

Phytohormone-fungal coordination mediates functional trait adaptation in *Pleioblastus amarus* under elevational stress

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Abstract

Background and aims

Arbuscular mycorrhizal fungi (AMF) play crucial roles in shaping plant functional traits and adaptation strategies. However, the AMF diversity and plant functional trait relationships in bamboo forest remain unexplored. Given their unique clonal growth pattern, bamboo forest offers an intriguing ecosystem to study mycorrhizal-plant interactions across changing elevations.

Methods

We conducted a field study in bamboo forest dominated by the species *Pleioblastus amarus*. We measured the soil fungal community, endogenous hormones, non-structural carbon (NSC) content, shoot density, and shoot biomass, as well as soil physicochemical properties in four bamboo forests with different elevation.

Results

Although the alpha diversity of did not differ among the four bamboo forests, soil fungal diversity significantly correlated with phytohormones in the rhizome, taxonomically displaying varying correlations with plant traits. While shoot density and shoot biomass showed opposing trends or functional trade-off, endogenous hormones and NSC content showed significant changes among the four bamboo forests. Also, soil pH, SM, and total phosphorus significantly differed among the four bamboo forests.

Conclusions

The taxon-specific fungal correlation with plant traits suggests that specialized fungal symbionts promote plant hormonal adjustments and evolutionary adaptation strategies in a changing environment.

Introduction

Mycorrhizal fungi form symbiotic relationship with ~ 80% of terrestrial plants (Brundrett and Tedersoo 2018; Smith and Read 1997; Zobel et al. 2024), substantially providing critical regulatory services, including hormone balance, stress adaptation, and nutrient uptake to their host plants (Wagg et al. 2011; Jiang et al. 2021; Zhang and Feng 2021). Thus, plant-mycorrhizal fungal interactions are fundamental to functioning and productivity of terrestrial ecosystems such as bamboo forest (Chen et al. 2017; Zhang et al. 2023; Wang et al. 2024). Previous studies have shown that the belowground communities, especially fungal communities, vary across ecosystems owing to differences in elevation, soil properties, and plant community composition (Wilson et al. 2009; Wu et al. 2014; Adomako et al. 2025; Barbi et al. 2025). For instance, elevational gradients act as environmental filter due to temperature and soil biogeochemical dynamics (Shigyo et al. 2019; Větrovský et al. 2019), which can significantly alter mycorrhizal community composition and functional relationships with host plants. Despite being a key symbiont in plant-fungal association in many ecosystems and the extensive research coverage in field and controlled studies, knowledge on mycorrhizal fungi diversity and mutual interactions with plants along elevations remain limited in bamboo forest ecosystems. Understanding how such interactions shift across elevations is essential for predicting bamboo forest resilience to climate change in montane regions.

Bamboo forest is among the most important and promising forest ecosystems in Asia. As a clonal plant, bamboo possesses an extensive belowground rhizome system that facilitates its growth and population expansion (Luan et al. 2021). By their unique horizontal and vertical growth characteristics, bamboo often alters the environmental conditions, including nutrient levels, light availability, and spatial structure, significantly modulating bamboo shoot density, physiological, and biochemical processes (Guo et al. 2011; Xu et al. 2017; Xiao et al. 2021; Zuo et al. 2024). Especially, the extensive canopy architecture and litter accumulation strongly impact the growth of understory co-occurring plant communities (Luan et al. 2021) and soil properties and belowground microbial communities (Chang and Chiu 2015; Luo et al. 2024). For example, a recent meta-analysis found a marked changes in soil pH, ammonium nitrogen, fungal biomass, and bacterial Shannon diversity in a bamboo invaded ecosystems (Luo et al. 2024). Also, Luan et al. (2021) reported that bamboo litter decomposition reduced microbial carbon, increased soil nitrogen, and fungal communities in bamboo ecosystems. The majority of previous studies on bamboo have primarily focused on the growth and productivity (Van Dam et al. 2018), changes in hormonal and nutrients content, and soil communities (Jiang et al. 2013; Zhan et al. 2022; Mao et al. 2024). However, very few studies have examined bamboo effects on plant functional traits, soil properties, and rhizospheric soil communities, and their relationship along elevational gradients.

Plant functional traits, including shoot density, biomass, and physiological markers such as endogenous hormones and non-structural carbohydrates (NSC), are key indicators of growth strategies and environmental adaptation (Yu et al. 2024b). These traits are often mediated by soil microbial communities, particularly AMF, which enhance nutrient uptake and hormonal regulation (He et al. 2017; Adomako et al. 2021). For instance, AMF can modulate gibberellic acid (GA), abscisic acid (ABA), and cytokinin levels, thereby influencing plant growth and stress tolerance (Zhang et al. 2019). However, the mechanisms underlying AMF-driven hormonal adjustments and their effects on bamboo functional traits are not well understood. Furthermore, while soil properties such as pH, moisture, and phosphorus content are known to shape fungal communities (Barbi et al. 2025), their interactions with bamboo functional traits and AMF diversity have not been thoroughly investigated. Given the ecological and economic importance of bamboo forests, understanding these relationships is essential for predicting ecosystem resilience and optimizing management practices under changing environmental conditions.

Advancing knowledge on mycorrhizal fungi diversity, plant functional traits, and their relationship in bamboo forest is critical for understanding soil microbial communities' role in plant growth regulation and adaptation mechanisms under future environmental changes. Thus, we conducted a field study the bamboo forest dominated by the species *Pleioblastus amarus*. We measured the soil fungal community diversity, endogenous hormones, NSC content, shoot density,

and shoot biomass, as well as soil physicochemical parameters across four bamboo forests with contrasting elevation. Specifically, our study aimed to: (1) Determine whether mycorrhizal alpha diversity and relative abundance exhibit significant spatial variation within the bamboo forest ecosystem. (2) Assess variation in bamboo functional traits (shoot density, shoot biomass) and physiological characteristics (endogenous hormones, NSCs). (3) Identify relationships between mycorrhizal fungal diversity, bamboo functional traits, and soil physicochemical parameters. By integrating analyses of soil fungal communities, plant physiology, and edaphic factors, this study advances our understanding of mycorrhizal-plant interactions in bamboo ecosystems, providing insights into their ecological and adaptive significance.

Materials and Methods

Study species and sampling site

Pleioblastus amarus is a bamboo species belonging to the grass family Poaceae, and widely distributed across its native Asia-Pacific region (Guo et al. 2018; 2019). Its perennial, tall, hollow, and has cylindrical erect stem (known as culms) that reaches approximately 20 meters (Zuo et al. 2024). *Pleioblastus* sp. are characterized by their woody and lignified rhizomatous underground clonal network system that enhance their capacity to colonize and survive in diverse natural environments, including montane regions. Due to their incredibly adaptability and versatility, *P. amarus* has gain considerable economic and ecological importance and wide range of applications, especially in Asia. It has a rapid growth rate, especially in monoculture stands.

On June 2024, we conducted a field sampling study in Linhai, Taizhou city and Xianju County (120°17'-121°56'E, 28°01'-29°20"N) in the southeastern of Zhejiang Province. The region has a subtropical monsoon climate with moderate annual temperatures and abundant sunshine and rainfall. The annual mean temperature is 15–18°C but can be extremely high in summer with a maximum of 43°C in July and August. The mean annual precipitation ranges between 980–2000 mm, and a mean annual sunlight availability of 1710–2100 hours. Other co-occurring species that inhabit the understory of *P. amarus* includes perennial and annual herbs such as *Duchesnea indica* (Andr.) Focke, *Leptochloa panicea* (Retz.) Ohwi, *Trachelospermum jasminoides* (Lindl.) Lem, and *Patrinia scabiosifolia* Fisch. ex Trevir. In each of the sampling sites, we selected four bamboo forests (namely F1, F2, F3, F4) in both Linhai, Taizhou, and Xianju sampling sites for *P. amarus* forest along the elevation gradient (Fig. 1; Table 1).

Table 1
Description of sampling site information

Number	Sampling site	Elevation(m)	Longitude	Latitude
F1	Taizhou city	106	121°23'3.22"E	28°39'1.37"N
F2	Linhai city	375	121°14'39.08"E	28°32'6.80"N
F3	Xianju county	646	121°14'52.17"E	28°32'3.74"N
F4	Xianju county	1349	121°14'20.18"E	28°31'30.23"N

Experimental design

In each sampling plot, at least five 1 × 1m quadrats were randomly placed along the diagonal line for field investigation. In each quadrat, we counted the number of shoot of *P. amarus* and estimated the shoot density by using the number of shoots/m² in all quadrat. We randomly selected six shoots, clipped it at ground level, and randomly dig out three belowground rhizomes connected to the shoot. Each fresh shoot washed and weighed. The shoots and three corresponding rhizomes were weighed after washing, and clipped with a sharp razor into small strips and freeze immediately in liquid nitrogen for further hormone analysis. Thirty replicates for shoot and fifteen replicates for rhizome were used in each plot for endogenous hormone content determination. Lastly, six shoots per quadrat were oven-dried at 70°C for at least 48 hours, and weighed to obtain the biomass and also used for the soluble sugar and starch content determination. The soluble sugar and starch contents were expressed as percentages (%) based on the fresh weight, which thirty replicates were used from each plot. For soil sampling, we took five soil samples (0–10 cm deep) under each quadrat. The five soil samples from each container were thoroughly homogenized to form a composite sample. Then, a sub-sample of 10 mL was preserved at – 80°C until DNA extraction for soil microbial and physiochemical analysis (Table 2).

Table 2
Soil parameters in the four bamboo forests with different elevation

Soil parameters	Along contrasting elevational gradient				<i>F</i>	<i>P</i>
	F1	F2	F3	F 4		
PH	4.61 ± 0.06	4.96 ± 0.07	4.44 ± 0.08	4.51 ± 0.07	9.369	< 0.001
SM(%)	26.06 ± 1.35	29.00 ± 1.14	31.12 ± 0.66	32.60 ± 0.65	7.126	< 0.001
TC(mg/L)	124.64 ± 13.68	147.23 ± 14.70	135.53 ± 19.28	125.28 ± 8.62	0.683	> 0.05
TOC(mg/L)	133.13 ± 6.81	113.59 ± 13.02	142.37 ± 13.71	125.18 ± 18.51	0.596	< 0.05
TN(mg/L)	17.68 ± 1.16	27.52 ± 1.81	29.84 ± 6.50	24.54 ± 2.83	3.478	< 0.05
TP(mg/L)	3.54 ± 0.58	6.08 ± 0.40	2.94 ± 0.52	2.57 ± 0.20	13.621	< 0.001
IC(mg/L)	11.04 ± 0.85	14.85 ± 1.06	10.35 ± 1.19	12.57 ± 0.86	3.943	< 0.05

Endogenous hormone determination

Endogenous hormones were determined in the laboratory for gibberellic acid (GA), abscisic acid (ABA), indolepropionic (IPA), indoleacetic acid (IAA), and zeatin riboside (ZR) with an enzyme-linked immunosorbent assay (ELISA) (Chen et al. 1998). The specific extraction procedures were as follows: (1) weighed 0.2 g of freeze-dried and ground sample, added 5 mL of extraction solution, shook well, and placed the mixture for 4 h at 4 °C according to the instructions of the ELISA kit manufacturer; (2) centrifuged the mixed extraction solution at 3500 rpm/min for 8 min at 4 °C and collected the supernatant with a pipette; then added 1 mL of extraction solution to the remaining precipitate, shook and extracted at 4 °C again, and collected the supernatant again; (3) passed supernatant through a C-18 solid-phase extraction column, dried the sample obtained after passing through the column, and then diluted it to 5 mL with sample diluent from the ELISA kit, then added the standard substance and placed the mixture for 0.5 h at 37 °C; (4) after color development, measured the OD values of the standard substance and each sample at 490 nm with an ELISA spectrophotometer; (5) fitted the standard curve of hormones and calculated the hormone content in each sample using a logit curve based on the measured values.

Soluble sugar and starch determination

For soluble sugar, the plant samples were ground after drying, weighed 0.1–0.15 g into test tubes, added 5 mL of 80% ethanol, and mixture thoroughly. The sample was then bathed in water at 80 °C for 30 minutes. The sample was then poured into a centrifuge tube, which was spun at 2000 RPM for 10 minutes, and the supernatant was collected in a 50 mL colorimetric tube. This extraction step was repeated twice. After the supernatant was mixed, the colorimetric tube was placed in an 85 °C water bath to evaporate the ethanol, resulting in approximately 2 mL. The solution was then filled with distilled water to a volume of 50 mL. A 1 mL aliquot of the extraction solution was transferred to a test tube, added 1 mL of distilled water, 0.5 mL of anthrone reagent, and 5 mL of concentrated sulfuric acid. The mixture was shaken well, and the solution was heated in a water bath for 1 minute, followed by cooling to room temperature. The absorbance at 630 nm was measured using a spectrophotometer (752 N Hengping). We obtained the starch after the precipitation after extraction of soluble sugar, and the above method was repeated for the determination of other samples.

Microbial sample collection and sequencing

Soil DNA was extracted using a PowerSoil™ DNA Isolation Kit (MoBio, Carlsbad, CA, USA) in accordance with the manufacturer's instructions. Subsequently, the extracted DNA was sent to Novogene Co., Ltd., Beijing, China, for amplification, library preparation, and sequencing. Additionally, the fungal ITS region rDNA was amplified using primers ITS5-1737F (GGAAGTAAAGTCGTAACAAGG) and ITS2-2043R (GCTGCGTTCTTCATCGATGC) (Wei et al. 2018). Sequencing was performed on an Illumina NovaSeq 6000 platform, generating 250 bp paired-end reads.

Bioinformatic analysis

Barcode extraction, paired read assembly, and quality filtering of the raw data were conducted using QIIME software version 1.9.1 (Caporaso et al. 2010). Chimeric sequences were identified and removed using UCHIME (Edgar et al. 2011). Operational taxonomic units (OTUs) were identified at a 97% similarity threshold with UPARSE version 7.1b (Edgar 2013). The taxonomy of each fungal OTU was assigned using the Uclust method with SILVA release 132 (<https://www.arb-silva.de/documentation/release-132>) and the UNITE database (http://qiime.org/scripts/assign_taxonomy.html), respectively.

Statistical Analysis

We used one-way ANOVA to determine the differences in belowground shoot density, biomass, physiological characteristics (endogenous hormone, soluble sugar, and starch), and soil fungi in the various sample site (F1, F2, F3, F4) along the elevation gradient. We performed Principal Coordinates Analysis (PCoA) and Adonis to test whether species composition of soil microbial communities differed between different plots based on Weighted Unifrac distance. Correlation analysis was used to assess the relationships of shoot density, biomass, physiological characteristics (endogenous hormone, soluble sugar and starch) with the alpha diversity index, and relative abundances of phyla and genera of fungi. Residuals of all variables were checked for homoscedasticity and normality. All statistical analysis and Tukey's test was performed using SPSS 20.0 (IBM, Inc., Armonk, NY, USA), calculated alpha diversity using the QIIME software (Version 1.9.1), and created all graphs using Origin 8.5.

Results

Shoot biomass and density

Shoot biomass and density significantly changed among four plots with different elevation ($P < 0.05$, Table 3). Thus, shoot density (20.16 ± 4.12) initially peaked at F1 plot, but decreased markedly at F2 with a slightly increased at plot F3. However, there was no significant difference between the change in shoot density in both plots F3 and F4 (Fig. 2). Contrary to the peak pattern of shoot density in plot F1, the shoot biomass (34.29 ± 5.78) significantly peaked at plot F4 ($P < 0.001$, Fig. 2) however, such an observation reversed at F3 before peaking again at F2 (Fig. 2).

Table 3
Summary of ANOVA analysis testing the effects of elevation on endogenous hormone, NSC content, shoot biomass and shoot density

Variable	df	F	P
Biomass	3,96	17.407	< 0.001
Number	3,14	4.989	0.015
Soluble sugar	3,104	0.960	0.415
Starch potato	3,104	7.424	< 0.001
Rh iaa	3,104	7.376	< 0.001
Rh zr	3,104	80.721	< 0.001
Rh aba	3,104	10.568	< 0.001
Rh ipa	3,104	24.508	< 0.001
Rh ga ₁₊₃	3,104	30.248	< 0.001
Rh ga ₄₊₇	3,104	23.590	< 0.001
Sh iaa	3,50	11.277	< 0.001
Sh zr	3,50	5.552	0.002
Sh aba	3,50	16.503	< 0.001
Sh ipa	3,50	17.932	< 0.001
Sh ga ₁₊₃	3,50	5.288	0.003
Sh ga ₄₊₇	3,50	2.848	0.047

Endogenous hormones and non-structural carbon (NSC)

Results of rhizome and shoot content determination for six endogenous hormones (IAA, ZR, ABA, IPA, GA₁₊₃, and GA₄₊₇) indicated that the mass fraction of the six hormones differed significantly among four bamboo forests with contrasting elevation (Fig. 3). Specifically, IAA, ZR, ABA and IPA contents in rhizomes significantly increased and then decreased at the higher elevational plot, and peaked at the F2 plot ($P < 0.001$, Fig. 3a-d; Table 3). For GA₁₊₃ and GA₄₊₇, the hormone contents in the rhizome decreased at the higher elevational plot ($P < 0.001$, Fig. 3e-f; Table 3). Similarly, the IAA, ZR, ABA, IPA and GA₁₊₃, hormones in the shoots significantly increased but decreased at the higher elevational plot ($P < 0.05$, Fig. 3g-i). While the IAA, ZR, and ABA hormones peaked at F2 plot, the contents of IPA and GA₁₊₃ peaked at F3 plot. For GA₄₊₇, hormones in shoot decreased at the higher elevational plot ($P < 0.05$, Fig. 3g-i). While soluble sugar content showed no significant difference among four plots (Fig. 4a; Table 3), starch content significantly changed among four plots with different elevation, which peaked at plot F4 (Fig. 4b; Table 3).

Alpha diversity and relative abundance of soil fungi community

Results indicate that elevation had no significant effect on the alpha diversity (OTUs, Shannon, Simpson, Chao1, Dominance and Pielou indices) of soil fungal communities (Fig. 5; Table 4). Regarding soil fungal taxa, Ascomycota, Basidiomycota, and Zoopagomycota were the three most abundant phyla (Fig. 6a). Among the 10 most abundant fungal genera, the relative abundance of Onygenales and Penicillium increased significantly with increasing elevation (Fig. 6b). Results of the Adonis test showed that species composition of soil fungal communities differed between the F1-F4 plots ($P < 0.001$, Table 5).

Table S1
The Correlation analysis of plant traits with soil fungal diversity

Variable	Rh iaa	Rh zr	Rh aba	Rh ipa	Rh ga ₁ + 3	Rh ga ₄ + 7	Sh iaa	Sh zr	Sh aba	Sh ipa	Sh ga ₁ + 3	Sh ga ₄ + 7	Biomass	Soluble sugar
1 Chao1	0.598	0.717	0.894	0.638	0.931	0.776	0.907	0.362	0.551	0.587	0.369	0.743	0.608	0.144
Dominance	0.504	0.992	0.597	0.469	0.22	0.277	0.642	0.099	0.555	0.124	0.454	0.485	0.716	0.397
Goods_coverage	0.571	0.999	0.746	0.846	0.776	0.801	0.893	0.602	0.542	0.771	0.462	0.919	0.503	0.251
OTUs	0.593	0.683	0.92	0.623	0.911	0.796	0.905	0.348	0.496	0.588	0.339	0.726	0.587	0.123
Pielou_e	0.508	0.934	0.642	0.608	0.416	0.363	0.685	0.16	0.969	0.218	0.379	0.613	0.746	0.204
Shannon	0.505	0.865	0.697	0.592	0.543	0.437	0.73	0.175	0.875	0.267	0.339	0.627	0.695	0.151
Simpson	0.504	0.992	0.597	0.469	0.22	0.277	0.642	0.099	0.555	0.124	0.454	0.485	0.716	0.397
2 Chao1	0.626	0.089	0.861	0.992	0.609	0.560	0.167	0.108	0.253	0.368	0.297	0.188	0.294	0.687
Dominance	0.654	0.696	0.923	0.071	0.138	0.362	0.002	0.024	0.983	0.250	0.381	0.213	0.292	0.528
Goods_coverage	0.706	0.017	0.826	0.568	0.971	0.390	0.274	0.071	0.117	0.208	0.132	0.243	0.125	0.283
OTUs	0.578	0.124	0.836	0.925	0.624	0.577	0.173	0.144	0.286	0.459	0.346	0.181	0.321	0.748
Pielou_e	0.796	0.737	0.631	0.222	0.137	0.381	0.056	0.120	0.701	0.590	0.856	0.166	0.527	0.858
Shannon	0.740	0.555	0.724	0.308	0.186	0.550	0.062	0.111	0.590	0.550	0.965	0.152	0.457	0.833
Simpson	0.654	0.696	0.923	0.071	0.138	0.362	0.002	0.024	0.983	0.250	0.381	0.213	0.292	0.528
3 Chao1	0.778	0.847	0.858	0.892	0.960	0.924	0.997	0.990	0.997	0.963	0.981	0.996	0.667	0.915
Dominance	0.357	0.578	0.565	0.719	0.575	0.706	0.521	0.512	0.613	0.492	0.616	0.538	0.698	0.932
Goods_coverage	0.463	0.921	0.747	0.999	0.727	0.892	0.624	0.715	0.690	0.719	0.632	0.613	0.345	0.866
OTUs	0.851	0.809	0.765	0.884	0.896	0.907	0.905	0.922	0.906	0.894	0.878	0.907	0.688	0.846
Pielou_e	0.220	0.248	0.671	0.272	0.305	0.284	0.635	0.255	0.911	0.261	0.813	0.455	0.371	0.658
Shannon	0.342	0.423	0.836	0.422	0.448	0.422	0.763	0.408	0.987	0.422	0.908	0.599	0.394	0.767
Simpson	0.357	0.578	0.565	0.719	0.575	0.706	0.521	0.512	0.613	0.492	0.616	0.538	0.698	0.932
4 Chao1	0.941	0.034	0.005	0.002	0.972	0.075	0.001	0.077	0.587	0.845	0.002	0.004	0.331	0.033
Dominance	0.767	0.048	0.001	0.071	0.965	0.001	0.337	0.410	0.511	0.393	0.088	0.003	0.336	0.001
Goods_coverage	0.558	0.270	0.035	0.027	0.956	0.198	0.002	0.081	0.192	0.887	0.025	0.022	0.541	0.105
OTUs	0.960	0.024	0.003	0.002	0.962	0.046	0.001	0.090	0.726	0.765	0.002	0.003	0.331	0.022
Pielou_e	0.917	0.043	0.005	0.135	0.902	0.001	0.588	0.710	0.191	0.226	0.173	0.011	0.464	0.002
Shannon	0.928	0.027	0.002	0.073	0.919	0.001	0.377	0.565	0.256	0.253	0.096	0.005	0.422	0.002
Simpson	0.767	0.048	0.001	0.071	0.965	0.001	0.337	0.410	0.511	0.393	0.088	0.003	0.336	0.001

Table 4
Effect of elevation on the alpha diversity
(OTUs, Shannon, Simpson, Chao1,
Dominance and Pielou indices) of soil fungi
community

Variable	df	F	P
Chao1	3,50	2.120	0.109
Dominance	3,50	0.631	0.598
Goods coverage	3,50	1.492	0.228
OTUs	3,50	2.436	0.076
Pieloue	3,50	0.371	0.774
Shannon	3,50	0.511	0.677
Simpson	3,50	0.631	0.598

Table 5
Adonis test for differences in community composition of fungi
between different plots based on Bray-Curtis distance

	<i>df</i>	<i>F</i>	<i>R</i> ²	<i>P</i>
F1 vs. F2	1(28)	4.79544	0.14622(0.85378)	< 0.001
F1 vs. F3	1(22)	2.58658	0.1052(0.8948)	< 0.001
F1 vs. F4	1(28)	2.98365	0.0963(0.9037)	< 0.001
F2 vs. F3	1(22)	4.3549	0.16524(0.83476)	< 0.001
F2 vs. F4	1(28)	6.94599	0.19876(0.80124)	< 0.001
F3 vs. F4	1(22)	2.7228	0.11013(0.88987)	< 0.001

Correlation among soil fungi, shoot density, shoot biomass, physiological characteristics

Both shoot biomass and shoot density negatively correlated with all the phytohormones (IAA, ZR, ABA, IPA, GA₁₊₃, and GA₄₊₇) measured. While shoot density negatively correlated with ABA hormones in the rhizome and shoot, it positively correlated with GA hormones in rhizome and shoot (Fig. 7). Alpha diversity of soil fungi community positively correlated with shoot biomass and ABA contents in the rhizome, but negatively correlated with shoot density ($P < 0.05$, Fig. 8a). Compared with endogenous hormones of rhizomes, alpha diversity of soil fungi community had no significant correlations with endogenous hormone of shoot (Table S1). Regarding soil fungal taxa, Ascomycota negatively correlated with endogenous hormones, meanwhile Basidiomycota positively correlated with the endogenous hormones and shoot biomass. Also, we found positive correlation between the fungal taxa Zoopagomycota with endogenous hormone and soluble sugar. While Mucoromycota negatively correlated with endogenous hormone, it positively correlated with starch. Moreover, Aphelidiomycota, Blastocladiomycota, and Chytridiomycota showed significant negative correlation with shoot density, it positively correlated with endogenous hormone ($P < 0.05$, Fig. 8b).

Discussion

Variation in shoot density and biomass among four bamboo forests with different elevation

Expectedly, results indicated that shoot biomass increased at higher elevation, shoot density significantly decreased. These results suggest that shoot density and shoot biomass exhibited a trade-off relationship and environmental filtering effects, representing a coping mechanism or adaptation strategies of bamboo populations against elevation-induced environmental stressors. The results aligned with some previous studies on how elevation shapes plant community structure and adaptation strategies under contrasting gradients (Halbritter et al. 2018; Liu et al. 2020; Pfennigwerth et al. 2017).

It is widely known that plants adjust their morphological, physiological, and functional characteristics along elevational gradients by, for example, shifting resources allocation, decreasing leaf surface area, and developing extensive belowground structures (Liu et al. 2020). Such changes enable plants to survive common elevational-induced stressors such as nutrient limitation, low moisture content, and a decreased photosynthetic efficiency and carbon assimilation capacity (Sundqvist et al. 2013; Guo et al. 2018). In the present study, bamboo allocated more resources into shoot growth instead of shoot production to cope with the limited total nitrogen and carbon. Given the limited resource availability along increasing elevation and the high energy demand for developing the thick and woody stem (called culms), bamboo tend to allocate more energy to shoot growth rather than increasing shoot production (Liu et al. 2020; Yu et al. 2024a). Notably, bamboo often prefer decreasing their clonal (vegetative) growth and limit ramet density to increasing shoot growth, offering strong competitive advantage via extensive canopy formation that limits light availability for co-occurring understory communities (Liu et al. 2024). Results indicate that bamboo adopt functional trade-offs as a coping mechanisms and competitive strategies when growing under harsh environmental conditions (Akram et al. 2022; Liu et al. 2024). Thus, results consistently align with the pattern observed in the functional traits of 77 woody bamboo species in a recent study (Liu et al. 2024), revealing an evolutionary strategy in bamboo and related species (Edwards et al. 2010; Strömberg, 2011).

Variation in endogenous hormones, NSC content, and soil fungal community

Results reveal significant variation in all measured endogenous hormones in the bamboo rhizomes and shoots, exhibiting a consistent pattern in previous studies (Fahad and Bano 2012; Rahman et al. 2020). Although ABA contents were higher followed by IAA in both rhizome and shoots, contents decreased at the higher elevational plot in rhizomes than in shoots. Increased accumulation of ABA and IAA play crucial role in bamboo responses to elevational-induced stress, including low temperature and dryness (Rahman et al. 2020; Sun et al. 2025; Zandalinas et al. 2022).

Plants, especially those in mountainous and arid environments, overcome elevational stress by producing endogenous hormones (e.g., ABA and IAA), serving as regulatory and coping mechanisms to ensure growth and survival (Hirayama and Shinozaki, 2007; Santner et al. 2009; Sun et al. 2025). For instance, ABA modulate stomatal closure to avoid excessive transpiration and optimizes root growth and architecture for soil water, which is adaptation in arid environment (Rahman et al. 2020; Zhu et al. 2014). Additionally, IAA promotes nutrient acquisition in nutrient-poor soils and limits plant growth under stress to conserve limited growth resources, especially along elevational gradients (Zheng et al. 2016; Zhu et al. 2014). Indeed, exceptional accumulation of ABA and IAA in bamboo shoots and rhizomes indicate their disproportionate roles in bamboo growth, water conservation, and elevational stress adaptation. For example, increased production of IAA and ABA in woody bamboo, *Cephalostachyum pingbianense* was found to mediate clonal growth all-year round (Mao et al.

2024). As a clonal plant, bamboo underground rhizomes form a closed and interconnected network architecture, facilitating transport and parental sharing of nutrients, water, and signals within the clone (Bai et al. 2002; Fan et al. 2024).

Although results of soluble sugars showed no appreciable variations, starch content showed significant variation in shoots and rhizomes, suggesting that non-storage carbohydrates (NSC) are vital for growth, fitness, and structural defense in bamboo (Chen et al. 2025). For instance, NSC has been suggested to maintain tree survival at low temperatures at high altitudes (Clark et al. 2024). While starch content represents the inactive carbon component stored in plants, while sugar is the active form of carbon, directly playing pivotal roles in metabolic processes such as photosynthesis, biogeochemical cyclings, and plant-fungal relationship (Martinez-Vilalta et al. 2016; MacNeill et al. 2017). Also, under conditions of sugar limitation in plants, starch can be metabolized or converted into sugar or sugar to starch to support growth and energy demand under stressful conditions (Scofield et al. 2009; Cao et al. 2018).

Surprisingly, the soil fungal diversity showed no significant difference among the four bamboo forests with different elevation in the present study, which is in contrast with most previous findings that showed positive and negative effects (Li et al. 2018; Rasmussen et al. 2022; Shigyo et al. 2019), although neutral effects have also been documented (Barbi et al. 2025). As such, the majority of previous studies have proposed soil physical properties, especially temperature and soil pH (Dumbrell et al. 2010; Shigyo and Hirao 2021; Tedersoo et al. 2014; Zhao et al. 2020) as the driving mechanism for these differential responses of mycorrhizal diversity to elevational gradients. However, the present results failed to support this explanation because both soil moisture and soil pH differed significantly along elevational gradient, but did not influence mycorrhizal diversity. It is worth noting that previous studies suggest plant species identity or vegetation type underlie the variation in mycorrhizal diversity along elevation (Rasmussen et al. 2022; Saitta et al. 2018; Zhang et al. 2025). Similarly, a recent study found that soil fungal communities varied with bamboo varieties (Guo et al. 2023), while moso bamboo invasion greatly decreased root-associated soil bacterial and fungal communities (Li et al. 2022). Thus, a lack of variation in mycorrhizal fungal diversity along elevation in bamboo forests may be attributed to the bamboo species identity and its capacity to modulate the soil community composition through strong allelopathic effects from its root exudates and litter leachates (Guo et al. 2023; Wang et al. 2024), potentially restructuring the soil fungal characteristics. One caveat is that this assumption requires experimental verification as we did not analyze allelochemicals in the present study.

Relationship between plant traits, physiology, and soil fungal community

Plant functional traits are key determinant of soil functioning via influencing the soil microbial community (Adomako et al. 2022; Delgado-Baquerizo et al. 2018; Liu et al. 2020), especially the soil fungal communities due to their direct interaction with plant roots (Faucon et al. 2017). As such, plants responses to environmental cues are jointly shaped by both plant functional traits and associated microbial communities (Ma et al. 2024). However, it remains unclear how bamboo functional traits relate with soil fungi communities along elevational gradients in bamboo forest. Our results showed a strong correlation between phytohormones (e.g., GA, ABA, and IAA) and bamboo shoots in bamboo forest, consistently aligning with previous studies on plant hormonal regulatory traits (Bhandawat et al. 2017; Yu et al. 2024b; Zheng et al. 2016).

Previous studies found that shoot burst in subtropical bamboo was regulated by the IAA and GA signaling pathways (Bhandawat et al. 2017), while shoot sprouting in *Indocalamus decorus* highly correlated with ZR and IAA or ABA (Gao et al. 2018). Apart from regulating stomatal closure and plant adaptation to arid environment, ABA play vital roles during bud dormancy induction and release (Zheng et al. 2016), meanwhile IAA hormones involvement in the activity of rhizome buds in *Phyllostachys praecox* have been documented (Huang et al. 2002). Overall, these findings provide empirical evidence of the role of endogenous hormones in the development of bamboo buds and shoots, especially under elevational induced harsh conditions.

Our study demonstrated that AMF significantly correlated with six of the examined hormones in both the rhizome and shoot, except for GA_{4+7} . While alpha diversity of soil fungal communities positively correlated shoot biomass, ABA, and GA_{4+7} content in rhizome, it negatively related with shoot density. Thus, these results are consistent with previous studies on the relatedness of alpha diversity and plant functional traits along elevational gradients (Chun and Lee 2017; Merino-Martin et al. 2023; Yakimov et al. 2020). For instance, Merino-Martin et al. (2022) found that the fungal α -diversity was closely related to plant identity and belowground plant traits. Thus, the observation in previous studies and our findings are reasonable considering the close association of AMF and plant hormonal regulation of rhizome or root traits. Furthermore, previous studies showed that AMF symbiosis altered plant phytohormonal levels, with ABA content significantly increasing in roots after mycorrhizal formation (Ma et al. 2022; Wang et al. 2024). Also, inoculated with AMF significantly decreased the concentration of IAA than IAA concentrations of uninoculated plants in controlled treatments (Meixner et al. 2005), suggesting that plant endogenous hormones and the soil fungal communities may jointly shape bamboo responses to elevational-induced stressors in bamboo ecosystems.

Regarding fungal taxa, Ascomycota was the most common and abundant phyla in bamboo soils, possessing more than 50% relative abundance in each sampling plots. Notably Ascomycota phylum contains a wide diversity of fungal taxa, ranging from pathogens to mutualists, collectively and ecological functioning as a unit (Fuke et al. 2021; Zhao et al. 2024). This suggests that Ascomycota may negatively impacts phytohormones, possibly explaining the inhibitory effects on endogenous hormone production, which may be partly caused by the emergence and pathogen accumulation in bamboo forest (Nett et al. 2022; Shao et al. 2024). The second most common phylum of soil fungi observed in the bamboo forest was Basidiomycota. The phyla Basidiomycota has the capacity to increase endogenous hormone levels by breaking down organic matter and root secretions (Lakshmipathi et al. 2019), aligning with our study findings that its abundance promotes endogenous hormone production. Together, Ascomycota and Basidiomycota are saprotrophs that uses organic matter, carbon sources, and plant root residue as primary energy sources (Clemmensen et al. 2013), buffering the resilience of bamboo forest against elevational induced pressures in montane regions.

Conclusions

Results of this study indicated that bamboo adopts functional trade-offs and environmental filtering effects as coping mechanisms when growing under harsh environmental conditions by decreasing shoot density but rather increase shoot biomass, especially along elevational gradients. Significant accumulation and changes in endogenous hormones, e.g., ABA and IAA, and non-structural carbon (NSC) with increasing elevation provide empirical

evidence of their disproportionate roles in bamboo growth, water conservation, and elevational stress adaptation. Soil fungal diversity showed no significant variation along elevation gradients, had greater abundance of the phyla Ascomycota and Basidiomycota (i.e., saprotrophs), and exhibited significant positive relationships with phytohormones and bamboo traits, overall suggesting that plant endogenous hormones and specific fungal communities but not their diversity may jointly shape bamboo responses to elevational-induced stressors in bamboo ecosystems.

Declarations

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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References

1. Adomako MO, Wu J, Yu FH (2025) Ecological and evolutionary responses of earthworm holobionts to environmental changes. *ISME J* 19: wraf044. <https://doi.org/10.1093/ismejo/wraf044>
2. Adomako MO, Xue W, Du DL, Yu FH (2022) Soil microbe-mediated N:P stoichiometric effects on *Solidago canadensis* performance depend on nutrient levels. *Microb Ecol* 83: 960-970. <https://doi.org/10.1007/s00248-021-01814-8>
3. Akram MA, Zhang Y, Wang X, Shrestha N, Malik K, Khan I, Deng J (2022) Phylogenetic independence in the variations in leaf functional traits among different plant life forms in an arid environment. *J Plant Physiol* 272: 153671. <https://doi.org/10.1016/j.jplph.2022.153671>
4. Bai Y, Cai M, Mu C, Cheng W, Zheng H, Cheng Z, Li J, Mu S, Gao J (2022) New insights into the local auxin biosynthesis and its effects on the rapid growth of Moso bamboo (*Phyllostachys edulis*). *Front Plant Sci* 13: 858686. <https://doi.org/10.3389/fpls.2022.858686>
5. Barbi F, Martinović T, Odriozola I, Machac A, Moravcová A, Algora C, Kohout P (2025) Disentangling drivers behind fungal diversity gradients along altitude and latitude. *New Phytol*. <https://doi.org/10.1111/nph.70012>
6. Bhandawat A, Singh G, Seth R, Singh P, Sharma R (2017) Genomewide transcriptional profiling to elucidate key candidates involved in bud burst and rattling growth in a subtropical bamboo (*Dendrocalamus hamiltonii*). *Front Plant Sci* 7: 2038. <https://doi.org/10.3389/fpls.2016.02038>
7. Brundrett MC, Tedersoo L (2018) Evolutionary history of mycorrhizal symbioses and global host plant diversity. *New Phytol* 220: 1108-1115. <https://doi.org/10.1111/nph.14976>
8. Cao Y, Li YA, Chen YM (2018) Non-structural carbon, nitrogen and phosphorus between black locust and Chinese pine plantations along a precipitation gradient on the Loess Plateau, China. *Trees* 32: 835-846. <https://doi.org/10.1007/s00468-018-1676-1>
9. Caporaso JG, Kuczynski J, Stombaugh J, Bittinger K, Bushman FD, Costello EK, Fierer N, Peña AG, Goodrich JK, Gordon JI (2010) QIIME allows analysis of high-throughput community sequencing data. *Nat Methods* 7: 335-336. <https://doi.org/10.1038/nmeth.f.303>
10. Chang EH, Chiu CY (2015) Changes in soil microbial community structure and activity in a cedar plantation invaded by moso bamboo. *Appl Soil Ecol* 91: 1-7. <https://doi.org/10.1016/j.apsoil.2015.02.001>
11. Chen JG, Cheng SH, Cao W, Zhou X (1998) Involvement of endogenous plant hormones in the effect of mixed nitrogen source on growth and tillering of wheat. *J Plant Nutr* 21: 87-97. <https://doi.org/10.1080/01904169809365385>
12. Chen S, Zhao H, Zou C, Li Y, Chen Y, Wang Z (2017) Combined inoculation with multiple arbuscular mycorrhizal fungi improves growth, nutrient uptake and photosynthesis in cucumber seedlings. *Front Microbiol* 8: 2516. <https://doi.org/10.3389/fmicb.2017.02516>
13. Chen Y, Tang M, Song YC, Zargar M, Chen MX, Lin SY, Song T (2025) Unlocking bamboo's fast growth: Exploring the vital role of non-structural carbohydrates (NSCs). *Plant J* 122: e70147. <https://doi.org/10.1111/tbj.70147>
14. Chun JH, Lee CB (2017) Disentangling the local-scale drivers of taxonomic, phylogenetic and functional diversity in woody plant assemblages along elevational gradients in South Korea. *PLoS One* 12: e0185763. <https://doi.org/10.1371/journal.pone.0185763>
15. Clark CM, Coughlin JG, Phelan J, Martin G, Austin K, Salem M, Sabo RD, Horn K, Thomas RQ, Dalton RM (2024) Winners and Losers From Climate Change: An Analysis of Climate Thresholds for Tree Growth and Survival for Roughly 150 Species Across the Contiguous United States. *Glob Chang Biol* 30: e17597. <https://doi.org/10.1111/gcb.17597>
16. Clemmensen KE, Bahr A, Ovaskainen O, Dahlberg A, Ekblad A, Wallander H, Lindahl BD (2013) Roots and associated fungi drive long-term carbon sequestration in boreal forest. *Science* 339: 1615-1618. <https://doi.org/10.1126/science.1231923>
17. Delgado-Baquerizo M, Fry EL, Eldridge DJ, de Vries FT, Manning P, Hamonts K, Bardgett RD (2018) Plant attributes explain the distribution of soil microbial communities in two contrasting regions of the globe. *New Phytol* 219: 574-587. <https://doi.org/10.1111/nph.15161>
18. Dumbrell AJ, Nelson M, Helgason T, Dytham C, Fitter AH (2010) Relative roles of niche and neutral processes in structuring a soil microbial community. *ISME J* 4: 337-345. <https://doi.org/10.1038/ismej.2009.122>
19. Edwards EJ, Osborne CP, Strömberg CAE, Smith SA, Consortium CG, Bond WJ, Tiplle B (2010) The origins of C4 grasslands: integrating evolutionary and ecosystem science. *Science* 328: 587-591. <https://doi.org/10.1126/science.1177216>

20. Edgar RC, Haas BJ, Clemente JC, Quince C, Knight R (2011) UCHIME improves sensitivity and speed of chimera detection. *Bioinformatics* 27: 2194-2200. <https://doi.org/10.1093/bioinformatics/btr381>
21. Edgar RC (2013) UPARSE: Highly accurate OTU sequences from microbial amplicon reads. *Nat Methods* 10: 996-998. <https://doi.org/10.1093/bioinformatics/btr381>
22. Fahad S, Bano A (2012) Ethnobotanical and physiological studies of some endangered plant species collected from two different altitudes in Gilgit Baltistan. *Pak J Bot* 44: 165-170
23. Fan LL, Chen SL, Cai ZM, Guo ZW, Yang J, Zheng R, Hu RC (2024) Expansion of *Pleiblastus amarus* in tea plantations significantly enhances the appearance and nutritional composition of bamboo shoots but adversely affects palatability. *BMC Plant Biol* 24: 1161. <https://doi.org/10.1186/s12870-024-05856-1>
24. Faucon MP, Houben D, Lambers H (2017) Plant functional traits: Soil and ecosystem services. *Trends Plant Sci* 22: 385-394. <https://doi.org/10.1016/j.tplants.2017.01.005>
25. Fuke P, Mohan MT, Kumar M, Sawarkar AD, Pandey A, Singh L (2021) Role of microbial diversity to influence the growth and environmental remediation capacity of bamboo: A review. *Ind Crop Prod* 167: 113567. <https://doi.org/10.1016/j.indcrop.2021.113567>
26. Gao G, Zhong H, Wu Z, Li N, Zhong Z, Pan Y, Wu L (2018) Effects of key growth conditions on endogenous hormone content in tillering stem bases, germination of lateral buds, and biomass allocation in *Indocalamus decorus*. *J For Res* 29: 1547-1555. <https://doi.org/10.1007/s11676-017-0577-2>
27. Guo W, Zhang J, Li MH, Qi L (2023) Soil fungal community characteristics vary with bamboo varieties and soil compartments. *Front Microbiol* 14: 1120679. <https://doi.org/10.3389/fmicb.2023.1120679>
28. Guo Z, Chen S, Xiao J (2011) Organochlorine pesticide residues in bamboo shoot. *J Sci Food Agric* 91: 593-6
29. Guo Z, Lin H, Chen S, Yang Q (2018) Altitudinal Patterns of Leaf Traits and Leaf Allometry in Bamboo *Pleiblastus amarus*. *Front Plant Sci* 9: 1110. <https://doi.org/10.1002/jsfa.4233>
30. Guo Z, Yang L, Lin H, Chen S, Yang Q (2019) Effects of altitude on the variation of appearance, nutrition, and taste for bamboo shoots of *Pleiblastus amarus* in Shaxian, Fujian Province. *Chin J Appl Ecol* 38: 83-33
31. Halbritter AH, Fior S, Keller I, Billeter R, Edwards PJ, Holderegger R, Alexander JM (2018) Trait differentiation and adaptation of plants along elevation gradients. *J Evol Biol* 31: 784-800. <https://doi.org/10.1111/jeb.13262>
32. Hirayama T, Shinozaki K (2007) Perception and transduction of abscisic acid signals: keys to the function of the versatile plant hormone ABA. *Trends Plant Sci* 12: 343-351. <https://doi.org/10.1016/j.tplants.2007.06.013>
33. Huang J, Liu L, Zhang B, Qiu L (2002) Dynamic changes of endophyt hormone in rhizomal buds of *Phyllostachys praecox*. *Sci Silvae Sin* 38: 38-41
34. Jiang F, Zhang L, Zhou J, George TS, Feng G (2021) Arbuscular mycorrhizal fungi enhance mineralisation of organic phosphorus by carrying bacteria along their extraradical hyphae. *New Phytol* 230: 304-315. <https://doi.org/10.1111/nph.17081>
35. Jiang W, Gou G, Ding Y (2013) Influences of arbuscular mycorrhizal fungi on growth and mineral element absorption of chenglu hybrid bamboo seedlings. *Pak J Bot* 45: 303-310
36. Kiba T, Kudo T, Kojima M, Sakakibara H (2011) Hormonal control of nitrogen acquisition: roles of auxin, abscisic acid, and cytokinin. *J Exp Bot* 62: 1399-1409. <https://doi.org/10.1093/jxb/erq410>
37. Lakshmipathi RN, Subramanyam B, Narotham Prasad BD (2019) Microorganisms, Organic Matter Recycling and Plant Health. In: Ansari R, Mahmood I (eds) *Plant Health Under Biotic Stress*. Springer, Singapore
38. Li S, Xie D, Ge X, Dong W, Luan J (2022) Altered diversity and functioning of soil and root-associated microbiomes by an invasive native plant. *Plant Soil* 473: 235-249. <https://doi.org/10.1007/s11104-022-05338-z>
39. Li X, Xu M, Christie P, Li X, Zhang J (2018) Large elevation and small host plant differences in the arbuscular mycorrhizal communities of montane and alpine grasslands on the Tibetan Plateau. *Mycorrhiza* 28: 1-15. <https://doi.org/10.1007/s00572-018-0850-z>
40. Li XL, Xu M, Li XL, Christie P, Wagg C, Zhang JL (2020) Linkages between changes in plant and mycorrhizal fungal community composition at high versus low elevation in alpine ecosystems. *Environ Microbiol* 12: 229-240. <https://doi.org/10.1111/1758-2229.12837>
41. Liu W, Zheng L, Qi D (2020) Variation in leaf traits at different altitudes reflects the adaptive strategy of plants to environmental changes. *Ecol Evol* 10: 8166-8175. <https://doi.org/10.1002/ece3.6519>
42. Liu X, Zhou S, Hu J, Zou X, Tie L, Li Y, Peñuelas J (2024) Variations and trade-offs in leaf and culm functional traits among 77 woody bamboo species. *BMC Plant Biol* 24: 387. <https://doi.org/10.1186/s12870-024-05108-2>
43. Luan J, Li S, Dong W, Liu Y, Wang Y, Liu S (2021) Litter decomposition affected by bamboo expansion is modulated by litter-mixing and microbial composition. *Funct Ecol* 35: 2562-2574. <https://doi.org/10.1111/1365-2435.13911>
44. Luo W, Zhang Q, Wang P, Luo J, She C, Guo X, Tao J (2024) Unveiling the impacts moso bamboo invasion on litter and soil properties: A meta-analysis. *Sci Total Environ* 909: 168532. <https://doi.org/10.1016/j.scitotenv.2023.168532>
45. Lugo MA, Ferrero M, Menoyo E, Estévez MC, Siñeriz F, Anton A (2008) Arbuscular Mycorrhizal Fungi and Rhizospheric Bacteria Diversity Along an Altitudinal Gradient in South American Puna Grassland. *Microb Ecol* 55: 705-713. <https://doi.org/10.1007/s00248-007-9313-3>
46. Ma JG, Wang XB, Hou FJ (2024) A general pattern of plant traits and their relationships with environmental factors and microbial life-history strategies. *Sci Total Environ* 931: 172670. <https://doi.org/10.1016/j.scitotenv.2024.172670>
47. Ma Z, Zhao X, He A, Cao Y, Han Q, Lu Y (2022) Mycorrhizal symbiosis reprograms ion fluxes and fatty acid metabolism in wild jujube during salt stress. *Plant Physiol* 189: 2481-2499. <https://doi.org/10.1093/plphys/kiac239>

48. MacNeill GJ, Mehrpouyan S, Minow MAA, Patterson JA, Tetlow IJ, Emes MJ (2017) Starch as a source, starch as a sink: the bifunctional role of starch in carbon allocation. *J Exp Bot* 68: 4433-4453. <https://doi.org/10.1093/jxb/erx291>
49. Mao W, Bao C, Cheng Q, Liang N, Wang L, Yang H (2024) All-Year High IAA and ABA Contents in Rhizome Buds May Contribute to Natural Four-Season Shooting in Woody Bamboo **Cephalostachyum pingbianense**. *Plants-Basel* 13: 410. <https://doi.org/10.3390/plants13030410>
50. Martinez-Vilalta J, Sala A, Asensio D, Galiano L, Hoch G, Palacio S, Piper FI, Lloret F (2016) Dynamics of non-structural carbohydrates in terrestrial plants: a global synthesis. *Ecol Monogr* 86: 495-516. <https://doi.org/10.1002/ecm.1231>
51. Merino-Martín L, Hernández-Cáceres D, Reverchon F, Angeles-Alvarez G, Zhang G, Dunoyer de Segonzac D, Stokes A (2023) Habitat partitioning of soil microbial communities along an elevation gradient: from plant root to landscape scale. *Oikos* 2023: e09034. <https://doi.org/10.1111/oik.09034>
52. Meixner C, Ludwig-Müller J, Miersch O, Gresshoff P, Staehelin C, Vierheilig H (2005) Lack of mycorrhizal autoregulation and phytohormonal changes in the supernodulating soybean mutant nts1007. *Planta* 222: 709-715. <https://doi.org/10.1007/s00425-005-0003-4>
53. Nett RS, Bender KS, Peters RJ (2022) Production of the plant hormone gibberellin by rhizobia increases host legume nodule size. *ISME J* 16: 1809-1817. <https://doi.org/10.1038/s41396-022-01236-5>
54. Oita S, Ibáñez A, Lutzoni F, Miadlikowska J, Geml J, Lewis LA, Arnold AE (2021) Climate and seasonality drive the richness and composition of tropical fungal endophytes at a landscape scale. *Commun Biol* 4: 313. <https://doi.org/10.1038/s42003-021-01826-7>
55. Pfennigwerth AA, Bailey JK, Schweitzer JA (2017) Trait variation along elevation gradients in a dominant woody shrub is population-specific and driven by plasticity. *Aob Plants* 9: plx027. <https://doi.org/10.1093/aobpla/plx027>
56. Rahman IU, Afzal A, Iqbal Z, Hart R, Abd_Allah EF, Alqarawi AA, Bussmann RW (2020) Response of plant physiological attributes to altitudinal gradient: Plant adaptation to temperature variation in the Himalayan region. *Sci Total Environ* 706: 135714. <https://doi.org/10.1016/j.scitotenv.2019.135714>
57. Rasmussen PU, Abrego N, Roslin T, Öpik M, Sepp SK, Blanchet FG, Tack AJM (2022) Elevation and plant species identity jointly shape a diverse arbuscular mycorrhizal fungal community in the High Arctic. *New Phytol* 236: 671-683. <https://doi.org/10.1111/nph.18342>
58. Saitta A, Anslan S, Bahram M, Brocca L, Tedersoo L (2018) Tree species identity and diversity drive fungal richness and community composition along an elevational gradient in a Mediterranean ecosystem. *Mycorrhiza* 28: 39-47. <https://doi.org/10.1007/s00572-017-0806-8>
59. Santner A, Calderon-Villalobos LIA, Estelle M (2009) Plant hormones are versatile chemical regulators of plant growth. *Nat Chem Biol* 5: 301-307. <https://doi.org/10.1038/nchembio.165>
60. Scofield GN, Ruuska SA, Aoki N, Lewis DC, Tabe LM, Jenkins CLD (2009) Starch storage in the stems of wheat plants: localization and temporal changes. *Ann Bot* 103: 859-868. <https://doi.org/10.1093/aob/mcp010>
61. Shao QY, Ran QS, Li X, Dong CB, Huang JZ, Han YF (2024) Deciphering the effect of phytohormones on the phyllosphere microbiota of **Eucommia ulmoides**. *Microbiol Res* 278: 127513. <https://doi.org/10.1016/j.micres.2023.127513>
62. Shen C, Ni Y, Liang W, Wang J, Chu H (2015) Distinct soil bacterial communities along a small-scale elevational gradient in alpine tundra. *Front Microbiol* 6: 582. <https://doi.org/10.3389/fmicb.2015.00582>
63. Shigyo N, Hirao T (2021) Saprotrophic and ectomycorrhizal fungi exhibit contrasting richness patterns along elevational gradients in cool-temperate montane forests. *Fungal Ecol* 50: 101036. <https://doi.org/10.1016/j.funeco.2020.101036>
64. Sundqvist MK, Sanders NJ, Wardle DA (2013) Community and ecosystem responses to elevational gradients: processes, mechanisms, and insights for global change. *Annu Rev Ecol Evol S* 44: 261-280. <https://doi.org/10.1146/annurev-ecolsys-110512-135750>
65. Shigyo N, Umeki K, Hirao T (2019) Plant functional diversity and soil properties control elevational diversity gradients of soil bacteria. *FEMS Microbiol Ecol* 95: fiz025. <https://doi.org/10.1093/femsec/fiz025>
66. Smith SE, Read DJ (1997) *Mycorrhizal Symbiosis*. Academic Press, San Diego.
67. Strömberg CAE (2011) Evolution of grasses and grassland ecosystems. *Annu Rev Earth Planet Sci* 39: 517-544. <https://doi.org/10.1146/annurev-earth-040809-152402>
68. Sun P, Hao R, Fan F, Wang Y, Zhu F (2025) Adaptation of high-altitude plants to plateau abiotic stresses: A case study of the Qinghai-Tibet Plateau. *Int J Mol Sci* 26: 2292. <https://doi.org/10.3390/ijms26052292>
69. Tedersoo L, Bahram M, Põlme S, Kõljalg U, Yorou NS, Wijesundera R, Abarenkov K (2014) Global diversity and geography of soil fungi. *Science* 346: 1256688. <https://doi.org/10.1126/science.1256688>
70. Van Dam JE, Elbersen HW, Montaña CMD (2018) Bamboo production for industrial utilization. In: Alexopoulou E (ed) *Perennial grasses for bioenergy and bioproducts*. *Ann N Y Acad Sci*: 175-216. (Note: Specific volume/page range for the chapter within the series volume is often omitted in this format unless it's a journal article. Page range included as per source).
71. Větrovský T, Kohout P, Kopecký M, Machac A, Man M, Bahnmann BD, Baldrian P (2019) A meta-analysis of global fungal distribution reveals climate-driven patterns. *Nat Commun* 10: 5142. <https://doi.org/10.1038/s41467-019-13164-8>
72. Wang A, Huang K, Ning Y, Bi Y (2024) Allelochemicals from moso bamboo: Identification and their effects on neighbor species. *Forests* 15: 2040. <https://doi.org/10.3390/f15112040>
73. Wang Q, Liu M, Wang Z, Li J, Liu K, Huang D (2024) The role of arbuscular mycorrhizal symbiosis in plant abiotic stress. *Front Microbiol* 14: 1323881. <https://doi.org/10.3389/fmicb.2023.1323881>
74. Wagg C, Jansa J, Stadler M, Schmid B, Van Der Heijden MGA (2011) Mycorrhizal fungal identity and diversity relaxes plant-plant competition. *Ecology* 92: 1303-1313. <https://doi.org/10.1890/10-1915.1>
75. Wei W, Yang M, Liu Y, Huang H, Ye C, Zheng J, Guo C, Hao M, He X, Zhu S (2018) Fertilizer N application rate impacts plant-soil feedback in a sanqi production system. *Sci Total Environ* 633: 796-807. <https://doi.org/10.1016/j.scitotenv.2018.03.219>

76. Wilson GWT, Rice CW, Rillig MC, Springer A, Hartnett DC (2009) Soil aggregation and carbon sequestration are tightly correlated with the abundance of arbuscular mycorrhizal fungi: results from long-term field experiments. *Ecol Lett* 12: 452-461. <https://doi.org/10.1111/j.1461-0248.2009.01303.x>
77. Wu QS, Cao MQ, Zou YN, He XH (2014) Direct and indirect effects of glomalin, mycorrhizal hyphae, and roots on aggregate stability in rhizosphere of trifoliate orange. *Sci Rep* 4: 5823. <https://doi.org/10.1038/srep05823>
78. Yakimov BN, Gerasimova AS, Zhang S, Ma K, Zhang Y (2020) Phylogenetic α - and β -diversity elevational gradients reveal consistent patterns of temperate forest community structure. *Acta Oecol* 109: 103657. <https://doi.org/10.1016/j.actao.2020.103657>
79. Xiao LD, Li C, Cai Y, Zhou MX, Zhou T, Gao XY, Du HQ, Zhou YF, Zhou GM (2021) Preliminary application of ground-penetrating radar for reconstruction of root system architecture in moso bamboo. *Remote Sens* 13: 2816. <https://doi.org/10.3390/rs13142816>
80. Xu M, Zhuang S, Gui R (2017) Soil hypoxia induced by an organic-material mulching technique stimulates the bamboo rhizome up-floating of *Phyllostachys praecox*. *Sci Rep* 7: 14353. <https://doi.org/10.1038/s41598-017-14798-8>
81. Xu M, Li X, Cai X, Gai J, Li X, Peter C, Zhang J (2014) Soil microbial community structure and activity along a montane elevational gradient on the Tibetan Plateau. *Eur J Soil Biol* 64: 6-14. <https://doi.org/10.1016/j.ejsobi.2014.06.002>
82. Yu H, Le X, Peñuelas J, Sardans J, Xu C, Zou Y, Zhong Q (2024a) Trait divergence and opposite above- and below-ground strategies facilitate moso bamboo invasion into subtropical evergreen broadleaf forest. *Front Plant Sci* 15: 1410372. <https://doi.org/10.3389/fpls.2024.1410372>
83. Yu M, Shi W, Liang Y, Shabala S (2024b) Hormonal regulation of plant adaptation to hostile soils. *Plant Soil* 505: 1-5. <https://doi.org/10.1007/s11104-024-07065-z>
84. Zandalinas SI, Balfagón D, Gómez-Cadenas A, Mittler R (2022) Plant responses to climate change: metabolic changes under combined abiotic stresses. *J Exp Bot* 73: 3339-3354. <https://doi.org/10.1093/jxb/erac073>
85. Zhang Z, Lu Y, Li L, Zeng F, Li X, Li L, Yue J (2025) Elevational patterns in the diversity and composition of soil archaeal and bacterial communities depend on climate, vegetation, and soil properties in an arid mountain ecosystem. *CATENA* 249: 108679. <https://doi.org/10.1016/j.catena.2024.108679>
86. Zhao F, Feng X, Guo Y, Ren C, Wang J, Doughty R (2020) Elevation gradients affect the differences of arbuscular mycorrhizal fungi diversity between root and rhizosphere soil. *Agric For Meteorol* 284: 107894. <https://doi.org/10.1016/j.agrformet.2019.107894>
87. Zhan H, He W, Li M, Yu L, Li J, Wang C, Wang S (2022) The Dynamics of Non-Structural Carbohydrates in Different Types of Bamboo in Response to Their Phenological Variations: Implications for Managing Bamboo Plantations. *Forests* 13: 1218. <https://doi.org/10.3390/f13081218>
88. Zhang Q, Wang S, Xie Q, Xia Q, Lu L, Wang M (2023) Control of arbuscule development by a transcriptional negative feedback loop in *Medicago*. *Nat Commun* 14: 5743. <https://doi.org/10.1038/s41467-023-41493-2>
89. Zhang T, Feng G (2021) Arbuscular mycorrhizal fungi alleviate the negative effects of increases in phosphorus (P) resource diversity on plant community structure by improving P resource utilization. *Plant Soil* 461: 295-307. <https://doi.org/10.1007/s11104-020-04825-5>
90. Zhao ZY, Mu TC, Keyhani NO, Pu HL, Lin YS, Lv ZY, Xiong JM, Chen XH, Zhan XY, Lv HJ, Jibola-Shittu MY, Jia PS, Wu JL, Huang SS, Qiu JZ, Guan XY (2024) Diversity and New Species of Ascomycota from Bamboo in China. *J Fungi* 10: 454. <https://doi.org/10.3390/jof10070454>
91. Zheng Z, Guo Y, Novák O, Chen W, Ljung K, Noel JP, Chory J (2016) Local auxin metabolism regulates environment-induced hypocotyl elongation. *Nat Plants* 2: 16025. <https://doi.org/10.1038/NPLANTS.2016.25>
92. Zhu WZ, Wang SG, Yu DZ, Jiang Y, Li MH (2014) Elevational patterns of endogenous hormones and their relation to resprouting ability of *Quercus aquifolioides* plants on the eastern edge of the Tibetan Plateau. *Trees* 28: 359-372. <https://doi.org/10.1007/s00468-013-0954-1>
93. Zuo K, Fan L, Guo Z, Zhang L, Duan Y, Zhang J (2024) High nutrient utilization and resorption efficiency promote bamboo expansion and invasion. *J Environ Manage* 362: 121370. <https://doi.org/10.1016/j.jenvman.2024.121370>
94. Zuo KY, Fan LL, Guo ZW, Zhang JR, Duan YY, Zhang L, Chen SL, Lin H, Hu R (2024) Aboveground Biomass Component Plasticity and Allocation Variations of Bamboo (*Pleioblastus amarus*) of Different Regions. *Forests* 15: 43. <https://doi.org/10.3390/f15010043>
95. Zobel M, Koorem K, Moora M, Semchenko M, Davison J (2024) Symbiont plasticity as a driver of plant success. *New Phytol* 241: 2340-2352. <https://doi.org/10.1111/nph.19566>

Figures

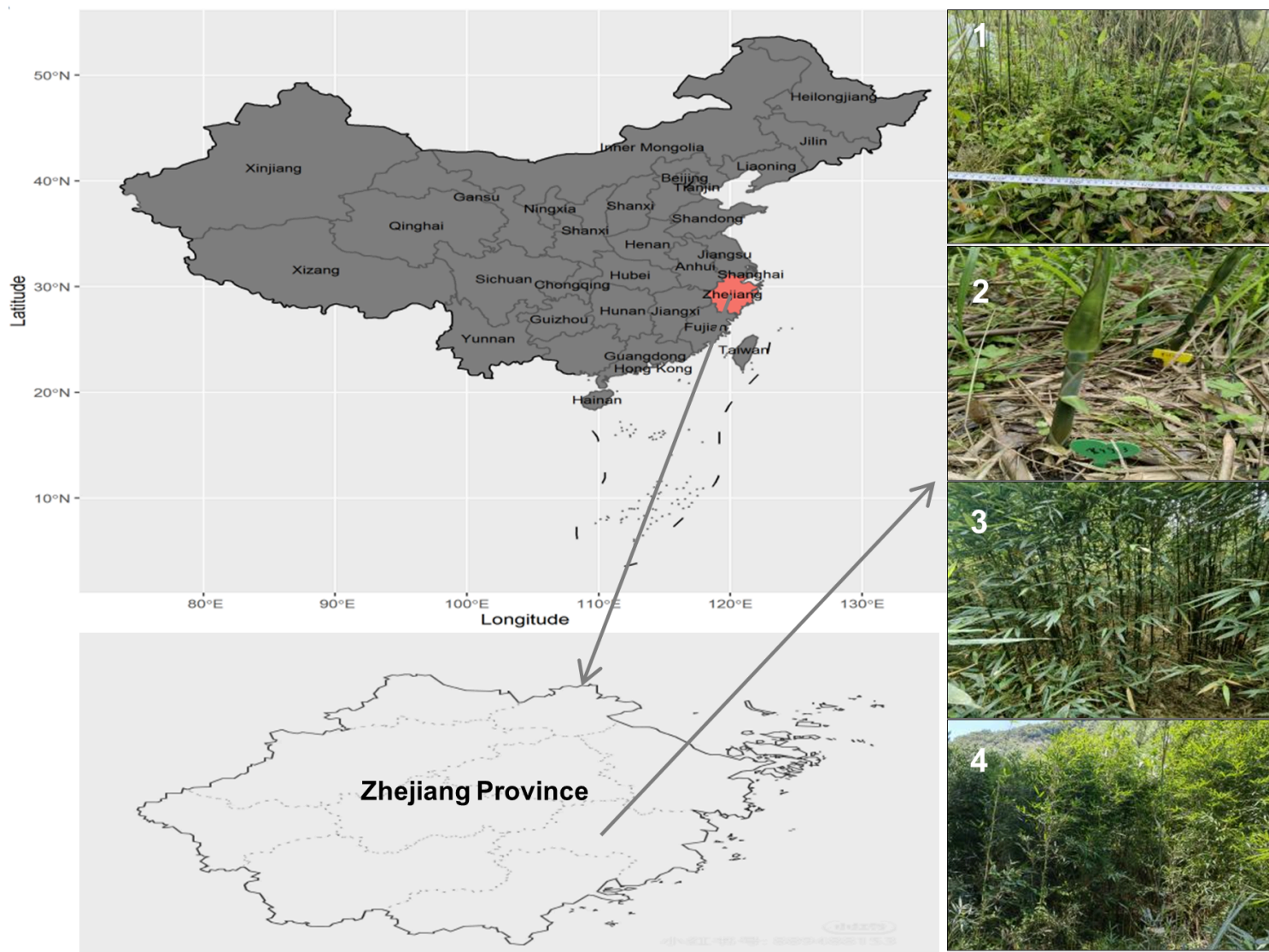


Figure 1

Pictures of the sampling sites along the increasing elevation.

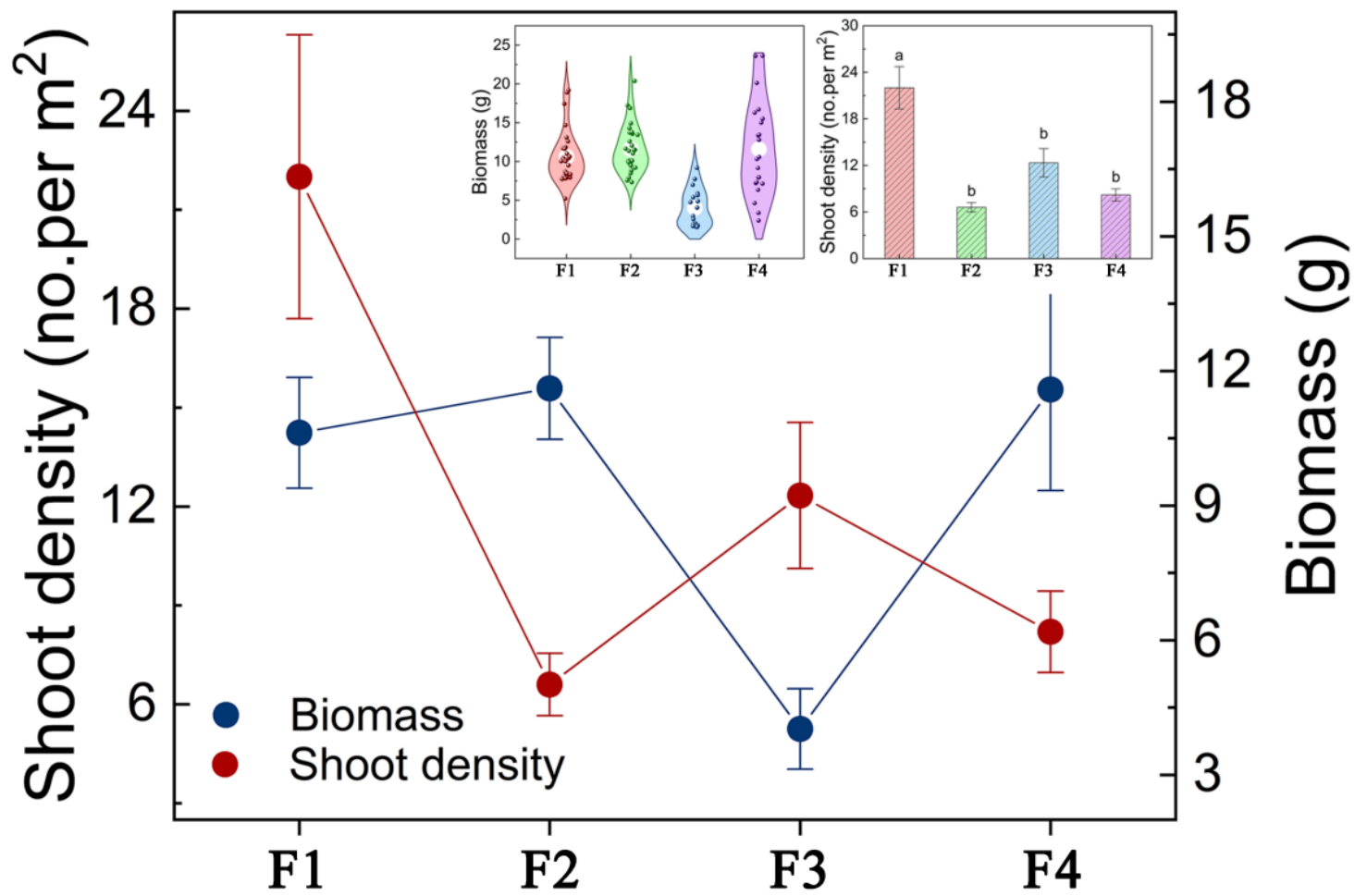


Figure 2

The changes of shoot biomass and shoot density of *P. amarus* along the increasing elevation. Different lowercase letters indicate a significant difference at the 0.05 level. Bars represent error bars.

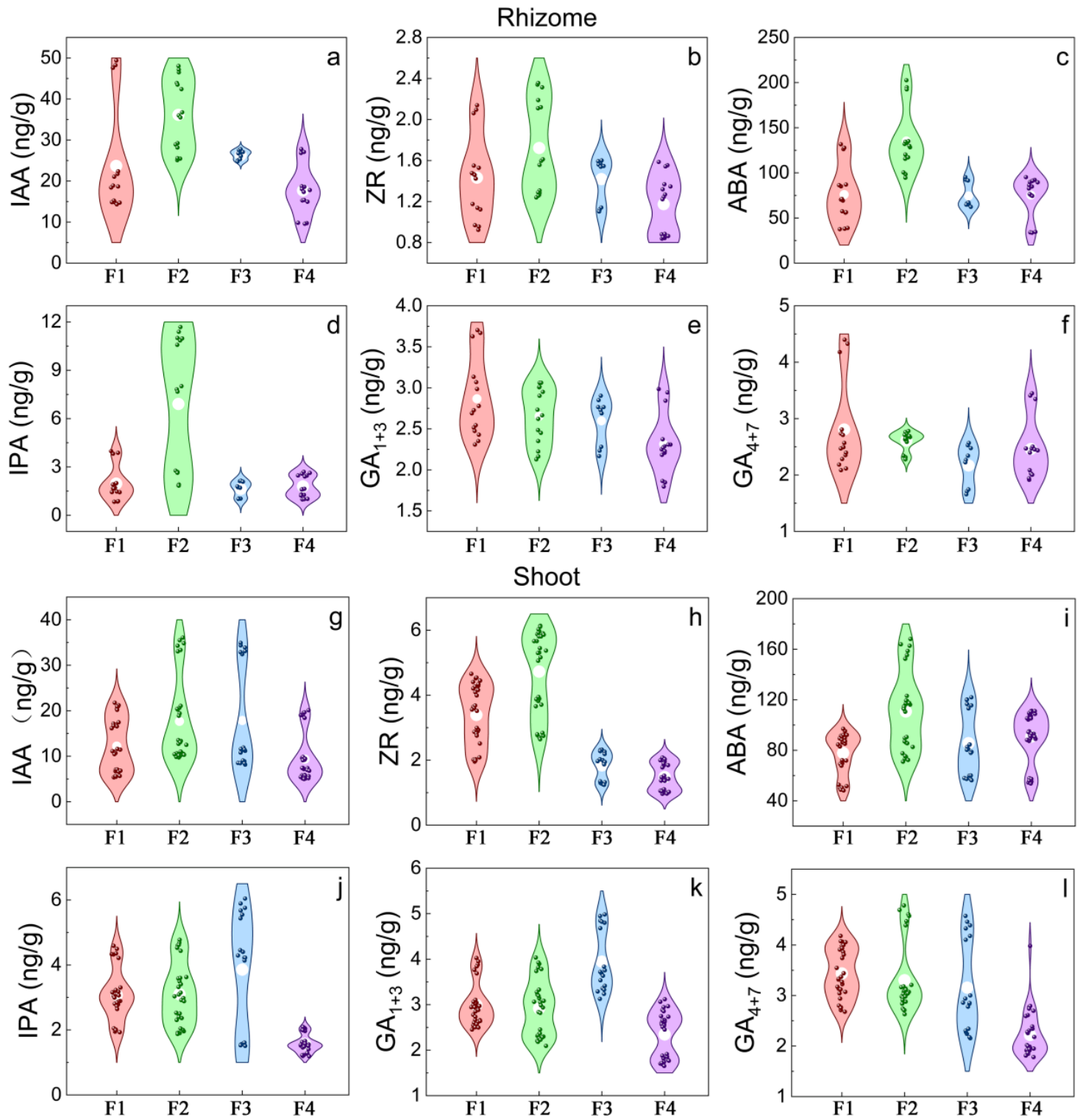


Figure 3

Changes of endogenous hormone contents of *P. amarus* in rhizome and shoot along the increasing elevation. IAA, indoleacetic acid; ZR, zeatin riboside; ABA, abscisic acid; IPA, indolepropionic acid; GA, gibberellins acid.

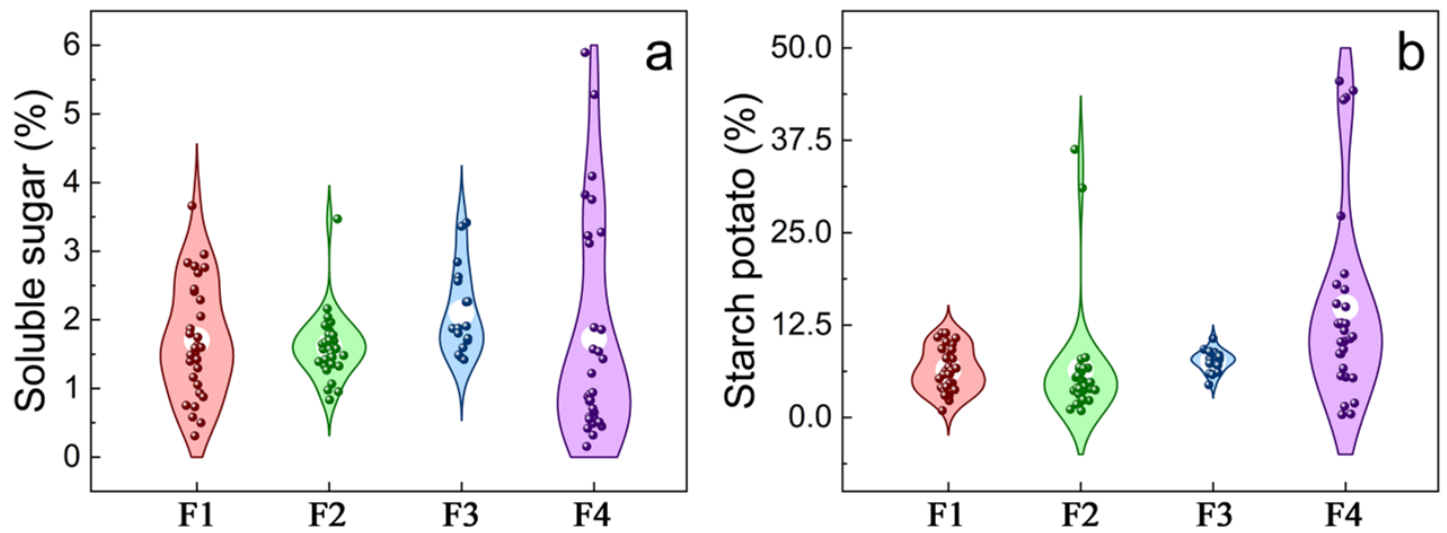


Figure 4

The changes of soluble sugar content and starch content contents of *P. amarus* in shoot along the increasing elevation.

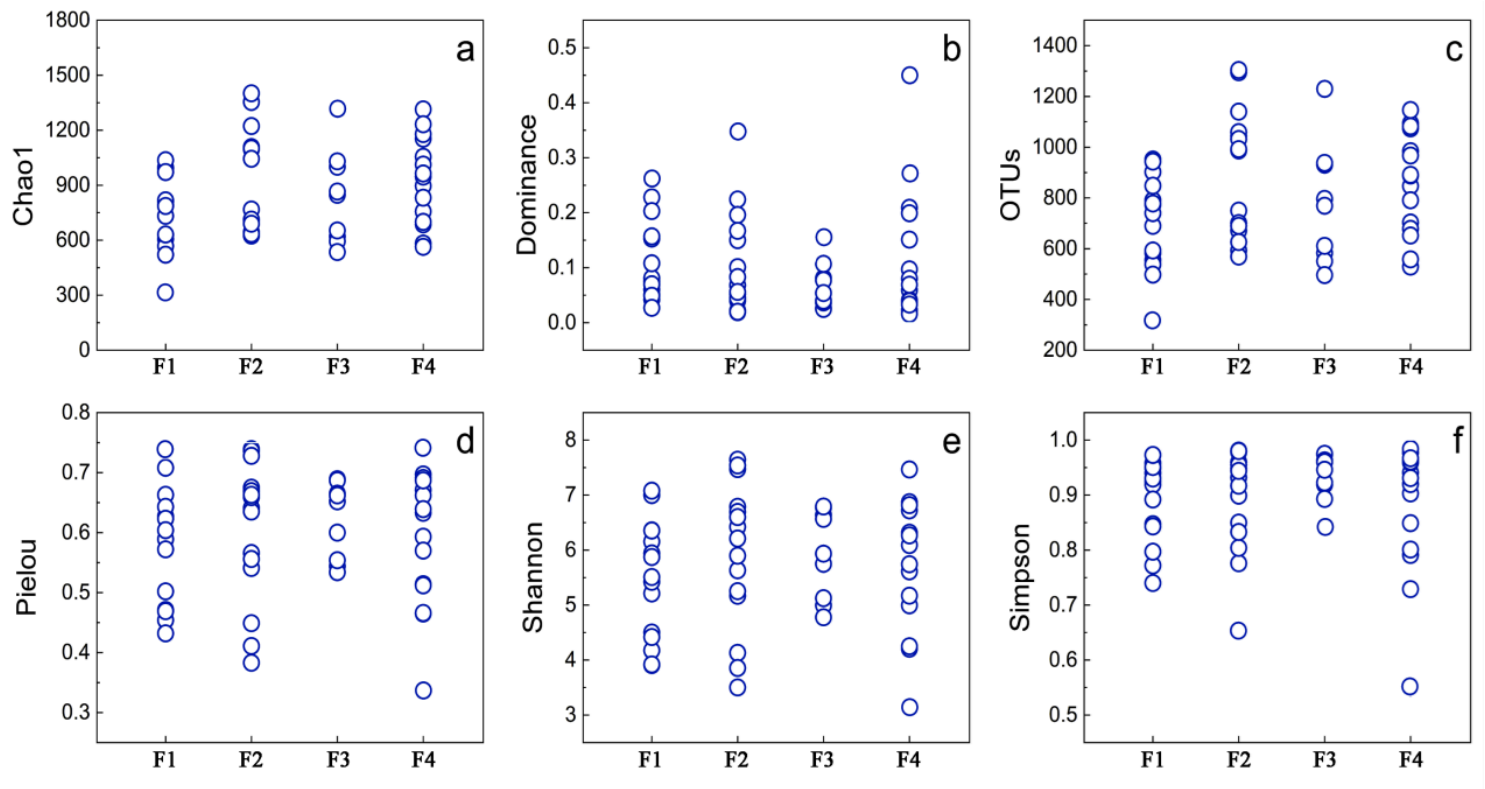


Figure 5

The change of Chao1, Dominance, OTUs, Shannon, Simpson and Pielou indices of soil fungal communities (a–f) along the increasing elevation.

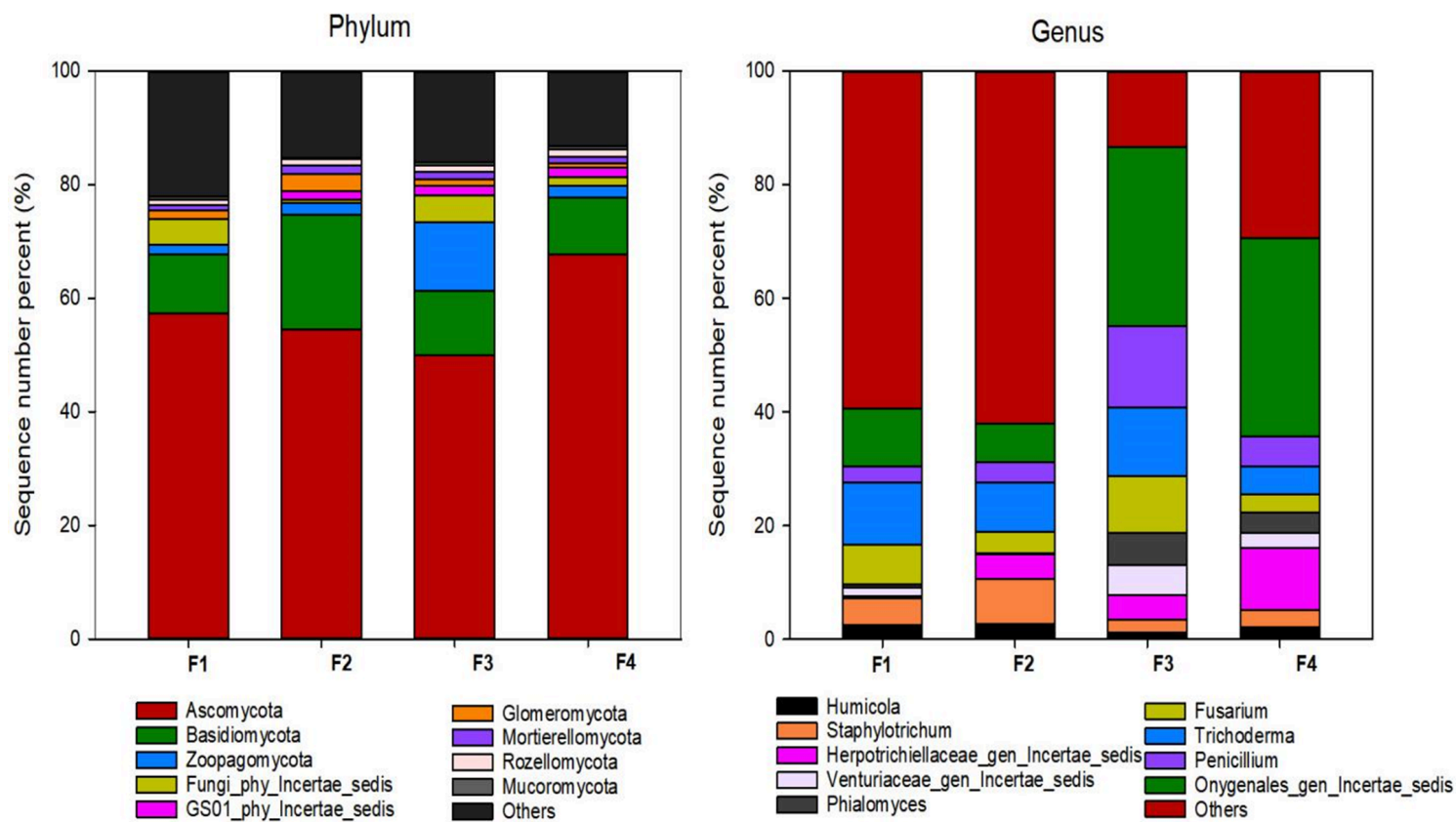


Figure 6

The change of Chao1, Dominance, OTUs, Shannon, Simpson and Pielou indices of soil fungal communities (a–f) along the increasing elevation. Figure 6 Relative abundance of the 10 most abundant phyla of soil fungi and the 20 most abundant genera of soil fungi under the communities along the increasing elevation.

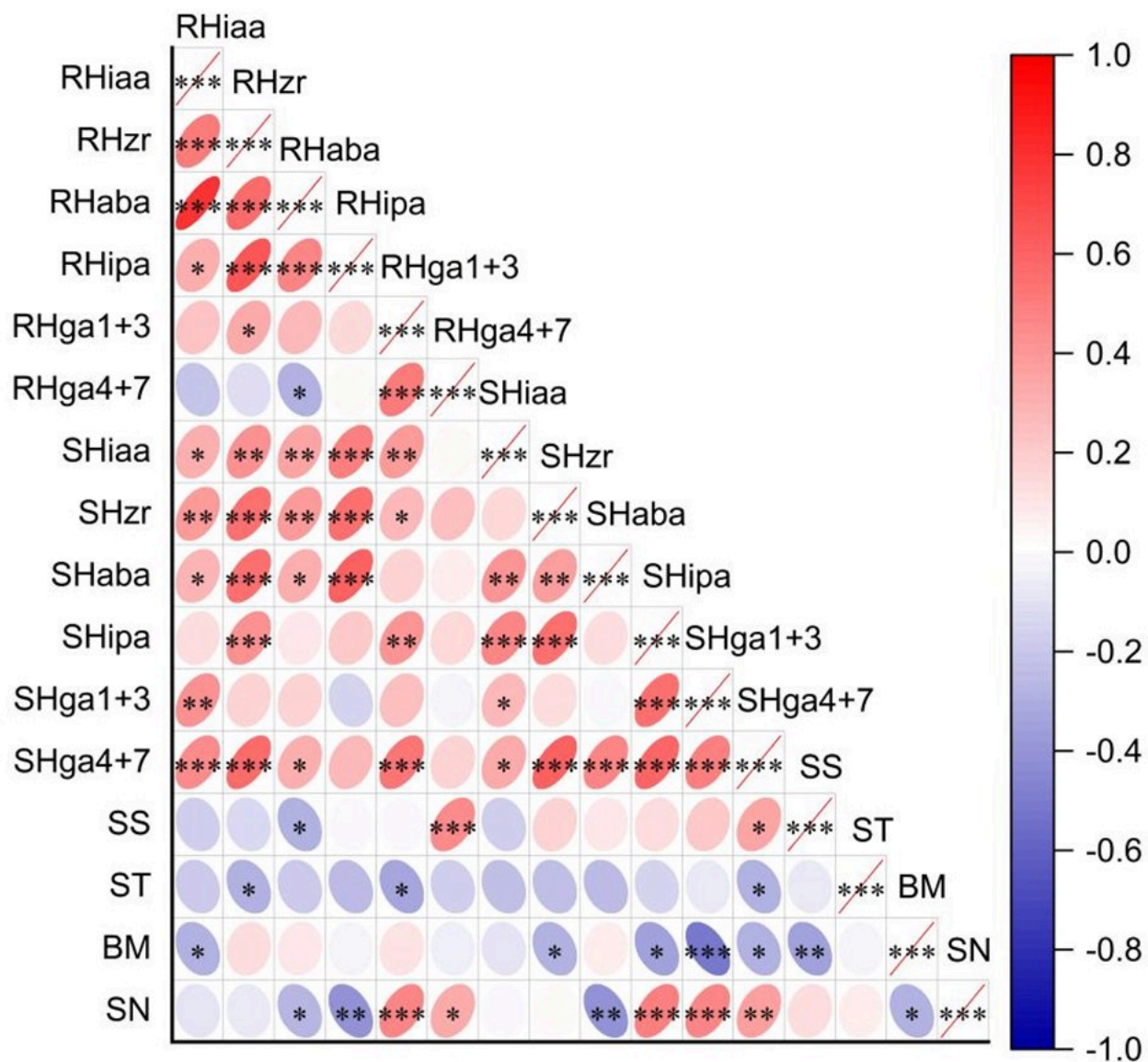


Figure 7

Correlation among endogenous hormone, NSC, shoot biomass and shoot density. SN, shoot density (no. Per m²); BM, shoot biomass (g); ST, starch content (%); SS, soluble sugar content (%); RH, rhizome and SH, shoot. * p < 0.05; ** p < 0.01.

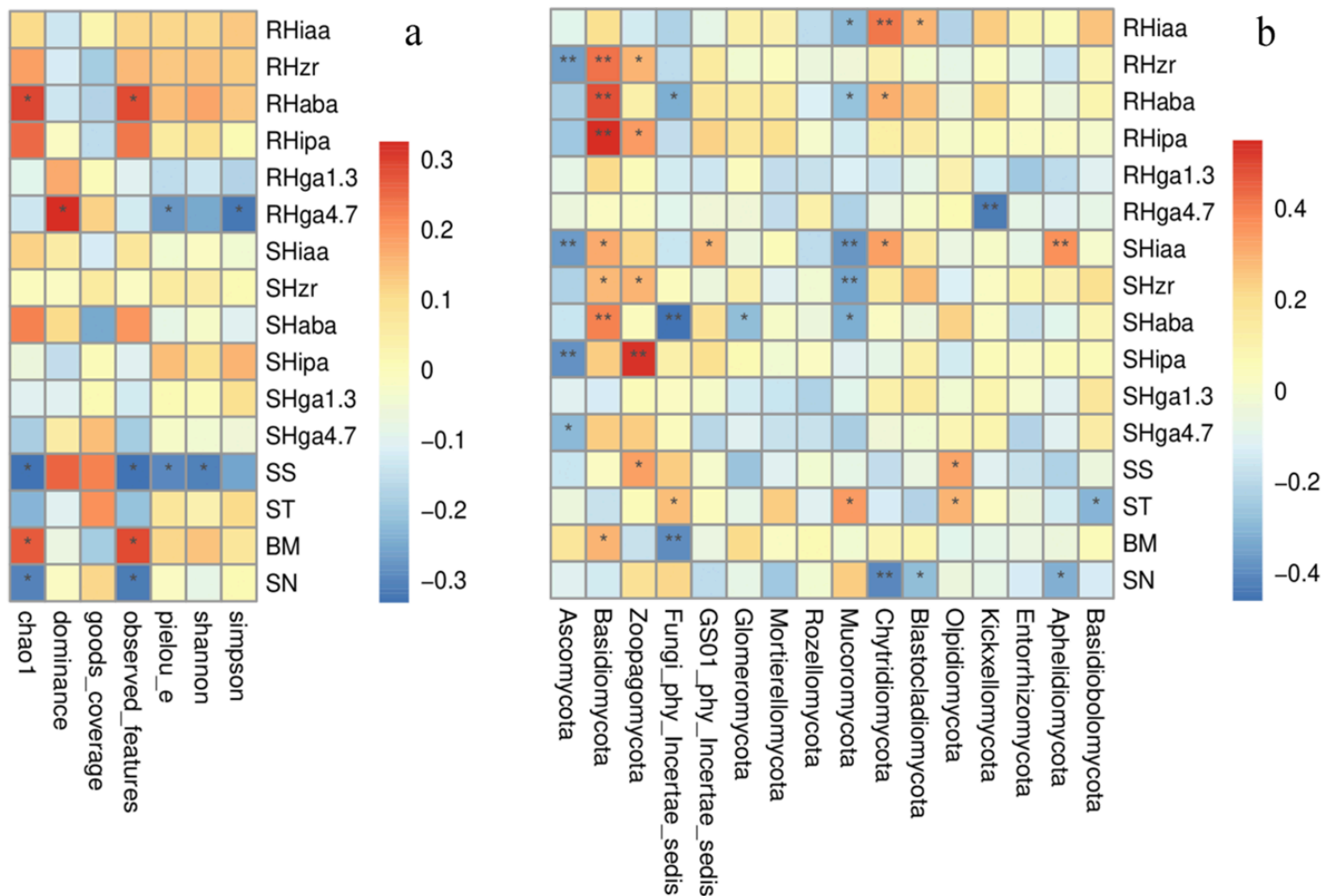


Figure 8

Relationships between diversity of soil fungi community and plant functional traits. SN, shoot density (no. Per m²); BM, shoot biomass (g); ST, starch content (%); SS, soluble sugar content (%); RH, rhizome and SH, shoot. * p < 0.05; ** p < 0.01.