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RESEARCH ARTICLE

Metagenomic highlight contrasting elevational pattern of bacteria- and fungi-derived compound decompositions in forest soils

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Abstract

Purpose Carbohydrate-active enzymes (CAZymes) mediate carbohydrate turnover and play vital roles in plant- and microbial-derived carbon decomposition. However, the changes of genes that encoding enzymes for plant- and microbial-derived carbon decomposition along environmental gradients remains unclear.

Methods We used metagenomic sequencing to explore changes in genes encoding enzymes for carbon decomposition in five forest sites along an elevational gradient (1503–3182 m) on Qinling Mountain, China.

Results The genes encoding CAZymes showed various patterns along the elevational gradient. In particular, the abundance of genes encoding auxiliary enzymes and glycoside hydrolases decreased with increasing elevation. The abundance of genes encoding enzymes for plant- and fungi-derived carbon decomposition was higher at low elevations than at high elevations, whereas the abundance of genes encoding enzymes for bacteria-derived carbon decomposition was higher at high elevations than at low elevations. The results indicate contrasting patterns of fungal- and bacterial-derived carbon decomposition with elevation. Proteobacteria and Acidobacteria were the dominant species that decomposed dead plant and microbial biomass. Moreover, our results reveal that soil properties (i.e., ammonium nitrogen and bulk density) and vegetation properties

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dominated the CAZymes gene distribution along the elevational gradient.
Conclusion Bacteria- and fungi-derived carbon decomposition potentials show contrasting elevational patterns in forest soils; soil and vegetation properties are common controls for the elevational patterns.

Keywords Metagenomics · CAZymes · Carbon cycle · Decomposition · Elevational gradient

Introduction

Forests are important carbon reservoirs in terrestrial ecosystems, with most carbon stored in the soil (Grace 2004; Vanguelova et al. 2016. Plant-derived carbon (cellulose, hemicellulose, and lignin) and microbial-derived carbon (chitin and glucans for fungi and peptidoglycan for bacteria) are the major sources of organic compounds entering the soil (Gao et al. 2021; Zhang et al. 2022). The degradation of these compounds is a key step in the forest soil carbon cycle (Eichorst and Kuske 2012). Microorganisms are the primary decomposers of plant- and microbial-derived carbon and produce various enzymes (Schimel and Weintraub 2003; Wallenstein and Weintraub 2008). Recent studies have shown that bacteria play important roles in the decomposition of both recalcitrant and simple compounds (Zifcakova et al. 2016). In particular, *Proteobacteria* and *Acidobacteria* produce a wide range of enzymes to decompose organic compounds (Llado et al. 2019). In particular, some enzymes are involved in the assembly and breakdown of diverse complex carbohydrate assemblies and breakdowns, collectively designated as carbohydrate-active enzymes (CAZymes), which play important roles in Carbon cycling in forest ecosystems (Lopez-Mondejar et al. 2020; Zifcakova et al. 2017).

Microbial CAZymes are classified into a hierarchy of families based on their structure and function, including glycosyl transferases (GTs), glycosyl hydrolases (GHs), carbohydrate esterases (CEs), auxiliary activities (AAs), polysaccharide lyases (PLs), and carbohydrate-binding modules (CBMs) (Lombard et al. 2014). Their action within microbial communities typically results in the decomposition of a variety of substrates and the production of specific polymers and sugar-modified proteins or metabolites (Gomez-Silva et al. 2019). For example, some GHs (e.g., cellulases, glucosidases, and hemicellulases), AAs (e.g., peroxidases, oxidoreductases, and laccases), and CEs are crucial for the degradation of plant-derived carbon (Bomble et al. 2017; Levasseur et al. 2013). Several GHs, including chitinases and peptidoglycan lytic transglycosylases, are involved in the degradation of fungi- and bacteria-derived carbon (Lopez-Mondejar et al. 2020; Zifcakova et al. 2017). Additionally, the composition of CAZymes genes reflects the ability of microorganisms to utilise various compounds, thereby affecting the accumulation of soil organic carbon (SOC) pools (Frey et al. 2022). Previous studies have shown lower soil carbon, soil C/N, and CAZymes gene abundance and diversity in forest-harvesting soils, indicating a lower potential for biomass decomposition (Cardenas et al. 2015). Ren et al. (2021) found that the abundance of CAZymes genes were associated with microbial metabolic activity and higher SOC in afforestation soil. Therefore, studying CAZymes is key to clarifying the cycling of soil nutrients in forest ecosystems. However, soil microbial community and function are affected by a wide array of factors, and the environmental factors controlling the genes encoding CAZymes for plant and microbial biomass decomposition remain unknown.

An elevational gradient can provide various environmental gradients that shape microbial properties and gene abundance, further influencing the decomposition capacity (Stokes et al. 2021). Ren et al. (2018) found that microbial alpha diversity was significantly affected by soil chemical properties (e.g., SOC and total nitrogen [TN]) and vegetation properties with elevation. Yang et al. (2022) found that the contribution of microbial residues to soil organic carbon showed a declining trend along an elevational gradient and was influenced by the interaction between vegetation and soil properties. In our recent study, Zhao et al. (2022) highlighted that the soil environment is a major factor influencing microbial functional genes, driving the positive priming effect along an elevational gradient. Zhou et al. (2015) found that temperature controls litter decomposition rates, with decomposition rates decreasing with increasing elevation. In this case, changes in soil environmental parameters can alter microbial potential decomposition, affecting carbon cycling in forest soils. Dai et al. (2021) found that microbial functional potential may

decline with the loss of microbial diversity along an elevational gradient. However, the potential decomposition of carbon by soil microorganisms derived from different sources and their influencing factors along an elevational gradient are unclear.

To fill the current knowledge gaps, we performed soil sampling and characterised CAZyme genes and soil and vegetation properties at five sites along an elevational gradient in a temperate forest. We hypothesised that the biomass carbon decomposition potential would be higher at low elevations than at high elevations, because Ren et al. (2018) found a decreasing trend in enzyme activity along an elevational gradient. Our aims were to (i) determine the trends of the microbial CAZymes genes pool along an elevational gradient, (ii) and investigate major factors affecting microbial CAZymes genes.

Materials and methods

Study area

The elevational transect in this study was located on the north-facing aspect of Taibai Mountain (33°45'–34°10' N and 107°19'–107°58' E), the main peak of the Qinling Mountains in Central China.. The annual mean temperature is 11.4 °C and the mean annual precipitation is 910.6 mm (Zhang et al. 2019). Taibai Mountain has rich vegetation types that cover an extensive area. The typical vertical vegetation belts from bottom to top are *Quercus aliena* var. *acuteserrata* (1100–1800 m), *Quercus wutaishanica* (1800–2200 m), *Betula albosinensis* (2200–2600 m), *Betula utilis* (2600–2800 m), *Abies fargesii Franch* (2800–3000 m), *Larix chinensis Beissn* (3000–3400 m), and alpine shrub meadow (> 3400 m).

Soil sampling and processing

Soil samples were collected from five elevation sites: low elevation (1503 m), low-mid elevation (1915 m), mid-elevation (2451 m), mid-high elevation (2753 m), and high elevation (3182 m) (Table S1). At each elevation, we randomly set three replicate plots (20 × 30 m). Surface litter and the humus layer were removed, and 0–10 cm surface soil samples were collected from 10 soil cores (5.0 cm inner diameter) in each replicate stand according to the "S" sampling method. We then mixed the 10 soil cores to get a composite sample. Finally, we obtained 15 soil samples (five elevation sites × three replicates). We removed rocks, roots, plant, animal residues, and other sundries from the soils, and filtered them through a 2-mm sieve. We used 60 g dry soil (calculated by fresh soil) to analyse basic soil properties; part of the fresh soil was stored in a − 80℃ refrigerator for metagenomic sequencing.

Soil and vegetation properties analysis

The soil moisture (SM) and soil temperature (ST) were measured using temperature and humidity sensors. Soil bulk density (BD) was calculated from the volume of the core sampler before and after oven drying at 105 °C for 24 h to assess the volume of each core (De Vos et al. 2005). Soil pH was estimated using a pH meter at a soil:water ratio of 1:2.5 (Zhang et al. 2016). SOC and TN were determined as described by Zhang et al. (2011). Ammonium nitrogen (NH_4^+) and nitrate nitrogen (NO_3^-) were extracted from samples using a 2 mol·L^{-1} KCl solution and Dionex ICS 1500 ion chromatograph (Dionex Co., Sunnyvale, CA) (Zhang et al. 2014). To determine the vegetation cover of each plot, quadrats were randomly selected near each elevation plot to determine the Arbor–Shannon index and canopy density using the method described by Zhao et al. (2015, 2022).

DNA extraction and sequencing

Total genomic soil DNA was extracted from a 0.5 g fresh soil sample using the FastDNA spin kit for soil (MP Biomedicals, Cleveland, United States), according to the manufacturer's protocol. To obtain sufficient DNA for whole-genome shotgun (WGS) sequencing, six replicates of each soil sample were analysed and a NanoDrop spectrophotometre was used to assess the quality and integrity of the DNA extracts. Extracted microbial DNA was processed to construct metagenomic shotgun sequencing libraries with an insert size of 400 bp. Each library was sequenced using an Illumina HiSeq and the PE150 strategy. The sequences were obtained from the National Center for Biotechnology Information (NCBI) website SRP345989.

Sequence quality control

The original data (FASTQ format) were used to determine the sequencing amount and high-quality base proportion. We also used FastQC (http://www.bioinformatics.babraham.ac.uk/projects/fastqc/) to control the quality of the original data generated by sequencing, including the base mass distribution, sequence average quality distribution, base content distribution, and GC content distribution. The valid sequences were screened and filtered. Cutadapt (v1.2.1) and a sliding-window algorithm were used to obtain a clean dataset for subsequent analysis, with a minimum sequence length of 50 bp and no fuzzy bases in the sequence.

Metagenome assembly

We used Megahit (https://hku-bal.github.io/megabox/) for the de novo assembly splicing of each sample's paired-end sequence. The Kaiju (https://github.com/bioinformatics-centre/kaiju) software was used to compare the effective sequences with the protein sequences of bacteria, archaea, fungi, viruses, and other micro-eukaryotes in the NCBI–NR database. The contigs obtained by splicing were aligned with NT using blastn (e-value of 0.001), the top5 hit were selected, and the LCA method was used to annotate the contigs to remove metazoans and greenery only. We then used MetaEuk to predict bacterial and fungal genes (e-value of 10^{-5}) and MetaGeneMark to predict bacterial genes (Zhu et al. 2010; Karin et al. 2020). After merging and removing redundancy from the prediction genes, the taxonomical annotation of the non-redundant proteins was performed using mmseqs2 (Steinegger and Soeding 2017) with the 'easy-taxonomy' mode and NR database. Information on the metagenome sequencing of samples from each elevation site is shown in Supplementary Table S2.

CAZymes annotation and selection

HMMER3 (Eddy 2011) based on the profile-hidden Markov model (Profile HMMs) sequence spectrum annotated the protein sequence set in dbCAN (http://csbl.bmb.uga.edu/dbCAN/) (Yin et al. 2012). To evaluate the abundance of these genes, salmon was used to map the high-quality sequence of each sample in order to the predicted gene sequences (Patro et al. 2017); TPM (transcripts per kilobase per million mapped reads) was used to normalise the abundance value in the metagenome. Specific CAZyme families were selected according to CAZy (http://www.CAZy.org) to link genes with plant-, bacteria-, and fungi-derived carbon decomposition (Lopez-Mondejar et al. 2020; Ren et al. 2021).

Statistical analyses

Data analyses were completed using Microsoft Excel 2016 and R4.0.2; visualization was performed using R4.0.2 and the 'ggplot2' package. One-way analysis of variance (ANOVA) was used to assess the α diversity of whole CAZymes genes, soil properties, vegetation properties, and microbial taxa of CAZymes genes based on the 'stats' package. Non-metric multidimensional scaling (NMDS) ordination analysis of the Bray–Curtis distances was performed in R using the 'vegan' package (Dixon 2003). Spearman correlations were used to examine the relationships between the abundance and environmental factors of the six CAZymes family classes. Principal coordinate analysis (PCoA) was used to analyse the dissimilarity in genes-encoding enzymes for plant-, fungi-, and bacteria-derived carbon decomposition among the elevation sites. Permutational multivariate analysis of variance (PERMANOVA) was used to assess the significance of the observed PCoA differences, based on *Adonis* function using the 'vegan' package. Relationships between the composition of gene encoding enzymes for plant-derived and microbial-derived carbon decomposition and soil physical, soil chemical, and vegetation properties were revealed by partial Mantel test with the packages of 'LinkET' (Huang 2021). Variation partitioning analysis, using the 'varpart' function of the R 'vegan' package, was performed to determine the relative importance of the environmental variables (soil physical, chemical properties, and vegetation properties), and their contribution to gene composition as described above.

Results

CAZymes genes along the elevational gradient

In total, we obtained 1,323,164,024 proteins from the entire metagenome and identified 50,883,616

CAZyme read counts, accounting for 3.85% of the total proteins. Among these, 66.71% and 0.04% were assigned to bacteria and fungi, respectively, whereas the remainder were assigned to 'other' or 'unknown'. In general, all CAZymes were identified as belonging to 128 GHs families, 12 AAs families, 53 CBMs families, 16 CEs families, 12 GTs families, and 26 PLs families. It was apparent that each elevation site was significantly different in the CAZymes (Fig. S1). The α diversity was higher at low elevation and lower at high elevation ($p < 0.05$) (Table S3). The gene abundance of GHs, AAs, CBMs, and PLs showed significant differences among sites along the elevational gradient (Fig. 1). The gene abundance of GHs and AAs declined with elevation, with GHs ranging from 5,763 at the low-elevation site to 5,132 at the high-elevation site, and AAs from 832 at the low-elevation site to 561 at the high-elevation site. AAs and GHs had significant negative relationships with SM, SOC, TN, and CD, and positive relationships with ST, NH_4^+, and NO_3^- ($p < 0.05$) (Fig. S2). The gene abundance of PLs increased with elevation, from 98 at the low-elevation site to 115 at the high-elevation site. Gene abundance of CBMs did not show elevational trends from low to mid-high elevation sites (1331–1387) ($p > 0.05$), but decreased significantly at the high elevation site (1,367) compared with sites at other elevations ($p < 0.05$). The gene abundance of GTs showed a U-shaped pattern with elevation, with a peak at the low-elevation site. The gene abundance of CEs did not show an elevational trend and was not related to environmental factors ($p > 0.05$).

CAZymes families participating in plant- and microbial-derived carbon decomposition

Our study showed that the abundance of CAZyme family genes encoding enzymes for plant-, fungi-, and bacteria-derived carbon decomposition exhibited different trends along the elevational gradient (Fig. 2). The abundance of the CAZyme gene for plant-derived carbon decomposition significantly decreased from 2,725 at the low-elevation site to 2,493 at the high-elevation site ($p < 0.05$) (Fig. 2a). Specifically, the abundance of the CAZyme

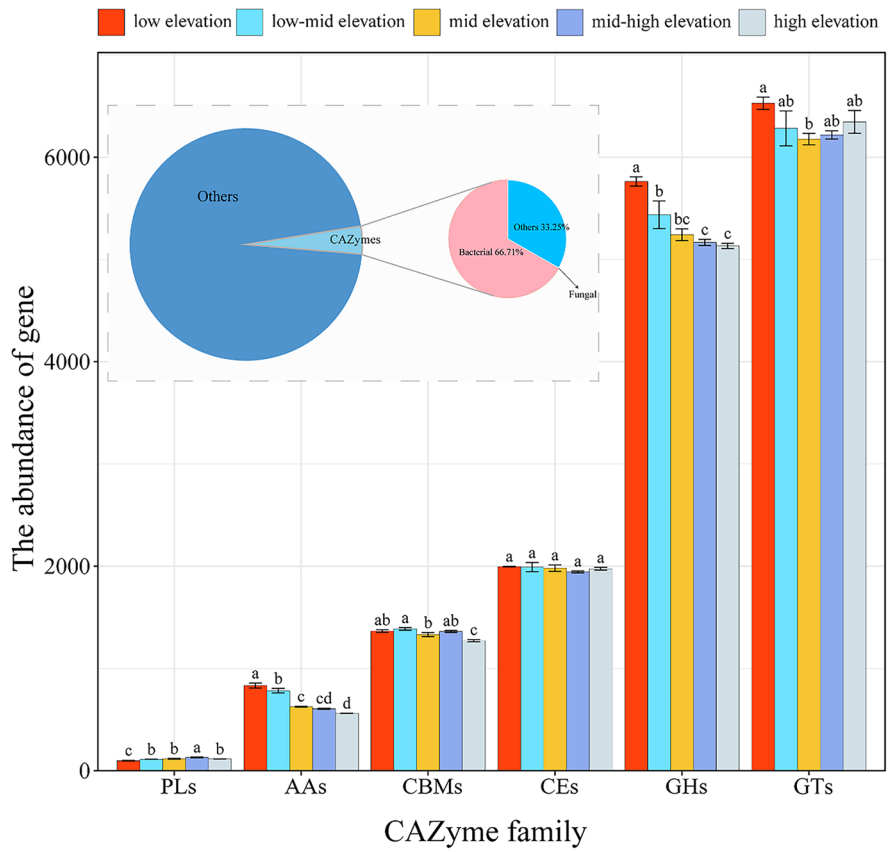

Fig. 1 The abundance (TPM: transcripts per kilobase per million mapped reads) of CAZyme family along the elevational gradient. Glycosyl Transferases (GTs), Glycosyl Hydrolases (GHs), Carbohydrate Esterases (CEs), Auxiliary Activities (AAs), Polysaccharide Lyases (PLs), and carbohydrate-binding modules (CBMs). Different lowercase letters represent significant differences at 0.05 level

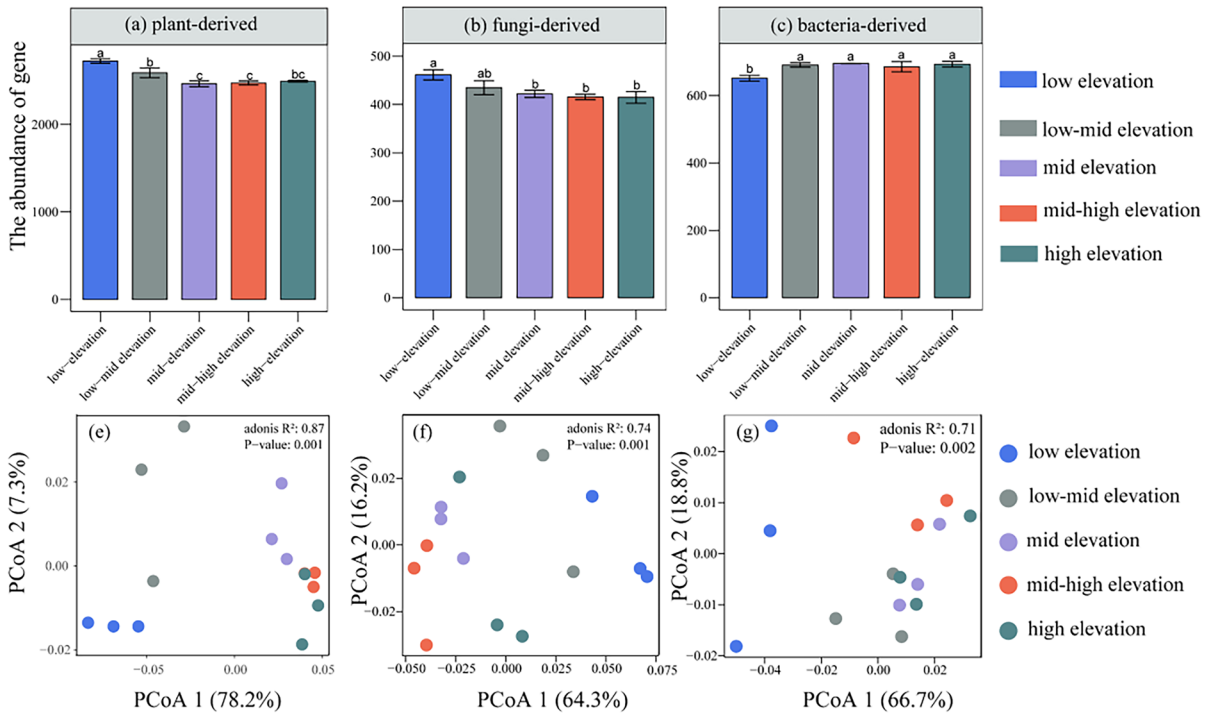

Fig. 2 The abundance (TPM: transcripts per kilobase per million mapped reads) of gene encoding enzymes for plant-derived (**a**), fungi-derived (**b**), and bacteria-derived (**c**) carbon decomposition along the elevational gradient. Error bar means ± SE; Different lowercase letters represent significant differences at 0.05 level. Principal coordinate analysis (PCoA) of CAZyme family gene encoding enzymes for plant-derived (**d**), fungi-derived (**e**), and bacteria-derived (**f**) carbon decomposition along the elevational gradient based on Bray–Curtis dissimilarity. Percentages indicate the amount of that variability explained by the corresponding axis

genes for plant-derived cellulose and hemicellulose decomposition showed no significant elevational trend; however, plant-derived lignin decomposition showed a significant decreasing trend ($p<0.05$) (Fig. S4), and all AA families associated with lignin decomposition showed a decreasing trend with elevation (Fig. S3a). The abundance of the CAZyme genes for fungi-derived carbon decomposition decreased from 461 at the low-elevation site to 414 at the high-elevation site ($p<0.05$) (Fig. 2b), with most families (e.g., GH19, GH55, GH20, GH17, GH18, and GH120) showing a decreasing trend (Fig. S3b). However, chitin decomposition did not change significantly with elevation (Fig. S4). Moreover, the abundance of the CAZyme gene for bacteria-derived carbon decomposition increased from 651 at the low-elevation site to 693 at the high-elevation site ($p<0.05$) (Fig. 2c); GH23 was the most abundant family gene, which showed an increasing trend along the elevational gradient (Fig. S3c). The composition of CAZyme genes shifted with elevation based on PCoA plotted using the Bray–Curtis distance (Fig. 2d, e, f). PERMANOVA showed that the compositional dissimilarities among elevations were significant (plant-derived carbon, $R^2=0.87$, $p=0.001$; fungi-derived carbon, $R^2=0.74$, $p=0.001$; bacteria-derived carbon, $R^2=0.71$, $p=0.002$).

Proteobacteria and Acidobacteria were the dominant bacterial phyla in the study area; Proteobacteria accounted for more than half of the bacteria responsible for bacteria-derived carbon decomposition, and had the highest relative abundance at lower elevation sites (Fig. 3). Furthermore, the relative abundance of Proteobacteria was highest at the low-mid elevation site for the decomposition of plant-derived carbon and highest at the high elevation site for the decomposition of fungi-derived carbon. Verrucomicrobia are important bacteria in the decomposition of fungi-derived carbon. The relative abundance of Acidobacteria, Actinobacteria, Firmicutes, Bacteroidetes, Verrucomicrobia, Candidatus Rokubacteria, and Gemmatimonadetes were lower at lower elevation

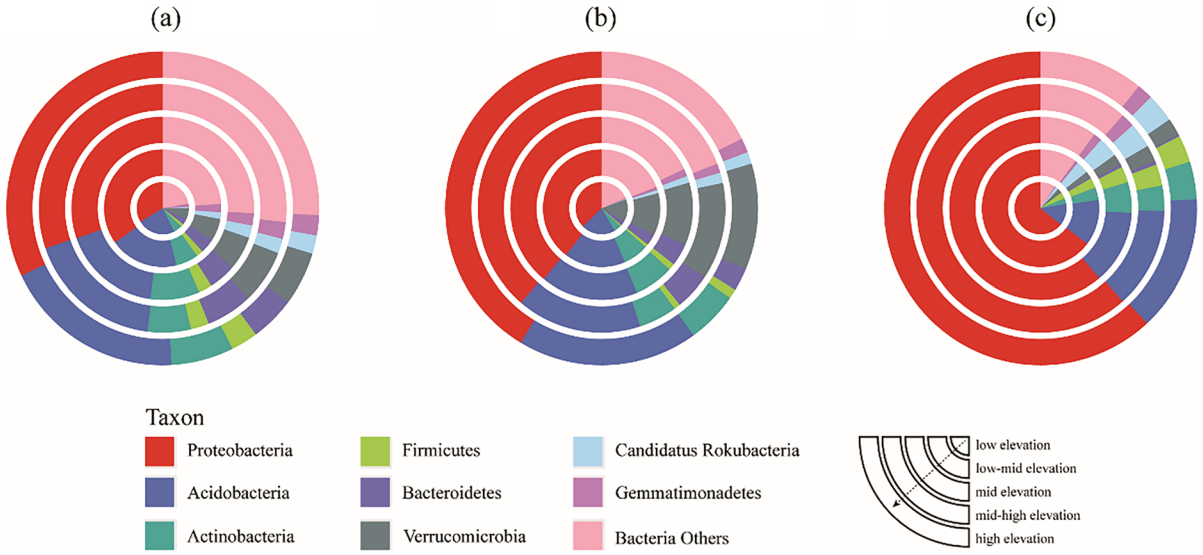

Fig. 3 Ring diagram showed the relative abundance of microbial taxon for decomposing plant-derived (**a**), fungi-derived (**b**), and bacteria-derived (**c**) carbon along the elevational gradient. The rings from inner to outer represent sites from low elevation to high elevation

sites than at higher elevation sites for decomposing biomass carbon.

Effects of soil and vegetation properties on microbial CAZymes genes

Mantel test analysis showed that soil physical properties (BD, SM, and ST) were significantly related to genes encoding enzymes for plant-derived decomposition (Mantel's $r > 0.5$, Mantel's $p < 0.05$) (Fig. 4a, Table S4). Soil NH_4^+ content is an important factor among soil chemical properties and had a strong correlation with genes encoding enzymes for plant-derived carbon decomposition (Mantel's $r = 0.89$, Mantel's $p < 0.05$). Soil BD (Mantel's $r = 0.64$, Mantel's $p < 0.05$) and NH_4^+ (Mantel's $r = 0.75$, Mantel's $p < 0.05$) were significantly related to genes encoding enzymes involved in fungi-derived carbon decomposition. Soil BD (Mantel's $r = 0.74$, Mantel's $p < 0.05$) and the Arbor–Shannon index (Mantel's $r = 0.63$, Mantel's $p < 0.05$) were significantly related to gene-encoding enzymes for bacteria-derived carbon decomposition. Furthermore, TN was significantly associated with the gene pools (Mantel's $p < 0.05$).

To further determine the relative importance of these variables, we conducted variation partitioning analysis to investigate their relative effects on the CAZyme genes. Variation partitioning analysis indicated that soil chemical properties explained a much greater portion of the variance (6.11%) in the genes encoding enzymes for plant-derived carbon decomposition than did soil physical (1.96%) and vegetation properties (1.41%) (Fig. 4b). For genes encoding enzymes involved in fungi-derived carbon decomposition, soil chemical properties explained a much greater proportion of the variance (5.28%) (Fig. 4c). Soil physical properties explained a much greater proportion of the variance in genes-encoding enzymes for bacteria-derived carbon decomposition (16.16%) than did soil chemical (8.80%) and vegetation properties (9.52%) (Fig. 4d). In addition, the three types of properties could interactively explain the variance in genes encoding enzymes for plant-, fungi-, and bacteria-derived carbon decomposition by 35.02%, 46.42%, and 47.31, respectively (Fig. 4b, c, d).

Discussion

Microbial CAZymes family genes variation along the elevational gradient

Our result showed that CAZymes gene α and β diversity differed among the elevation sites, especially

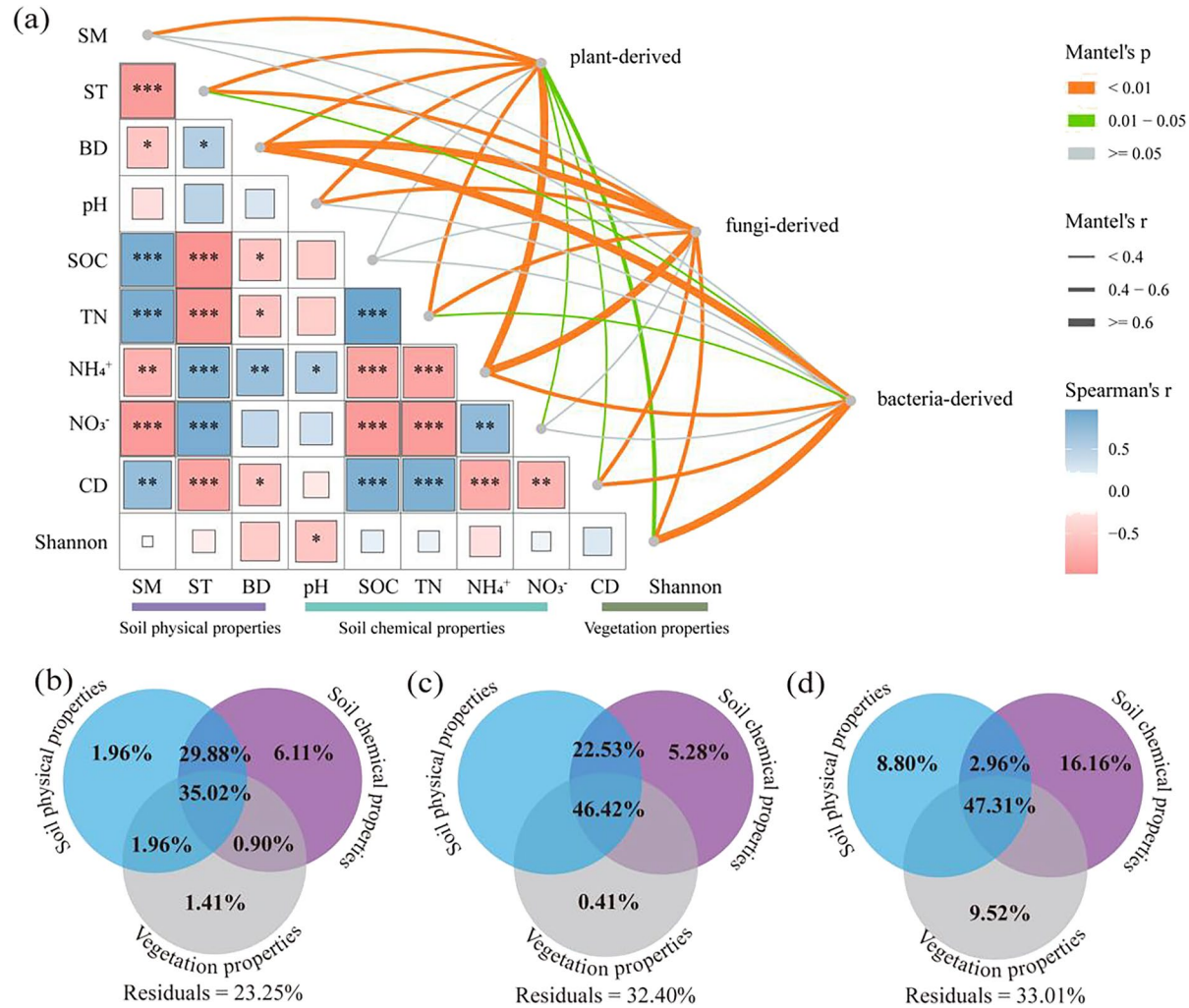

Fig. 4 CAZyme genes were related to each environmental factor by partial Mantel test (**a**). Edge width corresponds to the Mantel's r statistic for the corresponding distance correlations, and edge color denotes the statistical significance. Spearman's correlation based on pairwise comparisons of environmental factors. * $p<0.05$; ** $p<0.01$; *** $p<0.001$. And variation partitioning analysis (VPA) was conducted to identify the variance in gene encoding enzymes for plant-derived carbon (**b**), fungi-derived carbon (**c**), bacteria-derived carbon (**d**) decomposition

between low and high elevation sites, indicating variation of function along the elevational gradient (Table S3, Fig. S2). The abundance of genes encoding AAs, CBMs, and GHs decreased along the elevational gradient (Fig. 1). This indicates high metabolic activity of anabolic and catabolic processes at low-elevation sites. One possible explanation is that higher temperatures and lower water availability cause higher oxygen concentrations in the soil at lower elevations, which may be responsible for higher microbial activities, resulting in higher microbial decomposition potential (Mou et al. 2021). The temperature limitations of microbial and enzyme activities at higher elevation sites can cause a decline in the genes associated with enzymes (Liu et al. 2019). Our results also suggest strong correlations between ST and SM, with the genes encoding AAs, CBMs, and GHs (Fig. S2). Microbial GHs are key genes involved in the decomposition of SOM. However, Dai et al. (2021) reported that the abundance of GHs was higher at high-elevation sites, and there were no relationships between GHs and climatic, edaphic, and

vegetation variables, which was consistent with the lack of responses of overall organic C decomposition to the elevational gradient in their study area. A possible reason for this may be the response of organic decomposition to elevational gradients. In our recent study, Zhao et al. (2022) found a decline in the positive priming effect along an elevational gradient. Here, the gene for microbial anabolic activities (GTs) showed a U-shaped pattern along the elevational gradient, with the highest abundance in low elevation sites and a significant correlation with pH. In line with our results, Yang et al. (2022) found that pH was an important factor affecting microbial-derived carbon. This is not difficult to explain because pH plays an important role in influencing microbial community composition and diversity, thereby influencing functional genes (Li et al. 2018; Zhao et al. 2022).

Changes in plant- and microbial-derived carbon decomposition along the elevational gradient

The abundance of CAZyme genes encoding plant-derived carbon showed a declining trend along the elevational gradient, indicating that the potential for plant-derived carbon degradation decreases with increasing elevation (Fig. 2). One possible reason for this negative elevational trend is the higher plant-derived carbon input at lower elevation sites with vegetated deciduous broadleaf trees than at those with vegetated coniferous trees (Zhu et al. 2017). Studies have confirmed that an increase in plant residue input can increase the abundance of CAZyme genes (Ren et al. 2021; Yin and Zhang 2022).

Moreover, fungi-derived compounds had higher decomposition potentials at low elevations than at high elevations, whereas bacteria-derived compounds had higher decomposition potentials at higher elevations than at lower elevations (Fig. 2). In line with our results, previous evidence has indicated that the turnover of fungal and bacterial cell walls differs (Gunina et al. 2017). This can be attributed to three factors. First, microbes enhance their decomposition potential to meet their metabolic demand when the temperature declines and nutrients are limited at high elevation sites, resulting in faster turnover of dead bacterial biomass because bacteria-derived peptidoglycan is more readily decomposed and utilised by soil microbes (He et al. 2011; Hu et al. 2020; Liu et al. 2019). Second, some-glucans may indirectly increase the decomposability of dead fungal biomass by affecting water availability. Glucans can increase the water-holding capacity of the fungal cell wall, which is critically important when water availability is a limiting factor (e.g., at low elevation sites) (Fernandez et al. 2016; Kyanko et al. 2013). Finally, the acidic soils of coniferous forests favour fungi with larger residence times at higher elevations, indicating a slow turnover of fungal biomass (He and Xu 2021; Rousk and Baath 2011). Slower fungal biomass turnover leads to a lower fungal neuroma production rate, causing the decomposition capacity to decline (Fernandez et al. 2019; Wang et al. 2021, 2020).

Our results showed that most genes encoding enzymes for decomposing plant- and microbial-derived carbon belonged to Proteobacteria and Acidobacteria (Fig. 3), which have been widely shown to produce CAZymes (Ivanova et al. 2016; Zifcakova et al. 2016). This may be due to the high percentage of bacteria that potentially decompose cellulose found in forest soils, and the high frequency of genes involved in the decomposition of structural plant polysaccharides found in bacterial genomes (Lopez-Mondejar et al. 2020). Generally, Proteobacteria thrive in environments with high carbon utilisation because they are symbiotic bacteria that grow rapidly (Fierer et al. 2007). However, the relative abundance of Proteobacteria was inconsistent along the elevational gradient for fungi- and bacteria-derived compound decomposition, highlighting the critical role of *Proteobacteria* in biomass carbon decomposition. Acidobacteria are acidophilic and show an increasing trend with decreasing pH along the elevational gradient. This is in line with a previous study that reported a negative correlation between the abundance of Acidobacteria and soil pH (Sait et al. 2006). Overall, our results indicate the role of bacteria in biomass decomposition along an elevational gradient.

Factors affecting microbial CAZymes genes along elevational gradient

Our results demonstrate that soil and vegetation properties primarily control the distribution of microbial CAZyme genes encoding plant- and microbial-derived C decomposition in forest soils along an elevational gradient (Fig. 4). On the one hand,

vegetation can create microenvironments that influence soil microbial activity and functional diversity along an elevational gradient (Hernández-Cáceres et al. 2022). On the other hand, vegetation mainly shapes soil microbial biomass, growth, composition, and turnover (Lange et al. 2015; Prommer et al. 2020; Ren et al. 2018). Therefore, vegetation properties interact with soil properties to mediate microbial CAZyme genes (Liu et al. 2021; Tkacz et al. 2015). Among these properties, soil chemical properties play an important role (Fig. 4, Table S4). Consistent with our results, previous studies have shown that soil chemical properties and the diversity of microbial communities are significantly correlated (Fierer and Jackson 2006; Shen et al. 2013). Notably, the chemical properties related to nitrogen (TN, NH_4^+, and NO_3^-) are significantly associated with the gene pools. This may be because the soil nitrogen content regulates microbial diversity and composition (Luo et al. 2017; Shi et al. 2018; Tkacz et al. 2015), thereby influencing microbial CAZyme genes (Zhao et al. 2022). In addition, He et al. (2020) indicated that TN and soil microbial biomass were significantly correlated along an elevational gradient. Therefore, with the increase in TN along the elevational gradient in our study, we observed a significant effect on CAZymes. In particular, NH_4^+ is strongly correlated with genes encoding microbial-derived carbon decomposition. Previous studies have shown that NH_4^+ is preferred by microorganisms and affects the production of microbial residues (He et al. 2011). Furthermore, we observed the important role of soil physical properties on CAZyme genes production, with BD significantly influencing CAZyme genes function along an elevational gradient. This is consistent with our recent study showing that BD affects functional genes and alters the soil decomposition capacity of forest soils (Zhao et al. 2022). This may be because BD influences soil porosity and oxygen in the soil, and causes differences in soil temperature and moisture, both of which affect microbial community structure and function (Zhong et al. 2018). Therefore, BD is an important factor that influences CAZyme genes. ST is another important factor affecting CAZyme genes, which was confirmed by recent studies showing that temperature changes can alter the carbohydrate degradation potential in temperate forest soils (Pold et al. 2016). Overall, our results highlight that soil and vegetation properties drive the expression of microbial CAZyme genes associated with dead biomass decomposition in forest soils.

Conclusion

This study investigated functional genes relevant to C decomposition in forest soils along an elevational gradient. The key findings were as follows: 1) the genes encoding GHs and AAs decline with increasing elevation; 2) plant- and fungi-derived carbon decomposition potentials are higher at low elevation than at high elevation; 3) contrary to bacteria-derived carbon, fungi-derived carbon have higher decomposition potential at low elevation compared with high elevation; 4) dominant bacteria, such as Proteobacteria and Acidobacteria, play an important role in decomposing plant and microbial dead biomass; and 5) edaphic and vegetation factors primarily affect the distribution of microbial CAZyme genes. These findings advance our understanding of functional genes in association with ecosystem functions; the contrasting patterns of the functional genes of bacteria and fungi provide direct evidence of the different roles of microbes in decomposing dead biomass, which calls for model improvements in representing microbial community structure.

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Declarations

Conflict of interests The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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