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Original Research

Core fungal species strengthen microbial cooperation in a food-waste composting process

Yuxiang Zhao [a], Jingjie Cai [a], Pan Zhang [a], Weizhen Qin [a], Yicheng Lou [a], Zishu Liu [a, b], Baolan Hu [a, c, d, *]

[a] *Department of Environmental Engineering, Zhejiang University, Hangzhou, China*
[b] *State Key Laboratory of Urban Water Resource and Environment, Harbin Institute of Technology, Harbin, China*
[c] *Zhejiang Province Key Laboratory for Water Pollution Control and Environmental Safety, Hangzhou, China*
[d] *Key Laboratory of Environment Remediation and Ecological Health, Ministry of Education, College of Environmental Resource Sciences, Zhejiang University, Hangzhou, China*

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ABSTRACT

In ecosystem engineering research, the contribution of microbial cooperation to ecosystem function has been emphasized. Fungi are one of the predominant decomposers in composting, but thus far, less attention has been given to fungal than to bacterial cooperation. Therefore, network and cohesion analyses were combined to reveal the correlation between fungal cooperation and organic matter (OM) degradation in ten composting piles. Positive cohesion, reflecting the cooperation degree, was positively linked to the degradation rate of OM. From the community perspective, core species (i.e., *Candida tropicalis*, *Issatchenkia orientails*, *Kazachstania exigua*, and *Dipodascus australiensis*) with high occurrence frequency and abundance were the key in regulating positive cohesion. These species were highly relevant to functional genera associated with OM degradation in both fungal and bacterial domains. Therefore, focusing on these core fungal species might be an appropriate strategy for targeted regulation of functional microbes and promotion of degradation rates.

1. Introduction

The quantity of food waste (FW) is one of the largest among all kinds of waste, with its generation exceeding 120 million tons per year [1]. Composting is an effective way of rendering FW harmless. Additionally, composting can convert FW into stable mature compost [2], which is utilized as a soil conditioner [3]. The degradation of organic matter (OM) is one of the most important processes in composting. The low degradation rate of OM may not only hinder humus formation but also limit the harmlessness of FW. Without being completely harmless, FW has serious implications for both the environment and human health, as it is highly perishable, smelly and prone to harboring pathogens [4].

As the dominant contributors, various kinds of microbes play essential roles in OM degradation during composting, including fungi and bacteria [5]. Microbes do not exist in isolation, and they form complex microbial networks through positive (symbiotic), negative (amensualism) and neutral interactions. From an ecological standpoint, microbial interactions have a great impact on ecosystem function, especially in complex ecosystems [6]. Since the degradation of refractory OMs requires microbial interactions, focusing on microbial interactions may be a valuable strategy to promote OM degradation rates. During composting, it has been proven that bacterial cooperation is strongly linked with OM degradation, and highly structured bacterial networks can be observed [7]. Although fungi and bacteria are equally essential in composting [8], few investigations on microbial interactions have been reported for fungal communities [9]. Additionally, the microbial interaction between bacteria and fungi has been mentioned in other habitats, including negative interactions due to competition for niches [10] and positive interactions because of synergistic interactions [11]. Interactions between bacteria and fungi have a large impact on both community stability and function [12]. Although there is a division of labor between bacteria and fungi in

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* Corresponding author. Department of Environmental Engineering, Zhejiang University, Hangzhou, China.
E-mail address: blhu@zju.edu.cn (B. Hu).

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the composting process, interdomain interactions between fungi and bacteria have rarely been reported. Therefore, it is necessary to study microbial interactions in fungal communities as well as interdomain interactions between fungi and bacteria.

Microbial communities are complex and variable, and core microbial species are key to microbial interactions and functions [13]. The importance of core microbes has been mentioned in a variety of engineered habitats [14], such as *Achromobacter*, *Oceanobacillus*, *Bacilli* [15], and *Thermobifida* [16]. They were considered to promote microbial cooperation as well as OM degradation and were identified as the core bacterial microbes in the composting process. It has been proven that microbial inocula developed on the basis of key bacteria could facilitate the composting process by strengthening microbial cooperation [7,17]. Although alpha diversity and fungal community structure have been widely reported [18], core fungal microbes influence microbial interactions and have rarely been reported in comparison to bacteria. Therefore, analyses of the core of fungal microbes are crucial.

Therefore, in this study, ten different piles were investigated in an FW composting facility to reveal the relationships between fungal cooperation and the degradation of OM. Three criteria (i.e., high abundance (in the top 0.1%), high occurrence frequency (>80%), and key species in the network) were used to identify the core species, and their impact on the domain and interdomain microbial cooperation were explored according to the network and positive cohesion. We aimed to reveal the relationship between fungal cooperation and OM degradation and to reveal the core species that influenced microbial cooperation.

2. Materials and methods

2.1. Sampling

Composting samples were obtained from a local rural household FW composting facility (Changxing, Zhejiang Province), with ten piles investigated. Maize straw, collected from local residents, was used as a bulking agent and mixed in a 1:3 ratio with FW. After that, the waste was shredded into 3–5 cm pieces, and the moisture content was controlled by a press (approximately 72.8%) (Table S1). Each pile was composed of 8000 kg of FWs, and the size was dimensions of 3.0 m × 3.0 m × 1.2 m (i.e., L × W × H). The aeration rate was sustained at 0.9 L per kg dry matter (DM) per min. Nearly 0.5 kg of samples were collected on Days 0, 5, 12, 20, and 30 in each pile. Each sample consisted of five subsamples that were collected from different locations by using a tubular sampler. Each sample was split into two portions, with one stored at −20 °C and another stored at 4 °C.

2.2. Physicochemical analysis

The OM content was evaluated by measuring the weight loss after 4 h of ignition at 550 °C [19]. Starch content was detected by the anthrone colorimetric method. Cellulose, lignin, and hemicellulose contents were measured as previously described [20]. Three replicates were performed for each sample. The indices of these OMs were calculated to determine the degradation of these OMs based on the DM mass balance (e.g., cellulose content (g per kg DM)/ash content), which was an accurate method to evaluate the removal rate [21,22]. The physicochemical indicators of the raw materials and the composted material are shown in Table S1. All piles met the standards for maturity and phytotoxicity in NY/T 525–2021 (Ministry of Agriculture, China) and CJJ52-2014 (Ministry of Housing and Construction, China) (E4/E6 ratio >4, germination index value (GI value) > 80%, C/N ratio <15, moisture content (MC) < 30%).

2.3. DNA extraction and ITS high-throughput sequencing

Compost DNA (n = 50) was extracted by referring to the descriptions of the Power Soil DNA Kit (Mo Bio Laboratories, Carlsbad, CA). DNA quality and concentration were measured and guaranteed by a NanoDrop photometer (Isogen Life Science, The Netherlands). For fungal community analysis, the ITS genes were amplified with primer ITS5-1737F/ITS2-2043R and sequenced by Illumina MiSeq [23]. Based on a 97% similarity threshold, reads were clustered into OTUs, and OTUs observed less than two times were removed. The raw data were uploaded to NCBI under No. PRJNA791789.

2.4. Domain and interdomain network

A domain network was structured through the MENA pipeline to demonstrate potential microbial interactions in fungal communities [24]. For Pearson's or Spearman's correlation-based methods, the MENA pipeline identifies a threshold based on random matrix theory (RMT), which can be conducted automatically [24]. To overcome the double zeros problem caused by the calculation of the interdomain network, the IDEN pipeline calculates the adjacent matrix based on the SparCC correlation-based method, which uses logarithmically scaled variances to calculate correlations between species. The two pipelines use a targeted approach to avoid overfitting [25]. The interdomain network was constructed to discover the cross-trophic microbial associations between the fungal and bacterial communities, and the analyses of interdomain microbial cooperation were conducted according to the IDEN pipeline [25]. The bacterial community, collected from the same plies, was described in a previous study [20], and the bacterial data were No. PRJNA783737 in NCBI. After network construction, the topological indices were counted separately in the two pipelines [25]. The corresponding 100 rewired random networks were calculated to reveal the characteristics of the constructed network. In addition, the module value and Zi-Pi value were also computed to research the modularity and the key hubs [26].

2.5. Robustness calculation

Robustness represents the proportion of operational taxonomic units (OTUs) remaining in the network after the random or targeted removal of OTUs, indicating network stability. A proportion of nodes were randomly removed to simulate the random loss of OTUs. Additionally, core fungal species were individually removed to simulate targeted removal [6].

2.6. Cohesion calculation

To quantify positive microbial interactions in the fungal community, cohesion was calculated for each sample. Positive cohesion is the sum of abundance weighted on the basis of positive correlations from the model calibration (equation (1)) [27]. Thus, positive cohesion could reflect the degree of microbial cooperation in the microbial community.

$$\text{Positive cohesion } = connectedness_i \times \sum_{i=1}^{m} abundance_i \tag{1}$$

2.7. Statistical analysis

Three criteria were adopted to identify the core species in the composting fungal communities: (1) highly abundant species: species in the top 0.1%, (2) ubiquitous species: species occurring in over 80% of all composting samples, and (3) key species: Pi index

≥0.62 or Zi index ≥2.5 [14]. Structural equation modeling (SEM) was performed by the R package "*plspm*". The degradation rate of OM was one of the observed variables, and that of OM, starch, hemicellulose, cellulose, and lignin were regarded as the latent variables. Environmental factors were observed variables, whereas temperature, nitrate, ammonia, C/N ratio, E4/E6, EC value, pH value, total nitrogen, and MC were latent variables. Details of the environmental factors were described in a previous study [20]. The microbial community consisting of 452 species was an observed variable. Variance partitioning analysis (VPA) was performed by the *R* package "*vegan*". The random forest model (RFM) was performed by the *R* package "*randomForest*".

3. Results and discussion

3.1. The degradation of OM and its driving force

The degradation of OM could produce intermediates to improve composting quality; therefore, it was important to distinguish the contributions of various elements to composting (Fig. 1). The relative content of starch, hemicellulose, cellulose, and total OM showed a decreasing trend in all periods (Fig. S1). In contrast, the relative content of lignin remains constant at the start, as it was calculated as a proportion of lignin per kg of DM, and it might increase after the rapid degradation of other major OMs (starch, hemicellulose, and cellulose). To avoid the effect of weight loss on the relative content, the ash content was used to normalize the relative content of these OMs [28]. The results indicated that OM was effectively degraded in composting, reaching 63.5% (Fig. 1a). Obviously, OM was consumed to release energy and cause the temperature to increase [29]. In detail, significant differences could be observed in the degradation rates of different OMs (Fig. 1a). Starch had the highest degradation rate of 71.8%, followed by cellulose, hemicellulose and lignin with 65.8%, 69.9%, and 54.3%, respectively (Fig. 1a). The lower degradation rate of lignocellulose is caused by the crystal structure of lignocellulose, which is difficult for microbes to invade [30]. To identify the key factors affecting OM degradation, SEM analysis was adopted (Fig. 1b and c). The results showed that positive cohesion, indicating microbial cooperation, had the greatest impact on the degradation of OMs ($R^2 = 65.6\%$, $p < 0.001$). Furthermore, a significantly positive correlation could be observed between the positive cohesion and the degradation rate of these OMs (Fig. 1b). This was due to two main reasons: (1) Lignocellulose, the main kind of OM in FW composting, exists as recalcitrant crystals [31], the degradation of which requires the cooperation of various microbes [32]. Microbial cooperation could enable microbes to degrade these OMs more efficiently [33]. (2) Microbial cooperation could strengthen the microbial tolerance to extreme environments (e.g., high temperature) during the composting process. The results of SEM analysis also emphasized that the positive cohesion was negatively impacted by environmental factors (−30.9%, $p < 0.001$) and positively impacted by the microbial community (52.9%, $p < 0.001$). From the perspective of environmental factors, MC, pH, and the C/N ratio were the main latent variables modifying these factors (Fig. S2). These indices explain 41%, 49%, and 47% of the changes in positive cohesion, respectively (Fig. 1d). The importance of these environmental factors on positive cohesion has been mentioned for the bacterial domain [20]. Therefore, positive cohesion was the key factor in improving the degradation rate of OM, and the regulation of the C/N ratio and MC might be an effective strategy.

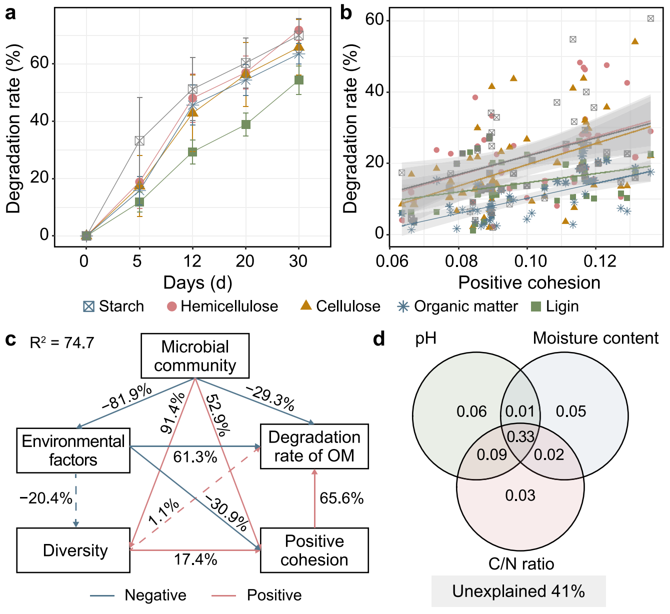

Fig. 1. Key factors affecting organic degradation. **a**, Degradation rates of different OMs. **b**, Relationship between positive cohesion and degradation rate of OMs. **c**, SEM analysis (dashed: insignificant, solid: significant). **d**, VPA analysis (relationship between latent environment factors and positive cohesion).

3.2. Identification of key fungal species

As positive cohesion was impacted by the environmental factors and the microbial communities, the fungal community was further explored, and the species associated with potential cohesion were examined (Fig. 2). Since 4019 OTUs and 452 species were obtained, RFM was adopted to reveal the species associated with high positive cohesion. Ten species, including *Candida tropicalis*, *Issatchenkia orientails*, *Kazachstania exigua*, and *Dipodascus australiensis*, were identified as the most basic species influencing positive cohesion, with the explanation reaching 20.3%, 15.6%, 15.5%, and 15.2%, respectively (Fig. 2a). To further confirm the ecological status of these species, three evaluation standards were combined to reveal the species with high occurrence frequency, high abundance, and substantial contributions to the community (Fig. 2b and c). According to the occurrence frequency, 56 species occurring in 80% of the samples were identified as the "ubiquitous species". Considered the "overall abundant species", the average relative abundance of 61 species was higher than 0.2% [14]. The ubiquitous species and overall abundant species were regarded as the species that could sustain functional stability. Furthermore, the Zi-Pi method was used to focus on the species contributing the most to the community, and 26 species were identified as the "key hubs". Remarkably, only *Candida tropicalis*, *Issatchenkia orientails*, *Kazachstania exigua*, and *Dipodascus australiensis* met all conditions simultaneously, indicating that these four species were the core fungal species in the composting process (Fig. 2c). In addition to the high abundance and occurrence frequency, the core species were also the network hubs and module hubs in the community (Fig. 2b). Both network hubs and modules were close to generalists, which had a great effect on the microbial structure and ecological function [13]. All these results emphasized that these species played an essential role in the fungal community. The sum of the relative abundances of these species was 46.5% at Day 0. With the rise in temperature, the number peaked on the 5th day at 69.3% (Fig. 2d). High temperature could be deemed an environmental stress factor, resulting in a decrease in alpha diversity and the enrichment of core species (Fig. S3). This result was supported by an early finding that significantly reduced diversity could be found in the thermophilic period [34], according to the nutrient limitation and high temperature (>55 °C). The consumption of readily decomposable OM led

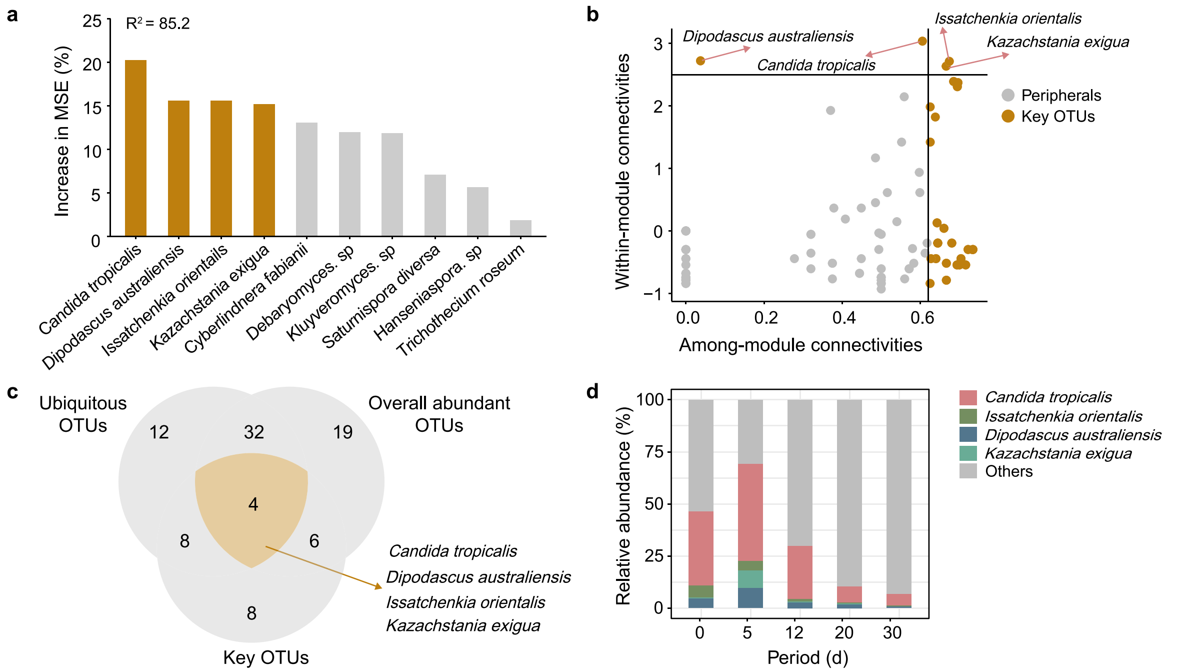

Fig. 2. Core species in the composting process. **a**, Screening for the species with high contributions to positive cohesion. **b**, The Zi-Pi method to reveal the function of core hubs. **c**, Screening for core species based on “ubiquitous species”, “overall abundant species”, and “high contribution species”. **d**, The relative abundance of core species in different periods.

to an increase in temperature and additional energy expenditure (In Ref. [35], which caused the elimination of nonfunctional microbes and the enrichment of target microbes [36]. Therefore, the relative abundance of core species peaked on Day 5. Subsequently, with the temperature drop and the recovery of alpha diversity, the minimum value of relative abundance of these core species could be observed on Day 30 (6.9%). *Aspergillus*, *Thermomyces*, and *Penicillium* were the focus of a previous study, owing to their ability to degrade lignocellulose [37]. However, the degradation of lignocellulose requires a division of labor, and the microbes associated with the hydrolysis process account for approximately 25% of the whole process [38]. Furthermore, these genera cannot adapt to a changeable environment and decline in the thermophilic period [39]. In contrast, these core fungal species, which could participate in microbial interactions, have been mentioned as high-abundance species in various periods of the composting process [5]. These species can maintain significant metabolic activity at high temperatures and are able to grow over a wide range of pH and moisture levels [40]. Their higher tolerance to the environment leads to their dominance and in turn underscores the potentially significant role of these species in the whole composting process [41]. Therefore, focusing on the core fungal species related to high microbial interactions might be an optimal strategy to strengthen the degradation of lignocellulose.

3.3. Network analysis of the fungal community

Correlation and best multiple regression analysis were further adopted to confirm the importance of these core species in the degradation rate of OM (Fig. 3). The correlation analysis showed that the relative abundance of core species was significantly associated with a higher degradation rate of OMs (Fig. S4a) and could explain 74.5–84.1% of the variation in the degradation rate of OM (Fig. S4b). These results emphasized the importance of these species in OM degradation. Although core fungal species have not been recognized as species with a high capacity to degrade OM, the strengthening of microbial interactions by them might be a potential strategy to promote the degradation of lignocellulose. Due to their ability to yield unique xylose reductase, beta-glucanase and alcohol dehydrogenase 1, the core fungal species could degrade furfural (typical microbial inhibitors in lignocellulose hydrolysate process) to promote the degradation of lignocellulose [42]. In addition, these core species could also produce xylitol, arabitol, dicarboxylic acid, citric acid, and uricase to promote the growth of other microbes [43,44]. Therefore, the core fungal species could facilitate microbial interactions to increase the degradation of lignocellulosic based on their unique metabolic processes. Furthermore, they could use hydrocarbons as raw materials to share tricarboxylic compounds and fatty acids with the environment, and these public goods would be used by other microbes. The addition of these public goods has been shown to improve composting efficiency and increase humic substances (Wang et al., 2019). This result implied that core species have the potential to strengthen microbial cooperation. Therefore, a microbial network was analyzed and visualized to further explore microbial cooperation in the composting process (Fig. 3). We found a significant difference in the topological indices (avgCC, GD, and M) between the constructed network and the randomized network (999 iterations). Higher M and avgCC and lower GD supported that the constructed network had small world, scale free, and modular properties (Table S2) [45]. These characteristics indicated that the potential interactions in the constructed network between different taxa were efficient and stable due to higher resistance to random node loss [46]. In contrast to the bacterial network, only 93 nodes could be found in the constructed fungal network, which was the result of low fungal diversity (Fig. 3a) [20]. However, a higher average degree (avgK), indicating the complexity of the network, implied that stronger microbial interactions existed in the fungal network [24]. Four-core fungal species accounted for only 4.0% of the total species, whereas they were involved in 40.2% of the

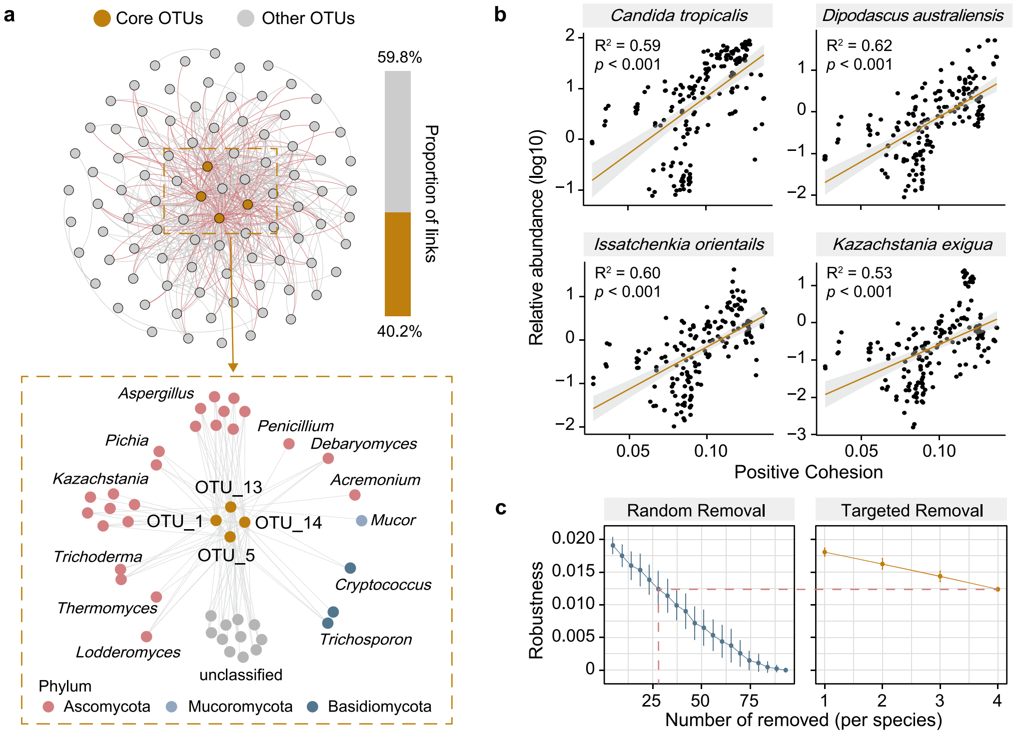

Fig. 3. Network analysis for the fungal community. **a**, Visualization of the network (yellow: core species, gray: other species). **b**, Relationship between the relative abundance of core species (log10) and positive cohesion. **c**, Robustness of random removal and target removal (The impact of the loss of the four-core species on robustness was consistent with the loss of 26 species, reaching 0.012).

network construction, suggesting their importance in the network. The microbes linked with these species were *Aspergillus*, *Thermomyces*, *Penicillium*, and *Mucor*, which are considered lignocellulose-degrading genera [18]. *Thermomyces* are major hemicellulose degraders [47]. *Aspergillus* can produce cellulases and hemicellulases, thus promoting compost maturation [48]. *Mucor* can yield simple sugars and motivate other microbes to decompose refractory compounds [49]. *Penicillium* degrades cellulose by high-yield cellulase and shares secondary metabolites [50].

Furthermore, species associated with the core species accounted for 65.9% of the degradation of OM, which was 1.8 times higher than that of unconnected species (Fig. S5). These results implied that the core species could be linked with the functional genera to carry out functions promoting OM degradation. To clarify the relationship between the relative abundance of core species and positive cohesion, correlation analysis was adopted. The results showed that the relative abundance of all core species was highly correlated with positive cohesion ($p < 0.001$); therefore, these species might promote other microbes through cooperation (Fig. 3b). The links between the four-core species and other microbes confirmed that these core species had significant positive correlations with other microbes, indicating that these OTUs might promote the growth of other microbes. The scale-free network had a higher dependence on the key hubs, although it had superior performance regarding random node loss [24]. The effect of random loss of nodes in the network and the loss of core OTUs on microbial stability was further simulated by iteration 999 [6]. It was found that the loss of four-core OTUs had a devastating impact on the network, leading to a 40% decrease in network stability (Fig. 3c), which was consistent with the impact of the loss of 26 nodes. Since these core OTUs played an important role in network construction, other microbes might be dependent on the core OTUs for growth. Therefore, the absence of these core OTUs might lead to the disappearance of microbes associated with them. Consequently, the core fungal species could strengthen the lignocellulose-degrading genera through microbial cooperation in the fungal domain.

3.4. Interdomain network between fungi and bacteria

The contributions of fungal and bacterial domains to OM degradation were similar, with more than 40% being a combination of fungi and bacteria (Fig. S6a). The importance of these core species was emphasized in the fungal domain, whereas the role of these core species in the interdomain was still unclear. Therefore, an interdomain network was constructed to reveal the relationship between fungal and bacterial domains (Fig. 4). According to the interdomain network, 21 bacterial OTUs and 41 fungal OTUs were chosen to illustrate the fungi-bacteria associations with 232 observed links. To prove the reliability of the observed topological indices, they were compared between the constructed interdomain network and the corresponding 100 rewired random networks. The significant difference between the constructed network and random network suggested that the small-world topology was a unique and inherent feature of this network ($p < 0.001$) (Table S3). This result implied that an intense microbial interaction could be observed in this interdomain network. The connectance of this interdomain network was 0.269, showing that 26.9% of potential links could be observed as fungi-bacteria links [25]. This connectance value was higher than that of other habitats, implying that the interdomain microbial interaction was more intensive in this type of habitat [51]. Furthermore, the web asymmetry was 0.33, and the contribution of fungi to the network was greater than that of bacteria. The skewed richness pattern indicated that fungi are more important than bacteria in influencing potential microbial interactions [52]. The high value of web asymmetry also indicated that fungi, as generalists, were connected with bacterial specialists.

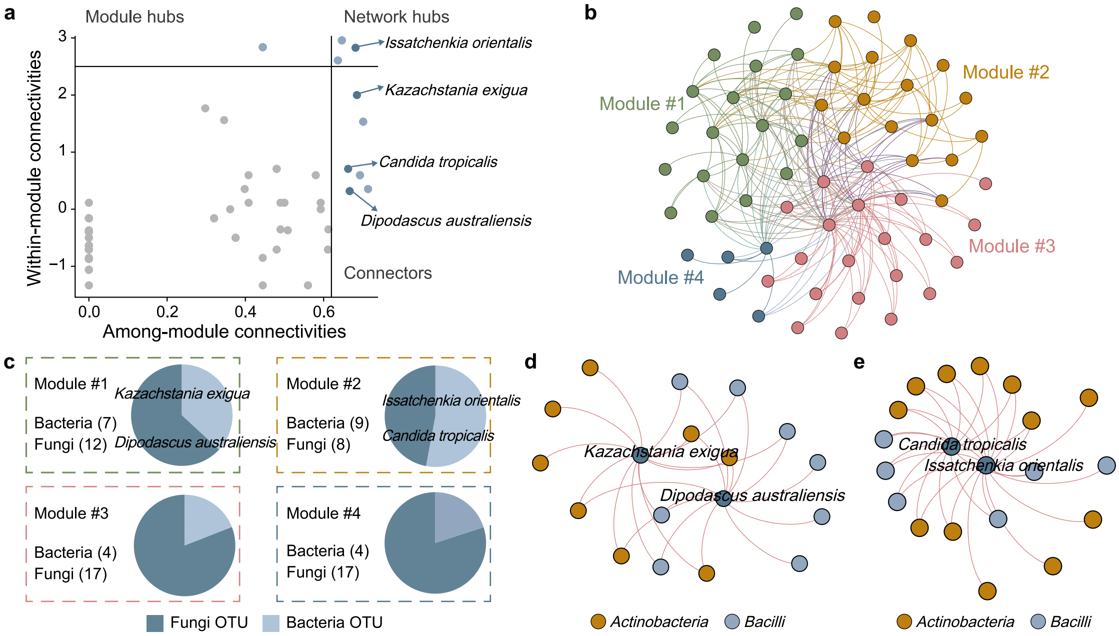

Fig. 4. Interdomain networks between fungal taxa and bacterial taxa. **a**, The Zi-Pi value of the interdomain network. **b**, The visualization of the network. **c**, The composition of different modules. **d**, The interaction between core species and functional bacterial taxa in Module #1. **e**, The interaction between core species and functional bacterial taxa in Module #2.

Additionally, a significantly modular structure ($p < 0.001$) found in this fungi-bacteria interdomain network indicated that an intensive interaction could be observed in different modules between bacteria and fungi. In contrast to the uneven distribution of total nodes within different modules in other habitats, this was similar in the composting interdomain network (17–21), and four different modules could be observed.

The Zi-Pi method was further adopted to reveal the key hubs in the interdomain network (Fig. 4a and b). Four fungal OTUs were classified as key hubs, which was consistent with the core fungal OTUs screened in the domain network (Fig. 4c). In comparison with the domain network, the core fungal species were classified as network hubs and connectors in the interdomain network; that is, these four-core fungal OTUs could interoperate with bacterial microbes within the same module (Fig. 4d and e). The obtained core fungal OTUs belonged to Module #1 and Module #2. The results showed that the OTUs of core fungi were positively correlated with Actinobacteria and Firmicutes in both modules. In addition, core fungal species could significantly promote positive cohesion, calculated from the interactions between fungi and bacteria (Fig. S6b). These results indicated that core fungal species could improve interdomian microbial cooperation. The bacterial phyla associated with the core fungal species were reported to be functional bacterial phyla in composting, playing a crucial role in mineralization and humification processes [53]. The genera were further explored, and the results showed that the core fungal OTUs were highly associated with *Paenibacillus*, *Saccharomonospora*, *Bacillus*, *Thermobifida*, and *Oceanobacillus* (Table S4). As previously described, *Bacillus, Thermobifida*, and *Peanibacillus* are genera associated with the degradation of OM [20]. In addition, *Saccharomonospora* and *Oceanobacillus* were identified as functional species in the maturity period [54] on account of their ability to hydrolyze phenolic compounds into nontoxic forms [41]. Accordingly, our research implied that the cooperation between key fungal species and functional bacteria could promote the composting process. Fungi can secrete a wide variety of extracellular enzymes and produce water-soluble polysaccharides as well as phenolic compounds [55]. All these compounds serve as major carbon and energy sources for both fungi and bacteria. The extracellular slime secreted by bacteria could be utilized as sugar storage for fungi [56]. These results implied that the fungal community had the potential to strengthen both domain and interdomain microbial cooperation to promote the degradation of OM. The aim to culture and regulate thousands of species in composting is not feasible; therefore, focusing on these core fungal species might be a reasonable strategy for managing and enhancing the composting process. Although this study hinted at the importance of core fungal species, further research based on metatranscriptomics and metaproteomics could be explored to confirm it.

4. Conclusions

Our research revealed the links between fungal cooperation and OM degradation in ten local rural household FW composting piles. Positive cohesion could promote the degradation of OM, which was modified by pH value, moisture content, C/N ratio, and microbial community. *Candida tropicalis*, *Issatchenkia orientails*, *Kazachstania exigua*, and *Dipodascus australiensis* were identified as the core species with high relative abundance and occurrence frequency. These species could strengthen both domain and interdomain microbial cooperation. Specifically, these core fungal species were positively correlated with the genera linked to the degradation of OM in both the fungal and bacterial domains. In conclusion, the relative abundance of core species was fundamental for maintaining high microbial cooperation and the functional potential of OM degradation.

Declaration of interests

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.

Acknowledgments

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ese.2022.100190.

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Abbreviations

OM: organic matter
FW: food waste
DM: dry matter
MC: moisture content
GI: germination index
RMT: random matrix theory
OTUs: operational taxonomic units
SEM: structural equation model
VPA: variance partitioning analysis
RFM: random forest model
avgCC: average clustering coefficient
GD: average path distance
M: modularity
avgK: average degree