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Effect of initial moisture content, resulting from different ratios of vegetable waste to maize straw, on compost was mediated by composting temperatures and microbial communities at low temperatures

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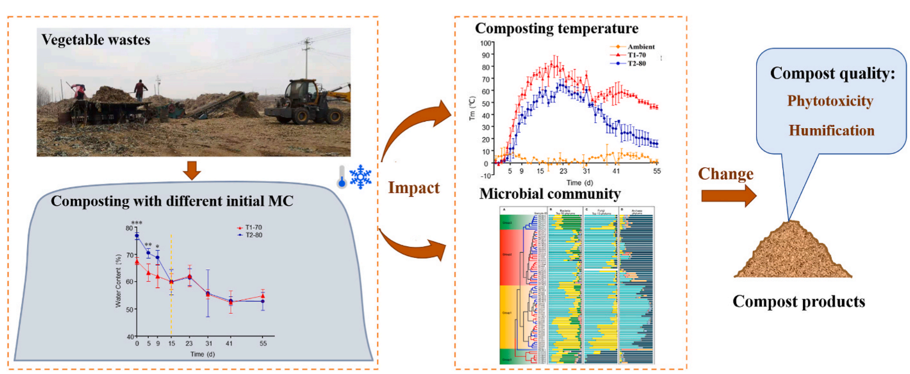
HIGHLIGHTS

- High MC in vegetable waste significantly impacted its composting at low temperatures.
- Initial MC of vegetable waste composting led to the greatest change during maturation.
- Differential microbes were correlated with germination index and humification.
- Initial MC of 70 % improved the maturity, humification and harmlessness of composts.

GRAPHICAL ABSTRACT



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ABSTRACT

Owing to the huge amounts and perishable character of vegetable wastes, composting is one of the best options for recycling vegetable wastes post-harvest. The initial moisture content (MC) is critical for optimizing composting process, but the effect of high MC in undehydrated vegetable wastes on composting was rarely reported. For this, the plant-scale windrows were prepared by mixing cauliflower waste and maize straw at different ratios to control initial MC of 70 % (T1-70) and 80 % (T2-80), respectively, and composted in winter. As composting progressed, substantial organic matter degradation, progressive humification, decreases in electrical conductivity

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Initial moisture content
Humification

and increases of pH and germination index (GI) were observed in both treatments. Nonetheless, T1-70 accelerated heating rate early during composting, prolonged high temperature period (>50 °C) by 30 d, thus increased the harmless level of composting, and significantly improved the humification of end-products compared to T2-80. Results also revealed that T1-70 activated more indigenous microbes and enhanced microbial interactions early during composting, with the fungi enriched in T1-70 playing an important role in accelerating the composting process. Remarkably, the difference in composting temperatures, humification degree, and microbial communities between the two treatments was most significant during the maturation phase. In this phase, *MWH_CFBk5*, *Planktosalinus*, *Pseudopedobacter*, and *Luteimonas* enriched in T1-70 were positively correlated with humification indices. It is suggested that the effect of initial MC, resulting from different ratios of vegetable waste to maize straw, on their composting was mediated by the composting temperature and microbial communities at low temperatures.

1. Introduction

With the significantly increasing demands of agrofood, the fresh and processing industries generate huge waste of vegetables, including their components, by-products and residues (FAO, 2014; Sagar et al., 2018). Example of the losses and waste in cabbages production reached up to 30 % (Wu et al., 2016). Moreover, due to the high moisture content (MC), perishability and logistic-related problems of vegetable waste, the management of vegetable waste is challenging nowadays (Esparza et al., 2020).

Composting is considered as an environmentally friendly and sustainable technology for handling organic waste, as it can inactivate potential pathogens and provide bioavailable nutrients and stable humified substances for the soil-plant system (Pergola et al., 2018; Ravindran et al., 2022; Shi et al., 2022). The MC is a critical factor in optimizing composting process, and the optimum MC is essential for maintaining microbial diversity and activity, and promoting organic matter degradation (Guo et al., 2012; Wan et al., 2020; Wang et al., 2022a). Prior studies have suggested a significant effect of initial MC on the composting of agro-biowastes when the ambient temperature is above 20 °C (Petric et al., 2009; Sarlaki et al., 2021). Compared to these raw materials, vegetable waste has a much higher MC of 80–90% (Zhang et al., 2020; Shi et al., 2022), and the dehydration of vegetable waste requires of more time and costs (Esparza et al., 2020). Therefore, it is of great importance to investigate the effect of high MC in un-dehydrated vegetable waste on its composting process, especially under low temperature conditions following post-harvest.

The low temperature reduces metabolic activities of microbial populations and thus suppresses the start-up of composting (Zhang et al., 2015a,b), which might present quite different phenomenon in terms of composing process. Our preliminary assessment of small/medium-scale composting experiments showed that compared to an initial MC of 63%, an initial MC of 68% prolonged the high temperature phase during the low-temperature composting of vegetable waste (Shi et al., 2022). The interesting result encouraged us to uncover the mechanism of high initial MC affecting natural composting process of vegetable waste under low temperature conditions.

Composting is a biological oxidation process, which is driven by the metabolic activity of microbiota dwelling in the raw materials (Tortosa et al., 2020; Zhang et al., 2020). A number of studies on the microbial communities throughout composting have been done and still ongoing, and these studies showed that biotic and abiotic factors can improve the compost quality by optimizing the microbial community in composting process (Yu et al., 2019; Zhang et al., 2022; Shi et al., 2022). Yu et al. (2019) emphasized the carrier role of bacterial community in boosting the formation of humic acids (HAs) during chicken manure composting, which was driven by the addition of minerals. Another case analyzed the impacts of biochar and palygorskite on fungal succession during corn stover and chicken manure composting to influence the formation of humic substances (Zhang et al., 2022). Nevertheless, relatively few studies have been published on the effect of initial MC on microbial communities and their microecological mechanisms during the composting process of vegetable wastes at low temperatures.

In this study, the plant-scale composting of cauliflower waste with maize straw at different ratios was carried out under low temperature conditions. The objectives were to (i) investigate the effect of high initial MC on the composting process and compost quality; (ii) assess the role of initial MC in the succession of microbial communities throughout composting process; and (iii) reveal the microecological mechanisms by which initial MC affected the composting of cauliflower waste.

2. Materials and methods

2.1. Materials preparation and experimental setup

In the present study, the raw materials for composting were collected locally in Tai'an, Shandong Province, China. Cauliflower wastes (root, stem, leaf and other waste after harvest) and maize straws were taken respectively from a vegetable production base and farmland. The shredded wastes (3–5 cm) including 24 t cauliflower wastes and 5 t maize straws were piled into two windrows. Each windrow was approximately 10 m × 3 m × 1.5 m (length × width × height) and 14.5 t (Fig. S1A). The physico-chemical properties of the raw materials were present in Fig. S1B. The initial C/N ratio and moisture content of raw materials, and aeration rate were the most important factors affecting the maturation of compost (Raj and Antil, 2011; Guo et al., 2012). In order to investigate the effect of high MC in un-dehydrated vegetable wastes on the composting process, the cauliflower waste and maize straw were mixed in a weight ratio of 3:1 and 12:1 to adjust the initial MC to about 70 % (T1-70) and 80 % (T2-80), and control the C/N ratios of 20.43 and 21.44, respectively. Additionally, the other initial properties of the two windrows were very similar (Fig. 1). This large windrow composting experiment was carried out at a composting plant located in Tai'an for 55 days (from 16th December 2018 to 9th February 2019). The ambient temperature of this composting plant ranged from −2 °C ±1.43 °C to 8.65 °C ± 2.66 °C during the composting process. The windrows were aerated by natural ventilation and artificially turned every 2 d to ensure adequate airflow.

2.2. Sampling and physicochemical analysis

The temperature of windrows was monitored daily at 9:00 a.m. and 15:00 p.m. using a digital thermometer. Five thermometer probes were inserted at the middle positions of the windrow (Fig. S1C), and readings were recorded when the temperature display stabilized. Ten records of each day were used as replicates for temperature measurement. Meanwhile, the ambient temperature was also measured every day by using five thermometers placed at a height of 1 m above the ground. According to the temperature curve, representative samples were collected from each windrow on day 0, 5, 9, 15, 23, 31, 41 and 55. As shown in Fig. S1C, five subsamples were collected from the middle position of windrows at each sampling point and set as replicates for subsequent analyses.

The protocols of our previous studies (Zhang et al., 2020; Shi et al., 2022) were followed for the measurement of physicochemical properties: MC, pH, electrical conductivity (EC), total organic carbon (TOC), total nitrogen (TN), C/N ratio, total phosphorus (TP), total potassium

(TK) and germination index (GI). The determination of humic substances (HA, fulvic acid (FA) and the HA/FA ratio) was performed as described by Duan et al. (2019) and Zhou et al. (2014).

2.3. High-throughput sequencing

The succession of bacterial, fungal and archaeal communities was monitored in T1-70 and T2-80 as composting proceeded. Total genomic DNA of compost samples (0, 5, 9, 15, 23, 31, 41 and 55 d) was extracted

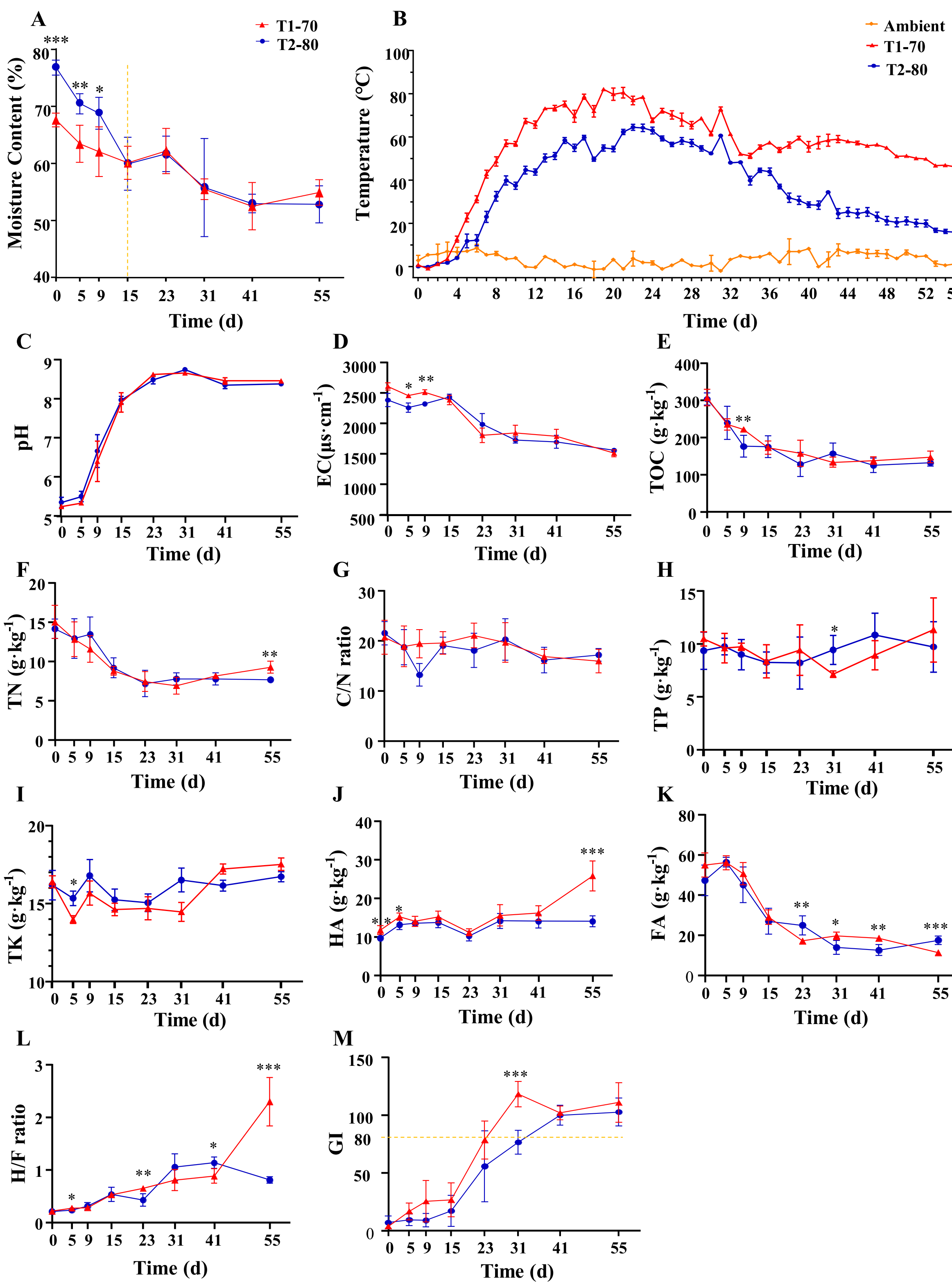

Fig. 1. Dynamics of moisture content (A), temperature (B), pH (C), electrical conductivity (EC, D), total organic carbon (TOC, E), total nitrogen (TN, F), C/N ratio (G), total phosphorus (TP, H), total potassium (TK, I), humic acid (HA, J) fulvic acid (FA, K), HA/FA ratio (L) and germination index (GI, M) during composting process. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

with MoBio DNeasy PowerSoil kit (Qiagen, Germany) and quantified by a NanoDrop ND-1000 UV–vis Spectrophotometer (Thermo Fisher Scientific, USA). The V4 hypervariable region of archaeal and bacterial 16S rRNA gene was amplified with universal archaeal primers (Uni519F: 5′-CAGYMGCCRCGGKAAHACC-3′, Arch806R: 5′-GGACTACNSGGGTMTCTAAT-3′) and bacterial primers (515F: 5′-GTGCCAGCMGCCGCGGTAA-3′, 806R: 5′-GGACTACHVGGGTWTCTAAT-3′), respectively (Zhou et al., 2016; Jiang et al., 2017). Meanwhile, fungal primers (ITS1-1F–F: 5′-CTTGGTCATTTAGAGGAAGTAA-3′, ITS1-1F–R: 5′-GCTGCGTTCT TCATCGATGC-3′) were used to target the fungal internal transcribed spacer (ITS) region (Zhang et al., 2015a,b). The amplicon libraries were prepared and sequenced with the Illumina Miseq platform (Illumina, USA) by Guangzhou Magigen Biotechnology Co. Ltd., China. Raw sequencing data have been submitted to the NCBI SRA database under accession number SUB11962975.

Raw data were pre-processed using QIIME 2 (v 2020. 08) toolkit (Callahan et al., 2016). The raw sequences were merged and quality-filtered using the Q2-Tools plugin and Q2-Demux plugin, respectively. The chimeric sequences were then removed using Q2-DADA2. High-quality sequences were used to generate amplicon sequencing variant (ASV) table. The ASVs were filtered using Q2-features-table plugin to remove sequences whose total abundance were less than 10 or that were only present in one sample. Taxonomy annotation was performed using Naive Bayes classifiers based on SILVA-138 database (https://www.arb-silva.de/) for bacterial and archaeal 16S rRNA gene and UNITE 8.2 database (http://unite.ut.ee/index.php) for ITS gene sequences (Bokulich et al., 2018; Shi et al., 2022). After that, Q2-alignment and Q2-phylogeny plugins were used for feature sequence alignment and phylogenetic tree establishment.

2.4. Statistical analysis

Statistical differences for physicochemical properties during composting were analyzed with the "*t.test*" function from package "stats" and visualized with package "ggplot2" in R (v 3.6.3). The R package "vegan" was used for permutational multivariate analysis of variance (PERMANOVA) and hierarchical clustering based on the abundance of all ASVs. The α- and β-diversity indices were calculated using Q2-Diversity plugin of QIIME 2. The linear discriminant analysis (LDA) with effect size (LEfSe) analysis was performed to determine the differential abundant taxa between the two treatments during composting and among different composting phases using the online tool (http://huttenhower.sph.harvard.edu/galaxy) (Xu et al., 2020). We set 3.5 as the threshold of logarithmic LDA score for discriminative features. Significant differences between the two treatments and among different composting phases were assessed using the factorial Kruskal-Wallis test with an alpha value of 0.05. The correlation coefficient among physicochemical properties, and between physicochemical factors and significantly differential microbes was calculated using R package "psych" and the $p < 0.05$ was considered as statistically significant. Co-occurrence network interactions of physicochemical factors and microbes as well as microbial communities were analyzed and visualized with the Molecular Ecological Network Analyses (MENA) Pipeline (http://ieg4.rccc.ou.edu/mena) and Cytoscape (v. 3.3.2), respectively (Shi et al., 2022).

3. Results and discussion

3.1. Effect of initial moisture content on composting temperature

The initial MC of T1-70 and T2-80 was 67.63 % and 76.80 %, respectively (Fig. 1A), which was consistent with our experimental settings. The composting processes of both treatments were continuous water loss processes due to evaporation that was caused by elevated temperature and aeration (Wang et al., 2021; Pottipati et al., 2022). The MC of T2-80 was significantly higher than that of T1-70 during the first 15 d. However, the MC of the two treatments was very similar thereafter and finally stabilized at 54.92 % (T1-70) and 52.83 % (T2-80) on the day 55, respectively (Fig. 1A). From 15 d to the end of composting, the MC of both treatments was 50 %–60 % which was reported to be the optimum conditions for the green waste and food waste composting (Kumar et al., 2010; Guo et al., 2012).

Different from the temperature profiles of composting reported previously (Zhang et al., 2020; Haouas et al., 2021; Chen et al., 2022), we observed an obvious lag phase of pile temperature in both treatments (Fig. 1B) which was proposed as the initial phase. Zhang et al. (2015a,b) have suggested that low temperature conditions (15 °C downward) reduce metabolic activity of the microbial population, resulting in the composting difficult to start-up. Subsequently, the temperature change rate differed between T1-70 and T2-80. The temperature of T1-70 sharply increased after 3 d of composting, exceeded 50 °C from day 9, peaked to 82.1 °C on day 19 and maintained high temperature phase (>50 °C) for 43 days (Fig. 1B). In comparison, the temperature of T1-80 started to increase on day 4, exceeded 50 °C from day 13, reached to a peak of 65.6 °C on day 22 and maintained above 50 °C for 18 days (Fig. 1B). Nonetheless, both treatments met the criteria for "non-hazardous" compost products, since the duration of high temperature phase (≥3 days) was sufficient to kill weed seeds and pathogenic microorganisms (Zhou et al., 2019; Yang and Zhang, 2022). On the other hand, both treatments entered the cooling stage from day 31 onward, when the most striking difference in temperature between the two treatments occurred. A quick decrease of temperature in T2-80 was observed and the composting temperature dropped to 15.9 °C on day 55 (Fig. 1B). In contrast, the temperature of T1-70 decreased slowly, maintained around 55 °C for a long time and reached to 46.3 °C on day 55 (Fig. 1B). Overall, T1-70 outperformed T2-80 in terms of heating rate, average temperature and duration of high temperature phase, accelerating the composting process.

As previous studies demonstrated that the high heat capacity of water as well as the compaction of raw materials caused by high ratio of vegetable waste to maize straw would restrict the heat transmission of compost windrows (Guo et al., 2012; White et al., 2020). Moreover, T2-80 had more water loss by endothermic evaporation during the first 15 days. These could explain why T2-80 presented lower heating rate during the initial and ascending phases. Composting temperature influences and reflects microbial diversity and activity, the decomposition rate, and the humification degree of compost products (Zhang and Sun, 2017). The different temperature caused by initial MC early during composting might have influenced other biotic and abiotic factors, which in turn resulted in differential composting temperature profiles thereafter. Therefore, when the MC of both treatments was very similar (after 15 d of composting), significant difference in temperature curves was still observed.

Petrica et al. (2012) previously showed that when the ambient temperature was over 20 °C, the relatively high initial MC was better at achieving higher temperatures and prolonging thermophilic period during poultry manure and wheat straw composting. However, this study revealed that high initial MC suppressed the warming of vegetable waste composting under low temperature conditions, which further led to the lower temperatures during the whole composting process.

3.2. Effect of initial moisture content on physicochemical properties

3.2.1. pH and electrical conductivity during composting

In this work, the changes in pH were very similar for the two treatments, which increased significantly in 31 days, then slightly decreased and remained 8.38–8.54 on day 55 (Fig. 1C). The large increase of pH in the two treatments could be explained by the production and accumulation of ammonium during the mineralization of proteins and other nitrogenous compounds (Reyes-Torres et al., 2018; Sarlaki et al., 2021). EC indicates the soluble salt content in the compost samples, and high EC (>4 mS cm^{-1}) of compost products might pose phytotoxic/negative effects on plant growth (Karak et al., 2013; Zhang et al., 2021a,b). For the both treatments, EC had high initial values, but exhibited a downward trend during the composting process (Fig. 1D). Initial MC directly affected EC within the first 15 days, showing that EC value of T1-70 was significantly higher than that of T2-80. On day 55, the final EC values of T1-70 and T2-80 were 1.48 mS cm^{-1} and 1.56 mS cm^{-1}, respectively. The results indicate that there was no phytotoxicity caused by the salt content of compost products in either treatment (Karak et al., 2013; Yang and Zhang, 2022).

3.2.2. Nutrient contents during composting

In both the treatments, the TOC content suffered a rapid decrease in the first 23 days (Fig. 1E), which corresponded to the increasing temperature that would enhance the microbial-mediated decomposition of organic carbon (Fig. S2). Subsequently, the TOC content remained relatively constant until the completion of composting because of the exhaustion of readily degradable carbon and the formation of more stable organic structures through the humification process (Amir et al., 2010; Sun et al., 2021; Wang et al., 2022b). The changes of TN content in the two treatments showed a similar trend to that of TOC (Fig. 1F). The loss of N during composting is generally caused by the volatilization of ammonia because of the alkaline pH and possibly high temperature (Yang and Zhang, 2022). The initial C/N ratio for T1-70 and T2-80 were 20.43 and 21.44, respectively (Fig. 1G), which was in the optimum range (20–30) for composting (Wan et al., 2020). From day 31 onward, the C/N value of the two treatments gradually declined, indicating the increased degree of maturity (Amir et al., 2010; Haouas et al., 2021). Additionally, the content of TP and TK for the two treatments was also monitored, which fluctuated but maintained a relatively stable level during the composting process (Fig. 1H and I). Collectively, the effect of the initial MC, resulting from different ratios of vegetable waste to maize straw, on nutrient contents of the compost was not distinct. Coincidentally, Guo et al. (2012) reported that the MC had an insignificant effect on the quality of pig feces and corn stalks compost (including TOC, TN and C/N ratio).

3.2.3. The humification process during composting

The general trend of HA content was the same in the two treatments over 31 days, showing a slow increase from 11.76 g kg^{-1} to 9.67 g kg^{-1} to 15.56 g kg^{-1} and 14.14 g kg^{-1} for T1-70 and T2-80, respectively (Fig. 1J). Nonetheless, the HA content of T1-70 was significantly higher than that of T2-80 in the ascending phase. From day 31 onward, the HA content of T2-80 remained fairly constant and the final value was 14.0 g kg^{-1} on day 55. However, the HA content in T1-70 continued to increase after 31 days of composting and sharply peaked to 25.81 g kg^{-1} on day 55, presenting an increase of 65.87 % during the maturation phase (Fig. 1J).

In contrast, the FA content of T1-70 exhibited a downward trend from the initial value of 54.87 g kg^{-1} to 11.39 g kg^{-1} during the composting process, while the FA content of T2-80 suffered a decreased from 47.39 g kg^{-1} to 12.90 g kg^{-1} within the first 31 days and then increased slowly to the final value of 17.47 g kg^{-1} (Fig. 1K). The decreased FA content observed in this work was consistent with the results of previous studies (Raj and Antil, 2011; Zhang et al., 2021a,b; Shi et al., 2022), since FA in the raw material could be used as the energy resource for microbes' growth and as precursors for forming more stable organic structures like HA (Amir et al., 2010; Zhou et al., 2014). Hence, the transformation between FA and HA induced by microbe activities might contribute to the significant difference in the content of HA and FA between the treatments.

The HA/FA ratios for the two treatments were very similar in the first 15 days, but significantly differed thereafter (Fig. 1L). The HA/FA ratio in T1-70 increased throughout composting from 0.21 to 2.27, with the greatest increase in the maturation phase. While the HA/FA ratio of T2-80 increased first and then declined, with the significant change coinciding with the active phase of composting (thermophilic stage) (Fig. 1L). The mentioned increase of HA/FA ratio indicated a growing predominance of humified substances with a more stable structure. As the humification index, HA/FA ratio have been employed as quality criteria for evaluating the maturity and stability of composts (Raj and Antil, 2011; Awasthi et al., 2017). Jimenez and Garcia (1992) proposed that the HA/FA ratio greater than 1 indicated the occurrence of humification. Moreover, the value of HA/FA ratio greater than 1.9 was deemed to be the maturity index of composts from different origins like poultry waste composting and sewage sludge composting (Iglesias-Jimenez and Perez-Garcia, 1992; Raj and Antil, 2011). In our case, the final value of HA/FA ratio in T1-70 was much higher than that in T2-80 and even greater than 1.9, indicating the more maturity and stability of composts in T1-70. These results suggested that the initial MC, resulting from different ratios of vegetable waste to maize straw, crucially impacted the humification process during the maturation phase, and the initial MC of 70 % markedly increased the humification degree of compost products.

3.3. Effect of initial moisture content on phytotoxicity

The meager values of GI in both treatments early during composting (0 d–15 d) (Fig. 1M) indicated low germination capacity of compost materials, which might be attributed to the high content of salt or phytotoxic fatty acids formed from organic matter decomposition (Haouas et al., 2021; Pottipati et al., 2022). Along with the increase in duration of high temperature and the reduction in EC, the GI value increased strongly after 15 d, with final values were 110.96 % and 102.68 % for T1-70 and T2-80, respectively (Fig. 1M and Fig. S2). GI is a frequently used indictor for evaluating the maturity and phytotoxicity of compost products (Barje et al., 2013; Haouas et al., 2021). According to the ideal GI range (>80 %) recommended by previous reports (Zhang et al., 2021a,b; Pottipati et al., 2022), compost products obtained in this study could be considered mature and non-phytotoxic. Nonetheless, comparing with T2-80, T1-70 presented higher GI values. Since the Spearman's correlation indicated that the composting temperature depicted significant and positive correlations with GI in the T1-70 treatment (Fig. S2A), this phenomenon could be ascribed to the higher temperatures that inactivated phytotoxic compounds.

3.4. Effect of initial moisture content on microbial community

3.4.1. The composition of microbial community during composting

Bacterial, fungal and archaeal sequences were clustered into 4065, 1939 and 3234 ASVs, respectively. The hierarchical cluster analysis of all composting samples in the two treatments was performed based on the relative abundance of all ASVs at phylum- and genus-levels, respectively. Despite the different ratios of vegetable waste to maize straw in the two treatments, 0 d samples from T1-70 and T2-80 were clustered. All the samples were grouped into three clusters, which could correspond to the different composting phase combined with temperature curves (Fig. 2 and Fig. S3). Recent studies demonstrated that the composition of microbial communities at different phase of composting was significantly different (Zhang et al., 2021a,b; Wang et al., 2022b). Consistent with these reports, we also noticed a significant temporal dynamic in the microbial community composition at the phylum (Fig. 2) and genus levels (Fig. S3) as composting progressed.

Remarkably, cluster III corresponding to maturation phase of composting was branched into two divisions: samples from T1-70 and samples from T2-80 (Fig. 2 and Fig. S3). The result implied the significant difference in the composition of microbial communities between the two treatments during the maturation phase. Ascomycota were the main fungal phylum in both treatments during ascending and thermophilic phase (Fig. 2). This phylum has been described as the dominant phylum in vegetable waste composting (Shi et al., 2022) and olive mill waste composting (Tortosa et al., 2020). However, in the maturation phase, Ascomycota dominated overwhelmingly in T2-80, whereas over 90 % of fungal ASVs in T1-70 were assigned as unclassified fungi, and

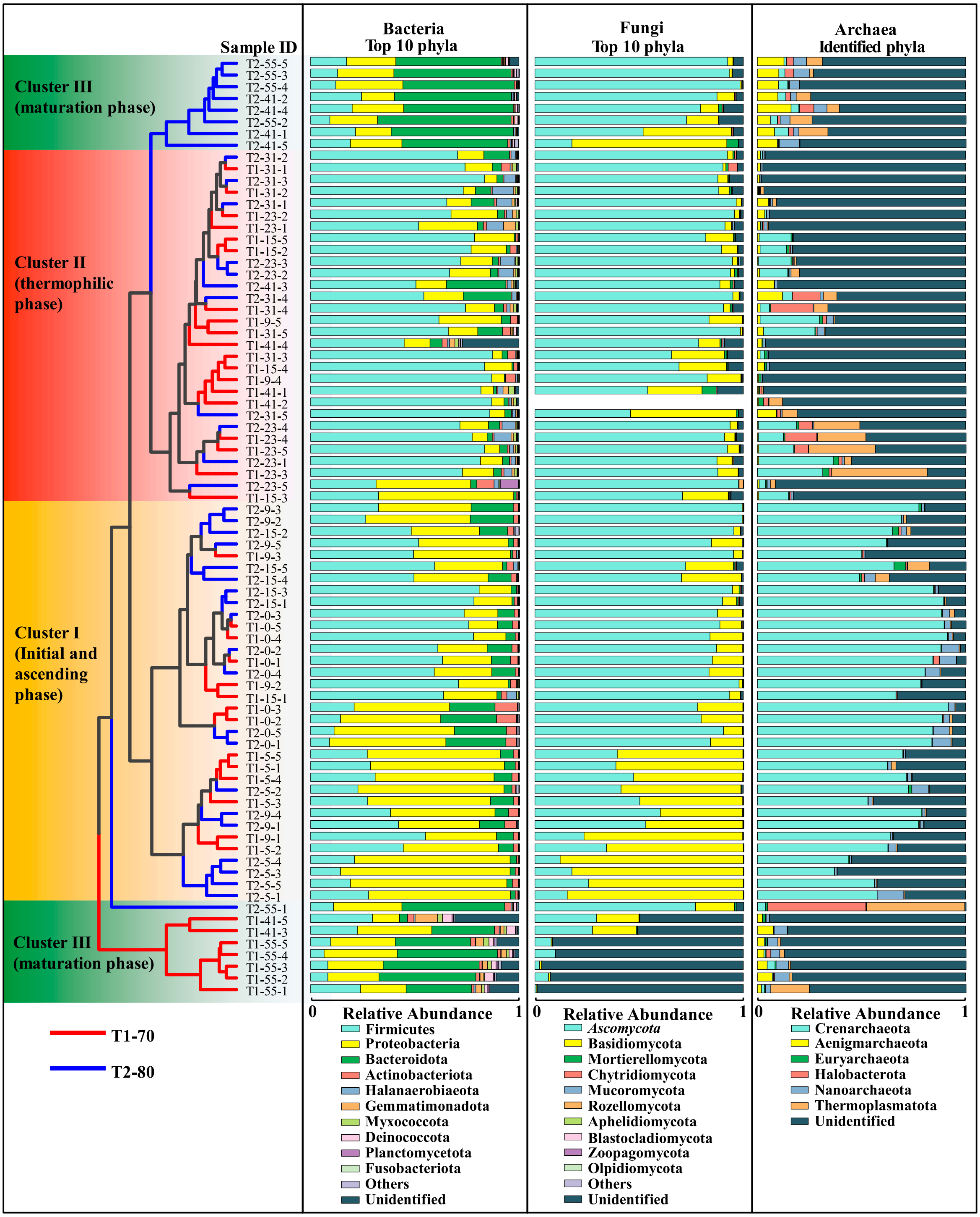

Fig. 2. Dynamic changes in microbial community composition at the phylum level during composting process.

the relative abundance of Ascomycota was only 5.44 % (Fig. 2). The initial MC, resulting from different ratios of vegetable waste to maize straw, critically affected the composition of fungal community in maturation phase.

3.4.2. The microbial diversities during composting

The α-diversity (Shannon) of bacterial, fungal and archaeal communities in both treatments had a similar trend in the initial phase of composting, but was higher in T1-70 (Fig. 3A), which was beneficial for composting start-up (Wang et al., 2021). In the ascending and thermophilic phase, microbial α-diversity in T1-70 was general higher than that in T2-80 (Fig. 3A). Shi et al. (2022) reported a similar phenomenon in the composting of vegetable waste, i.e., high temperature did not reduce the bacterial α-diversity. In the maturation phase, archaeal α-diversity in T1-70 was higher than that in T2-80, while bacterial α-diversity in T1-70 exhibited a downward trend and significantly lower than that in T2-80 on day 55 (Fig. 3A), which was mostly due to the enhanced specialization of microbial metabolic function (Wang et al., 2021; Zhang et al., 2021a,b). The fungal α-diversity in T1-70 decreased sharply from day 41 onward due to the large proportion of unclassified ASVs, while fungal α-diversity in T2-80 remained relatively stable from 15 d to 55 d (Fig. 3A).

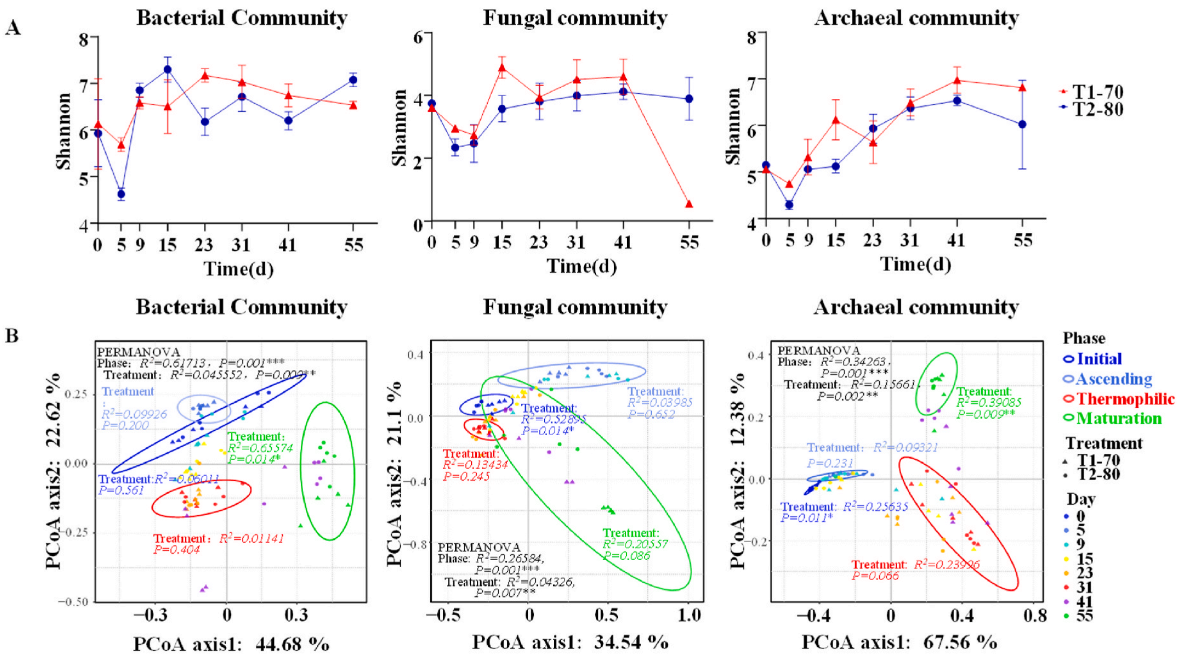

Fig. 3. Indices of α-diversity (A) and β-diversity (B) in bacterial, fungal and archaeal communities.

On the other hand, PCoA indicated that β-diversity distribution patterns of bacterial, fungal and archaeal communities were similar in the two treatments, showing significant temporal succession patterns between composting phases (Fig. 3B). Furthermore, PERMANOVA examined variations in the microbial communities with respect to the treatments and composting phases. Although the composting phase was that main factor contributing to the variation, the bacterial and archaeal communities differed significantly between the treatments during the maturation phase. Additionally, the fungal and archaeal communities differed significantly between the treatments in the initial phase, which could be attributed not only to the different initial MC, but also to the different mixing ratios of vegetable waste to maize straw.

3.4.3. *Correlation analysis between physicochemical properties and potentially functional microorganisms*

LEfSe analysis was performed to determine the influence of initial MC on specific microbial taxa from the phylum to genus levels in each phase of composting. A total of 23, 21, 15 and 64 clades (microbial taxa with significant differences (LDA>3.5, $P < 0.05$)) were enriched during the initial, ascending, thermophilic and maturation phases, respectively (Fig. S4).

In the initial phase, significant difference between T1-70 and T2-80 was observed for the abundances of some fungal and archaeal taxa, especially fungal Basidiomycota (Fig. S4A). Basidiomycota is frequently found in composts, playing an important role in organic matter degradation and humic substances formation (Goud et al., 2011; Tortosa et al., 2012, 2020). Belonging to Basidiomycota, the genus *Filobasidium* enriched in T1-70 was negatively correlated with TK, TOC and water content, but positively correlated with composting temperature, GI, FA and HA during the initial phase (Fig. 4). It was reported that *Filobasidium* not only possessed the ability to degrade fats and proteins but also positively associated to the synthesis of HA during straw composting (Suzuki et al., 2013; Zhao et al., 2022). It was believed that the proliferation of *Filobasidium* in T1-70 contributed to the higher composting temperature, GI, FA and HA during the initial phase. Coincidentally, a fungal genus *Aspergillu* that was more abundant in T1-70 showed positive correlations with composting temperature during the ascending phase (Fig. S4B and Fig. 4), presumably because of its important ligninolytic activity in composting (He et al., 2022; Shi et al., 2022). These results demonstrated the key role of differential fungi between the two treatments early during composting.

Compared to other stages of composting, bacterial and fungal taxa were enriched in the thermophilic and maturation phase (Fig. S5). In the thermophilic phase, the correlation between physicochemical properties and the differential microbiota showed that bacterial genus *Ureibacillu* enriched in T1-70 was negatively correlated with FA (Fig. S4C and Fig. 4). *Ureibacillu* might enhance the decomposition of FA in T1-70 during the thermophilic phase. When the treatments entered the maturation period, the largest number of differential microbes correlated with physicochemical properties were identified at genus level (Fig. 4). Most of these microbes were enriched in T2-80 (Fig. S4D), which was attributed to the depletion of thermal sensitive microbes in T1-70. Four bacteria including *MWH_CFBk5*, *Planktosalinus*, *Pseudopedobacter*, and *Luteimonas* were more abundant in T1-70. The Pearson correlation analysis showed that these bacterial genera were positively correlated with humification parameters in T1-70 during the maturation phase (Fig. 4), indicating their potential roles in improving the humification degree of the compost. *Planktosalinus* and *Luteimonas* were the primary bacteria in the maturation phase of composts from different origins, like livestock manure composting (Gong et al., 2021; Xie et al., 2021; Wang et al., 2021, 2022a), sewage sludge and municipal green waste composting (Chen et al., 2022), and agro-industrial waste composting (Hernández-Lara et al., 2022). *Planktosalinus* was reported to be involved in nutrient element (C/N/P/S) transformation (Zhao et al., 2019). Also, the intense activity of *Luteimonas* was linked to the organic matter degradation and maintaining high temperature, thus increasing the harmless level of composting (Chen et al., 2021; Wang et al., 2021, 2022a). These might explain their relationship with TN content and GI.

In comparison, many genera enriched in T2-80 preferentially showed negative correlations with humification indices during maturation (Fig. 4). This correlation was strongly notable for genera belonging to Ascomycota, the overwhelmingly dominate fungi found in the maturation phase of T2-80. *Penicillium*, *Candida* and *Trichoderma* were negatively correlated with HA content and HA/FA ratio (Fig. 4); *Ascobolus* and *Kernia* were positively correlated with FA content, and negatively correlated HA/FA ratio, indicating that these genera might be involved in FA formation. Previous studies have reported the similar results, i.e., belonging to Ascomycota, *Capnodiales* was involved in lignin

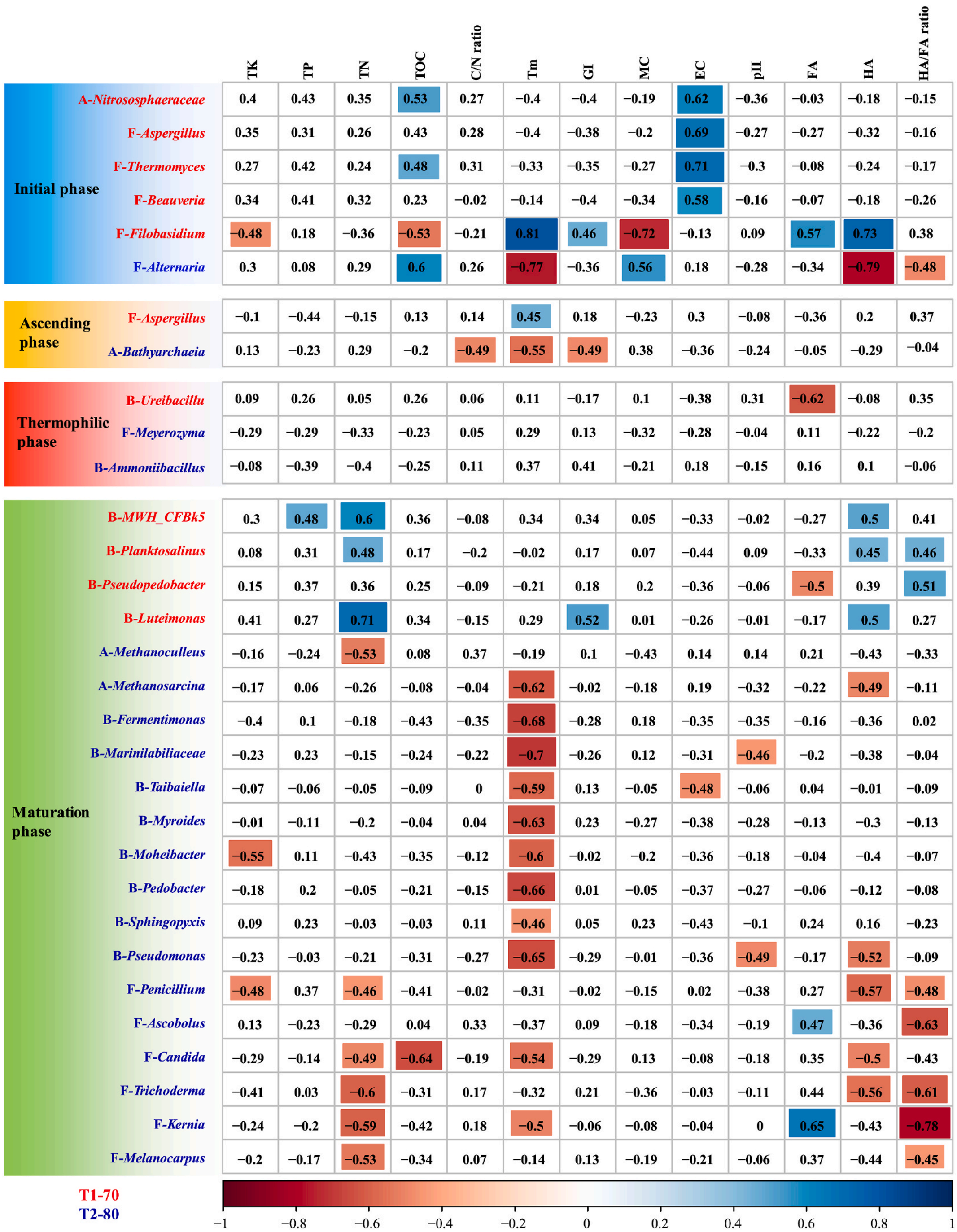

Fig. 4. Correlation analysis between physicochemical properties (total potassium, TK; total phosphorus, TP; total nitrogen, TN; total organic carbon, TOC; C/N ratio; temperature; germination index, GI; moisture content, MC; electrical conductivity, Eh; pH; fulvic acid, FA; humic acid, HA and HA/FA ratio) and significantly differential genera between the two treatments during composting process. Color folders represent significant correlation ($p < 0.05$). A, archaea; F, fungi; B, bacteria. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

degradation, but negatively correlated with humification degree and the percentage of HA (Tortosa et al., 2020); *Sarocladium* was positively correlated with FA content, and negatively correlated with HA content (Zhang et al., 2022).

3.4.4. Effect of initial moisture content on microbial co-occurrence network relationships

To further decipher the relationship between physicochemical properties and microbial communities as well as the species-species (ASV) interactions during composting process, the molecular ecological networks were constructed (Fig. S6 and Fig. 5). As shown in Fig. S6, pH, TOC and FA were the main factors directly associated to the microbial populations in T1-70, but composting temperature had time-delayed associations with all the three factors. In the network of T2-80, pH and H/F ratio were the main factors associated to microbes, and temperature had time-delayed associations with pH. Composting temperature is the major factor driving the succession of microbial communities, crucially affecting the composting process (Chen et al., 2022; Ravindran et al., 2022). It is speculated that the effect of initial MC on composting process was mediated by the composting temperature.

On the other hand, the co-occurrence network of microbiota showed that the total link number of T1-70 network was much higher than that of T2-80 network (Fig. 5), indicating more complex microbial communities in T1-70. Moreover, the networks of both treatments were divided into distinct modules and these modules could correspond to composting phases according to the dynamics of the microbial abundance (Fig. S7). For example, in T2-80, the sequence abundance for module 2 increased dramatically from 31 d onward and then was much higher than that for other modules (Fig. S7A). Thus module 2 represented the main microbiota during the maturation phases of composting in T2-80. Additionally, the links in the networks of both treatments generally occurred within the modules (Fig. 5), which not only confirmed the succession of microbial communities but also highlighted microbial interactions within composting phases.

Compared to T2-80, the numbers of nodes and links in the modules corresponding to the initial and ascending phases was much higher in T1-70 network (Fig. S7B). These topological features suggested that the ratio of 3:1 of vegetable waste: maize straw in 70% initial MC could activate more indigenous microbes and enhance microbial interactions early during composting. Recent studies have reported that inoculation of functional microbes could optimize microbial communities by enhancing their interactions during the composting, thus improving composting efficiency (Wang et al., 2021; Shi et al., 2022). On the contrary, the number of nodes in the module corresponding to the

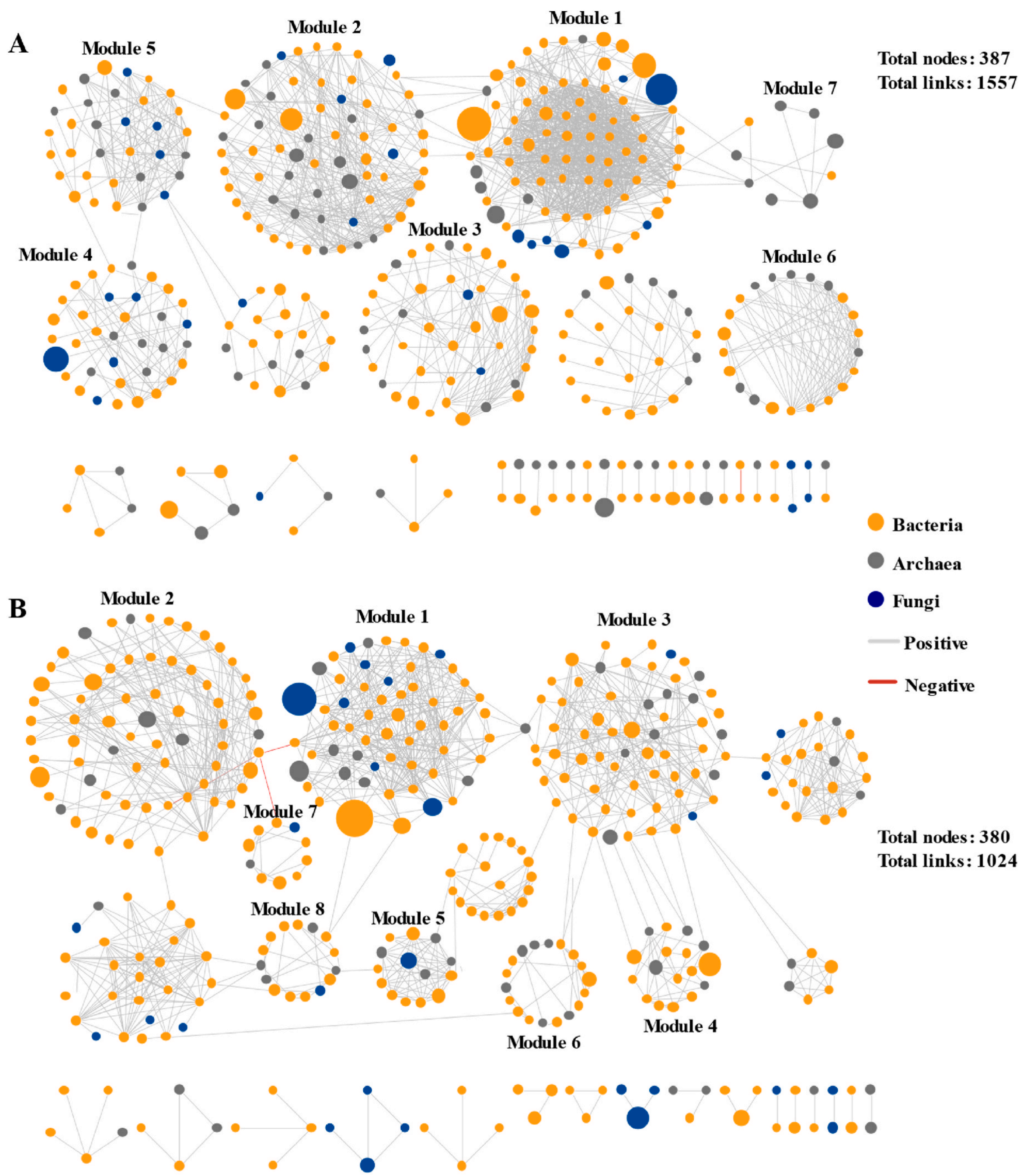

Fig. 5. Microbial co-occurrence networks in the T1-70 (A) and T2-80 (B) during composting processes. The link indicates a significant correlation ($P < 0.05$). Light grey and red lines respectively represent the positive and negative correlations between OTUs. Orange, grey and navy-blue nodes represent bacterial ASVs, archaeal ASVs and fungal ASVs, respectively. The size of each node is proportional to the degree of each ASVs. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

maturation phase was lower for T1-70 due to its greater heat pressure in the thermophilic period (Fig. S7B). The reduced active microbes in the maturation phase of T1-70 surprisingly improved the humification degree of the compost, which was presumably due to the enhanced specialization of microbial metabolic function as discussed above.

4. Conclusion

This study revealed that initial MC, resulting from different ratios of vegetable waste to maize straw, significantly influenced their plant-scale composting under the low temperature conditions, even though both T1-70 and T2-80 treatments achieved mature and non-hazardous composts. Moreover, our data highlighted that the difference in composting temperatures, humification degree, and microbial communities between the two treatments was most significant during the maturation phase. Differential microbes between the two treatments were significantly correlated with composting temperatures, GI and humification indices, which improved compost quality in T1-70 by achieving higher temperatures and promoting humification.

CRediT authorship contribution statement

Shanshan Sun: Conceptualization, Formal analysis, Writing – original draft. **Cheng Guo:** Formal analysis, Investigation, Methodology. **Jianyu Wang:** Data curation, Investigation, Validation. **Li Ren:** Methodology, Validation. **Jianping Qu:** Investigation. **Qi Guan:** Investigation. **Nongxiao Dou:** Methodology. **Jiahui Zhang:** Methodology. **Qiuhua Chen:** Investigation. **Qi Wang:** Investigation. **Jiguang Wang:** Investigation. **Jieming Li:** Resources, Writing – review & editing. **Zheng Gao:** Supervision, Writing – review & editing. **Bo Zhou:** Conceptualization, Funding acquisition, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to 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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