil Biology & Biochemistry, 2018, 116: 419-430.
[28] Singh S, Mayes M A, Kivlin S N, et al. How the Birch effect differs in mechanisms and magnitudes due to soil texture[J]. Soil Biology & Biochemistry, 2023, 179: 108973.
[29] Eichorst S A, Breznak J A, Schmidt T M. Isolation and characterization of soil bacteria that define Terriglobus gen. nov., in the phylum Acidobacteria[J]. Applied and Environmental Microbiology, 2007, 73(8): 2708-2717.
[30] Malik A A, Martiny J B, Brodie E L, et al. Defining trait-based microbial strategies with consequences for soil carbon cycling under climate change[J]. The ISME Journal, 2020, 14(1): 1-9.
[31] Feng M, Zhang M, Cai P, et al. Increased microbial extracellular polymeric substances as a key factor in deep soil organic carbon accumulation[J]. Soil Biology & Biochemistry, 2026, 212: 109998.
[32] Zhang H, Chen J, Hu Y, et al. Increased contributions of microbial extracellular polymeric substance to soil organic carbon during grassland degradation[J]. Global Change Biology, 2026, 32(3): e70821.
[33] Shi K, Zheng Q, Wang B, et al. Continental-scale drivers of soil microbial extracellular polymeric substances[J]. Nature Communications, 2026, 17: 3334.
[34] Flemming H-C, van Hullebusch E D, Neu T R, et al. The biofilm matrix: Multitasking in a shared space[J]. Nature Reviews Microbiology, 2023, 21(2): 70-86.
[35] Rashid M, Siddiqui K. The stability of extracellular β-glucosidase from Aspergillus niger is significantly enhanced by non-covalently attached polysaccharides[J]. Folia microbiologica, 1996, 41(4): 341-346.
[36] Iwashita K, Shimoi H, Ito K. Extracellular soluble polysaccharide (ESP) from Aspergillus kawachii improves the stability of extracellular β-gluocosidases (EX-1 and EX-2) and is involved in their localization[J]. Journal of Bioscience and Bioengineering, 2001, 91(2): 134-140.
[37] Op De Beeck M, Troein C, Siregar S, et al. Regulation of fungal decomposition at single-cell level[J]. The ISME Journal, 2020, 14(4): 896-905.
[38] De Beeck M O, Persson P, Tunlid A. Fungal extracellular polymeric substance matrices–highly specialized microenvironments that allow fungi to control soil organic matter decomposition reactions[J]. Soil Biology & Biochemistry, 2021, 159: 108304.
[39] Tielen P, Kuhn H, Rosenau F, et al. Interaction between extracellular lipase LipA and the polysaccharide alginate of Pseudomonas aeruginosa[J]. BMC Microbiology, 2013, 13(1): 159.
[40] Redmile-Gordon M, Brookes P, Evershed R, et al. Measuring the soil-microbial interface: Extraction of extracellular polymeric substances (EPS) from soil biofilms[J]. Soil Biology & Biochemistry, 2014, 72: 163-171.
[41] Chen Y, Luo X, Wu Y, et al. Quantifying the trade-off between yield and contamination in soil EPS extraction

using cation exchange resin[J]. Journal of Soils & Sediments, 2025, 25: 2008-2016.
[42] Wang S, Redmile-Gordon M, Mortimer M, et al. Extraction of extracellular polymeric substances (EPS) from red soils (Ultisols)[J]. Soil Biology & Biochemistry, 2019, 135: 283-285.
[43] Luo Y, Lopez J B G, van Veelen H P J, et al. Effects of different soil organic amendments (OAs) on extracellular polymeric substances (EPS)[J]. European Journal of Soil Biology, 2024, 121: 103624.
[44] Giri S, Debroy A, Nag A, et al. Evaluating the role of soil EPS in modifying the toxicity potential of the mixture of polystyrene nanoplastics and xenoestrogen, Bisphenol A (BPA) in *Allium cepa* L.[J]. Journal of Hazardous Materials, 2024, 477: 135252.
[45] Nazari M, Bickel S, Benard P, et al. Biogels in soils: Plant mucilage as a biofilm matrix that shapes the rhizosphere microbial habitat[J]. Frontiers in Plant Science, 2022, 12: 798992.
[46] Hu W, Cai Y, Li X, et al. Microbial carbon accumulation efficiency in global soils resolved via 13C‐glucose amendment experiments[J]. Global Biogeochemical Cycles, 2025, 39(6): e2025GB008553.
[47] Bölscher T, Vogel C, Olagoke F K, et al. Beyond growth: The significance of non-growth anabolism for microbial carbon-use efficiency in the light of soil carbon stabilisation[J]. Soil Biology & Biochemistry, 2024, 193: 109400.
[48] Kögel‐Knabner I, Guggenberger G, Kleber M, et al. Organo‐mineral associations in temperate soils: Integrating biology, mineralogy, and organic matter chemistry[J]. Journal of Plant Nutrition and Soil Science, 2008, 171(1): 61-82.
[49] Bol R, Poirier N, Balesdent J, et al. Molecular turnover time of soil organic matter in particle‐size fractions of an arable soil[J]. Rapid Communications in Mass Spectrometry, 2009, 23(16): 2551-2558.
[50] Dümig A, Häusler W, Steffens M, et al. Clay fractions from a soil chronosequence after glacier retreat reveal the initial evolution of organo–mineral associations[J]. Geochimica et Cosmochimica Acta, 2012, 85: 1-18.
[51] Grandy A S, Neff J C. Molecular C dynamics downstream: The biochemical decomposition sequence and its impact on soil organic matter structure and function[J]. Science of the Total Environment, 2008, 404(2/3): 297-307.
[52] Grandy A S, Neff J C, Weintraub M N. Carbon structure and enzyme activities in alpine and forest ecosystems[J]. Soil Biology and Biochemistry, 2007, 39(11): 2701-2711.
[53] Prater I, Zubrzycki S, Buegger F, et al. From fibrous plant residues to mineral-associated organic carbon–the fate of organic matter in Arctic permafrost soils[J]. Biogeosciences, 2020, 17(13): 3367-3383.
[54] Oades J M. Soil organic matter and structural stability: Mechanisms and implications for management[J]. Plant and Soil, 1984, 76(1): 319-337.
[55] Gunina A, Kuzyakov Y. Sugars in soil and sweets for microorganisms: Review of origin, content, composition and fate[J]. Soil Biology & Biochemistry, 2015, 90: 87-100.
[56] Amelung W, Flach K W, Zech W. Neutral and acidic sugars in particle‐size fractions as influenced by climate[J]. Soil Science Society of America Journal, 1999, 63(4): 865-873.
[57] Ludwig M, Achtenhagen J, Miltner A, et al. Microbial contribution to SOM quantity and quality in density fractions of temperate arable soils[J]. Soil Biology & Biochemistry, 2015, 81: 311-322.
[58] Schnitzer M, Hindle C, Meglic M. Supercritical gas extraction of alkanes and alkanoic acids from soils and humic materials[J]. Soil Science Society of America Journal, 1986, 50(4): 913-919.
[59] Angers D, Mehuys G R. Barley and alfalfa cropping effects on carbohydrate contents of a clay soil and its size fractions[J]. Soil Biology & Biochemistry, 1990, 22(3): 285-288.
[60] Angst G, John S, Mueller C W, et al. Tracing the sources and spatial distribution of organic carbon in subsoils using a multi-biomarker approach[J]. Scientific Reports, 2016, 6(1): 29478.
[61] Saiz‐Jimenez C, Hermosín B, Guggenberger G, et al. Land use effects on the composition of organic matter

in soil particle size separates. III. Analytical pyrolysis[J]. European Journal of Soil Science, 1996, 47(1): 61-69.
[62] Angst G, Mueller K E, Nierop K G, et al. Plant- or microbial-derived: A review on the molecular composition of stabilized soil organic matter[J]. Soil Biology & Biochemistry, 2021, 156: 108189.
[63] Lin D, Ma W, Jin Z, et al. Interactions of EPS with soil minerals: A combination study by ITC and CLSM[J]. Colloids and Surfaces B: Biointerfaces, 2016, 138: 10-16.
[64] Mikutta R, Zang U, Chorover J, et al. Stabilization of extracellular polymeric substances (Bacillus subtilis) by adsorption to and coprecipitation with Al forms[J]. Geochimica et Cosmochimica Acta, 2011, 75(11): 3135-3154.
[65] Cao Y, Wei X, Cai P, et al. Preferential adsorption of extracellular polymeric substances from bacteria on clay minerals and iron oxide[J]. Colloids and Surfaces B: Biointerfaces, 2011, 83(1): 122-127.
[66] Fang L, Cao Y, Huang Q, et al. Reactions between bacterial exopolymers and goethite: A combined macroscopic and spectroscopic investigation[J]. Water Research, 2012, 46(17): 5613-5620.
[67] Cai P, Lin D, Peacock C L, et al. EPS adsorption to goethite: Molecular level adsorption mechanisms using 2D correlation spectroscopy[J]. Chemical Geology, 2018, 494: 127-135.
[68] Flynn R M, Yang X, Hofmann T, et al. Bovine serum albumin adsorption to iron-oxide coated sands can change microsphere deposition mechanisms[J]. Environmental Science & Technology, 2012, 46(5): 2583-2591.
[69] Zhao W, Walker S L, Huang Q, et al. Contrasting effects of extracellular polymeric substances on the surface characteristics of bacterial pathogens and cell attachment to soil particles[J]. Chemical Geology, 2015, 410: 79-88.
[70] Moore O W, Curti L, Woulds C, et al. Long-term organic carbon preservation enhanced by iron and manganese[J]. Nature, 2023, 621(7978): 312-317.
[71] Xiao K-Q, Zhao Y, Liang C, et al. Introducing the soil mineral carbon pump[J]. Nature Reviews Earth & Environment, 2023, 4(3): 135-136.
[72] Lopez A M, Avila C C E, VanderRoest J P, et al. Molecular insights and impacts of wildfire-induced soil chemical changes[J]. Nature Reviews Earth & Environment, 2024, 5(6): 431-446.
[73] Bahureksa W, Young R B, McKenna A M, et al. Nitrogen enrichment during soil organic matter burning and molecular evidence of Maillard reactions[J]. Environmental Science & Technology, 2022, 56(7): 4597-4609.
[74] Jokic A, Frenkel A, Vairavamurthy M, et al. Birnessite catalysis of the Maillard reaction: Its significance in natural humification[J]. Geophysical Research Letters, 2001, 28(20): 3899-3902.
[75] Wang Z, Zhao H, Shi Z, et al. Manganese dioxides induce the transformation and protection of dissolved organic matter simultaneously: A significance of crystallinity[J]. Environmental Science & Technology, 2025, 59(2): 1222-1231.
[76] Peng S, Hu A, Ai J, et al. Changes in molecular structure of extracellular polymeric substances (EPS) with temperature in relation to sludge macro-physical properties[J]. Water Research, 2021, 201: 117316.
[77] Wang Q, Xu Q, Du Z, et al. Mechanistic insights into the effects of biopolymer conversion on macroscopic physical properties of waste activated sludge during hydrothermal treatment: Importance of the Maillard reaction[J]. Science of the Total Environment, 2021, 769: 144798.
[78] Yang N, Zhang Y, Yang S. Structural characteristics of organics released from sludge pretreatment and their performance in the synthesis of biomass plastics[J]. Chemical Engineering Journal, 2024, 490: 151391.
[79] Yang N, Yang S, Yang L, et al. Exploration of browning reactions during alkaline thermal hydrolysis of sludge: Maillard reaction, caramelization and humic acid desorption[J]. Environmental Research, 2023, 217: 114814.
[80] Six J, Bossuyt H, Degryze S, et al. A history of research on the link between (micro) aggregates, soil biota, and soil organic matter dynamics[J]. Soil and Tillage Research, 2004, 79(1): 7-31.
[81] Totsche K U, Amelung W, Gerzabek M H, et al. Microaggregates in soils[J]. Journal of Plant Nutrition and Soil

Science, 2018, 181(1): 104-136.
[82] Ghasemzadeh Z, Parhizkar M, Zomorodian M, et al. The role of extracellular polysaccharide produced by Bradyrhizobium strain in root growth, improvement of soil aggregate stability and reduction of soil detachment capacity[J]. Rhizosphere, 2023, 27: 100771.
[83] Mai Z, Zeng X, Wei X, et al. Mangrove restoration promotes the anti-scouribility of the sediments by modifying inherent microbial community and extracellular polymeric substance[J]. Science of the Total Environment, 2022, 811: 152369.
[84] Olagoke F K, Bettermann A, Nguyen P T B, et al. Importance of substrate quality and clay content on microbial extracellular polymeric substances production and aggregate stability in soils[J]. Biology and Fertility of Soils, 2022, 58(4): 435-457.
[85] Peng Y, Zhang H, Li G, et al. Microbial inoculum improved soil aggregate formation and increased cucumber yield in a greenhouse under secondary salinization conditions[J]. Journal of Environmental Management, 2025, 376: 124576.
[86] Wang L, Huang Y, Yang Q, et al. Biocrust reduces the soil erodibility of coral calcareous sand by regulating microbial community and extracellular polymeric substances on tropical coral island, South China Sea[J]. Frontiers in Microbiology, 2023, 14: 1283073.
[87] Wang L, Li J, Zhang S, et al. Biological soil crust elicits microbial community and extracellular polymeric substances restructuring to reduce the soil erosion on tropical island, South China Sea[J]. Marine Environmental Research, 2024, 197: 106449.
[88] Zethof J H, Bettermann A, Vogel C, et al. Prokaryotic community composition and extracellular polymeric substances affect soil microaggregation in carbonate containing semiarid grasslands[J]. Frontiers in Environmental Science, 2020, 8: 51.
[89] Guhra T, Stolze K, Totsche K U. Pathways of biogenically excreted organic matter into soil aggregates[J]. Soil Biology & Biochemistry, 2022, 164: 108483.
[90] Lin D, Story S D, Walker S L, et al. Influence of extracellular polymeric substances on the aggregation kinetics of TiO2 nanoparticles[J]. Water Research, 2016, 104: 381-388.
[91] Guhra T, Ritschel T, Totsche K U. Formation of mineral–mineral and organo–mineral composite building units from microaggregate - forming materials including microbially produced extracellular polymeric substances[J]. European Journal of Soil Science, 2019, 70(3): 604-615.
[92] Pen Y, Zhang Z J, Morales-García A L, et al. Effect of extracellular polymeric substances on the mechanical properties of Rhodococcus[J]. Biochimica et Biophysica Acta (BBA)-Biomembranes, 2015, 1848(2): 518-526.
[93] Yu X, Xiao B, Cao Y, et al. Microbial-induced extracellular polymers are fundamentally responsible for the mechanical stability of biocrusts in drylands[J]. Catena, 2024, 245: 108349.
[94] Lehmann J, Hansel C M, Kaiser C, et al. Persistence of soil organic carbon caused by functional complexity[J]. Nature Geoscience, 2020, 13(8): 529-534.
[95] Mangalassery S, Sjögersten S, Sparkes D, et al. The effect of soil aggregate size on pore structure and its consequence on emission of greenhouse gases[J]. Soil and Tillage Research, 2013, 132: 39-46.
[96] Ruamps L S, Nunan N, Pouteau V, et al. Regulation of soil organic C mineralisation at the pore scale[J]. FEMS Microbiology Ecology, 2013, 86(1): 26-35.
[97] Kravchenko A N, Guber A K. Soil pores and their contributions to soil carbon processes[J]. Geoderma, 2017, 287: 31-39.
[98] Kravchenko A N, Negassa W C, Guber A K, et al. Protection of soil carbon within macro-aggregates depends on intra-aggregate pore characteristics[J]. Scientific Reports, 2015, 5(1): 16261.
[99] Ananyeva K, Wang W, Smucker A, et al. Can intra-aggregate pore structures affect the aggregate's effectiveness

in protecting carbon [J]. Soil Biology & Biochemistry, 2013, 57: 868-875.

[100] Fu C, Wu Y, Sørensen S J, et al. The mitigation of spatial constraint in porous environments enhances biofilm phylogenetic and functional diversity[J]. Microbiome, 2025, 13(1): 84.

[101] Chenu C. Clay- or sand-polysaccharide associations as models for the interface between micro-organisms and soil: Water related properties and microstructure[M]. Amsterdam: Elsevier, 1993.

[102] Kidron G J, Wang Y, Herzberg M. Exopolysaccharides may increase biocrust rigidity and induce runoff generation[J]. Journal of Hydrology, 2020, 588: 125081.

[103] Or D, Phutane S, Dechesne A. Extracellular polymeric substances affecting pore-scale hydrologic conditions for bacterial activity in unsaturated soils[J]. Vadose Zone Journal, 2007, 6(2): 298-305.

[104] Fei W, Ge Z, Zheng T, et al. Isolation, identification, and potential biotechnological application on soil porosity of the microbial exopolysaccharides (EPS) from bacillus polymyxa[J]. Biomacromolecules, 2025, 26(6): 3771-3785.

[105] Chenu C, Roberson E. Diffusion of glucose in microbial extracellular polysaccharide as affected by water potential[J]. Soil Biology & Biochemistry, 1996, 28(7): 877-884.

[106] Tao F, Huang Y, Hungate B A, et al. Microbial carbon use efficiency promotes global soil carbon storage[J]. Nature, 2023, 618(7967): 981-985.

[107] Zou M, Wu Y, Qu C, et al. Molecular composition determines the adsorption behaviors of loosely-and tightly-bound extracellular polymeric substances (EPS) from Shewanella oneidensis MR-1 on hematite nanoparticles[J]. Environmental Science: Nano, 2022, 9(12): 4459-4467.

[108] Felz S, Vermeulen P, van Loosdrecht M C, et al. Chemical characterization methods for the analysis of structural extracellular polymeric substances (EPS)[J]. Water Research, 2019, 157: 201-208.

[109] Shi K, Liao J, Zou X, et al. Accumulation of soil microbial extracellular and cellular residues during forest rewilding: Implications for soil carbon stabilization in older plantations[J]. Soil Biology & Biochemistry, 2024, 188: 109250.

[110] Fu Y, Xu Y, Wang Q, et al. Deciphering the microbial players driving straw decomposition and accumulation in soil components of particulate and mineral-associated organic matter[J]. Soil Biology & Biochemistry, 2025, 209: 109871.

[111] Costa O Y, De Hollander M, Pijl A, et al. Cultivation-independent and cultivation-dependent metagenomes reveal genetic and enzymatic potential of microbial community involved in the degradation of a complex microbial polymer[J]. Microbiome, 2020, 8(1): 76.

[112] Costa O Y, Pijl A, Kuramae E E. Dynamics of active potential bacterial and fungal interactions in the assimilation of acidobacterial EPS in soil[J]. Soil Biology & Biochemistry, 2020, 148: 107916.

[113] Li X Y, Yang S F. Influence of loosely bound extracellular polymeric substances (EPS) on the flocculation, sedimentation and dewaterability of activated sludge[J]. Water Research, 2007, 41(5): 1022-1030.

[114] Pal A, Paul A. Optimization of cultural conditions for production of extracellular polymeric substances (EPS) by serpentine rhizobacterium Cupriavidus pauculus KPS 201[J]. Journal of Polymers, 2013(1): 692374.

[115] Ye F, Ye Y, Li Y. Effect of C/N ratio on extracellular polymeric substances (EPS) and physicochemical properties of activated sludge flocs[J]. Journal of Hazardous Materials, 2011, 188(1/3): 37-43.

[116] Bradford M A, Wieder W R, Bonan G B, et al. Managing uncertainty in soil carbon feedbacks to climate change[J]. Nature Climate Change, 2016, 6(8): 751-758.

[117] Saha I, Datta S, Biswas D. Exploring the role of bacterial extracellular polymeric substances for sustainable development in agriculture[J]. Current Microbiology, 2020, 77(11): 3224-3239.

（责任编辑：檀满枝）