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Microbial Communities in Composting: Succession, Functional Ecology, and Bioaugmentation Design — A Narrative Critical Review

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Received: 16/08/2026

Accepted: 26/09/2026

Available online: 30/09/2026

DOI: <https://doi.org/10.63964/atjb.2026.2.3.1>

ABSTRACT

Composting is an aerobic, self-heating biodegradation process driven by an ordered succession of microbial populations that occupy distinct thermal and nutritional niches. This narrative critical review synthesises culture-independent evidence published mainly between 2016 and 2026 (with emphasis on 2021–2026), drawn from PubMed, Scopus and Web of Science searches on compost microbiology, genome-resolved metagenomics, metatranscriptomics, ecological network analysis and machine-learning modelling of composting performance. Four conclusions emerge. First, taxonomically dissimilar compost communities repeatedly converge on similar functional gene repertoires, indicating that functional redundancy rather than taxonomic composition underlies process stability. Second, thermophilic fungi and thermophilic bacteria contribute complementary steps to lignocellulose deconstruction, and the best-documented bioaugmentation gains have come from cross-kingdom consortia delivered at the appropriate process phase. Third, microbial co-occurrence networks and keystone taxa carry information on process efficiency that abundance-based profiling alone does not capture. Fourth, although antibiotic resistance genes (ARGs) are substantially reduced by thermophilic composting, their persistence in mature manure-derived compost remains an under-regulated biosafety issue, and the archaeal fraction of the compost community, which includes ammonia-oxidising and methanogenic groups, remains poorly characterised despite its relevance to nitrogen retention and greenhouse-gas emissions. Integrated multi-omics combined with machine-learning frameworks offers a promising route towards predictive process engineering. Priority needs include rigorous characterisation of archaeal function, industrial-scale validation of laboratory findings, and harmonised reporting standards for composting microbiome studies.

Keywords: *composting; microbial succession; functional redundancy; CAZymes; thermophilic fungi; bioaugmentation; keystone taxa; antibiotic resistance genes; archaea; nitrogen cycling*

1. INTRODUCTION

Composting is among the oldest biotransformation practices known to humanity. In modern terms it is defined as the aerobic biological decomposition of organic matter by a succession of microorganisms, during which metabolic heat accumulates and drives the material through mesophilic, thermophilic, cooling and maturation phases [1]. Although the practice has been applied empirically for millennia, a mechanistic understanding of the process only became possible with culture-independent methods. High-throughput 16S rRNA gene sequencing, shotgun metagenomics and long-read sequencing have revealed a taxonomic and functional diversity in composting systems that far exceeds what culture-based studies could detect [2, 3, 4].

A striking example of this hidden diversity comes from genome-resolved metagenomics of thermophilic composting. Lopez-Mondejar et al. [2] reconstructed 60 high-quality metagenome-assembled genomes (MAGs) from time-series sampling of two thermophilic composting systems; 47 represented putative novel bacterial species and 24 had no close relative in public MAG databases at the 95% average nucleotide identity threshold. This “microbial dark matter” is simultaneously a fundamental knowledge gap and a bioprospecting opportunity.

Composting also occupies a distinctive position at the interface of environmental microbiology, industrial biotechnology, food safety and public health. It functions as a waste-valorisation platform, as a source of thermostable biocatalysts, and, particularly when livestock manure or sewage sludge is a principal feedstock, as a node in the environmental dissemination of antibiotic resistance genes (ARGs) [5, 6, 7]. These three roles justify a review framework that is critical rather than merely descriptive.

Despite the rapid growth of composting microbiome datasets over the past decade, a conceptual gap persists between how compost communities are described and how they are manipulated. Much bioaugmentation work continues to select inoculant strains primarily by taxonomic identity, although screening by enzyme activity is increasingly common [8, 9]. At the same time, metagenomic evidence consistently indicates that stability and degradation efficiency are determined less by which taxa are present than by the functional repertoire the community encodes [2, 3]. Bacillota (Firmicutes), Pseudomonadota (Proteobacteria), Actinomycetota (Actinobacteria) and Bacteroidota are generally reported as the dominant phyla, yet their relative abundances vary considerably among studies as a result of feedstock composition, aeration regime, reactor design, DNA extraction method, sequencing depth and bioinformatic pipeline [10, 11]. Direct comparison of abundance profiles across independent studies therefore requires caution.

This review argues that composting microbiome engineering should move from a taxonomy-centred to a function-centred paradigm, in which the primary design criteria for inoculant consortia and process optimisation are the carbohydrate-active enzyme (CAZyme) repertoire, the nitrogen-cycling gene complement and inter-kingdom enzymatic complementarity, rather than species identity. Because recent metagenomic studies show that bacteria dominate both the taxonomic composition and the functional gene repertoire of thermophilic composts [2, 3], the review concentrates on bacterial succession and CAZyme systems, while devoting dedicated sections to thermophilic fungi and to the archaeal fraction. Section 2 describes the review approach. Sections 3 and 4 address community succession and fungal ecology; Section 5 examines CAZyme systems, interaction networks and bioaugmentation design; Sections 6 and 7 cover nitrogen cycling and the biosafety dimensions of pathogens and ARGs; Sections 8 and 9 discuss advanced meta-omics, predictive modelling and archaeal communities; and Section 10 sets out knowledge gaps, methodological needs and limitations of the review.

2. REVIEW APPROACH

This is a narrative critical review rather than a systematic review or meta-analysis. Literature was identified through searches of PubMed, Scopus and Web of Science using combinations of the terms “compost*” with “microbial community”, “succession”, “metagenom*”, “metatranscriptom*”, “metagenome-assembled genome”, “CAZyme”, “lignocellulose”, “bioaugmentation” or “inoculant”, “co-occurrence network” or “keystone”, “antibiotic resistance gene”, “archaea” or “ammonia-oxidizing archaea”, “nitrous oxide”, and “machine learning” or “random forest”. Reference lists of retrieved articles were screened for additional sources. Primary emphasis was placed on peer-reviewed studies published between 2021 and 2026 that applied culture-independent methods to composting systems; earlier studies (2007–2020) were included where they provide foundational evidence (for example on archaeal communities, inoculation timing and enrichment-culture metagenomics) that has not been superseded. One preprint [12] is cited and is identified as such wherever it is used. Studies were appraised for scale (laboratory, pilot or industrial), replication, whether functional data (enzyme activity, metatranscriptomics or metaproteomics) accompanied sequence data, and whether findings were validated beyond a single system (Table 2). No formal screening counts were recorded, and the selection therefore reflects the authors’ judgement of relevance and quality; this limitation is discussed in Section 10.4.

3. MICROBIAL COMMUNITY SUCCESSION: PATTERNS, DRIVERS, AND INTERPRETIVE CAVEATS

3.1 Mesophilic phase

The mesophilic phase begins with rapid colonisation of newly available substrate by heterotrophs already present in the raw material. In the co-composting of food-waste digestate with garden waste, Wang et al. [11] reported that Firmicutes, Proteobacteria and Bacteroidota dominated the early bacterial community, while Ascomycota accounted for most fungal sequences throughout the process, with Basidiomycota rising in the later stages. Chloroflexi are also frequently recorded during the initial phase of manure–straw composts [10]. Soluble carbohydrates and proteins are preferentially consumed during this period, generating enough metabolic heat to drive the pile into thermophilic conditions within roughly three to seven days [1]. Although this phase determines how quickly composting initiates, it has received comparatively little attention from a meta-omics perspective; most genome-resolved studies have sampled the thermophilic and maturation stages [2, 4].

3.2 Thermophilic phase

Once pile temperatures exceed about 45 °C, thermal filtering selects for taxa able to grow and metabolise at high temperature. In cow manure–tobacco straw composting analysed by shotgun metagenomics, the zoonotic pathogen *Rhodococcus equi* declined steadily while *Thermopolyspora* and *Sphaerobacter* became the dominant lignocellulolytic genera, a pattern consistent with competitive exclusion acting alongside thermal inactivation during hygienisation [13]. Thermophilic conditions favour organisms with high substrate-acquisition rates and strong extracellular enzyme production, including actinomycetes such as *Thermobifida* and *Thermomonospora* that hydrolyse cellulose and hemicellulose [14].

An important observation is that thermophilic communities that differ taxonomically can reach comparable degradation performance. Santos-Pereira et al. [3] found that composts of different feedstock and origin shared the same dominant glycoside hydrolase families, and Lopez-Mondejar et al. [2] showed that distinct MAG clusters in two composting systems encoded overlapping metabolic capacities. Together with the convergent lignocellulose losses achieved by different inoculant consortia [8, 9, 15], these results support, although they do not yet prove, the view that functional redundancy rather than taxonomic identity governs process performance.

3.3 Cooling and maturation phases

As thermophilic activity declines, mesophiles recolonise the pile. Actinobacteria are typically prominent during cooling and maturation. In compost-derived consortia enriched on lignocellulose, Actinobacteria contributed about 46% of all CAZyme-encoding genes, with cellobiohydrolase, β -glucosidase, acetyl xylan esterase, arabinofuranosidase and ligninase genes forming the core of that contribution [16]; because these data come from enrichment cultures rather than composting in situ, they indicate metabolic potential rather than the in-pile contribution of the phylum. Using combined Illumina and Nanopore sequencing of straw and leaf composts, Kimeklis et al. [4] demonstrated that the chemical composition of the hemicellulose fraction shapes community development through substrate-specific polysaccharide utilisation loci (PULs), with xylan- and pectin-targeting PULs most frequent among the high-performing MAGs.

Nitrification is suppressed during the thermophilic phase because ammonia oxidisers are heat-sensitive, and it resumes during cooling and maturation. In sludge–corn straw composting under continuous aeration, nitrate accumulated to a maximum of 5.33 g kg⁻¹ [17]. Co-occurrence networks generally become more complex during maturation, which has been interpreted as

increasing ecological stability and metabolic cooperation within a diverse, functionally redundant climax community ([11, 18], in soil amended with compost); this interpretation remains inferential because network metrics are not direct measurements of interaction.

3.4 Synthesis

The successional pattern across composting phases is reproducible along temperature and substrate gradients (Table 1). Between-study variation in the relative abundance of individual taxa reflects real differences in feedstock, C/N ratio and aeration, but also, in part, technical differences in extraction, sequencing and analysis [10, 11]. Several independent studies now report that communities with divergent taxonomy exhibit similar functional potential through redundant CAZyme and nitrogen-metabolism genes [2, 3, 4]. This suggests that compost quality monitoring would benefit from function-specific gene markers alongside, rather than instead of, taxonomic indices.

Table (1): Microbial succession across composting phases as reported in sequencing-based studies.

Phase	Approx. temperature (°C)	Dominant bacterial groups	Dominant fungal groups	Key functional processes	Sources
Mesophilic	15–45	Firmicutes, Proteobacteria, Bacteroidota, Chloroflexi	Ascomycota (e.g. <i>Cladosporium</i> , <i>Aspergillus</i>)	Hydrolysis of soluble C and N; heat generation; pioneer community assembly	[10, 11, 1]
Thermophilic	45–75	<i>Bacillus</i> , <i>Geobacillus</i> , <i>Thermopolyspora</i> , <i>Sphaerobacter</i> , <i>Saccharomonospora</i> , <i>Thermobifida</i>	<i>Thermomyces lanuginosus</i> , <i>Talaromyces thermophilus</i> , <i>Aspergillus fumigatus</i>	Lignocellulose degradation; pathogen inactivation; ARG reduction; N ₂ O risk during aeration cycling	[13, 19, 20, 21]
Cooling	45→25	<i>Thermobifida</i> , <i>Streptomyces</i> ; Actinobacteria resurgence	<i>Myceliophthora thermophila</i> ; Basidiomycota recolonisation	Attack on recalcitrant substrate; nitrification resumes; PUL-driven substrate specialisation	[16, 4, 20]
Maturation	Ambient	Diverse Actinobacteria; <i>Nitrospira</i> / <i>Nitrosomonas</i> lineages	Stable Ascomycota; <i>Trichoderma</i> ; Basidiomycota	Humification; NO ₃ ⁻ accumulation; increased network complexity	[17, 11]

ARG, antibiotic resistance gene; PUL, polysaccharide utilisation locus. Temperature ranges follow the conventional phase definitions of Ryckeboer et al. [1].

4. FUNGAL COMMUNITIES: ECOLOGICAL SIGNIFICANCE AND ENZYMATIC COMPLEMENTARITY

Although bacteria contribute most of the functional gene pool of compost metagenomes, fungi are the principal agents of oxidative lignin depolymerisation, humification and the production of thermostable oxidoreductases [21]. Culture-based surveys indicate that a very high proportion of thermophilic fungal isolates from compost are lignocellulolytic, whereas only a minority of thermophilic bacterial isolates are, and those mostly attack hemicellulose (reviewed in [21]). Such figures are subject to cultivation bias and should not be generalised to the whole community. Moreover, thermophilic actinomycetes such as *Thermobifida fusca* possess complete cellulolytic systems, and several bacterial lineages carry AA10 lytic polysaccharide monooxygenases (LPMOs) and peroxidases capable of acting on lignin-derived aromatics [24, 25, 14]. The evidence therefore supports a model in which fungi are the dominant but not the sole contributors to lignin oxidation, and in which complete lignocellulose mineralisation is most efficient when fungal and bacterial enzyme systems act together.

Table (2): Critical appraisal of the principal primary studies drawn on in this review.

Study	System and method	Scale / replication	Functional data	Key finding	Consistency with field	Main limitation
[11]	Food-waste digestate + garden waste; Illumina 16S/ITS	Pilot; single site, two feedstock mixes	None	Firmicutes, Proteobacteria, Bacteroidota dominate; temperature is primary driver	Consistent with [10] and [13] at phylum level	No functional gene or enzyme data
[10]	Cow manure + corn straw; Illumina 16S/ITS	Pilot; triplicate piles	None	Proteobacteria, Bacteroidetes, Firmicutes, Chloroflexi, Actinobacteria; TN, NH ₄ ⁺ , NO ₃ ⁻ , temperature and moisture drive succession	Consistent with [11]	Amplicon only; no functional data
[13]	Cow manure + tobacco straw; shotgun metagenomics	Pilot; single system	Gene-level only	<i>Thermopolyspora</i> and <i>Sphaerobacter</i> dominate thermophilic phase; <i>R. equi</i> declines	Consistent with hygienisation literature	Tobacco residues may confound; single study
[2]	Two thermophilic composting systems; MAGs + metatranscriptomics	Time series; two systems	Metatranscriptomics	60 MAGs, 47 putative new species; metabolic dependencies among MAG clusters	Supports functional-redundancy hypothesis	Two systems only; no industrial-scale validation
[3]	Portuguese composts; sequence- and function-based metagenomics (fosmid library)	Several composts, single region	Functional screening of clones	GH5/GH9/GH3 dominant regardless of feedstock	CAZyme universality across feedstocks	Gene abundance ≠ activity; no metatranscriptomics
[4]	Straw and leaf composts; Illumina + Nanopore	Laboratory microcosms	Enzyme assays	Substrate-specific PULs drive differential assembly	Consistent with substrate-driven succession	Laboratory inoculum may not represent field composting
[16]	Compost-derived consortia enriched on lignocellulose; shotgun metagenomics	Laboratory enrichment	None	Actinobacteria contribute ~46% of CAZyme genes	Consistent with actinobacterial prominence in cooling phase	Enrichment culture, not in-situ composting
[8]	Green waste; three-strain inoculum (<i>B. amyloliquefaciens</i> , <i>C. rogersoniana</i> , <i>S. thermotolerans</i>)	Laboratory; replicated treatments	Enzyme assays	Cellulose, hemicellulose and lignin losses 197%, 145% and 113% higher than control	Consistent with bioaugmentation literature	Controlled conditions; industrial performance unvalidated
[9]	Synthetic community inoculated in	Laboratory; replicated	Enzyme assays; random forest	Xylanase +85.4%, cellobiohydrolase	Consistent with [8]	Predictive performance metrics not

Study	System and method	Scale / replication	Functional data	Key finding	Consistency with field	Main limitation
	thermophilic phase; metagenomics			se +43.1%; keystone taxa enriched		reported in abstract
[15]	Green waste; same inoculum applied at mesophilic, thermophilic or cooling phase	Laboratory ; replicated	Enzyme assays	Thermophilic-phase inoculation gave the largest gains (cellulose +193%, laccase +1034%)	Consistent with earlier timing studies	Single inoculum; laboratory scale
[22]	Straw composting with thermophilic inoculant ± commercial agent; qPCR of N-cycle genes	Laboratory ; replicated	Functional gene quantification	N ₂ O reduced 33.3% (thermophiles) and 50.8% (combined); <i>amoA</i> most influential	Consistent with [23]	Mechanism inferred from correlation

TN, total nitrogen; MAG, metagenome-assembled genome; PUL, polysaccharide utilisation locus.

4.1 Thermophilic fungal succession and phenotypic plasticity

In a culture-based survey of 21 days of compost maturation at an Italian facility, Di Piazza et al. [20] recovered 45 fungal species from 25 genera, with Ascomycota dominating the thermophilic mycobiota; thermophilic *Thermomyces* and *Thermascus* species were prominent, and the thermotolerant *Aspergillus fumigatus* was among the most frequently recovered taxa. An observation of practical importance, drawn from the enzyme-screening literature summarised by Tiquia-Arashiro and Mormile [21], is that strains of the same thermophilic species can display different enzymatic expression profiles across composting stages. This phenotypic plasticity means that inoculant performance cannot be predicted from strain identity alone and should be assessed under the conditions prevailing at the time of inoculation.

During the cooling phase *Myceliophthora thermophila*, which grows optimally at 45–50 °C, degrades residual cellulose and contributes to humification [20]. Its sequenced genome encodes a complete cellulolytic CAZyme repertoire, including AA9 LPMOs, GH7 cellobiohydrolases and GH3 β -glucosidases, which has made it a model for the discovery of thermostable biocatalysts [26]. Basidiomycota recolonise the pile late in maturation and complete the oxidative attack on lignin, releasing aromatic fragments that serve as humic-acid precursors [11, 20]. From a biosafety standpoint, *A. fumigatus* persists throughout the process and in the final product [20]. As an opportunistic pathogen causing invasive aspergillosis in immunocompromised individuals, its presence in mature compost merits attention, yet product standards such as EU Regulation 2019/1009 [27] specify limits for *Salmonella* and *Escherichia coli* but not for fungal pathogens.

4.2 Cross-kingdom fungal–bacterial enzymatic synergies

The mechanistic basis of fungal–bacterial cooperation during composting has been examined at the genomic level. Chang et al. [25] showed that colonisation of compost by *Agaricus bisporus* mycelium was accompanied by increased laccase activity, reduced lignin content and enrichment of thermophilic bacteria carrying AA10 LPMO genes, chiefly *Thermobifida* and *Thermotaphylospora*. This pattern suggests that lignocellulose degradation in compost is cooperative rather than parallel: fungal oxidative enzymes open the lignin macromolecule to yield low-molecular-weight aromatics, which bacterial peroxidases and LPMOs then process further. On this basis we propose, as an interpretation that extends beyond the original authors' conclusions, that bioaugmentation strategies restricted to bacteria are likely to underperform on high-lignin substrates relative to mixed consortia.

Direct experimental support comes from Feng et al. [8], who constructed a three-strain inoculum of *Bacillus amyloliquefaciens*, *Clonostachys rogersoniana* and *Streptomyces thermoviolaceus* at a 3:3:2 volume ratio for green-waste composting. Relative to the uninoculated control, cellulose, hemicellulose and lignin losses increased by 197%, 145% and 113%, and laccase, manganese peroxidase (MnP), lignin peroxidase (LiP) and carboxymethyl cellulase activities by 605%, 269%, 180% and 228%, respectively; humic acid content rose by 291% and mature compost was obtained within 32 days. These are consortium-level responses expressed relative to low control activities, so the absolute magnitudes should not be extrapolated across systems. Nevertheless, together with the five-member bacterial–fungal community of Chen et al. [28], which raised lignin degradation by 19.3% and humus content by 34.4%, they indicate that cross-kingdom complementarity is a defensible design principle.

4.3 Phase-specific inoculation: temporal coordination as a design principle

Inoculation timing matters as much as inoculant identity. *Phanerochaete chrysosporium*, a mesophilic white-rot basidiomycete, cannot survive thermophilic conditions, and studies spanning more than a decade have shown that its ligninolytic contribution is greatest when it is introduced after the thermophilic peak: inoculation at later time points increased ligninolytic enzyme activities [29], and inoculation during the cooling period enhanced humification of maize straw and canola residue relative to early inoculation [30]. Conversely, thermophilic bacterial–fungal inocula perform best when delivered at the onset of the thermophilic phase: applying the same compound inoculum at the mesophilic, thermophilic or cooling stage of green-waste com-

posting, Wang et al. [15] found that thermophilic-phase inoculation gave the largest improvements (cellulose, hemicellulose and lignin degradation +193%, +125% and +69%; laccase +1034%; composting time reduced to 28 days). Matching the thermal tolerance and enzymatic role of the inoculant to the prevailing phase is therefore a readily implementable route to better organic matter stabilisation in industrial operations.

Table (3): Key fungal taxa in composting: thermal preferences, characteristic enzymes and biosafety notes.

Taxon	Phylum	Optimum growth temperature	Characteristic enzymes	Ecological role	Note	Sources
<i>Thermomyces lanuginosus</i>	Ascomycota	50–55 °C	Xylanase, cellulase, amylase, lipase	Primary thermophilic hemicellulose/cellulose degrader; co-dominant in thermophilic phase	Strain-level plasticity in enzyme expression	[20, 21]
<i>Aspergillus fumigatus</i>	Ascomycota	37–45 °C (thermotolerant)	Protease, CMCase, amylase	Thermotolerant degrader; persists in final product	Opportunistic human pathogen; not covered by product standards	[20]
<i>Myceliophthora thermophila</i>	Ascomycota	45–50 °C	AA9 LPMO, GH7, GH3	Cooling-phase cellulose degrader; humification	Sequenced genome; model for thermostable enzyme discovery	[26, 20]
<i>Talaromyces thermophilus</i>	Ascomycota	45–50 °C	Xylanase, endoglucanase	Thermophilic hemicellulose degrader	Under-represented in amplicon surveys owing to primer and database bias	[21]
<i>Clonostachys rogersiana</i>	Ascomycota	20–30 °C	Laccase, cellulases	Fungal component of an effective three-strain inoculum	Mesophilic; consortium raised laccase by 605%	[8]
<i>Agaricus bisporus</i>	Basidiomycota	20–25 °C	Laccase (AA1), MnP	Mycelial colonisation enriches AA10 LPMO-bearing bacteria	Cross-kingdom synergy demonstrated	[25]
<i>Phanerochaete chrysosporium</i>	Basidiomycota	35–40 °C	LiP, MnP, H ₂ O ₂ -generating oxidases	Post-thermophilic lignin oxidation; humification	Cannot survive thermophilic phase; inoculate during cooling	[29, 30]

CMCase, carboxymethyl cellulase; LPMO, lytic polysaccharide monooxygenase; MnP, manganese peroxidase; LiP, lignin peroxidase. Optimum temperatures are approximate values compiled from Tiquia-Arashiro and Mormile [21] and Di Piazza et al. [20].

5. CAZYME SYSTEMS, INTERACTION NETWORKS, AND BIOAUGMENTATION DESIGN

Carbohydrate-active enzymes are the molecular machinery through which compost microorganisms deconstruct lignocellulose. Understanding the diversity of these systems, and above all the gap between genomic potential and realised catalytic activity, is central to the function-centred paradigm proposed here.

5.1 Metagenomic CAZyme landscape

Functional profiling of compost metagenomes from Portugal identified GH5 and GH9 cellulases and GH3 oligosaccharide hydrolases as the dominant glycoside hydrolases irrespective of feedstock or process conditions [3]. The recurrence of this GH5/GH9/GH3 signature across studies supports the view that compost is a reliable source for the bioprospecting of industrial biocatalysts. In lignocellulose-enriched consortia derived from compost, Actinobacteria contributed roughly 46% of all CAZyme

genes [16], consistent with their competitive advantage during cooling and maturation when readily degradable carbon has been depleted; as noted above, enrichment-culture data describe potential rather than in-pile contribution.

A major interpretive caveat is that gene presence does not demonstrate enzyme synthesis. Metagenomes describe potential function under notionally permissive conditions, whereas compost communities experience steep spatial and temporal gradients under which transcriptional regulation and post-translational control may decouple activity from gene abundance. Direct comparison of metagenome and metatranscriptome CAZyme profiles in thermophilic compost has shown that expression is dynamic and only partly predictable from gene content [31, 2]. Until metatranscriptomic and metaproteomic measurements become routine, CAZyme profiles should be read as indicators of catalytic potential rather than confirmed metabolic function—a distinction that also bears on how bioaugmentation efficacy and enzyme-discovery programmes are evaluated.

5.2 Microbial interaction networks and keystone taxa

Co-occurrence network analyses portray compost communities as interconnected systems rather than collections of independent taxa. Thermophilic composting produces modular networks in which some taxa act as hubs—nodes with high degree, high betweenness centrality or module-hub status—whose ecological influence exceeds what their abundance would suggest [11, 18]. Thermophilic Actinobacteria, *Bacillus*-like taxa and lignocellulolytic Proteobacteria are frequently identified as such hubs, and SynCom inoculation has been shown to enrich keystone genera including *Sphaerobacter*, *Paenibacillus* and *Thermopolyspora* [9]. Network complexity generally increases from the mesophilic to the maturation stage, which is interpreted as reflecting metabolic cooperation through hydrolysis, metabolite exchange and syntrophy [11].

A plausible but as yet untested hypothesis is that disturbances such as aeration failure, excessive moisture or mistimed inoculation act disproportionately on hub taxa, leading to loss of cooperative degradation modules, reduced efficiency and higher greenhouse-gas emissions. Because keystone status is inferred from correlation networks, this causal chain requires experimental confirmation. If it holds, bioaugmentation strategies that target hub taxa may be more effective at the ecosystem level than those that target isolated enzymatic functions [2]. Network analysis combined with functional gene profiling is, in any case, emerging as a useful approach for identifying microbial indicators of compost quality and for designing inoculant consortia.

5.3 Bioaugmentation: phase-specific design principles

The evidence for bioaugmentation efficacy described in Section 4 is consistent across several independent laboratory studies. Cross-kingdom consortia achieved larger gains in lignocellulose degradation than single-organism inoculants in the same experimental series [8, 28], and delivery timed to the metabolic demands of the prevailing phase outperformed untimed application [29, 30, 15]. In the study of Chen et al. [9], random-forest modelling identified key bacterial and fungal taxa, ligninase and cellulase/hemicellulase activities, and CAZyme gene abundance as the most important predictors of degradation efficiency (Section 8.3). Three design principles follow: select inoculants by enzymatic complement and thermal tolerance rather than genus; combine fungal oxidative capacity with bacterial hydrolytic and LPMO activity; and time delivery to the phase in which the inoculant can function.

6. MICROBIAL NITROGEN CYCLING, GREENHOUSE GAS EMISSIONS, AND MITIGATION STRATEGIES

Nitrogen transformations determine both the fertiliser value of compost and its environmental footprint. They are carried out by several functional guilds whose combined activity governs plant-available nitrogen, ammonia volatilisation and nitrous oxide (N_2O) release. N_2O has a 100-year global warming potential of 265–298 relative to CO_2 [32]. It is produced by two main routes in compost: as a by-product of ammonia oxidation by nitrifiers, and through denitrification from nitrate (*narG*) to nitrite, nitric oxide (*nirK/nirS*) and N_2O (*norB*); nitrous oxide reductase (*nosZ*) completes the pathway to N_2 , and the balance between *nor* and *nosZ* activity is central to mitigation [33]. He et al. [22] showed that a thermophilic bacterial inoculant reduced cumulative N_2O emissions from straw composting by 33.3%, and by 50.8% when combined with a commercial decomposition agent, with *amoA* abundance identified as the most influential gene; in hyperthermophilic composting of refinery sludge, an extreme-thermophile inoculum lowered NH_3 and N_2O emissions by 32.4% and 10.2% while raising peak temperature to 80.5 °C [23]. These studies illustrate targeted manipulation of the microbiome to reduce the greenhouse-gas burden of composting without slowing decomposition.

Aeration mode strongly affects nitrogen fate. Under continuous aeration, nitrification proceeds and nitrate accumulates (Section 3.3), whereas intermittent aeration reduces ammonia loss but increases N_2O release because alternating aerobic and anaerobic conditions promote coupled nitrification–denitrification [17]. No universal optimum exists between nitrogen conservation and greenhouse-gas mitigation; the balance must be established case by case, ideally with monitoring of *amoA*, *narG*, *nirK*, *nirS*, *norB* and *nosZ*. Complete ammonia oxidisers (comammox *Nitrospira*), which convert ammonium directly to nitrate without releasing nitrite and with lower N_2O yield, have been characterised in engineered and soil systems [34, 35]; whether they contribute measurably to nitrification in mature compost is an open question worth testing.

7. PATHOGEN FATE AND ANTIBIOTIC RESISTANCE GENES: THE SAFETY DIMENSIONS OF COMPOSTING

Beyond decomposition, composting performs a public-health function by reducing pathogens and other biological hazards in raw feedstocks. Two related dimensions are considered here: classical pathogen suppression and the dissemination of ARGs.

7.1 Pathogen suppression through thermophilic succession

Pathogen populations decline during thermophilic composting through two synergistic routes: thermal inactivation above

about 55 °C, and biological inhibition through competitive exclusion, antimicrobial production by *Bacillus* and *Streptomyces*, and, plausibly, bacteriophage predation, although phage-mediated control has not been quantified in compost [1, 13]. Liu et al. [13] documented the decline of *Rhodococcus equi* during thermophilic composting at the metagenomic level, one of the few such reports for this zoonotic pathogen, and a metagenomic time series of urban compost piles reported that the heat phase reduced foodborne-associated genera and ARG-carrying organisms [12]. The two mechanisms should not be conflated: heat acts indiscriminately, whereas biological antagonism is selective and may be more important against thermotolerant organisms that survive direct heat exposure.

7.2 Antibiotic resistance genes: a persistent and under-regulated biosafety issue

The fate of ARGs during composting has been studied extensively. Manure and sewage sludge are recognised reservoirs of ARGs and of the mobile genetic elements (MGEs)—integrations, transposons and conjugative plasmids—that mediate their horizontal transfer [5]. Conventional thermophilic composting substantially reduces the abundance of most ARGs and MGEs through thermal inactivation and successional replacement of their hosts [7], and hyperthermophilic composting (>80 °C) accelerates their removal in sewage sludge [6]. Complete elimination is nevertheless rarely achieved: some ARGs persist or even rebound during maturation, especially in cooler, poorly aerated microenvironments [7, 12], and their persistence raises the possibility of transfer to soil microbiomes and the food chain after land application.

The efficacy of composting as an ARG-mitigation measure depends on peak temperature, duration, aeration efficiency, moisture control and the specific ARG classes present, so quantitative risk assessment still requires further data. Long-read metagenomics now allows ARGs to be resolved together with their genomic context, distinguishing plasmid- from chromosome-borne genes and linking them to horizontal-transfer machinery. Routine ARG surveillance of mature compost is technically feasible and scientifically justified, yet neither EU Regulation 2019/1009 [27] on fertilising products nor the US EPA biosolids rule (40 CFR Part 503 [36]) includes ARG criteria; both rely on pathogen indicators and time–temperature requirements.

8. ADVANCED META-OMICS AND PREDICTIVE MODELLING: TOWARD MECHANISTIC PROCESS ENGINEERING

Closing the gaps identified above—from genomic potential versus activity in CAZyme profiling to the uncharacterised archaeal fraction and ARG dynamics—requires tools beyond conventional metagenomics.

8.1 Genome-resolved metagenomics

Shotgun sequencing and MAG assembly have transformed compost microbial ecology. As described in the Introduction, Lopez-Mondejar et al. [2] recovered 60 high-quality MAGs from two thermophilic composting systems, most representing putative novel species, and metabolic modelling of MAG gene content revealed likely cross-feeding dependencies that provide a mechanistic basis for the cooperative degradation networks inferred from co-occurrence data. Hybrid Illumina–Nanopore sequencing has since yielded near-complete genomes from straw and leaf composts and linked phylogenetic identity to PUL and CAZyme content at higher resolution [4].

8.2 Integration of metatranscriptomics, metaproteomics and metabolomics

Metagenomics indicates potential; it does not demonstrate function. Metatranscriptomic profiling of thermophilic compost shows that MAG-derived gene clusters exhibit dynamically regulated expression that cannot be forecast from genomic information alone [31, 2]. Metatranscriptomics captures actively transcribed hydrolases and nitrogen-cycling genes at the time of sampling; metaproteomics provides evidence of extracellular enzyme production, the closest proxy for function; and metabolomics reveals intermediate breakdown products, volatile organic compounds and humification-associated metabolites invisible to nucleic-acid methods. Multi-omics integration has begun to appear in bioaugmentation studies [28]. To our knowledge, however, no composting study has yet combined all four layers over a complete process time course. Such integration would directly address the potential-versus-activity problem, identify manipulable metabolic bottlenecks and support the design of inoculants on the basis of dynamic metabolic flux.

8.3 Machine learning and predictive process modelling

Machine-learning approaches are beginning to be applied to composting data. In the study of Chen et al. [9], random-forest analysis of SynCom composting data attributed lignocellulose degradation efficiency mainly to key bacterial (19.8%) and fungal (22.1%) taxa, ligninase (10.2%) and cellulase/hemicellulase (23.7%) activities, and CAZyme gene abundance (23.1%). The practical value of such models lies in ranking controllable variables rather than in prediction alone. Their evidential weight is currently limited, however, because predictive performance (for example cross-validated R^2 or error) is seldom reported and because models trained on single systems have not been tested on independent data. A longer-term vision is an intelligent monitoring system that adjusts aeration, moisture, turning frequency and inoculation schedules in real time. This will require standardised multi-omics datasets, industrial-scale validation and sensors capable of providing real-time readouts of the functional state of the microbiome.

9. ARCHAEOAL COMMUNITIES IN COMPOSTING: AN UNDER-CHARACTERISED COMPONENT

Archaea are regularly detected in compost yet remain far less studied than bacteria and fungi, even though their involvement in nitrogen cycling and greenhouse-gas dynamics is potentially significant. Archaeal sequences typically constitute a few per cent of prokaryotic reads in compost amplicon libraries when archaea-specific primers are used [37, 38], but bacterial-optimised 16S rRNA primer sets amplify archaeal templates poorly, so their contribution is underestimated in most surveys. Archaea-targeted amplicon sequencing with primer pairs such as Arch349F/Arch806R [39] is rarely applied in composting studies.

Nitrification in compost has commonly been attributed to ammonia-oxidising bacteria (AOB), and quantitative studies in manure composts support AOB dominance during the process [37]. Ammonia-oxidising archaea (AOA), including members of the genus *Nitrososphaera* (phylum Nitrososphaerota, formerly Thaumarchaeota), have nevertheless been detected during cattle-manure composting, and their growth is favoured by moderate temperatures and low ammonia concentrations [37, 40]. This is consistent with the far higher ammonia affinity of AOA compared with AOB [41], and suggests that AOA may become relevant during cooling and maturation once ammonia is depleted. Simultaneous quantification of archaeal and bacterial *amoA* by qPCR has been used in a number of compost studies [37, 40, 22], but the relative contribution of AOA and AOB to nitrification, and to N₂O formation, across feedstocks and operating regimes remains unresolved.

Hydrogenotrophic methanogens such as *Methanothermobacter* and *Methanoculleus* have been detected in aerobic compost, where micro-aerobic and anaerobic zones provide suitable conditions for methanogenesis [38]. Methane production by these organisms adds to greenhouse-gas emissions and represents a thermodynamically inefficient route of carbon turnover. The spatial extent of methanogenic activity within aerated piles has not been resolved at the scale needed to guide aeration management. Thermoacidophilic Crenarchaeota-related lineages have also been reported during the thermophilic phase, but their functional roles are unknown.

In summary, the archaeal fraction is the least characterised component of the composting microbiome despite its likely relevance to nitrogen retention and greenhouse-gas mitigation. We suggest that future composting microbiome studies adopt, as a minimum reporting standard, paired bacterial and archaeal 16S rRNA amplicon sequencing together with qPCR of bacterial and archaeal *amoA*.

10. KNOWLEDGE GAPS, METHODOLOGICAL CHALLENGES, AND FUTURE RESEARCH PRIORITIES

10.1 Persistent scientific knowledge gaps

Two further gaps deserve attention alongside the archaeal question. First, the compost virome is poorly understood. Bacteriophages can exert top-down control on bacterial communities and may drive succession through “kill-the-winner” dynamics, in which lysis of dominant hosts releases nutrients that facilitate colonisation by other populations [42]. Viral metagenomic methods developed for soils and other complex matrices [43] are directly applicable to compost, and their systematic application represents a tractable research opportunity. Second, many organisms characterised genomically in compost have never been isolated; this uncultured “dark matter” holds enzymatic products that remain inaccessible to direct biochemical characterisation, and targeted cultivation remains a methodological priority.

10.2 Methodological heterogeneity and standardisation needs

Lack of harmonisation in sampling strategy, DNA extraction, primer choice, sequencing platform, OTU versus ASV clustering and bioinformatic pipeline hampers meta-analysis and cross-study synthesis. The 16S rRNA variable region sequenced (V3–V4, V4 or full length), sequencing depth and the taxonomic reference database all influence apparent composition and diversity indices. A minimum reporting standard for composting microbiome studies, modelled on the MIMARKS/MIxS specifications [44], is therefore recommended. It should include feedstock composition and C/N ratio, pile dimensions, turning frequency and aeration rate, sampling location and depth, temperature at sampling, and a compost maturity index.

10.3 Emerging research frontiers

Spatially resolved metagenomics—describing communities at defined coordinates within the pile—would illuminate the microscale heterogeneity that allows aerobic, microaerophilic and anaerobic niches to coexist within macroscopically aerobic heaps, and may clarify how ARGs and pathogens persist in thermally shielded microenvironments. Synthetic biology offers a longer-term route to engineering thermostable traits, enhanced enzyme secretion or quorum-sensing-regulated cooperation in inoculant strains, although regulatory and biosafety considerations will constrain deployment. In the near term, the combination of ecological network modelling with functional genomics to identify keystone and hub taxa, and the rational assembly of bacterial–fungal consortia around enzymatic complementarity [8, 28], appear to be the most productive directions.

10.4 Limitations of this review

This is a narrative rather than a systematic review; no formal screening protocol or quantitative synthesis was applied, and study selection reflects the authors’ judgement. The evidence base is modest, and most bioaugmentation and multi-omics studies cited were conducted at laboratory or pilot scale, so their transferability to industrial operations is untested. Several central claims—functional redundancy as the determinant of performance, and keystone-taxon vulnerability—rest on inference from sequence data and correlation networks rather than manipulative experiments. One cited study is a preprint. These limitations should be borne in mind when interpreting the conclusions below.

11. CONCLUSIONS

The evidence compiled here supports a shift in compost microbiome research from taxonomy-based description towards functional and mechanistic analysis. Composting performance appears to be governed less by taxonomic diversity than by functional redundancy, inter-kingdom enzymatic complementarity and the organisation of microbial interaction networks. Specifically:

Functional redundancy is a recurring property of composting microbiomes: taxonomically distinct communities encode similar CAZyme and nitrogen-metabolism repertoires. Inoculant design should therefore weight enzymatic complement and thermostability range above genus-level identity; several recent studies already do so, but the principle has not yet been adopted uni-

formly.

Thermophilic fungi are the dominant, though not the only, agents of lignin oxidation, and the best-documented bioaugmentation gains have come from consortia that combine fungal oxidative capacity with bacterial hydrolytic and LPMO activity. Strategies that omit a fungal component are likely to underperform on high-lignin substrates.

Until metatranscriptomic and metaproteomic analyses accompany metagenomic surveys routinely, CAZyme gene abundance must be regarded as an indicator of catalytic potential rather than of realised activity.

Archaea, including ammonia oxidisers and methanogens, are the most under-explored source of functional information relevant to nitrogen retention and greenhouse-gas mitigation; archaea-targeted molecular assays should become a minimum reporting standard.

Thermophilic composting substantially reduces but does not eliminate ARGs in manure- and sludge-derived compost. Long-read metagenomic surveillance of ARGs in mature compost is feasible and scientifically justified, yet current regulatory frameworks do not require it.

Integrated multi-omics combined with machine-learning models is a promising route towards predictive process engineering, provided that predictive performance is reported and models are validated on independent, industrial-scale data.

The composting microbiome is more than an empirical biochemical reactor: it is a tractable experimental ecosystem for testing questions in microbial ecology, functional redundancy theory, inter-kingdom interaction and microbiome engineering. Realising its scientific and biotechnological potential will depend on methodological standardisation, multi-omics integration and a conceptual framework that places ecological function above taxonomic identity.

Author contributions: [to be completed]. **Funding:** [to be completed]. **Conflicts of interest:** The authors declare no conflict of interest. **Data availability:** Not applicable; no new data were generated.

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