

添加菌剂对厨余垃圾堆肥细菌共现网络和代谢功能的影响

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摘 要:为解决厨余垃圾堆肥周期长、臭气排放强的问题, 构建接种固定化功能菌剂的堆肥体系, 以未接种组为对照, 系统监测堆体理化性质, 结合 16S rRNA 高通量测序分析细菌群落结构, 构建不同阶段的细菌共现网络, 并运用功能预测与偏最小二乘路径模型, 解析固定化功能菌剂在堆肥系统中的生态调控作用及其对微生物网络与代谢功能的影响机制。菌剂组高温期更持久、温度更稳定。第 15 天堆肥成熟时, 种子发芽指数达到 88.89%, 高于对照组的 58.89%。菌剂处理显著改变了细菌群落结构, 并增强了确定性组装过程。与对照组相比, 增强了与降解和营养转化相关的功能菌群富集, 提高了网络连通性与协同互作水平。功能预测结果显示, 菌剂提升了碳氮循环相关功能的相对丰度, 降低了硫循环相关功能的相对丰度, 降低了臭气生成潜势。固定化菌剂通过改善堆体理化环境、重构微生物网络与代谢功能, 实现堆肥效率提升与臭气减排的协同优化, 为厨余垃圾堆肥的高效与清洁化提供了生态学依据。

关键词:厨余垃圾; 菌剂; 细菌群落; 共现网络; 代谢功能; 偏最小二乘路径模型

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0 引 言

随着人口增长和饮食结构变化, 厨余垃圾 (kitchen waste, KW) 产生量迅速增加, 已成为城市固体垃圾的重要组成部分。全球评估数据显示, 厨余垃圾年产生量已超 13 亿 t, 预计到 2050 年将增加至 22 亿 t^[1]。厨余垃圾成分复杂、异质性强, 通常富含易降解有机物 (如淀粉、蛋白质、脂质等) 和结构复杂、生物可利用性差的木质纤维素等物质^[2], 同时具有高油盐、高有机质、高含水率等特征。若管理不当, 厨余垃圾会迅速腐解, 产生渗滤液和恶臭气体, 滋生病原微生物, 对空气、水体、土壤环境及人类健康造成威胁^[3-4]。

堆肥是目前处理高有机质固废的主要生物技术之一, 具有操作简便、过程可控、成本较低、资源化程度高等优点^[5]。通过微生物的分解和矿化作用, 堆肥可将淀粉、纤维素和蛋白质等有机物转化为腐殖质和养分, 实现养分循环与资源再利用^[6]。然而, 传统堆肥工艺仍存在发酵周期长、产品质量不稳定及臭气排放难以控制等问题,

限制了其在厨余垃圾资源化领域的广泛推广^[7-8]。

近年来, 针对堆肥性能的优化研究持续深入, 调控通风效率、碳氮比、湿度和 pH 等工艺参数, 或应用添加剂, 均被证实可改善堆肥过程^[9-10]。然而, 这些措施往往增加成本, 并可能抑制部分微生物活性甚至引发二次污染。相比之下, 微生物接种技术作为一种生物强化策略, 具有低成本、高选择性和可持续性等优势。研究表明, 由功能菌株组成的微生物菌剂可加速有机物降解、改善堆肥理化条件, 并抑制恶臭气体产生^[11-13]。CHEN 等^[14]构建了含有耐热硫化物氧化菌的复合菌群, 减少了堆肥过程中的臭气排放, 增加了营养保存, 加速了堆肥进程。LI 等^[15]发现, 添加微生物菌剂可以调节高温阶段的酶活性, 促进碳水化合物和蛋白质的代谢转化, 从而提高堆肥成熟度。考虑到厨余垃圾堆肥体系具有高含水率、高温和强油盐胁迫等特征, 外加游离菌在堆肥过程中易发生快速流失或失活。采用固定化方式可提高外源功能菌在堆肥环境中的存活稳定性和持续作用能力, 固定化载体兼具微生物附着支撑和缓释营养的功能, 有利于功能菌在堆肥体系中的定植与协同作用^[16]。

微生物是堆肥系统的核心驱动力, 在有机物降解、养分转化及腐殖质形成过程中发挥关键作用。外源微生物的引入可能改变原有堆肥系统的微生物生态位, 影响群落组成、相互作用和系统功能。近年来, 微生物共现网络分析被广泛应用于解析环境微生物群落间的潜在互作关系。该方法能够定量刻画微生物之间的协同与拮抗模式, 识别关键类群 (keystone taxa), 并揭示系统稳定性。ZHANG 等^[17]在堆肥系统接种嗜热菌, 提高了细菌

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丰富度和多样性,增加了微生物共现网络的连通性和复杂性;LIU等^[18]发现微生物接种有利于有益菌群富集,强化碳、氮、硫等养分代谢通路;ZHAO等^[19]和LIU等^[16]报道了不同微生物接种物可能对微生物群落和功能产生不同影响,表现为富集有益菌群,促进养分转化与保留,增强微生物之间交互作用,作为微生物网络的核心物种等,表明微生物网络结构可能是堆肥系统功能差异的重要生态基础。

然而,已有研究多从群落组成和功能基因层面探讨菌剂在堆肥过程中的作用,但关于菌剂如何通过改变微生物互作关系影响堆肥系统稳定性与功能表现的机制仍不清楚。特别是不同堆肥阶段微生物网络结构的动态演变及其与系统功能(如有机物降解与堆肥成熟度)的关联尚缺乏系统性分析。本研究以自制功能型微生物菌剂堆肥体系为研究对象,设置对照组和菌剂组,系统监测堆肥过程中理化参数及微生物群落结构变化。通过构建4个堆肥阶段的微生物共现网络,分析菌剂接种对堆肥系统微生物群落和功能的影响,并结合理化指标与腐熟度指标评价堆肥效率,以期揭示菌剂调控堆肥微生物网络结构和系统稳定性的生态机制。

1 材料与方法

1.1 堆肥原料和试验设计

试验所用厨余垃圾收集自内蒙古巴彦淖尔市餐厅。玉米秸秆从巴彦淖尔市周边农田收集,经自然风干后机械粉碎至小于5 cm,用于调节厨余垃圾堆肥的含水率和碳氮比。原料的初始理化性质见表1。试验设置两种处理:1)对照组堆肥:170 kg厨余垃圾与60 kg玉米秸秆混合堆肥;2)菌剂组堆肥:170 kg厨余垃圾与60 kg玉米秸秆混合堆肥,并接种前期研发的固定化菌剂(IBC,4%)。菌剂包含根据厨余垃圾主要组分降解、养分转化和臭气控制性能筛选出的功能互补的六株功能菌:*Bacillus velezensis* (AS 1.923)、*Bacillus licheniformis* (ATCC 11946)、*Bacillus megaterium* (CICC 22681)、*Bacillus subtilis* (CGMCC 1.14985)、*Aneurinibacillus thermoaerophilus* (DSM 10154)和*Bacillus safensis* (CICC 21743),采用的固定化载体为碎花生壳、小麦麸皮和鱼骨粉按照质量比8:3:3混合制备。

表1 原料初始理化性质

指标 Parameter	厨余垃圾 Kitchen waste	玉米秸秆 Maize stover	混合物 Mixture
含水率 Moisture content/%	77.80±5.63	20.17±0.50	63.32±2.29
pH	4.33±0.04	5.56±0.03	4.53±0.08
总碳 Total carbon (TC)/%	42.26±2.73	43.61±0.94	43.66±2.23
总氮 Total nitrogen (TN)/%	3.10±0.70	1.18±0.09	2.05±0.31
碳氮比 Carbon-to-nitrogen ratio (C/N)	13.63±2.52	36.96±3.36	21.26±2.07

注:含水率、pH值基于样品鲜质量测定,总碳、总氮、碳氮比基于样品干质量计算,数值表示为平均值±标准差。

Note: Moisture content and pH value were measured on a fresh weight basis, while total carbon, total nitrogen, and carbon-to-nitrogen ratio were determined on a dry weight basis, values are expressed as mean ± standard deviation.

堆肥过程在好氧生物反应器进行,反应器工作容积

2.5 m³,配备底部曝气系统(曝气量为2.5 m³/d)。堆肥过程持续15 d,根据堆体温度分为四个阶段:升温期(1~2 d,温度由环境温度升高至55℃)、高温期(3~8 d,55~60℃)、降温期(9~12 d,自然降温)和腐熟期(13~15 d,堆体稳定化与腐殖化)。堆体每两天翻堆一次,以维持充足供氧。在每个堆肥阶段(升温期、高温期、降温期和腐熟期)分别采集6个重复样品,采样时,从堆体的不同位置采集堆肥样本,将其混合成一个复合样本,用于分子生物学和理化性质分析:鲜样用于含水率、pH值、无机氮测定;部分样本经冷冻干燥并研磨均匀用于元素分析;部分储存在-80℃下用于DNA提取。

1.2 测定指标和方法

1.2.1 理化性质

堆肥过程中温度采用插入式温度探针进行监测,每天测量3次并取平均值。含水率通过将新鲜样品于105℃烘干至质量恒定测定。pH值采用去离子水按1:10比例提取,250 r/min振荡1 h后,用便携式pH计测定。堆肥样品冷冻干燥并研磨均匀,采用元素分析仪(Elementar UNICUBE,德国)测定TC和TN含量,并计算碳氮比(C/N)。铵态氮(NH₄⁺)、硝态氮(NO₃⁻)和亚硝态氮(NO₂⁻)的测定方法如下:称取10 g新鲜样品,用2 mol/L的KCl溶液按1:10比例提取,200 r/min振荡30 min,5000 r/min离心10 min后经0.45 μm孔径滤膜过滤。NH₄⁺浓度采用靛酚蓝比色法测定,NO₂⁻浓度采用N-(1-萘基)-乙二胺比色法测定,NO₃⁻浓度采用水杨酸比色法测定。

种子发芽指数(germination index, GI)以小白菜种子为指示生物测定。按1:10比例将堆肥与去离子水混合,250 r/min振荡1 h后以5000 r/min离心10 min,并经0.45 μm滤膜过滤获得堆肥提取液。在培养皿中铺滤纸,放置10粒小白菜种子,以堆肥提取液润湿,蒸馏水为对照,在25℃黑暗环境中培养24 h,种子发芽率和种子平均根长的乘积与对照的比值为种子发芽指数。

1.2.2 分子生物学性质

根据E.Z.N.A.® Soil DNA Kit (Omega Bio-tek, Norcross, GA, USA)说明书提取堆肥样品中微生物群落的总基因组DNA。采用1%琼脂糖凝胶电泳检测DNA提取质量,并使用NanoDrop 2000分光光度计(Thermo Scientific, USA)测定DNA浓度和纯度。以细菌16S rRNA基因V3~V4可变区为扩增靶标,使用引物338F(5'-ACTCCTACGGGAGGCAGCAG-3')和806R(5'-GGACTACHVGGGTWTCTAAT-3')进行PCR扩增。PCR反应体系总量为20 μL,包括:5×TransStart FastPfu缓冲液4 μL,2.5 mM dNTPs 2 μL,引物(5 μM)各0.8 μL,TransStart FastPfu DNA聚合酶0.4 μL,模板DNA约10 ng。扩增程序为:95℃预变性3 min;27个循环(95℃,30 s;55℃,30 s;72℃,30 s);72℃延伸10 min,4℃保存。扩增产物经2%琼脂糖凝胶电泳检测后,利用DNA凝胶回收纯化试剂盒(PCR Clean-Up Kit, 逾华生物,中国)进行纯化,并通过Qubit 4.0荧光计(Thermo Fisher Scientific, USA)定量。

纯化产物采用NEXTFLEX® Rapid DNA-Seq Kit (Bioo Scientific, USA)进行文库构建,包括接头连接、

磁珠筛选、PCR 富集及文库纯化等步骤,使用 Illumina NextSeq 2000 平台进行双端测序。原始序列经 fastp (v0.19.6) 进行质量控制,并使用 FLASH (v1.2.11) 拼接双端序列。经质控优化后的序列在 QIIME2 平台去噪,生成扩增子序列变体 (ASVs)。基于 Silva 16S rRNA 基因数据库 (v138) 进行分类学注释。采用 FAPROTAX 对细菌群落的潜在功能进行预测分析。

1.3 数据处理与分析

采用 R (v4.2.1) 中的“vegan”包,基于 ASV 水平计算阿尔法多样性指数 (Shannon 指数和 Chao 指数)。不同处理组及堆肥阶段间阿尔法多样性指数的差异采用单因素方差分析 (one-way ANOVA) 进行检验。基于 Bray-Curtis 距离矩阵的贝塔多样性分析通过主坐标分析 (principal coordinate analysis, PCoA) 进行,使用 R (v4.2.1) 中的“vegan”包完成计算。

为揭示不同堆肥阶段及菌剂处理对微生物互作的影响,基于 16S rRNA 测序数据构建共现网络。以 Spearman 相关分析为基础,分别计算各处理各阶段样本间的物种相关性矩阵。在每个样本集中,若某 ASV 在样本中零值超过样本总数一半,则予以剔除,以减少稀有序列干扰;仅保留 $|r| \geq 0.65$ 且 FDR 校正后 $P < 0.05$ 的相关性作为显著关联,相关系数矩阵经对称化处理生成邻接矩阵,在 R (v4.2.1) 中利用“igraph”包构建无向加权网络,识别网络的拓扑特征 (包括节点数、边数、平均度、网络密度、平均路径长度、聚类系数等),解析堆肥微生物群落中复杂的互作关系,使用 Gephi (v0.9.2) 进行网络的可视化。基于网络的模块划分结果,按照节点在模块内和模块间的连接度对关键类群进行识别:网络枢纽 (network hubs): $Z_i > 2.5$ 且 $P_i > 0.62$; 模块枢纽 (module hubs): $Z_i > 2.5$ 且 $P_i < 0.62$; 连接者 (connectors): $Z_i < 2.5$ 且 $P_i > 0.62$; 其余节点定义为边缘类群 (peripherals)。

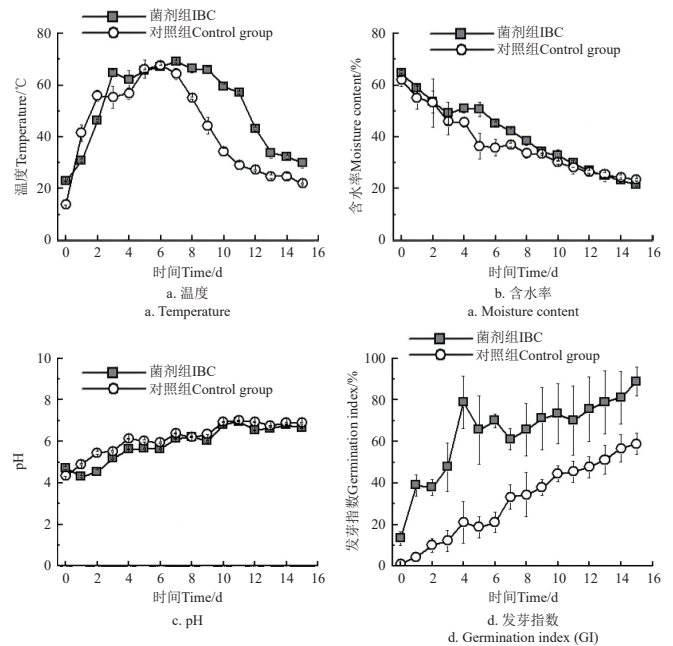
为探讨环境因子、微生物群落特征、碳氮硫代谢功能以及堆肥效率之间的潜在关系,采用 R (v4.2.1) 中的“plsmpm”包开展偏最小二乘路径模型 (partial least squares path model, PLS-PM) 进行结构方程建模分析。模型路径系数的显著性通过 bootstrap 进行检验,显著性水平设定为 $P < 0.05$ 。PLS-PM 结果计算导出后使用 Microsoft PowerPoint 进行可视化。除网络图与 PLS-PM 图外,其余图件均使用 Origin 2022 绘制。

2 结果与分析

2.1 堆肥系统理化性质变化

菌剂处理组和对照组堆肥过程中理化性质的变化如图 1 所示。可以看出,两组均表现出典型的堆肥温度变化规律,经历升温期、高温期、降温期和腐熟期。其中,菌剂组的高温期持续时间长于对照组,表明菌剂接种增强了微生物活性,加速了有机物的分解。高温期的延长有利于致病菌的灭活及恶臭物质的控制^[20-21]。随着堆肥过程的进行,两组堆肥物料含水率总体呈下降趋势。在堆肥 3~9 d,对照组含水率低于菌剂组;10~15 d,两组含水率趋于一致。这一差异可能与两组微生物代谢强度及水分耗散方式有关:对照组前期微生物活性相对较弱,堆体中自由水更易在通风和翻堆过程中快速蒸发;

而菌剂组前期代谢活动强,有机质代谢过程伴随一定量代谢水的生成;随着堆肥进入降温和腐熟阶段,易降解底物减少,堆体结构逐步稳定,水分迁移主要受通风和环境条件控制,两组含水率差异随之缩小^[22]。pH 在两组中变化趋势相似,均由初期的微酸性逐渐升高至接近中性后趋于稳定,这一变化可能是含水率降低、有机酸的降解及氨的积累等因素的综合作用。菌剂组的 GI 高于对照组,通常认为 GI 值高于 70% 可被认为堆肥达到无毒、稳定状态^[23]。第 15 天时,菌剂组 GI 达到 88.89%,对照组 GI 为 58.89%,说明菌剂处理促进了堆肥的稳定化与无害化进程。



注: IBC 为菌剂组,即添加固定化菌剂的堆肥系统;Control group 为对照组,即不添加固定化菌剂的堆肥系统。下同。

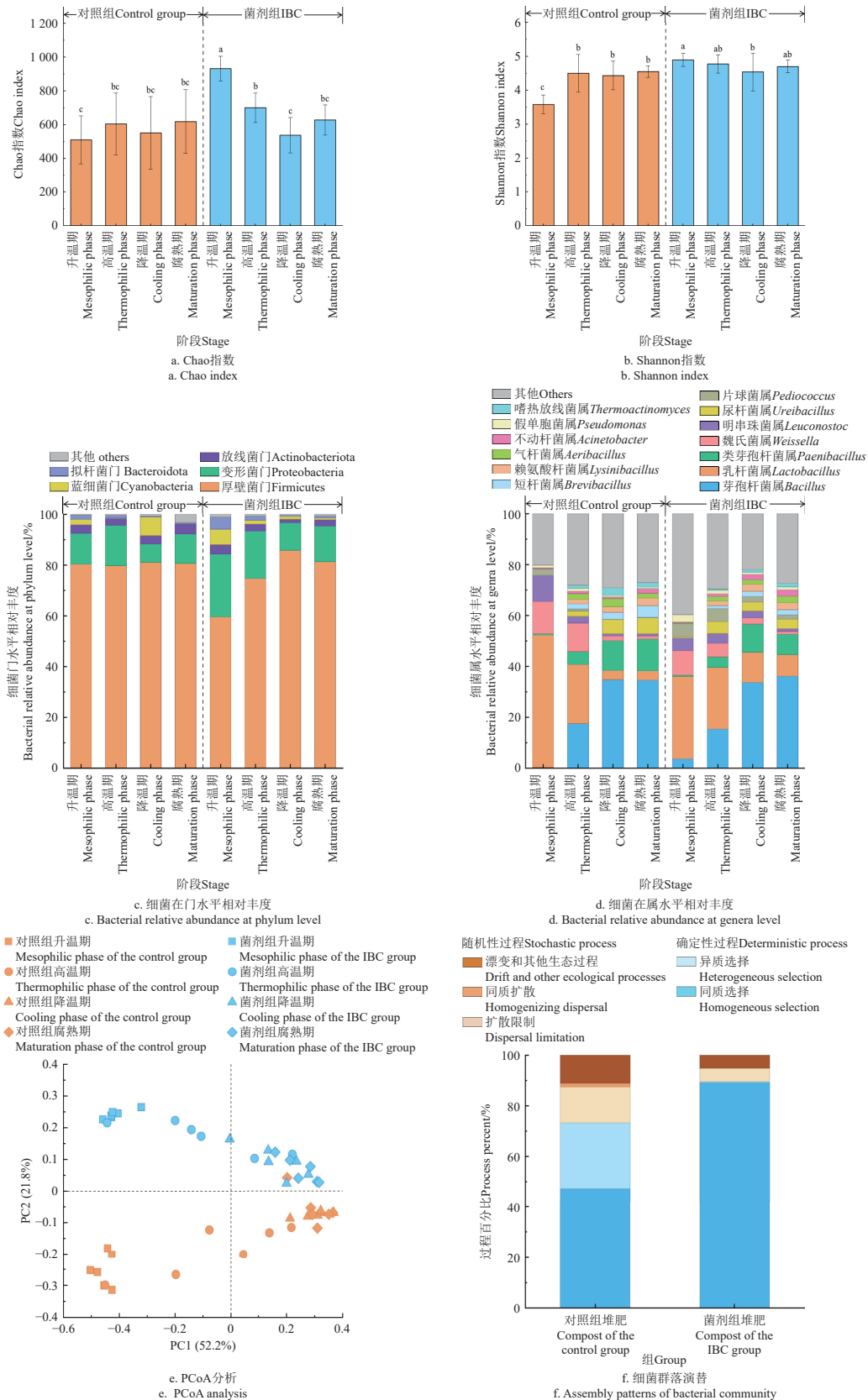
Note: IBC represents the inoculated group, i.e., the composting system with immobilized bacterial consortium; the control group represents the non-inoculated group, i.e., the composting system without immobilized bacterial consortium. Same below.

图 1 不同处理堆肥系统理化性质

Fig.1 Physicochemical properties of composting systems under different treatments

2.2 堆肥系统细菌群落结构变化

堆肥过程中细菌群落的多样性、组成及生态过程如图 2 所示。整体来看,菌剂组与对照组在堆肥的不同阶段均表现出明显的群落差异。菌剂组升温期的丰富度指数 (Chao 指数, 图 2a) 显著高于其他堆肥阶段 ($P < 0.05$), 说明菌剂在堆肥早期作为外源功能菌群引入, 促进了细菌的物种丰富度提升。随着堆肥过程的推进, 外源菌逐渐适应堆肥环境, 受到底物消耗、微生物间互作及资源竞争的共同影响, 群落丰富度趋于稳定。多样性指数 (Shannon 指数, 图 2b) 显示, 菌剂组在整个堆肥过程中保持较高且波动较小的多样性水平。菌剂的加入通过引入耐热且代谢类型多样的菌株, 增强了系统中种群的均匀性与结构稳定性。研究表明, 堆肥过程中较高的 Shannon 指数有助于提高堆体的代谢冗余度与抗扰动能力, 促进堆肥有机物分解与营养保留^[24]。



注：不同小写字母表示不同处理或堆肥阶段间差异显著 ($P < 0.05$)。

Note: Different lowercase letters indicate significant differences among treatments and composting stages ($P < 0.05$).

图2 不同处理堆肥系统细菌多样性、组成和演替规律

Fig.2 Diversity, composition, and assembly patterns of bacterial communities during composting systems under different treatments

菌剂组和对照组堆肥各个阶段细菌在门水平和属水平的群落组成如图 2c 和图 2d 所示。从门水平来看，对照组和菌剂组的群落均以 Firmicutes、Proteobacteria、

Actinobacteriota、Cyanobacteria 和 Bacteroidota 为主要优势菌门，菌剂组堆肥 Firmicutes 相对丰度低于对照组，Proteobacteria 相对丰度高于对照组。属水平上，*Bacillus*、

Lactobacillus、*Paenibacillus*、*Weissella*、*Leuconostoc*、*Ureibacillus* 等为对照组和菌剂组主要的细菌属。*Lactobacillus* 在升温期是相对丰度最高的细菌属，随着堆肥过程的进行，*Lactobacillus* 的相对丰度降低。*Lactobacillus* 是一种乳酸菌，偏好酸性环境^[25]，通常将可溶性糖发酵为有机酸（乳酸、挥发性脂肪酸等），这些有机酸会进一步降低堆肥的 pH 值^[26]。随着底物的消耗和 pH 的升高，*Lactobacillus* 相对丰度逐渐降低。*Weissella*、*Leuconostoc* 属等为乳酸菌，是堆肥初期出现的重要产酸属^[27-28]。相反，*Bacillus*、*Paenibacillus*、*Ureibacillus* 属的相对丰度随着堆肥进程逐渐增加。*Bacillus* 是堆肥过程中常见菌属，耐受多种环境压力，且可以快速降解有机质^[29-30]，从升温期到腐熟期逐步成为主导菌属。此外，*Bacillus* 也是目前最常用的堆肥菌剂^[31-32]，本研究中外源添加的菌剂中有 5 种属于 *Bacillus* 属。*Paenibacillus* 对木质纤维素降解和氮转化起积极作用^[33]。*Ureibacillus* 在厨余或餐厨垃圾堆肥中常见，且与 Na^+ 和 Cl^- 等盐度指标呈正相关关系，与总磷和 GI 等堆肥安全性和腐熟度指标密切相关^[34-35]。

主坐标分析结果显示（图 2e），前两个主坐标轴分别解释了 52.2% 和 21.8% 的群落差异。菌剂组与对照组在 PC2 轴上明显分离，形成清晰的聚类区间，表明菌剂接种改变了细菌群落结构。PC1 轴上的聚类主要反映堆肥阶段的差异（升温期、高温期、降温期和腐熟期），说明堆肥阶段是驱动细菌群落演替的主要因素，而菌剂接种发挥了显著但次要的调节作用。类似的调控现象也在 LI 等^[36] 和 WANG 等^[37] 的研究中得到报道。

为进一步揭示堆肥过程中细菌群落的演替机制，基于 βNTI 和 RCbray 分析结果，对群落组装过程进行了定量解析（图 2f）。总体来看，堆肥系统的群落组装由确定性与随机性过程共同驱动，且确定性过程占主导。对照组和菌剂组堆肥的细菌演替中，确定性过程占比分别为 73.26% 和 89.59%，且以同质选择为主要驱动方式，占比分别为 47.22% 和 89.24%。异质选择和随机过程的相对贡献明显降低，表明菌剂的接种可能通过改善堆肥体系理化性质，增强了资源利用的一致性，降低了堆肥体系内的环境异质性。微生物在群落尺度上受到更加统一的环境筛选，其定植、竞争与资源分配更受环境选择与生理适应的影响^[38-39]。

2.3 堆肥系统细菌共现网络特征

为揭示菌剂接种对堆肥系统中细菌互作关系的影响，构建了不同堆肥阶段的细菌共现网络（图 3），并计算其拓扑参数（表 2）。细菌共现网络在堆肥各个阶段的互作强度与复杂度均呈现动态变化。升温期网络的边数和平均度最高，表明此阶段微生物间联系最为密集，可能由于堆体中有机物种类丰富，易降解底物（如糖类、氨基酸、脂肪酸等）充足，促使多种代谢类型的微生物快速繁殖并形成高复杂度网络^[40]。随着堆肥进入高温期，底物逐渐消耗、网络节点与边数减少、平均路径长度增大、网络复杂度下降，群落结构逐渐简化，说明营养物质的丰度对塑造细菌群落相互作用强度具有重要意义^[41]。模块度反映了节点的聚集程度，模块度高通常反映网络具有更明显的模块化特征，不同模块可能主要承担不同

的生态功能^[42]。不同堆肥阶段的共现网络依据拓扑特征识别得到的 5~7 个模块，模块内部的微生物之间存在更紧密的潜在互作关系。高温期网络的模块度最低，表明在高温胁迫条件下，微生物群落的潜在互作关系趋于简化，模块的功能界限减弱。降温期和腐熟期网络结构再度趋于紧密，正向边数/负向边数比值升高，原因可能是木质纤维素等难降解底物的降解依赖于多种酶系统的协同作用^[43]。为了增加酶合成和微生物生长所需能量，微生物之间可能形成更多的潜在协同互作关系，通过代谢交换完成有机物的降解转化^[41, 44]。

与对照组相比，菌剂接种增加了网络节点数、边数和平均度，降低了平均路径长度和网络直径，说明菌剂促进了细菌之间更紧密的连接与潜在的协同代谢作用，这种高连通、低距离的网络结构有助于代谢物交换与协同降解过程^[45]。菌剂组的正向边数/负向边数比值先增加后降低，在降温期最高，可能是菌剂接种初期外源菌与土著菌竞争资源与生态位，导致负相关比例相对较高；而经过高温阶段的环境筛选后，菌剂组逐渐形成以协同互作为主的网络结构，特别在降温期表现出最强的正向协作特征。综上，菌剂通过在早期阶段促进菌群互作的重构，在中后期形成更紧密、更高效的正向互作网络，强化了堆体的降解功能与生态稳定性。

2.4 堆肥系统细菌代谢功能预测

为揭示堆肥过程中微生物潜在代谢功能的动态变化，本研究基于 FAPROTAX 功能预测结果，分析了 C、N、S 循环及有机质降解等关键功能在各个堆肥阶段的变化特征（图 4）。

堆肥过程中，有机质的降解是驱动 C、N、S 等元素循环及臭气生成的重要代谢基础。有机质降解功能主要包括多糖（纤维素、木聚糖、几丁质）、芳香族化合物、木质素及含氮有机物等分解过程（图 4a）。有机质降解功能在升温期较弱，在降温期和腐熟期增强。该结果说明堆体早期主要利用小分子可溶性底物；随着堆肥进行，微生物逐渐转向对难降解大分子物质的分解。这一转变可能与高温阶段后复杂有机物逐步被分解为小分子化合物有关，从而提高有机质的生物可利用性，加快腐殖化与堆体成熟^[46]。

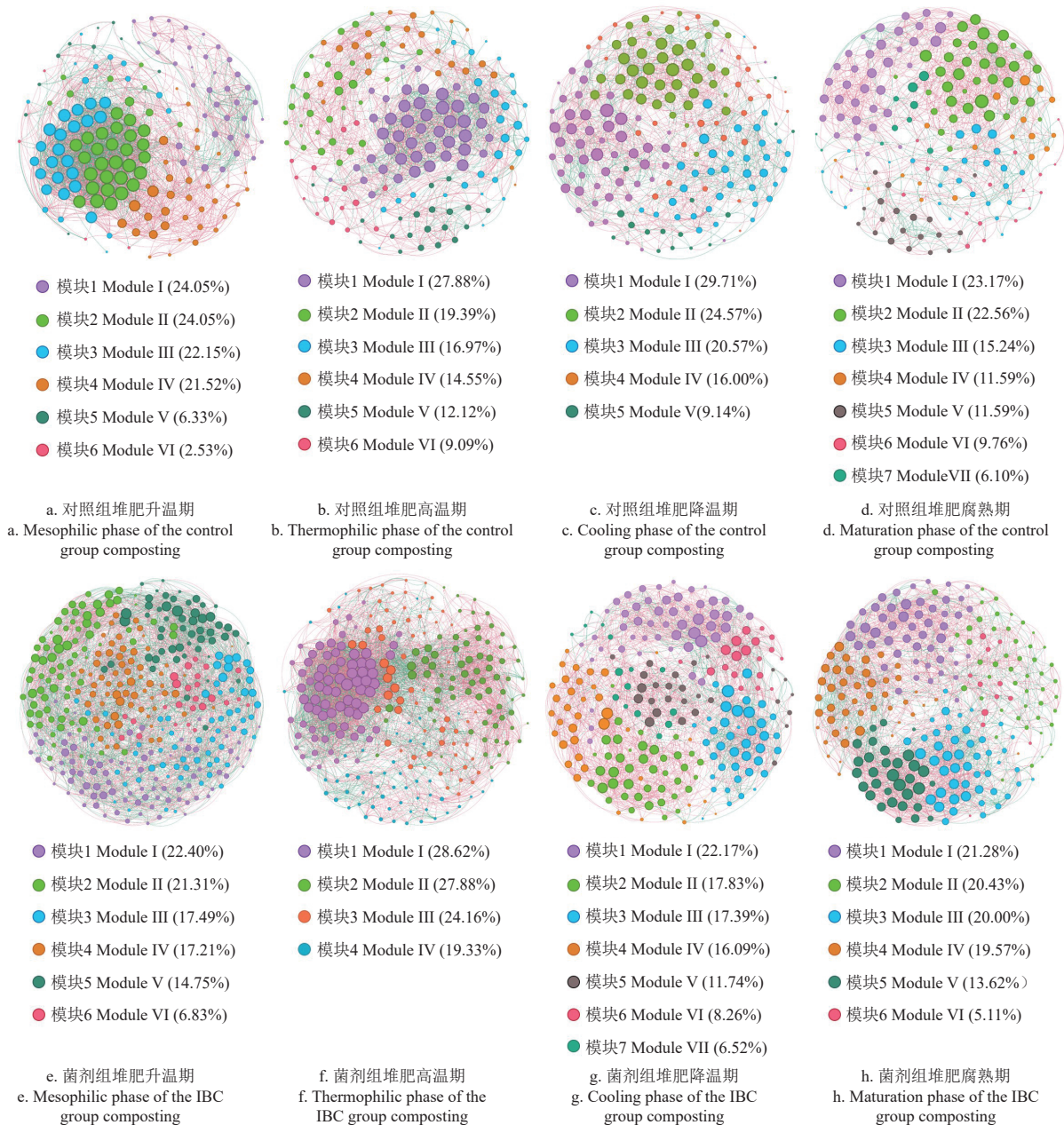
堆肥体系的 C 循环主要包括化能异养作用、发酵作用及好氧化能异养作用等过程^[46]（图 4b）。化能异养作用和有氧化能异养作用相对丰度随堆肥进程逐渐增加，而发酵作用的相对丰度逐渐下降，这一趋势与 XU 等^[47-48] 的研究结果一致，表明堆肥系统前期可能有氧气不足现象，随着通风和翻堆，发酵作用相对丰度下降，系统转向以有氧分解为主的稳定状态。这一变化有助于促进可溶性有机物的快速矿化与腐殖化，同时减少还原性发酵中间产物（如有机酸、醇类、硫化物等）的积累，从源头上削弱臭气生成潜势。

堆肥体系的 N 循环相关功能包括氮呼吸、硝酸盐和亚硝酸盐呼吸、异化铵化、反硝化及固氮等过程（图 4c）。亚硝酸盐呼吸、亚硝酸盐异化铵化和硝酸盐异化铵化在堆肥初期相对丰度较高，随后随堆肥进程下降。这可能是因为堆肥早期反硝化菌相对丰度较高，以硝酸盐/亚硝酸盐为电子受体的还原代谢较为活跃；随着温度升高与通气条件改善，反硝化相关的潜在功能相对丰度下降，硝

化与固氮等有氧氮转化潜在功能的贡献增加^[49-50]。硝酸盐还原作用在各阶段变化不大，而固氮作用在降温期与腐熟期增强，说明后期堆体中氮素的固定与再生能力提高，从而降低氮损失并有助于堆肥品质提升。

堆肥体系中的 S 循环功能主要包括硫化物呼吸、硫酸盐呼吸、亚硫酸盐呼吸、元素硫呼吸及硫代硫酸盐

呼吸等过程（图 4 d）。对照组中，与硫循环相关的潜在功能在高温期具有最高的相对丰度，随后逐步降低；而菌剂组的各类硫呼吸功能相对丰度均低于对照组，表明菌剂接种有效削弱了还原性硫代谢途径，这可能与菌剂改善堆体通气性、提高氧化代谢活性及竞争性抑制硫酸盐还原菌相关。



注：不同模块表示网络中具有较强潜在关联关系的节点聚类；括号中的百分比表示该模块所包含节点数占网络总节点数的比例。
Note: Different modules represent clusters of nodes with relatively strong potential associations within the network. The percentage in parentheses represents the proportion of nodes contained in each module relative to the total number of nodes in the network.

图 3 不同处理堆肥系统细菌共现网络
Fig.3 Co-occurrence network of bacterial communities during composting systems under different treatments

2.5 堆肥体系理化性质、微生物群落结构和功能对堆肥效率的影响

为进一步揭示堆肥过程中理化性质、微生物群落结构、网络复杂性、代谢功能及堆肥效率之间的关系，基于 PLS-PM 构建对照组堆肥和菌剂组堆肥模型。对照组堆肥 PLS-PM 模型和各指标对堆肥效率的影响如图 5a 和

图 5c 所示；菌剂组如图 5b 和图 5d 所示。两组模型拟合优度（goodness of fit, GoF）均高于 0.6，说明拟合效果较好。

在对照组中，理化性质对细菌群落结构呈显著负向作用（路径系数 = -0.853, $P < 0.05$ ），表明堆肥理化性质变化可能是影响细菌群落多样性、组成和演替的重要

因素。群落结构对代谢功能表现出显著的正向影响（路径系数 = 0.777, $P < 0.05$ ），说明堆肥微生物群落多样性和组成变化与 C、N、S 及有机物降解等代谢途径的强度有显著关联。网络复杂性对堆肥效率的直接作用为显著正向的（路径系数 = 0.227, $P < 0.05$ ），表明在自

然堆肥体系中，网络的高连通度与协同互动对维持堆体功能稳定性和促进有机质转化具有重要作用。然而，理化性质对堆肥效率的直接效应和总效应最强（图 5c），说明对照体系的整体效率仍主要受温度和水分等理化条件制约。

表 2 不同处理堆肥过程中细菌共现网络的拓扑特征参数
Table 2 Topological parameters of bacterial co-occurrence networks during composting systems under different treatments

处理 Treatment	阶段 Stage	节点数 Number of nodes	边数 Number of edges	正向边数 Number of positive edges	负向边数 Number of negative edges	正向边数/ 负向边数 Ratio of positive to negative edges	平均度 Average degree	平均路径长度 Average path length	网络直径 Network diameter	网络密度 Network density	平均聚类系数 Average clustering coefficient	模块化度 Modularity
对照组堆肥 Compost of the control group	升温期 Mesophilic phase	158	2 238	1 421	817	1.739	28.329	1.113	2.951	0.180	0.736	0.335
	高温期 Thermophilic phase	165	1 469	985	484	2.035	17.806	1.227	3.898	0.109	0.618	0.499
	降温期 Cooling phase	175	1 370	938	432	2.171	15.657	1.242	2.999	0.090	0.550	0.542
	腐熟期 Maturation phase	164	1 176	936	240	3.900	14.341	1.283	2.924	0.088	0.539	0.531
菌剂组堆肥 Compost of the IBC group	升温期 Mesophilic phase	366	4 364	2 333	2031	1.149	23.847	1.181	2.075	0.065	0.481	0.561
	高温期 Thermophilic phase	269	4 328	2 755	1 573	1.751	32.178	1.129	2.474	0.120	0.638	0.445
	降温期 Cooling phase	230	2 229	1811	418	4.333	19.383	1.205	2.508	0.085	0.545	0.593
	腐熟期 Maturation phase	235	2 393	1 777	616	2.885	20.366	1.206	2.560	0.087	0.544	0.551

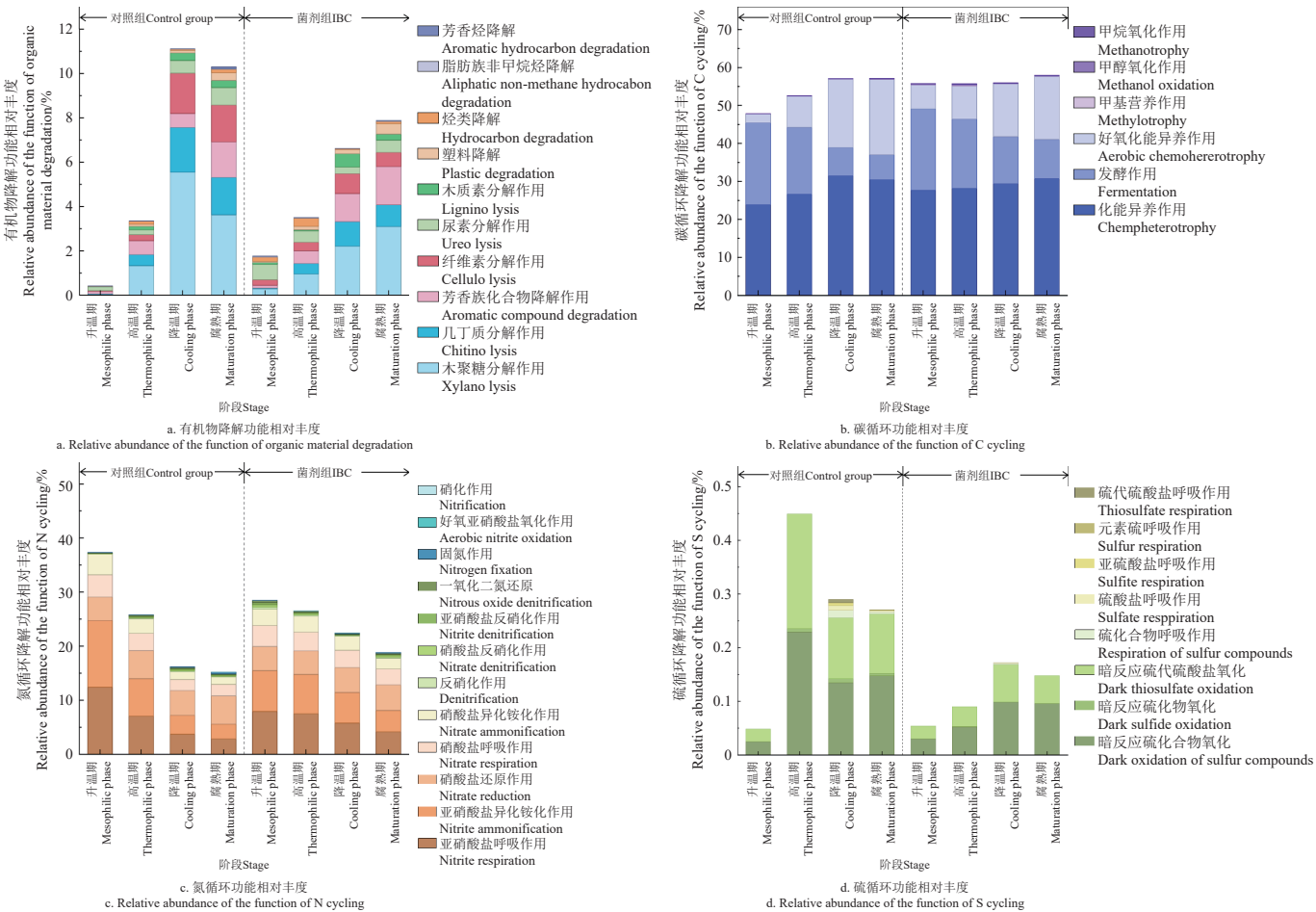
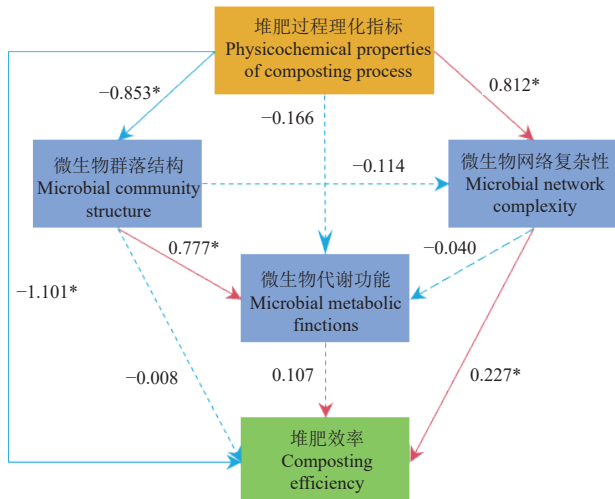


图 4 不同处理堆肥过程中细菌群落的代谢功能预测
Fig.4 Predicted metabolic functions of bacterial communities during composting systems under different treatments

在菌剂组堆肥中，模型潜变量路径关系发生明显变化。理化性质对群落结构的作用由对照组的显著负向转为显著正向（ $P < 0.05$ ），说明菌剂接种后，堆体理化条件变化可能更有利于优势功能菌群的富集。理化性质对

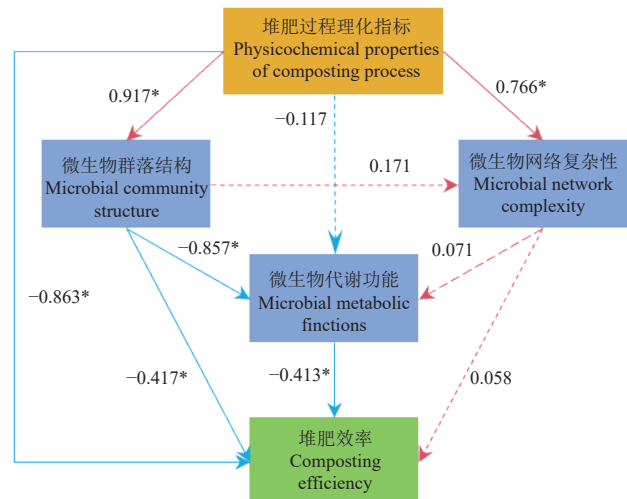
堆肥效率的影响仍然表现出较强的影响,但其直接负向作用相对减弱,间接效应比例提高(图5d)。群落结构对代谢功能的作用方向由正向转为显著负向($P < 0.05$),表明菌剂堆肥体系中代谢功能可能更多依赖于关键功能菌群,而与微生物群落尺度的多样性或组分关系减弱。此外,菌剂组中网络复杂性对堆肥效率的直接影响减弱且不显著,群落结构对堆肥效率的路径系数由对照组中较弱且不显著的负向关系转变为显著负向($P < 0.05$),

代谢功能对堆肥效率的路径系数也由正向转为显著负向($P < 0.05$)。这并非表明微生物群落、网络和代谢对堆肥效率的影响减弱甚至抑制,可能的原因是菌剂的接种在早期显著强化微生物的互作关系,促进有机物分解和代谢反应,后期逐渐减弱,从而在统计上表现为代谢增强与GI下降的负相关;随着降温与腐熟阶段到来,这些中间产物被进一步转化,GI迅速升高,体现出菌剂对堆肥周期的整体缩短效应^[14]。



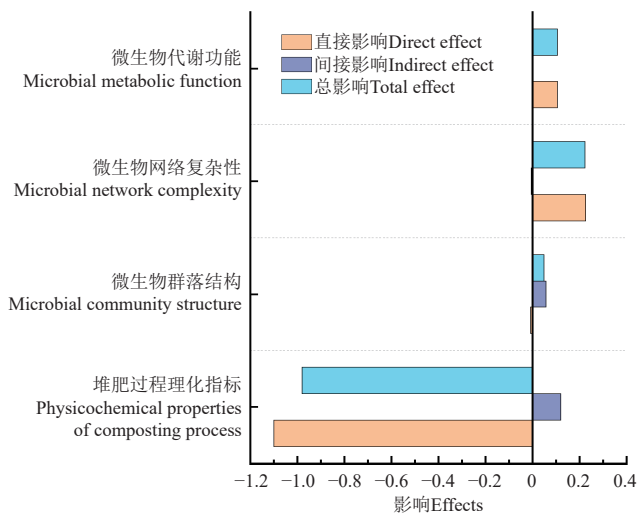
Goodness of fit (GoF)=0.795

a. 对照组堆肥系统PLS-PM模型
a. PLS-PM model of the control composting system

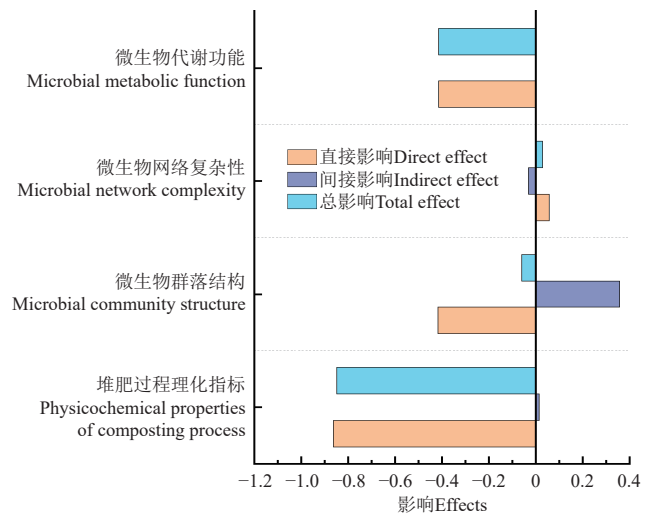


Goodness of fit (GoF)=0.731

b. 菌剂组堆肥系统PLS-PM模型
b. PLS-PM model of the IBC composting system



c. 对照组堆肥指标对堆肥效率的直接和间接影响
c. Direct and indirect effects of composting parameters on composting efficiency in the control group



d. 菌剂组堆肥指标对堆肥效率的直接和间接影响
d. Direct and indirect effects of composting parameters on composting efficiency in the IBC group

注: 蓝色箭头表示负向影响, 红色箭头表示正向影响, 实线表示影响显著, 虚线表示影响不显著, 线条旁数字表示路径系数, *表示 $P < 0.05$ 。

Note: Blue arrows indicate negative effects, red arrows indicate positive effects. Solid lines represent significant relationships, while dashed lines indicate non-significant ones. The numbers beside the lines denote the path coefficient values. Asterisks * indicate significance at $P < 0.05$.

图5 不同处理堆肥体系中理化性质、微生物群落、网络与代谢功能与堆肥效率的PLS-PM结构方程模型

Fig.5 PLS-PM structural equation models illustrating the relationships among physicochemical properties, microbial community, network, metabolic functions and composting efficiency systems under different treatments

综上, PLS-PM 结果揭示菌剂接种对堆肥生态过程的调控作用, 改变理化性质与群落结构的关系, 促进优势功能菌的定植与富集, 群落结构与代谢功能的关系由多样性驱动转向以关键功能菌为核心的高效代谢模式; 菌剂强化了前期有机物利用分解、加速了堆肥后期稳定, 整体上加快了堆体由高反应性向稳定腐熟的转变, 从而

实现堆肥周期缩短与效率提升。

3 结论

1) 固定化功能菌剂的接种延长了厨余垃圾堆肥的高温期并提高了体系稳定性, 促进堆肥在 15 d 内达到较高腐熟水平 (发芽指数为 88.89%)。

2) 菌剂改变了堆肥细菌群落结构与演替特征, 确定性组装过程占比提高, 由 73.26% 提升至 89.59%, 使群落在环境筛选下向耐热、降解及养分转化等功能性方向演替。菌剂增强了微生物共现网络的复杂性与协同性, 表现为节点数、边数、平均度提升, 平均路径长度降低, 系统稳定性与有机物降解效率提高。

3) 菌剂处理增强了碳、氮循环相关潜在功能, 降低了硫还原相关功能的相对丰度, 降低了臭气生成潜势。

4) PLS-PM 模型揭示菌剂改变了堆肥理化性质、微生物群落结构和功能与堆肥效率之间的耦合关系, 堆肥体系转向以关键功能菌为核心的高效代谢模式, 实现堆肥周期缩短与效率提升。

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Effects of microbial consortium on the bacterial co-occurrence network and metabolic functions in kitchen waste composting systems

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Abstract: Kitchen waste (KW) composting often suffers from prolonged processing time and strong odor emissions due to the high moisture content and complex organic composition of the substrate. This study aimed to elucidate how inoculation with an immobilized bacterial consortium (IBC) regulates the microbial community, co-occurrence network structure, and metabolic functions in a KW composting system, thereby improving composting efficiency and mitigating odor generation. A composting system inoculated with an IBC composed of six functional bacterial strains was established, with a non-inoculated treatment serving as control. The physicochemical parameters of the compost, including temperature, moisture content, pH, and germination index (GI), were continuously monitored throughout the 15-day process. Bacterial community composition and succession were analyzed via 16S rRNA gene sequencing. Co-occurrence networks were constructed for different composting phases to reveal changes in microbial interactions. Functional Annotation of Prokaryotic Taxa (FAPROTAX) was applied to predict metabolic pathways related to carbon, nitrogen, and sulfur cycling. Partial Least Squares Path Modeling (PLS-PM) was used to explore causal relationships among physicochemical conditions, microbial community structure, network complexity, metabolic functions, and composting efficiency. The IBC treatment sustained a longer and more stable thermophilic phase than the control, accelerating compost maturity, with the GI reaching 88.89% on day 15 compared to 58.89% in the control. Inoculation significantly reshaped the bacterial community structure and enhanced deterministic assembly processes, guiding microbial succession toward functional guilds specialized in organic degradation and nutrient transformation. The inoculated compost exhibited greater network complexity, characterized by increased node and edge numbers, higher average degree, and reduced path length and network diameter, indicating stronger microbial connectivity and synergistic metabolic cooperation. Functional prediction showed that carbon cycling was dominated by chemoheterotrophy and aerobic chemoheterotrophy, both increasing over time, while fermentation functions gradually declined. In the nitrogen cycle, nitrite respiration and dissimilatory ammonification were most active during the early phase, but nitrogen fixation became dominant in the later cooling and maturation stages. Sulfur respiration pathways were markedly suppressed in the inoculated group, implying the inhibition of reductive sulfur metabolism and reduced potential for odor emission. PLS-PM analysis further demonstrated that microbial inoculation reversed the relationship between physicochemical properties and bacterial community from negative to positive, promoting the enrichment of core functional taxa. The relationship between community structure and metabolic function shifted from diversity-driven to functional taxa-driven patterns. Although the direct effect of network complexity on composting efficiency declined, it indirectly enhanced system functionality through improved robustness and cooperative stability. The immobilized bacterial consortium effectively optimized the composting physicochemical environment, reconstructed microbial interaction networks, and reinforced functional coupling among key taxa. These integrated effects accelerated organic matter degradation, shortened the composting period, and reduced odor emissions. The study provides new ecological insights into the microbial regulatory mechanisms of KW composting and supports the development of efficient, low-emission, and sustainable biotechnological strategies for organic waste recycling.

Keywords: kitchen waste; microbial inoculant; bacterial community; co-occurrence network; metabolic function; partial least squares path modeling (PLS-PM)