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Multi-Trophic Species Diversity Contributes to the Restoration of Soil Multifunctionality in Degraded Karst Forests through Cascading Effects

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Abstract: The biodiversity–ecosystem function (BEF) relationship is the basis for studying the restoration of degraded ecosystems, and the simultaneous assessment of multi-trophic-level biodiversity and ecosystem multifunctionality relationship is more conducive to unravelling the restoration mechanism of degraded ecosystems, especially for degraded forest ecosystems with harsh habitats and infertile soils such as karst. In this study, we evaluated the biodiversity and soil multifunctionality (SMF) of degraded karst forests (scrub, SB; secondary growth forests, SG; old-growth forests, OG) in the Maolan National Nature Reserve, China, using 30 sample plots. Biodiversity and soil multifunctionality (SMF) at three trophic levels (plant–soil fauna–soil microorganisms), were assessed through vegetation surveys and soil sampling. One-way ANOVA showed that SMF increased with natural restoration, but multi-trophic level biodiversity showed different trends. Pearson's correlation analysis showed a positive correlation between plant species diversity and SMF ($p < 0.001$), whereas soil fauna and soil microorganisms were negatively correlated with SMF. Structural equation modeling revealed a cascading effect of the multi-trophic level on the stimulation of the SMF during restoration. Only soil microorganisms exhibited a direct driving effect on SMF ($p < 0.001$), whereas plants indirectly influenced soil microorganisms through soil fauna, which subsequently affected the SMF. Although we observed the negative effects of increased plant diversity on soil fauna and soil microbial diversity in terms of quantitative relationships, the increase in soil fauna species and the evenness of soil microbial function still contributed to SMF restoration. This study revealed the cascading effects of multi-trophic diversity in promoting SMF restoration and emphasized that soil microbes are key to unraveling restoration mechanisms and processes, whereas soil fauna is an important intermediate link.

Keywords: degraded karst; multi-trophic level; natural restoration; soil fauna; soil microorganisms

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1. Introduction

Soil is an important component of terrestrial ecosystems and a material basis for the survival of many plants and animals. It is the carrier of numerous ecological processes, connecting the material cycle and energy flow between above-ground plants and below-ground organisms [1,2]. Soil multifunctionality (SMF) provides and maintains multiple ecological functions, such as soil nutrient cycling, nutrient storage, and physical stability [3]. SMF serves as a comprehensive indicator of soil quality [4–6]. More importantly, its integrity is the basis of ecosystem functions and services [7]. Karst landscapes are characterized by environmental fragility, high sensitivity, and poor water-holding capacity. They are highly susceptible to vegetation cover degradation and soil erosion [8–12]. The regional

SMF can reflect ecosystem conditions, especially in degraded karst forest environments. Biodiversity has been recognized as a determinant of fulfilling ecosystem functions [13,14]. In traditional studies on biodiversity–ecosystem function, greater emphasis has been placed on biodiversity at the primary trophic level [15]. The role of biodiversity across multi-trophic levels is crucial to ecosystem function yet has gained limited attention. Thus, examining the effect of biodiversity on ecosystem multifunctionality from a multi-trophic viewpoint can advance our thorough understanding of BEF.

Of the three trophic levels (producer–consumer–decomposer), most early studies have focused on the primary trophic level (i.e., plant diversity). Research has indicated that there is a positive correlation between ecosystem functioning and plant diversity [16,17], and that the majority of the effects of plant diversity on ecosystem functioning are caused by changes in plant species composition and functional features [6]. The species composition of plant communities can directly influence changes in soil microbial composition (e.g., through litter quantity and quality inputs) or indirectly (e.g., through changes in abiotic factors), ultimately modulating ecosystem functioning [18]. The influence of soil microorganisms on ecosystem multifunctionality has received increasing attention since the advent of high-throughput sequencing technology [19]. Most studies have reported a positive correlation between soil microbial diversity and ecosystem function [20,21]; however, some studies have found a negative correlation between ecosystem functioning and bacterial diversity [22]. A growing body of work has confirmed the significant role of soil microbial diversity in ecosystem functioning [20,21,23]. Microbial diversity is involved in the biogeochemical cycling of soil nutrients; it acts as a decomposer of organic matter, plant mutualists, and pathogens, affecting the growth of macro-organisms [24], and can emit greenhouse gases that may accelerate global climate change [25]. In summary, microorganisms play a key role in maintaining ecosystem function in a variety of ways [26].

Soil fauna, a key element of soil biodiversity, is vital to terrestrial ecosystem processes and acts as an important consumer in ecosystems [27,28]. Compared with producer and decomposer trophic levels, there have been relatively few studies on ecosystem functions involving the consumer trophic level. The temporal and spatial patterns of the ecological functions of soil fauna have long been underexplored [29]. Following the launch of the Global Soil Biodiversity Initiative, the distribution patterns of soil fauna diversity have began to receive increased attention [15,30]. The prevailing idea believes that soil microorganisms directly drive soil ecological processes, whereas a soil fauna primarily act as a regulator for microbial communities. In other words, the soil fauna fulfills its ecological function mainly through indirect effects [31]. The ecological functions of soil fauna are complex and influenced by environmental conditions and functional taxa at various spatial and temporal scales. These impacts typically extend across feeding relationships in the food web and can have cascading effects on the entire body [32]. Overall, the ecological functions of soil fauna include structural modifications (i.e., habitat formation and destruction) [33–35], soil organic carbon accumulation (such as decomposition and transformation of organic matter) [36–38], and plant health maintenance (i.e., growth, pathogen control, and stress resistance) [39,40]). Given that soil fauna may have different effects (e.g., positive vs. negative) on the key ecological functions of soil physical structure, organic carbon, and plant growth, an increasing number of recent studies have focused on the concept of ecosystem multifunctionality to elucidate the combined effects of soil fauna from the perspective of SMF [41]. Although numerous studies have elucidated the relationships governing ecosystems functioning at a single trophic level, understanding the impact of biodiversity loss on ecosystem functioning in complex natural ecosystems requires integrating processes across multiple trophic levels and considering species competition within each trophic level [13]. In degraded karst forest ecosystems, the ecological function of soils as a scarce resource, with higher trophic levels often functioning as potential components and more important predictors of multifunctionality, has become exceptionally important. Therefore, it is necessary to include soil fauna in restoration studies on degraded karst forest ecosystems.

Although tens of thousands of studies have been published since the development of BEF, numerous studies have confirmed the driving role of plant diversity and soil biodiversity for soil multifunctionality, most of these studies have focused on a single trophic level of biodiversity. For example, overwhelming research on the relationship between functional diversity and ecosystem functioning has been limited to a single trophic level, plant diversity, ignoring the important role of the functional traits of soil microbes and fauna in ecosystem processes [42,43]. Research on ecosystem functioning that integrates multiple trophic levels, particularly those that include all three trophic levels of producers, consumers, and decomposers, is still lacking. As of 1 January 2024, according to Web of Science, this study conducted an econometric analysis of the literature using "plant diversity", "soil microbial diversity", "soil fauna diversity", "ecosystem function", and "ecosystem multifunctionality" as the combinations of subject headings. Overall, the greatest number of studies were obtained by searching for a single trophic level and ecosystem function simultaneously. In contrast, the number of studies decreased significantly by more than one order of magnitude when searching for both a single trophic level and ecosystem multifunctionality. For both ecosystem function and ecosystem multifunctionality, the largest number of studies have focused on plant diversity, followed by soil microbes. Studies on the trophic level of soil fauna have been less frequent, with a decreasing trend as trophic levels gradually increased (Table 1).

Table 1. Bibliometric characterization of polytrophic biodiversity and multifunctionality based on Web of Science online research data from 2008 to 1 January 2024.

Heading	Ecosystem Function	Ecosystem Multifunctionality
Plant diversity	15,895	719
Soil microbial diversity	5420	328
Soil fauna diversity	751	26
Plant diversity + Soil microbial diversity	4149	274
Plant diversity + Soil fauna diversity	593	21
Soil microbial diversity + Soil fauna diversity	294	8
Plant diversity + Soil fauna diversity + Soil microbial diversity	241	8

In addition to anthropogenic disruptions and destruction, the karst zone constitutes a mosaic of several microhabitats, which are non-uniformly distributed or discontinuous (e.g., unsustainable farming and extensive logging), leading to severe ecosystem degradation in the southwestern part [44–46]. Due to these landscape characteristics, this region has more challenges for restoration than a normal landscape, and it is prone to irreversible damage. In such extreme environments, SMF is highly sensitive to natural restoration. To investigate the restoration of each ecosystem component during the degradation restoration, this study focused on the natural restoration of degraded karst forests across shrubs (SBs), secondary growth forest (SG), and old-growth forest (OG) stages. Ten fixed sample plots were set up in each gradient, totaling 30. The restoration of plant diversity, soil microbial diversity, soil fauna diversity, and soil multifunctionality in karst forests were analyzed. We also investigated how above-ground and below-ground species diversity drives SMF. For one thing, it addresses the gap in research on the function of multi-trophic ecosystems containing soil fauna in karst areas. For another, it helps to advance the understanding of the restoration mechanism in degraded karst forests and provides a reference for the conservation and restoration of these ecosystems. In this study, we solved the following questions: (1) how plants, soil fauna, soil microbes, and SMF respond to natural restoration in degraded karst forests and (2) what the relationship between multi-trophic level species diversity and SMF is, as well as the role of these factors in driving SMF. The aim of this study is to investigate in depth the changes in multi-trophic-level species diversity during natural restoration of degraded karst forests and their impact on soil multifunctionality, with a view to improving the understanding of the restoration mechanisms and providing a scientific basis and reference for the conservation and restoration of these ecosystems.

2. Data and Methods

2.1. Study Area

The research site is situated in Maolan National Nature Reserve in Libo County, Guizhou Province (107°52′10″–108°5′40″ E, 25°09′20″–25°20′50″ N) (Figure 1). It stands at an elevation of 430–1078 m and is dominated by a subtropical monsoon climate. The average annual temperature is 15.3 °C. This area has annual mean precipitation surpassing 1700 mm, mostly in April–October, with an average annual relative humidity of 83%. The area belongs to a typical karst landscape (karst peak forests and peaks and depressions), the ground bedrock is exposed, the soil-forming parent rock is mainly dolomite and limestone, the soil is mainly black limestone soil, the soil layer is shallow and discontinuous, and is mostly stored in rock crevices, calcium-rich and salt-rich, and has a high organic matter content. Subtropical evergreen deciduous broad-leaved mixed woods make up the majority of the vegetation type.

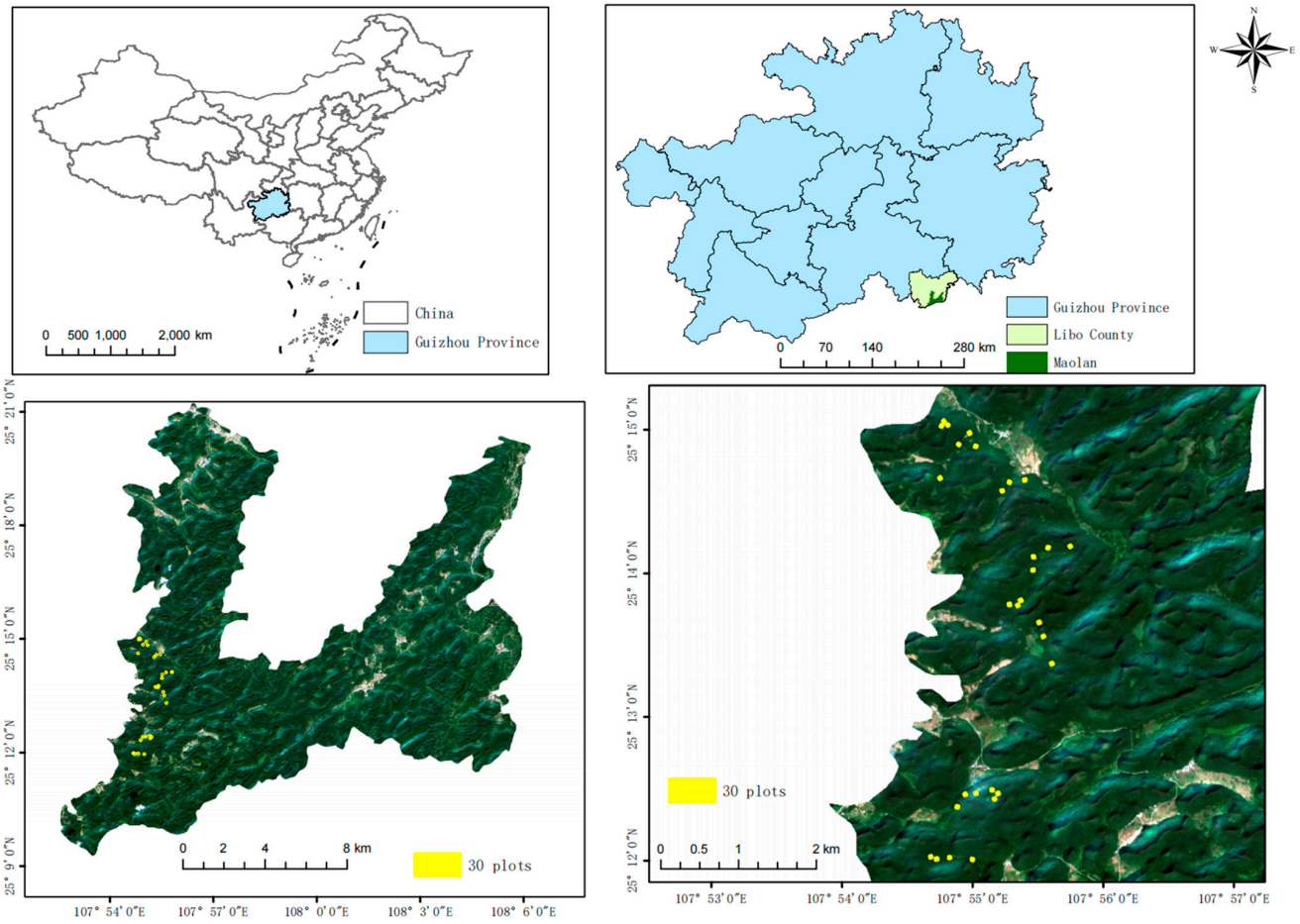

Figure 1. Location of karst landscape study sites (30 forest dynamic plots) in Maolan National Nature Reserve, Guizhou, China.

2.2. Sample Plot Setting

Based on the standards of Condit (1998) [47] and the standard of "Technical specification for investigation and assessment of national ecological status-Field observation of forest ecosystem" (HJ 1167-2021) raised by the Ministry of Ecology and Environment of China [48], as well as the investigation of the community structure of the sample plots, the spatial and temporal replacement method was used to construct the sample plots, and the test areas were selected in accordance with the principles of representativeness, consistency, and exemplary character. In this study, three stages (SB, SG, and OG) were selected as typical natural restoration stages in the karst region [49]. To prevent community-based

crossbreeding zones and the effects of spatial autocorrelation, the distance between every two adjacent plots was greater than 50 m. Thirty sample plots were established from June to August 2021, consisting of ten 10 m × 10 m SB plots, ten 30 m × 30 m SG plots, and ten 30 m × 30 m OG plots. In the SB phase, the last selective logging occurred 11 years ago in 2010 and propagules were left behind to allow for the natural restoration of shrubbery into the old-growth forest. The SG stage had the same anthropogenic disturbances as the SB stage (selective cutting), with the most recent occurring 37 years ago in 1984. Based on historical evidence and enquiries from local elders, natural restoration continued for more than 100 years during the OG stage. In addition, they share the same regional species pool in all stages of restoration, with no anthropogenic disturbance during natural restoration.

2.3. Data Acquisition

2.3.1. Soil Sampling and Plant Survey

The soil samples were taken in October 2021 with a five-point sampling technique. In each sample plot, a midpoint on the diagonal was selected as the center sampling point. On the diagonal, four points at equal distances from the central sample point were selected as sampling points. We ensured that these five points were evenly distributed to guarantee a representative sample. For every sampling site, five soil samples were taken from the 0 to 20 cm soil layer. These samples were then homogenized and mixed to obtain uniform soil samples. Thirty composite soil samples were collected (Figure S1). For each sample plot, one portion of the soil sample was air-dried for the determination of soil physicochemical properties and mineral content (referring to Bauerstein's Agrochemical Analysis of Soil), and the other was cryopreserved at −20 °C for the analysis of DNA extraction from soil organisms (soil fauna and microorganisms). Plant species surveys were conducted for each plot following the methodology proposed by Condit (1998), and diameter at breast height > 1 cm diameter were labeled. Given that the hierarchy of our study follows a sequence from plants to soil fauna and then deeper to soil microbes, this coincides with the top-down cascade effect of the three trophic levels in ecology (surface to the depth). Through the detailed investigation of the community characteristics of different natural stages, the forest microhabitat is complex, diverse, and very rich in biological resources, with a total of 396 species of plants in the sample site. There were 72 species of plants in the SB stage, belonging to 42 families and 62 genera, and the shrubs were diverse and generally low, with *Lindera communis* and *Celtis sinensis* as the main dominant species. In the SG stage, there were 172 species of plants belonging to 57 families and 109 genera, the diameter at breast height (DBH) and the height of trees increased significantly, and the tree l restoration layer dominated, with *Platycarya strobilacea* and *Cornus parviflorus* as the main dominant species. In the OG stage, there were 152 species of plants belonging to 53 families and 99 genera, dominated by tall and robust trees, with *Acer wangchii* and *Boniodendron minus* as the main dominant species (Table S9).

2.3.2. Soil DNA Extraction and Metagenomic Sequencing

The extraction of total genomic DNA (0.5 g) from each soil sample was carried out utilizing the FastDNA®Spin Kit for soil, following the manufacturer's directions provided by MP Biomedicals (Irvine, CA, USA). Subsequently, the quality of the extracted DNA was thoroughly assessed by quantifying its concentration and purity using a TPS-380 microfluorometer (TurnerBio-Systems, Sunnyvale, CA, USA) as well as a NanoDrop 2000 Ultra Microspectrophotometer (Thermo Scientific, Waltham, MA, USA). To achieve an average fragment size of approximately 400 bp, the isolated DNA was fragmented using a Covaris M220 sonicator from Gene Company Limited (Shanghai, China). For the construction of a paired-end library, these fragmented DNAs were integrated with the NEXTflex™ Rapid DNA Sequencing Kit sourced from Bioo Scientific (Austin, TX, USA). Adapters, equipped with hybridization sites compatible with all sequencing primers, were appended to the blunt ends of the fragments. The paired-end sequencing process was executed at Majorbio Bio-Pharm Technology Co. Ltd. (Shanghai, China), adhering to the manufacturer's instruc-

tions and utilizing the Illumina NovaSeq platform (Illumina Inc., San Diego, CA, USA) in conjunction with the NovaSeq Reagent Kit for sequencing (www.illumina.com).

Multiple samples were sequenced, and subsequently appending indexed tagged sequences were investigated to identify their respective sources. Upon extracting the data, raw reads were generated and archived in the FASTQ format v0.20.0 (https://github.com/OpenGene/fastp, accessed on 19 February 2024). We utilized the FASTQ tool on the Majorbio cloud platform (accessible free of charge at https://cloud.majorbio.com/, accessed on 24 August 2023) to eliminate adaptor sequences, trim, and discard low-quality reads containing N bases. These reads were filtered based on a minimum length threshold of 50 bp and a quality threshold of 20 [50]. After rigorous quality control measures, we obtained a total of 1,776,367,626 clean reads. To assemble these high-quality reads into contigs, we employed MEGAHIT with the following parameters: kmer_min = 47, kmer_max = 97, step = 10 (v1.1.2, https://github.com/voutcn/megahit, accessed on 19 February 2024). This tool utilizes compressed de Bruijn graphs for the assembly process [51]. Only contigs with a bp value of at least 300 were considered for the final assembly.

The high-quality reads were submitted to the NCBI database and the accession number PRJNA951346 (https://submit.ncbi.nlm.nih.gov/, accessed on 24 August 2023) for ORF identification in contigs using MetaGene [52]. Genes with nucleic acid lengths of 100 bp or longer were chosen and translated into amino acid sequences based on the NCBI translation table. Utilizing CD-HIT software v4.6.1 (http://www.bioinformatics.org/cd-hit/, accessed on 24 August 2023) [53], we constructed non-redundant gene sets with a sequence identity and coverage threshold of >90%. The representative sequences of these genes were compared with NCBI-n and KEGG databases v94.2 (https://www.genome.jp/kegg/, accessed on 24 August 2023) using a strict evaluation threshold of 1×10^{-5} based on the NCBI NR database. Additionally, the non-redundant gene catalog was taxonomically and functionally annotated by using BLASTP implemented in DIAMOND v0.9.19 [54].

Gene-based taxonomic annotation of species against the NR database was performed to obtain species and abundance information at each taxonomic level (domain, kingdom, phylum, order, order, family, genus, species) in each sample. Subsequent statistical analyses at the species level could be performed based on this table. Here, abundance was calculated as Reads Number.

2.3.3. Soil Fauna Taxa Selection

Based on the results of the gene-based taxonomic annotation of species in the NR database and the species abundance calculated by summarizing the corresponding gene abundance in the species, we obtained species and abundance information tables for soil fauna at the species level. Since our study area was formerly marine (the region was marine until the Middle–Late Triassic age) [55,56], we screened soil fauna species at the phylum level according to habitat, excluding aquatic and marine-inhabiting species. Six soil fauna phyla were finally retained, including Chordata, Invertebrata, Arthropoda, Nematoda, Platyhelminthes, and Rotifera.

2.3.4. Soil Microorganism Taxa Selection

Considering the fact that bacteria and fungi are commonly used as decomposers in ecosystems as well as the importance and widespread value of bacteria, archaea, and fungi in soil ecosystems, the three taxa of bacteria, fungi, and archaea were therefore combined to represent the trophic level of soil microorganisms for subsequent statistical analyses.

2.3.5. Determination of Soil Physical and Chemical Properties

Fifteen functional indicators were selected to calculate the SMF, including soil physical properties (soil mechanical composition: clay, silt, and sand) and soil chemical properties, such as total carbon (TC), particulate organic carbon (POC), easily oxidized carbon (EOC), light fraction organic carbon (LFOC), total nitrogen (TN), available nitrogen (AN), total phosphorus (TP), total calcium (TCa), exchanged calcium (Eca), soil urease (SUE),

soil neutral phosphatase (S-NP), and pH. An elemental analyzer was used to determine the concentrations of TC and TN (UNICUBE trace, Elemental, Langenselbold, Hess, Germany). POC was measured by the wet sieving method, EOC by oxidation with potassium permanganate, and LFOC by the extraction method with 1.7 g cm^{-3} NaI solution. AN determination was performed by using alkaline diffusion, and TP measurement was performed by using the molybdenum–antimony colorimetric method. TCa and Eca were evaluated by using primary absorption spectrometry and soil pH using a pH meter (Leici, PHS-3C, Shanghai, China). The Solarbio Activity Assay Kit (Solarbio International Inc., Beijing, China) was used to gauge SUE activity and S-NP.

2.3.6. Species Diversity Calculations

Species diversity was calculated for each trophic level based on species abundance information (plants, soil fauna, and soil microorganism) (Table S4). Species richness, SR, is represented using the total number of species. The Shannon–Wiener diversity index H′ was determined by using the following equation [57]. Margalef Margalef's richness index F was calculated as follows [58]:

$$SR = S \quad (1)$$

$$H' = -\sum_{i=1}^{S} P_i ln P_i \quad (2)$$

$$D = \frac{S-1}{lnN} \quad (3)$$

where S denotes the total number of species; P_i represents the proportion of the ith species to the total; and N represents the total number of individuals.

Statistical analyses of soil fauna and soil microorganisms in this study were calculated using species level (Tables S5 and S6).

Beta diversity is defined as the degree of species substitution along an environmental gradient, also known as the rate of species turnover and the rate of species substitution [59,60]. In addition to this, β-diversity includes differences in species composition between communities; the fewer the species shared between different communities or between different points on a given environmental gradient, the greater the β-diversity [61]. The species richness of the soil fauna and soil microorganisms were represented by the OTU (Optical Transport Unit) richness (Tables S2 and S3). Bray–Curtis distances were calculated based on the abundance information of the species, which is one of the commonly used metrics for reflecting the variability among communities in ecology. PCoA (principal coordinate analysis) is a classic multidimensional scaling (MDS) analysis method [62], and the biggest difference with PCA is that PCoA can evaluate the similarity between samples based on other distance scales except the Euclidean distance. PCoA can simplify the data structure by down-scaling the distance matrix of the samples to show the natural distribution of the samples under a specific distance scale. Finally, we adopted the first principal component PC1 axis with the largest variance contribution to characterize the beta diversity (the larger the value means that this principal component can distinguish the samples better) (Tables S7 and S8).

2.3.7. Calculation of *SMF*

In order to assess the ability of soils to fulfil multiple functions at the same time, a soil multifunctionality index needs to be calculated. Firstly, it is necessary to classify the functions of the soil and determine the relevant soil indicators; secondly, the soil multifunctionality index is calculated. Since no uniform standards for the quantitative index and calculation method of SMF are available, researchers have adopted different calculation methods and indicators. Based on the existing literature on soil multifunctionality, this study, similar to most ecological studies, selected soil indicators that were mainly related to ecosystem carbon, nitrogen, and phosphorus cycles. These included TC, POC, LFOC, EOC, TN, AN, TP, SU, S-NP, TCa, ECa, and pH (Figure S3). In addition to the indicators of soil chemical properties, soil physical properties were also considered in the

quantification of soil multifunctionality. Overall, these variables are good indicators of important soil functions such as nutrient cycling and nutrient pool building. To estimate soil multifunctionality, we used three methods (mean value, factor analysis, and threshold method) to calculate soil multifunctionality. The results of the three methods showed that the results of the three multifunctionality calculation methods are very close (Pearson $r = 0.99$) (Figure S2). The threshold method can avoid the bias caused by the excessive weight of some ecosystem function categories and does not affect the final results regardless of whether the factor-multifunctionality relationship is linear or not, with a wide range of applications. Therefore, the soil multifunctionality index, calculated using the threshold method, was selected for the subsequent analysis.

2.4. Data Analysis

All analyses were performed by using R 4.2.3 [63]. Biodiversity indices were calculated using the "vegan" package, and trends in soil physico-chemical properties, polytrophic biodiversity, and SMF during the three restoration stages were compared using one-way analysis of variance (ANOVA) and multiple comparisons with the least significant difference ($p < 0.05$). Correlations between plant species diversity, soil fauna diversity, soil microbial diversity, and SMF were tested using the linear Pearson correlation coefficient ($p < 0.05$). A structural equation model was created with SMF as the response variable and five diversity indices as predictors to investigate the direct and indirect causal links between plant diversity, soil faunal diversity, soil microbiological diversity, and SMF. The α and β scales were utilized to group predictor variables, including soil microorganisms and soil fauna, and we calculated the relative contribution of diversity to SMF on both scales. The validity of the model structure was evaluated using traditional structural equation modeling (lavaan) by performing a *chi*-square test on the sum of squares of the differences in the variance–covariance matrices between the two multivariate variables generated from the observed data and the model predictions. Due to the limitations of the requirements of structural equation modeling, our data could not be constructed in the model. For this reason, we performed a principal component analysis on the SEM analysis dataset. This allowed for fully leveraging the first principal component (α-diversity). Specifically, we extracted three α-diversity variables of plants, soil fauna, and soil microorganisms with reduced dimensionality. For plant diversity in this model, the plant SR, plant Shannon–Wiener, and plant Margalef indices were used. In the case of soil fauna diversity, the soil SR, Shannon–Wiener, Margalef, and β-diversity indices were introduced. In addition, the soil β-diversity, microbial Shannon–Wiener, microbial Margalef, and microbial SR indices were selected for soil microbial diversity. The constructed structural equation models were evaluated using the great likelihood, non-significant chi-square test (chi-square/df < 3, $p > 0.05$), and relative fitness index ($CFI > 0.95$), and the goodness-of-fit index ($GFI > 0.90$) was used for fitting.

3. Results

3.1. Responses of Plant Species Diversity, Soil Fauna Diversity, Soil Microbial Diversity, and SMF to the Restoration Stage

During the natural restoration of degraded karst forests, plants, soil fauna, soil microorganisms, and soil multifunctionality different responses to the restoration stage were shown. Both soil multifunctionality and plant diversity increased significantly with natural restoration, particularly the transition from the shrub stage to secondary growth forest, and they reached a saturation state in the late stage of restoration (old-growth forest) (Figure 2A–D). The fauna species richness index and β-diversity index decreased significantly with natural restoration (Figure 2E,H). However, the Shannon–Winner index of soil fauna increased significantly with natural restoration (Figure 2F). The soil microbial species diversity did not change significantly during natural restoration, and the soil microbial β-diversity index decreased significantly with natural restoration (Figure 2L).

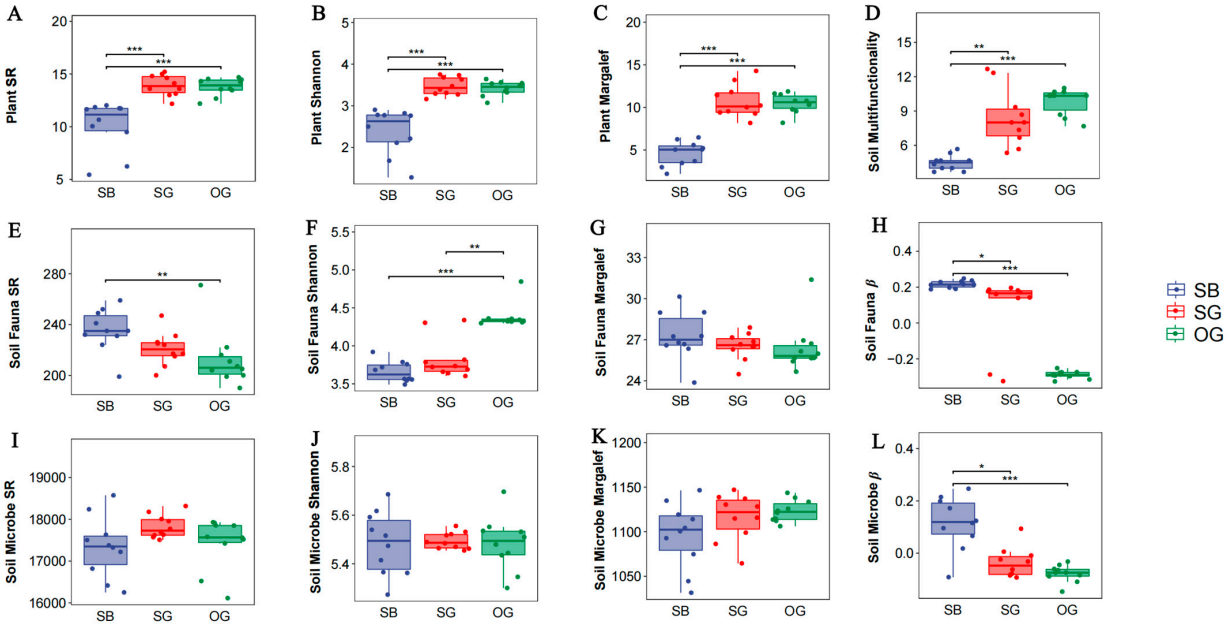

Figure 2. Responses of plant diversity (**A**–**C**), soil fauna diversity (**E**–**H**), soil microbial diversity (**I**–**L**), and SMF (**D**) to the restoration stages, where *p* value represents the total difference between groups and indicates the significance level of differences between groups (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$).

3.2. Relationship between Species Diversity at Multiple Trophic Levels and SMF

SMF was significantly and positively correlated to the plant SR, plant Shannon–Wiener, and plant Margalef indices (Figure 3A–C). By comparison, the soil fauna SR and soil fauna *β*-diversity indices were significantly negatively correlated to SMF (Figure 3D,G), whereas Figure 3G exhibits a peculiarly discontinuous distribution due to the discrete distribution of samples from the three phases on the PC1 axis (Figure S6). A significantly positive correlation was found between SMF and the soil fauna Shannon index (Figure 3E). The soil microbial SR, soil microbial Shannon–Wiener, and soil microbial Margalef indices were not significantly correlated with SMF. The soil microbial *β*-diversity index exhibited a significantly negative correlation to SMF (Figure 3K), and the remaining diversity had no significant correlations with SMF.

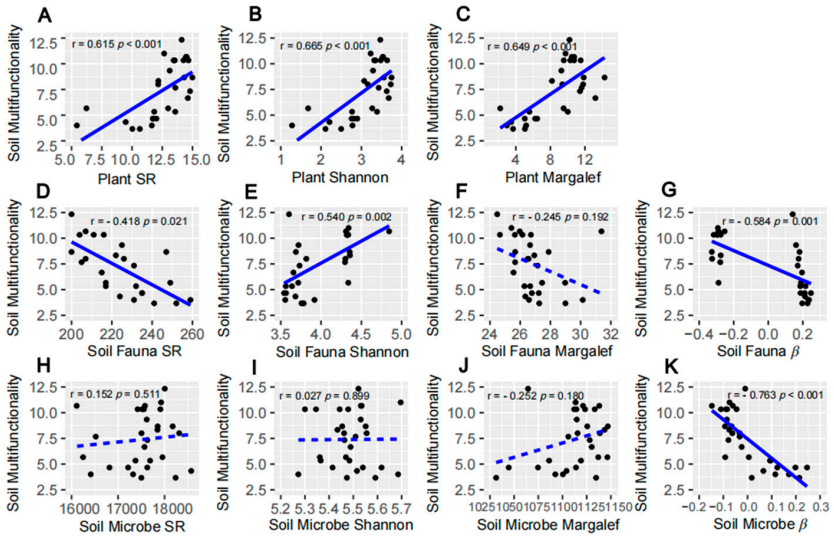

Figure 3. Correlations between plant diversity (**A**–**C**), soil fauna diversity (**D**–**G**), soil microbial diversity (**H**–**K**), and SMF. The blue line indicates the trend and the solid black dots indicate the values of the test samples.

3.3. Driving Mechanism of Single Trophic Levelon SMF

The results of the SEM model showed that plant diversity had a significant positive effect on SMF during natural restoration (Figure 4A); soil microbial diversity had a significant negative effect on SMF (Figure 4B); and the α-diversity of soil fauna did not have a significant effect on SMF; meanwhile, β-diversity had a significant negative effect on SMF (Figure 4C). The model fit indices satisfied the fit criteria (p = 0.426, chi-square/df < 3, CFI > 0.95, GFI > 0.90), indicating a good model fit.

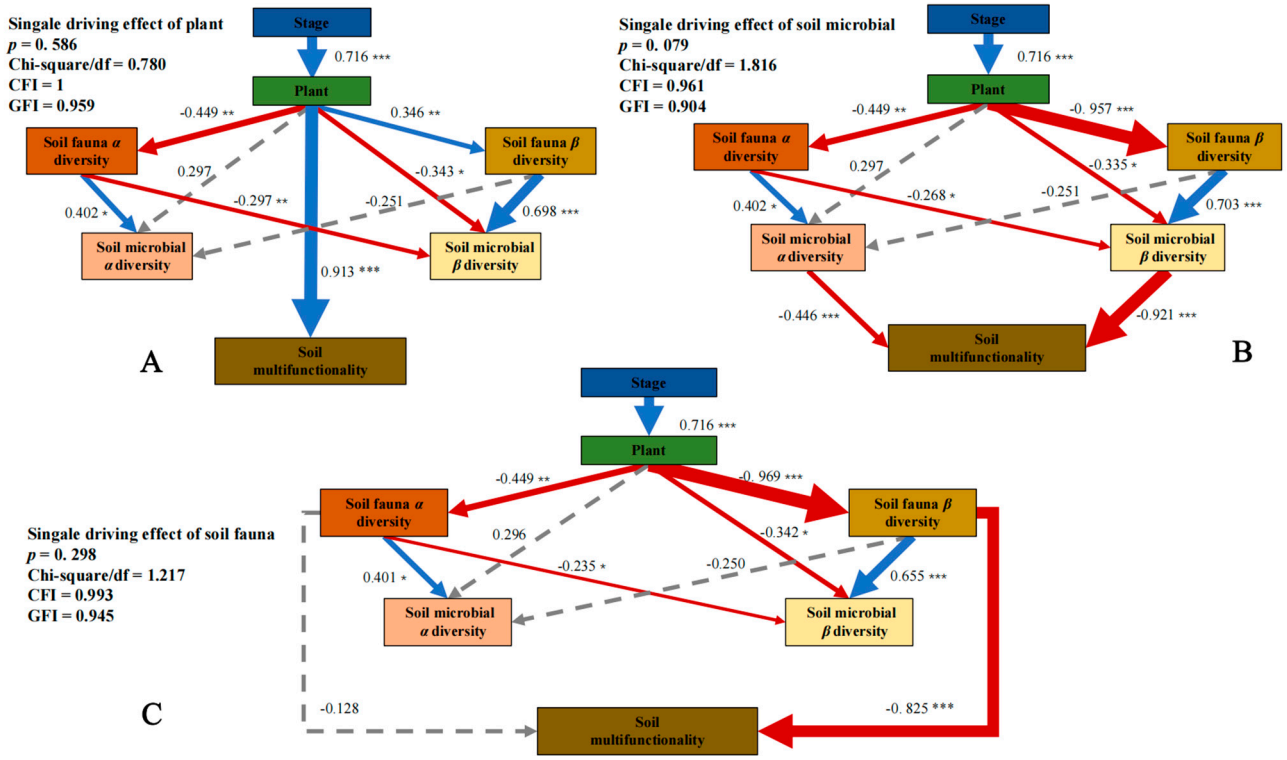

Figure 4. The effects of plant (**A**), soil microorganisms (**B**), and soil fauna (**C**) on SMF based on structural equation models. The arrows indicates the direction of the effect. The blue arrows represent positive effects, the red ones represent negative effects, and the grey dashed arrows indicate non-significant effects. The numbers next to the arrows represent the effect sizes of the relationship. The asterisk after the number indicates the significance level (*, p < 0.05; **, p < 0.01; ***, p < 0.001).

3.4. Driving Mechanism of Species Diversity at Multiple Trophic Levels on SMF

The SEM results showed that plant diversity indirectly drives SMF by influencing soil fauna and soil microorganisms during natural restoration. The natural restoration of degraded karst vegetation had a significant negative effect on soil fauna, whereas soil microorganisms were significantly positively influenced by soil fauna. Additionally, soil microorganisms delivered a significant negative effect on SMF. A multi-trophic cascade pathway for the natural restoration of degraded karst vegetation–plant–soil fauna–soil microorganism–SMF was formed (Figure 5). The model fit indices satisfied the fit criteria (p = 0.426, chi-square/df < 3, CFI = 1, GFI = 0.956), indicating a good model fit.

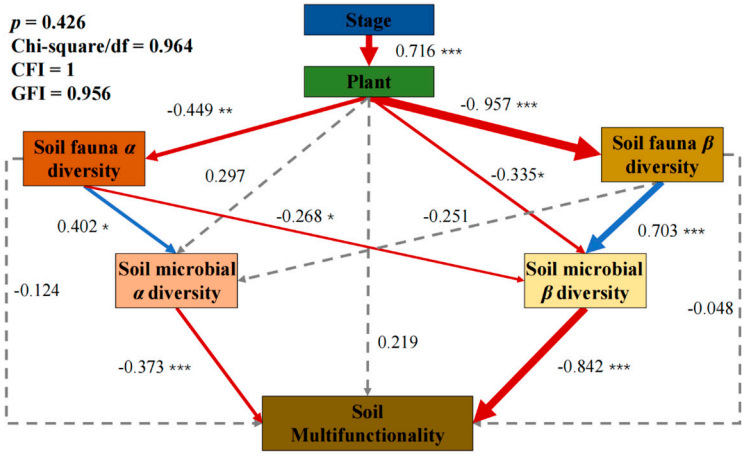

Figure 5. Direct and indirect effects of plant, soil fauna, and soil microorganism on soil multifunctionality based on structural equation models. The arrows indicates the direction of the effect. The blue arrows represent positive effects, the red arrows represent negative effects, and the grey dashed arrows indicate non-significant effects. The numbers next to the arrows represent the effect sizes of the relationship. The asterisk after the number indicates the significance size (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$).

4. Discussion

4.1. Species Diversity at Multiple Trophic Levels and SMF Respond Differently to Restoration

In general, as the natural restoration of degraded forest ecosystems proceeds, biodiversity at all trophic levels in the ecosystem and soil function are restored. The positive effects of restoration on biodiversity and ecosystem functioning in degraded ecosystems have long been proved [64,65], and the response trends may vary over trophic levels of biodiversity. For example, Deak et al. [66] and Guo et al. [67] have shown that an increasing trend in above-ground plant diversity with restoration exists; however, the results of Liu et al. [68] have shown a saturation trend in plant diversity in the later restoration stages. Soil faunas have also been reported to show different results, with significant increases [69,70] or decreases [71,72] in response to the restoration sequences. The soil microbial community has also shown an increasing [68], hump-like, or insignificant [70] pattern of restoration. In contrast, SMF shows a positive response to restoration [73] or a significant lag [68]. These differences in responses to restoration across trophic levels may be due to differences in habitats or ecosystem types [74,75], such as soil physicochemical properties, dispersal constraints, and historical contingencies, potentially affecting the restoration of different biomes [67,76,77].

In this study, the natural restoration of degraded karst forests resulted in unsynchronized or even opposite patterns of changes in biodiversity at different trophic levels and SMF. Specifically, plant species diversity and SMF increased with restoration. In contrast, soil fauna exhibited a decreasing trend in SR and β-diversity but an increasing trend in species evenness (Figure 2). Soil microorganisms did not show significant changes in α diversity, but did exhibit decreases in β-diversity. The increase in the diversity of primary producers (plants) and soil functioning is intuitive. In contrast, the trend in the diversity of consumers and decomposers in response to restoration is unexpected. This is possibly attributed to the complex cascading interactions between trophic levels during this process [31,78–80]. Since the history of disturbance in the study area is woodcutting, all the forests were old-growth forests before the disturbance. The above-ground vegetation was most directly affected by the disturbance and began to undergo classical secondary succession, leading to an increase in plant diversity as the restoration proceeded. As woodcutting does not have a direct impact on the soil community, the soil community remains in its original top state at the beginning of the secondary succession. Soil faunas are more sensitive to litter supply [81–83]. The soil fauna community had the highest SR in the

initial SB and showed a decreasing trend in the SG and OG stages. This may be due to the higher rate of nutrient cycling and the faster rate of litter return in the SB stage, accelerating food source replenishment. Consequently, a high level of SR was maintained in the SB stage. As succession progressed, the plant community advanced to the SG and OG stages. The plants tended to reach maturity, and the proportion of deciduous species decreased (Table S1). As a result, the rate of community nutrient cycling dropped with the quantity and rate of litter material return. Additionally, the diversity of plant species became more homogeneous, leading to lower individual, SR, and β-diversity of the soil fauna. Compared with soil faunas, soil microbial communities are less sensitive to the rate of nutrient cycling (apoplast return), and they are more susceptible to environmental factors (temperature, pH, etc.) [84–87]. This indicated that the secondary succession process did not affect the α-diversity of soil microorganisms. β-diversity may decline for the same reasons and be regulated by soil fauna, as evidenced by the significant correlations between the plant diversity and soil fauna diversity and between the soil fauna diversity and β-diversity of soil microorganisms (Figure S4). Although the size of the soil microbial community remained constant, variations in community composition between the sample sites decreased as the attributes of the food source became homogeneous in the later stages of succession.

4.2. Stepwise Action of Multiple Trophic Levels Ultimately Drives the Increase in SMF

The study by Esteban Lucas-Borja and Delgado-Baquerizo [88] has demonstrated that every single trophic level in the ecosystem plays a role in driving SMF. Specifically, this study showed that plant communities drive changes in SMF during the secondary succession of *Pinus taeda*. Increased plant diversity can provide additional resources, such as leaf litter and root secretions, leading to soil nutrient accumulation. This promotes soil nutrient cycling, accelerates resource recirculation, increases plant productivity, and enhances litter decomposition, improving SMF [73,89,90]. Soil fauna were found to boost SMF in studies by Tresch et al. [91] and Schittko et al. [92]. Soil fauna can drive an increase in SMF by regulating pH, organic matter decomposition, and nutrient cycling [33,93,94]. SMF is not only driven by plant communities and soil fauna but also by microbial communities during ecological succession [73,95]. Most studies have shown that microorganisms play a crucial role in driving SMF by participating in nutrient mineralization and apoplastic decomposition in biogeochemical cycles [21,96,97]. In contrast, the driving force of each trophic level on SMF in natural ecosystems is not exerted independently. Instead, it is the ultimate outcome of the movement of matter and energy, as they flow through each trophic level, cascade by cascade. When analyzing the driving effect of a single trophic level on SMF in previous studies, the functions exercised by other trophic levels are often neglected, whereas the interaction between trophic levels is often the most realistic representation of the driving effect and is essential for a comprehensive description of the process of multi-trophic-level action on SMF. The processes of material cycling and energy flow between trophic levels also play a role between trophic levels, necessitating consideration. We detected significant correlations between single trophic levels and SMF (Figure 3), and a significant individual driving effect of single trophic levels on SMF was verified by using SEM (Figure 4). When the driving effect of each trophic level on SMF was evaluated, and the three trophic levels were linked in SEM according to the direction of energy flow, only soil microorganisms showed a significant direct effect on SMF. The direct effects of plants and soil fauna on SMF became insignificant and acted indirectly through the transfer of energy between trophic levels. This suggests that the individual driving effect of each trophic level on the SMF does not accurately reflect the contribution of each trophic level and ignores the role of the ecological processes between these levels.

Our study found that of the three trophic levels, only soil microorganisms had a significant direct effect on SMF. In contrast, soil fauna significantly influenced soil microorganisms, and plants only had a significant direct effect on soil fauna, constituting a cascading order of trophic regulation from low to high (Figure 5). Soil microorganisms are the only trophic level with a direct effect on SMF for two possible reasons. On the one hand,

soil fauna and soil microorganisms are more likely to directly influence SMF than plants due to their presence in the soil and their high interaction with the soil. On the other hand, the effects of plants on soil fertility are largely dependent on soil microorganisms [68,98]. For example, during the return of nutrients from apoplastic material to the soil, soil microorganisms accelerate litter decomposition as well as soil nutrient accumulation and cycling, which ultimately contributes to increased SMF [99–101]. Although the soil fauna is also instrumental in the early steps of litter decomposition, most of its contribution comes from the fragmentation segment, whereas the final decomposition is mainly exercised by soil microorganisms [102–105].

Although no significant direct effects of the trophic plants and soil fauna on SMF were found, these two trophic levels exerted significant indirect effects. In general, as plant diversity increases, the soil provides a more diverse substrate that supports higher soil fauna diversity, especially during the restoration of ecosystems near primary succession. For example, Salamon and Alphei [106] have found that soil fauna community diversity increases with the improvement of plant diversity in a restoration succession, starting from bare sand (mobile dunes). The reason for this is that a higher diversity of plant species contributes to a higher diversity in the quality or type of litter entering the subsurface subsystem and more apoplastic materials, increasing the diversity of soil fauna. In contrast, plant diversity had a significant negative effect on soil fauna in this study (Figure 5). That is, the diversity of soil fauna tended to decrease as plants were restored during succession. The reasons for the different results from other studies may be explained as follows. For one thing, the disturbance context of the secondary succession sequence selected in this study was the woodcutting of the old-growth forests. Compared to the restoration of the near-primary succession, the soil fauna of the present secondary succession did not need to be constructed from scratch. Soil faunal communities are primarily controlled by top-down food resources [107–109]. Additionally, the community selected at the beginning of the successional sequence in this study was the SB stage, with the herbaceous layer still showing some signs of survival. In contrast, the plant community in the shrub–grass mixed stage was characterized by higher nutrient cycling rates and a greater mass of litter, providing the soil fauna community with ample food sources. As restoration proceeded at the SG and OG stages due to increasing canopy density and dropping light conditions, herbaceous shrubs were ruled out by competition and replaced by mature and stable tall tree communities. The rate of nutrient cycling was greatly reduced, resulting in a single supply of nutrient resources for soil fauna and a decrease in the number of soil fauna species [108].

Soil microbial diversity is influenced by both upward (bottom-up) and downward (top-down) factors, such as resources and consumers [110–113]. In this study, the effects of plant diversity were found to be relatively insignificant (Figure 5). The relationship between soil fauna and soil microorganisms can be summarized as “predation” and “facilitation”. Direct trophic relationships between microfauna and microorganisms are important drivers of soil microbial diversity [114]. For example, microbivorous nematodes are selective feeders for soil microorganisms that directly regulate the size of soil microbial communities. The contribution of soil fauna to soil microorganisms was reflected in the crushing, stirring, and mixing of soil fauna. Through these roles, soil fauna increases the opportunity for materials, e.g., litter fully contacting with soil microorganisms and delivering a dispersal effect on soil microbial objects or spores during their movement [115,116]. In addition, the digestion of plant residues and their excretion through feces, together with their residues after death, are good sources of nutrients for soil microorganisms [117,118]. In this study, SEM was used to detect the promoting effect of soil fauna on soil microorganisms, indicating that soil fauna had limited predatory effects on soil microorganisms during natural restoration. Although soil fauna diversity showed a decreasing trend, the positive correlation between the two resulted in a decreasing trend in soil microbial diversity. Although soil microorganisms were the only direct drivers of SMF, their decline led to an increase in SMF, which seems counterintuitive. Therefore, we further tested the trend of

soil microbial functional diversity with succession and its relationship with SMF and found that soil microbial functional evenness increased with restoration, and that it was highly significantly positively correlated with SMF (Figure S5). Therefore, although we found that declining soil microbial species diversity drives the increase in SMF when we constructed SEM using species diversity metrics, the real role is played by the simplified structure of the soil microbial community, which reduces the redundancy of species and functions, so its functions are performed more evenly, ultimately contributing to the increase in SMF.

5. Conclusions

By analyzing the plant community, soil fauna, and soil microbial diversity in 30 sample plots across three restoration gradients in degraded karst ecosystems, this study found that natural restoration promoted the restoration of soil multifunctionality, with soil microorganisms being the only direct driver of soil multifunctionality, that plants indirectly affect soil multifunctionality through soil fauna, which then influences soil multifunctionality, and that multi-trophic levels function through cascading effects. The cascading action among trophic levels in the restoration process of degraded karst forests is key to understanding natural restoration mechanisms and processes, which implies that the intermediary roles of soil fauna and soil microorganisms are important bridges for the functioning of primary trophic levels. We suggest that future studies on degraded ecosystems should avoid focusing too much on the functioning of a single trophic level and should instead comprehensively consider the integrated roles of multiple trophic levels to comprehensively reveal the restoration process.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f15030559/s1, Figure S1. Diagram of the five-point sampling method; Figure S2. The linear relationship between soil multifunctional index was obtained based on mean value method, factor analysis method and threshold method; Figure S3. Changes in soil physicochemical properties at different stages of restoration of degraded karst forests; Figure S4. Relationship between soil microbial functional diversity index and soil multifunctionality; Figure S5. Responses of soil microbial function diversity to the restoration stage (A); Relationship between soil microbial function diversity and soil multifunctionality (B); Figure S6. PCoA analyses of the three natural recovery stages, where the distances of the points represent the distances of the samples, and samples in the same area on the plane are shown to be similar; Table S1. Number and proportion of deciduous species during natural restoration; Table S2. OTU data form for soil fauna; Table S3. OTU data form for soil microorganisms; Table S4. Biodiversity index data; Table S5. Level of soil fauna classification; Table S6. Level of classification of soil microorganisms; Table S7. Results of PCoA analyses of soil fauna; Table S8. Results of PCoA analyses of soil microorganisms; Table S9. Basic information on the vegetation of the sample site. References [119,120] are cited in the Supplementary Materials.

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