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Stochastic Processes Dominate Soil Microbial Community Assembly during the Restoration of Degraded Karst Forests

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Abstract: The mechanisms underpinning the soil microbial community assembly are important, particularly in the fragile karst forest ecosystem. Despite such significance, relevant topics remain limited. We investigated a typical karst area, the Maolan National Nature Reserve in China. For this purpose, 30 forest dynamics plots were established on three restoration gradients in degraded karst forests, namely shrub, pioneer tree, and climax communities. Using vegetation surveys, we explored the diversity patterns, driving factors, and community assembly of the soil microbial communities during the restoration of degraded karst forest ecosystems. In addition, the soil physicochemical properties and macrogenomic sequencing data were examined. One-way analysis of variance and principal coordinates analysis showed no significant changes in soil microbial α-diversity during restoration, and the opposite pattern was observed for β-diversity. Variation partitioning analysis revealed that the combined effect of both soil microbial β-diversity and soil was significant (28% and 32% for bacteria and fungi, respectively). Pearson correlation analyses showed that plant species diversity and soil multifunctionality correlated significantly with soil microbial β-diversity. In contrast, the direct effect of plants was smaller (2% and 3% for bacteria and fungi, respectively). According to the dispersal–niche continuum index, stochastic processes were responsible for the assembly of the bacterial and fungal soil microbial communities. During restoration, the dominant influence of stochastic effects on the assembly of bacterial communities intensified. In contrast, the reverse tendency was observed in soil fungi. The investigation of the diversity pattern of soil microbial communities and their assembly can provide theoretical references for the restoration of degraded ecosystems.

Keywords: dispersal–niche continuum index; karst forests; plant species diversity; soil multifunctionality; succession

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1. Introduction

Soil microorganisms are highly active and play a crucial role in terrestrial ecosystems [1]. They participate directly or indirectly in most soil ecological processes [2], including material cycling, energy conversion, and pollutant degradation, contributing to the functioning of ecosystems. Another importance lies in their ability to link soil and vegetation [3]. The composition of the soil microbial community undergoes changes when the degraded ecosystems are restored. The mechanisms shaping microbial community diversity and its influencing factors, especially in degraded karst forests, are crucial, yet have limited discussion in soil ecology [4]. It is necessary to investigate how the thin soils and harsh habitats with high vulnerability and complexity contribute to the spatiotemporal evolution of soil microbial communities, as well as the influencing factors and assembly of

these communities [5]. In this sense, exploring the characteristics of the changes, driving forces, and assembly of soil microbial communities can guide the ecological restoration of degraded karst forests.

The concept of α-diversity encompasses both species richness (number of species) and evenness (distribution of species within a community or environment); the β-diversity of soil microorganisms describes differences in species composition between sites and is one of the fundamental components of species diversity. The composition and diversity of the soil microbial community are indicators of soil ecosystem stability and functionality, and they also affect ecosystem processes [6], including nutrient acquisition [7], soil formation [8], plant productivity, and plant diversity [9]. Soil microbial communities exhibit various successional patterns in the recovery process of degraded ecosystems. For instance, the soil microbial α-diversity ascends and stabilizes throughout due to changes in abiotic variables [10–12]. In some studies, no significant differences or changes were reported in soil pH [12,13]; consequently, the microbiological community of soil α-diversity in succession was not significantly changed [14]. For forest restoration, research has reported significant changes in the β-diversity of soil microorganisms between restoration stages [4,15,16]. In contrast, some reports demonstrated no significant differences in forest succession in karst regions [13,17]. The diversity of soil microbial communities is impacted by plant diversity and soil properties with progressive succession [18]. Soil microorganisms change with the succession of above-ground vegetation, and varying types of apoplastic materials provide a rich source of nutrients for soil microorganisms [19]. Due to diverse vegetation types, the organic matter and root secretions entering the soil vary, altering the nutrient soil properties, such as organic matter content, moisture content, and pH value. These factors affect soil microbial diversity by regulating the qualitative input for microbial survival, habitat, and metabolic conditions, thus changing the distribution and composition of microbial communities [20]. Yuan et al. [21] reported soil carbon and ammonium nitrogen as the primary environmental elements influencing soil microbial communities. However, Zhang et al. [22] suggested that soil nutrients played an important role in forming inorganic and organic substrates for soil microbes. It was indicated that plants have an indirect effect on soil microbial communities, which are directly influenced by soil physicochemical features.

To predict how ecosystems respond to environmental change, we need to clarify the relative contributions of stochastic (e.g., stochastic births, deaths, and dispersal events) and deterministic (such as environmental selection, species interactions, and niche differentiation) processes controlling the assembly of soil microbial communities during succession [23]. Deterministic processes support the role of biotic and abiotic filtration, leading to significant variations in community composition under various environmental conditions. In comparison, stochastic processes emphasize the contribution of probabilistic dispersal and ecological drift to the community composition patterns [24]. Dini-Andreote et al. [25] proposed that deterministic selection increased when forest succession progressed; more importantly, deterministic processes were impacted by environmental changes in soil organic matter content. Initially, stochasticity governs soil microbial communities throughout forest succession. Liu et al. [26] suggested that regarding the composition of soil microbial communities, deterministic mechanisms dominated in the early stages of subtropical forest secondary succession; when secondary succession progressed, the role of stochasticity stood out. Increasing investigations have reported on the synergic effects of determinism and stochasticity in the assembly of microbial communities [27,28]. Despite these achievements, a research gap exists on the relative importance of these two processes between bacteria and fungi as well as at different stages of forest succession. It is widely acknowledged that deterministic and stochastic mechanisms form microbial communities [29]. Inspired by the idea put forth by Gravel et al. [30] that purely neutral and niche communities could be considered two ends of a continuum, the dispersal–niche continuum index (DNCI) was proposed to address this issue [31]. Using a quantitative approach, DNCI can illustrate community formation using the PER-SIMPER [32] algorithm. Furthermore, it enables the direct computation of DNCI values among datasets

(e.g., populations and successional stages) to determine changes in the assembly process's strength. Vilmi et al. [31] and Gibert et al. [33] demonstrated the effectiveness of the PER-SIMPER/DNCI framework in clarifying the respective roles of dispersal and niche processes in shaping riverine macroinvertebrate communities and fleas as well as their small mammalian hosts. For soil microbial communities, revealing the basic processes of assembly can predict the successive trajectories of the community structure, enabling the assessment and prediction of ecosystem functioning and guiding the restoration of degraded karst forest ecosystems [34].

Despite considerable research on soil microbial diversity patterns and community assembly across different ecosystems, the following issues merit further consideration: (1) Most previous studies have focused on terrestrial or aquatic ecosystems in normal landscapes, and investigations on soil microbial communities in karstic landscapes, especially within degraded karstic forest ecosystems, are lacking. (2) The majority of earlier research has not evaluated soil microbial community diversity patterns on the recovery gradient, instead focusing on the current state of these patterns and their influencing factors, which more accurately depict the variations in environment and the evaluation of the diversity pattern of the soil microbial community [35]. Changes in the soil microbial community can be observed more clearly on the recovery gradient. In order to better understand the natural recovery mechanism and offer guidance for the degraded ecosystem restoration, research on the diversity of the soil microbial community and its assembly during the natural recovery of degraded karst forest ecosystems is necessary. This study assessed soil microbial diversity, driving forces, and their assembly during the natural restoration of karst vegetation using a macrogenomic approach. The objective is to address the following issues: (a) What are the responses of soil microbial diversity to natural restoration and its driving factors during this process? (b) Do the niche- or dispersal-based processes determine the soil microbial community assembly throughout the restoration?

2. Material and Methods

2.1. Study Area

The study site is the Maolan National Nature Reserve (107°52′10″–108°05′40″ E, 25°09′20″–25°20′50″ N) of the Guizhou Province, located in Libo County, China, and adjacent to Guangxi Mulun National Nature Reserve (Figure 1). It covers a total area of 21,285 km^2. This reserve has an average annual temperature of 18.3 °C, annual mean precipitation of 1752.5 mm, 83% relative humidity, an average height of 550–850 m, and 1272.8 h of sunshine. It is dominated by the middle subtropical monsoon humid climate. Typical vegetation types include native evergreen deciduous broadleaf mixed forests. The soil-forming parent rock of the Maolan Reserve is carbonate rock, so the soil formed by its weathering and development is all limestone soil, mainly calcareous soil, followed by yellow soil, soil with a shallow and discontinuous layer, low water retention, and rich calcification. This area is characterized by a rare karstic peaked landscape.

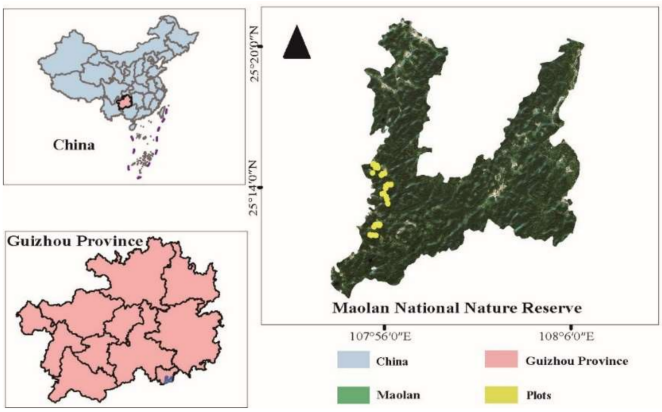

Figure 1. Overview map of the study area.

2.2. Data Acquisition

2.2.1. Demarcation of Plots and Sample Collection

The subtropical karst evergreen deciduous broadleaf mixed forest is susceptible to biotic and abiotic disturbances responsible for forest degradation. The main disturbance in the study area is selective cutting. When the disturbance is removed, the forest undergoes succession. Gradually developing from the shrub (SB) and pioneer tree (SG) stages, the degraded karst forest recovers to the climax community of evergreen and deciduous broad-leaved mixed forest (OG). Following the standard manual for establishing forest dynamic plots [36], we demarcated forest dynamics plots in the nature reserve in June–September 2021 to explore the soil microbial diversity patterns and the community assembly in this process. Ten forest dynamic plots on each gradient were built for SB and SG as well as OG stages, measuring 10 m^2 and 30 m^2, respectively. For the SB stage, selective cutting has been initiated since 2002, and the vegetation propagule was not destroyed. At the SG stage, the mentioned disturbance remained, with the most recent one occurring in 1984. Based on past data and discussions with local elders, no human disturbance for at least a century was determined at the OG stage. All restoration stages share the same regional species pool, and no human disturbance is allowed during the natural restoration. The five-point sampling approach was used to gather samples in October 2021. At each sampling location, five soil samples were obtained from the 0–20 cm soil layer after litter layer removal. Subsequently, they were evenly mixed to a composite state, and thirty composite samples were acquired. Every sample was split into two halves. To ascertain the physical and chemical characteristics of the soil, one part was air-dried, and the other was instantly frozen in liquid nitrogen at −80 °C for microbiological examination.

2.2.2. DNA Extraction, Library Construction, and Metagenomic Sequencing Analysis

Following the manufacturer's instructions, 0.5 g of each soil sample was selected to extract the total genomic DNA variation partitioning analysis (VPA) using the FastDNA® Spin Kit (MP Biomedicals, CA, USA). Next, a 1% agarose gel was added to assess the purity of the extractant. The extracted DNA was broken up to an average size of about 400 bp using Covaris M220 (Gene Company Limited, Shanghai, China) to obtain a library of paired-end reads with NEXTflexTM Rapid DNA-Seq (Bioo Scientific, Austin, TX, USA). The blunt ends of the fragments were ligated to adapters that contained the whole complement of sequencing primer hybridization sites. At Majorbio Bio-Pharm Technology Co, Ltd. (Shanghai, China), paired-end sequencing was carried out on an Illumina NovaSeq (Illumina Inc., San Diego, CA, USA) using NovaSeq Reagent Kits in accordance with the manufacturer's instructions (www.illumina.com, accessed on 5 June 2023).

2.2.3. Sequence Quality Control and Genome Assembly

A total of 1,813,610,194 raw readings were obtained. These raw reads from metagenome sequencing were processed to produce clean reads by removing adaptor sequences and trimming low-quality reads (those with N bases, a minimum length threshold of 50 bp, and a minimum quality threshold of 20) using the FASTP (https://github.com/OpenGene/fastp, version 0.20.0, accessed on 5 June 2023) on the Majorbio Cloud Platform (cloud.majorbio.com), a free online resource. Following a quality check, 1,776,367,626 clean readings were obtained. These high-quality reads were then assembled into contigs using condensed de Bruijn graphs and MEGAHIT [37] (parameters: kmer_min = 47, kmer_max = 97, and step = 10) as a guide.

2.2.4. Gene Prediction, Taxonomy, and Species Annotation

Predicted ORFs spanning 100 bp or more were retrieved using the NCBI translation table, and corresponding amino acid sequences were obtained (http://www.ncbi.nlm.nih.gov/Taxonomy/taxonomyhome.html/index.cgi?chapter=tgencodes#SG1, accessed on 5 June 2023). A non-redundant gene catalog with 90% sequence identity and coverage was produced using CD-HIT [38] (http://www.bioinformatics.org/cd-hit/, version 4.6.1, accessed on 5 June 2023). BLASTP (BLAST V.2.2.28+, http://blast.ncbi.nlm.nih.gov/Blast.cgi, (accessed on 5 June

2023) BLAST comparison parameter with expected E-value of 1×10^{-5}) was used to compare non-redundant gene sets on the NR database. Species annotation was performed using the corresponding taxonomic information database of the NR library and used to calculate the abundance of the species by summing up the corresponding gene abundances in species. The abundance of the species in each sample was counted at each taxonomic level. An abundance profile was constructed for the corresponding taxonomic level.

2.2.5. Calculating Species Diversity

Based on the species richness information of plants and soil microorganisms, the species richness index (SR) and Shannon–Wiener index were calculated as follows:

$$\text{Plant SR} = S \quad (1)$$

$$\text{Plant Shannon} - \text{Wiener} = -\sum_{i=1}^{s} P_i \ln P_i \quad (2)$$

where S represents the total number of species, P_i is the proportion of the i_{th} species to the total as the number of the i_{th} species, and N is the total number of individuals.

The SR of soil microorganisms was represented by OTU richness. Principal coordinates analysis (PCoA) was performed based on the Bray–Curtis distance matrix between samples, with information on the first axis of PCoA (PCoA1) representing species differences (β-diversity) between samples.

2.2.6. Determination of Soil Physical and Chemical Properties and Calculation of Soil Versatility

Fifteen soil functional indicators were selected to determine soil multifunctionality in this study, including physical (soil mechanical composition: clayey grains %, powdery grains %, and sandy grains %) and chemical (carbon content, organic carbon that is particle, easily oxidizable, and light fractioned, nitrogen content, alkaline dissolved nitrogen, total phosphorus, calcium content, exchanged calcium, urease, neutral phosphatase, and pH) properties. Carbon (C %) and nitrogen (N %) contents were determined using an elemental analyzer (UNICUBE trace, Elementar, Germany). The wet sieving method was used to quantify particulate organic carbon (POC). Based on the oxidation with potassium permanganate, the content of easily oxidized organic carbon was determined. Using an extraction method with 1.7 g/cm^3 NaI solution, the light fraction of organic carbon was detected. The alkaline dissolved nitrogen (AN) content was measured based on alkaline dissolved nitrogen levels using the alkaline diffusion method. The total phosphorus was assessed with the molybdenum-antimony colorimetric method. The calcium content (Ca %) and exchangeable calcium concentration were determined using the primary absorption spectrometry. A pH meter (LeiMagnet, PHS-3C, Shanghai, China) was used to assess the soil, and Solepol kits were applied to measure the levels of urease and neutral phosphatase.

Quantitative indicators and calculation methods for soil multifunctionality have not been standardized. For this reason, researchers have adopted various calculation methods and indicators. Based on the existing literature on soil multifunctionality, this study, similar to most ecological reports, selected soil indicators related to the ecological carbon, nitrogen, and phosphorus cycles. These include carbon content, particulate organic carbon, light fraction organic carbon, readily oxidizable organic carbon, nitrogen content, effective nitrogen, total phosphorus, neutral phosphatase, urease, calcium content, exchangeable calcium, and pH. In addition to indicators of soil chemical properties, soil physical properties were included in the quantification of soil multifunctionality. Overall, these variables are helpful for characterizing important soil functions, such as nutrient cycling and nutrient pool building. The mean, factor analysis, and threshold methods were used to calculate soil multifunctionality. Estimates using the three multifunctionality calculation methods were close (r = 0.99) (Figure S1). The threshold method can avoid biases arising from the excessive weight of some ecosystem function categories without affecting the final results. Despite the linearity of the factor–multifunctionality relationship, it has wide applications.

In this sense, the soil multifunctionality index calculated using the threshold method was selected for subsequent analyses.

2.3. Statistical Analysis

We used Excel 2016 for data collation. The "vegan" package in R (V.4.3.0) was deployed to construct the species richness index (SR and Shannon–Wiener index) and PCoA based on the Bray–Curtis dissimilarity matrix. For both the PCoA results and the PC1 axis of the α-diversity index, a Kruskal–Wallis rank-sum test was performed. We used permutation multivariate analysis of variance (ANOVA) (999 permutations) to evaluate pairwise differences in the compositions of the fungal and bacterial communities. Linear Pearson correlation coefficients were introduced to assess the correlation between plant species diversity, α- and β-diversity indices of soil bacteria and fungi, and SMF (soil multifunctionality). Variance decomposition analysis (VPA), with wide applications in ecological process identification, was used to quantify the relative effects of plant species diversity and soil multifunctionality on the β-diversity of soil bacteria and fungi. Specifically, the β-diversity of soil bacteria and fungi served as the response variable, and plant species diversity and soil multifunctionality were explanatory variables. The VPA results are presented in Venn diagrams to show the proportion of variation explained by each dataset and the coincidence [39].

We evaluated the relative significance of dispersion and niche mechanisms in guiding the assemblages of bacteria and fungi over successional stages using the PER- (similarity percentage) SIMPER/DNCI framework [31,33]. SIMPER analysis is a distance-based algorithm to calculate the relative contribution of each taxonomic unit to the overall average difference observed between two or more groups of class combinations. Based on SIMPER analysis, the PER-SIMPER approach was developed, and three null distributions were obtained using three rearrangements of empirical data. Briefly, row-fixed, column-fixed, and both row- and column-fixed were included to simulate niche assembly, dispersal assembly, and both during permutations. These data were analyzed using SIMPER analysis to obtain the empirical SIMPER and the three different null SIMPERs. The empirical SIMPER's logarithm of the total squared variances between each null SIMPER was calculated to acquire three E-values (Ed, En, and Edn) to qualitatively identify the main processes of assembly (dispersal assembly vs. niche assembly) [32]. Qualitative techniques, however, do not yield an accurate picture of the dominant assembly because biome assembly is driven by a combination of dispersal and niche processes [40], especially when the effects of dispersal and niche processes are identical. In order to resolve this problem, DNCI used the PER-SIMPER method, which can be used for the quantitative identification of dominant assembly processes by comparing the standardized effect sizes of Ed and En and contrasting the relative significance of dispersal/niche processes among various community groups. While negative DNCI values point to a larger role for dispersal processes, positive values indicate that niche processes predominate in community assembly. The associated assembly's dominance increases with the larger absolute value of DNCI. The "DNCImper" software package in R (V. 4.3.0) was used for all PER-SIMPER/DNCI analyses. We conducted a pairwise comparison of DNCI values between different phase combinations to examine the relative importance of dispersal/niche between two stages; pairwise analyses were performed using the "DNCI_multigroup" function.

3. Results

3.1. Trends in SOIL Microbial Species Diversity and Community Composition during Succession

One-way ANOVA showed that the differences in the α-diversity of species at different stages of recovery were not significant ($p > 0.05$) for either fungi (Figure 2C,D) or bacteria (Figure 2A,B).

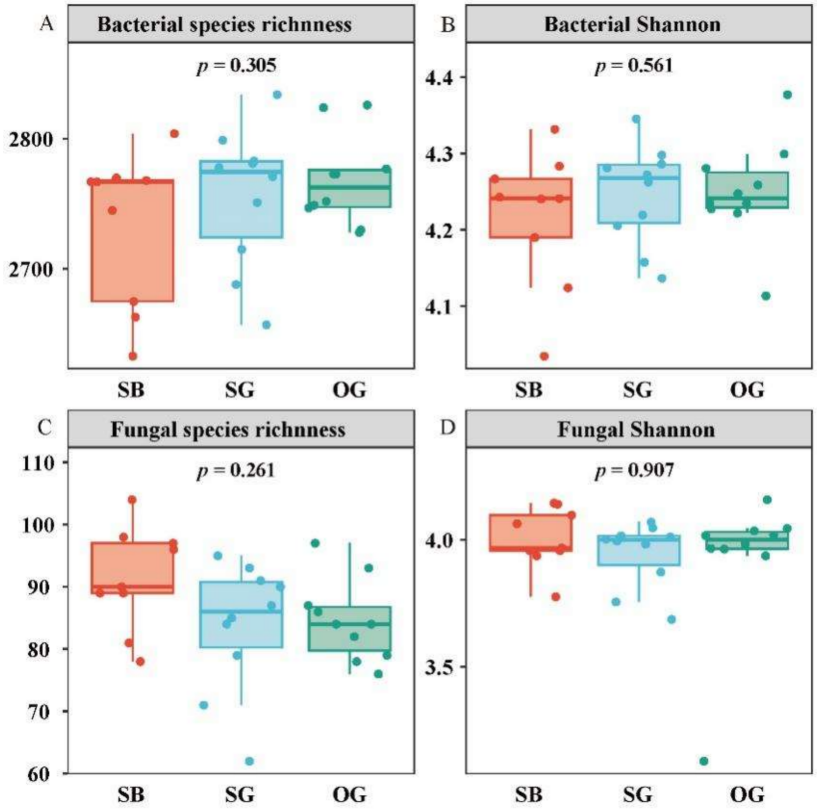

Figure 2. Differences in species α-diversity across different stages of restoration for bacteria (**A**,**B**) and fungi (**C**,**D**). SB, SG, and OG denote the shrub stage, pioneer tree stage, and climax community stage, respectively.

Following NR species annotation, a total of 24,922 bacterial and 394 fungal species were obtained. The dominant bacterial phyla in the SB, SG, and OG stages were Protcobacteria (46.9%, 40.1%, and 37.5%, respectively), Acidobacteria (16.09%, 25.3%, and 27.1%, respectively), and Actinobacteria (10.6%, 10.2%, and 11.1%, respectively) (Figure 3A). The dominant fungal phyla in SB, SG, and OG stages were Ascomycota (61.3%, 66.7%, and 60.7%, respectively), Basidiomycota (14.3%, 13%, and 23%, respectively), and Mucoromycota (17.3%, 14.7%, and 11.6%, respectively) (Figure 3B). Among them, Chytridiomycota, Zoopagomycota, Microsporidia, and Cryptomycota accounted for a small proportion. Among the fungi, Mucoromycota and Zoopagomycota decreased in abundance with recovery, whereas among bacteria, Protcobacteria and Verrucomicrobia showed reduced abundance with recovery, and Actinobacteria gradually increased with recovery (Figure 3A).

Between the SB-SG and SB-OG, PCoA revealed significant differences in the species community composition of soil bacteria (PERMANOVA: SB-SG, $p = 0.001$; SB-OG, $p = 0.001$), and insignificant differences between the SG-OG successional stages (PERMANOVA: SG-OG, $p = 0.099$) (Figure 4A). Soil fungal species community composition differed across successional stages (PERMANOVA: SB-SG, $p = 0.003$; SB-OG, $p = 0.001$; SG-OG, $p = 0.001$) (Figure 4B). The box plots at the top show the overall distribution of PCoA1 within each interval analyzed based on the PC1 principal coordinates. Small letters indicate significant differences between stages (Tukey's multiple effects test). The box plot at the top shows the overall distribution of PC1 principal coordinates, PCoA1, within each interval. Small letters indicate significant differences between stages (Tukey's multiple effects test).

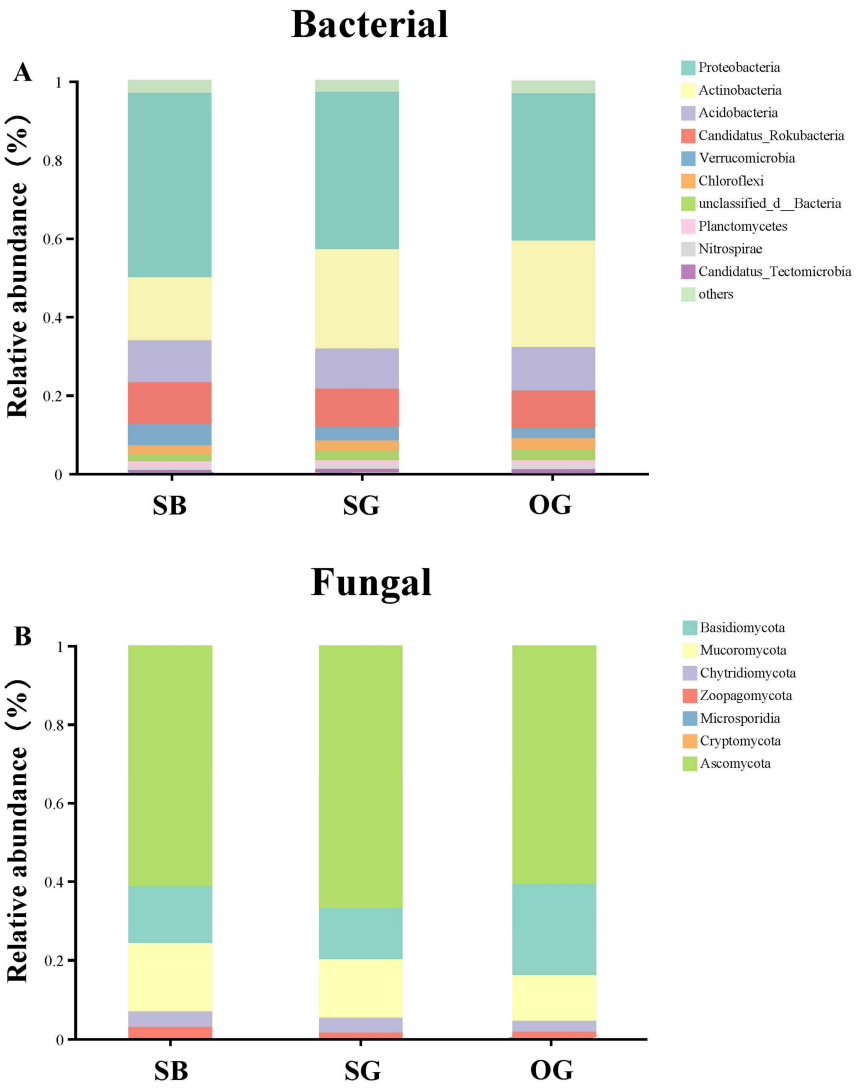

Figure 3. Relative abundance of bacterial and fungal phyla at each stage. (**A**) Relative abundance of bacterial phyla; (**B**) relative abundance of fungal phyla. SB, SG, and OG denote the shrub stage, pioneer tree stage, and climax community stage, respectively.

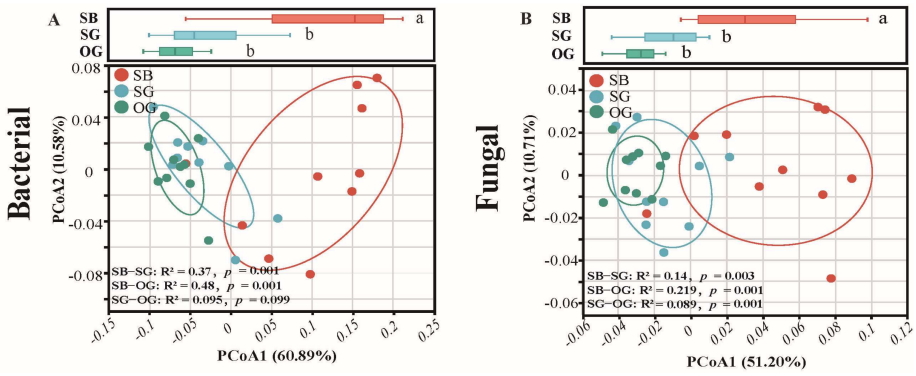

Figure 4. Species community composition of bacteria (**A**) and fungi (**B**). Principal coordinate analysis (PCoA) shows Bray–Curtis distances between successional stages. The box plots at the top show the overall distribution of successional stages in PCoA1, with different small letters indicating significant differences between stages (Tukey's multiple effects test). SB, SG, and OG denote the shrub stage, pioneer tree stage, and climax community stage, respectively.

3.2. Plant Species Diversity and Soil Multifunctionality as Drivers of Soil Microbes

Pearson correlation analyses showed that α-diversity indices of bacteria and fungi were not significantly correlated with either plant species diversity or soil multifunctionality (Figure 5A,B,E,F) but β-diversity showed significant correlations with α-diversity for both bacteria and fungi (Figure 5C,D,G,H).

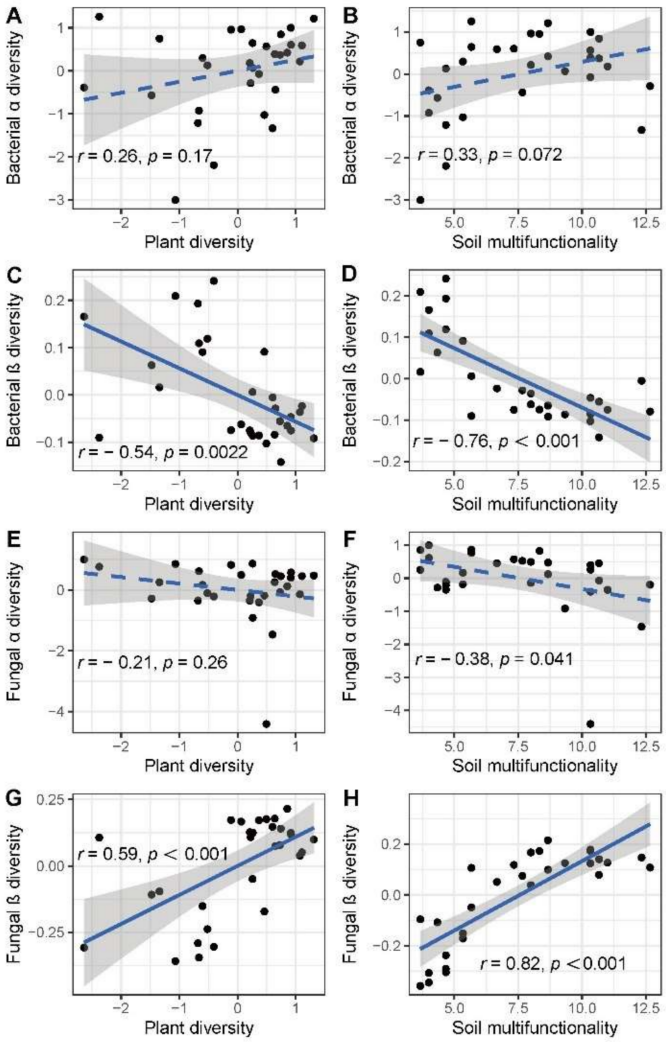

Figure 5. Relationship between plant species diversity and soil bacterial α-diversity (**A**), soil multifunctionality and soil bacterial α-diversity (**B**), plant species diversity and soil bacterial β-diversity (**C**), soil multifunctionality and soil bacterial β-diversity (**D**), plant species diversity and soil fungal α-diversity (**E**), soil multifunctionality and soil fungal α-diversity (**F**), plant species diversity and soil fungal β-diversity (**G**), soil multifunctionality soil fungal β-diversity (**H**). The blue line shows the trend, and the black circles show the values of the test samples.

The results of VPA showed (Figure 6) that plant species diversity and soil multifunctionality had a large, combined effect on bacterial (28%) and fungal (35%) β-diversity but only soil multifunctionality showed a strong individual effect on bacterial (28%) and fungal (32%) β-diversity, whereas the individual effect of plant species diversity was only on bacteria (2%) and fungi (3%).

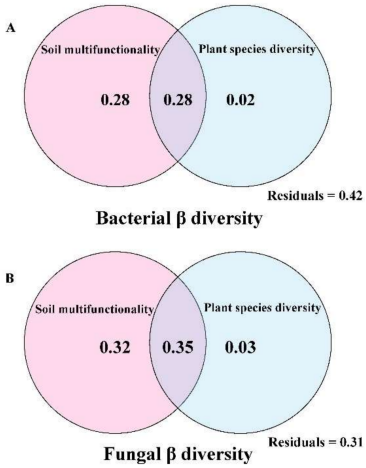

Figure 6. Venn diagram showing the results of the variation partitioning analysis (VPA) with the relative contributions of plant species diversity and soil multifunctionality to bacterial β-diversity (**A**) and fungal β-diversity (**B**). Numbers represent specific explanatory contributions as a percentage.

3.3. Soil Microbial Community Assembly Process

According to the PER-SIMPER analysis (Figures 7 and 8), it can be qualitatively known that both bacterial and fungal communities are dominated by stochastic processes in their community assembly processes during the recovery process.

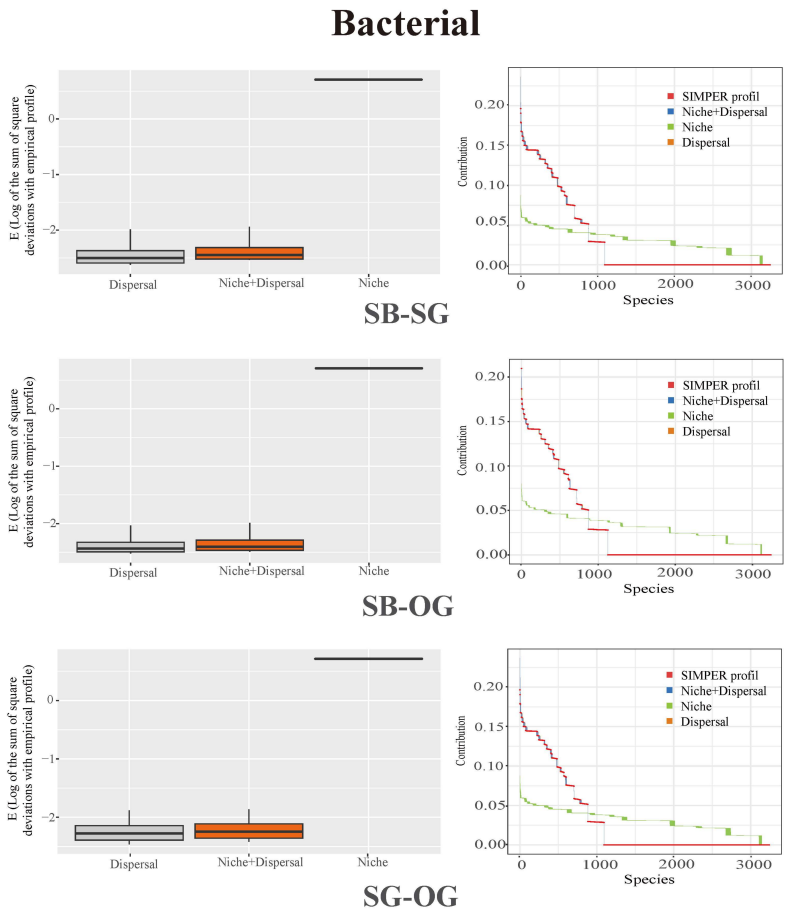

Figure 7. Boxplots of E-values between the various stages of bacterial recovery (left) and empirical SIMPERs created based on our empirical data (bacterial or fungal) (red on the right) compared with aligned models representing niche-controlled distributions (green on the right; row-fixed, deterministic processes) and diffusion process-controlled distributions (orange on the right; column-fixed, stochastic processes).

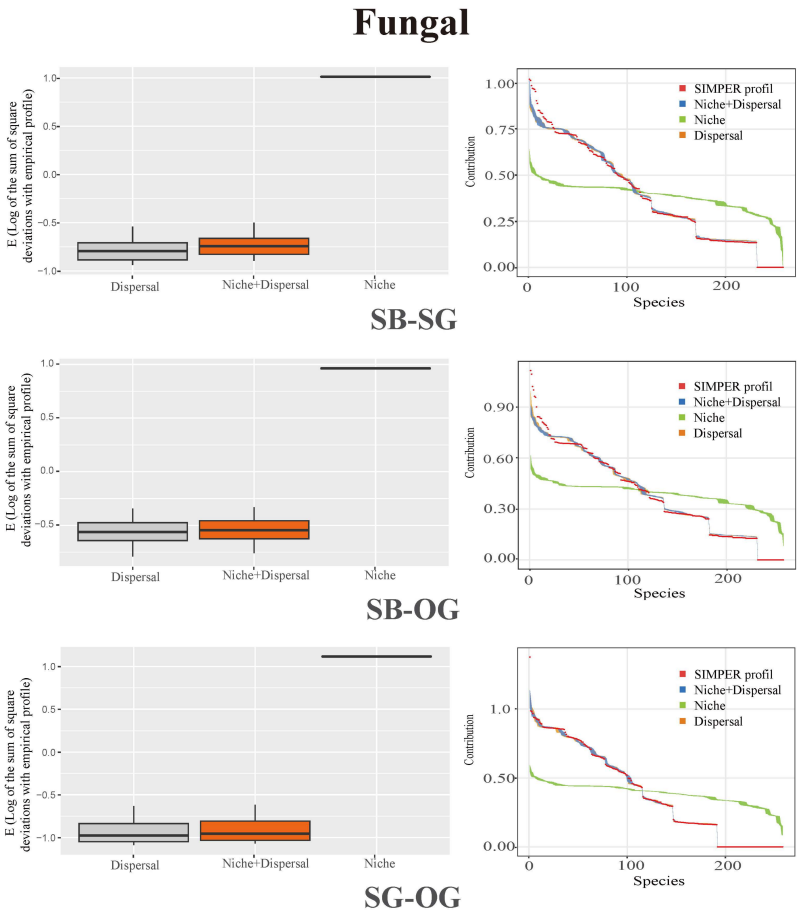

Figure 8. Boxplots of E-values between the various stages of fungal recovery (left) and empirical SIMPERs created based on our empirical data (bacterial or fungal) (red on the right) compared with aligned models representing niche-controlled distributions (green on the right; row-fixed, deterministic processes) and diffusion process-controlled distributions (orange on the right; column-fixed, stochastic processes).

The DNCI was negative between the three restoration stages (Figure 9), indicating that both bacterial and fungal communities were dominated by stochastic processes in their community assembly process during recovery.

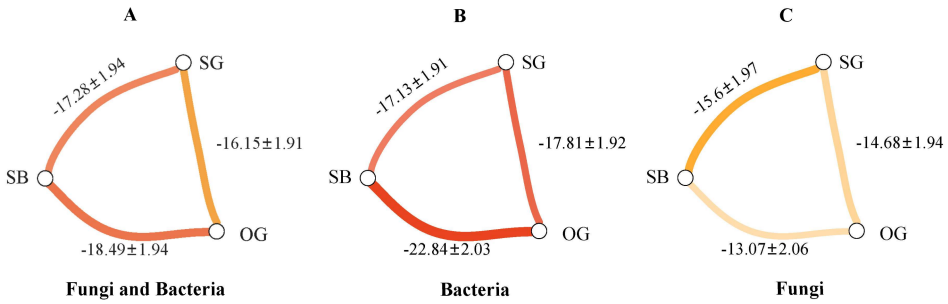

Figure 9. Dispersal–niche continuum index (DNCI) distributions for bacteria and fungi (N = 3500) (**A**), bacteria (N = 3242) (**B**), and fungi (N = 258) (**C**), between SB, SG, and OG stages two by two. Nodes represent different stages of recovery (ten sample plots per node) and connecting lines between nodes indicate community assembly processes (here, diffusion processes in all deterministic processes are indicated in red and yellow). The color and thickness of the connecting lines are proportional to the assembly process, with darker and thicker colors indicating a higher dominance of the assembly process.

According to the DNCI, dispersal processes dominated community assembly between each pair of recovery stages, while stochastic processes were primarily responsible for driving the assembly of bacterial and fungal communities (Figure 9A). The bacterial community SG-OG had a lower DNCI value (−17.13 ± 1.91) than SB-SG (−17.81 ± 1.92), suggesting that the bacterial community was gradually driven by dispersal effects during recovery (Figure 9B). Between stages, dispersal predominantly drove fungi. Dispersal processes dominated community assemblages between each pair of restoration stages. Although community dispersal processes outweighed niche processes between restoration stages, the deterministic driving effect on fungal communities increased gradually with restoration, evidenced by higher DNCI values for SG-OG (−14.68 ± 1.94) compared to SB-SG (−15.6 ± 1.97) (Figure 9C).

4. Discussion

4.1. Soil Microbial α- and β-Diversity Indices Show Different Trends during Restoration Processes

Succession alters the soil microbial α-diversity [41,42]. Our results suggested that the α-diversity indices of both bacteria and fungi did not change significantly with the natural restoration of degraded karst forests (Figure 2). This is consistent with research on Arctic sand dunes [43] and the Inner Mongolian Desert [44]. The following could be one explanation for the disparity: the forests of this succession already reached the climax community stage of succession before damage, and after the forests were subjected to anthropogenic disturbances such as woodcutting, only the above-ground vegetation was damaged, whereas the soil microorganisms were not seriously disturbed, and remained in their original state. Consistent with our results, earlier research [45,46] indicates that the OTU richness of bacteria and fungi was considerably impacted by the successional stage. This OTU richness is highly correlated with the richness of uncommon species [47]. Unlike the α-diversity, we discovered that there were notable differences in the β-diversity of soil fungi and bacteria between the restoration stages, and only the β-diversity of bacteria was similar between the SG-OG stages (R^2 = 0.095, p = 0.099) (Figure 4). The alteration of soil nutrients by different plant species through changes in apoplastic inputs and root secretions can specifically promote or restrict microbial communities in the soil [48–50], resulting in changes to the composition of the soil microbial community [51]. Soil fungi establish biotrophic relationships with plants through mycorrhizae, rhizomes, and other symbiotic systems [51]. It explains why fungal communities react to changes in different vegetation habitats more strongly than bacterial communities.

4.2. Soil Multifunctionality Drives the β-Diversity of Soil Microbial Communities

Soil microorganisms are susceptible to external environmental disturbances, along with changes in the species composition. The two primary factors influencing the composition of soil microbial communities are vegetation and soil physicochemical properties [51–53]. Using variance decomposition and Pearson correlation analysis, we tested the role of vegetation and soil on the species composition of soil microbes on the restoration gradient. The results of the Pearson correlation analyses indicated a correlation between the soil microbial β-diversity and plant species diversity as well as soil multifunctionality (Figure 5), but in variance decomposition, we found that the role of plants alone was very weak, whereas that of soil alone and its combined role with plants were strong (Figure 6). This shows that the primary and direct factors affecting the composition of soil microbial communities are the physical and chemical features of the soil, while vegetation succession may indirectly affect soil microbial communities through soil properties [54]. Changes in soil conditions, including moisture, texture, and pH, along with the contents of various nutrients, affect soil microbial communities [55]. The physical properties of soil, as a site for the vital metabolism and reproduction of soil microorganisms, directly regulate the conditions for microbial survival, with more than 80% of soil bacteria inhabiting the micropores of soil stabilization aggregates, which provide the most favorable conditions for growth in terms of water and nutrients [56]. Chemical properties of the soil underpin microbial nutrition; for example, SOC is an important carbon source for soil microbes [46], and soil

ammonium nitrogen is a key biochemical molecule for microbes to synthesize proteins and nucleic acids [21]. Plant succession alters the organic matter and root secretions that enter the soil, which in turn affects the distribution and composition of the microbial community as well as the nutrient inputs from the root system [57,58]; however, this effect first passes through the soil and ultimately manifests itself more as an indirect effect on the microbial community, consistent with the results of our variance decomposition analysis.

4.3. Stochastic Processes Dominate the Assembly of Soil Microbial Community during the Restoration of Degraded Karst Forests

Gaining a greater grasp of the recovery process of soil microorganisms in degraded ecosystems requires an understanding of the ecological mechanisms behind their community assembly [59]. Our results suggest that communities of both bacteria and fungi, two-by-two across the three successional stages, were driven by dispersal (Figure 9). A negative dispersal-niche continuum index (DNCI) does not imply that niche processes have no role in community assembly; rather, it suggests that niche processes are weaker and have a smaller impact than dispersal in community assembly. Yan et al. [60] show that deterministic processes usually dominate during the succession of microbial communities, and their relative importance decreases as succession progresses [26], in accordance with the literature. Our results do not support the dominance of deterministic processes for microbial community assembly in subtropical forests. Recent studies provide increasing support for the dominant role of stochasticity in microbial systems [61–63], where migration, population colonization, and the lack of an ordered community structure are characteristic of microbial communities in the early stages of succession [64]. The high diversity of soil microbial communities is dominated by taxa that are able to utilize an extensive variety of resources [65,66]. This implies weak selection due to less competition, and the large effect of stochasticity. According to Badri et al. [67] and Chaparro et al. [68], sugars released by seedling roots in the soil create a resource-rich environment that lessens competitive pressures, resulting in a dominance of stochasticity during the early establishment of the soil microbial communities. In this study, soil microorganisms were not severely disturbed after vegetation destruction. Stochasticity is expected to predominate in the early stages of community assembly when a diverse variety of organisms thrive well in a particular environment [27].

One significant finding is that, in karst forest succession, the relative contributions of deterministic and stochastic processes to the assembly of bacterial and fungal communities differ, and that these contributions vary depending on the stage at which the bacterial and fungal communities are assembled. (Figure 9). For bacteria, stochastic processes drive bacterial communities more strongly later in succession. This suggests that bacteria are subject to a gradually increasing dispersal between successions. Plant resource inputs and soil nutrient accumulation gradually rise with succession. Plant communities diversify and grow more complex as they approach the mid-successional stages [69]. This probably causes soil bacteria to have access to a wider range of plant resources at the same time that environmental variability rises [26], while stochasticity becomes more important with increasing resource availability [25], thus enhancing the dispersal limitation on soil bacteria. Stochastic processes become less important in the case of fungi as succession progresses. Fungi form intimate relationships with plants during succession, including mutualism. Variations in the composition of plants can function as powerful filters in their own right, leading to different fungal communities [12]. Furthermore, through variations in the biochemistry of litter during succession, plants may indirectly cause changes in the fungal communities that live in the soil [70]. The plant community's influence on fungal assembly processes may, therefore, result from selection pressure (e.g., nutrient limitation causes a higher proportion of symbionts) on soil fungal fitness and the survival of variational plant communities of the studied forests in the early stages of succession. This suggests that the structure of fungal communities is mainly determined by deterministic processes.

5. Conclusions and Suggestions for Future Research

In summary, we analyzed the plant, soil, and soil microbial data from 30 sample plots across three restoration gradients in the degraded karst forest ecosystems. It was found that secondary succession in karst forests affected by selective logging delivered no effects on the α-diversity of soil microorganisms since the subsurface was not immediately disturbed. However, succession considerably changes the composition of soil microbial communities (β-diversity). The synergic effect of plant species diversity and soil physical and chemical characteristics influences microbial community composition, and this influence is more significant than that of a single factor. Plant succession changes soil microbial community composition by affecting soil physical and chemical properties, a relatively indirect effect responsible for weakening the separate effect of plants. Microbial community composition change is affected more by the combined effect of soil physical and chemical properties than by either individual type of factor. Stochastic processes dominate the assembly of soil bacterial and fungal communities during restoration. However, the intensity of such a role in the bacterial community varies over the number of soil microbes and total soil microbes in the community. The latter increased with succession in bacterial communities and decreased with succession in fungal communities. Based on the understanding of the diversity, composition, and dominant factors of soil microbial community assembly during degradation and restoration. Soil microorganisms serve as a pivotal conduit between vegetation and soil interactions. By elucidating the mechanisms behind community assembly during their restoration processes, this provides a foundation for future artificial restoration efforts. For instance, bacterial communities, which are often driven by stochastic processes, can be artificially supplemented with a more diversified nutrient source to enhance their community diversity. Conversely, fungal communities, which readily form symbiotic relationships with plants, are more influenced by deterministic processes. This insight can inform the selection of plant species for artificial restoration initiatives.

We have suggested that the functional and phylogenetic diversity of soil microbial communities in naturally restored karst forests, as well as the diversity of rare microorganisms and the mechanism of community assembly, can be studied in future research, so as to improve the study of soil microbial communities in naturally restored karst forests.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f15040594/s1. References [71,72] are cited in the supplementary materials.

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