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## Soil microbial community, dissolved organic matter and nutrient cycling interactions change along an elevation gradient in subtropical China

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# Soil microbial community, dissolved organic matter and nutrient cycling interactions change along an elevation gradient in subtropical China

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**ABSTRACT**

To identify possible dominating processes involved in soil microbial community assembly, dissolved organic matter (DOM) and multi-nutrient cycling (MNC) interactions and contribute to understanding of climate change effects on these important cycles, we investigated the interaction of soil chemistry, DOM components and microbial communities in five vegetation zones - ranging from evergreen broad-leaved forest to alpine meadow - along an elevation gradient of 290 to 1960 m in the Wuyi Mountains, Fujian Province, China. Soil DOM composition and microbial community assembly were characterized using Fourier transform ion cyclotron resonance mass spectrometry (FT-ICR MS) and Illumina MiSeq high-throughput sequencing, respectively. Sloan's neutral model and the modified stochasticity ratio were used to infer community assembly processes. Key microbial drivers of the soil MNC index were identified from partial least squares path models. Our results showed that soil DOM composition is closely related to the vegetation types along an elevation gradient, the structure and composition of the microbial community, and soil nutrient status. Overall, values of the double bond equivalent (DBE), modified aromaticity index ($AI_{mod}$) increased, and H/C ratio and molecular lability boundary ($MLB_L$) percentage decreased with elevation. Lignins/CRAM-like structures compounds dominated soil DOM in each vegetation type and its relative abundance decreased with elevation. Aliphatic/protein and lipids components also decreased, but the relative abundance of aromatic structures and tannin increased with elevation. The alpha diversity index of soil bacteria gradually decreased with elevation, with deterministic processes dominating the microbial community assembly in the highest elevation zone. Bacterial communities were conducive to the decomposition of labile degradable DOM compounds (H/C≥1.5) at low elevation. In the cooler and wetter conditions at higher-elevation sites the relative abundance of potentially resistant soil DOM components (H/C<1.5) gradually increased. Microbial community diversity and composition were important predictors of potential soil nutrient cycling. Although higher elevation sites have higher nutrient cycling potential, soil DOM was assessed to be a more stable carbon store, with apparent lower lability and bioavailability than at lower elevation sites. Overall, this study increases understanding of the potential linkage between soil microbial community, multiple nutrient cycling and DOM fate in subtropical mountain ecosystems that can help predict the effect of climate change on soil carbon

58   sequestration and thus inform ecosystem management.

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## 1. Introduction

64   Globally, the carbon (C) content of soil organic matter (SOM) is more than three times that of the

65   atmospheric C pool or the C storage of living terrestrial vegetation (Schmidt et al., 2011;

66   Gougoulias et al., 2014). Climate warming significantly affects the stock and stability of SOM and

67   increases the release of $CO_2$ from the soil carbon pool, thereby causing a positive feedback between

68   the terrestrial carbon cycle and climate change (Koven et al., 2011). Soil microorganisms play a

69   pivotal role in global C cycling (Abatenh et al., 2018), because a large proportion of SOM is derived

70   from storage and reprocessing within the microbial food web (Liang et al., 2019).

71       Although dissolved organic matter (DOM) accounts for less than 2% of SOM (Swenson et al.,

72   2015), it plays an important role in regulating nutrient cycles and soil micro-ecology as a dynamic

73   soil carbon pool (Fouché et al., 2020). Soil DOM compounds provide soluble organic substrates for

74   heterotrophic microbes and play a role in extracellular electron transfer across cell membranes,

75   changing the cellular redox state (Wang Y. H. et al., 2021). This alters the microbial niche and

76   thereby affects the composition and diversity of the functional microbial community (Li et al., 2019;

77   Mladenov et al., 2010; Wang Y. H. et al., 2021). The production and degradation of the different

78   components of DOM are inseparable from DOM-microbe interactions (Wang W. X. et al., 2021).

79   For example, low molecular mass plant-derived DOM molecules are consumed and transformed by

80   microorganisms, generating larger molecular mass DOM compounds with increasing soil depth

81   (Roth et al., 2019). Furthermore, changes in structure and composition of the microbial community

82   are tightly coupled to DOM turnover (Wu X. Q. et al., 2018). Analysis of changes in the temporal

83   and spatial distribution of DOM compounds and their chemodiversity is key for evaluating SOM

84   stabilization mechanisms. Fourier transform ion cyclotron resonance mass spectrometry (FT-ICR

85   MS) provides detailed information on various DOM compounds at the molecular level (e.g., Roth et

86   al., 2019; Wang W. X. et al., 2021; Wu X. Q. et al., 2018).

87　　　　Artificial simulation warming experiments allow us to explore the response of SOM to

88　short-term temperature increase. For example, in a 4 ℃ soil warming experiment conducted for 4.5

89　years, it was reported that soil nutrient availability changed, which affected the composition and

90　metabolism processes of the microbial community (Dove et al., 2021). However, the applicability of

91　these results to understanding SOM processing under complex environmental conditions and over

92　long-time scales is questionable. Moreover, these experiments did not fully consider the impact of

93　substrate availability on microbial activities. An alternative approach is to use elevation gradients as

94　natural experiments to test the ecological and evolutionary responses of biological groups to climate

95　change (Körner, 2007). Climate, vegetation types, and soil heterogeneity vary greatly over short

96　spatial distances in mountain ecosystems (Tang et al., 2020). These differences have been exploited

97　in "temporal and spatial substitution" studies across geographic gradients (Rustad, 2008) in which

98　soil transplant experiments have been conducted along elevation gradients to explore the response

99　of surface SOM components to rising temperature (Cao et al., 2020; Luan et al., 2014).

100　Bioavailability of DOM, the most bioavailable fraction of SOM, is controlled by its intrinsic

101　characteristics, soil properties and external factors such as temperature and precipitation patterns

102　(Marschner and Kalbitz, 2003). The sharply heterogeneous environment along an elevation

103　gradient, such as precipitation, temperature, rainfall and vegetation type, may lead to variation in

104　water-extractable SOM (Huang et al., 2015). Hence, soil heterogeneity and environmental

105　variability have a great impact on the DOM inventory along elevation gradients. For example, Dai

106　et al. (2021) reported a positive correlation between the total genetic diversity of microorganisms

107　related to C cycling and elevation.

108　　　　Niche and neutral processes are complementary in regulating the assembly of microbial

109　communities simultaneously (Chen Q. L. et al., 2021; Zhou and Ning, 2017). Niche-based theory

110　holds that the assembly of microbial community structure is controlled by deterministic processes

111　due to the different habitat preferences and fitness among microorganisms, including abiotic factors

112　(environmental filtering) and biotic interactions (such as facilitation and predation) (Chen et al.,

113　2019; Zhou and Ning, 2017). Thus, environmental heterogeneity is the dominant driver of microbial

114　assembly. Conversely, neutral theory asserts that microbial assemblage is generated by stochastic

115　processes, including probabilistic dispersal, random speciation and extinction, and ecological drift

(Zhou and Ning, 2017). A recent study showed that stochastic processes mainly determined the assembly of *phoD*-harboring bacteria (an indicator of organic phosphorus transformation) at high elevations (> 1500 m) with less environmental constraint, compared to the bacteria assembly at low elevation (< 1500 m), in the pristine Shennongjia forest, north-western Hubei Province, China (Wan et al., 2021). Nevertheless, the relationship between soil DOM compositions and its molecular properties and the assembly patterns of microbial community along subtropical elevation gradients remain largely unexplored.

Microbial community assembly determines the presence, abundance, and composition of microbes, thereby impacting multiple ecosystem functions (Wan et al., 2021; Xun et al., 2019). One of the methods for assessing ecosystem multi-functionality is to standardize and then average the values of multiple functions to a single index (Byrnes et al., 2014). The multiple nutrient cycling (MNC) index provides a quantifiable measure of an ecosystem to sustain multiple functions simultaneously (Delgado-Baquerizo et al., 2016; Jiao et al., 2018; Jiao et al., 2021). Microorganisms drive the soil nutrient cycling in terrestrial ecosystems (Zhou et al., 2023). Thus, analyzing microbial community assembly processes and DOM compounds, and investigating how microbial community diversity and composition drive soil multiple nutrient cycling, are needed for predicting the effect of climate change on soil microbial community and the drivers of soil C cycling.

The Wuyi Mountains have a distinct vertical zonation of vegetation types and strong climatic variation along an elevation gradient in subtropical south-eastern China, providing a unique experimental platform to explore soil-plant-microbial interactions (Wang et al., 2009; Wu et al., 2016). To identify the soil microbial community assembly process, diversity patterns, and soil DOM components, we applied FT ICR-MS to characterize soil DOM components, combined with Illumina MiSeq sequencing, to soil samples along an elevation gradient in the Wuyi Mountains, subtropical China. Specifically, we hypothesized that: i) the chemodiversity of DOM molecules and the content of refractory components increases with elevation due to the shift to specialized microbes with greater C degradation ability; ii) deterministic processes control soil bacterial and fungal community assembly at high elevation; iii) changes in soil microbial diversity result in variation in multi-nutrient cycling along the elevation gradient.

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## 2. Material and methods

### 2.1. Site description, soil sample collection and preparation, and soil chemical analysis

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Our study was conducted in the Wuyi Mountain National Nature Reserve (27°33′-27°54′ N, 117°27′-117°51′ E) in northern Fujian Province, south-eastern China. Five sites with different vegetation zones along an elevation gradient were selected, which are long-term ecological study sites described in Bu et al. (2011). The vegetation zones and elevations of the five sites were: evergreen broad-leaved forest (EB), coniferous and broad-leaved mixed forest (CB), coniferous forest (CF), subalpine dwarf forest (DF), and alpine meadow (AM), located at 290, 1070, 1400, 1800 and 1960 m above sea level, respectively. Additional information about soil type, climate (mean annual air temperature (MAT), and mean annual precipitation (MAP)) and the main plant species in each vegetation zone are in Table S1. Winter was selected as the optimal time for sampling to explore soil microbial effects on DOM as previous research in the same area reported higher soil microbial biomass in winter (He et al., 2009).

We randomly demarcated three plots (20 m × 20 m) in each vegetation zone. Eight cores (3 cm diameter) were taken in the upper 20 cm of soil in an S-shape in each plot on 19 January 2019 (in winter) at mid-slope positions. For each plot, all eight soil samples were mixed thoroughly to form a single composite sample (~1 kg) and then placed in an airtight bag. Thus 15 soil samples were generated, consisting of one composite sample from each of the three plots for each of the five vegetation zones. The samples were stored at 4 °C for transport to the laboratory within 48 hours (Roth et al., 2019). In the laboratory, fresh soil samples were sieved (2 mm) to remove gravel and plant debris.

Part of the sieved soil was air-dried at room temperature and used to determine soil pH, available phosphorus (AP) and available potassium (AK). Some of the 2-mm sieved air-dried soil was ground by hand and passed through a 0.149 mm nylon sieve and used for determination of soil total carbon (TC) and total nitrogen (TN) contents. The remaining fresh soil samples (< 2 mm) were cryopreserved at -80 °C and then thawed as required to represent "fresh" soil for determination of ammoniacal-nitrogen ($NH_4^+$-N), nitrate-nitrogen ($NO_3^-$-N), dissolved organic carbon (DOC), and the characterization of DOM molecular composition and the soil microbial community. The

6

174 analysis methods for soil chemical properties and the molecular composition of soil DOM are

175 detailed in Supplementary Material Sections S1 and S2, respectively. We mixed equally the three

176 replicate soil samples at each site into one sample (Ye et al., 2020) for DOM extraction.

177

178 **2.2. Soil microbial community analysis**

179 Bacterial and fungal DNA were extracted from each fresh soil sample using a Power Soil DNA

180 Isolation Kit (MoBio Laboratories, Inc., CA). We subjected soil samples to high-throughput

181 sequencing using the Illumina Miseq PE300 sequencing platform at Beijing Allwegene Technology

182 Co., Ltd. (Beijing, China). DNA quality was detected by 1% agarose gel electrophoresis. The

183 primers 338F (5′-ACTCCTACGGGAGGCAGCAG-3′) and 806R

184 (5′-GGACTACHVGGGTWTCTAAT-3′) were used to amplify the V3–V4 region of the bacterial

185 16S rRNA. For fungal communities, the ribosomal ITS1-ITS2 region was targeted using primers

186 ITS1 (5′- CTTGGTCATTTAGAGGAAGTAA-3′) and ITS2 (5′-TGCGTTCTTCATCGATGC-3′).

187 The PCR reaction mixtures and PCR amplification procedures used for soil bacteria and fungi were

188 the same as in Zhang et al. (2022), and are detailed in Supplementary Material Section S3. Reads

189 were demultiplexed, quality-filtered, and processed to obtain valid sequences. Effective sequences

190 with a similarity of 97% were clustered into the same operational taxonomic unit (OTU).

191 Trimmomatic (v 0.36) and PEAR (v 0.9.6) were used to control the quality of raw sequence reads,

192 and the paired-end sequences were merged using Flash (v1.20) and PEAR (v0.9.6). Chimeric

193 sequences were removed with the Vsearch (v2.7.1) (uchime method) (Zhang et al., 2022). The

194 functional annotation of prokaryotic taxa (FAPROTAX) database was used for annotation of the

195 bacterial community (Sansupa et al., 2021) using the online tools

196 (http://cloud.biomicroclass.com/CloudPlatform/SoftPage/FAP).

197

198 **2.3. Soil multi-nutrient cycling analysis and DOM molecular properties**

199 We determined the soil MNC index from the seven nutrient variables measured: TC, TN, $NH_4^+$-N,

200 $NO_3^-$-N, AP, AK, and DOC. The MNC value was calculated for the average value of the

201 standardized score of each soil nutrient variable, normalized for individual nutrient concentrations

202 on a common scale ranging from 0 to 1 (Jiao et al., 2021; Zhang et al., 2022) (Eqs. 1 and 2).

$$STD_i = \frac{X_i - X_{min}}{X_{max} - X_{min}} \quad\quad \text{(Eq. 1)}$$

$$MNC = \frac{\sum_{i=1}^{n} STD_i}{n} \quad\quad \text{(Eq. 2)}$$

where $STD_i$ is the standardized individual soil nutrient variable i and $X_i$, $X_{min}$, and $X_{max}$ are the individual soil nutrient concentrations and their minimum and maximum values across all soil samples, respectively. n represents the number of all nutrient variables. Classification and calculation of soil DOM molecular properties (DBE, $AI_{mod}$, average nominal oxidation state of carbon (NOSC), molecular lability boundary ($MLB_L$) percentage, and Shannon index) are detailed in Supplementary Material Section S4 and Table S2.

**2.4. Data and statistical analysis**

Apart from where stated, all statistical analyses were conducted using R v4.1.3 (R Core Team, 2018) and the significance level used was $P < 0.05$. Differences in soil chemical properties and the relative abundance and alpha diversity indexes of microbes were tested using one-way analysis of variance (ANOVA), with multiple comparisons among vegetation zones conducted using least significant difference (LSD) tests (SPSSv19, SPSS Inc., Chicago, IL, USA). The Shapiro-Wilk test and Levene's test were used to check that data fulfilled the normality and homogeneity of variance assumptions for ANOVA, respectively. If these assumptions were not met, we applied the non-parametric Kruskal-Wallis test with Bonferroni-adjusted $P$ values using the "agricolae" (v1.3-5) package (de Mendiburu, 2021).

We calculated the alpha diversity indices (Chao1 index, Shannon index, and Faith's phylogenetic diversity whole tree index (Faith's PD whole tree index)) of microbial communities in each of the 15 soil samples using Qiime (v.1.8.0) (Taketani et al., 2017). Differences in microbial communities between elevations and the degree of separation between- and within- elevations were evaluated using the NMDS and analysis of similarities (ANOSIM) (Chen et al., 2019).

We calculated Spearman's rank correlation coefficients between the soil bacterial and the fungal OTUs with the top 300 relative abundances using the "Hmisc" and "igraph" packages in R. We used the False Discovery Rate (FDR) method to adjust the $P$ values. Only correlations with absolute correlation coefficient values $> 0.8$ correlations and adjusted $P$ values $< 0.01$ were

considered. The "igraph" package was also used to calculate the topological characteristics of the co-occurring network compared with 10,000 random networks generated according to the Erdös–Réyni model whose edges were assigned to any node with the same probability (Jiao et al., 2016). The degree distributions of the co-occurring networks were plotted to assess their form (Fig. S1). Gephi (0.9.3) (https://gephi.org/) was used to visualize the co-occurrence networks.

To assess the contribution of neutral processes to microbial community assembly, we fitted Sloan's neutral community model (NCM) to estimate the relationship between the occurrence frequency and mean relative abundance variations of OTUs, as described in detail in Jiao et al. (2021). The modified stochasticity ratio (MST) to infer microbial community assembly processes (Qiu et al., 2020) and Levins' niche breadth index were calculated for the soil microbial community using the "NST" package and the "niche.width" function in the "spaa" package (Chen Q. L. et al., 2021), respectively. The "EcolUtils" package was used to randomly arrange the occurrences of OTUs 1000 times to simulate the OTU occurrence frequency. OTUs with observed occurrence exceeding the upper 95% confidence interval were considered generalists, with those below the lower 95% confidence interval considered specialists, and the remainder considered neutral taxa (Zhang et al., 2018).

Associations between soil DOM composition and microbial OTUs were assessed by Pearson product-moment correlation analysis and visualized as co-occurrence network diagrams using Cytoscape 3.5.1. The "random-forest" package was used to identify the main microbial predictors of soil MNC values along the elevation gradient. The most important predictors were assessed as those with higher percentage increases in the MSE (mean squared error) of the variable. The "A3" package was used to assess the significance of the model with 5000 permutations of the response variables (Gao et al., 2021; Jiao et al., 2018), whilst the "rfPermute" package was used to estimate the significance of each predictor on the MNC index with 5000 trees. We used partial least squares path models (PLS-PM) through the "plspm" package to investigate the direct and indirect effects of microbial community characteristics on the MNC index. From initial modeling, variables with loading values < 0.7 and variance inflation factor (VIF) > 10 were removed, with the final PLS-PM constructed using the remaining variables (Yun et al., 2022). DOM data used in this manuscript can be found at https://www.zenodo.org/record/8188815.

**3. Results**

**3.1. Soil chemical properties and DOM composition along the elevation gradient**

Soils were acidic and pH values were very similar among sites, ranging from mean pH of 4.55 in the subalpine dwarf forest (DF) vegetation zone to 4.73 in the alpine meadow (AM) zone (Table 1). Soil $NH_4^+$-N concentration generally increased with elevation, whilst $NO_3^-$-N and AP did not vary significantly between zones. DOC concentration increased with elevation, reaching a mean of 109.4 mg $kg^{-1}$ at AM, double that in the EB and coniferous and broad-leaved mixed forest (CB) vegetation zones. Soil TN and TC concentrations also increased significantly with elevation, although the C/N ratio remained relatively constant. In general, the MNC index increased with elevation (Table 1).

An UpSet plot were used to visualize the common-shared, partial-shared, and unique DOM molecules for the five vegetation zones along the elevation gradients in the Wuyi Mountains (Fig. S1). The number of detected molecular formulae of soil DOM at the five different vegetation zones ascending with altitude from evergreen broad-leaved forest (EB) to AM was 1168, 3106, 1206, 3392, and 2325, respectively. The common shared molecules (present in all five samples) accounted for the largest proportion from the intersection of different vegetation zones. Inter sample rankings analysis was performed to reveal possible differences in quality in the 703 common DOM components present in the five vegetation zones (Fig. 1). DOM qualities differed considerably across the vegetation zones at different elevations. At the EB site, DOM molecular formulae ranked 1 (relatively high peak intensities) exhibited H/C > 0.9 and O/C ≤ 0.5, whilst those ranked 4 and 5 mainly had O/C > 0.5. In contrast, at sites DF and AM, DOM formulae ranked 4 and 5 mainly exhibited H/C > 1 and O/C ≤ 0.55. The DOM molecular formulae ranked 1 at site AM were dominated by H/C < 1, whilst formulae ranked 1 and 2 at DF displayed high m/z values (> 400) with O/C > 0.5. Unique DOM molecular formulae at DF and AM were dominated by tannin- and aromatic structures- like compounds, respectively (Fig. S2).

Lignins/CRAM-like (carboxylic rich alicyclic molecule) structures dominated soil DOM composition in all vegetation zones, and its abundance decreased with increasing elevation (Fig. S3). The relative abundance of aliphatic/proteins and lipids also decreased with elevation, whilst those of tannin and aromatic structures increased with elevation (Fig. S3d). The weighted mean

289  O/C ratio, AI$_{mod}$, and NOSC values of DOM molecules showed increasing trends with elevation,

290  whilst the H/C ratio and molecular lability boundary (MLB$_L$) percentage decreased (Table 2). The

291  Shannon index values of DOM molecules in the coniferous forest (CF) were slightly lower than in

292  the other vegetation zones (Table 2). This is consistent with the narrower ranges of the distribution

293  curves for the number of C and O atoms and M/Z values of DOM compositions in CF compared

294  to the other vegetation zones (Fig. S3).

295

296  **3.2. Soil microbial diversity, community structure and assembly processes along the elevation**

297  **gradient**

298  Within the soil bacterial community, *Acidobacteria* (36.2%–42.6%), *Proteobacteria* (24.5%–

299  32.3%), *Chloroflexi* (7.51%–14.2%), *Actinobacteria* (5.97%–8.4%) and *Planctomycetes* (2.14%–

300  5.77%) were the five most abundant phyla in all five vegetation types (numbers in parentheses are

301  minimum and maximum values of mean % abundance amongst the different sites, Fig. S4a). They

302  displayed no clear trend in abundance with elevation, although the relative abundance of

303  *Verrucomicrobia* (0.99%–2.69%) decreased with elevation (Fig. S3b). In the fungal community,

304  *Basidiomycota* (53.7%–82.5%) dominated at all sites. Its relative abundance was highest at the

305  lowest elevation in the evergreen broad-leaved forest (EB) zone, and then decreased before

306  increasing with elevation. The relative abundance of *Mortierellomycota* phylum also generally

307  increased with elevation (Fig. S4c).

308  The Chao1 index and Faith's PD index of soil bacteria decreased with increasing elevation (Fig.

309  S5a and Fig. S6a), whilst the indices for fungi were not significantly different between elevations

310  (Fig. S5d and Fig. S6b). The Shannon indices for both the bacterial and fungal communities

311  increased from EB to the coniferous and broad-leaved mixed forest (CB) zone and then showed a

312  decreasing trend with elevation (Fig. S5b, e). Non-metric multidimensional scaling (NMDS)

313  analysis showed that the soil bacterial and fungal communities at the different sites formed distinct

314  clusters, which are completely separate in the ordination space (Anosim test, Global R = 1, $P <$

315  0.001) (Fig. S5c, f). Beta diversity, estimated among the microbial communities in all 15 soil

316  samples based on Bray-Curtis dissimilarities, was significantly lower among bacteria than fungi

317  (Fig. S7).

318       The potential linkages among soil bacteria and fungi OTUs were revealed by the co-occurring

319    network analysis (Fig. 2a, b). Compared with the Erdös-Réyni random network, a higher clustering

320    coefficient and average path length were observed in the co-occurrence networks of bacterial and

321    fungal communities (Fig. 2a, b). This displayed that the generated networks were more clustered

322    than the identically sized random networks and that their degree distributions are non-random. The

323    modularity and average path length of the fungal community were greater than for the bacterial

324    network. In the fungal community most connections were positive (93%), in contrast to the bacterial

325    community where only 55% of connections were positive.

326       Neutral processes dominated assembly of the bacterial and fungal communities overall along

327    the elevation gradient, with 72.9% and 56.6% of the community variation explained by the neutral

328    community model (NCM), respectively (Fig. 2c, d). The values of $m$ (migration rate) were 0.561

329    and 0.123 for the bacterial and fungal community, respectively (Fig. 2c, d). To detect the relative

330    importance of stochastic and deterministic processes in the assembly of the bacterial and fungal

331    communities at different elevations, we calculated the modified stochasticity ratio (MST) in each

332    vegetation zone (Fig. 2e). The MST value for the fungal community in CB was significantly higher

333    than in other vegetation zones. In addition, MST values were < 0.5 for both bacteria and fungi in the

334    AM zone.

335

336    **3.3. Correlation between soil chemical properties, DOM components, and microbial**

337    **community characteristics**

338    Correlation analysis across all elevations revealed that the Chao 1 index for the bacterial community

339    was significantly negatively correlated with tannins, aromatic structures, and the $AI_{mod}$ value of

340    DOM compounds (Fig. 3a). Conversely, lignins/CRAM-like structures and aliphatic/proteins

341    components were significantly positively correlated with the bacterial Chao1 index (Fig. 3a). The

342    relative abundance of lignins/CRAM-like structures and aliphatic/proteins compounds were

343    significantly negatively correlated with soil TC、$NH_4^+$-N, and TN contents ($P < 0.05$). However,

344    the relative abundance of tannins was significantly positively correlated with soil TN and TC

345    contents (Fig. S8).

346       Highly significant correlations ($P < 0.01$) between the 100 most abundant DOM molecular

formulae and bacteria and fungi OTUs at the phylum level were selected to construct network diagrams. For bacteria (Fig. 3b), formulae of lignins/CRAM-like structures were positively correlated with most microbes, whilst *Chloroflexi* was negatively correlated with some tannin molecules. *Proteobacteria* was only positively correlated with individual DOM molecules, whilst *Chloroflexi* only had negative correlations. The number of C atoms in DOM formulae correlated with *Proteobacteria* had a small range of 15–21, while those correlated with *Acidobacteria* had a relatively large range of 13–23. For fungi (Fig. 3c), there were a smaller number of correlations between phyla and individual DOM molecules, and all correlations were positive and with lignins/CRAM-like structures, apart from one formula. More DOM molecular formulae were correlated with *Ascomycota* than with *Basidiomycota*.

**3.4. Microbial drivers of soil multi-nutrient cycling**

We applied random forest (RF) analysis to identify the major potential microbial drivers of soil multiple nutrient cycling across all sites. Site elevation, alpha diversity (PD whole tree and Chao1 indices), and the relative abundance of *Verrucomicrobia* and *Firmicutes* were the most important bacterial community indicators of the soil multi-nutrient cycling (MNC) index (Fig. 4a). The significant fungal community predictors were site elevation, relative abundance of three fungal phyla, and the alpha diversity (PD whole tree and Shannon indices). Partial least squares path models (PLS-PM) analyzed the effects of microbial community characteristics on the soil MNC index, which had best fit goodness-of-fit (GOF) values of $> 0.70$ for microbial communities (Fig. 4c). The PLS-PM also highlighted the strong direct effects of elevation on soil microbial community diversity, although the effects are in opposite directions: high elevation has a negative effect on the bacterial alpha diversity index (path coefficient = -0.91, $P < 0.001$) but a positive effect on the fungal alpha diversity index (path coefficient = 0.59, $P < 0.05$). The Shannon diversity index of fungal community exhibited direct negative effects on MNC (path coefficient = -0.56, $P < 0.05$).

**4. Discussion**

**4.1. Refractory components of soil DOM molecules gradually increase along the elevation**

376 **gradient**

377 In our study elevation transect in the Wuyi Mountains, the $MLB_L$ (%) decreased and $AI_{mod}$ and

378 NOSC values of DOM molecules increased with elevation. Since higher $AI_{mod}$ and NOSC values

379 indicate greater recalcitrance (low bioavailability) of DOM compounds (Cai and Jiao, 2023; Hu et

380 al., 2022), this indicates that soil DOM resistance increased with elevation. The DBE and O/C ratio

381 of soil DOM molecules increased along our study elevation gradient (Table 2), which is consistent

382 with the elevational variation in DOM components in restored areas of the Loess Plateau (Hu et al.,

383 2021), but contrasts with results in the higher altitude Sygera Mountains on the Tibetan Plateau

384 (Zhang et al., 2022). The DBE value reflects the degree of unsaturation of the DOM molecules

385 (Melendez-Perez et al., 2016), with higher values indicating greater unsaturation and lower

386 bioavailability (Cai and Jiao, 2023). Ligand exchange between the carboxyl / hydroxyl functional

387 groups of the DOM compounds and the surface of Fe oxides is the main mechanism of adsorption of

388 soil DOM molecules (Ding, 2020). An experimental study demonstrated that adsorption of the more

389 oxidized DOM components increased at low DOM concentrations, whilst at high DOM

390 concentrations selective adsorption of the less oxidized DOM components occurred (Avneri-Katz et

391 al., 2017). These processes appear to occur along our study elevation transect, with more oxidized

392 DOM components remaining in the soil liquid phase at the high-elevation sites. In contrast, at the

393 lower elevation sites, the oxidized DOM components were more readily adsorbed at soil solid phase

394 surfaces (and not extracted for analysis in our ultrapure water extraction (Bahureksa et al., 2021)),

395 thus decreasing the C accessibility for microbial degradation. Soil iron-containing minerals retain

396 great quantities of SOM (Lv et al., 2017). Highly oxidized and more aromatic DOM molecules are

397 preferentially adsorbed on hematite surfaces (Lv et al., 2017), and preferential adsorption of high

398 molar mass organic solutes occurs on goethite surfaces (Liu et al., 2014). The soil in the Wuyi

399 Mountains is highly leached, with mineral composition dominated by hematite in low-elevation red

400 earth soils and goethite at higher elevations in yellow earth soils (Lin, 2010). Soil mineralogy,

401 therefore, helps explain the lower molar mass (M/Z) and O/C values of the DOC molecules

402 extracted at the lowest elevation EB site.

403     The abundances of DOM molecules with lipids- and aliphatic/proteins-like compositions

404 decreased with increasing elevation on our study transect. Conversely, aromatic- and tannin- like

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compounds increased, indicating DOM compounds derived from microbe to plants along the elevation gradient (Shen et al., 2023). Tannins are secondary metabolites of polyphenols produced by higher plants, which can leach from litter into soil, and are toxic to microbial metabolism and can inhibit enzyme activity, thereby affecting nutrient cycling (Triebwasser et al., 2012; Kraus et al., 2003). Feng et al. (2021) showed that soil microbial metabolic efficiency decreased with elevation, which was attributed partly to the microbial community increasing investment in nutrient acquisition via enzymes. Thereby, the decrease with elevation of microbial-derived DOM along our elevation transect is attributed to the expected inhibition of microbial activity. We also found that the relative abundance of lignin/CRAM-like structure compounds decreased with increasing altitude. Lignins in soil are mainly generated from above-ground and subsurface (root) litter of higher plants, though biotic, aerobic and co-metabolic degradation processes (Thevenot et al., 2010). For example, white rot fungi of *Basidiomycetes* secrete ligninolytic enzymes, which can convert and mineralize refractory DOM into $CO_2$ and water by co-metabolizing aliphatic and aromatic substances (Agrawal et al., 2021). The change of lignin input source during the transition from trees to graminaceous plants and the strong degradation of saprophytic fungi at higher elevation may explain the change of lignin-like compounds to some extent along the study transect.

Interestingly, the DOM molecules in soil from the coniferous forest (CF) site had a narrower range of number of C and O atoms and M/Z values (Fig. S3), which is consistent with the results of Li et al. (2021) for soil DOM of monoculture Chinese fir (*Cunninghamia lanceolata* (Lamb.) Hook.) plantations. Soil DOM provides carbon-containing substrates for the soil microbial community, and the latter affects DOM composition by supplying metabolites and residues (Wu M. et al., 2021). Plant litter is an important main source of soil DOC (Don and Kalbitz, 2005). Therefore, differences in litter-fall and the metabolites and residues of microorganisms in vegetation zones along elevation gradients may be one important cause of changes in DOM molecular composition. For instance, the low input of soil nutrients from litter-fall (Ma et al., 2007) may partly explain the soil DOM variation in Chinese fir plantations of different ages.

The van Krevelen diagram is widely used for visualization of DOM molecular types and

characters, and identification of possible chemical reactions (Kim et al., 2003). Nevertheless, it is important to note that the molecular composition (molecular formulae) only of DOM is obtained based on FT-ICR MS but not the isomer features (Hu et al., 2022). It is therefore necessary in future studies to identify the structural features of DOM molecules to reveal their full role in soil ecosystems (Qi et al., 2022).

**4.2. Deterministic processes dominate the low-diversity microbial assembly at high elevation**

The MST values of the soil bacteria and fungi communities were below the 0.5 threshold in the alpine meadow zone, indicating that deterministic processes dominate microbial assembly at the highest elevation site (Fig. 2e). Furthermore, the microbial community at this site had low Shannon diversity indices compared to many of the lower elevation vegetation zones (Fig. S5b, e). Environmental filters, including temperature, precipitation, soil available nutrient contents and physical properties, and vegetation types can select for microbial species with specific traits, such as stress tolerances and nutrient acquisition (Anthony et al., 2020). Such effects have been reported in a number of studies. For instance, microbial community diversity and enzyme activity were affected more by changing climatic factors, such as mean annual temperature and precipitation, than soil characteristics along an elevation gradient on Taibai Mountain in eastern China (Ren et al., 2020). Mo et al. (2021) reported that deterministic processes influenced the microeukaryotic plankton community assembly with narrow habitat niche breadths under high salinity conditions. Furthermore, Xun et al. (2019) indicated that environmental selection increased in low-diversity bacterial communities, which contributed to the dominance of deterministic processes. Reduced soil temperature and increased soil moisture were observed with elevation in the Wuyi Mountains related to lower air temperature and elevated precipitation (Table S1), which results in slower decomposition rates of SOM at high elevation (Bu et al., 2012). Collectively, increasing environmental and physiological stress on microorganisms along the elevation gradient (Ren et al., 2020), including the reduced abundance of labile DOM (H/C $\geq$ 1.5), high C/N ratio substrates (Anthony et al., 2020) and increasing abundance of tannins, are suggested to lead to the dominance of deterministic assembly processes for the microbial community at the highest elevation site in the Wuyi Mountains.

Co-occurring network analysis is a useful method for identifying potential microbial interactions and functional distribution (Chen W. J. et al., 2021). The results of co-occurring network analysis showed that positive associations were more dominant among the fungal community than the bacterial community at the study sites (Fig. 2a, b), suggesting possible niche overlap and mutualistic or facilitative interactions between the fungal species (Zhu et al., 2021). The lower average path length and higher average degree of the bacterial co-occurring network indicates closer relationships among the OTUs and rapid distribution of any perturbation (Li et al., 2020; Yuan et al., 2021).

The emergence and maintenance of soil microbial diversity are underpinned by soil heterogeneity (Nunan et al., 2020). In this study, soil fungal communities had higher beta diversity than bacterial communities (Fig. S7) which is consistent with the results of Jiao et al. (2018). The bacterial community across all sites had lower path length, lower dispersal limitation (lower $m$ value), and wider habitat niche breadths than fungal taxa (Fig. 2a, c, d and Fig. S9), which have a smaller body size and more flexible metabolic plasticity, and therefore are less environmentally filtered (Wu W. X. et al., 2018). The interaction between disturbance and dispersal can homogenize species composition, which was observed to cause decreased beta diversity (Catano et al., 2017). The relative proportions of soil heterotrophic microorganisms are determined by the local geographic environment, vegetation types, and soil factors (Zhuang et al., 1997). For example, Li et al. (2021) found that the soil fungal Faith's PD index declined with elevation in the cold temperate zone at high latitudes in China. Microbial diversity positively regulates the service functions of terrestrial ecosystems by changing the nutrient supply and distribution of terrestrial ecosystems (Delgado-Baquerizo et al., 2016).

Overall, in this study, the Chao 1 and Faith's PD diversity indexes of bacterial communities decreased along a subtropical elevation gradient (Fig. S5a and Fig. S6a). Ma et al. (2022) also reported that the bacteria community richness index and Faith's PD index decreased with elevation in subtropical forests, with soil temperature largely explaining the changes in soil bacterial and fungal diversity. Bacterial community diversity largely drives the utilization efficiency of C (Domeignoz-Horta et al., 2020). Reduced abundance of labile DOM (H/C $\geq$ 1.5) and increasing abundance of tannins may reduce soil enzyme activity, thereby reducing bacterial community

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492   diversity.

493       Microbial life history strategies also influence soil DOM composition. For example, Zeng et al.

494   (2022) found that microbial assemblies shifted from using labile to recalcitrant carbon with

495   increasing elevation. In our study, *Chloroflexi* had higher relative abundance at the highest

496   elevation AM site (Fig. S4a) and also its abundance was negatively correlated with

497   lignins/CRAM-like structures and tannins in DOM molecules (Fig. 3b). Positive correlations

498   between microbial compositions and DOM molecules are indicative of the generation of new

499   molecules by microbial activity, whilst negative correlations are interpreted as the decomposition

500   of DOM molecules based on resource-consumer relationships (Hu et al., 2022). *Chloroflexi* can

501   decompose recalcitrant C-containing components and are considered a *K*-selected microbe

502   (Adamczyk et al., 2021). Combined with our study results, this suggests the selection of substrates

503   with low bioavailability by *Chloroflexi.*

504

505   **4.3. Bacteria drive the degradation of labile soil DOM components, and the fungal**

506   **community is the key control on soil nutrient cycling**

507   The soil bacterial community contained a slightly higher percentage of habitat generalists and had

508   a larger niche breadth compared to the fungal community, which had a higher percentage of

509   habitat specialists (Fig. S9), indicating that the soil bacterial community had more competitive

510   ability than the fungi. Highly labile substrates, for which bacterial communities have a high affinity

511   (Osterholz et al., 2016), can reach steady-state equilibrium concentrations below detection limits.

512   The significant correlations across the study sites between the Chao1 index for bacteria and the H/C

513   and O/C ratios of DOM components (positive and negative, respectively) (Fig. 3a), indicate that the

514   bacterial community plays an important role in the degradation of labile components. The Chao1

515   index of the bacterial community was also significantly positively correlated with soil DOM

516   aliphatic/protein compounds, concurring with other studies reporting positive associations between

517   bacterial abundance and activity and aliphatic DOM components (Kamjunke et al., 2019). From the

518   results of the FAPROTAX database functional annotation, we found that bacterial OTUs with

519   functional photoheterotrophy increased with elevation, whilst those with functional nitrification

520   and aerobic nitrite oxidation decreased overall with altitude (Fig. S10). Furthermore, the soil MNC

521　index increased along the altitude gradient (Table 1). Thus, changes in microbial investment in

522　nutrient acquisition may lead to this interaction between soil nutrients and microbial communities.

523　　　Fungal extracellular polymeric substances and hyphae networks are conducive to the

524　transmission and aggregation of plant-derived litter derivatives to increase the decomposition

525　efficiency and persistence of SOM (De Beeck et al., 2021; Witzgall et al., 2021). Fungi are

526　regarded as oligotrophs, exhibiting effective degradation of refractory carbon substrates (Ho et al.,

527　2017). The soil fungal community plays a vital role in nutrient cycling and organic matter

528　transformation, such that fungal community structure and biomass provide an early indicator of soil

529　environmental changes (Wu et al., 2019). Specifically, the relative abundance of the fungal phylum

530　*Mortierellomycota* increased with elevation and was significantly positively correlated with soil AK

531　and DOC concentrations (Fig. S4c and S11a). *Mortierellomycota* are *r*-selected saprotrophic

532　microorganisms that have a low life expectancy and stronger growth in environments with high

533　available resources and low-stress exposure (Wu et al., 2021).

534　　　In contrast, the relative abundance of the bacterial phylum *Verrucomicrobia* was significantly

535　negatively correlated with soil $NH_4^+$-N, AK, and DOC concentrations (Fig. S11b, c), and with

536　tannin abundance (Fig. S12). This is interpreted as indicative of the oligotrophic lifestyle of

537　*Verrucomicrobia* (Navarrete et al., 2015). In our study, the relative abundance of tannins were

538　significantly positively correlated with soil TC and TN concentrations (Fig. S8), which showed

539　that tannins was beneficial to the sequestration of carbon and nitrogen. The dominant fungal

540　phylum *Basidiomycota* in our study had the highest relative abundance in the lowest elevation

541　vegetation zone EB, and then decreased, followed by an increasing trend with elevation from CB to

542　AM (Fig. S4c). *Basidiomycota* are representative of oligotrophic fungi, which can degrade

543　refractory compounds, and were found to be most abundant in warmer soil conditions along a

544　temperate forest transect characterized by a K-strategy fungal community (Li et al., 2021). Thus the

545　increase in the relative abundance of *Basidiomycota* with elevation in our study can partly explain

546　the shift to K strategy due to the refractory components (H/C < 1.5) of soil DOM with elevation.

547

548　**5. Conclusions**

549　It is well-known that the soil microbial community has a profound impact on DOM composition and

multi-nutrient cycling in ecosystems. Changes in the functional group of soil bacterial community with elevation, related to investment in nutrient acquisition, may account for changes in soil nutrient cycling. Neutral processes dominated overall the bacterial and fungal communities assembly along the elevation transect, and bacteria have a higher niche breadth and lower dispersal limitation than fungi. However, deterministic selection dominated the microbial community assembly at the highest elevation site, which may be attributed to the reduced soil temperature and increased soil moisture, and increased relative abundance of tannin and aromatic structures in soil DOM. This increased abundance of potentially resistant DOM components could be interpreted as enhanced soil carbon sequestration capacity with increasing elevation, but their stability is not assured if vegetation zones at lower elevations with higher rates of DOM degradation move upwards in response to climate warming. As a relatively active fraction of the soil C pool, DOM molecules are greatly affected by microbial community, and anthropogenic-driven climate change increases the possibility of DOM degradation. Since sampling was conducted in winter, care should be taken in interpreting the interconnection between soil DOM components and microorganisms in the Wuyi Mountains in other seasons.

**References**

Abatenh, E., Gizaw, B., Tsegaye, Z., Tefera, G., 2018. Microbial Function on Climate Change - A Review. Open Journal of Environmental Biology 3(1), 1-7. https://doi.org/10.17352/ojeb.000008.

Adamczyk, M., Rüthi, J., Frey, B., 2021. Root exudates increase soil respiration and alter microbial community structure in alpine permafrost and active layer soils. Environmental Microbiology 23(4), 2152-2168. https://doi.org/10.1111/1462-2920.15383.

Agrawal, N., Barapatre, A., Shahi, M.P., Shahi, S.K., 2021. Biodegradation Pathway of Polycyclic Aromatic Hydrocarbons by Ligninolytic Fungus *Podoscypha elegans* Strain FTG4 and Phytotoxicity Evaluation of their Metabolites. Environmental Processes 8(3), 1307-1335. https://doi.org/10.1007/s40710-021-00525-z.

Anthony, M. A., Crowther, T. W., Maynard, D. S., van den Hoogen, J., Averill, C., 2020. Distinct

579        Assembly Processes and Microbial Communities Constrain Soil Organic Carbon Formation.

580        One Earth 2(4), 349-360. https://doi.org/10.1016/j.oneear.2020.03.006.

581    Avneri-Katz, S., Young, R. B., McKenna, A. M., Chen, H., Corilo, Y. E., Polubesova, T., Borch, T.,

582        Chefetz, B., 2017. Adsorptive fractionation of dissolved organic matter (DOM) by mineral soil:

583        Macroscale approach and molecular insight. Organic Geochemistry 103, 113-124.

584        https://doi.org/10.1016/j.orggeochem.2016.11.004.

585    Bae, E. J., Yeo, I. J., Jeong, B., Shin, Y., Shin, K. H., Kim, S., 2011. Study of double bond

586        equivalents and the numbers of carbon and oxygen atom distribution of dissolved organic

587        matter with negative-mode FT-ICR MS. Analytical Chemistry 83(11), 4193-4199.

588        https://doi.org/10.1021/ac200464q

589    Bahureksa, W., Tfaily, M. M., Boiteau, R. M., Young, R. B., Logan, M. N., McKenna, A. M., Borch,

590        T., 2021. Soil Organic Matter Characterization by Fourier Transform Ion Cyclotron Resonance

591        Mass Spectrometry (FTICR MS): A Critical Review of Sample Preparation, Analysis, and

592        Data Interpretation. Environmental Science & Technology 55(14), 9637-9656.

593        https://doi.org/10.1021/acs.est.1c01135.

594    Bu, X. L., Ding, J. M., Wang, L. M., Yu, X. N., Huang, W., Ruan, H. H., 2011. Biodegradation and

595        chemical characteristics of hot-water extractable organic matter from soils under four different

596        vegetation types in the Wuyi Mountains, southeastern China. European Journal of Soil Biology

597        47(2), 102-107. https://doi.org/10.1016/j.ejsobi.2010.11.009.

598    Bu, X. L., Ruan, H. H., Wang, L. M., Ma, W. B., Ding, J. M., Yu, X. N., 2012. Soil organic matter in

599        density fractions as related to vegetation changes along an altitude gradient in the Wuyi

600        Mountains, southeastern China. Applied Soil Ecology 52, 42-47.

601        https://doi.org/10.1016/j.apsoil.2011.10.005.

602    Byrnes, J. E. K., Gamfeldt, L., Isbell, F., Lefcheck, J. S., Griffin, J. N., Hector, A., Cardinale, B. J.,

603        Hooper, D. U., Dee, L. E., Duffy, J. E., 2014. Investigating the relationship between

604        biodiversity and ecosystem multifunctionality: challenges and solutions. Methods in Ecology

605        and Evolution, 5(2), 111-124. https://doi.org/10.1111/2041-210X.12143.

606    Cai, R. H., Jiao, N. Z. 2023. Recalcitrant dissolved organic matter and its major production and

607        removal processes in the ocean. Deep Sea Research Part I: Oceanographic Research Papers,

608    191, 103922. https://doi.org/10.1016/j.dsr.2022.103922.

609    Cao, C., Ruan, C. Y., Ren, Y. B., Zhang, S. L., Xiong, X. L., Li, X. J., Lyu, M. K., Xie, J. S., 2020.

610        Effects of stimulating warming on surface soil carbon, nitrogen and its enzyme activities across

611        a subtropical elevation gradient in Wuyi Mountain, China. Acta Ecologica Sinica 40(15),

612        5347-5356. (in Chinese).

613    Catano, C. P., Dickson, T. L., Myers, J. A., 2017. Dispersal and neutral sampling mediate contingent

614        effects of disturbance on plant beta-diversity: a meta-analysis. Ecology Letters 20(3), 347-356.

615        https://doi.org/10.1111/ele.12733.

616    Chen, Q. L., Hu, H. W., Yan, Z. Z., Li, C. Y., Nguyen, BA. T., Sun, A. Q., Zhu, Y. G., He, J. Z., 2021.

617        Deterministic selection dominates microbial community assembly in termite mounds. Soil

618        Biology & Biochemistry 152, 108073. https://doi.org/10.1016/j.soilbio.2020.108073.

619    Chen, W. D., Ren, K. X., Isabwe, A., Chen, H. H., Liu, M., Yang, J., 2019. Stochastic processes

620        shape microeukaryotic community assembly in a subtropical river across wet and dry seasons.

621        Microbiome 7, 148. https://doi.org/10.1186/s40168-019-0749-8.

622    Chen, W. J., Zhou, H. K., Wu, Y., Li, Y. Z., Qiao, L. L., Wang, J., Zhai, J. Y., Song, Y. H., Zhao, Z.

623        W., Zhang, Z. H., Liu, G. B., Zhao, X. Q., You, Q. M., Xue, S., 2021. Plant-mediated effects of

624        long-term warming on soil microorganisms on the Qinghai-Tibet Plateau. Catena 204, 105391.

625        https://doi.org/10.1016/j.catena.2021.105391.

626    Dai, Z. M., Zang, H. D., Chen, J., Fu, Y. Y., Wang, X. H., Liu, H. T., Shen, C. C., Wang, J. J.,

627        Kuzyakov, Y., Becker, J. N., Hemp, A., Barberán, A., Gunina, A., Chen, H. H., Luo, Y., Xu, J.

628        M., 2021. Metagenomic insights into soil microbial communities involved in carbon cycling

629        along an elevation climosequences. Environmental Microbiology 23(8), 4631-4645.

630        https://doi.org/10.1111/1462-2920.15655.

631    De Beeck, M. O., Persson, P., Tunlid, A., 2021. Fungal extracellular polymeric substance matrices –

632        Highly specialized microenvironments that allow fungi to control soil organic matter

633        decomposition    reactions.    Soil    Biology    and    Biochemistry    159,    108304.

634        https://doi.org/10.1016/j.soilbio.2021.108304.

635    Delgado-Baquerizo, M., Maestre, F. T., Reich, P. B., Jeffries, T. C., Gaitan, J. J., Encinar, D.,

636        Berdugo, M., Campbell, C. D., Singh, B. K., 2016. Microbial diversity drives

22

multifunctionality in terrestrial ecosystems. Nature Communications 7, 10541. https://doi.org/10.1038/ncomms10541.

de Mendiburu, F. (2021). Package `agricolae': Statistical Procedures for Agricultural Research. R package v1.3-5. https://CRAN.R-project.org/package=agricolae.

Domeignoz-Horta, L. A., Pold, G., Liu, X.-J. A., Frey, S. D., Melillo, J. M., DeAngelis, K. M., 2020. Microbial diversity drives carbon use efficiency in a model soil. Nature Communications 11, 3684. https://doi.org/10.1038/s41467-020-17502-z.

Don, A., Kalbitz, K., 2005. Amounts and degradability of dissolved organic carbon from foliar litter at different decomposition stages. Soil Biology and Biochemistry, 37(12), 2171-2179. https://doi.org/10.1016/j.soilbio.2005.03.019.

Dove, N. C., Torn, M. S., Hart, S. C., Taş, N., 2021. Metabolic capabilities mute positive response to direct and indirect impacts of warming throughout the soil profile. Nature Communications 12, 2089. https://doi.org/10.1038/s41467-021-22408-5.

Feng, J., Zeng, X. M., Zhang, Q. G., Zhou, X. Q., Liu, Y. R., Huang, Q. Y., 2021. Soil microbial trait-based strategies drive metabolic efficiency along an altitude gradient. IS ME Communication, 1, 71. https://doi.org/10.1038/s43705-021-00076-2.

Fouché, J., Christiansen, C. T., Lafrenière, M. J., Grogan, P., Lamoureux, S. F., 2020. Canadian permafrost stores large pools of ammonium and optically distinct dissolved organic matter. Nature Communications 11, 4500. https://doi.org/10.1038/s41467-020-18331-w.

Gao, X. F., Chen, H. H., Gu, B. H., Jeppesen, E., Xue, Y. Y., Yang, J., 2021. Particulate organic matter as causative factor to eutrophication of subtropical deep freshwater: Role of typhoon (tropical cyclone) in the nutrient cycling. Water Research 188, 116470. https://doi.org/10.1016/j.watres.2020.116470.

Gougoulias, C., Clark, J. M., Shaw, L. J., 2014. The role of soil microbes in the global carbon cycle: tracking the below-ground microbial processing of plant-derived carbon for manipulating carbon dynamics in agricultural systems. Journal of the Science of Food and Agriculture 94(12), 2362-2371. https://doi.org/10.1002/jsfa.6577.

He, R., Wang, G. B., Wang, J. S., Xu, B. F., Wang, K. J., Fang, Y. H., Shi, Z., Ruan, H. H., 2009. Seasonal variation and its main affecting factors of soil microbial biomass under different

vegetations along an elevation gradient in Wuyi Mountains of China. Chinese Journal of Ecology, 28(3), 394-399. (in Chinese).

Ho, A., Di Lonardo, D. P., Bodelier, P. L. E., 2017. Revisiting life strategy concepts in environmental microbial ecology. FEMS Microbiology Ecology 93(3), fix006. https://doi.org/10.1093/femsec/fix006.

Hu, A., Choi, M., Tanentzap, A. J., Liu, J. F. Jang, K. S., Lennon, J. T., Liu, Y. Q., Soininen, J., Lu, X. C., Zhang, Y. L., 2022. Ecological networks of dissolved organic matter and microorganisms under global change. Nature Communications, 13(1), 3600. https://doi.org/10.1038/s41467-022-31251-1.

Hu, H. Y., Umbreen, S., Zhang, Y. L., Bao, M. Z., Huang, C. F., Zhou, C. F., 2021. Significant association between soil dissolved organic matter and soil microbial communities following vegetation restoration in the Loess Plateau. Ecological Engineering, 169, 106305. https://doi.org/10.1016/j.ecoleng.2021.106305.

Huang, W., McDowell, W. H., Zou, X. M., Ruan, H. H.,Wang, J. S., Ma, Z. L., 2015. Qualitative differences in headwater stream dissolved organic matter and riparian water-extractable soil organic matter under four different vegetation types along an altitudinal gradient in the Wuyi Mountains of China. Applied Geochemistry 52, 67-75. https://doi.org/10.1016/j.apgeochem.2014.11.014.

Jiao, S., Liu, Z. S., Lin, Y. B., Yang, J., Chen, W. M., Wei, G. H., 2016. Bacterial communities in oil contaminated soils: Biogeography and co-occurrence patterns. Soil Biology and Biochemistry 98, 64-73. https://doi.org/10.1016/j.soilbio.2016.04.005.

Jiao, S., Chen, W. M., Wang, J. L., Du, N. N., Li, Q. P., Wei, G. H., 2018. Soil microbiomes with distinct assemblies through vertical soil profiles drive the cycling of multiple nutrients in reforested ecosystems. Microbiome 6, 146. https://doi.org/10.1186/s40168-018-0526-0.

Jiao, S., Peng, Z. H., Qi, J. J., Gao, J. M., Wei, G. H., 2021. Linking Bacterial-Fungal Relationships to Microbial Diversity and Soil Nutrient Cycling. mSystems 6(2), e01052-20. https://doi.org/10.1128/mSystems.01052-20.

Kamjunke, N., Hertkorn, N., Harir, M., Schmitt-Kopplin, P., Griebler, C., Brauns, M., von Tümpling, W., Weitere, M., Herzsprung, P., 2019. Molecular change of dissolved organic

695      matter and patterns of bacterial activity in a stream along a land-use gradient. Water Research

696      164, 114919. https://doi.org/10.1016/j.watres.2019.114919.

697      Kim, S., Kramer, R. W., Hatcher, P. G., 2003. Graphical method for analysis of ultrahigh-resolution

698      broadband mass spectra of natural organic matter, the van Krevelen diagram. Analytical

699      Chemistry, 75(20), 5336-5344. https://doi.org/10.1021/ac034415p.

700      Kraus, T. E. C., Dahlgren, R. A., Zasoski, R. J., 2003. Tannins in nutrient dynamics of forest

701      ecosystems - a review. Plant and Soil 256(1), 41-66.

702      https://doi.org/10.1023/A:1026206511084.

703      Körner, C., 2007. The use of 'altitude' in ecological research. Trends in Ecology & Evolution 22(11),

704      569-574. https://doi.org/10.1016/j.tree.2007.09.006.

705      Koven, C. D., Ringeval, B., Friedlingstein, P., Ciais, P., Cadule, P., Khvorostyanov, D., Krinner, G.,

706      Tarnocai, C., 2011. Permafrost carbon-climate feedbacks accelerate global warming.

707      Proceedings of the National Academy of Sciences of the United States of America 108(36),

708      14769-14774. https://doi.org/10.1073/pnas.1103910108.

709      Li, J. B., Li, C. N., Kou, Y. P., Yao, M. J., He, Z. L., Li, X. Z., 2020. Distinct mechanisms shape soil

710      bacterial and fungal co-occurrence networks in a mountain ecosystem. FEMS Microbiology

711      Ecology 96(4), fiaa030. https://doi.org/10.1093/femsec/fiaa030.

712      Li, H., Yang, S., Semenov, M. V., Yao, F., Ye J., Bu, R. C., Ma, R. A., Lin, J. J., Kurganova, I., Wang,

713      X. G., Deng, Y., Kravchenko, I., Jiang, Y., Kuzyakov, Y., 2021. Temperature sensitivity of

714      SOM decomposition is linked with a K-selected microbial community. Global Change Biology

715      27(12), 2763-2779. https://doi.org/10.1111/gcb.15593.

716      Li, J., Yang, Y. C., Yang, L. X., 2021. Seasonal variations in soil fungal communities and

717      co-occurrence networks along an altitudinal gradient in the cold temperate zone of China: A

718      case study on Oakley Mountain. Catena 204, 105448.

719      https://doi.org/10.1016/j.catena.2021.105448.

720      Li, X. M., Chen, Q. L., He, C., Shi, Q., Chen, S. C., Reid, B. J., Zhu, Y. G., Sun, G. X., 2019.

721      Organic Carbon Amendments Affect the Chemodiversity of Soil Dissolved Organic Matter

722      and Its Associations with Soil Microbial Communities. Environmental Science & Technology

723      53(1), 50-59. https://doi.org/10.1021/acs.est.8b04673.

724    Liang, C., Amelung, W., Lehmann, J., Kästner, M., 2019. Quantitative assessment of microbial

725        necromass contribution to soil organic matter. Global Change Biology 25(11), 3578-3590.

726        https://doi.org/10.1111/gcb.14781.

727    Lin, L. Q., 2010. The Vertical Distribution of Iron Oxide in Wuyi Mountain and Its Causes Analysis.

728        Hunan Agricultural Sciences 17, 70-71+75. (in Chinese).

729    Liu, H., Liu, X., Li, X., Fu, Z., Lian, B., 2021. The molecular regulatory mechanisms of the bacteria

730        involved in serpentine weathering coupled with carbonation. Chemical Geology 565, 120069.

731        https://doi.org/10.1016/j.chemgeo.2021.120069.

732    Liu, H. B., Chen, T. H., Frost R. L., 2014. An overview of the role of goethite surfaces in the

733        environment. Chemosphere 103, 1-11. https://doi.org/10.1016/j.chemosphere.2013.11.065.

734    Liu, Y., Li, J., Sun, H., Chen, Y. W., Li, X., 2020. Stability of soil organic carbon along the

735        altitudinal gradient in alpine of the west of Sichuan Province. Research of Soil and Water

736        Conservation 27(02), 123-127+135. (in Chinese).

737    Luan, J. W., Liu, S. R., Chang, S. X., Wang, J. X., Zhu, X. L., Liu, K., Wu, J. H., 2014. Different

738        effects of warming and cooling on the decomposition of soil organic matter in warm–temperate

739        oak forests: a reciprocal translocation experiment. Biogeochemistry 121(3), 551-564.

740        https://doi.org/10.1007/s10533-014-0022-y.

741    Lv, J. T., Miao, Y. X., Huang, Z. Q., Han, R. X., Zhang, S. Z., 2018. Facet-Mediated Adsorption and

742        Molecular Fractionation of Humic Substances on Hematite Surfaces. Environmental Science

743        & Technology 52(20), 11660-11669. https://doi.org/10.1021/acs.est.8b03940.

744    Ma, L. W., Liu, L., Lu, Y. S., Chen, L., Zhang, Z. C., Zhang, H. W., Wang, X. R., Shu, L., Yang, Q. P.,

745        Song, Q. N., Peng, Q. H., Yu, Z. P., Zhang, J., 2022. When microclimates meet soil microbes:

746        Temperature controls soil microbial diversity along an elevational gradient in subtropical

747        forests.     Soil     Biology     and     Biochemistry     166,     108566.

748        https://doi.org/10.1016/j.soilbio.2022.108566.

749    Ma,     X.     Q.,     Heal,     K.     V.,     Liu,     A.     Q.,     Jarvis,     P.     G.,     2007.

750        Nutrient cycling and distribution in different-aged plantations of Chinese fir in     southern

751        China.     Forest     Ecology     and     Management     243(1),     61-74.

752        https://doi.org/10.1016/j.foreco.2007.02.018.

753  Marschner, B., Kalbitz, K., 2003. Controls of bioavailability and biodegradability of dissolved

754  organic matter in soils. Geoderma 113(3-4), 211-235.

755  https://doi.org/10.1016/S0016-7061(02)00362-2.

756  Melendez-Perez, J. J., Martínez-Mejia, M. J., Eberlin, M. N., 2016. A reformulated aromaticity

757  index equation under consideration for non-aromatic and non-condensed aromatic cyclic

758  carbonyl compounds. Organic Geochemistry 95, 29-33.

759  https://doi.org/10.1016/j.orggeochem.2016.02.002.

760  Mladenov, N., Zheng, Y., Miller, M. P., Nemergut, D. R., Legg, T., Simone, B., Hageman, C.,

761  Rahman, M. M., Ahmed, K. M., McKnight, D. M., 2010. Dissolved organic matter sources and

762  consequences for iron and arsenic mobilization in Bangladesh aquifers. Environmental

763  Science & Technology 44(1), 123-128. https://doi.org/10.1021/es901472g.

764  Mo, Y. Y., Peng, F., Gao, X. F., Xiao, P., Logares, R., Jeppesen, E., Ren, K. X., Xue, Y. Y., Yang, J.,

765  2021. Low shifts in salinity determined assembly processes and network stability of

766  microeukaryotic plankton communities in a subtropical urban reservoir. Microbiome 9, 128.

767  https://doi.org/10.1186/s40168-021-01079-w.

768  Navarrete, A. A., Soares, T., Rossetto, R., van Veen, J. A., Tsai, S. M., Kuramae, E. E., 2015.

769  Verrucomicrobial community structure and abundance as indicators for changes in chemical

770  factors linked to soil fertility. Antonie van Leeuwenhoek 108(3), 741-752.

771  https://doi.org/10.1007/s10482-015-0530-3.

772  Nunan, N., Schmidt, H., Raynaud, X., 2020. The ecology of heterogeneity: soil bacterial

773  communities and C dynamics. Philosophical Transactions of The Royal Society B 375,

774  20190249. http://doi.org/10.1098/rstb.2019.0249.

775  Osterholz, H., Singer, G., Wemheuer, B., Daniel, R., Simon, M., Niggemann, J., Thorsten, D., 2016.

776  Deciphering associations between dissolved organic molecules and bacterial communities in a

777  pelagic marine system. ISME Journal 10, 1717–1730. https://doi.org/10.1038/ismej.2015.231.

778  Qi, Y. L., Xie, Q. R., Wang, J. J., He, D., Bao, H. Y., Fu, Q. L., Su, S. H., Sheng, M., Li, S. L., Volmer,

779  D. A., Wu, F. C., Jiang, G. B., Liu, C. Q., Fu, P. Q., 2022. Deciphering dissolved organic matter

780  by Fourier transform ion cyclotron resonance mass spectrometry (FT-ICR MS): from bulk to

781  fractions and individuals. Carbon Research, 1, 3. https://doi.org/10.1007/s44246-022-00002-8.

782    Qiu, L., Fang, W. W., He, H. Z., Liang, Z. W., Zhan, Y. Y., Lu, Q. H., Liang, D. W., He, Z. L., Mai, B.

783        X., Wang, S. Q., 2020. Organohalide-Respiring Bacteria in Polluted Urban Rivers Employ

784        Novel Bifunctional Reductive Dehalogenases to Dechlorinate Polychlorinated Biphenyls and

785        Tetrachloroethene. Environmental Science & Technology 54(14), 8791-8800.

786        https://doi.org/10.1021/acs.est.0c01569.

787    R Core Team, 2018. R: A language and environment for statistical computing.

788    Ren, C. J., Zhou, Z. H., Guo, Y. X., Yang, G. H., Zhao, F. Z., Wei, G. H., Han, X. H., Feng, L., Feng,

789        Y. Z., Ren, G. X., 2020. Contrasting patterns of microbial community and enzyme activity

790        between rhizosphere and bulk soil along an elevation gradient. Catena 196, 104921.

791        https://doi.org/10.1016/j.catena.2020.104921.

792    Roth, V.-N., Lange, M., Simon, C., Hertkorn, N., Bucher, S., Goodall, T., Griffiths, R. I.,

793        Mellado-Vázquez, P. G., Mommer, L., Oram, N. J., Weigelt, A., Dittmar, T., Gleixner, G., 2019.

794        Persistence of dissolved organic matter explained by molecular changes during its passage

795        through soil. Nature Geoscience 12(9), 755-761. https://doi.org/10.1038/s41561-019-0417-4.

796    Rustad, L. E., 2008. The response of terrestrial ecosystems to global climate change: Towards an

797        integrated approach. Science of The Total Environment 404(2-3), 222-235.

798        https://doi.org/10.1016/j.scitotenv.2008.04.050.

799    Sansupa, C., Wahdan, S. F. M., Hossen, S., Disayathanoowat, T., Wubet, T., Purahong, W., 2021.

800        Can We Use Functional Annotation of Prokaryotic Taxa (FAPROTAX) to Assign the

801        Ecological Functions of Soil Bacteria? Applied Sciences 11(2), 688.

802        https://doi.org/10.3390/app11020688.

803    Schmidt, M. W. I., Torn, M. S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I. A., Kleber,

804        M., Kogel-Knabner, I., Lehmann, J., Manning, D. A. C., Nannipieri, P., Rasse, D. P., Weiner, S.,

805        Trumbore, S.E., 2011. Persistence of soil organic matter as an ecosystem property. Nature 478,

806        49-56. https://doi.org/10.1038/nature10386.

807    Shen, J., Liang, Z. Y., Kuzyakov, Y., Li, W. T., He, Y. T., Wang, C. Q., Xiao, Y., Chen, K., Sun, G.,

808        Lei, Y. B., 2023. Dissolved organic matter defines microbial communities during initial soil

809        formation after deglaciation. Science of The Total Environment, 878, 163171.

810        https://doi.org/10.1016/j.scitotenv.2023.163171.

811    Swenson, T. L., Bowen, B. P., Nico, P. S., Northen, T. R., 2015. Competitive sorption of microbial

812          metabolites on an iron oxide mineral. Soil Biology and Biochemistry 90, 34-41.

813          https://doi.org/10.1016/j.soilbio.2015.07.022.

814    Taketani, R. G., Lanconi, M. D., Kavamura, V. N., Durrer, A., Andreote, F. D., Melo, I. S., 2017.

815          Dry Season Constrains Bacterial Phylogenetic Diversity in a Semi-Arid Rhizosphere System.

816          Microbial Ecology 73 (1), 153-161. https://doi.org/10.1007/s00248-016-0835-4.

817    Tang, M. Z., Li, L., Wang, X. L., You, J., Li, J. N., Chen, X., 2020. Elevational is the main factor

818          controlling the soil microbial community structure in alpine tundra of the Changbai Mountain.

819          Scientific Reports 10, 12442. https://doi.org/10.1038/s41598-020-69441-w.

820    Trivedi, P., Anderson, I. C., Singh, B. K., 2013. Microbial modulators of soil carbon storage:

821          integrating genomic and metabolic knowledge for global prediction. Trends in Microbiology

822          21(12), 641-651. https://doi.org/10.1016/j.tim.2013.09.005.

823    Thevenot, M., Dignac, M. F., Rumpel, C., 2010. Fate of lignins in soils: A review. Soil Biology and

824          Biochemistry, 42(8), 1200-1211. https://doi.org/10.1016/j.soilbio.2010.03.017.

825    Triebwasser, D. J., Tharayil, N., Preston, C. M., Gerard, P. D., 2012. The susceptibility of soil

826          enzymes to inhibition by leaf litter tannins is dependent on the tannin chemistry, enzyme class

827          and vegetation history. New Phytologist, 196(4), 1122-1132.

828          https://doi.org/10.1111/j.1469-8137.2012.04346.x.

829    Wan, W. J., He, D. L., Li, X., Xing, Y. H., Liu, S., Ye, L. P., Njoroge, D. M., Yang, Y. Y., 2021.

830          Adaptation of *pho*D-harboring bacteria to broader environmental gradients at high elevations

831          than at low elevations in the Shennongjia primeval forest. Geoderma 401, 115210.

832          https://doi.org/10.1016/j.geoderma.2021.115210.

833    Wang, W. X., Tao, J. C., Yu, K., He, C., Wang, J. J., Li, P. H., Chen, H. M., Xu, B., Shi, Q., Zhang, C.

834          L., 2021. Vertical stratification of dissolved organic matter linked to distinct microbial

835          communities in subtropic estuarine sediments. Frontiers in Microbiology 12, 697860.

836          https://doi.org/10.3389/fmicb.2021.697860.

837    Wang, Y. H., Zhang, G. L., Wang, H. L., Cheng, Y., Liu, H., Jiang, Z., Li, P., Wang, Y. X., 2021.

838          Effects of different dissolved organic matter on microbial communities and arsenic

839          mobilization in aquifers. Journal of Hazardous Materials 411, 125146.

29

840         https://doi.org/10.1016/j.jhazmat.2021.125146.

841 Wang, S. J., Ruan, H. H., Wang, B., 2009. Effects of soil microarthropods on plant litter

842         decomposition across an elevation gradient in the Wuyi Mountains. Soil Biology and

843         Biochemistry 41(5), 891-897. https://doi.org/10.1016/j.soilbio.2008.12.016.

844 Witzgall, K., Vidal, A., Schubert, D. I., Höschen, C., Schweizer, S. A., Buegger, F., Pouteau, V.,

845         Chenu, C., Mueller, C. W., 2021. Particulate organic matter as a functional soil component for

846         persistent soil organic carbon. Nature Communications 12, 4115.

847         https://doi.org/10.1038/s41467-021-24192-8.

848 Wu, D., Zhang, M. M., Peng, M., Sui, X., Li, W., Sun, G. Y., 2019. Variations in Soil Functional

849         Fungal Community Structure Associated With Pure and Mixed Plantations in Typical

850         Temperate Forests of China. Frontiers in Microbiology 10, 1636.

851         https://doi.org/10.3389/fmicb.2019.01636.

852 Wu, M., Li, P. F., Li, G. L., Petropoulos, E., Feng, Y. Z., Li, Z. P., 2021. The chemodiversity of

853         paddy soil dissolved organic matter is shaped and homogenized by bacterial communities that

854         are orchestrated by geographic distance and fertilizations. Soil Biology and Biochemistry 161,

855         108374. https://doi.org/10.1016/j.soilbio.2021.108374.

856 Wu, W. X., Lu, H. P., Sastri, A., Yeh, Y. C., Gong, G. C., Chou, W. C., Hsieh, C. H., 2018.

857         Contrasting the relative importance of species sorting and dispersal limitation in shaping

858         marine bacterial versus protist communities. ISME Journal, 12(12) 485-494.

859         https://doi.org/10.1038/ismej.2017.183.

860 Wu, X. J., Liu, P. F., Wegner, C. E., Luo, Y., Xiao, K. Q., Cui, Z. L., Zhang, F. S., Liesack, W., Peng,

861         J. J., 2021. Deciphering microbial mechanisms underlying soil organic carbon storage in a

862         wheat-maize rotation system. Science of The Total Environment 788, 147798.

863         https://doi.org/10.1016/j.scitotenv.2021.147798.

864 Wu, X. Q., Wu, L. Y., Liu, Y. N., Zhang, P., Li, Q. H., Zhou, J. Z., Hess, N. J., Hazen, T. C., Yang, W.

865         L, Chakraborty, R., 2018. Microbial interactions with dissolved organic matter drive carbon

866         dynamics and community succession. Frontiers in Microbiology 9, 1234.

867         https://doi.org/10.3389/fmicb.2018.01234.

868 Wu, Z. Y., Lin, W. X., Li, J. J., Liu, J. F., Li, B. L., Wu, L. K., Fang, C. X., Zhang, Z. X., 2016.

Effects of seasonal variations on soil microbial community composition of two typical zonal

vegetation types in the Wuyi Mountains. Journal of Mountain Science 13(6), 1056-1065.

https://doi.org/10.1007/s11629-015-3599-2.

Xun, W. B., Li, W., Xiong, W., Ren, Y., Liu, Y. P., Miao, Y. Z., Xu, Z. H., Zhang, N., Shen, Q. R.,

Zhang, R. F., 2019. Diversity-triggered deterministic bacterial assembly constrains community

functions. Nature Communications 10, 3833. https://doi.org/10.1038/s41467-019-11787-5.

Ye, Q. H., Wang, Y. H., Zhang, Z. T., Huang, W. L., Li, L. P., Li, J. T., Liu, J. S., Zheng, Y., Mo, J.

M., Zhang, W., Wang, J. J., 2020. Dissolved organic matter characteristics in soils of tropical

legume and non-legume tree plantations. Soil Biology and Biochemistry 148, 107880.

https://doi.org/10.1016/j.soilbio.2020.107880.

Yuan, M. M., Guo, X., Wu, L. W., Zhang, Y., Xiao, N. J., Ning, D. L., Shi, Z., Zhou, X. S., Wu, L.

Y., Yang, Y. F., Tiedje, J. M., Zhou, J. Z., 2021.

Climate warming enhances microbial network complexity and   stability.   Nature   Climate

Change, 11(4), 343-U100. https://doi.org/10.1038/s41558-021-00989-9.

Yun, Y., Gui, Z. Y., Su, T. Q., Tian, X. F., Wang, S. J., Chen, Y., Su, Z. Y., Fan, H. Q., Xie, J. X., Li,

G. Q., Xia, W. J., Ma, T., 2022. Deep mining decreases the microbial taxonomic and functional

diversity of subsurface oil reservoirs. Science of The Total Environment 821, 153564.

https://doi.org/10.1016/j.scitotenv.2022.153564.

Zeng, X. M., Feng, J., Chen, J., Delgado-Baquerizo, M., Zhang, Q. G., Zhou, X. Q., Yuan, Y. S.,

Feng, S. H., Zhang, K. X., Liu, Y. R., Huang, Q. Y., 2022. Microbial assemblies associated

with temperature sensitivity of soil respiration along an altitudinal gradient. Science of The

Total Environment, 820, 153257. https://doi.org/10.1016/j.scitotenv.2022.153257.

Zhang, J., Zhang, B. G., Liu, Y., Guo, Y. Q., Shi, P., Wei, G. H., 2018.

Distinct large-scale biogeographic patterns of fungal communities in bulk soil and soybean rh

izosphere in China.   Science   of   The   Total   Environment   644,   791-800.

https://doi.org/10.1016/j.scitotenv.2018.07.016.

Zhang, Y. L., Heal, K. V., Shi, M. J., Chen, W. X., Zhou, C. F., 2022. Decreasing molecular diversity

of soil dissolved organic matter related to microbial community along an alpine elevation

gradient.   Science   of   The   Total   Environment   818,   151823.

898     https://doi.org/10.1016/j.scitotenv.2021.151823.

899     Zhou, J. Z., Ning, D. L., 2017. Stochastic Community Assembly: Does It Matter in Microbial

900         Ecology? Microbiology and Molecular Biology Reviews 81(4), e00002-17.

901         https://doi.org/10.1128/MMBR.00002-17.

902     Zhou, L., Bai, C. R., Cai, J., Hu, Y., Shao, K. Q., Gao, G., Jeppesen, E., Tang, X. M., 2018. Bio-cord

903         plays a similar role as submerged macrophytes in harboring bacterial assemblages in an

904         eco-ditch. Environmental Science and Pollution Research 25(26), 26550-26561.

905         https://do.iorg/10.1007/s11356-018-2697-4.

906     Zhou, X. R., Chen, X. K., Qi, X. N., Zeng, Y. Y., Guo, X. W., Zhuang, G. Q., Ma, A. Z., 2023. Soil

907         bacterial communities associated with multi-nutrient cycling under long-term warming in the

908         alpine meadow. Frontiers in Microbiology, 14, 1136187.

909         https://doi.org/10.3389/fmicb.2023.1136187.

910     Zhu, D., Ma, J., Li, G., Rillig M. C., Zhu, Y. G., 2021. Soil plastispheres as hotpots of antibiotic

911         resistance genes and potential pathogens. The ISME Journal 16(2), 521-532.

912         https://doi.org/10.1038/s41396-021-01103-9.

913     Zhuang, T. C., Lin, P., Chen, R.H., 1997. Seasonal Variation on Amounts and Groups of

914         Heterotrophic Microorganisms in Forest Soil at Wuyishan National Nature Reserve. Journal of

915         Xiamen University (Natural Science) 35(4), 655-658. (in Chinese).

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**Author Contributions**

918

919     All authors contributed to the study conception and design. **Shuzhen Wang**: Investigation,

920     Validation, Data Curation, Data analysis, Writing - first draft; **Kate V. Heal**: Supervision, Writing -

921     review & editing; **Qin Zhang**: Validation, Data analysis; **Yuanchun Yu**: Supervision; **Mulualem**

922     **Tigabu**: Reading and polishing the manuscript; **Shide Huang**: Soil sampling, **Chuifan Zhou**:

923     Conceptualization, Visualization, Resources, Supervision. All authors commented on previous

924     versions of the manuscript. All authors read and approved the final manuscript.

925

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**Figure captions**

932 **Fig. 1.** Inter sample rankings analysis of common-shared DOM molecules in five vegetation zones

933 along the elevation gradient in the Wuyi Mountains, Fujian Province, China. Codes for the

934 different vegetation zones - EB: evergreen broad-leaved forest; CB: coniferous and broad-leaved

935 mixed forest; CF: coniferous forest; DF: subalpine dwarf forest; AM: alpine meadow.

936

937 **Fig. 2.** Co-occurring network diagrams for soil bacteria (a) and fungi (b) (top 300 OTUs) across

938 all soil samples along the elevation gradient in the Wuyi Mountains, Fujian Province, China. The

939 box below each of (a) and (b) contains summary characteristics of the results of 10,000 random

940 networks generated for bacteria and fungi, respectively, according to the Erdös–Réyni model. Fit

941 of Sloan's neutral community model (NCM) to the OTUs of the soil (c) bacterial and (d) fungal

942 community assemblies for all soil samples. The solid black line represents the best-fitting neutral

943 model and the dashed black lines represent the 95% confidence intervals around it. Blue points

944 between the dashed black lines represent OTUs that follow the neutral process. The green and

945 orange points indicate OTUs that occur more and less frequently than predicted by the NCM,

946 respectively. $R^2$ indicates the fit to the NCM, $m$ is the estimated migration rate, and Nm is the

947 product of metacommunity size and $m$ values. (e) Bar plots of the modified stochasticity ratio

948 (MST) values of the soil bacterial and fungal community assemblies in different vegetation zones

949 along the elevation gradient. The horizontal dashed purple line (MST = 0.5) was set as the

950 boundary between deterministic (MST < 0.5) and stochastic (MST > 0.5) assembly processes.

951 Values are means ± standard error ($n$ = 3). Different lowercase letters for bacteria/fungi indicate

952 significant differences between vegetation zones at different elevations according to LSD tests ($P$

953 < 0.05). See Fig. 1 for explanation of the codes for the different vegetation zones.

954

**Fig. 3.** (a) Heatmap of correlation between microbial community characteristics (Chao1, Shannon and Faith's PD indices, modified stochasticity ratio (MST)) and site elevation and DOM components/characteristics (defined in Supplementary Material Section S1). *, $0.01 \leq P < 0.05$; **, $0.001 \leq P < 0.01$ indicate significant coefficients. Co-occurrence network diagrams of significant ($P < 0.01$) correlations between the 100 most abundant soil DOM molecular formulae and the 100 highest relative abundance OTUs for bacteria (b) and fungi (c) in soil samples across the elevation gradient of different vegetation zones. Blue circles represent the OTUs of bacterial and fungal phyla. Green and red circles represent the lignin/CRAM-like structure and tannin molecules, respectively. The sizes of the circles indicate the relative abundance of the OTUs and DOM molecular formulae. The blue and red lines indicate significant positive and negative correlations, respectively, between DOM formulae and microbial phyla.

**Fig. 4.** Random forest (RF) analysis to identify the importance of different microbial predictors of the multiple nutrient cycling (MNC) index of the 15 soil samples along an elevation gradient in the Wuyi Mountains, Fujian Province, China. (a) Bacterial community predictors: relative abundance of the 10 most abundant bacterial phyla, alpha diversity indices (Shannon index, Chao1 index, Faith's PD index), the site pH, and elevation. (b) Fungal community predictors: relative abundance of the 3 most abundant fungal phyla, alpha diversity indices (Shannon index, Chao1 index, Faith's PD index), the site pH, and elevation. Partial least squares path models (PLS-PM) showing the effects of soil microbial communities characteristics on MNC (c). The line width is proportional to the magnitude of the path coefficient. Numbers adjacent to arrows indicate the direct effect size of the relationship. The black and blue lines indicate positive and negative path coefficient, respectively. $R^2$ indicates the variance of the dependent variable explained by the model. GOF is the goodness-of-fit index of the model. *, $0.01 \leq P < 0.05$; **, $0.001 \leq P < 0.01$; ***, $P < 0.001$ indicate significant predictors or path coefficients.

**Fig. 2**

a



b



c

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986    **Fig. 4**

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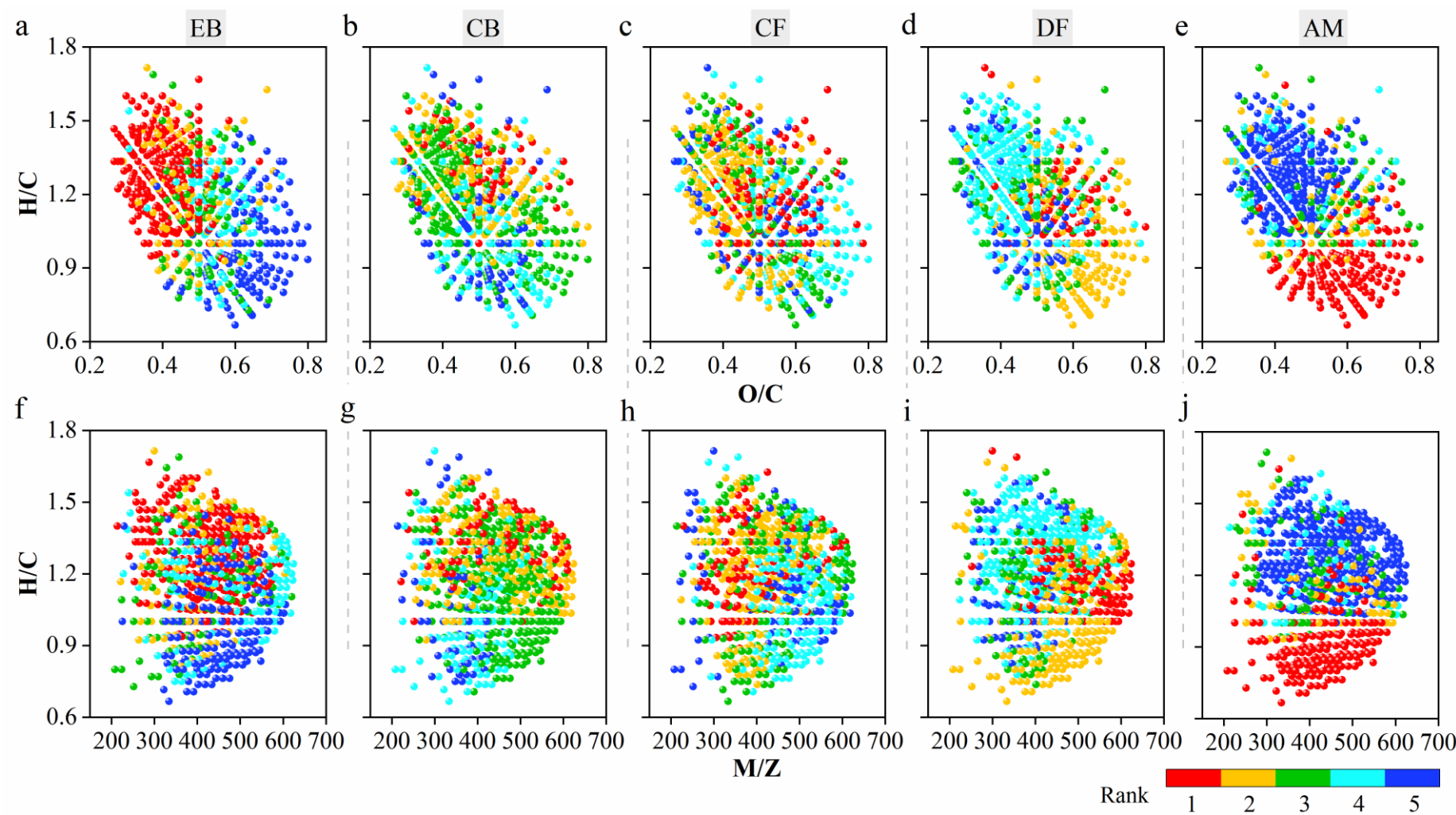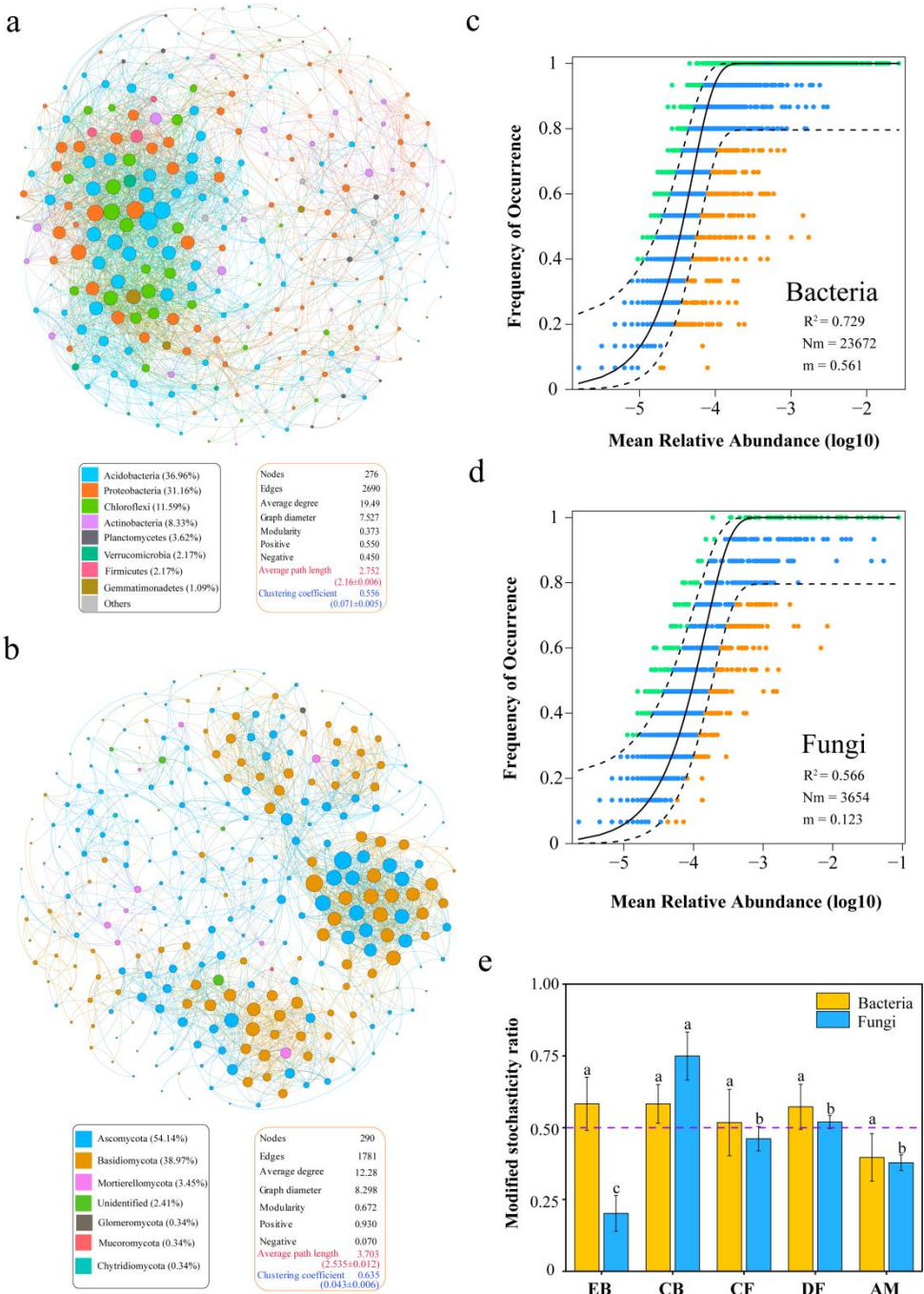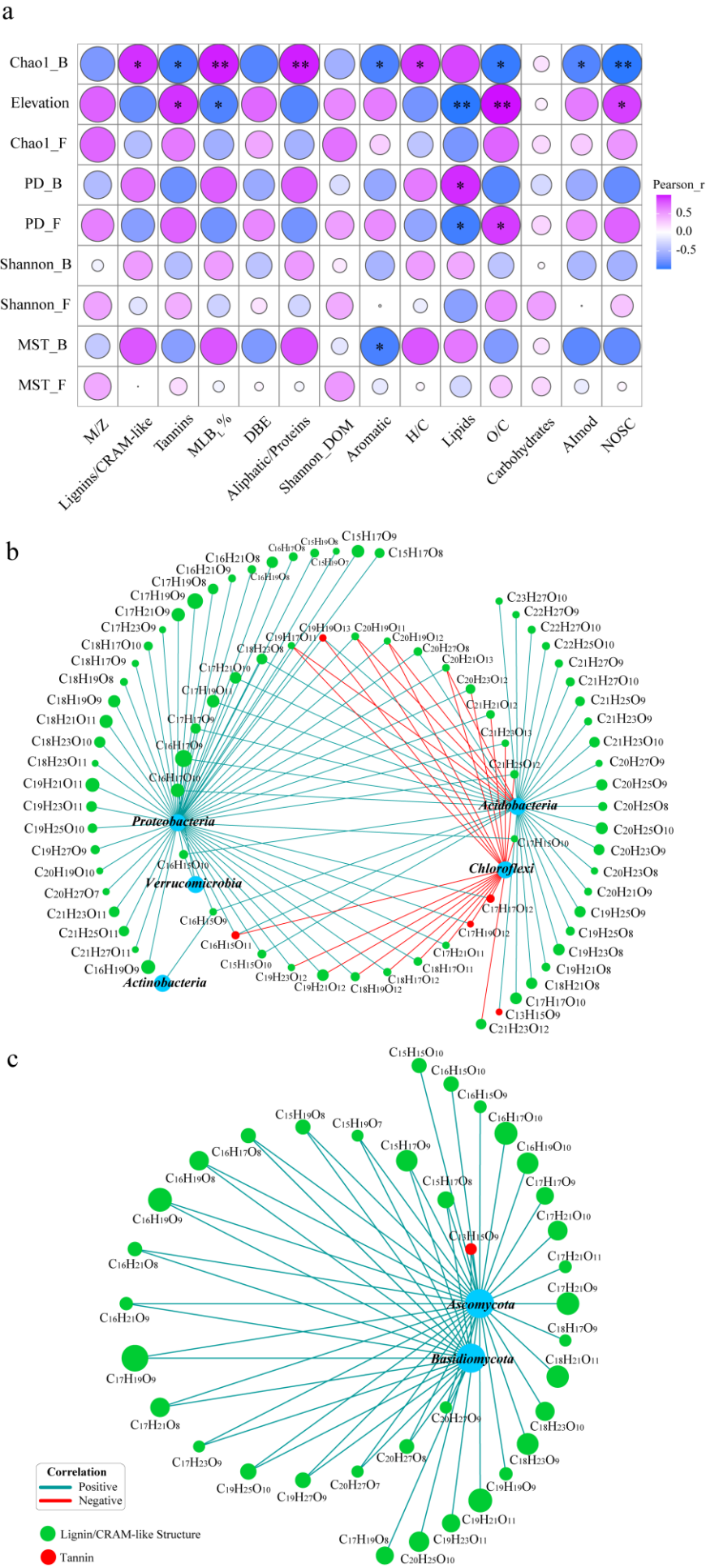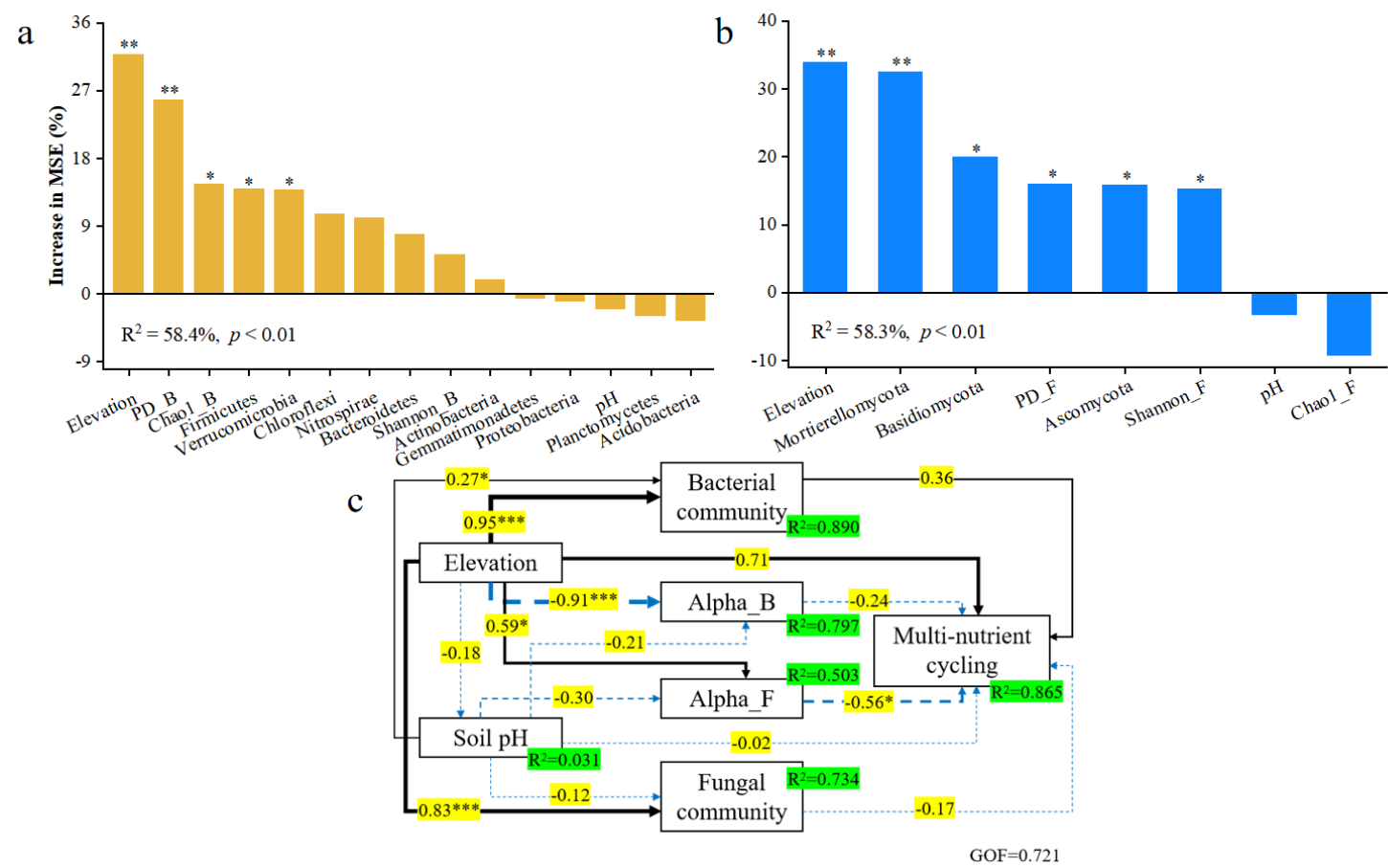
**Tables**

990 **Table 1.** Soil properties in different vegetation zones along an elevation gradient in the Wuyi Mountains, Fujian Province, China. All data are presented as means $\pm$

991 standard error ($n$ = 3). EB: evergreen broad-leaved forest; CB: coniferous and broad-leaved mixed forest; CF: coniferous forest; DF: subalpine dwarf forest; AM:

992 Alpine meadow). Ammoniacal-nitrogen ($NH_4^+$-N); nitrate-nitrogen ($NO_3^-$-N); available phosphorus (AP); available potassium (AK); dissolved organic carbon (DOC);

993 total nitrogen (TN); total carbon (TC); C/N ratio: TC/TN; MNC: soil multiple nutrient cycling index, calculated as explained in Section 2.5. $NO_3^-$-N, $NH_4^+$-N, and

994 DOC reported as mg kg$^{-1}$ fresh weight. Different lowercase letters in a row indicate significant differences between elevations ($P$ < 0.05).

| Soil property | Vegetation zone and elevation | | | | |
|---|---|---|---|---|---|
| | EB (290 m) | CB (1070 m) | CF (1400 m) | DF (1800 m) | AM (1960 m) |
| pH | 4.70±0.04ab | 4.64±0.09ab | 4.58±0.04ab | 4.55±0.04b | 4.73±0.03a |
| $NH_4^+$-N (mg kg$^{-1}$) | 12.71±0.64a | 15.23±1.70a | 13.38±0.28a | 14.23±0.62a | 18.20±2.18a |
| $NO_3^-$-N (mg kg$^{-1}$) | 1.89±0.60a | 1.11±0.04a | 1.99±0.10a | 1.48±0.21a | 1.37±0.11a |
| AP (mg kg$^{-1}$) | 5.38±1.09b | 5.11±0.49b | 11.64±4.89ab | 7.95±0.41ab | 11.67±0.93a |
| AK (mg kg$^{-1}$) | 156.96±15.91ab | 113.33±16.53b | 130.85±20.32b | 200.07±7.48a | 223.74±16.17a |
| DOC (mg kg$^{-1}$) | 54.28±4.06c | 56.21±8.07c | 93.93±9.80ab | 80.08±4.71b | 109.43±4.36a |
| TN (g kg$^{-1}$) | 1.47±0.26c | 1.20±0.55c | 3.42±0.21b | 4.53±0.30b | 6.96±0.67a |
| TC (g kg$^{-1}$) | 20.88±1.23cd | 19.29±7.70d | 45.53±1.54bc | 60.29±3.12ab | 98.15±14.76a |
| C/N | 14.78±1.78a | 16.80±0.89a | 13.36±0.39a | 13.36±0.50a | 14.01±1.34a |
| MNC | 0.22±0.03c | 0.16±0.07c | 0.41±0.03b | 0.43±0.02b | 0.68±0.08a |

**Table 2.** Intensity weighted average (wa) values of the different characteristics of DOM molecules and relative abundance of different element combinations from soils along an elevation gradient, Wuyi Mountains, Fujian Province, China. $n = 1$ as a composite sample for the three plots at each elevation was analyzed by FT-ICR MS. DBE: double bond equivalent; NOSC: average nominal oxidation state of carbon; $AI_{mod}$: modified aromaticity index; $MLB_L$: molecular lability boundary. The calculation methods are described in Supplementary Material Section S4. Vegetation zone codes are as given in Table 1.

| Vegetation zone code and elevation | DBE wa | M/Z wa | H/C wa | O/C wa | NOSC wa | $AI_{mod}$ wa | $MLB_L$ % | Shannon index | Characteristics of soil DOM molecules | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | | | | | | | | | CHO % | CHON % | CHOS % |
| EB (290 m) | 8.49 | 409.15 | 1.25 | 0.48 | -0.26 | 0.25 | 14.47 | 6.78 | 88.39 | 8.12 | 3.48 |
| CB (1070 m) | 9.20 | 439.60 | 1.21 | 0.52 | -0.16 | 0.26 | 11.63 | 7.42 | 90.43 | 5.54 | 4.03 |
| CF (1400 m) | 8.37 | 414.03 | 1.24 | 0.53 | -0.13 | 0.24 | 11.44 | 6.70 | 80.17 | 9.46 | 10.37 |
| DF (1800 m) | 10.20 | 455.60 | 1.13 | 0.55 | 0.004 | 0.29 | 7.96 | 7.60 | 86.79 | 7.83 | 5.39 |
| AM (1960 m) | 11.59 | 453.73 | 0.98 | 0.57 | 0.19 | 0.39 | 3.20 | 7.45 | 88.53 | 10.91 | 0.56 |