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Research article

# Enhancing C and N turnover, functional bacteria abundance, and the efficiency of biowaste conversion using *Streptomyces-Bacillus* inoculation

Ziyan Zhou<sup>a,1</sup>, Xiaofei Shi<sup>a,1</sup>, Parag Bhople<sup>b</sup>, Jishao Jiang<sup>c</sup>, Caspar C.C. Chater<sup>d,e</sup>, Shimei Yang<sup>a</sup>, Jesus Perez-Moreno<sup>f</sup>, Fuqiang Yu<sup>a,\*\*</sup>, Dong Liu<sup>a,\*</sup>

<sup>a</sup> The Germplasm Bank of Wild Species & Yunnan Key Laboratory for Fungal Diversity and Green Development, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, 650201, Yunnan, China

<sup>b</sup> Crops, Environment, And Land Use Department, Environment Research Centre, Teagasc, Johnstown Castle, Wexford, Y35TC98, Ireland

<sup>c</sup> School of Environment, Henan Normal University, Xinxiang, Henan, 453007, China

<sup>d</sup> Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AE, UK

e Plants, Photosynthesis, and Soil, School of Biosciences, University of Sheffield, Sheffield, S10 2TN, UK

<sup>f</sup> Colegio de Postgraduados, Campus Montecillo, Edafologia, Texcoco, 56230, Mexico

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### ABSTRACT

Microbial inoculation plays a significant role in promoting the efficiency of biowaste conversion. This study investigates the function of *Streptomyces-Bacillus* Inoculants (SBI) on carbon (C) and nitrogen (N) conversion, and microbial dynamics, during cow manure (10% and 20% addition) and corn straw co-composting. Compared to inoculant-free controls, inoculant application accelerated the compost's thermophilic stage (8 vs 15 days), and significantly increased compost total N contents (+47%) and N-reductase activities (nitrate reductase: +60%; nitrite reductase: +219%). Both bacterial and fungal community succession were significantly affected by DOC, urease, and NH<sup>4</sup><sub>4</sub>-N, while the fungal community was also significantly affected by cellulase. The contribution rate of *Cupriavidus* to the physicochemical factors of compost was as high as 83.40%, but by contrast there were no significantly different contributions ( $\sim60\%$ ) among the top 20 fungal genera. Application of SBI induced significant correlations between bacteria, compost C/N ratio, and catalase enzymes, indicative of compost maturation. We recommend SBI as a promising bio-composting additive to accelerate C and N turnover and high-quality biowaste maturation. SBI boosts organic cycling by transforming biowastes into bio-fertilizers efficiently. This highlights the potential for SBI application to improve plant growth and soil quality in multiple contexts.

#### 1. Introduction

Agricultural intensification and large-scale livestock production cause high volume organic waste streams (Cui et al., 2023). Across the world, 140 billion tons of cellulose-lignin-based biomass from crops and 125 million tons of N waste from livestock are generated annually (FAO, 2020). China's yearly contribution to this is about 900 million tons of straw and 3.8 billion tons of manure (Chen et al., 2021). Indiscriminate disposal of livestock manure and crop straw has brought new challenges to ecological environments worldwide. Processing treatments are required to minimize damaging environmental effects of these waste products. In traditional composting, the rate of humus formation and stabilization of organic matter (OM) from plant residues is limited by the slow decomposition of recalcitrant polymeric materials (Su et al., 2023; Sun et al., 2023). This drawback of traditional methods can be addressed by co-composting techniques. These employ simultaneous treatment of at least two different organic wastes (manure and agricultural biowaste) using microbial inoculants, causing a quicker and more efficient conversion of OM into stable humic substances (Cheng et al., 2021; Li et al., 2022a), This method resolves limitations of single-straw composting (large pores and low moisture) and transforms biowaste into an important raw substrate for agricultural production (Bernal et al., 2009; de Nijs et al., 2023).

During composting, indigenous microbial communities vary

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<sup>\*</sup> Corresponding author.

<sup>\*\*</sup> Corresponding author

E-mail addresses: fqyu@mail.kib.ac.cn (F. Yu), liudongc@mail.kib.ac.cn (D. Liu).

<sup>&</sup>lt;sup>1</sup> These authors contribute equal to this work.

substantially and in succession, following initial, thermophilic, cooling, and mature stages respectively (Bello et al., 2020; He et al., 2022a; Meng et al., 2019c; Zhu et al., 2021). The bioactivity of thermophilic microorganisms is restricted during the later stages, which limits their roles in OM transformation and humus formation (Villar et al., 2016). To overcome this, microorganism inoculants are applied during composting to accelerate OM decomposition, reduce nitrogen loss and ammonia volatilization, and improve the quality of compost (Abdellah et al., 2022; Zhang et al., 2022b). The addition of exogenous inoculants can also accelerate the formation of a dominant microbial community, increase the abundance of functional microorganisms, and degrade toxic and harmful substances (Harindintwali et al., 2020; Wu et al., 2019; Yin et al., 2021).

Microbial inoculants are increasingly attractive solutions to promote rapid compost maturation. They do this by improving C degradation (cellulose, hemicellulose, and lignin) from straw and sawdust while supporting microbial metabolism and further accelerating compost formation (Huang et al., 2004; Jiang et al., 2022; Yu et al., 2019; Zhang et al., 2021c). Firmicutes and Actinobacteria are two types of Gram-positive bacteria (Cheng et al., 2015). Within these two phyla, Bacillus, Pseudomonas, and Streptomyces are the most common genera detected in composts (Ventorino et al., 2016). For instance, Bacillus subtilis, gaining central importance as a dominant bacterial strain (Siu-Rodas et al., 2018), survives in different environmental niches, efficiently degrading lignocellulose and enhancing compost quality. B. subtilis can accelerate the thermophilic stage of composting by secreting broad-spectrum enzymes capable of degrading a range of OM (Guo et al., 2022). Besides Bacillus, Streptomyces, a widely-used Actinobacterium, is resistant to extreme environments (Shinde et al., 2022). As beneficial microbial inoculants, Bacillus and Streptomyces have the potential to improve enzyme activity in biochemical processes (Li et al., 2022c). The interaction between C- and N-cycling enzymes and the microbe is synergistic and simultaneously co-regulated by factors including moisture, pH, and composting C-additive substrates (Li et al., 2020; Zhang and Lynd, 2004). However, compared to traditional composting, our understanding of the associations among these factors remains limited.

Compost stability is not ensured without proper decomposition. Supplementing plant residues with co-substrates such as manure can provide ample N during composting (Abdellah et al., 2022). Manure's low C/N ratio, easily degradable OM content, and higher moisture content (~60%) create ideal conditions for decomposition. In comparison to poultry, pig, and donkey manure, supplementation with cattle manure significantly improves humus formation and final compost quality in terms of lower C/N ratios and increased total nitrogen and phosphorus contents, all of which correlate with higher microbial biomass C contents (Meng et al., 2019a; Pan et al., 2023). Co-composting production of mature and stable compost is therefore an effective strategy to reuse organic wastes and enhance soil fertility, recycle nutrient supply, and promote crop growth.

Rapid co-composting of plant residue and manure is usually achieved using single-strain inoculants, but there are synergistic benefits of optimizing combinations. Although fungi are the principle cellulose degraders, the roles of bacteria and other microorganisms are no less important. Microbial inoculant addition to chicken manure and corn straw compost can increase seed germination rates (Wan et al., 2020) and adding exogenous nitrifying bacteria to compost can improve the nitrification process and reduce nitrogen loss (Naghdi et al., 2018). Compound bacterial preparations in mixed cow manure-reed rod compost prolonged the thermophilic period of compost and improved the degradation efficiency of lignocellulose (Zhou et al., 2023a). Among bacteria, Bacillus is the most abundantly recovered genus from feedstock materials and demonstrates longevity during the composting process due to spore formation under thermophilic conditions (S.P et al., 2021; Zhang et al., 2021a). This reflects their ability to thrive in stressful abiotic and biotic conditions. Despite these advantages, Bacillus has

limited lignin mineralization potential, which must be upscaled by using other spore-forming filamentous actinomycete bacteria such as *Streptomyces*; these can potentially solubilize lignin and are occasionally found in lignocellulolytic materials (Rainisalo et al., 2011).

In the present study, we investigate the benefits of Streptomyces-Bacillus Inoculant (SBI) concentrations, and their effects on physicochemistry, enzymatic properties, and microbial communities during co-composting of corn plant residues and cow manure. There are potential broader applications of SBI in composting. For example, inoculants can i) serve as pioneer microbial groups for degrading recalcitrant C-containing compounds; ii) favor the release of easily degradable C sources which can synergistically promote growth of mesophilic bacteria and accelerate overall microbial succession in composts (Shi et al., 2021); and iii) enhance the versatility of compost by improving compost nutrients, enzyme activities, and diversity of functional genes (Hoang et al., 2022; Li et al., 2020; Xi et al., 2015; Xie et al., 2023). We hypothesized that: (i) the application of SBI would accelerate C- and N-conversion during the cow manure and agroforestry biowaste co-composting; (ii) SBI would significantly change key C- and N-cycling enzyme activities, and shift microbial community structures during composting; and (iii) the correlations between physicochemical properties, and C- and N-cycling microbes would be altered by SBI.

### 2. Substrates and methods

### 2.1. Composting experiment design and sample collection

The bio-composts were prepared in September 2022 at Kunming Institute of Botany, Chinese Academy of Sciences (102°43'E, 25°14'N). The basic physicochemical characteristics of compost substrates (cow manure, corn stalks, and corn cobs) are shown in Table S1. Treatments were set up based on variations in the proportion of cow manure (10% vs. 20% in dry weight) and with/without Streptomyces-Bacillus inoculant (SBI) (Luoyang Biotechnology Co., LTD, Streptomyces-Bacillus 1:1). SBI functions to accelerate compost temperature increases, shortening maturation period, and improve deodorization. In total, there were four treatments: Low cow manure addition of 10% (L), low cow manure with SBI (LM), high cow manure addition of 20% (H), and high cow manure with SBI (HM). Detailed substrate ratios are shown in Table 1. Corn cob enhances water absorption, has high sugar content, and improves soil quality after fermentation. After adding quicklime (CaO) to the compost, it reacts with water, releases a lot of heat, and adjusts the pH, aiding sterilization and disease prevention.

Raw substrates were mixed evenly according to their treatment's ratio (Table 1). The mixture pile for each treatment was  $\sim 2 \text{ m}^3$ . Each pile's moisture content was adjusted to 60–70%. Piles were turned at 3-day intervals to ensure adequate air circulation.

As sampling dates were based on temperature indicators of the thermophilic stage, sampling was conducted earlier for inoculant treatments (Fig. 1). The sampling intervals were based on temperature data from the outdoor automatic temperature and humidity recorder (HOBO® Micro Station, H21-USB). Specific sampling points were: at ~20 °C for the initial stage, >60 °C for the thermophilic stage, ~40 °C for the cooling stage, and ~20 °C for final sampling at maturation (Fig. 1). Information on composting piles sampling dates is shown in Table S2. In order to minimize sampling heterogeneity, we collected

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Substrate ratio of four composting trea	atments.

Treatment	Cow manure (%)	Corn stalk (%)	Corn cob (%)	Lime (%)	SBI (g)
L	10	86	3	1	0
Н	20	76	3	1	0
LM	10	86	3	1	31.5
HM	20	76	3	1	31.5

Table 1



**Fig. 1.** Temperature (a), Moisture content (b) and pH (c) change of the four composts across different stages (Initial, day 2; thermophilic, days 8–15; cooling, days 15–32; maturation, days 32–40). Lowercase letters above the bars indicate significant differences between treatments (L, low manure addition (10% W/W); LM, low manure with *Streptomyces-Bacillus* inoculant; H, high manure addition (20% W/W); HM, high manure with *Streptomyces-Bacillus* inoculant). Asterisks denote significance among stages (\*P < 0.05; \*\*P < 0.01; \*\*\*P < 0.001). Within boxplots, the black square represents three replicates, the white square represents the mean, and the black line represents the median.

composts from the top, middle, and bottom parts of individual piles, and mixed them as a representative sample for each time point. At each date, the collected samples were divided into three portions. The first portion (~50 g) for moisture and pH analysis; the second portion (~100 g) was freeze-dried, sieved (150–300  $\mu$ m), and stored at 4 °C for total carbon (TC), dissolved carbon (DOC), total nitrogen (TN), ammonium nitrogen (NH<sup>4</sup><sub>4</sub>-N), nitrate nitrogen (NO<sup>3</sup><sub>3</sub>-N), urease, catalase, cellulase, lignin peroxidase, nitrate reductase, and nitrite reductase analyses; and the third part (~50 g) was stored at–80 °C for metagenomics sequencing.

## 2.2. Physicochemical properties, C- and N- cycling enzyme activities and biological analysis

Compost temperature, pH, moisture, total carbon (TC), dissolved organic carbon (DOC), total nitrogen (TN), ammonium nitrogen (NH<sub>4</sub><sup>+</sup>-N), and nitrate nitrogen (NO3-N) were tracked. Temperature and moisture content were automatically recorded in real-time at 1-h intervals with an automatic temperature and humidity recorder (HOBO® Micro Station, H21-USB) at 30 cm depth below the compost pile surface. Compost moisture was also determined using fresh sample ( $\sim 2$  g) mass to dry mass after oven-drying at 60 °C to constant weight. Compost pH was determined in ultra-pure water at a 1:1 soil-water ratio using a pH meter (PHS-3C, Shanghai, China) (Liu et al., 2023). TC was determined by the Potassium dichromate oxidation external heating process (Bu et al., 2022). DOC was determined using a carbon-nitrogen analyzer (Shimadzu total organic carbon analyzer, TOC-L, Shimadzu Corp., Tokyo) (Hernandez-Lara et al., 2022). TN was determined by the sulfuric acid-hydrogen peroxide digestion method (Li et al., 2012). Concentrations of NH<sub>4</sub><sup>+</sup>-N and NO<sub>3</sub><sup>-</sup>N were determined with ultraviolet spectrophotometry after potassium chloride extraction (Chen et al., 2017). Enzymes related to N conversion and OM mineralization (urease), antioxidant defense (catalase), OM biodegradation (cellulase, lignin peroxidase), and N conservation (nitrate reductase and nitrite reductase), were analyzed using a full wavelength enzyme labeling instrument (Molecular devices, SpectraMax 190, USA) (Feng et al., 2023; He et al., 2022a; Pan et al., 2023; Su et al., 2023; Yin et al., 2021, 2023). Urease, produced by both fungi and bacteria, are closely related to N conversion and OM mineralization processes. Lignocellulose in compost is hydrolyzed by urease to produce unstable ammonia compounds, which causes N loss. Reducing urease activity can restrict ammonia emissions in composting (Zhou et al., 2021). Catalase is involved in antioxidant defense systems (Pan et al., 2023). Cellulase and lignin peroxidase are the main C-degrading enzymes involved in OM biodegradation. Increased N-reductase activities reflect their roles in N conservation because i) N-reductase promoted the formation of ammonium-N through organic N mineralization (Schimel and Bennett, 2004), and ii) ammonium-N would be further transformed into stable N compounds by N-reductase (Chen et al., 2019).

DNA was extracted from freeze-dried compost samples (0.2g) using a Fast DNA Spin Kit. Extracted DNA sample concentrations were determined with an ultra-fine ultraviolet spectrophotometer (Quawell Q3000). Extracted DNA quality was achieved with A260/A280 of 1.8–2.0. High-throughput quantitative PCR and metagenomics amplicon sequencing were then performed. Sequencing was conducted on the HiSeq 2500 platform (Illumina, PE150 mode, Guangdong Meige Gene Technology Co., Ltd). After obtaining metagenomic sequencing data of each sample, quality control was performed using Trimmomatic software to remove low-quality data. Metagenomic assembly was then

performed on each sample based on clean reads after quality control. Sequence data is available in the NCBI SRA database under project ID PRJNA996558.

### 2.3. Statistical analysis

All data were tested for normal distribution and homogeneity before statistics using Shapiro-Wilk test and Levene test. One-way analysis of variance (ANOVA) and post-hoc Tukey's test were performed to examine significant differences (P < 0.05) among treatments and composting time. The structural equation model was used to assess the direct and indirect effects of compost environmental variables.

Differences in microbial community composition were analyzed using Bray-Curtis dissimilarities calculated from normalized microbial abundance. We used principal coordinate analysis (PCA) to plot microbial community structure dissimilarities in space and permutational multivariate analysis of variance (PERMANOVA) to test the effect of composting properties on bacterial and fungal community structure. Redundancy analysis (RDA) and Mantel test were used to clarify relationships between composting properties and microbial communities. All statistics were completed using the "vegan" and "linKET" packages in R (version 4.2.3) (Oksanen et al., 2020).

To identify physicochemical indicators mediating changes in compost microbial community diversity and relative abundance of bacterial and fungal genera, we correlated these values with physicochemical differences between each pair of compost samples. Correlations between the physical and chemical properties of compost, microbial community diversity, and the relative abundance of microbial genera were analyzed by heat map, using the "ComplexHeatmap" and "circlize" packages in R (version 4.2.3). Regression analysis was then performed by constructing the diversity index using the relative abundance of microorganisms at each genus level and the physicochemical properties of the compost data, to obtain  $R^2$  value. The total explanatory quantity (the  $R^2$  value of the best model) was determined by the best regression.

The contributions of composting properties to microbial community dissimilarities in genus relative abundances (based on correlation and best multiple regression model) were plotted using "psych", "reshape2", "ggplot2", and "randomForest" packages in R. Structural equation model between composting properties and microbial diversity indices (Chao 1 and Shannon) was constructed using the "lavaan", "haven", "Hmsic" and "semPlot" packages. Detailed R scripts relative to the analysis were shown in supplementary file 1.

### 3. Result and discussion

### 3.1. Physicochemical and nutrient changes during composting

Aerobic composting is a microbially-mediated process (Wang et al., 2020c; Zhang et al., 2021b), and changes in physicochemical properties over time correlate with the process of organic matter decomposition during composting (Awasthi et al., 2016; Lv et al., 2023; Zhang et al., 2022a). In the present study, we closely tracked physical and chemical properties during the four stages of decomposition. In the thermophilic stage, the compost temperature reached  $\sim$ 65 °C (Fig. 1a) and this high-temperature duration is an important indicator for maturation (Meng et al., 2019a, 2019b). According to Zhang et al. (2013), microbial involvement in OM decomposition is the main cause of compost temperature increases. Adding exogenous Streptomyces-Bacillus inoculant (SBI) could reduce the time it takes for compost temperatures to peak. In our study, treatments of exogenous inoculant almost halved their time to reach maximum temperature (8 vs 15 days), which could be closely associated with the roles of SBI in accelerating degradation of carbon components (i.e., hemicellulose, cellulose, and lignocellulose) (He et al., 2022b; Hu et al., 2021). The rate of temperature elevation and duration at high temperature are important factors affecting composting efficiency (Wang et al., 2022a). After adding SBI, the time to reach the highest temperature was halved, which accelerated organic cycling (Javed et al., 2021) and increased compost N content (Ahmed et al., 2023). Moreover, the speeding up of high temperatures triggers shifts in microbial composition, promoting accumulation of N-functional micro-organisms (Ahmed et al., 2023) and pathogen suppression (Chang et al., 2021b).

Moisture content declined during composting and was significantly lower upon maturation than in the initial and thermophilic stages (Fig. 2), stabilizing at ~55% by the end (Fig. 1b). This decline is driven by evaporation caused by high temperature and ventilation during composting (Huang et al., 2022b). Compost moisture continues to evaporate, and the addition of microbial inoculants accelerates water loss rates (Wang et al., 2024). The moisture content of HM compost (containing high cow manure with inoculant) was significantly lower than that of H (high cow manure without inoculant) during the cooling stage. This difference can be attributed to the legacy effect of SBI from the thermophilic stage, demonstrating *Streptomyces-Bacillus*'s strong resistance to harsh conditions (Feng et al., 2021; Li et al., 2022b). In the cooling stage, the compost microbial abundance remained higher in HM, with greater microbial growth and metabolic activity contributing to accelerated evaporation.

Compost pH increased sharply during the initial and thermophilic stages (Fig. 1c), likely caused by the ammonification of organic matter nitrogen and release of nitrate (Chan et al., 2016; Li et al., 2021; Zhang et al., 2023). With intensifying microbial activity, OM degradation was accelerated, forming lower molecular weight organic acids and acidic phenols (Ravindran et al., 2022; Sun et al., 2023). We observed a drop in compost pH after the thermophilic stage (due largely to the presence of organic acids), stabilizing at  $\sim$  pH 7.7 upon maturation (Fig. 1c). Alkalinity was in agreement with the results of Zhang et al. (2018). Moreover, our results showed that inoculants induced significant pH change related to both the amount of manure addition (10% vs. 20%) and composting stage. At the thermophilic stage, high manure addition (20% W/W) resulted in a significantly higher pH in inoculant-treated (HM) than in inoculant-free manure (H). Under the higher N and higher temperature conditions, SBI might promote ammonification of compost, resulting in a large accumulation of ammonium nitrogen and consequent increase in pH; whereas, with low manure addition (10%), significant pH differences between SBI and inoculant-free treatments appeared during cooling, which may be attributed to alkaline metabolites produced by the Streptomyces-Bacillus inoculant (Ning et al., 2017; Wu et al., 2021). Optimal pH for the composting process varies with initial substrate and pile moisture, and it also affects microbial metabolism and compost maturity (Yang et al., 2020). A large amount of NH<sub>4</sub><sup>+</sup> in the initial composting stage leads to an increase in pH, while the carboxyl and phenolic groups formed by humic acid can trigger a decline in pH which is accompanied by N loss (Cao et al., 2022; Dong et al., 2024). Thus, monitoring pH at an alkalescent range (7.8–8.8 in our case) can be a useful indicator for N content maintained in final composts.

Total carbon (TC) content of the four composts decreased significantly from ~48 % to ~38% on average during the composting stages (P < 0.05; Fig. 2a). At the end of composting, TC content of inoculated treatments (LM, HM) was significantly higher than inoculant-free treatments (L, H). Accelerated C degradation under SBI treatments could result from greater C-degrading enzyme activity, on carbon-containing OM, releasing gaseous carbon (i.e., CO<sub>2</sub> and CH<sub>4</sub>) (He et al., 2018; Swati and Hait, 2018). Apart from total carbon, the dissolved organic carbon (DOC) of all composts decreased significantly from ~2.8 % to ~0.1 % (P < 0.05; Fig. 2b). Decrease in DOC was associated with microbial metabolic utilization during composting (Raj and Antil, 2011) and was consistent with the results from previous studies (Hue and Liu, 1995; Straathof and Comans, 2015; Zmora-Nahum et al., 2005).

Total nitrogen (TN) content across the four compost treatments increased significantly from 1.0, 1.2, 1.0, and 1.2% to 1.1(+10.4%), 1.5



**Fig. 2.** Total carbon (TC; a), dissolved carbon (DOC; b), total nitrogen (TN; c), ammonium nitrogen  $(NH_{4}^{+}-N; d)$ , nitrate nitrogen  $(NO_{3}^{-}-N; e)$  and carbon to nitrogen (C/N ratio; f) change during different composting stages (Initial, day 2; thermophilic, days 8–15; cooling, days 15–32; maturation, days 32–40). Lowercase letters above the bars indicate significant differences between treatments (L, low manure addition (10% W/W); LM, low manure with SBI (*Streptomyces-Bacillus* inoculant); H, high manure addition (20% W/W); HM, high manure with SBI). Asterisks denote significance among stages (\*P < 0.05; \*\*P < 0.01; \*\*\*P < 0.001).

(+33.04%), 1.9 (+91.7%), and 1.9% (+64.3%) (P < 0.05), respectively (Fig. 2c). Carbon loss in compost is largely driven by the needs of microbial growth and metabolism (Huang et al., 2022a). Although carbon loss in the composting process is inevitable, high carbon loss can reduce the amount and quality of final composts. Carbon conversion in compost

is always accompanied by complex biochemical metabolism (Cao et al., 2019); the longer the duration of the thermophilic period, the more effective is carbon loss control during composting (Ye et al., 2023). After the addition of SBI, the time to reach the thermophilic phase was significantly shortened (Fig. 1). In addition, we found that the activity of

C-degrading enzymes was significantly boosted in the inoculant treatments. Lignocellulose-degrading micro-organisms, those that produce C-degrading enzymes targeting cellulose (cellulase) and lignin (peroxidase), favor high temperatures (Pérez et al., 2002); this phenomenon may be closely linked to the optimal activities of these enzymes under high temperatures. Similar to the changes in compost TC, inoculant treatments exhibited a significantly higher TN content compared to inoculant-free treatments at the maturation stage. The later composting stage was accompanied by a decrease in temperature, which favors the proliferation of nitrifying bacteria that convert ammonium nitrogen into nitrate nitrogen (Li et al., 2020). This reaction leads to the concentration and increase in nitrogen content over time (Stein, 2020; Straka et al., 2019). Biological enrichment with the addition of SBI enhances the process of organic N degradation as the microbial community converts mineral N to humic N (Duan et al., 2020; Harindintwali et al., 2020). Higher temperatures normally coincided with high CO<sub>2</sub> production and matter loss, which contributed to high N content in the final compost.

During aerobic composting, organic N degrades into dissolved N and eventually into  $NH_4^+$ -N (Wang et al., 2020b). At the thermophilic stage, a significant decrease in  $NH_4^+$ -N content was found in all composts,



Fig. 3. Variations in C- and N-cycling enzyme activities at different composting stages (Initial, day 2; thermophilic, days 8–15; cooling, days 15–32; maturation, days 32–40). Treatments (L, low manure addition (10% W/W); LM, low manure with SBI; H, high manure addition (20% W/W); HM, high manure with SBI).

probably due to high-temperature volatilization of ammonium as NH<sub>3</sub> (Liu et al., 2023), and NO<sub>3</sub>-N content reached its peak, potentially related to attenuation of nitrifying bacteria at around 65-70 °C (Chen et al., 2022; Jiang et al., 2021). Similarly, HM had the highest NO<sub>3</sub>-N content, with a two-fold increase compared to the initial stage. Initial cow manure concentration (L vs H) also affected NO<sub>3</sub>-N content: with NO<sub>3</sub>-N significantly lower in L than LM, but significantly higher in H than HM (Fig. 3e). This may be caused by the proliferation in thermophilic bacteria involved in nitrification and denitrification at the thermophilic stage, leading to an increase in NO3-N content (Zhou et al., 2022a). After composting, the C/N of the four composting treatments were 38.3, 16.9, 23.7, and 22.4, respectively, and L was significantly higher than LM, but H was significantly lower than HM (Fig. 3f). An appropriate C/N ratio is a key factor for composting (Azim et al., 2017; Kumar et al., 2010). In the present composts, the value of the initial C/N > 40, but the C/N ratio of the SBI treatment (LM and HM) stayed at  $\sim$  23 after maturation, indicating microbial inoculation strongly influenced the degradation rate of organic matter in composting and then affects the conversion of C and N nutrition (Jia et al., 2023; Ou et al., 2019).

### 3.2. Key C- and N-cycle enzyme activities and their correlations with other parameters

The degradation and conversion of compost C-substances mainly depend on a range of enzymes secreted by microorganisms (Hoang et al., 2022; Xie et al., 2023). Microorganisms secrete extracellular enzymes such as dehydrogenases, cellulases, amylases, proteases, and phosphatases to decompose organic matter (Costa et al., 2016; Zhang and Sun, 2014). The activity of these enzymes also reflects the intensity of microorganisms transforming organic matter into humus. Among the Cand N- cycling enzymes investigated in this study (urease, cellulase, lignin peroxidase, nitrate reductase, nitrite reductase, and catalase) (Fig. 3), ureases produced by both fungi and bacteria are closely associated with nitrogen conversion and OM mineralization processes (Tavares et al., 2023). Our results show that changes in urease activity are negatively correlated with NH<sub>4</sub><sup>+</sup>-N (r = -0.61; P < 0.05) and NO<sub>3</sub><sup>-</sup>N content (r = -0.45; P < 0.05; Fig. S1). Urease activity ranged from 2.91 to 7.35 mg  $g^{-1}$ , gradually increasing over the composting stages (Fig. 3a). With an initial activity around 3 mg  $g^{-1}$ , the process of composting more than doubled urease activity possibly co-mediated by OM carbonization and nitrification (Gao et al., 2023; Meng et al., 2023). Urease hydrolyzes compost lignocellulose and produces unstable ammonia compounds. A deceleration of urease activity can reduce ammonia emissions, thus increasing the final N content in compost (Zhou et al., 2021). Compared to inoculant-free treatments, inoculant treatments showed significantly lower urease activity, testimony to their ability to mitigate the release of N and minimizing the harmful effects of excessive N concentrations (Meng et al., 2023). Catalases are involved in antioxidant defense systems (Pan et al., 2023). Catalase activity ranged from 164 to 236 mg g  $^{-1}$  in our experiments and was  ${\sim}200$  mg g  $^{-1}$  at the initial stage (Fig. 3b). As a whole, the catalase activity of inoculant treatments (LM, HM) was significantly higher than that in inoculant-free treatments (L, H), indicating that SBI can enhance the removal of hydrogen peroxide and limit oxidative stress during composting. This could reflect Streptomyces species' ability to produce diverse secondary metabolites and their resulting abundance of reactive-oxygen-scavenging enzymes (Chen et al., 2023; Yang et al., 2023). Applying agroforestry byproducts like straw and cornstalks as exogenous C-additives is a useful way to accelerate compost maturity (He et al., 2022a). Our results showed that the activities of both cellulase and lignin peroxidase steadily increased during composting, reflecting an accelerating maturation process in co-ordination with microbial C-metabolism (Yu et al., 2019; Zhang et al., 2021c). Nitrate reductase ranged from 2 to 41  $\mu$ mol g<sup>-1</sup> (Fig. 3d) and nitrite reductase ranged from 4 to 11  $\mu$ mol g<sup>-1</sup> (Fig. 3e) in our experiments. Both enzymes were significantly correlated (r = 0.71, P < 0.05; Fig. S2) and exhibited

similar changes; N-cycling is a redox reaction, and it interconverts N-containing compounds between the highest oxidation state nitrate and the lowest reducing state ammonium salt (Kuypers et al., 2018). The global biogeochemical N cycle mainly includes six N-transformation processes: assimilation, ammonization, nitrification, denitrification, anaerobic ammoxidation, and N fixation (Shi et al., 2020). N fluxes of these nitrogen conversion processes are quite different. Among them, nitrification and denitrification are the two important linkages to N conversion, and nitrification is a key step to reduce ammonia volatilization (Wang et al., 2019). However, N loss caused by denitrification in the composting process cannot be ignored (Lycus et al., 2018). N accumulation can be promoted by adding N-converting microorganisms. Thus, the two important oxidoreductases, nitrate reductase and nitrite reductase, were mainly considered in the present work. The higher the nitrate reductase and nitrite reductase activities of the inoculant treatment, the stronger the nitrogen retention ability. N-reductase activities of inoculant treatments were all significantly higher than those of inoculant-free treatments at maturation (Fig. 3). Increased N-reductase activities reflect their leading roles in N storage because i) N-reductase promoted the formation of ammonium-N through organic N mineralization (Schimel and Bennett, 2004), and ii) ammonium-N would be further transformed into stable N compounds by N-reductase (Chen et al., 2019). The higher activity of these two nitrogen reductases in the inoculated group indicates greater nitrogen retention capacity.

### 3.3. Characteristics of bacterial and fungal communities during composting

During aerobic composting, C and N cycling are mainly mediated by microbial communities (Wei et al., 2017; Zhou et al., 2019; Zhu et al., 2019). Relative abundances of bacteria differed significantly in each compost (Fig. 4a) and bacterial community composition differed between stages, as shown by a diverse distribution of community composition (Fig. 4a). In each stage, a close distance of bacterial community structure between low (L) and high (H) cow manure composts indicated that the addition ratio (10% vs 20%) of cow manure did not significantly affect it (Fig. S2). At the initial stage, bacterial composition of L1 and H1 treatments was dominated by Pantoea. However, at the thermophilic stage, SBI clearly increased the relative abundances of Agrobacterium and Pseudomonas in low (LM) and high (HM) cow manure treatments (Fig. 4), possibly due to SBI's effect on indigenous microorganism metabolism and degradation rates (Feng et al., 2021; Oviedo-Ocaña et al., 2022). Inoculant stimulated the relative abundance of cellulolytic (Cupriavidus (+89%) and Sorangium (+87%)) and N-fixing (Agrobacterium (+72%) and Pseudomonas (+23%)) bacteria (Fig. S2). Alteration of the compost environment in the transition to the thermophilic stage gradually replaced the originally dominant microbial taxa associated with the compost substrates (Du et al., 2019; Li et al., 2023; Zhou et al., 2023b).

For fungal community structure, we found the two initial treatments (L1 and H1) significantly separated from the others along the PC1 axis, but there was no significant difference in fungal community structure between SBI-treated and untreated composts in the later composting stages (Fig. S2). This might due to the severe selection pressure effect of high temperatures on the fungal communities (Huhe et al., 2017).

Microbial community in compost is the key to compost quality. The addition of SBI changed the abundance and community succession of microorganisms involved in carbon and nitrogen metabolism, improving C and N metabolism and resulting in efficient composting (Hou et al., 2023; Wang et al., 2021). A range of microorganisms are involved in the biological oxidation composting processes (Lu et al., 2022). Proteobacteria, Bacteroides, Firmicutes, and Actinobacteria are the dominant phyla involved in the degradation and transformation of organic matter (Henry et al., 2020; Ma et al., 2023). In cow manure composting, *Bacillus, Pseudomonas*, and *Streptomyces* are the dominant bacterial genera across various stages. *Pseudomonas* have exhibited



**Fig. 4.** Dynamics of bacterial and fungal community composition and structure at the genus level in different treatments during composting. (**a**, bacterial community composition; **b**, bacterial community structure). Contributions of compost properties to bacterial (**c**) and fungal (**d**) community dissimilarities (at the genus level) based on correlation and best multiple regression model. Circle size represents variable importance (the proportion of explained variability calculated via multiple regression modeling and variance partitioning analysis). Colors represent Spearman correlations.

N-fixing and lignin-degrading functions in cow-manure and C-additive substrate experiments (Ren et al., 2016). Bacteroides are also capable of degrading macromolecular organic matter including cellulose, chitin, and starch (Ren et al., 2016). Streptomyces tend to dominate the later composting stages, especially in degrading cellulose and hemicellulose (Steger et al., 2007; Zhou et al., 2022b). Fungi use numerous C-containing compounds as carbon sources, playing a crucial role in the rapid degradation of cellulose and lignin (Bonito et al., 2010). For instance, Ascomycetes (such as Fusarium) and Basidiomycetes are the dominant fungi in the composting process and secrete a variety of cellulose and hemicellulose degrading enzymes (Wang et al., 2018; Yin et al., 2023). In the thermophilic stage, Aspergillus and Humicola are abundant, producing heat-stable cellulase, lignin enzyme, and amylase, and contributing significantly to C-substrate degradation at high-temperature (Chang et al., 2021a; Kumar et al., 2007). Penicillium, Trichoderma, Chaetomium, and Neurospora can produce strongly penetrating mycelia which maximize the contacting interface between C-substrates and degrading enzymes.

The potential biological contribution of the core bacterial and fungal microbiota to the physicochemical properties of compost at the generic level is shown in Fig. 4b and d. Compost-dissolved organic C (DOC), C/N ratio, nitrate reductase, and pH are the three strongest positive predictors of bacterial community differences. For instance, DOC was positively associated with *Pantoea, Agrobacterium, Pseudomonas*, Hydrogenophaga, Brevundimonas, Pseudoxanthomonas, and Plantibacter. The core bacterial genera with a more than 50% potential biological contribution to the physical and chemical properties of compost were Cupriavidus (~80%), Sorangium (~70%), Streptomyces (~55%), and Agrobacterium (50%) (Fig. 4b). This can be explained by the increased abundance of these copiotrophic taxa and their abilities to utilize readily available C for carbohydrate transport and energy conversion (Liu et al., 2019). The beneficial roles of these bacteria can further improve compost maturation efficiency (Wang et al., 2020a). For fungi, DOC, NH<sub>4</sub><sup>+</sup>-N, and moisture were the three strongest positive predictors in community differences (Fig. 4d). In contrast to bacteria, fungal taxa explained the changes of compost physicochemical properties more equally, at around 60% (Fig. 4d), and these parameters showed comparable correlations with the top 20 abundant fungal genera. This indicated that the bacterial community was more sensitive to environmental fluctuations than the fungal community (Huhe et al., 2017; Meng et al., 2019c).

### 3.4. Relationships between microbial community composition and physicochemical factors

To ascertain relationships between environmental variables and microbial communities during composting, RDA showed that the explanatory variables for bacterial communities represented 96.87 %

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(62.87% and 27.01% in the two axes, respectively) of the total variation (Fig. 5a). As evaluated by arrow length, the strength of environmental factors explaining the variation in bacterial communities was: DOC > urease > cellulase > lignin peroxidase > TC > pH > C/N ratio > NH<sub>4</sub><sup>+</sup>-N > TN > moisture > nitrate reductase > nitrite reductase > catalase > NO<sub>3</sub><sup>-</sup>N. Among them, the C/N ratio was positively correlated with pH and TC, as shown by an aggregation of the three parameters in RDA. Compost fungal community change was mainly explained by the variables along the first axes (93.9%; Fig. 5b). Overall, compost physicochemical properties (C, N, pH) drove bacterial community changes (as shown by the longest arrows alongside the RDA 1), while the C and N decomposing enzymes (cellulase, lignin peroxidase, and urease) as well as readily-available C (DOC), played secondary roles (as indicated by the length of these variables along the RDA 2) (Fig. 5a). Fungal community was mainly controlled by C-degrading enzymes (cellulose and lignin peroxidase) and the release of readily-available C and N nutrients (DOC, NH<sup>+</sup><sub>4</sub>-N). This might be due to differences in the mechanisms by which

bacteria and fungi participate in the conversion of nutrients during composting (Liu et al., 2020; Wang et al., 2022d; Xiong et al., 2023). The results of RDA analysis showed that bacterial and fungal community structure were regulated by physicochemical properties, thus accelerating the decomposition and transformation of C-substances (Wang et al., 2024). However, during composting, the key factors driving bacterial and fungal community succession were different, due to the divergent mechanisms driving nutrient conversion in bacteria and fungi (Liu et al., 2020; Wang et al., 2022b; Xiong et al., 2023). The bacterial life-history strategy consists of rapid development, a small body size, early reproduction, and a short lifespan (r-strategist) (Jeschke et al., 2019), mediated by easily-available nutrients during composting. In contrast, fungi are marked by slow development, a large body size, delayed reproduction, and a long lifespan (K-strategist). Thus, fungal community succession is mainly controlled by total carbon, total nitrogen, and the activity of C-substrate transformation during composting. These findings can contribute to the development of effective microbial



**Fig. 5.** Redundancy analysis (RDA) and Mantel test analysis between environment factors and microbial community structure in different treatments during composting. For RDA between environment factors and bacterial (a) or fungal (b) community structure, the percentage of variation explained by each axis is shown, and the relationship is significant (P < 0.001). Points of different colors represent samples under different treatments. The length of the arrows in the RDA plot indicates the degree of correlation between environmental factors and the sample distribution. For Mantel test between environment factors and bacterial (c) or fungal (d) community structure, the dotted- and solid gold triangles represent the treatments with and without SBI (*Streptomyces-Bacillus* 1:1 inoculant), respectively. Color column and square on the top right corner, denote Pearson's correlation coefficients. Line breadth and color represent correlation coefficient and significance levels, respectively. Asterisks in the square indicate significance levels (\*, P < 0.05; \*\*, P < 0.01; \*\*\*, P < 0.001).

combinations to boost SBI applications in composting.

Compared to inoculant-free treatments, the SBI-boosted bacterial community was significantly correlated with C/N ratios (Mental test, P < 0.01) and with catalase (P < 0.01) (Fig. 6c), indicating SBI's role in improving maturation and oxidative stress defense during composting. However, the fungal community was mainly affected by easily-available C and N nutrients (Mental test, r > 0.4; P < 0.01; Fig. 6d), regardless of inoculant. The dominant influence of DOC and NH<sup>+</sup><sub>4</sub>-N on the fungal community was sustained across all composting stages (Fig. S3) and could be linked to the processes of C mineralization and organic N decomposition; usually the drivers of succession in fungal community composition (Maleki et al., 2023). In particular, the proliferation of fungi was more likely to be sensitive to the conversion of NH<sup>+</sup><sub>4</sub>-N (nitrification) as an important nitrogen energy resource (Liu et al., 2023).

Numerous composting studies have compared C and N losses during composting (Walling et al., 2020; Zhao et al., 2020). Although very important, microbial physiological parameters (such as microbial biomass carbon, carbon use efficiency, and turnover rate) have until now often been overlooked in composting studies. Diverse microorganisms play essential roles in C, N conversion during composting. In addition to assimilation of labile carbon for growth (as revealed by the amounts of C and N incorporated into biomass), their residues also make a high contribution to stable carbon content. In recent years, the relationship between organic carbon and microbial necromass has been extensively explored in natural ecosystems, however, whether microbial physiological traits affect microbial necromass and how to link microbial biomass, microbial necromass, and total carbon during composting are points that need to be further explored.

Carbon and nitrogen transformations in composting are mainly driven by microorganisms, including degradation and fixation, methane metabolism, nitrification, and denitrification (Deng et al., 2023; Wang et al., 2022c). Each step of the C, N metabolic process is controlled by one or more functional marker genes (Bae et al., 2015; Lammel et al., 2015; Zhang et al., 2020). For example, *naglu, isoplu, amyA, exochi, amyX, manB, xylA, smtA, rbcL, mcrA,* and *pccA* are the main genes involved in the carbon cycle in compost. Functional genes such as *hao, narG/H, nirK, norB, nosZ,* and *nifH* are commonly used to study microbial community structure succession in the N cycle (Wen et al., 2022). Cellular carbon and nitrogen decomposition and anabolism are the main sources of energy and nutrients required for microbial metabolism (Yang et al., 2019; Zhang et al., 2018) and are tightly coupled in different organisms; often a restriction or oversupply of one element can have a strong effect on the metabolism of the other. The ko00910 metabolic pathway (Nitrogen Metabolism - reference pathway from KEGG) shows that  $HCO_3^-$  can interact with cyanates to form an important intermediate of carbon-nitrogen coupling; carbamate (Hennessy et al., 2018).

The Structural equation model (SEM) showed that the selected environmental parameters had different significant effects on microbial richness and diversity (Fig. 6 and Fig. S5). The SEM was capable of postulating direct and in-direct functions among different factors during the composting process based on microbial inoculant use. For bacteria, TC and TN contents were directly affected by bacterial Shannon index ( $R^2 = 0.96$ ) and moisture ( $R^2 = 1.00$ ), out of all interactions among dominant factors (TC, TN, C/N ratio, and pH). Out of the secondary important factors (cellulase, DOC, urease, and NH<sup>+</sup><sub>4</sub>-N), C- and Ndegrading enzymes (cellulase and urease) were directly affected by bacterial community (both richness and diversity). DOC was coregulated by the direct functions of pH, cellulase, and bacterial community; while NH<sup>+</sup><sub>4</sub>-N content was the only factor affected by nitrate reductase ( $R^2 = 0.12$ ).

In terms of fungal indices, compost moisture directly affected fungal diversity ( $R^2 = 0.80$ ) and richness ( $R^2 = 0.87$ ). The altered fungal community was further significantly influenced by TN, N-reductases (nitrite- and nitrate-reductase) and NO<sub>3</sub><sup>-</sup>-N contents (Fig. 6b). The change of TC content was positively affected (in a direct way, P < 0.05) by fungal richness and pH; TN was also significantly influenced by both fungal richness and fungal diversity (Fig. 6b) indicating the roles of these fungal communities in C-substrate degradation (Tian et al., 2017; Zhang et al., 2016) and N transformation (Guo et al., 2012; Qiao et al., 2021).

### 4. Conclusion

Cow manure and corn residues are transformed into humus products through a series of biochemical reactions. These substances are rich in nitrogen, phosphorus, potassium, and other nutrients, and provide a stable source of high-quality fertilizer. After proper application to soil, it



**Fig. 6.** Structural equation model (SEM) shows the effect of environmental factors on bacterial (a) and (b) fungal richness (Chao 1 index) and diversity (Shannon) indices during composting. Red and blue (significant influence with P < 0.05) arrows reflect positive and negative relationships, respectively. R<sup>2</sup> indicates the percentage of variation that can be explained in respective SEM. For each variable, the standardized path coefficients adjacent to each arrow can be found in Fig. S4.

can enhance the diversity and richness of soil microorganisms; improve soil structure, fertility, and soil ecology; and ultimately promote the growth and yield of crops. This work highlights the positive effects of Streptomyces-Bacillus inoculants (SBI) on co-composting of crop residual biomass combined with cow manure. SBI shortened the thermophilic stage, increased the content of total nitrogen and the activities of N reductase (nitrate reductase: +60%; nitrite reductase: +219%), and improved the final compost quality with a high C/N ratio of  $\sim$ 23:1). In the thermophilic phase, inoculation of SBI significantly increased the relative abundance of Agrobacterium and Pseudomonas, and changed C-, N-metabolism pathways in the composting process. The response of the fungal community to environmental factors was weaker than that of bacteria. The rapidly-reproducing bacterial community was significantly affected by easily-available nutrients during composting, while the fungal community was more tightly regulated by cellulase and urease. Overall, the use of SBI in the co-composting process is a suitable approach to accelerate composting time, facilitate biodegradation, and increase N concentration in the final compost of cow manure and agroforestry biowaste. In this way, for sustainable waste management practitioners or end-users, SBI-mediated co-composting has the potential to speed up biowaste conversion and application as an effective organic fertilizer for maximum soil and plant health.

### CRediT authorship contribution statement

Ziyan Zhou: Investigation, Methodology, Writing – original draft. Xiaofei Shi: Investigation, Resources. Parag Bhople: Methodology, Software, Validation. Jishao Jiang: Resources, Validation, Visualization. Caspar C.C. Chater: Resources, Validation, Writing – review & editing. Shimei Yang: Investigation, Validation. Jesus Perez-Moreno: Writing – review & editing. Fuqiang Yu: Project administration, Writing – review & editing. Dong Liu: Conceptualization, Project administration, Supervision, Writing – review & editing.

#### Declaration of competing interest

The authors declare that they have no competing financial interests or personal relationships that could influence the work reported in this paper.

### Data availability

Data will be made available on request.

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### Appendix A. Supplementary data

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### References

Abdellah, Y.A.Y., Shi, Z.-J., Sun, S.-S., Luo, Y.-S., Yang, X., Hou, W.-T., Wang, R.-L., 2022. An assessment of composting conditions, humic matters formation and product maturity in response to different additives: a meta-analysis. J. Clean. Prod. 366, 132953.

- Ahmed, I., Zhang, Y., Sun, P., Zhang, B., 2023. Co-occurrence pattern of ARGs and Nfunctional genes in the aerobic composting system with initial elevated temperature. J. Environ. Manag. 343, 118073.
- Awasthi, M.K., Pandey, A.K., Bundela, P.S., Wong, J.W.C., Li, R., Zhang, Z., 2016. Cocomposting of gelatin industry sludge combined with organic fraction of municipal solid waste and poultry waste employing zeolite mixed with enriched nitrifying bacterial consortium. Bioresour. Technol. 213, 181–189.
- Azim, K., Soudi, B., Boukhari, S., Perissol, C., Roussos, S., Thami Alami, I., 2017. Composting parameters and compost quality: a literature review. Org Agr 8 (2), 141–158.
- Bae, H.-S., Holmes, M.E., Chanton, J.P., Reddy, K.R., Ogram, A., Voordouw, G., 2015. Distribution, activities, and interactions of methanogens and sulfate-reducing prokaryotes in the Florida everglades. Appl. Environ. Microbiol. 81 (21), 7431–7442.
- Bello, A., Han, Y., Zhu, H., Deng, L., Yang, W., Meng, Q., Sun, Y., Egbeagu, U.U., Sheng, S., Wu, X., Jiang, X., Xu, X., 2020. Microbial community composition, cooccurrence network pattern and nitrogen transformation genera response to biochar addition in cattle manure-maize straw composting. Sci. Total Environ. 721, 137759.
- Bernal, M.P., Alburquerque, J.A., Moral, R., 2009. Composting of animal manures and chemical criteria for compost maturity assessment. A review. Bioresour. Technol. 100 (22), 5444–5453.
- Bonito, G., Isikhuemhen, O.S., Vilgalys, R., 2010. Identification of fungi associated with municipal compost using DNA-based techniques. Bioresour. Technol. 101 (3), 1021–1027.
- Bu, W., Wan, J., Zhang, H., Liu, N., Wang, K., Wang, Y., 2022. Effects of pilot-scale cocomposting of gentamicin mycelial residue with rice chaff on gentamicin degradation, compost maturity and microbial mommunity dynamics. Waste Biomass Valori 13 (12), 4797–4812.
- Cao, Y., Gu, J., Zhang, J., Chen, B., Xu, Y., Liu, D., Hu, H., Huang, H., 2022. Reduced pH is the primary factor promoting humic acid formation during hyperthermophilic pretreatment composting. J. Environ. Manag. 316, 115215.
- Cao, Y., Wang, J., Huang, H., Sun, E., Butterly, C., Xu, Y., He, H., Zhang, J., Chang, Z., 2019. Spectroscopic evidence for hyperthermophilic pretreatment intensifying humification during pig manure and rice straw composting. Bioresour. Technol. 294, 122131.
- Chan, M.T., Selvam, A., Wong, J.W., 2016. Reducing nitrogen loss and salinity during 'struvite' food waste composting by zeolite amendment. Bioresour. Technol. 200, 838–844.
- Chang, H.-q., Zhu, X.-h., Wu, J., Guo, D.-y., Zhang, L.-h., Feng, Y., 2021a. Dynamics of microbial diversity during the composting of agricultural straw. J. Integr. Agric. 20 (5), 1121–1136.
- Chang, R., Li, Y., Li, N., Wu, X., Chen, Q., 2021b. Effect of microbial transformation induced by metallic compound additives and temperature variations during composting on suppression of soil-borne pathogens. J. Environ. Manag. 279, 111816.
- Chen, H., Huang, R., Wu, J., Zhang, W., Han, Y., Xiao, B., Wang, D., Zhou, Y., Liu, B., Yu, G., 2021. Biohythane production and microbial characteristics of two alternating mesophilic and thermophilic two-stage anaerobic co-digesters fed with rice straw and pig manure. Bioresour. Technol. 320 (Pt A), 124303.
- Chen, J., Qiao, M., Yang, Y., Gao, Z., Yang, Z., Lin, W., 2023. Exogenous *Streptomyces* spp. benefit naked oat growth under dry farming conditions by modifying rhizosphere bacterial communities. Appl. Soil Ecol. 189, 104946.
- Chen, L., Li, W., Zhao, Y., Zhang, S., Meng, L., 2022. Evaluation of bacterial agent/nitrate coupling on enhancing sulfur conversion and bacterial community succession during aerobic composting. Bioresour. Technol. 362, 127848.
- Chen, M., Wang, C., Wang, B., Bai, X., Gao, H., Huang, Y., 2019. Enzymatic mechanism of organic nitrogen conversion and ammonia formation during vegetable waste composting using two amendments. Waste Manag. 95, 306–315.
- Chen, W., Liao, X., Wu, Y., Liang, J.B., Mi, J., Huang, J., Zhang, H., Wu, Y., Qiao, Z., Li, X., Wang, Y., 2017. Effects of different types of biochar on methane and ammonia mitigation during layer manure composting. Waste Manag. 61, 506–515.
- Cheng, D., Liu, Y., Shehata, E., Feng, Y., Lin, H., Xue, J., Li, Z., 2021. In-feed antibiotic use changed the behaviors of oxytetracycline, sulfamerazine, and ciprofloxacin and related antibiotic resistance genes during swine manure composting. J. Hazard Mater, 402. 123710.
- Cheng, K., Rong, X., Pinto-Tomás, A.A., Fernández-Villalobos, M., Murillo-Cruz, C., Huang, Y., Voordouw, G., 2015. Population genetic analysis of *Streptomyces albidoflavus* reveals habitat barriers to homologous recombination in the diversification of Streptomycetes. Appl. Environ. Microbiol. 81 (3), 966–975.
- Costa, M., Lorin, H.E.F., Costa, L.A.M., Cestonaro, T., Pereira, D.C., Bernardi, F.H., 2016. Performance of four stabilization bioprocesses of beef cattle feedlot manure. J. Environ. Manag. 181, 443–448.
- Cui, H., Wang, J., Cai, X., Feng, K., Xie, G.J., Liu, B.F., Xing, D., 2023. Chemical pretreatments and anaerobic digestion shape the virome and functional microbiome in fecal sludge. Environ. Sci. Technol. 57 (14), 6008–6020.
- de Nijs, E.A., Maas, L.M.E., Bol, R., Tietema, A., 2023. Assessing the potential of cocomposting rose waste as a sustainable waste management strategy: nutrient availability and disease control. J. Clean. Prod. 399, 136685.
- Deng, W.-K., He, J.-L., Chen, J.-Y., Wu, R.-T., Xing, S.-C., Liao, X.-D., 2023. Effects of microplastics on functional genes related to CH<sub>4</sub> and N<sub>2</sub>O metabolism in bacteriophages during manure composting and its planting applications. J. Hazard Mater. 460, 132288.
- Dong, S., Wei, Y., Yu, Q., Gao, Y., Chen, H., Zhou, K., Cheng, M., Wang, B., Wei, Y., Hu, X., 2024. Inoculating functional bacteria improved the humification process by

#### Z. Zhou et al.

regulating microbial networks and key genera in straw composting by adding different nitrogen sources. Bioresour. Technol. 393, 130022.

- Du, J., Zhang, Y., Qu, M., Yin, Y., Fan, K., Hu, B., Zhang, H., Wei, M., Ma, C., 2019. Effects of biochar on the microbial activity and community structure during sewage sludge composting. Bioresour. Technol. 272, 171–179.
- Duan, M., Zhang, Y., Zhou, B., Qin, Z., Wu, J., Wang, Q., Yin, Y., 2020. Effects of *Bacillus subtilis* on carbon components and microbial functional metabolism during cow manure-straw composting. Bioresour. Technol. 303, 122868.
- FAO, 2020. Livestock and Environment Statistics: Manure and Greenhouse Gas Emissions. Global, Regional and Country Trends, 1990–2018. FAOSTAT Analytical Brief Series, Rome, 14.
- Feng, J., Wang, B., Zhang, D., Chu, S., Zhi, Y., Hayat, K., Wang, J., Chen, X., Hui, N., Zhou, P., 2021. Streptomyces griseorubens JSD-1 promotes rice straw composting efficiency in industrial-scale fermenter: evaluation of change in physicochemical properties and microbial community. Bioresour. Technol. 321, 124465.
- Feng, Y., Wang, N., Fu, H., Xie, H., Xue, L., Feng, Y., Poinern, G.E.J., Chen, D., 2023. Manure-derived hydrochar superior to manure: reducing non-point pollution risk by altering nitrogen and phosphorus fugacity in the soil-water system. Waste Manag. 168, 440–451.
- Gao, Y., Tan, Z., Wang, H., Zhu, Y., 2023. Nitrogen fertilization and the rhizosphere effect on nitrogen cycling: a meta-analysis. Appl. Soil Ecol. 186, 104788.

Guo, R., Li, G., Jiang, T., Schuchardt, F., Chen, T., Zhao, Y., Shen, Y., 2012. Effect of aeration rate, C/N ratio and moisture content on the stability and maturity of compost. Bioresour. Technol. 112, 171–178.

- Guo, X., Guo, W., Yang, M., Sun, Y., Wang, Y., Yan, Y., Zhu, B., 2022. Effect of *Bacillus* additives on fermentation quality and bacterial community during the ensiling process of whole-plant corn silage. Processes 10 (5).
- Harindintwali, J.D., Zhou, J., Yu, X., 2020. Lignocellulosic crop residue composting by cellulolytic nitrogen-fixing bacteria: a novel tool for environmental sustainability. Sci. Total Environ. 715, 136912.
- He, X., Yin, H., Sun, X., Han, L., Huang, G., 2018. Effect of different particle-size biochar on methane emissions during pig manure/wheat straw aerobic composting: insights into pore characterization and microbial mechanisms. Bioresour. Technol. 268, 633–637.
- He, Y., Liu, D., He, X., Wang, Y., Liu, J., Shi, X., Chater, C.C.C., Yu, F., 2022a. Characteristics of bacterial and fungal communities and their impact during cow manure and agroforestry biowaste co-composting. J. Environ. Manag. 324, 116377.
- He, Y., Zhang, Y., Huang, X., Xu, J., Zhang, H., Dai, X., Xie, L., 2022b. Deciphering the internal driving mechanism of microbial community for carbon conversion and nitrogen fixation during food waste composting with multifunctional microbial inoculation. Bioresour. Technol. 360, 127623.
- Hennessy, J.E., Latter, M.J., Fazelinejad, S., Philbrook, A., Bartkus, D.M., Kim, H.-K., Onagi, H., Oakeshott, J.G., Scott, C., Alissandratos, A., Easton, C.J., Vieille, C., 2018. Hyperthermophilic carbamate kinase stability and anabolic in vitro activity at alkaline pH. Appl. Environ. Microbiol. 84 (3).
- Henry, A.B., Maung, C.E.H., Kim, K.Y.P., 2020. Metagenomic analysis reveals enhanced biodiversity and composting efficiency of lignocellulosic waste by thermoacidophilic effective microorganism (tEM). J. Environ. Manag. 276, 111252.
- Hernandez-Lara, A., Ros, M., Cuartero, J., Bustamante, M.A., Moral, R., Andreu-Rodriguez, F.J., Fernandez, J.A., Egea-Gilabert, C., Pascual, J.A., 2022. Bacterial and fungal community dynamics during different stages of agro-industrial waste composting and its relationship with compost suppressiveness. Sci. Total Environ. 805, 150330.
- Hoang, H.G., Thuy, B.T.P., Lin, C., Vo, D.N., Tran, H.T., Bahari, M.B., Le, V.G., Vu, C.T., 2022. The nitrogen cycle and mitigation strategies for nitrogen loss during organic waste composting: a review. Chemosphere 300, 134514.
- Hou, T., Zhou, Y., Cao, X., Li, W., Zhang, S., Zhao, Y., Chen, L., An, Q., Meng, L., 2023. Effects of microbial inoculum on microbial community and enzyme activity involved in nitrogen-sulfur metabolism during sewage sludge composting. Sci. Total Environ. 858, 159954.
- Hu, T., Wang, X., Zhen, L., Gu, J., Song, Z., Sun, W., Xie, J., 2021. Succession of diazotroph community and functional gene response to inoculating swine manure compost with a lignocellulose-degrading consortium. Bioresour. Technol. 337, 125469.
- Huang, D., Gao, L., Cheng, M., Yan, M., Zhang, G., Chen, S., Du, L., Wang, G., Li, R., Tao, J., Zhou, W., Yin, L., 2022a. Carbon and N conservation during composting: a review. Sci. Total Environ. 840, 156355.
- Huang, G.F., Wong, J.W., Wu, Q.T., Nagar, B.B., 2004. Effect of C/N on composting of pig manure with sawdust. Waste Manag. 24 (8), 805–813.
- Huang, Y., Yang, H., Li, K., Meng, Q., Wang, S., Wang, Y., Zhu, P., Niu, Q., Yan, H., Li, X., Li, Q., 2022b. Red mud conserved compost nitrogen by enhancing nitrogen fixation and inhibiting denitrification revealed via metagenomic analysis. Bioresour. Technol. 346, 126654.
- Hue, N.V., Liu, J., 1995. Predicting compost stability. Compost Sci. Util. 3 (2), 8-15.

Huhe, Jiang, C., Wu, Y., Cheng, Y., 2017. Bacterial and fungal communities and contribution of physicochemical factors during cattle farm waste composting. MicrobiologyOpen 6 (6).

- Javed, Z., Tripathi, G.D., Mishra, M., Dashora, K., 2021. Actinomycetes the microbial machinery for the organic-cycling, plant growth, and sustainable soil health. Biocatal. Agric. Biotechnol. 31, 101893.
- Jeschke, J.M., Gabriel, W., Kokko, H., 2019. r-Strategists/K-Strategists. In: Fath, B. (Ed.), Encyclopedia of Ecology, second ed. Elsevier, Oxford, pp. 193–201.
- Jia, P., Wang, X., Liu, S., Hua, Y., Zhou, S., Jiang, Z., 2023. Combined use of biochar and microbial agent can promote lignocellulose degradation and humic acid formation during sewage sludge-reed straw composting. Bioresour. Technol. 370, 128525.

- Jiang, J., Wang, Y., Yu, D., Hou, R., Ma, X., Liu, J., Cao, Z., Cheng, K., Yan, G., Zhang, C., Li, Y., 2022. Combined addition of biochar and garbage enzyme improving the humification and succession of fungal community during sewage sludge composting. Bioresour. Technol. 346, 126344.
- Jiang, J., Wang, Y., Yu, D., Yao, X., Han, J., Cheng, R., Cui, H., Yan, G., Zhang, X., Zhu, G., 2021. Garbage enzymes effectively regulated the succession of enzymatic activities and the bacterial community during sewage sludge composting. Bioresour. Technol. 327, 124792.
- Kumar, A., Gaind, S., Nain, L., 2007. Evaluation of thermophilic fungal consortium for paddy straw composting. Biodegradation 19 (3), 395–402.
- Kumar, M., Ou, Y.L., Lin, J.G., 2010. Co-composting of green waste and food waste at low C/N ratio. Waste Manag. 30 (4), 602–609.
- Kuypers, M.M.M., Marchant, H.K., Kartal, B., 2018. The microbial nitrogen-cycling network. Nat. Rev. Microbiol. 16 (5), 263–276.
- Lammel, D.R., Feigl, B.J., Cerri, C.C., Nüsslein, K., 2015. Specific microbial gene abundances and soil parameters contribute to C, N, and greenhouse gas process rates after land use change in Southern Amazonian Soils. Front. Microbiol. 6.
- Li, C., Li, H., Yao, T., Su, M., Li, J., Liu, Z., Xin, Y., Wang, L., Chen, J., Gun, S., 2020. Effects of microbial inoculation on enzyme activity, available nitrogen content, and bacterial succession during pig manure composting. Bioresour. Technol. 306, 123167.
- Li, H., Li, X., Zhang, D., Xu, Y., 2023. Addition of exogenous microbial agents increases hydrogen sulfide emissions during aerobic composting of kitchen waste by improving bio-synergistic effects. Bioresour. Technol. 384, 129334.
- Li, H., Zhang, T., Shaheen, S.M., Abdelrahman, H., Ali, E.F., Bolan, N.S., Li, G., Rinklebe, J., 2022a. Microbial inoculants and struvite improved organic matter humification and stabilized phosphorus during swine manure composting: multivariate and multiscale investigations. Bioresour. Technol. 351, 126976.
- Li, M.X., He, X.S., Tang, J., Li, X., Zhao, R., Tao, Y.Q., Wang, C., Qiu, Z.P., 2021. Influence of moisture content on chicken manure stabilization during microbial agent-enhanced composting. Chemosphere 264 (Pt 2), 128549.
- Li, R., Wang, J.J., Zhang, Z., Shen, F., Zhang, G., Qin, R., Li, X., Xiao, R., 2012. Nutrient transformations during composting of pig manure with bentonite. Bioresour. Technol. 121, 362–368.
- Li, Y., Wu, Y., Liu, Y., Li, J., Du, G., Lv, X., Liu, L., 2022b. A genetic toolkit for efficient production of secretory protein in *Bacillus subtilis*. Bioresour. Technol. 363, 127885.
- Li, Z., Alami, M.M., Tang, H., Zhao, J., Nie, Z., Hu, J., Shu, S., Zhu, D., Yang, T., 2022c. Applications of *Streptomyces jingyangensis* T. and *Bacillus mucilaginosus* A. improve soil health and mitigate the continuous cropping obstacles for *Pinellia ternata* (Thunb.) Breit. Ind. Crops Prod. 180, 114691.
- Liu, D., Keiblinger, K.M., Leitner, S., Wegner, U., Zimmermann, M., Fuchs, S., Lassek, C., Riedel, K., Zechmeister-Boltenstern, S., 2019. Response of microbial communities and their metabolic functions to drying-rewetting stress in a temperate forest soil. Microorganisms 7 (5).
- Liu, H., Huang, Y., Duan, W., Qiao, C., Shen, Q., Li, R., 2020. Microbial community composition turnover and function in the mesophilic phase predetermine chicken manure composting efficiency. Bioresour. Technol. 313, 123658.
- Liu, X., Zubair, M., Kong, L., Shi, Y., Zhou, H., Tong, L., Zhu, R., Lv, Y., Li, Z., 2023. Shifts in bacterial diversity characteristics during the primary and secondary fermentation stages of bio-compost inoculated with effective microorganisms agent. Bioresour. Technol. 382, 129163.
- Lu, X., Yang, Y., Hong, C., Zhu, W., Yao, Y., Zhu, F., Hong, L., Wang, W., 2022. Optimization of vegetable waste composting and the exploration of microbial mechanisms related to fungal communities during composting. J. Environ. Manag. 319, 115694.
- Lv, Y., Bao, J., Liu, D., Gao, X., Yu, Y., Zhu, L., 2023. Synergistic effects of rice husk biochar and aerobic composting for heavy oil-contaminated soil remediation and microbial community succession evaluation. J. Hazard Mater. 448, 130929.
- Lycus, P., Soriano-Laguna, M.J., Kjos, M., Richardson, D.J., Gates, A.J., Milligan, D.A., Frostegård, Å., Bergaust, L., Bakken, L.R., 2018. A bet-hedging strategy for denitrifying bacteria curtails their release of N<sub>2</sub>O. Proc Natl Acad Sci 115 (46), 11820–11825.
- Ma, R., Wang, J., Liu, Y., Wang, G., Yang, Y., Liu, Y., Kong, Y., Lin, J., Li, Q., Li, G., Yuan, J., 2023. Dynamics of antibiotic resistance genes and bacterial community during pig manure, kitchen waste, and sewage sludge composting. J. Environ. Manag. 345, 118651.
- Maleki, S., Ranjbar, F., Beheshti-Alagha, A., Sharifi, R., 2023. Release kinetics of carbon, nitrogen, phosphorus, and potassium during co-composting of poultry manure mixed with diferent ratios of wheat straw and zeolite. Waster Biomass Valori 14, 57–68.
- Meng, C., Wu, M., Yang, L., Liang, H., Wu, Q., Li, Y., Shen, P., 2023. Rational utilization of urease and nitrification inhibitors improve the ammonia-oxidizing bacteria community, nitrogen use efficiency and peanut growth. Arch. Agron Soil Sci. 69 (14), 2938–2955.
- Meng, Q., Xu, X., Zhang, W., Cheng, L., Men, M., Xu, B., Deng, L., Sun, X., 2019a. Diversity and abundance of denitrifiers during cow manure composting. Rev. Argent. Microbiol. 51 (3), 191–200.
- Meng, Q., Xu, X., Zhang, W., Men, M., Xu, B., Deng, L., Bello, A., Jiang, X., Sheng, S., Wu, X., 2019b. Bacterial community succession in dairy manure composting with a static composting technique. Can. J. Microbiol. 65 (6), 436–449.
- Meng, Q., Yang, W., Men, M., Bello, A., Xu, X., Xu, B., Deng, L., Jiang, X., Sheng, S., Wu, X., Han, Y., Zhu, H., 2019c. Microbial community succession and response to environmental variables during cow manure and corn straw composting. Front. Microbiol. 10, 529.
- Naghdi, M., Cledon, M., Brar, S.K., Ramirez, A.A., 2018. Nitrification of vegetable waste using nitrifying bacteria. Ecol. Eng. 121, 83–88.

Ning, T., Wang, H., Zheng, M., Niu, D., Zuo, S., Xu, C., 2017. Effects of microbial enzymes on starch and hemicellulose degradation in total mixed ration silages. Asian-Australas. J. Anim. Sci. 30 (2), 171–180.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Wagner, H.H., 2020. Vegan community ecology package version 2.5-7 (Accessed November 2020).

Oviedo-Ocaña, E.R., Soto-Paz, J., Torres, V.S., Castellanos-Suarez, L.J., Komilis, D., 2022. Effect of the addition of the *Bacillus* sp., *Paenibacillus* sp. bacterial strains on the cocomposting of green and food waste. J. Environ. Chem. Eng. 10 (3).

Pan, S., Wang, G., Fan, Y., Wang, X., Liu, J., Guo, M., Chen, H., Zhang, S., Chen, G., 2023. Enhancing the compost maturation of deer manure and corn straw by supplementation via black liquor. Heliyon 9 (2), e13246.

Pérez, J., Muñoz-Dorado, J., de la Rubia, T., Martínez, J., 2002. Biodegradation and biological treatments of cellulose, hemicellulose and lignin: an overview. Int. Microbiol. 5 (2), 53–63.

Qiao, C., Penton, C.R., Liu, C., Tao, C., Deng, X., Ou, Y., Liu, H., Li, R., 2021. Patterns of fungal community succession triggered by C/N ratios during composting. J. Hazard Mater. 401, 123344.

Qu, G., Cai, Y., Lv, P., Ma, X., Xie, R., Xu, Y., Ning, P., 2019. Effect of EM microbial agent on aerobic composting for dairy cattle manure. Int J Environ Sci Te 16 (11), 6945–6958.

Rainisalo, A., Romantschuk, M., Kontro, M.H., 2011. Evolution of *clostridia* and *streptomycetes* in full-scale compositing facilities and pilot drums equipped with online temperature monitoring and aeration. Bioresour. Technol. 102 (17), 7975–7983.Raj, D., Antil, R.S., 2011. Evaluation of maturity and stability parameters of composts

prepared from agro-industrial wastes. Bioresour. Technol. 102 (3), 2868–2873. Ravindran, B., Karmegam, N., Awasthi, M.K., Chang, S.W., Selvi, P.K., Balachandar, R., Chinnappan, S., Azelee, N.I.W., Munuswamy-Ramanujam, G., 2022. Valorization of

food waste and poultry manure through co-composting amending saw dust, biochar and mineral salts for value-added compost production. Bioresour. Technol. 346, 126442.

Ren, G., Xu, X., Qu, J., Zhu, L., Wang, T., 2016. Evaluation of microbial population dynamics in the co-composting of cow manure and rice straw using high throughput sequencing analysis. World J. Microbiol. Biotechnol. 32 (6), 101.

S P, Z., Zhou, H.Y., Xia, S.N., Ying, J.M., Ke, X., Zou, S.P., Xue, Y.P., Zheng, Y.G., 2021. Efficient bio-degradation of food waste through improving the microbial community compositions by newly isolated *Bacillus* strains. Bioresour. Technol. 321, 124451.

Schimel, J.P., Bennett, J., 2004. Nitrogen mineralization: challenges of a changing paradigm. Ecology 85 (3), 591–602.

Shi, F., Yu, H., Zhang, N., Wang, S., Li, P., Yu, Q., Liu, J., Pei, Z., 2021. Microbial succession of lignocellulose degrading bacteria during composting of corn stalk. Bioengineered 12 (2), 12372–12382.

Shi, M., Zhao, X., Zhu, L., Wu, J., Mohamed, T.A., Zhang, X., Chen, X., Zhao, Y., Wei, Z., 2020. Elucidating the negative effect of denitrification on aromatic humic substance formation during sludge aerobic fermentation. J. Hazard Mater. 388.

Shinde, R., Shahi, D.K., Mahapatra, P., Naik, S.K., Thombare, N., Singh, A.K., 2022. Potential of lignocellulose degrading microorganisms for agricultural residue decomposition in soil: a review. J. Environ. Manag. 320, 115843.

Siu-Rodas, Y., Calixto-Romo, M.d.I.A., Guillén-Navarro, K., Sánchez, J.E., Zamora-Briseño, J.A., Amaya-Delgado, L., 2018. *Bacillus subtilis* with endocellulase and exocellulase activities isolated in the thermophilic phase from composting with coffee residues. Rev. Argent. Microbiol. 50 (3), 234–243.

Steger, K., Jarvis, A., Vasara, T., Romantschuk, M., Sundh, I., 2007. Effects of differing temperature management on development of Actinobacteria populations during composting. Res. Microbiol. 158 (7), 617–624.

Stein, L.Y., 2020. The long-term relationship between microbial metabolism and greenhouse gases. Trends Microbiol. 28 (6), 500–511.

 Straathof, A.L., Comans, R.N.J., 2015. Input materials and processing conditions control compost dissolved organic carbon quality. Bioresour. Technol. 179, 619–623.
Straka, L.L., Meinhardt, K.A., Bollmann, A., Stahl, D.A., Winkler, M.H., 2019. Affinity

Straka, L.L., Meinhardt, K.A., Bollmann, A., Stahl, D.A., Winkler, M.H., 2019. Affinity informs environmental cooperation between ammonia-oxidizing archaea (AOA) and anaerobic ammonia-oxidizing (Anammox) bacteria. ISME J. 13 (8), 1997–2004.

Su, Q., Wu, Y., Wang, S., Li, Y., Zhao, J., Huang, F., Wu, J., 2023. The reverse function of lignin-degrading enzymes: the polymerization ability to promote the formation of humic substances in domesticated composting. Bioresour. Technol. 380, 129059.

Sun, H., Chen, S., Zhu, N., Jeyakumar, P., Wang, J., Xie, W., Feng, Y., 2023. Hydrothermal carbonization aqueous phase promotes nutrient retention and humic substance formation during aerobic composting of chicken manure. Bioresour. Technol. 385, 129418.

Swati, A., Hait, S., 2018. Greenhouse gas emission during composting and vermicomposting of organic wastes - a Review. CLEAN - Soil Air Water 46 (6).

Tavares, M.C., Dos Santos Nascimento, I.J., de Aquino, T.M., de Oliveira Brito, T., Macedo Jr., F., Modolo, L.V., de Fatima, A., Santos, J.C.C., 2023. The influence of Nalkyl chains in benzoyl-thiourea derivatives on urease inhibition: soil studies and biophysical and theoretical investigations on the mechanism of interaction. Biophys. Chem. 299, 107042.

Tian, X., Yang, T., He, J., Chu, Q., Jia, X., Huang, J., 2017. Fungal community and cellulose-degrading genes in the composting process of Chinese medicinal herbal residues. Bioresour. Technol. 241, 374–383.

Ventorino, Parillo, Testa, Viscardi, Espresso, Pepe, 2016. Chestnut green waste composting for sustainable forest management: microbiota dynamics and impact on plant disease control. J. Environ. Manag. 166 (-), 168–177, 2016.

Villar, I., Alves, D., Garrido, J., Mato, S., 2016. Evolution of microbial dynamics during the maturation phase of the composting of different types of waste. Waste Manag. 54, 83–92.

Walling, E., Trémier, A., Vaneeckhaute, C., 2020. A review of mathematical models for composting, Waste Manage. (Tucson, Ariz.) 113, 379–394. Wan, W., Wang, Y., Tan, J., Qin, Y., Zuo, W., Wu, H., He, H., He, D., 2020. Alkaline phosphatase-harboring bacterial community and multiple enzyme activity contribute to phosphorus transformation during vegetable waste and chicken manure composting. Bioresour. Technol. 297, 122406.

Wang, G., Kong, Y., Yang, Y., Ma, R., Li, L., Li, G., Yuan, J., 2022a. Composting temperature directly affects the removal of antibiotic resistance genes and mobile genetic elements in livestock manure. Environ. Pollut. 303, 119174.

Wang, G., Yang, Y., Kong, Y., Ma, R., Yuan, J., Li, G., 2022b. Key factors affecting seed germination in phytotoxicity tests during sheep manure composting with carbon additives. J. Hazard Mater. 421.

Wang, K., Yin, X., Mao, H., Chu, C., Tian, Y., 2018. Changes in structure and function of fungal community in cow manure composting. Bioresour. Technol. 255, 123–130.

Wang, N., Awasthi, M.K., Pan, J., Jiang, S., Wan, F., Lin, X., Yan, B., Zhang, J., Zhang, L., Huang, H., Li, H., 2022c. Effects of biochar and biogas residue amendments on N2O emission, enzyme activities and functional genes related with nitrification and denitrification during rice straw composting. Bioresour. Technol. 357.

Wang, N., Zhao, K., Li, F., Peng, H., Lu, Y., Zhang, L., Pan, J., Jiang, S., Chen, A., Yan, B., Luo, L., Huang, H., Li, H., Wu, G., Zhang, J., 2022d. Characteristics of carbon, nitrogen, phosphorus and sulfur cycling genes, microbial community metabolism and key influencing factors during composting process supplemented with biochar and biogas residue. Bioresour. Technol. 366, 128224.

Wang, Q., Gu, J., Wang, X., Ma, J., Hu, T., Peng, H., Bao, J., Zhang, R., 2020a. Effects of nano-zerovalent iron on antibiotic resistance genes and mobile genetic elements during swine manure composting. Environ. Pollut. 258, 113654.

Wang, R., Zhao, Y., Xie, X., Mohamed, T.A., Zhu, L., Tang, Y., Chen, Y., Wei, Z., 2020b. Role of NH(3) recycling on nitrogen fractions during sludge composting. Bioresour. Technol. 295, 122175.

Wang, S.-P., Wang, L., Sun, Z.-Y., Wang, S.-T., Shen, C.-H., Tang, Y.-Q., Kida, K., 2021. Biochar addition reduces nitrogen loss and accelerates composting process by affecting the core microbial community during distilled grain waste composting. Bioresour. Technol. 337, 125492.

Wang, S., Long, H., Hu, X., Wang, H., Wang, Y., Guo, J., Zheng, X., Ye, Y., Shao, R., Yang, Q., 2024. The co-inoculation of *Trichoderma viridis* and *Bacillus subtilis* improved the aerobic composting efficiency and degradation of lignocellulose. Bioresour. Technol. 394, 130285.

Wang, X., Tamiev, D., Alagurajan, J., DiSpirito, A.A., Phillips, G.J., Hargrove, M.S., 2019. The role of the NADH-dependent nitrite reductase, Nir, from *Escherichia coli* in fermentative ammonification. Arch. Microbiol. 201 (4), 519–530.

Wang, Y., Gong, J., Li, J., Xin, Y., Hao, Z., Chen, C., Li, H., Wang, B., Ding, M., Li, W., Zhang, Z., Xu, P., Xu, T., Ding, G.C., Li, J., 2020c. Insights into bacterial diversity in compost: core microbiome and prevalence of potential pathogenic bacteria. Sci. Total Environ. 718, 137304.

Wei, Y., Zhao, Y., Fan, Y., Lu, Q., Li, M., Wei, Q., Zhao, Y., Cao, Z., Wei, Z., 2017. Impact of phosphate-solubilizing bacteria inoculation methods on phosphorus transformation and long-term utilization in composting. Bioresour. Technol. 241, 134–141.

Wen, X., Sun, R., Cao, Z., Huang, Y., Li, J., Zhou, Y., Fu, M., Ma, L., Zhu, P., Li, Q., 2022. Synergistic metabolism of carbon and nitrogen: cyanate drives nitrogen cycle to conserve nitrogen in composting system. Bioresour. Technol. 361, 127708.

Wu, D., Xia, T., Zhang, Y., Wei, Z., Qu, F., Zheng, G., Song, C., Zhao, Y., Kang, K., Yang, H., 2021. Identifying driving factors of humic acid formation during rice straw composting based on Fenton pretreatment with bacterial inoculation. Bioresour. Technol. 337, 125403.

Wu, J., Zhang, A., Li, G., Wei, Y., He, S., Lin, Z., Shen, X., Wang, Q., 2019. Effect of different components of single superphosphate on organic matter degradation and maturity during pig manure composting. Sci. Total Environ. 646, 587–594.

Xi, B., He, X., Dang, Q., Yang, T., Li, M., Wang, X., Li, D., Tang, J., 2015. Effect of multistage inoculation on the bacterial and fungal community structure during organic municipal solid wastes composting. Bioresour. Technol. 196, 399–405.

Xie, S., Tran, H.-T., Pu, M., Zhang, T., 2023. Transformation characteristics of organic matter and phosphorus in composting processes of agricultural organic waste: Research trends. Mater Sci Energy Technol 6, 331–342.

Xiong, J., Su, Y., He, X., Han, L., Huang, G., 2023. Effects of functional membrane coverings on carbon and nitrogen evolution during aerobic composting: insight into the succession of bacterial and fungal communities. Bioresour. Technol. 369, 128463.

Yang, M., Lu, D., Yang, J., Zhao, Y., Zhao, Q., Sun, Y., Liu, H., Ma, J., 2019. Carbon and nitrogen metabolic pathways and interaction of cold-resistant heterotrophic nitrifying bacteria under aerobic and anaerobic conditions. Chemosphere 234, 162–170.

Yang, M., Zhang, W., Lv, Z., Shi, L., Zhang, K., Ge, B., 2023. Induced defense response in soybean to sclerotinia sclerotiorum using wuyiencin from *Streptomyces albulus* CK-15. Plant Dis. 107 (1), 107–115.

Yang, Y., Awasthi, M.K., Bao, H., Bie, J., Lei, S., Lv, J., 2020. Exploring the microbial mechanisms of organic matter transformation during pig manure composting amended with bean dregs and biochar. Bioresour. Technol. 313, 123647.

Ye, P., Fang, L., Song, D., Zhang, M., Li, R., Awasthi, M.K., Zhang, Z., Xiao, R., Chen, X., 2023. Insights into carbon loss reduction during aerobic composting of organic solid waste: a meta-analysis and comprehensive literature review. Sci. Total Environ. 862, 160787.

Yin, Y., Li, M., Tao, X., Yang, C., Zhang, W., Li, H., Zheng, Y., Wang, X., Chen, R., 2023. Biochar enhanced organic matter transformation during pig manure composting: roles of the cellulase activity and fungal community. J. Environ. Manag. 333, 117464.

Yin, Y., Yang, C., Tang, J., Gu, J., Li, H., Duan, M., Wang, X., Chen, R., 2021. Bamboo charcoal enhances cellulase and urease activities during chicken manure

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composting: roles of the bacterial community and metabolic functions. J. Environ. Sci. (China) 108, 84–95.

- Yu, H., Xie, B., Khan, R., Shen, G., 2019. The changes in carbon, nitrogen components and humic substances during organic-inorganic aerobic co-composting. Bioresour. Technol. 271, 228–235.
- Zhang, J., Wu, Z., Huang, Y., Zhan, X., Zhang, Y., Cai, C., 2023. Industrial-scale composting of swine manure with a novel additive-yellow phosphorus slag: variation in maturity indicators, compost quality and phosphorus speciation. Bioresour. Technol. 384, 129356.
- Zhang, L., Sun, X., Tian, Y., Gong, X., 2013. Effects of brown sugar and calcium superphosphate on the secondary fermentation of green waste. Bioresour. Technol. 131, 68–75.
- Zhang, L., Sun, X., 2014. Changes in physical, chemical, and microbiological properties during the two-stage co-composting of green waste with spent mushroom compost and biochar. Bioresour. Technol. 171, 274–284.
- Zhang, L., Zhang, H., Wang, Z., Chen, G., Wang, L., 2016. Dynamic changes of the dominant functioning microbial community in the compost of a 90-m(3) aerobic solid state fermentor revealed by integrated meta-omics. Bioresour. Technol. 203, 1–10.
- Zhang, M., Li, Y., Sun, Q., Chen, P., Wei, X., 2020. Correlations of functional genes involved in methane, nitrogen and sulfur cycling in river sediments. Ecol Indic 115, 106411.
- Zhang, Q., Tang, D., Liu, M., Ruan, J., 2018. Integrated analyses of the transcriptome and metabolome of the leaves of albino tea cultivars reveal coordinated regulation of the carbon and nitrogen metabolism. Sci. Hortic. 231, 272–281.
- Zhang, S., Xia, T., Wang, J., Zhao, Y., Xie, X., Wei, Z., Zhang, X., Song, C., Song, X., 2021a. Role of *Bacillus* inoculation in rice straw composting and bacterial community stability after inoculation: unite resistance or individual collapse. Bioresour. Technol. 337, 125464.
- Zhang, S., Zhong, B., An, X., Han, Y., Xiao, X., Zhang, Q., 2022a. Effect of moisture content on the evolution of bacterial communities and organic matter degradation during bioaugmented biogas residues composting. World J. Microbiol. Biotechnol. 39 (1), 1.
- Zhang, X., Zhan, Y., Zhang, H., Wang, R., Tao, X., Zhang, L., Zuo, Y., Zhang, L., Wei, Y., Li, J., 2021b. Inoculation of phosphate-solubilizing bacteria (*Bacillus*) regulates microbial interaction to improve phosphorus fractions mobilization during kitchen waste composting. Bioresour. Technol. 340, 125714.
- Zhang, Y., Sun, Q., Wang, J., Ma, Y., Cao, B., 2021c. Responses of heavy metals mobility and resistant bacteria to adding time of activated carbon during chicken manure composting. Environ. Pollut. 290, 118070.
- Zhang, Y., Wei, Z., Guo, J., Zhang, S., Zhao, L., Pan, C., Wang, L., Zhang, R., Chen, Y., 2022b. Resource utilization of mink manure: functional microbial inoculation to

elevate the bioavailability of organic nitrogen during composting. Bioresour. Technol. 353, 127149.

- Zhang, Y.H., Lynd, L.R., 2004. Toward an aggregated understanding of enzymatic hydrolysis of cellulose: noncomplexed cellulase systems. Biotechnol. Bioeng. 88 (7), 797–824.
- Zhao, S., Schmidt, S., Qin, W., Li, J., Li, G., Zhang, W., 2020. Towards the circular nitrogen economy – a global meta-analysis of composting technologies reveals much potential for mitigating nitrogen losses. Sci. Total Environ. 704, 135401.
- Zhou, G., Xu, X., Qiu, X., Zhang, J., 2019. Biochar influences the succession of microbial communities and the metabolic functions during rice straw composting with pig manure. Bioresour. Technol. 272, 10–18.
- Zhou, L., Yang, X., Wang, X., Feng, L., Wang, Z., Dai, J., Zhang, H., Xie, Y., 2023a. Effects of bacterial inoculation on lignocellulose degradation and microbial properties during cow dung composting. Bioengineered 14 (1).
- Zhou, S., Song, Z., Li, Z., Qiao, R., Li, M., Chen, Y., Guo, H., 2022a. Mechanisms of nitrogen transformation driven by functional microbes during thermophilic fermentation in an ex situ fermentation system. Bioresour. Technol. 350, 126917.
- Zhou, S.P., Tang, S.Q., Ke, X., Zhou, H.Y., Zou, S.P., Xue, Y.P., Zheng, Y.G., 2023b. Hyperthermophilic pretreatment significantly accelerates thermophilic composting humification through improving bacterial communities and promoting microbial cooperation. Bioresour. Technol. 385, 129467.
- Zhou, S.P., Zhou, H.Y., Xia, S.N., Ying, J.M., Ke, X., Zou, S.P., Xue, Y.P., Zheng, Y.G., 2021. Efficient bio-degradation of food waste through improving the microbial community compositions by newly isolated *Bacillus* strains. Bioresour. Technol. 321, 124451.
- Zhou, Z., Song, Z., Gu, J., Wang, X., Hu, T., Guo, H., Xie, J., Lei, L., Ding, Q., Jiang, H., Xu, L., 2022b. Dynamics and key drivers of antibiotic resistance genes during aerobic composting amended with plant-derived and animal manure-derived biochars. Bioresour. Technol. 355, 127236.
- Zhu, L., Zhao, Y., Zhang, W., Zhou, H., Chen, X., Li, Y., Wei, D., Wei, Z., 2019. Roles of bacterial community in the transformation of organic nitrogen toward enhanced bioavailability during composting with different wastes. Bioresour. Technol. 285, 121326.
- Zhu, P., Li, Y., Gao, Y., Yin, M., Wu, Y., Liu, L., Du, N., Liu, J., Yu, X., Wang, L., Guo, W., 2021. Insight into the effect of nitrogen-rich substrates on the community structure and the co-occurrence network of thermophiles during lignocellulose-based composting. Bioresour. Technol. 319, 124111.
- Zmora-Nahum, S., Markovitch, O., Tarchitzky, J., Chen, Y., 2005. Dissolved organic carbon (DOC) as a parameter of compost maturity. Soil Biol. Biochem. 37 (11), 2109–2116.