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A Fungi-Driven Sustainable Circular Model Restores Saline Coastal Soils and Boosts Farm Returns

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Abstract

Agricultural production in the saline–alkaline soils of the Yellow River Delta faces persistent challenges in waste recycling and soil improvement. We developed a three-stage circular agriculture model integrating "crop straw–edible mushrooms–vegetables," enabling simultaneous waste utilization and soil remediation within one year (two mushroom and two vegetable cycles annually). Crop straw was first used to cultivate *Pleurotus eryngii*, achieving 80% biological efficiency and reducing substrate costs by ~36.3%. The spent mushroom substrate (SMS) was then reused for *Ganoderma lucidum* and vegetable cultivation, maximizing the resource efficiency. SMS application significantly improved soil properties: organic matter increased 11-fold (from 14.8 to 162.78 g/kg) and pH decreased from 8.34 to ~6.75. The available phosphorus and potassium contents increased several-fold compared to untreated soil. Metagenomic analysis showed the enrichment of beneficial decomposer bacteria (*Hyphomicrobiales*, *Burkholderiales*, and *Streptomyces*) and functional genes involved in glyoxylate metabolism, nitrogen cycling, and lignocellulose degradation. These changes shifted the microbial community from a stress-tolerant to a nutrient-cycling profile. The vegetable yield and quality improved markedly: cabbage and cauliflower yields increased by 34–38%, and the tomato lycopene content rose by 179%. Economically, the system generated 1,695,000–1,962,881.4 CNY per hectare annually and reduced fertilizer costs by ~450,000 CNY per hectare. This mushroom–vegetable rotation addresses ecological bottlenecks in saline–alkaline lands through lignin-driven carbon release, organic acid-mediated pH reduction, and actinomycete-dominated decomposition, offering a sustainable agricultural strategy for coastal regions.

Keywords: circular agriculture; edible fungi; saline–alkaline soil; spent mushroom substrate; microbial community; economic benefits

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1. Introduction

Land degradation represents a global ecological challenge, with soil salinization as one of its primary manifestations. Soil salinization inhibits plant growth, reduces crop yields, deteriorates the soil and water quality, and severely constrains socioeconomic development [1,2]. Current remediation strategies for saline–alkaline soils include biological

approaches such as breeding salt-tolerant crop varieties [3], chemical methods involving soil amendments [4,5], microbial inoculants [6], and physical-engineering measures like hydrological management [7]. While these methods may temporarily improve soil conditions, they often increase agricultural inputs and operational costs, potentially creating additional environmental pressures, limiting their widespread adoption [8]. Thus, developing novel remediation techniques that integrate agricultural productivity and environmental restoration through resource recycling, thereby breaking the vicious cycle of "remediation and re-salinization," is a critical challenge for sustainable saline soil management [9].

The Yellow River Delta, China's largest eastern coastal saline–alkaline area, comprises approximately 240,000 hectares of saline soil, accounting for about half of the region's total land area [10]. Although tasked with significant national grain and cotton production responsibilities, crop yields under traditional management remain low due to severe soil salinization; many coastal farmlands produce less than 1500 kg per hectare, markedly below yields of non-saline areas [11]. Currently, a widespread corn–wheat rotation system generates substantial agricultural residues annually. For instance, in 2019, corn production in the Yellow River Delta reached 3.97 million tons [12], generating large quantities of straw that often remain unused or are openly burned. Although straw incorporation into soil is effective in mitigating salinity, its practical implementation is limited by the soil conditions, straw quality, and agronomic requirements [13]. Therefore, there is an urgent need for circular strategies that effectively transform agricultural waste locally, facilitating ecological restoration alongside economic value generation.

The edible mushroom industry is pivotal within modern ecological agriculture due to its short cultivation cycle, low input requirement, and high output, effectively serving as a central node facilitating material and energy recycling within agricultural ecosystems. Studies have demonstrated that substituting traditional sawdust with crop straw as a substrate for cultivating *Pleurotus eryngii* can reduce cultivation costs by over 40% [14]. Spent mushroom substrate (SMS), produced from *P. eryngii* cultivation, represents a sustainable bio-organic fertilizer, significantly improving the soil organic matter content, fertility, and structure when returned to fields [15]. Additionally, SMS reuse can realize dual harvests from a single input, substantially enhancing the resource efficiency [16]. Thus, a circular agricultural chain incorporating "crop straw–edible mushrooms–organic fertilizer–crops" exhibits considerable potential in saline–alkaline agriculture. However, comprehensive circular agricultural models centered on edible mushrooms remain scarce. For example, Ye et al. established a model using reed straw to cultivate *P. eryngii* and oyster mushrooms, composting the resulting SMS and evaluating the economic benefits [17]. Similarly, Li et al. proposed a reed–mushroom–organic fertilizer chain, enhancing ecological functions in saline wetlands [18]. Still, systematic circular agricultural models centered on edible mushrooms, specifically tailored for coastal saline–alkaline areas like the Yellow River Delta, including ecological–economic impact evaluations, are lacking.

Numerous studies indicate that soil salinization profoundly alters the soil microbial community structure and function, markedly reducing diversity [19–21]. Current research on soil microbes in the Yellow River Delta focuses primarily on how salinity stress impacts the microbial community composition and function [21–23] and specific beneficial plant-associated microbes under saline conditions [24,25]. To date, few studies have systematically investigated concurrent changes in soil properties, microbial communities, and economic benefits within integrated circular agricultural systems, or elucidated the underlying microbial functional mechanisms during remediation.

In response, this study developed and validated a novel three-stage circular agricultural model ("crop straw–edible mushrooms–vegetables") in the saline–alkaline soils of the Yellow River Delta. Specifically, this model aimed to achieve ecological restoration and

agricultural productivity enhancement by: (1) implementing an annual crop rotation comprising two mushroom cycles (factory-scale cultivation of *P. eryngii* using straw substrates) followed sequentially by *Ganoderma lucidum* cultivation, vegetable planting, and inducing secondary mushroom flushes from *P. eryngii* to maximize resource utilization; (2) improving the soil quality through SMS incorporation and crop rotation, thereby modulating soil microbial functional networks and mitigating salt accumulation; and (3) conducting comprehensive ecological–economic evaluations across the entire agricultural chain, combining field trial data and metagenomic analyses to quantify synergistic short-term agricultural outputs and long-term soil restoration effects. Through cultivation experiments and metagenomic sequencing, we illustrate the cost advantages and scalability potential of this circular approach compared to traditional saline soil remediation methods, providing theoretical foundations and practical solutions for green transformation in coastal saline agricultural areas.

2. Materials and Methods

2.1. Experimental Site and Materials

The experiment was conducted from April 2019 to November 2021 at the Yellow River Delta Modern Agricultural Experimental Demonstration Base, Shandong Academy of Agricultural Sciences. Strains of *P. eryngii* and *G. lucidum* used in the experiment were provided by Shandong Academy of Agricultural Sciences (Jinan, China). Vegetable crops including cauliflower, cabbage, celery, and tomato were cultivated with seeds provided by the experimental base. Wheat straw, sorghum straw, maize straw, and peanut shells used as cultivation substrates were all collected from the experimental base.

2.2. Experimental Design

A three-stage circular planting model was established, including factory cultivation of *P. eryngii*, cultivation of *G. lucidum* using *P. eryngii* spent substrate and its secondary fruiting, vegetable cultivation using *G. lucidum* spent substrate returned to the field, and secondary fruiting of *P. eryngii* from waste mushroom sticks. Initially, *P. eryngii* was grown industrially on straw-based substrates and harvested upon maturity. Subsequently, *P. eryngii* SMS was reused for *G. lucidum* cultivation in saline–alkaline greenhouses (April–May), with the first harvest in July–August. Residual substrates were then managed in situ for a second *G. lucidum* harvest (August–October). After mushroom cropping, all *G. lucidum* SMS was incorporated into soil as organic amendment for vegetable planting (celery, cauliflower, and cabbage), harvested the following January. Additionally, unused *P. eryngii* substrates from the factory were buried in fields to induce secondary fruiting, harvested in March. Alternatively, *P. eryngii* SMS was buried in October after factory harvest, with second fruiting in December and SMS reused for tomato planting, harvested the next March (Figure 1). These systems enabled annual rotation of two mushroom and two vegetable cycles, adaptable to seasonal changes. Initial soil characteristics (pH, organic matter, and salinity) of rotation and control plots were measured to ensure comparability.

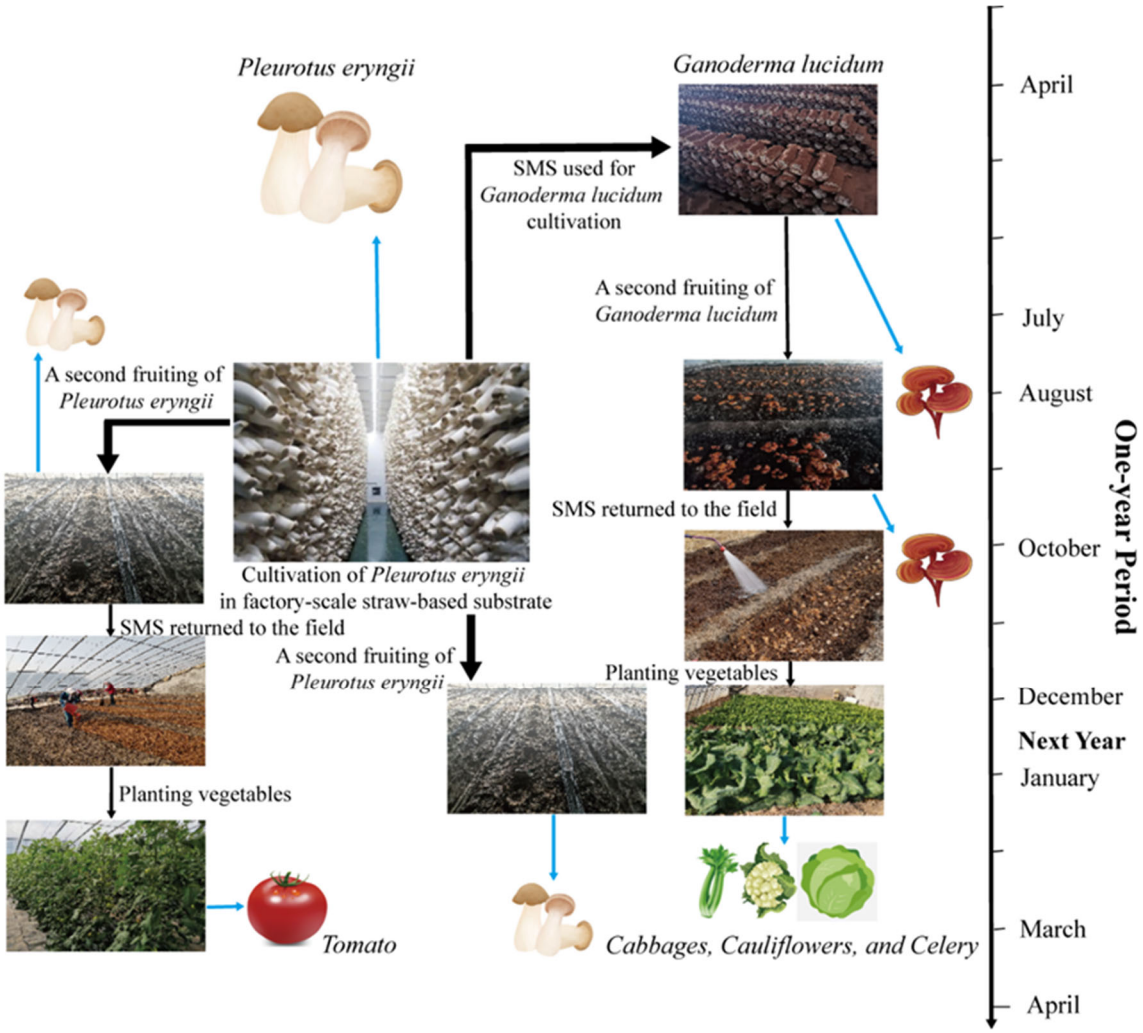


Figure 1. Schematic diagram of a sustainable one-year crop rotation system integrating *Pleurotus eryngii*, *Ganoderma lucidum*, and various vegetables.

2.3. Mushroom Cultivation

P. eryngii was cultivated under factory conditions. The original cultivation substrate consisted of 38% cotton seed hulls, 38% sawdust, 18% wheat bran, 4% corn flour, 1% lime, and 1% gypsum. In the improved formulation, sawdust was replaced with straw. The new substrate was composed of 50% shredded and sterilized mixed straw (a 1:1:1:1 mixture of wheat, corn, and sorghum straw and peanut shells), combined with 26% cottonseed hulls, 18% wheat bran, 4% corn flour, 1% lime, and 1% gypsum. The moisture content was adjusted to 60–65%.

The original cultivation substrate for *G. lucidum* consisted of 45% cottonseed hulls, 44% sawdust, 10% wheat bran, and 1% gypsum. In the modified formulation, 45% *P. eryngii* spent substrate was used to replace an equal proportion of sawdust, combined with 44% cottonseed hulls, 10% wheat bran, and 1% gypsum. Each cultivation bag was filled with 400 g of dry substrate.

Following the first *G. lucidum* harvest, a secondary crop was induced by applying a soil-covering method, arranging substrate bags in double rows with their bottoms outward. Secondary fruiting of *P. eryngii* was achieved by burying discarded mushroom sticks from factory production in the soil during a suitable season, followed by soil coverage and moisture retention to induce fruiting.

2.4. Raw Material Composition Analysis

The cultivation substrate materials (wheat, sorghum, and maize straw and peanut shells) were air-dried, ground, and sieved through a 100-mesh screen. Cellulose, hemicellulose, and lignin contents were analyzed via the Van Soest method [26]. Crude protein, fat, ash, and moisture were measured following the national food safety standard (GB 5009.5-2016) [27], with carbohydrate content calculated by difference. Total carbon and nitrogen were determined using an elemental analyzer to calculate the C/N ratio. Total polysaccharides were quantified by the phenol–sulfuric acid method [28], while total triterpenes and phytosterols were measured by the vanillin–glacial acetic acid–perchloric acid colorimetric method [29]. Alkaloids were determined by LC-MS (GB/T 38571-2020) [30]. Trace elements including iron (GB 5009.90-2016) [31] and selenium (GB 5009.93-2017) [32] were detected via atomic fluorescence spectrometry. Vitamin C was determined using the extraction–colorimetric method (GB 5009.86-2016) [33]. Moisture and dry matter were measured by direct drying (GB 5009.3-2016) [34], and crude fiber by the sulfuric acid–potassium hydroxide method (GB/T 5009.10-2003) [35]. Soluble solids were measured by refractometry (NY/T 2637-2014) [36], titratable acidity by NaOH titration, and soluble sugars by the phenol–sulfuric acid method [37]. Lycopene in tomatoes was quantified by UPLC (GB/T 41133-2022) [38]. Soil analysis included available nitrogen by alkaline hydrolysis diffusion, phosphorus by bicarbonate extraction and molybdenum-antimony colorimetry, potassium by ammonium acetate extraction with flame atomic absorption spectrometry, organic matter via potassium dichromate oxidation, and pH by pH meter (FE28-Standard, METTLER TOLEDO, Columbus, OH, USA).

2.5. Vegetables Growth and Yield

At harvest, vegetable growth and yield traits were measured based on sampling at three points per plot. At each point, 10 plants were randomly collected. The measured indicators included plant canopy spread, plant height, horizontal and vertical diameter of the head (if applicable), and number of outer leaves. Based on these data, the average gross and net weight per plant were calculated. Yield per hectare was estimated using the formula:

$$\text{Yield} = \text{Net weight per plant} \times \text{Planting density} \times 0.9$$

where 0.9 is a shrinkage coefficient accounting for post-harvest loss.

In the rotation plots, the plant spacing was 40 cm × 70 cm for cauliflower, 40 cm × 40 cm for cabbage, and 18 cm × 20 cm for celery. In the control plots, the plant spacing for cauliflower, cabbage and celery remained the same as in the rotation plots.

2.6. DNA Extraction and Metagenomic Analysis

Soil samples were collected from rotation plots and non-rotation controls (monoculture vegetable plots and untreated saline–alkaline soil) at two depths (0–20 cm and 20–40 cm), totaling 30 samples (Supplementary Materials Table S1). Microbial genomic DNA was extracted using the QIAamp Fast DNA Extraction Kit (Qiagen, Hilden, Germany). Short insert libraries (insert size 300 bp) were constructed and sequenced on the Illumina (Illumina Inc., San Diego, CA, USA) NovaSeq 6000 platform (150 bp × 2 PE reads). Raw reads were processed to cut adaptor sequences and to remove low-quality reads by using fastp version 0.23.4 [39]. Clean reads were assembled by using MEGAHIT version 1.2.9 [40]. Open reading frames were predicted by using Prodigal version 2.6.3 [41]. A non-redundant gene set was constructed by using MMseqs2 version 13.45111 [42] (identity cutoff 95% and coverage cutoff 90%). Gene abundance was quantified by mapping clean reads to the gene set by using BBMap version 38.93. Microbial composition and function were analyzed using tools including Krona, pathway enrichment, and CAZy family analysis.

Experimental data were analyzed in R software (version 4.2.2, R Foundation for Statistical Computing, Vienna, Austria). ANOVA or Kruskal–Wallis tests which assessed differences in crop yield, soil properties, and gene abundance ($p < 0.05$). PCoA and NMDS visualized microbial functional differences, and LEfSe identified significantly enriched taxa and genes. Economic benefits were evaluated using an input–output accounting model.

2.7. Economic Value

The economic value was assessed based on reduced substrate costs, mushroom and vegetable sales revenue, and fertilizer savings from SMS application.

2.7.1. Reduction in Substrate Cost and Sales Revenue of *P. eryngii*

The prices of raw materials for mushroom cultivation substrates were as follows: wheat straw (0.37 CNY/kg), sorghum straw (0.25 CNY/kg), corn straw (0.28 CNY/kg), peanut shells (0.50 CNY/kg), cottonseed hulls (2.40 CNY/kg), and sawdust (0.90 CNY/kg). The average price of straw materials was calculated as:

Average straw price = (0.37 + 0.25 + 0.28 + 0.50)/4 = 0.35 CNY/kg.

Each cultivation bag contained 562.5 g of dry substrate (based on a moisture content of 62.5%). Economic calculations were based on a scale of 10,000 cultivation bags.

Total straw consumption in modified formula = 10,000 bags × (0.5625 kg/bag × 50%) = 2812.5 kg.

Substrate cost of original formula = 10,000 × [(0.5625 kg × 38% × 2.4 CNY/kg) + (0.5625 kg × 38% × 0.9 CNY/kg)].

Substrate cost of modified formula = 10,000 × (0.5625 kg × 50% × 0.35 CNY/kg).

Cost savings from substrate modification = original cost − modified cost = 2560 CNY.

Sales revenue from factory-cultivated *P. eryngii* = average fresh yield per bag × 10,000 bags × 15.51 CNY/kg.

2.7.2. Sales Revenue of *G. lucidum* Grown on *P. eryngii* SMS

The sales revenue of *G. lucidum* grown on *P. eryngii* SMS was estimated based on a cultivation scale of 10,000 bags. Each cultivation bag contained 0.4 kg of dry substrate, with the modified formulation consisting of 45% *P. eryngii* SMS. Therefore, the total amount of SMS used was

Total SMS consumed = 10,000 bags × (0.4 kg × 45%) = 1800 kg.

By replacing cottonseed hulls (2.40 CNY/kg) with SMS (0.28 CNY/kg), the substrate cost savings amounted to: Cost savings = 1800 kg × (2.4 − 0.28) CNY/kg = 3816 CNY.

The market price of fresh *G. lucidum* fruiting bodies was 23.85 CNY/kg. Assuming a conversion rate of 2% from fresh fruiting bodies to spore powder, and a spore powder market price of 400 CNY/kg, the total sales revenue was calculated as:

Fruiting body revenue = 10,000 × average fresh weight per bag × 23.85 CNY/kg.

Spore powder sales revenue = 10,000 × average fresh weight per bag × 2% × 400 CNY/kg.

Total *G. lucidum* sales revenue = Fruiting body revenue + Spore powder revenue.

2.7.3. Secondary Fruiting of *G. lucidum* and *P. eryngii*

The economic output from the secondary fruiting of *G. lucidum* and *P. eryngii* was estimated based on standard cultivation densities.

For *G. lucidum*, assuming a planting density of 150,000 cultivation bags per hectare, the income was calculated as follows:

Fruiting body revenue = yield per spent substrate stick × 150,000 × 23.85 CNY/kg.

Spore powder revenue = yield per spent substrate stick × 150,000 × 400 CNY/kg × 2%.

For *P. eryngii*, assuming a planting density of 270,000 cultivation bags per hectare, the total yield and corresponding revenue were calculated as:

Total yield = 270,000 bags × average yield per spent substrate stick.

Sales revenue = total yield × 15.51 CNY/kg.

2.7.4. Increased Yield and Income from Leafy Vegetables and Tomato

The economic benefits from increased yields of leafy vegetables and tomato were estimated based on yield improvements and market prices. For leafy vegetables, the total revenue per hectare was calculated as follows:

Total vegetable yield income = total vegetable yield per hectare × market price ÷ 3.

Increased revenue from yield improvement = (yield after SMS application − original yield) × market price ÷ 3.

This one-third factor accounts for the allocation of land or production cycles among three vegetable types. Market prices used in the calculations were as follows: cauliflower, 7.00 CNY/kg; cabbage, 1.46 CNY/kg; celery, 2.62 CNY/kg; and tomato, 8.00 CNY/kg.

For tomato, the total sales revenue was calculated as follows:

Tomato revenue = tomato yield per hectare × 8.00 CNY/kg.

In addition, the cost of chemical fertilizer was estimated at 22,500 CNY per hectare and fertilizer savings due to SMS application were considered in the total economic assessment.

2.7.5. Integrated per Hectare Income from the Circular System

The annual total output value per hectare was calculated as the sum of revenues from all production components in the circular mushroom–vegetable system:

Total output value per hectare = *P. eryngii* secondary fruiting income + *G. lucidum* fruiting body income + *G. lucidum* spore powder income + total vegetable income.

2.8. Statistical Analysis

All data were analyzed using SPSS Statistics 26.0 (IBM Corp., Armonk, NY, USA) for statistical tests. Results are presented as mean ± standard deviation (SD) based on three biological replicates (n = 3), unless otherwise specified. Differences among multiple groups were assessed using one-way analysis of variance (ANOVA) followed by Tukey's HSD test for multiple comparisons, with a significance threshold of $p < 0.05$. Independent-sample t-tests were used to compare treatment groups with their respective control groups for each parameter. Significance levels were denoted as: ns ($p \geq 0.05$), * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$).

3. Results

3.1. Mushroom Cultivation and Substrate Generation

3.1.1. Straw-Based Cultivation of *P. eryngii*

The lignocellulose content (cellulose, hemicellulose, and lignin) in agricultural and forestry residues was measured to assess their potential as carbon sources for *P. eryngii*. In this study, the total lignocellulose contents of wheat straw, sorghum straw, corn straw, and peanut shells were approximately 35.8%, 49.8%, 52.6%, and 52.9%, respectively (Table 1). Corn straw had the highest cellulose and hemicellulose contents (33.58% ± 0.78 and 12.97% ± 0.26, respectively), while peanut shells exhibited a high lignin content (32.71% ± 1.97), exceeding that of commonly used substrates such as cottonseed hulls (26.97%) and poplar sawdust (28.79%) [17].

Table 1. Composition analysis of different straw contents.

Raw Materials	Component Measurement of the Raw Materials								
	Moisture g/100 g (H_2O)	Ash g/100 g	Total Nitrogen g/100 g (N)	The Carbohydrate g/100 g	Cellulose g/100 g	Lignin %	Hemicellulose g/100 g	C/N %	pH
wheat straw	4.13 ± 0.17 d	5.80 ± 0.20 d	1.33 ± 0.06 b	83.49 ± 3.68 a	20.95 ± 1.16 c	5.28 ± 0.22 d	8.57 ± 0.52 c	36.30 ± 1.64 d	7.24 ± 0.27 a
sorghum straw	5.31 ± 0.16 b	6.27 ± 0.27 b	1.18 ± 0.07 c	79.62 ± 2.03 c	31.63 ± 2.89 b	5.64 ± 0.05 c	12.66 ± 0.32 b	68.38 ± 2.67 b	6.08 ± 0.36 d
corn straw	5.05 ± 0.28 c	7.07 ± 0.14 a	0.75 ± 0.08 d	83.11 ± 2.46 b	33.58 ± 0.78 a	6.71 ± 0.21 b	12.97 ± 0.26 a	98.08 ± 6.21 a	7.23 ± 0.48 b
peanut shell	7.14 ± 0.11 a	6.20 ± 0.47 c	4.47 ± 0.03 a	55.30 ± 0.77 d	11.47 ± 0.13 d	32.71 ± 1.97 a	8.14 ± 0.02 d	54.19 ± 3.25 c	6.37 ± 0.08 c

Note: mean ± SD (n = 3). Different lowercase letters in the same row indicate significant differences (ANOVA, $p < 0.05$).

To optimize the cultivation substrate for *P. eryngii*, sawdust in conventional substrates was replaced with an equal-proportion mixture of four types of straw, increasing the total straw content to 50% and reducing the cottonseed hull content from 38% to 26%. The modified substrate exhibited a carbon-to-nitrogen ratio (C/N) ranging from 36 to 101. The average fresh yield of *P. eryngii* was approximately 450 g per cultivation bag under this substrate formulation, with a biological efficiency (BE) of 80%, calculated using a dry substrate weight of 562.5 g (moisture content: 62.5%).

3.1.2. *G. lucidum* Cultivation and Secondary Fruiting

SMS from factory cultivation of *P. eryngii* was repurposed as a substrate for *G. lucidum* cultivation. The experiment was conducted in spring using bag cultivation in greenhouses. *G. lucidum* was inoculated in April, with full mycelial colonization achieved by May. Fruiting body formation began approximately 30 days later, and the first flush was harvested in early August. Under a dry substrate weight of 400 g per bag, the average fresh weight of *G. lucidum* per cultivation bag was approximately 104.15 g. The biological efficiency (BE) was calculated as 26.04% using the formula: (104.15 g/400 g) × 100%.

After harvesting the first flush, cultivation bags were opened in place, covered with soil, and kept moist to induce a second fruiting. The bags were arranged bottom-side outward in a stacked structure and fully covered with soil. Mycelial regrowth occurred within 10–15 days, and pinhead primordia emerged from soil cracks after 9–12 days of management. Fruiting bodies matured asynchronously, allowing batch harvesting over a one-month period. The second fruiting was completed by October. With 150,000 cultivation bags per hectare, the average fresh yield reached approximately 200 g per bag. This approach enabled two harvests per substrate cycle, with all spent substrate retained in the field.

3.2. Vegetable Yield and Quality Enhancement

3.2.1. Increased Leafy Vegetable Yield

Vegetables grown in saline–alkaline soils amended with SMS showed significant yield increases, particularly cabbage and cauliflower. Cabbage plants in the experimental group had a significantly greater height and net weight per plant than the controls, with an average yield of 71,460 kg per hectare—a 38% increase (Table 2). Cabbage heads were also more compact with improved formation, indicating notable quality enhancements (Figure 2). Cauliflower showed similar responses, with increases in the height, leaf number, and net weight. Its average yield reached 39,231.6 kg per hectare, nearly doubling that of

the control (20,892.9 kg/ha) (Table 2). For celery, the yield increase was modest at 0.3%, but plants developed stronger roots and thicker stems, suggesting SMS promoted root growth. With an extended harvest period, the total yield may increase further (Figure 2). The yield responses varied by crop type, with cruciferous vegetables showing the strongest gains, likely due to improved soil fertility and physicochemical properties. In addition to the yield and appearance, these findings underscore the crop production benefits of the circular cultivation model.

Table 2. Comparison of plant growth parameters and yield of cabbages, cauliflowers, and celery grown in mushroom residue-amended soil versus short-season vegetables in alternative greenhouses.

	Plant Canopy Spread (cm)	Plant Height (cm)	Horizontal Diameter of the Head (cm)	Vertical Diameter of the Head (cm)	Number of Outer Leaves	Average Net Weight (kg)	Yield Per Hectare (kg)	*t*-Value	*p*-Value	Significance
Cauliflower	109.55 ± 4.41	80.23 ± 3.50	18.89 ± 0.56	21.33 ± 1.01	22.91 ± 1.51	1.22 ± 0.072	39,231.6 ± 2314.29	23.64	<0.0001	***
Cauliflower (CK)	97.22 ± 2.88	73.0 ± 2.75	10.67 ± 0.43	18.33 ± 0.91	19.23 ± 1.21	0.65 ± 0.03	20,892.9 ± 964.29			
Cabbage	55.87 ± 7.18	47.8 ± 3.98	18.23 ± 0.85	20.03 ± 1.00	10.4 ± 0.50	1.27 ± 0.06	71,460.3 ± 3375.0	9.99	0.0027	**
Cabbage (CK)	46.31 ± 2.02	37.7 ± 1.31	15.5 ± 0.31	17.8 ± 0.42	9.62 ± 1.51	0.92 ± 0.05	51,766.5 ± 2812.5			
Celery	-	77.39 ± 0.82	-	-	12.27 ± 0.67	0.394 ± 0.02	98,545.1 ± 5000	−0.89	0.4376	ns
Celery (CK)	-	75.5 ± 3.75	-	-	9 ± 0.53	0.393 ± 0.02	98.295.0 ± 5000			

Note: Data are presented as mean ± SD (n = 3). t- and p-values were calculated by independent-sample t-test comparing yield per hectare between the treatment and control (CK) groups. Significance levels: ns, not significant ($p > 0.05$); ** $p < 0.01$; *** $p < 0.001$.

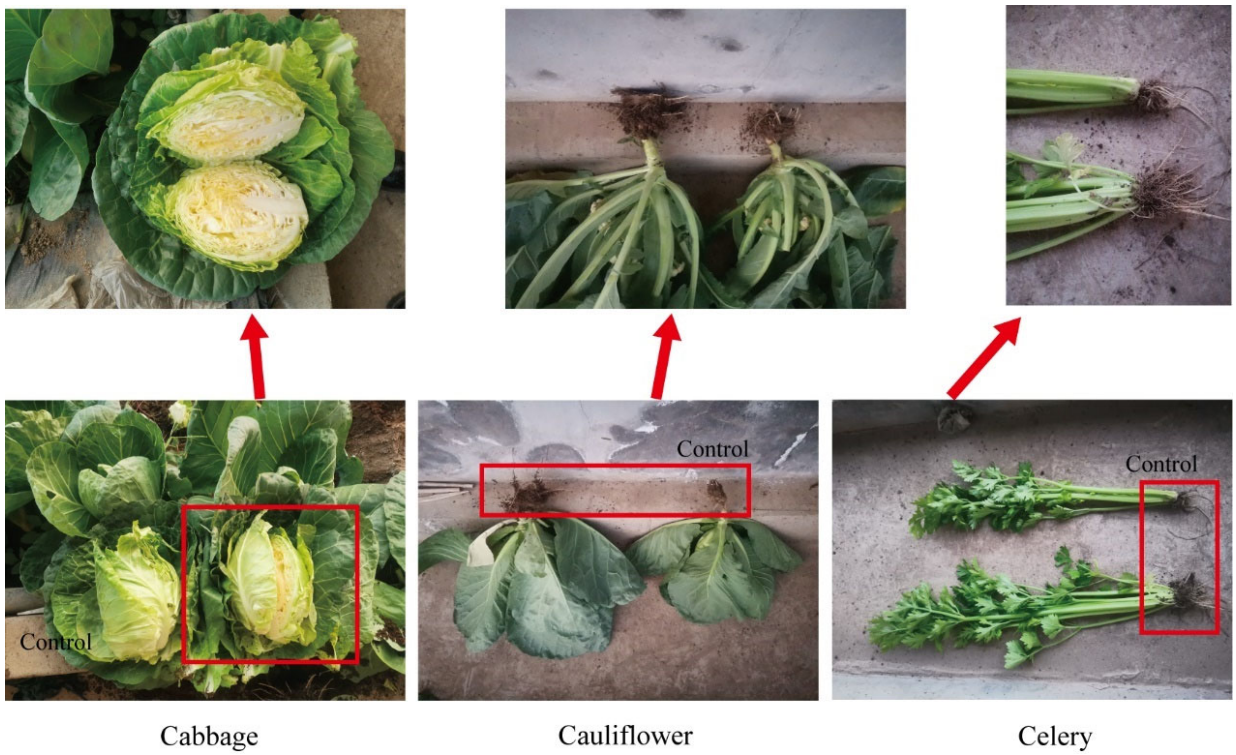


Figure 2. Comparison of the quality of cabbage, cauliflower, and celery grown in mushroom residue-amended soil versus short-season vegetables cultivated in conventional greenhouses.

SMS application also enhanced nutrient accumulation in vegetables, as reflected by higher protein, soluble sugar, and mineral (iron and potassium) levels (Table 3). Cauliflower

protein increased by 21% (p = 0.089), soluble sugars by 29.1% (p = 0.028); cabbage and celery's soluble total sugar increased by 11.6% (p = 0.074) and 80.8% (p = 0.003), respectively. These enhancements suggested that the SMS likely provided ample nitrogen and nutrients, promoting metabolite synthesis and nutritional quality. The dry matter content increased across all vegetables, notably in cauliflower (+15.2%, p = 0.044) and celery (+20.8%, p = 0.048) (Table 3), indicating the enhanced synthesis of biomass compounds like cellulose and starch. The SMS also improved the water retention and nutrient uptake. The iron (Fe) content increased by 136.2% in cauliflower ($p < 0.001$), 39.1% in cabbage (p = 0.007), and 28.7% in celery (p = 0.017), highlighting the role of SMS in improving the soil conditions and enhancing the plant mineral uptake efficiency.

Table 3. Nutrient composition of cabbages, cauliflowers, and celery grown in mushroom residue-amended soil versus control plots in short-season greenhouses.

	Cauliflower	Cauliflower (CK)	*p*-Value	Signifigance	Cabbage	Cabbage (CK)	*p*-Value	Signifigance	Celery	Celery (CK)	*p*-Value	Signifigance
Crude protein, g/100 g	1.67 ± 0.08	1.38 ± 0.03	0.0089	**	1.26 ± 0.04	1.16 ± 0.05	0.052	ns	0.90 ± 0.01	0.93 ± 0.02	0.2412	ns
Vitamin C, mg/100 g	38.0 ± 1.7	39.7 ± 0.49	0.469	ns	35.5 ± 1.36	35.1 ±1.19	0.525	ns	1.36 ± 0.07	2.00 ± 0.02	0.031	*
Moisture, %	92.4 ± 1.71	93.4 ± 4.04	0.312	ns	93.3 ± 1.62	93.7 ± 1.62	0.657	ns	94.2 ± 2.92	95.2 ± 2.11	0.331	ns
Dry matter, %	7.6 ± 0.16	6.6 ± 0.18	0.021	*	6.7 ± 0.1	6.3 ± 0.22	0.288	ns	5.8 ± 0.14	4.8 ± 0.1	0.008	**
Crude fiber, %	1.0 ± 0.04	0.9 ± 0.01	0.044	*	0.6 ± 0.02	0.6 ± 0.01	0.864	ns	0.7 ± 0.01	0.6 ± 0.02	0.048	*
Soluble total sugar, %	2.75 ± 0.05	2.13 ± 0.07	0.028	*	3.17 ± 0.15	2.84 ± 0.04	0.074	ns	0.94 ± 0.04	0.52 ± 0.03	0.003	**
Fe, mg/kg	7.30 ± 0.1	3.09 ± 0.07	<0.001	***	3.84 ± 0.11	2.76 ± 0.1	0.007	**	9.35 ± 0.28	7.26 ± 0.11	0.017	*
Ca, mg/kg	215 ± 9.97	2052± 2.33	0.341	ns	366 ± 13.36	363 ± 7.39	0.839	ns	845 ± 26.01	1062 ± 23.86	0.001	**
K, mg/kg	327 ± 5.69	261 ± 8.32	0.025	*	217 ± 8.9	188 ± 9.17	0.052	ns	355 ± 16.26	305 ± 14.51	0.2412	ns
Mg, mg/kg	146 ± 6.84	126 ± 4.27	0.057	**	140 ± 2.5	142 ± 1.92	0.694	ns	186 ± 3.34	183 ± 2.16	0.25	ns
Zinc, mg/kg	2.80 ± 0.01	2.09 ± 0.05	0.014	ns	1.31 ± 0.03	1.28 ± 0.06	0.409	ns	1.42 ± 0.05	1.00 ± 0.02	0.043	*

Note: Data are presented as mean ± SD (n = 3) for each treatment group. Statistical differences between rotation and control (CK) treatments were assessed using independent-sample t-tests (n = 3). Significance levels: ns (not significant), $p \geq 0.05$; $p < 0.05$ (*); $p < 0.01$ (**); $p < 0.001$ (***).

3.2.2. Improved Tomato Quality

In early spring of the following year, tomatoes were cultivated on SMS-amended saline–alkaline soil, with untreated saline–alkaline soil and traditional manure-amended soil as the controls. Plants grown in SMS-treated plots exhibited vigorous growth, higher fruit set rates, and visibly improved fruit quality compared to the controls.

Tomatoes from SMS-treated soil had soluble sugar and titratable acid contents of 0.23% and 0.29%, respectively, resulting in a sugar-to-acid ratio of 4.16. This was significantly higher than that of the saline–alkaline soil control (2.76) (p = 0.0004) and manure-treated soil (3.12) (Table 4). A higher sugar-to-acid ratio enhances the tomato flavor by achieving a better balance of sweetness and acidity, improving the commercial quality.

Notably, the lycopene content in tomatoes from SMS-treated soil reached 539.37 mg/kg, representing a 179% increase compared to the saline–alkaline soil control (193.28 mg/kg, $p < 0.0001$) and a 39.25% increase over manure-treated soil (387.35 mg/kg). As lycopene is a key determinant of the tomato color and antioxidant nutritional value, its significant increase suggests that the SMS amendment effectively promotes nutrient accumulation, enhancing both the product quality and market value [43].

Table 4. Tomato quality traits under control, cow dung, and mushroom residue treatments.

	Soluble Solid Content, %	Titrable Acid (Measured in Malic Acid), %	Soluble Sugar, %	Sugar-Acid Ratio	Lycopene, mg/kg
Tomato (CK)	4.45 ± 0.11 a	0.2 ± 0.02 a	0.13 ± 0.01 b	2.76 ± 0.11 a	193.28 ± 9.17 a
Tomato (cow dung)	4.72 ± 0.23 a	0.23 ± 0.02 a	0.04 ± 0 a	3.12 ± 0.02 b	387.35 ± 7.14 b
Tomato (SMS treatment)	4.9 ± 0.19 b	0.29 ± 0.02 b	0.23 ± 0.01 c	4.16 ± 0.12 c	539.37 ± 8.37 c
p-value	0.0074	0.0061	0.0001	0.0004	<0.0001
Significance	**	**	***	***	***

Note: Data are presented as mean ± SD (n = 3). Different lowercase letters within the same column indicate significant differences among treatments based on Tukey's HSD test ($p < 0.05$). p-values and significance levels refer to independent-sample t-tests comparing the SMS treatment and CK group for each parameter. Significance levels: ** ($p < 0.01$); *** ($p < 0.001$).

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3.3. Improved Soil Physicochemical Properties

This study evaluated the physicochemical properties of six soil types: slightly saline–alkaline soil, heavily saline–alkaline soil, conventional greenhouse substrate soil, cow manure-amended soil, SMS soil (SMS applied without crop planting), and post-cropped SMS-amended soil (after vegetable cultivation) (Table 5). SMS soil exhibited superior properties, with available phosphorus reaching 669.93 mg/kg—1.47 times higher than cow manure-amended soil (456.83 mg/kg, $p = 0.0003$) and conventional substrate soil (454.85 mg/kg, $p = 0.0003$) and 21–31 times higher than untreated saline–alkaline soils (31.52 mg/kg and 22.17 mg/kg)—meeting the phosphorus demands for fruiting crops while reducing fertilizer application. Available potassium reached 1402.5 mg/kg, the highest among treatments, approximately 8.8–13.1 times higher than in untreated saline–alkaline soil (159 mg/kg and 107 mg/kg, $p < 0.0001$), supporting tuber enlargement and enhancing stress tolerance. The total nitrogen content (248.85 mg/kg) was comparable to conventional substrate soil (271.36 mg/kg) and significantly higher than saline–alkaline soils (73.5–213.2 mg/kg), ensuring a balanced nitrogen supply without excessive vegetative growth. The SMS soil pH (7.66) was within the optimal range (6.0–7.5) and significantly lower than heavily saline–alkaline soil (≈8.3), improving the micronutrient availability. The electrical conductivity (EC) was 1789 μS/cm, 53% lower than heavily saline–alkaline soil (3840 μS/cm, $p = 0.0007$), reducing the salinity stress risk. The organic matter content (16.55 g/kg) met the threshold for cultivated substrates (>15 g/kg, $p = 0.0132$).

After a single vegetable-growing season, post-cropped SMS-amended soil exhibited significant changes compared to SMS soil. Hydrolytic nitrogen decreased from 248.85 mg/kg to 100.98 mg/kg (a 59.4% reduction, $p < 0.0001$), indicating a strong nitrogen uptake by crops and suggesting that SMS alone may not fully sustain the crop nitrogen demands throughout the growth cycle, necessitating supplementary fertilization. The available phosphorus declined by 25.0% to 502.38 mg/kg ($p = 0.0005$) and available potassium decreased by 9.1% to 1275 mg/kg ($p = 0.0807$, ns), reflecting the slow-release characteristics of lignin–polysaccharide complexes in SMS, with potassium remaining at sufficiently high levels post-harvest. Notably, the EC increased by 107.6% to 3711 μS/cm

($p < 0.0001$), exceeding typical vegetable salt tolerance thresholds, likely due to cation accumulation (K^+, Ca^{2+}) from organic matter mineralization, posing a risk of secondary salinization. Meanwhile, the pH further declined to 6.75 ($p = 0.0002$), attributed to root exudates, microbial metabolism, and nitrogen transformations, enhancing nutrient bioavailability and explaining the significant increase in the mineral element content in harvested vegetables (Table 3). The organic matter content surged from 16.55 to 162.78 g/kg (an 883% increase, $p < 0.0001$), driven by the gradual decomposition of recalcitrant SMS components (e.g., cellulose and chitin) and the crop residue return, greatly improving the soil structure and moisture retention. After one growing season, post-cropped SMS-amended soil showed further changes. Total nitrogen declined by 59.4% to 100.98 mg/kg, while available phosphorus and potassium decreased by 25.0% and 9.1%, respectively. The EC increased by 107.6% to 3711 μS/cm, exceeding typical vegetable salt tolerance levels. The soil pH further declined to 6.75. The organic matter content surged to 162.78 g/kg (an 883% increase), driven by the gradual decomposition of recalcitrant SMS components (e.g., cellulose and chitin) and the crop residue return, greatly improving the soil structure and moisture retention.

Table 5. Physical and chemical properties of different kinds of soils.

	Hydrolytic Nitrogen (mg/kg)	Available Phosphorus (mg/kg)	Available Potassium (mg/kg)	pH	Electric Conductivity (μS/cm)	Soil Organic Matter (g/kg)
Slightly saline soil	213.21 ± 5.33 c	31.52 ± 0.39 d	159 ± 6.88 d	8.01 ± 0.22 b	1132 ± 31.97 c	14.80 ± 0.51 c
Heavily saline–alkaline soil	73.47 ± 3.53 e	22.17 ± 0.90 d	107 ± 1.98 e	8.34 ± 0.19 a	3840 ± 89.91 a	9.29 ± 0.16 d
Conventional substrate soil	271.36 ± 10.69 b	454.85 ± 15.49 b	517.5 ± 8.94 c	7.45 ± 0.26 c	966 ± 25.92 d	19.56 ± 0.25 b
Cow manure-amended soil	436.43 ± 14.92 a	456.83 ± 17.51 b	592.5 ± 10.27 b	7.32 ± 0.11 cd	644 ± 17.38 e	27.98 ± 1.34 b
SMS soil	248.85 ± 4.04 b	669.93 ± 7.25 a	1402.5 ± 31.09 a	7.66 ± 0.17 bc	1789 ± 60.28 b	16.55 ± 0.8 c
post-cropped SMS-amended soil	100.98 ± 1.64 d	502.38 ± 24.51 b	1275 ± 39.51 a	6.75 ± 0.23 e	3711 ± 44.01 a	162.78 ± 6.89 a

Data are presented as mean ± SD ($n = 3$). Different lowercase letters within the same column indicate significant differences among soil types based on Tukey's HSD test ($p < 0.05$).

3.4. Soil Microbial Community Response (Metagenomic Analysis)

3.4.1. Taxonomic Composition and Indicator Species

To further elucidate microbial community changes under the mushroom–vegetable rotation system, metagenomic analysis was conducted on rotation-treated and control soils. Biological replicates exhibited high data similarity, with most samples clustering into distinct branches (Supplementary Materials Figures S1–S4). In terms of the species composition, the soil microbial community was dominated by bacteria, with *Proteobacteria* and *Actinobacteria* being the predominant phyla (Figure 3). At a more specific taxonomic level, the top three orders in terms of the average relative abundance were *Hyphomicrobiales*, *Burkholderiales*, and *Streptomycetales* (Figure 4a). At the genus level, *Streptomyces* exhibited the highest average abundance (Figure 4b). LEfSe analysis revealed the enrichment of specific functionals across different treatments (Figure 5). For example, order *Hyphomicrobiales*, enriched in the mushroom–cabbage rotation group (20–40 cm), is a nitrogen-fixing group within *Proteobacteria*, closely associated with nitrogen cycling and the plant nutrient supply [44]. In the mushroom–cauliflower rotation group (20–40 cm), order *Burkholderiales*, a well-known plant rhizosphere-associated microbial group involved in plant growth

promotion and pathogen antagonism, was significantly enriched. In contrast, severely saline–alkaline soil (ZY20_40) was enriched with order *Rhodospirillales*, a group adapted to high-salinity and high-pH conditions and involved in carbon cycling and metabolic diversity [45,46]. In contrast, severely saline–alkaline soil (ZY20_40) was enriched with order *Rhodospirillales*, a group adapted to high-salinity and high-pH conditions and involved in carbon cycling and metabolic diversity. Consistent with previous studies, *Rhodospirillales* exhibited higher abundance in high-EC soils, whereas *Burkholderiales* were more abundant in low-EC soils, aligning with our findings [47].

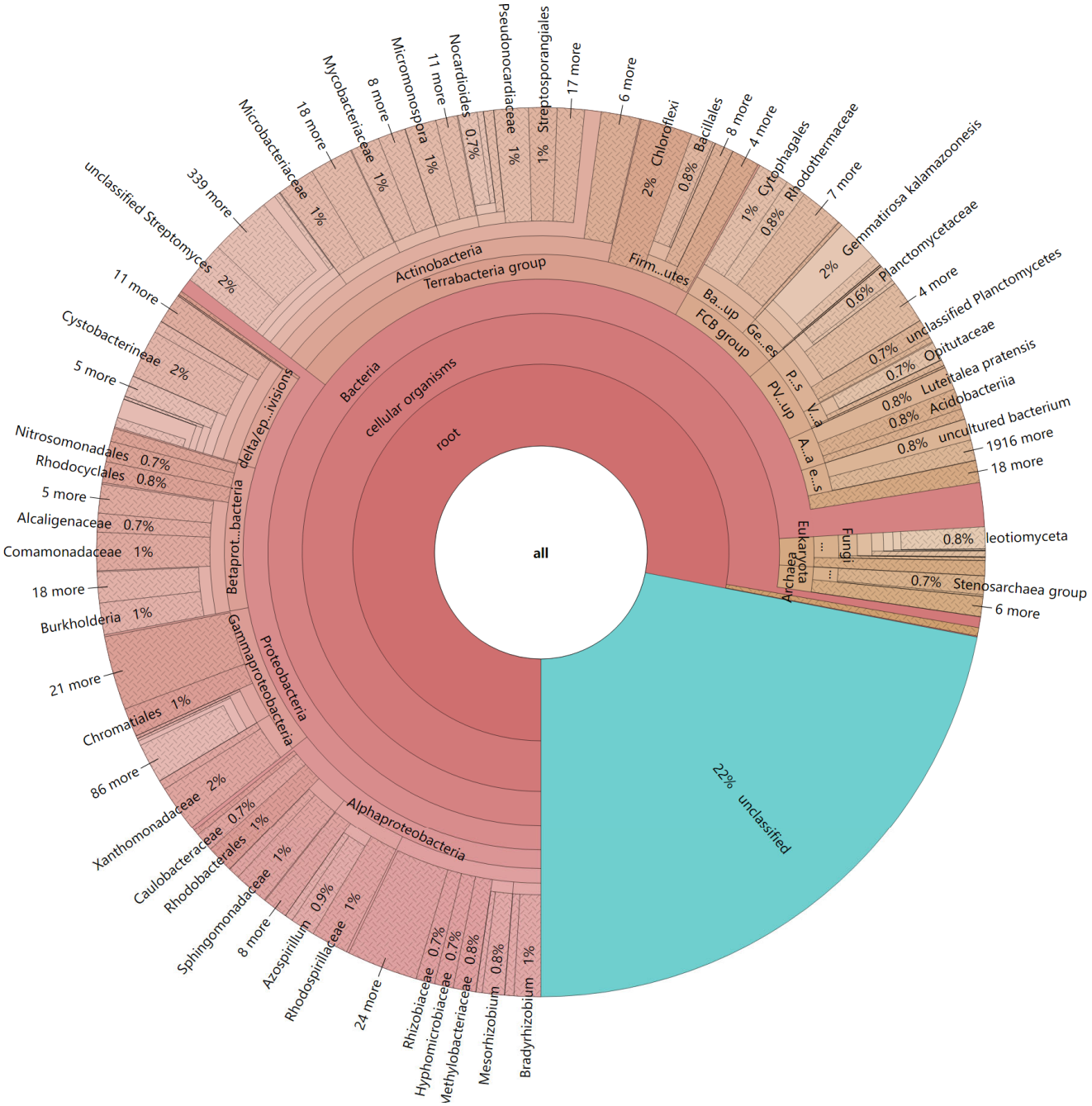


Figure 3. Taxonomic composition and relative abundance of soil microbial communities visualized using Krona plots.

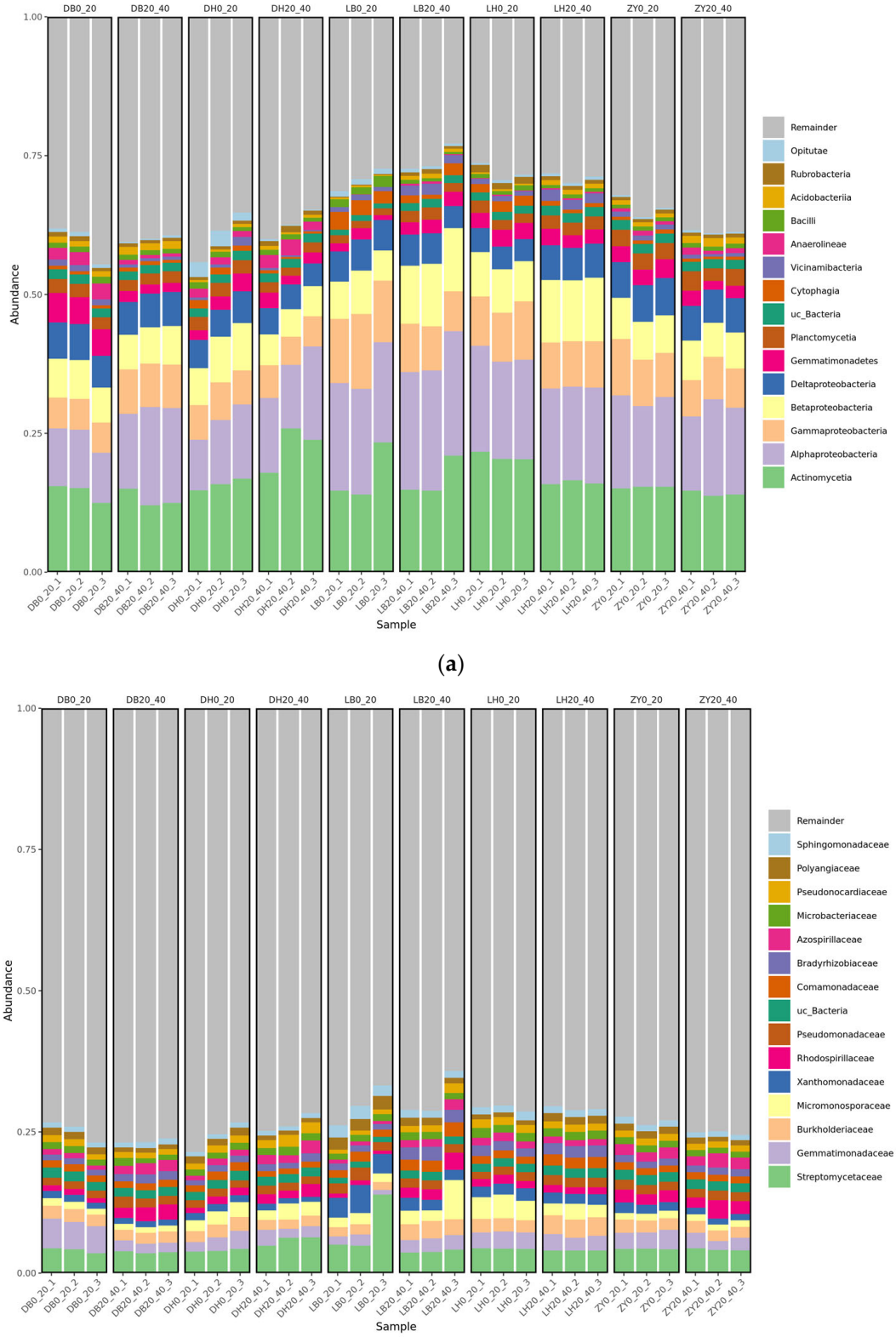


Figure 4. Relative abundance of dominant microbial taxa at different taxonomic levels. (**a**) Top 15 taxa at the order level. (**b**) Top 15 taxa at the genus level. These plots highlight key differences in microbial community composition under different treatments.

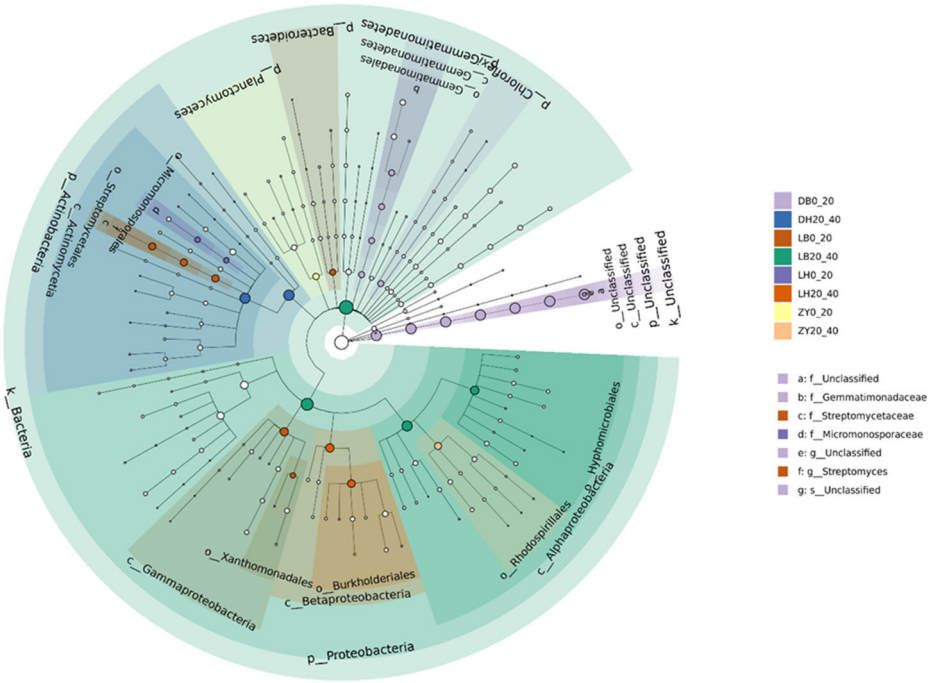


Figure 5. LEfSe cladogram showing taxonomic hierarchies of microbial groups significantly enriched in different sample groups. Colored nodes represent enriched taxa, with colors indicating the corresponding group. Inner circles denote higher taxonomic levels (e.g., phylum or class) and outer circles represent lower levels (e.g., order, family, or genus). Node size indicates relative abundance.

3.4.2. Functional Shifts in Microbial Metabolism

Functional annotation revealed significant differences in the microbial metabolic potential among treatments (Figure 6). In the unplanted, heavily saline–alkaline soil, genes associated with metabolic pathways such as butanoate metabolism, carbon fixation pathways in prokaryotes, the citrate (TCA) cycle, oxidative phosphorylation, propanoate metabolism, and RNA degradation were highly enriched. This suggests that the microbial community was primarily engaged in energy-intensive metabolic processes (e.g., the TCA cycle and oxidative phosphorylation) and autotrophic carbon fixation. Microbial communities in this environment were mainly characterized by stress adaptation and conservative survival metabolism, with low carbon and nitrogen cycling efficiency, indicating a relatively stagnant ecosystem. In contrast, monoculture vegetable plots exhibited moderate microbial activation due to root exudate stimulation, but also showed signs of intensified carbon competition (e.g., the enrichment of ABC transporters) and increased microaerophilic conditions (e.g., enhanced methane metabolism), suggesting ecological vulnerability. Notably, the mushroom–vegetable rotation system induced the functional reconstruction of the soil microbiota. Genes involved in flagellar assembly, two-component systems, chemotaxis, glyoxylate and benzoate metabolism, nitrogen metabolism, amino acid biosynthesis (e.g., valine and phenylalanine), glutathione metabolism, and CAMP resistance were significantly enriched. These results suggest that microorganisms actively utilized carbon sources from the SMS, enhanced nitrogen transformation and amino acid biosynthesis, and activated pathways related to antioxidant defense and pathogen resistance. This led to the establishment of a stable microbial community with an efficient degradation capacity, strong stress resistance, and interconnected metabolic functions, indicating a functional shift from stress adaptation to ecosystem service. Similar functional transitions in microbial communities have been observed in mushroom–crop rotation systems, where organic amendments and cross-kingdom interactions promote microbial diversity, metabolic integration, and nutrient cycling [48–50]. Overall, the combined effects of SMS amendment and rotation-induced

soil disturbance transformed microbial communities from a high-energy survival mode to a synergistic system characterized by efficient degradation, organic matter cycling, and stress resilience. This functional shift supports microbial community-driven soil remediation, fostering a self-sustaining recovery mechanism in saline–alkaline soils.

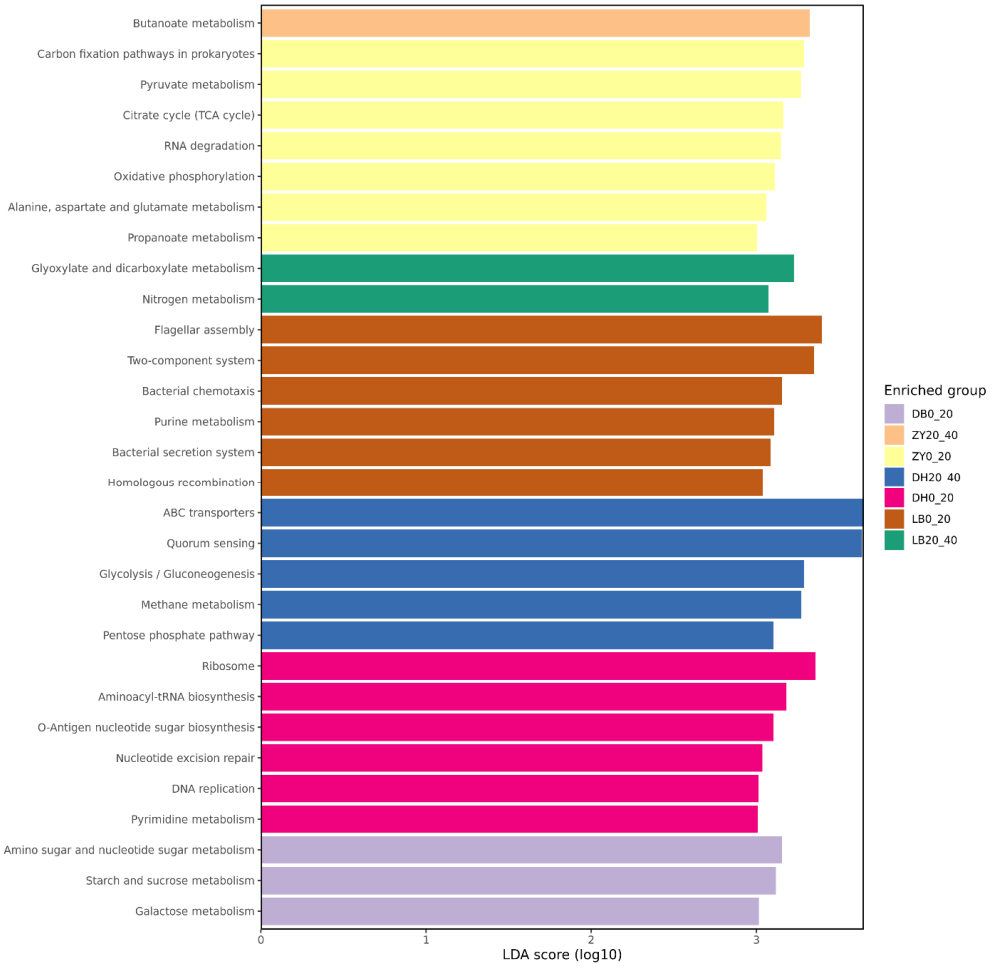


Figure 6. Differentially enriched gene functional pathways in soils under different cultivation practices, identified by LEfSe analysis based on KEGG functional annotations.

3.4.3. CAZy Gene Enrichment and Organic Matter Decomposition

Further analysis of carbohydrate-active enzymes (CAZy) highlighted the enhanced degradation potential of complex organic matter in rotation-treated soils. Principal coordinate analysis (PCoA) and Adonis tests demonstrated significant differences in CAZy gene profiles among soil treatments (R^2 = 0.806, p = 0.001), with clear separation between rotation-treated and control groups (Supplementary Materials Figure S5). Among the top 30 significantly different CAZy families, 17 (56.7%) belonged to glycoside hydrolases (GH) and 13 (76.5% of GH families) were significantly enriched in rotation-treated soils (Figure 7). GH enzymes play a crucial role in breaking down cellulose, hemicellulose, and other plant-derived macromolecular carbohydrates, providing bioavailable nutrients for soil microbes and plants. The enrichment of GH genes in rotation soils likely resulted from the microbial degradation of residual lignocellulose in SMS. Microbial taxonomic contribution analysis supported this, showing that *Streptomyces* contributed substantially to multiple CAZy enzyme families, including polysaccharide lyases (PL), glycoside hydrolases (GH), glycosyltransferases (GT), and auxiliary activity (AA) enzymes. *Aspergillus* fungi also contributed across treatments (Figure 8). These findings align with the observed increase

in soil organic matter, reinforcing the notion that a sustained organic substrate supply supports functional decomposer communities, thereby enhancing soil carbon cycling.

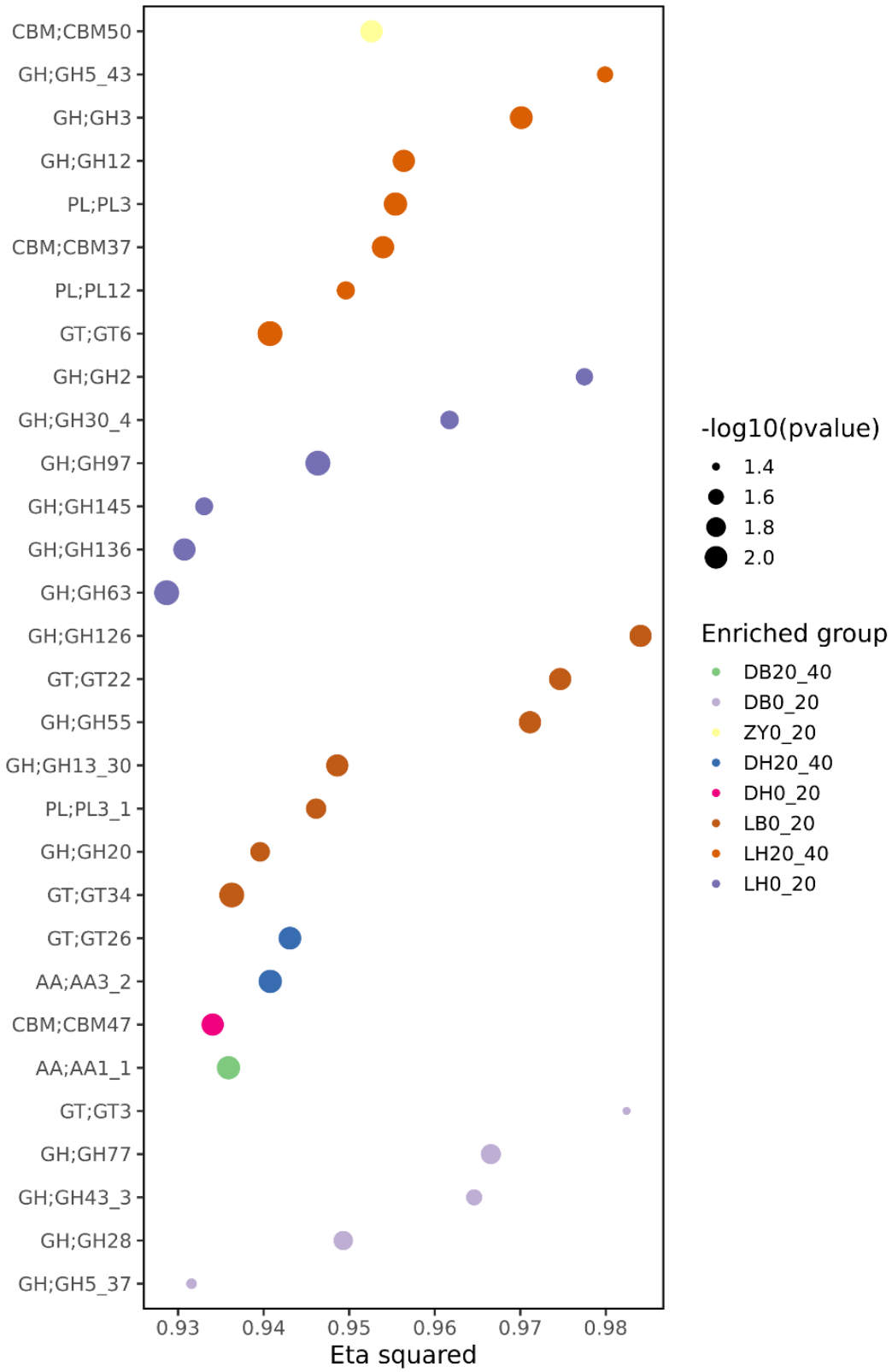


Figure 7. Top 30 significantly different carbohydrate-active enzyme (CAZyme) functions identified using the CAZy database. Bubble size represents the effect size and bubble color indicates the level of statistical significance.

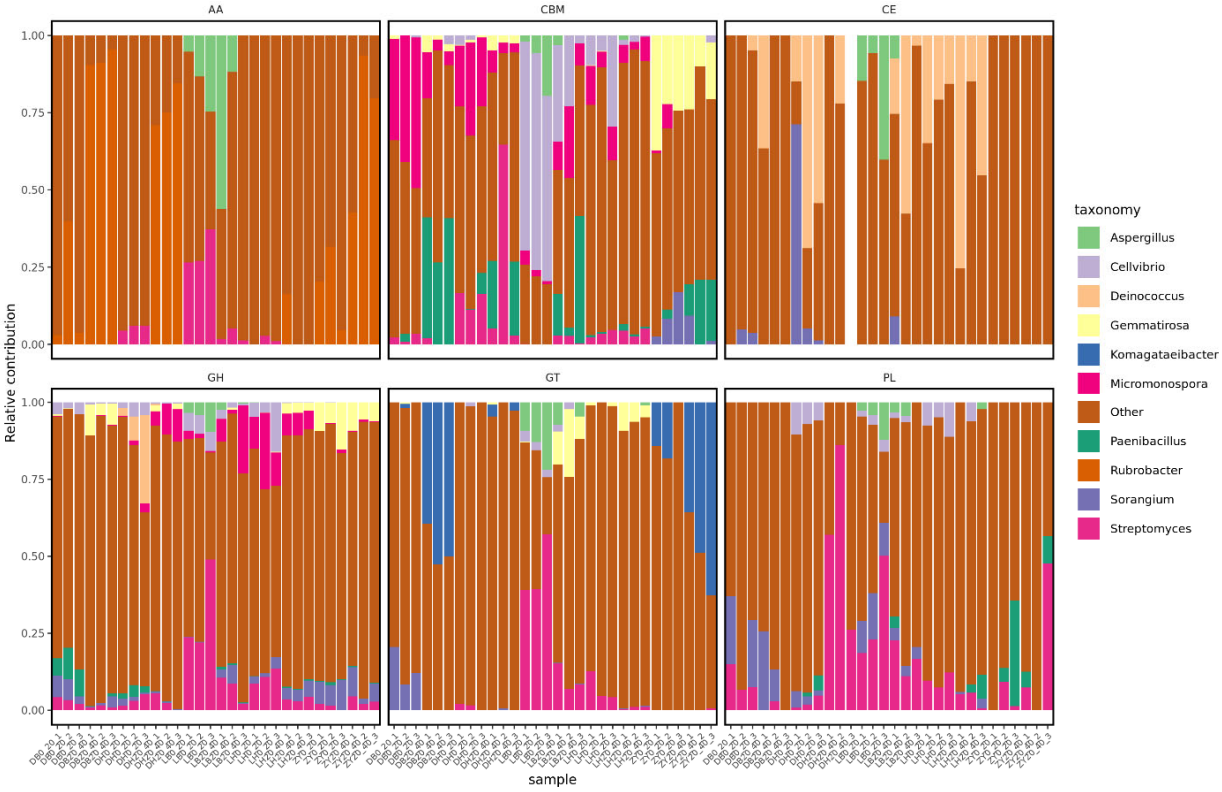


Figure 8. Correlations between dominant microbial genera and carbohydrate-active enzyme (CAZyme) functions.

3.5. Economic Benefit Assessment

In the factory-scale cultivation of *P. eryngii*, replacing sawdust entirely with a mixture of agricultural straws and reducing the amount of cottonseed hulls resulted in the use of 2812.5 kg of straw per 10,000 cultivation bags. This formulation modification reduced substrate costs by 2560 CNY. Based on an average fresh yield of approximately 450 g per bag, the estimated sales revenue from 10,000 bags reached 69,795 CNY, indicating clear economic benefits of the optimized substrate composition.

In the cultivation of *G. lucidum*, a total of 1800 kg of spent substrate was consumed per 10,000 cultivation bags, resulting in substrate cost savings of 3816 CNY. Based on an average fresh fruiting body yield of 104.15 g per bag, the estimated sales revenues from *G. lucidum* fruiting bodies and spore powder were 24,839.78 CNY and 8332 CNY, respectively. Therefore, the total sales revenue from *G. lucidum* cultivation reached 33,172 CNY.

For the secondary fruiting of *G. lucidum*, the average yield per spent substrate stick was 200 g. Based on a planting density of 150,000 cultivation bags per hectare, the total yield reached 30,000 kg/ha. The corresponding sales revenues from fruiting bodies and spore powder were 715,500 CNY/ha and 240,000 CNY/ha, respectively, resulting in a total revenue of 955,500 CNY/ha.

For *P. eryngii*, the average yield per spent substrate stick was 190 g. At a planting density of 270,000 cultivation bags per hectare, the total yield was 51,300 kg/ha, generating a sales revenue of 796,263 CNY/ha.

These results demonstrate that the reuse of spent substrate sticks for secondary fruiting provides significant economic returns and supports the circular utilization of cultivation materials in mushroom production systems.

In the control plots without SMS application, the vegetable yields were as follows: cauliflower, 29,264.7 kg/ha; cabbage, 51,766.5 kg/ha; and celery, 98,295 kg/ha. The corresponding average sales revenue was 179,003.3 CNY/ha

In the mushroom–vegetable rotation plots, the yields increased to 39,231.6 kg/ha for cauliflower, 71,460.3 kg/ha for cabbage, and 98,545.1 kg/ha for celery. The average sales revenue in these plots reached 212,380.1 CNY/ha, representing an income increase of 33,376.8 CNY/ha compared to the control.

Additionally, due to the improvement in soil fertility following SMS application, the input cost for chemical fertilizers was reduced by approximately 22,500 CNY per hectare.

For tomato cultivation, the yield reached approximately 112,500 kg/ha, resulting in a total sales revenue of 900,000 CNY/ha. Fertilizer cost savings of around 22,500 CNY/ha were also observed due to reduced dependence on chemical inputs.

Integrated economic benefits from the circular cultivation system were substantial. Based on two representative rotation models:

For the rotation "secondary *G. lucidum* fruiting (August–October) → leafy vegetables (harvested in January) → secondary *P. eryngii* fruiting (harvested in March of the following year)", the total annual revenue reached 955,500 CNY/ha + 212,380.1 CNY/ha + 796,263 CNY/ha = 1,964,143.1 CNY/ha.

For the rotation "secondary *P. eryngii* fruiting (December) → tomato (harvested in March)", the total annual revenue reached 796,263 CNY/ha + 900,000 CNY/ha = 1,696,263 CNY/ha.

In both rotation systems, fertilizer cost savings were approximately 45,000 CNY/ha due to improved soil fertility and reduced chemical fertilizer use.

4. Discussion

This study demonstrates the effectiveness of a straw–mushroom–vegetable circular cultivation model as an integrated strategy for saline–alkaline land utilization. By optimizing substrates, reusing SMS, and leveraging plant–microbe–soil interactions, this system simultaneously improved soil fertility, enhanced crop quality, and increased economic returns—offering both ecological and agronomic benefits.

4.1. Efficient Mushroom Production Based on Straw Integration and SMS Reuse

This study demonstrates a circular and resource-efficient mushroom cultivation model, in which agricultural straw is integrated into the primary substrate for *P. eryngii*, and the resulting SMS is reused for *G. lucidum* fruiting. Rather than simply replacing conventional materials like sawdust, this approach leverages the structural and compositional advantages of straw-based substrates and creates a two-stage production system that reduces waste, lowers cost, and increases the biomass output.

The optimized straw substrate supports high-efficiency *P. eryngii* production not just by supplying nutrients, but by improving the substrate's physical structure and biochemical balance. Unlike sawdust, the mixture of wheat, sorghum, corn straw, and peanut shells offers a diverse lignocellulosic matrix. Corn straw contributes high cellulose and hemicellulose levels that serve as accessible carbon sources for fungal metabolism, while peanut shells add lignin that maintains substrate porosity over time. This combination provides a gradual and sustained release of carbon, supports aeration, and regulates moisture, all of which are crucial for stable mycelial growth and fruiting [51]. The high C/N ratio (36–101) of the substrate may also activate lignocellulolytic enzyme expression, accelerating biomass conversion and enhancing the biological efficiency.

Beyond biological efficiency, economic analysis reinforces the value of substrate optimization. Replacing sawdust with straw mixtures significantly reduced input costs while maintaining high yields. This demonstrates that lignocellulose-rich agricultural residues, often treated as waste, can be transformed into a reliable and profitable substrate component.

The reuse of SMS for *G. lucidum* cultivation further illustrates the versatility and residual value of the optimized substrate. The enzymatic pre-conditioning by *P. eryngii* likely improved the substrate porosity and water retention, enabling effective colonization and fruiting by *G. lucidum*. Two successive flushes were achieved without composting or supplementation—highlighting the dual utility of a single substrate cycle. Such reuse reduces substrate waste, labor input, and energy consumption, aligning the system with circular economy principles [52].

Overall, this two-stage cropping model showcases how a rational substrate design, grounded in both biochemical and economic logic, can unlock the full potential of lignocellulosic waste. It provides a replicable framework for improving productivity and sustainability in the edible and medicinal mushroom industry, particularly in regions with abundant agricultural residues.

4.2. SMS Enhances Vegetable Yield and Quality in Saline–Alkaline Soils

The reuse of the SMS in saline–alkaline soils presents a compelling strategy for both crop productivity improvement and sustainable soil management. Beyond serving as a nutrient source, the SMS acts as a multifunctional soil conditioner—enhancing the soil structure, microbial activity, and water retention capacity. These effects are particularly valuable in salt-affected soils where a poor physical structure and ion imbalance restrict plant growth.

Cruciferous vegetables such as cabbage and cauliflower showed the strongest response to SMS applications, likely due to their high nutrient demand and sensitivity to soil salinity. The SMS may have mitigated salt stress by enhancing the cation exchange capacity, buffering the pH, and increasing the bioavailability of essential elements like Fe and K. Moreover, increased dry matter and sugar accumulation suggest an improved photosynthetic performance and carbon partitioning, consistent with prior studies that report an enhanced metabolic function under organic amendment regimes [53,54].

The improvement in the tomato fruit quality, especially the sugar–acid balance and lycopene content, highlights the potential of SMS to influence not just the yield, but also the nutritional and market value of the produce. This aligns with previous findings that organic matter enrichment in saline soils can stimulate secondary metabolism, leading to higher antioxidant compound accumulation [55].

From an economic perspective, the combination of an increased yield, improved quality, and reduced chemical fertilizer use translates into substantial income gains. In this context, the SMS becomes more than a waste byproduct—it becomes a valuable agronomic input that supports both environmental goals and economic resilience for farmers. Particularly in regions facing saline soil degradation and high fertilizer dependency, integrating the SMS into cropping systems could contribute to circular agriculture and input self-sufficiency.

It is also worth noting that different crops showed varying degrees of response to SMS, suggesting a need for the crop-specific optimization of application rates and timing. Future studies could explore the microbial mechanisms underlying improved nutrient cycling and salt tolerance, as well as the long-term impacts of repeated SMS use on soil health and productivity.

4.3. SMS Improves Soil Physicochemical Properties

The application of the SMS significantly improved the physicochemical properties of saline–alkaline soils, yet its benefits and limitations must be interpreted in the context of the plant nutrient dynamics, soil salinity buffering capacity, and long-term sustainability.

The elevated levels of available potassium and phosphorus in SMS-amended soil provide a favorable nutrient environment for crop development. Potassium, in particular, plays a dual role—not only supporting plant physiological processes like osmotic regulation and enzyme activation, but also participating in cation exchange processes that can reduce the sodium adsorption ratio (SAR), thereby alleviating sodicity-related stress [53,56]. The presence of humic substances and lignin derivatives in the SMS may further improve the soil structure by stabilizing macroaggregates and increasing permeability, accelerating salt leaching and enhancing root zone aeration.

The moderate acidification observed after one cropping cycle (pH 6.75) may be attributed to root exudation, microbial respiration, and nitrification processes—all enhanced by the labile carbon pool provided by the SMS [57]. This acidification is beneficial in alkaline soils as it increases the solubility and plant availability of micronutrients such as Fe, Mn, and Zn.

Moreover, the sharp increase in the soil organic matter (to 162.78 g/kg) highlights the role of SMS as a long-lasting organic input. The slow decomposition of recalcitrant components such as cellulose, hemicellulose, and chitin not only enriches the soil carbon pool, but also provides substrates for beneficial microbial communities. These microbial populations play a critical role in salt tolerance by enhancing soil enzymatic activity, producing exopolysaccharides that aid in soil aggregation, and modulating ion transport at the rhizosphere level [58].

However, the marked rise in EC (to 3711 μS/cm) after one season indicates a risk of secondary salinization. This may be due to the mineralization of potassium-, calcium-, and magnesium-rich organic matter, as well as concentration effects from limited leaching. In this context, management strategies such as controlled irrigation, gypsum or dolomite application, and crop rotation with salt-tolerant species should be considered to avoid a yield decline in subsequent crops.

Thus, while SMS demonstrates strong potential for saline–alkaline soil improvement, its application must be integrated with careful nutrient and salt management to fully realize its agronomic and environmental benefits over the long term.

4.4. Microbial Mechanism Underpinning Soil Recovery in a Circular Mushroom–Vegetable System

Metagenomic analysis demonstrated that integrating straw-based substrates with mushroom cultivation and subsequent vegetable planting significantly altered the soil microbial community structure and function. This straw–mushroom–vegetable circular model not only reshaped microbial taxonomic profiles, but also reprogrammed their metabolic pathways, driving a shift from stress-adapted to ecosystem-service-oriented communities. Such transformation is critical in saline–alkaline soil remediation, where microbial plasticity determines the success of soil functional restoration.

A key finding is the consistent enrichment of *Streptomyces*, *Hyphomicrobiales*, and *Burkholderiales*—microbial taxa known for their synergistic roles in soil health. *Streptomyces* species are prolific decomposers, secreting diverse carbohydrate-active enzymes (CAZymes), particularly glycoside hydrolases (GHs), that break down cellulose, hemicellulose, and lignin residues in the SMS [59]. Their abundance correlates with increased soil organic matter and nutrient bioavailability. *Hyphomicrobiales* contribute nitrogen fixation and carbon cycling [44], while *Burkholderiales* include many plant-growth-promoting rhizobacteria (PGPRs), known for siderophore production, pathogen suppression, and root colonization under salt stress [46].

Functionally, rotation-treated soils showed a significant upregulation of genes involved in nitrogen metabolism, glutathione biosynthesis, chemotaxis, and two-component signal transduction systems, reflecting an activated microbial state responsive to nutrient

signals and environmental cues. The enrichment of glutathione metabolism is particularly important, as this pathway mitigates oxidative stress induced by saline conditions, thereby enhancing microbial and plant tolerance.

Moreover, the enrichment of flagellar assembly and chemotaxis genes implies increased microbial motility and rhizosphere competence, essential for efficient root colonization and plant–microbe interactions. These functions, absent or suppressed in unplanted saline–alkaline soils, illustrate the ecological reprogramming enabled by circular bioresidue utilization.

In terms of carbon cycling, the rotation system markedly increased the abundance and diversity of CAZy families, especially GHs, GTs (glycosyltransferases), and AAs (auxiliary activity enzymes). This expansion of the enzymatic capacity enhances the breakdown of recalcitrant SMS components into simpler compounds, reinforcing a functional feedback loop: as microbes decompose the SMS, more bioavailable carbon and nitrogen become accessible, further supporting microbial growth, diversity, and soil aggregation [60].

Collectively, these results suggest that the circular use of straw and SMS fosters a microbial community optimized for organic matter degradation, nutrient mobilization, and abiotic stress resilience. This microbial reassembly forms the core of a self-sustaining soil recovery mechanism, transitioning saline–alkaline soils from degradation-prone systems to biologically enriched, crop-supportive environments.

5. Conclusions

This study established an integrated, closed-loop circular agricultural system of "straw–edible mushrooms–vegetables" in coastal saline–alkaline land, achieving both ecological restoration and economic value enhancement. By combining agricultural waste recycling, dual mushroom cropping, and microbial ecological engineering, this model significantly improved soil physicochemical and biological properties, increased crop yields, and generated much higher economic returns than conventional systems. Specifically:

1. Efficient resource utilization: Mixed straw replaced sawdust as the substrate for *P. eryngii*, achieving a biological efficiency of 80% and yield of 450 g per bag, reducing costs by 36.3%. The SMS was sequentially reused for *G. lucidum* cultivation, vegetables, and secondary mushroom fruiting, forming a full chain of Straw → *P. eryngii* → *G. lucidum* → Secondary *G. lucidum* → Vegetables → Secondary *P. eryngii* → Tomato, with 100% SMS returned to the soil, minimizing the external inputs.
2. Soil ecological restoration: The SMS increased the soil organic matter from 16.55 to 162.78 g/kg (+883%), reduced the pH from 8.34 to 6.75, and raised the available phosphorus and potassium by 21–31 times and 8.8–13.1 times, respectively. Rotation enriched functional microbes, notably *Actinobacteria*, *Hyphomicrobiales*, and *Burkholderiales*, and upregulated key metabolic pathways for the glyoxylate cycle, nitrogen cycling, and lignin degradation, shifting the microbial network from "stress survival" to "efficient degradation–resistance–nutrient cycling", supporting self-sustaining soil health.
3. Agricultural productivity and economic returns: Vegetable yields increased by over 30%, with the tomato quality (lycopene + 179%) notably enhanced. *G. lucidum* achieved "one substrate, two harvests" with bioactive compounds comparable to standard cultivation. The system yielded 1,695,000–1,962,881.4 CNY/ha annually—several times higher than traditional systems—while reducing chemical fertilizer use.

This is the first study to fully integrate edible mushrooms into saline land remediation, linking waste recycling with soil restoration and balancing ecology with economy. It offers a replicable "waste-to-value" circular agriculture model. Future directions include opti-

mizing secondary mushroom cropping, developing high-value products (e.g., *G. lucidum* spore powder), and applying microbiome engineering to enhance salt leaching and soil aggregation, improving system resilience and profitability. This model provides a novel strategy and technological reference for the green transformation of saline–alkaline agriculture worldwide. In addition, while our economic assessment focused on direct input costs and product revenues, future research should include a more comprehensive life-cycle cost analysis—including labor, energy, and infrastructure expenses—to provide a more accurate estimation of net economic benefits.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/horticulturae11070730/s1, Figure S1: Correlation heatmap of gene abundance across soil samples collected from different crop rotation systems and depths. Figure S2: Hierarchical clustering dendrogram of soil samples based on Bray–Curtis distances calculated from gene abundance profiles. Figure S3: Principal co-ordinate analysis (PCoA) based on species-level data, illustrating the distribution of different samples across taxonomic levels: phylum (a), order (b), genus (c), and species (d). Figure S4: Principal co-ordinate analysis (PCoA) of different samples based on gene functional annotations from the KEGG database. The analysis was conducted at three functional classification levels: Functional Category 1 (a), Functional Category 2 (b), and Functional Category 3 (c). Figure S5: Principal co-ordinate analysis (PCoA) of samples based on the abundance of CAZyme family (a) and subfamily (b). Table S1: Description of soil samples collected from rotation and non-rotation plots.

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