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Dynamic Coupling Mechanism of Soil Microbial Community Shifts and Nutrient Fluxes During the Life Cycle of *Dictyophora rubrovolvata*

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Abstract

As a rare edible mushroom, *Dictyophora rubrovolvata* possesses remarkable anti-tumor, anti-inflammatory, and antioxidant properties. However, continuous-cropping obstacles during cultivation significantly reduce soil reuse efficiency and adversely affect yield. To reveal a potential mechanism of continuous-cropping soil obstacles and propose some green precision cultivation strategies, the soil samples throughout the five growth stages of *D. rubrovolvata* were collected and systematically analyzed, including soil nutrient contents, pH, and dynamic changes in soil microbial communities. The results showed that soil organic carbon consumption was relatively high during the whole growth cycle. The total nitrogen consumption was greater during mycelial and primordium stages. The total phosphorus content began to exceed control from the egg stage. The total potassium and pH levels were both higher than control, exhibiting an upward trend. The bacterial species in the soil gradually increased with the growth of fruiting bodies, while the fungal species showed a declining trend. Moreover, there were significant differences in dominant bacteria and fungi in the soil during different growth stages. Further analysis revealed a dynamic coupling relationship among the soil microbial community, soil nutrient content, and pH during whole life cycle. This research would provide theoretical and technical support for the sustainable development of the edible mushroom industry.

Keywords: *Dictyophora rubrovolvata*; soil physicochemical properties; continuous-cropping obstacles; high-throughput sequencing; diversity

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1. Introduction

Dictyophora rubrovolvata belongs to the order Phallales, family Phallaceae, and genus *Dictyophora* and is hailed as the "Queen of mushrooms" and "Flower of fungi" [1]. As a rare edible fungus, *D. rubrovolvata* demonstrates significant application potential in treating diseases, such as anti-tumor effects, immune regulation, anti-inflammatory properties, antioxidant activity, and antibacterial functions [2–4]. Due to its high nutritional, medicinal, and economic value, it is widely cultivated in China [5]. After removing the bags and covering with soil, the cultivated species of *D. rubrovolvata* undergoes four distinct growth stages: mycelial stage, primordium stage, egg stage, and harvesting stage.

Soil covering can provide thermal insulation and moisture retention while also supplying nutrients and beneficial microorganisms, which facilitates the early formation of mushroom primordia [6]. It is evident that the growth and development of *D. rubrovolvata* are closely related to the nutrient content and microbial population in the soil. However, a major challenge in successive plantings of *D. rubrovolvata* is the emergence of continuous-cropping soil obstacles, rendering the soil unsuitable for reuse. If reused, the yield of *D. rubrovolvata* will significantly decline or even fail to produce mushrooms.

Research on continuous-cropping obstacles in edible fungi primarily focuses on soil-covered cultivation of *Morchella* and *Ganoderma lucidum* [7]. Continuous cultivation of morel can negatively impact the microbial diversity and community structure in the soil [8,9], and secondary cultivation is only possible after soil restoration. The bacterial species and abundance of multiple phyla, including Proteobacteria, Actinobacteria, and Acidobacteria, are associated with different soils cultivated with *Morchella* [10]. The excessive proliferation of pathogenic fungi, such as *Penicillium*, *Trichoderma*, and *Aspergillus*, may be the primary cause of the decline in *Morchella* yield [9]. Following soil fumigation with dazomet, subsequent *Morchella* cultivation demonstrated a significant reduction in soil-borne fungal pathogen abundance alongside increased beneficial bacterial populations, resulting in markedly improved yields of *Morchella* in continuous cropping systems [11]. This experiment verifies that the relationship between continuous-cropping obstacles of *Morchella* and soil microbial communities, demonstrating that continuous-cropping obstacles can be improved through appropriate soil treatment. The dynamic changes in bacterial and fungal community structures in soil are associated with variations in nitrogen and phosphorus levels. And the abundance of pathogenic fungi in the soil gradually increases with the growth of *Morchella* [9]. Zhang et al. have discovered that the primary causes of continuous-cropping obstacles in *Morchella* cultivation are the significant changes in soil nutrient composition and the imbalance of soil microbial community structure [12]. When studying the cropping soil samples of four growth stages of *Ganoderma lucidum*, Zaheer et al. have found that soil pH and total phosphorus content exhibit an upward trend [13], whereas the total nitrogen and total potassium contents show a decline [14]. Continuous cultivation of *G. lucidum* results in a marked decline in soil organic matter content, demonstrating that consecutive cropping systems accelerate soil organic matter depletion [15]. The decline in yield and alterations in soil physicochemical properties caused by continuous cropping of *G. lucidum* are highly likely associated with *Penicillium* fungi [16]. This indicates a close correlation between the composition of fungal and bacterial communities and the nutrient contents in soil [17]. In summary, it can be inferred that continuous-cropping obstacles arise not merely from the depletion of individual nutrients but rather result from complex interactions between soil nutrient profiles and the composition of the soil microbial community.

The continuous-cropping obstacle of *D. rubrovolvata* leads to a sharp decline in yield. The spent soil becomes unsuitable for replanting, resulting in the wastage of valuable soil components, including minerals and humus within the soil matrix, while simultaneously compromising both arable land productivity and ecological restoration potential. This situation poses a latent threat to the sustainability of agricultural development by undermining long-term resource availability and ecosystem resilience. Fu et al. has found that biochar, as a soil amendment, can improve the physicochemical and biological properties of soil, thereby increasing the yield of *D. rubrovolvata* [18], highlighting the role of soil composition in the cultivation of *D. rubrovolvata*. Green mold disease was detected on the fruiting bodies of *D. rubrovolvata* [19], leading to its demise or inhibiting the formation of a sporocarp, thereby suggesting that microorganisms have the potential to impact the growth and development of *D. rubrovolvata*. Although there have been analyses of soil nutrient composition and microbial communities in edible fungi cultivation, current research pri-

marily focuses on a single growth stage of edible fungi, neglecting the variations in the whole life cycle. Research on *D. rubrovolvata* is still in its preliminary stages, and systematic investigations remain inadequate. Based on these studies, it is hypothesized that there exists a close and dynamic coupling relationship between soil microorganisms and nutrients throughout the growth cycle of *D. rubrovolvata*, and this relationship plays a pivotal role in the emergence of continuous-cropping obstacles. To reveal a potential mechanism of soil continuous-cropping obstacles and propose green precision cultivation strategies based on microecological regulation, this study systematically analyzed the dynamic coupling patterns between soil microorganisms and nutrients throughout the entire growth cycle of *D. rubrovolvata*. This research provides both theoretical frameworks and practical technical solutions to support the sustainable development of the edible fungi industry.

2. Materials and Methods

2.1. Experimental Site and Experimental Design

The experiment on the soil-covered cultivation of *D. rubrovolvata* was conducted from May to September 2024 at Bailu Modern Agricultural Science and Technology Co., Ltd. in Taihe County, Fuyang City, Anhui Province, China.

The experimental design comprised five treatments (including a control) with three biological replicates each, utilizing rhizosphere soil samples collected during different growth stages of *D. rubrovolvata*. They were bare soil stage (CK, before planting), mycelial stage (Dr1, when mycelium fully covered the soil surface on the 30th day), primordium stage (Dr2, when spherical primordia with a diameter of 0.5–1 mm appeared on the surface on the 43rd day), egg stage (Dr3, when the average diameter of egg-shaped fruiting bodies reached 4–4.5 cm on the 68th day), and harvesting stage (Dr4, upon completion of fruiting body harvest) (Figure 1A).

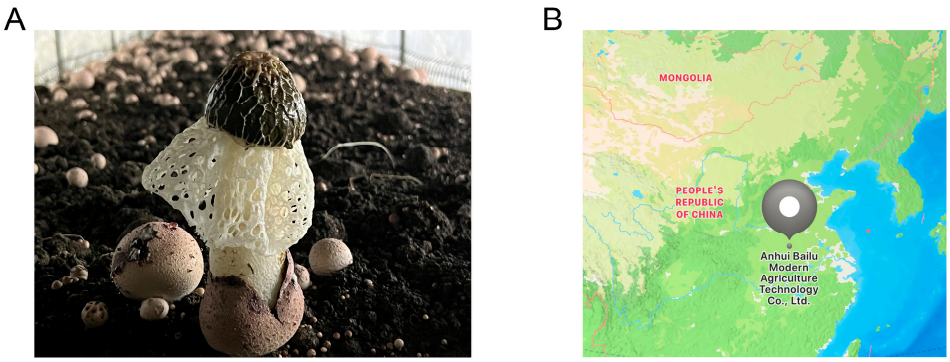


Figure 1. (**A**) Growth environment and fruiting body morphology of *D. rubrovolvata*. (**B**) Georeferenced map of the experimental plots.

2.2. Cultivation Conditions

The entire cultivation process of *D. rubrovolvata* was carried out in greenhouses in Ireland (Figure 1B), where environmental parameters such as soil temperature (maintained at 22–25 °C), air humidity (kept at 80–90%), and cultivation environment (with light exclusion treatment) were carefully regulated to ensure stable growth conditions. The soil-covering material was composed of a 75% red soil and 25% peat soil mixture. The measured parameters were as follows: organic carbon (152.38 ± 1.57 g/kg), total nitrogen (4.34 ± 0.03 g/kg), total phosphorus (0.75 ± 0.02 g/kg), total potassium (14.85 ± 0.26 g/kg), and pH (4.8 ± 0.006).

2.3. Experimental Process

Soil samples were collected from the covering soil layer at different growth stages of *D. rubrovolvata*, namely the bare soil stage, mycelial stage, primordium stage, egg stage, and harvesting stage. Three biological replicates were collected for each growth stage, with samples for each replicate obtained using the five-point sampling method. During collection, the top 2–3 cm of the soil layer was removed, and soil (excluding the mycelium and fruiting bodies of *D. rubrovolvata*) was collected using a soil auger with an inner diameter of 5 cm and a 100 cm^3 ring sampler. After removing stones, visible plant and animal residues, and other debris from the soil, the samples were sieved through an 80-mesh sieve. The samples were then stored at −80 °C for the determination of soil microbial community diversity and soil physicochemical properties. The air-dried soils were employed for determining total nitrogen, total phosphorus, total potassium, and organic carbon.

2.4. Determination of Soil Physicochemical Properties

The pH, organic carbon (OC), total nitrogen (TN), total phosphorus (TP) and total potassium (TK) were analyzed according to NY/T 1377-2007, NY/T 1121.6-2006, LY/T 1228-2015, GB/T 9837-1988, and NY/T 87-1988 standards [9]. The average value was obtained after three repeated samples.

2.5. High-Throughput Sequencing Analysis

Total soil DNA was extracted from 0.5 g of fresh soil using the TGuide S96 Magnetic Bead-Based Soil Genomic DNA Extraction Kit (Tiangen Biotech (Beijing) Co., Ltd., Beijing, China, Model: DP812), following the manufacturer's instructions. The nucleic acid concentration was determined using a microplate reader (Synergy HTX, GeneCompany Limited, Hong Kong, China) after adding the 1X dsDNA HS Working Solution (Yeasen Biotechnology (Shanghai) Co., Ltd., Shanghai, China). For the bacterial community analysis, primers 338F (5′-ACTCCTACGGGAGGCAGCA-3′) and 806R (5′-GGACTACHVGGGTWTCTAAT-3′) were used to amplify the V3-V4 hypervariable region of the 16S rRNA gene. For the fungal community analysis, primers ITS1F (5′-CTTGGTCATTTAGAGGAAGTAA-3′) and ITS2 (5′-GCTGCGTTCTTCATCGATGC-3′) were employed to amplify the internal transcribed spacer (ITS) region. Amplicon library preparation and high-throughput sequencing were conducted by Nanjing Tsingke Biotechnology Co., Ltd. (Nanjing, China).

The raw image data files obtained from high-throughput sequencing undergo base calling analysis to be converted into raw sequenced reads, with the results stored in FASTQ (abbreviated as fq) file format. This format contains both the sequence information of the reads and their corresponding sequencing quality scores.

Raw sequencing data were subjected to quality filtering by using Trimmomatic [20] (version 0.33) with the following parameters: a 50 bp sliding window was applied, and reads were truncated from the window's start if the average quality score fell below 20. Primer sequences were subsequently identified and removed by using Cutadapt [21] (version 1.8.3), with parameters set to allow a maximum error rate of 20% and require a minimum overlap of 15 bp for primer matching. Length filtering was performed according to the amplified regions: sequences with lengths between 350 and 490 bp were retained for 16S V3 + V4 regions, while 300–500 bp sequences were kept for ITS regions.

Further quality control, paired-end read merging, and chimera removal were conducted by using the DADA2 package in R v3.1.1. The filterAndTrim function was applied with a maximum expected error threshold of 2 (where EE = sum (10^(−Q/10))), with other parameters set to default values. Error model learning was performed using the learnErrors function, followed by denoising with the dada function. Paired-end reads were merged

using the mergePairs function (parameters: minOverlap = 18, maxMismatch = 18 × 0.2), and chimeric sequences were removed using the removeBimeraDenovo function with the consensus method.

Additionally, USEARCH [22] (version 10) was employed to merge reads from each sample with parameters set to a minimum overlap length of 10 bp, a minimum similarity of 90% in the overlap region, and a maximum of five mismatched bases (default settings). Chimeric sequences were identified and removed using USEARCH [22] (version 10) in combination with UCHIME [23] (version 8.1). The resulting high-quality sequences were used for subsequent downstream analyses. After quality control, quantification, and normalization of the DNA libraries, the obtained high-quality sequences were merged as operational taxonomic units (OTUs) by using VSEARCH (version 2.4.3) at a 97% similarity threshold cutoff. To process the taxonomic classification of OTUs, the representative sequences of each OTU were generated and aligned against the Greengenes database (version 13.5, https://greengenes.lbl.gov/Download/, accessed on 12 October 2024), Sliva database (Release138, https://www.arb-silva.de, accessed on 12 October 2024), fungene database (http://fungene.cme.msu.edu/, accessed on 12 October 2024), MaarjAM database (https://maarjam.ut.ee, accessed on 12 October 2024), and UNITE database (Release 8.0, https://unite.ut.ee/, accessed on 12 October 2024) for bacterial OTUs and fungal OTUs. The relative abundance data for taxa were generated based on the read count for each taxon across samples by using the total-sum scaling method.

The raw Illumina sequencing data of bacterial 16S rRNA genes and fungal internal transcribed spacer (ITS) regions have been deposited in the National Center for Biotechnology Information (NCBI), with the BioProject accession numbers PRJNA1285843 and PRJNA1285854, respectively.

2.6. Statistical Analyses

The bar chart comparing nutrient components across different samples was made by Origin 2021 and Excel 2016. And the variance analysis of experimental data was carried out by SPSS 23.0. To elucidate the soil microbial community diversity across distinct developmental phases, taxonomic annotation of feature sequences was performed by integrating a Naive Bayes classifier with sequence alignment methodologies, utilizing the Silva database (Release 138, https://www.arb-silva.de, accessed on 12 October 2024) as the reference database. The analysis pipeline enabled the acquisition of species classification information for each feature sequence. Subsequently, statistical characterization of microbial community composition was conducted across samples at multiple taxonomic levels. Species abundance tables were systematically generated using QIIME 2 software, followed by visualization through R-based tools: Venn diagrams were constructed to illustrate shared/unique features among samples, while stacked bar plots were generated to depict community structure at both phylum and genus levels for each sample.

Based on the species composition distribution and nutrient content in each sample, Origin 2021 and Excel 2016 were utilized to construct the heatmap for the analysis of the correlation between soil factors and microbial communities. The co-occurrence network was constructed by conducting Spearman rank correlation analysis and screening data with correlation coefficients greater than 0.1 and p-values less than 0.05. Fungal genera and bacterial genera with the top 50 relative abundances in each group were selected for this analysis. The predictions of functional genes of soil bacteria under CK and Dr4 conditions were predicted by using PICRUST2 (2.3.0) [24] software based on the COG database.

3. Results

3.1. Physical and Chemical Properties of Soil in Different Growth Stages

As shown in Figure 2A, Dr1 consumed 45.86% of the soil OC, and the consumption reached the minimum value in Dr2. That is, the original soil OC was consumed by 49.64% in the two stages. The soil OC content in Dr3 and 4 stages gradually stabilized at 55.09%. From Dr1 to 4, the content of TN and TP decreased first and then increased, reaching the lowest point in Dr2, which consumed 28.80% and 13.33% of the original total amount of soil, respectively. Then, it increased rapidly and reached the peak in Dr4, which increased to 100.46% and 137.33% of CK, respectively (Figure 2B,C). The TK content and pH value of the soil increased steadily throughout the growth cycle. At the Dr4, TP and pH reached the highest level, increasing to 114.41% and 150.83% of control, respectively (Figure 2D,E). Further analysis showed that the contents of OC, TN, TP, TK, and pH value in the soil layer at different growth stages showed significant differences.

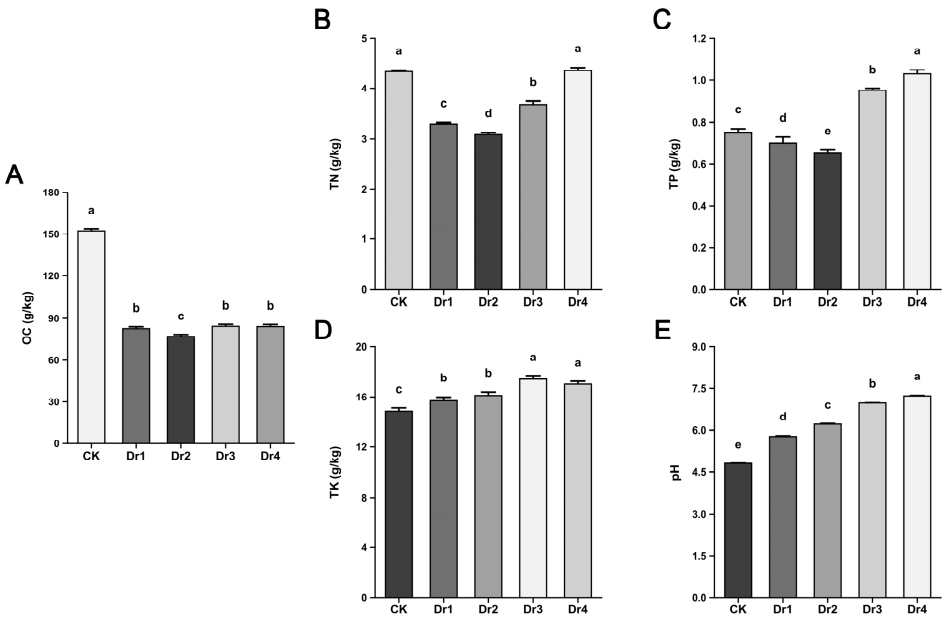


Figure 2. Soil basic physical and chemical properties during the growth of *D. rubrovolvata*. (**A**) OC (organic carbon); (**B**) TN (total nitrogen); (**C**) TP (total phosphorus); (**D**) TK (total potassium); (**E**) pH. CK: bare soil stage; Dr1: mycelial stage; Dr2: primordium stage; Dr3: egg stage; Dr4: harvesting stage. Different lowercase letters (a, b, c, d and e) indicate significant differences among stages. Stages sharing the same lowercase letter are not significantly different, whereas those with distinct letters differ at $p < 0.05$.

3.2. Diversity of Soil Microorganisms in Different Growth Stages

3.2.1. Analysis of Soil Bacteria and Fungi in Different Stages

The Venn diagram can show the number of common and unique characteristics of bacteria and fungi in soil samples of each stage and intuitively show the overlap of characteristics between soil samples of *D. rubrovolvata* in different growth stages. Combined with the species represented by the characteristics, the common microorganisms in soil at different stages can be identified. The results showed that the OTUs of bacteria were the least, and the OTUs of fungi were the most during CK. The OTUs of bacteria were the most during Dr3, and the OTUs of fungi were the least during Dr2 (Figure 3). Comprehensive analysis presented that during the whole cultivation process, the OTUs of bacteria in the soil increased steadily, while the OTUs of fungi decreased (to 44.07% of the CK) and then increased (to 75.37% of the CK).

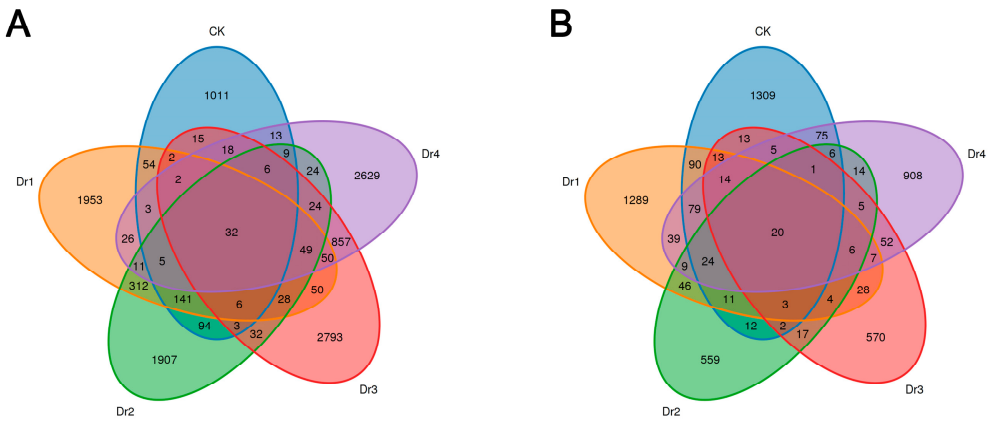


Figure 3. Venn diagram. Each circle in the figure represents a sample group. The numbers in the overlapping parts of the circles represent the number of OTUs shared between the sample groups, and the numbers in the non-overlapping parts represent the number of OTUs unique to the sample groups (bacteria (**A**) and fungi (**B**)). CK: bare soil stage; Dr1: mycelial stage; Dr2: primordium stage; Dr3: egg stage; Dr4: harvesting stage.

3.2.2. Diversity of Soil Microbial Communities in Different Stages

Figure 4A illustrates the distribution of bacteria at the phylum level in soil samples from different stages. The top six most abundant phyla were Proteobacteria, Actinobacteriota, Acidobacteriota, Bacteroidota, Gemmatimonadota, and Chloroflexi, accounting for over 85%. Further analysis showed that there was no significant difference between CK, Dr1, and Dr2. In Dr3 and Dr4, Bacteroidota, Gemmatimonadota, and Chloroflexi showed a significant increase, while Actinobacteriota showed a significant decrease. At the fungal phylum level (Figure 4B), the top three species in soil at each stage were Ascomycota, Basidiomycota, and Moriterellomycota, accounting for more than 90%. The Ascomycota in Dr2 was much lower than that in other stages, while the Basidiomycota was much higher than that in other stages. The Moriterellomycota was much higher than other stages during Dr3. The relative abundance of each fungus during the harvest period was comparable to that in the bare soil period.

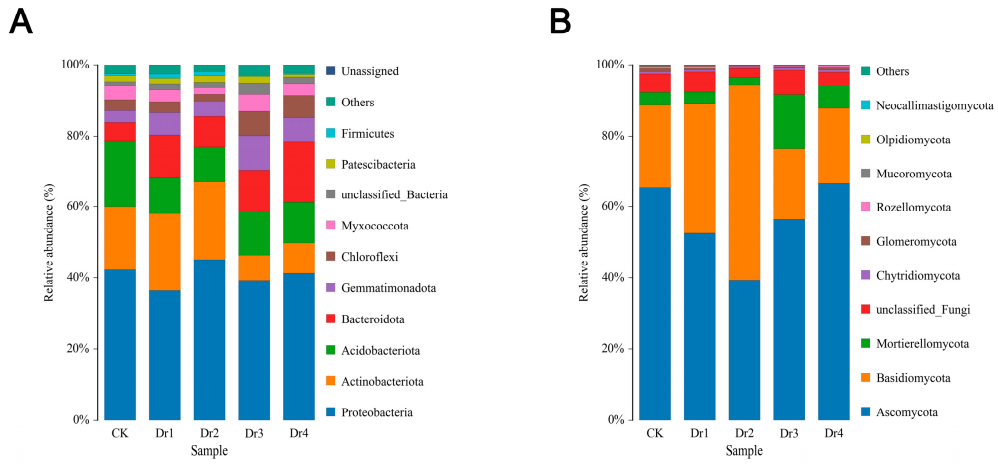


Figure 4. Relative abundance of bacteria (**A**) and fungi (**B**) at the phylum level. The different color represents different phylum of bacteria or fungi. CK: bare soil stage; Dr1: mycelial stage; Dr2: primordium stage; Dr3: egg stage; Dr4: harvesting stage.

As can be seen from Figure 5, at the genus level, the abundance of soil bacteria in each period was different. Unclassified_*Microscillaceae* was excluded because its function was unknown. *Streptomyces* accounted for the highest proportion in CK, which was significantly

higher than that in other stages. Among all stages, *Lappillicoccus* exhibited the highest relative abundance in Dr1, showing a statistically significant difference compared to the other stages. The proportion of *Burkholderia_Caballeronia_Paraburkholderia* in Dr2 was the highest. Unclassified_*Gemmatimonadaceae* accounted for the highest proportion in Dr3 and Dr4 (Figure 5A). Likewise, the relative abundance of fungal genera in soil varied greatly in different stages. The most abundant species are *Mortierella*, *Trichoderma*, *Fusarium*, *Cladosporium*, *Penicillium*, and unclassified_*Cordycipitaceae*. The proportion of *Fusarium* and *Cladosporium* in CK was markedly greater compared to other stages. Conversely, *Trichoderma* and *Penicillium* exhibited a significantly higher proportion in Dr2 than in the remaining stages. Additionally, the unclassified_*Cordycipitaceae* demonstrated a notably higher proportion in Dr3 relative to other stages. (Figure 5B).

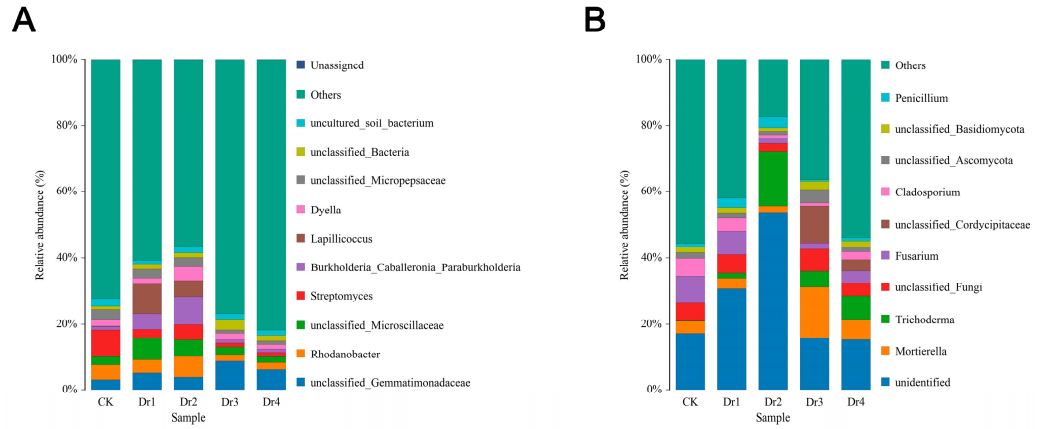


Figure 5. Relative abundance of bacteria (**A**) and fungi (**B**) at the genus level. The different colors represent different genera of bacteria or fungi. CK: bare soil stage; Dr1: mycelial stage; Dr2: primordium stage; Dr3: egg stage; Dr4: harvesting stage.

3.2.3. Co-Occurrence Network Analysis

Co-occurrence network analysis serves as a powerful tool to elucidate potential correlations among species. When such a correlation exists between any two species, they are visually connected by a line within the network, thereby offering a clear depiction of their interrelationships. In the network topological structures characterizing soil ecosystems at different stages, bacterial nodes predominantly fell within the phylum Actinobacteriota, Proteobacteria, Chloroflexi, Gemmatimonadota, Acidobacteriota, and Bacterioidota. Among them, Gemmatimonadota, Acidobacteriota, and Actinobacteriota exhibited relatively high abundances. The correlations exhibited among genera within the same phyla, as well as between genera belonging to distinct phyla, were notably robust (Figure 6A). Network analysis revealed that Ascomycota, Basidiomycota, and Mortierellomycota were the dominant fungal phyla. Notably, *Trichoderma*, *Mortierella*, *Fusarium*, and *Cladosporium* showed numerous connections, indicating that they were correlated with most fungal genera. A deeper analysis revealed that *Trichoderma* and *Mortierella* predominantly displayed negative correlations, varying from weak to strong, with other fungal genera. In contrast, *Fusarium* and *Cladosporium* predominantly demonstrated positive correlations, also ranging from weak to strong, with their fungal counterparts (Figure 6B).

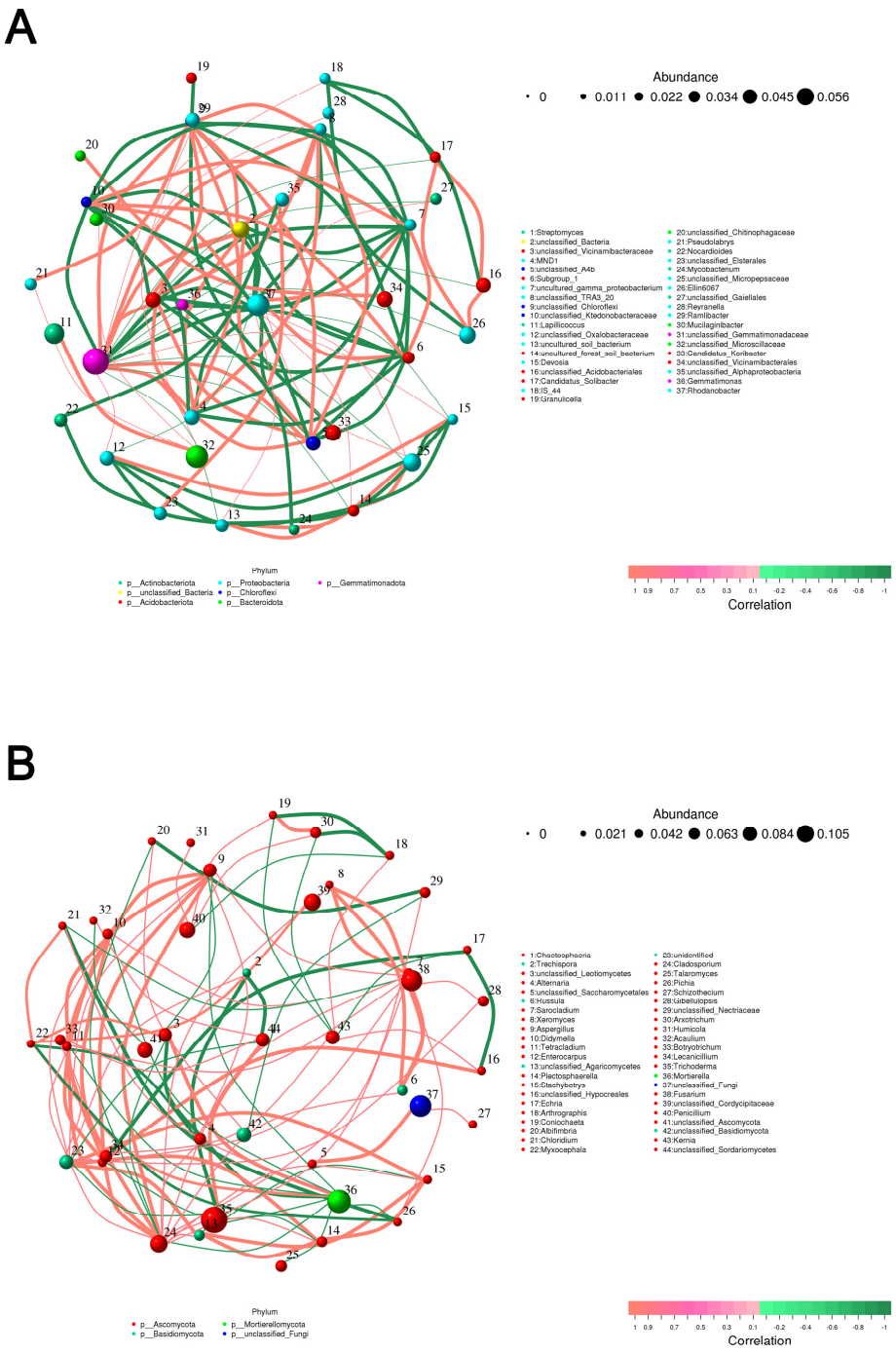


Figure 6. Co-occurrence network analysis of bacteria (**A**) and fungi (**B**). The different colors of the circle represent different genera of bacteria or fungi. The top 50 genera were shown ($p < 0.05$). When a correlation exists between any two genera, they are visually connected by a line within the network. The thicker the line, the stronger the correlation. The larger the circle, the higher the abundance of the species.

3.2.4. Analysis of Correlation Between Soil Factors and Microbial Communities

To delve deeper into the intricate relationships between diverse physicochemical soil factors and the microbial communities inhabiting the soil at various developmental stages, correlation heat maps were constructed, which visually depict the associations between soil factors and microbial communities. As shown in Figure 7A, the correlation between an array of physicochemical soil factors and bacterial communities was exceptionally high. A highly significant positive correlation was observed between *Streptomyces* and OC, with a

correlation coefficient of 0.83. TN displayed a highly significant negative correlation with unclassified_*Microscillaceae* (−0.82) and *Burkholderia_Caballeronia_Paraburkholderia* (−0.85). *Rhodanobacter* and the unclassified_*Micropepsaceae* exhibited a highly significant negative correlation with TP (−0.91 and −0.95, respectively).

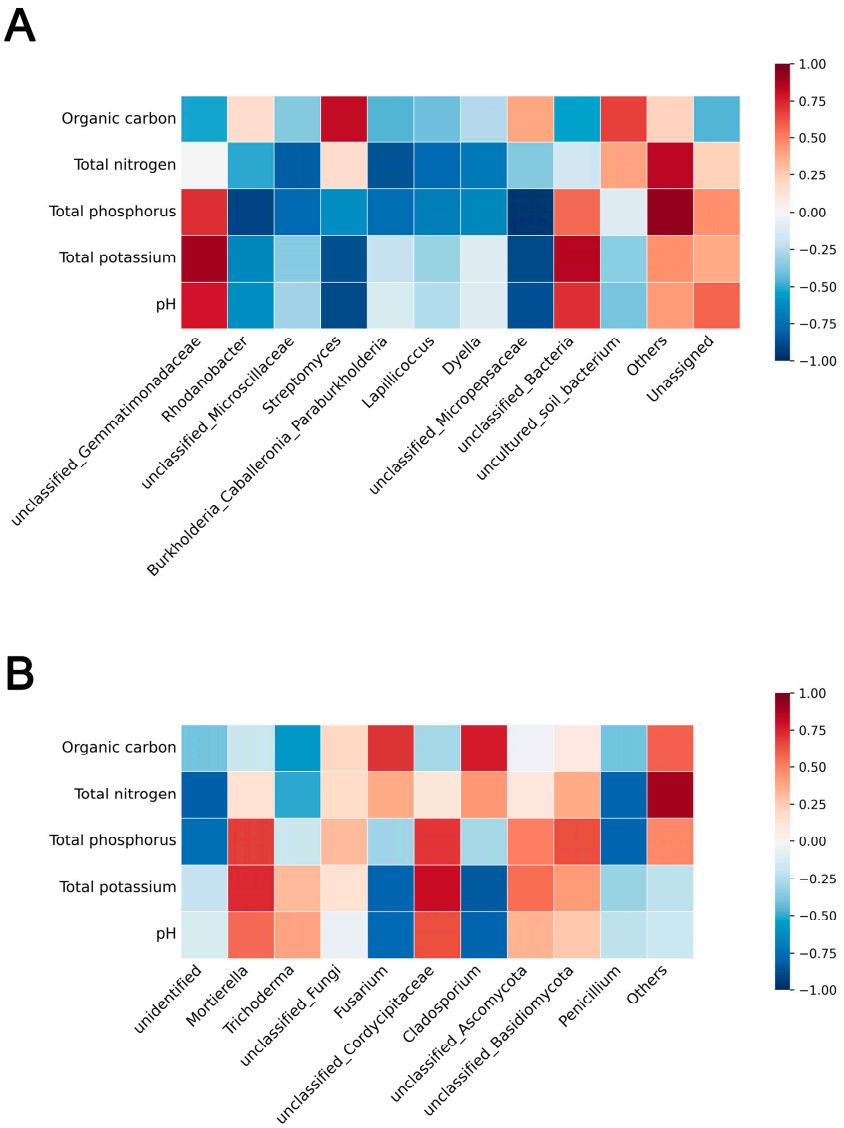


Figure 7. Heat map of the correlation between soil physicochemical properties and bacterial (**A**) and fungal (**B**) communities. The maps intuitively illustrate the associations between soil factors and microbial communities. Red indicates positive correlation, and blue denotes negative correlation. The color intensity reflects the strength of correlation.

TK and pH exhibited a notably strong and statistically significant negative correlation with both unclassified_*Micropepsaceae* (−0.89 for TK, −0.86 for pH) and *Streptomyces* (−0.88 for TK, −0.90 for pH). Conversely, unclassified_*Gemmatimonadaceae* displayed a highly significant positive correlation with TP (0.73), TK (0.88), and pH (0.78).

As shown in Figure 7B, among the correlations between physicochemical soil factors and fungi, *Fusarium* (0.70) and *Cladosporium* (0.77) showed a significantly strong positive correlation with OC. *Penicillium* demonstrated a pronounced and statistically significant negative correlation with TN (−0.80) and TP (−0.80). Similarly, *Fusarium* and *Cladosporium* each showed a significant negative correlation with TK (−0.80 for *Fusarium*, −0.83 for *Cladosporium*) and pH (−0.78 for *Fusarium*, −0.80 for *Cladosporium*). *Mortierella* and unclas-

sified_*Cordycipitaceae* presented a relatively significant positive correlation with TP (0.68 for *Mortierella*, 0.70 for unclassified_*Cordycipitaceae*), TK (0.74 for *Mortierella*, 0.81 for unclassified_*Cordycipitaceae*), and pH (0.57 for *Mortierella*, 0.65 for unclassified_*Cordycipitaceae*).

3.2.5. Comparison of Predicted Bacteria Functional Genes During Bare Soil and Harvest Stage

The functional genes of soil bacteria during CK and Dr4 were predicted by PICRUSt2 software based on the COG database. The results were shown in Figure 8. Except for the genes with unknown functions and those with only general function prediction, the functional genes of soil bacteria in the two stages mainly involved metabolic, genetic information transmission, cell process and signal transduction, and other life activities. These functional genes were predominantly implicated in the metabolic processes of amino acids, carbohydrates, inorganic ions, and secondary metabolites. Notably, the proportion of functional genes associated with amino acid, carbohydrate, and secondary product metabolism was more pronounced in CK bacteria compared to Dr4. Conversely, the level of genes involved in inorganic ion metabolism was observed to be lower in CK bacteria than in Dr4.

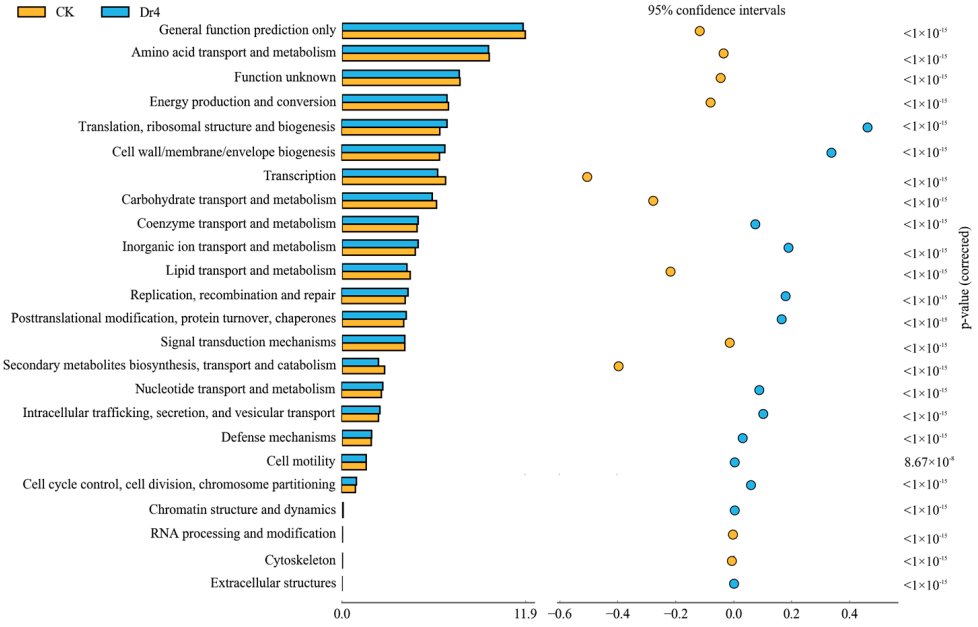


Figure 8. Function prediction of soil bacterial genes between CK (bare soil stage) and Dr4 (harvest stage). The left panel shows the abundance ratios of different function genes in CK and Dr4. The middle panel displays the differential ratios of functional abundances within the 95% confidence interval. The values on the rightmost side represent *p*-values.

4. Discussion

Soil cover is an essential step for the development of *Dictyophora rubrovolvata*. Studies have found that using different proportions of *Pseudomonas* and the substrate of line grass and seafood mushroom waste instead of bamboo cultivation can enhance soil nutrient accumulation and microbial community stability, and significantly affect the quality and yield of the fruiting body of *Dictyophora indusiata* [25]. A study on the sugarcane–*Dictyophora indusiata* intercropping system reveals that the content of soil nutrients is mainly affected by fungi, bacteria, the soil metabolome, and soil enzyme activity [26]. This highlights the importance of microbial communities and soil nutrients in cultivating *Dictyophora*. Therefore, during the whole growth cycle of *D. rubrovolvata*, studying the changes in microbial communities and physical and chemical properties of the soil and its dynamic coupling rules would

be helpful to reveal the possible mechanism of continuous-cropping soil obstacles. It also provides a theoretical reference for improving soil utilization, reducing production costs, and constructing a green and precise cultivation mode based on microecological regulation in production practice.

The growth of *D. rubrovolvata* requires a sufficient carbon source from the outside. After covering the soil, the mycelium can only obtain a carbon source from the soil to continue to proliferate. Organic carbon is an important component of soil [27] and is positively correlated with soil fertility. The results of this study showed that the organic carbon content was significantly reduced, indicating that the *D. rubrovolvata* took the organic carbon in the soil as the main carbon source for growth and development during the growth process. This resulted in a significant decrease in the organic carbon content in the soil after *D. rubrovolvata* cultivation, which further affected the repeated utilization of the soil. The nitrogen in the soil is also an important nitrogen source for the growth and utilization of mycelium. Therefore, in the early stage of *D. rubrovolvata* growth, the total nitrogen was utilized by the mycelium, resulting in a substantial reduction in its quantity. In the late growth stage, a large number of extracellular enzymes secreted by mycelium accelerated the decomposition of soil organic matter and promoted the release of nitrogen from the humic complex [28]. At the same time, as the activities of soil microorganisms, including those with nitrogen-fixing abilities, intensify, they could potentially facilitate the replenishment of nitrogen within the soil. The pH value functions as a critical indicator of the soil's acidity or alkalinity, exerting a direct influence on the solubility and bioavailability of essential nutrients, such as nitrogen, phosphorus, and potassium, within the soil environment. The possible reasons for the increase in soil pH in this study may be related to the ability of certain microorganisms (such as Actinomycetes and some bacteria) to decompose organic matter and release alkaline metabolites, as well as the depletion of acidic substances in the soil [29]. The low soil pH prevailing during the mycelium and primordium developmental stages facilitated the conversion of inorganic phosphorus into available phosphorus [30]. This available form was more readily taken up and utilized by the mycelium of *D. rubrovolvata*, consequently leading to a notable decline in the soil's phosphorus content. An elevation in the pH value during the egg and harvest stage hindered the conversion rate of inorganic phosphorus to available phosphorus. Consequently, this led to a corresponding decline in the consumption of organic phosphorus. As a result, the total phosphorus content showed a significant increase pattern. Therefore, it is inferred that the imbalance of soil nutrients and the change in pH led to the decline of soil texture [31], which may be the cause of continuous-cropping obstacles.

This study also revealed that, throughout the entire growth cycle of *D. rubrovolvata*, the organic carbon content in the soil underwent the most significant changes. Initially, it decreased markedly and then stabilized at a low level, well below that of the bare soil stage. In contrast, the nitrogen content in the soil rose until it reached the level observed in the bare soil stage. Meanwhile, the potassium content also increased and surpassed the level found in the bare soil. These changes suggest that the soil's nutrient composition has become imbalanced and disordered. This finding largely aligns with the outcomes of research conducted on other edible fungi [32–35]. Building upon this discovery, this study suggests the first green and precise cultivation strategy for *D. rubrovolvata* centered around microecological regulation. That is, during the production and cultivation of *D. rubrovolvata*, an appropriate amount of carbon sources should be added during the mycelial growth stage to sustain a high level of organic carbon in the soil, thereby meeting the growth requirements of the mycelium.

This study revealed a consistent upward trend in the number of bacterial species within the soil across the entire growth cycle of *D. rubrovolvata*. In contrast, the number of

fungal species exhibited a continuous decline. Notably, both the compositional diversity and relative abundance of soil bacterial and fungal communities underwent substantial changes at various growth stages, displaying distinct stage-specific patterns.

At the bacterial level, the soil of cultivating *D. rubrovolvata* mainly consists of Actinobacteriota, Proteobacteria, Chloroflexi, Gemmatimonadota, Acidobacteriota, and Bacterioidota. This outcome bears a resemblance to the predominant bacterial composition identified in the substrate following mushroom composting fermentation, as investigated by Wang et al. [36]. The findings of this study indicate that during the complete growth cycle, Actinobacteriota populations underwent a substantial reduction. Additionally, the organic carbon content in the soil dropped significantly, whereas the total nitrogen, phosphorus, and potassium contents showed an upward trend. Is there a correlation between the aforementioned increases and decreases? By conducting correlation analysis between soil physicochemical properties and bacterial communities, it was observed that *Streptomyces* (a typical genus within Actinomycetes) exhibited a notably positive correlation with organic carbon content. Conversely, it displayed a significant negative correlation with total phosphorus, total potassium, and soil pH. *Streptomyces*, as ubiquitous and vital microorganisms in soil, play a pivotal role in organic matter decomposition, particularly excelling in degrading complex compounds such as cellulose, lignin, and fatty acids [37]. Through secreting diverse enzymes, they efficiently break down organic carbon sources like plant residues and leaf litter [38], granting them a competitive advantage in organic-rich soils where they proliferate extensively. This process not only accelerates organic carbon transformation and release but also establishes a dynamic cycle, influencing soil organic carbon accumulation [39]. In other words, an elevated soil organic carbon content serves to further boost the metabolic vigor of *Streptomyces*, with its robust metabolism subsequently enhancing carbon transformation processes. Concurrently, *Streptomyces* metabolites modulate the soil microenvironment [40,41], creating a feedback mechanism conducive to organic carbon decomposition. These findings suggest that the dynamic fluctuations of Actinomycetes populations can substantially influence the variations in multiple soil nutrients and pH levels. Dorchenkova et al. have found that Actinomycetes can promote the formation of soil aggregates, enhance the production of organic carbon, and improve soil fertility. Moreover, their population size is notably regulated by soil pH, exhibiting dynamic response patterns [42]. These findings are highly consistent with the outcomes of our current study. Simultaneously, the prediction analysis of bacterial functional genes revealed that the proportion of functional genes implicated in amino acid, carbohydrate, and secondary product metabolism in bacteria at the harvest stage was lower compared to that at the bare soil stage. This discovery implies that bacterial metabolism during the harvest stage exhibits relatively low activity. Consequently, it can be deduced that the imbalance within the bacterial population in the soil exerts an influence on soil fertility [43]. Based on this discovery, this study proposes the second green and precise cultivation strategy for *D. rubrovolvata* based on microecological regulation. That is, during the production and cultivation of *D. rubrovolvata*, an appropriate amount of Actinomycetes inoculant could be added during the mycelium stage to increase the organic carbon content, promote the rapid growth of the mycelium of *D. rubrovolvata*, and help overcome the soil continuous-cropping obstacle caused by the deficiency of organic carbon.

At the level of the fungal kingdom, the abundance and diversity of fungi in the harvesting stage of *D. rubrovolvata* were significantly lower than that in the bare soil stage, which was consistent with the performance of soil fungi before and after the cultivation of *Morel* by Qi et al. [44]. The Ascomycota, Basidiomycota, and Moriterellomycota are the main groups, accounting for more than 90%. During the egg stage, the abundance of Moriterellomycota increased significantly, while that of Basidiomycota decreased sig-

nificantly. Tan et al. [45] have found that the Moriterellomycota is relatively high in the soil fungal community of morel, and some are suspected to be pathogenic bacteria, which may affect the transformation of morel mycelium into fruiting bodies. Consequently, it is hypothesized that the notable proliferation of Moriterellomycota fungi during the egg stage of *D. rubrovolvata* may also exert an influence on the formation of its eggs, consequently impacting the overall yield. The Ascomycetes fungi, *Trichoderma* and *Penicillium*, which attain their maximum abundance during the primordium stage, are extensively employed as biocontrol agents. These fungi can effectively suppress a diverse array of crop diseases. *Trichoderma* can inhibit the growth of many pathogenic fungi [46]. *Penicillium* fungi have the ability to produce metabolites, including antibiotics, antiviral agents, and mycotoxins [47]. *Fusarium*, a common pathogen of edible fungi [9,48,49], is effectively inhibited by the powerful synergistic action of *Trichoderma* and *Penicillium* fungi. Meanwhile, *Penicillium* and *Trichoderma* are also widespread and common opportunistic pathogens in the environment. Therefore, it is necessary to reasonably regulate their relative abundance in the soil. The findings indicate that an imbalance in the fungal population structure can potentially give rise to the occurrence of diseases during the whole growth cycle of *D. rubrovolvata*. On the basis of this discovery, this study proffers the third green and precise cultivation strategy of *D. rubrovolvata* revolved around microecological regulation. That is, prior to sowing *D. rubrovolvata*, the cultivation soil must undergo appropriate pre-sowing amendments. This involves exposing it to sunlight and applying beneficial microbial agents, such as Actinomycetes-based formulations, to suppress the growth of pathogenic fungi, restructure the microbial community, and thereby avert soil continuous-cropping obstacles.

5. Conclusions

This study systematically analyzed the soil nutrients, pH, and the dynamic changes in microbial communities in the whole growth cycle of *D. rubrovolvata*. It was found that there was a dynamic coupling relationship among the growth stage of *D. rubrovolvata*, soil microbial communities, soil nutrients, and pH. The imbalance of soil nutrient components, the disorder of soil pH value, and the dysbiosis of microbial community may be the important reasons for the continuous-cropping obstacles of *D. rubrovolvata*. This provides a theoretical reference for elucidating the interaction mechanisms between soil and edible fungi. Three green and precise cultivation strategies based on micro-ecological regulation have been proposed to address the problem of continuous-cropping obstacles. These measures involve disinfecting the cultivation soil prior to sowing *D. rubrovolvata*, as well as supplementing carbon sources and applying Actinomycetes inoculants during the mycelial growth phase. The strategies foster a synergistic relationship between the sustainable development of the edible fungi sector and the circular utilization of soil resources.

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