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Tourism disturbance gradient effects on soil fungal communities in southern China's karst grassland

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Global tourism intensifies ecological stress in karst destinations, hindering the conservation of World Natural Heritage sites. However, the mechanisms that underlie the effects of tourism disturbance on karst soil fungi remain unclear. This study examined Baicaoping Grassland, South China's most significant natural karst grassland tourism area. We established experimental sites representing no (ND), light (LD), moderate (MD), and severe (SD) tourism disturbance. Integrating ITS high-throughput sequencing with eight soil parameters, we systematically analysed disturbance impacts on soil chemical properties and fungal communities. Key findings: (i) The disturbance gradient significantly altered soil nutrient patterns. (ii) *Ascomycota* (48.01%) and *Basidiomycota* (28.22%) dominated at the phylum level, with unclassified_*Ascomycota* (17.52%) as the predominant genus. Moderate disturbance significantly increased fungal alpha diversity. Disturbance intensity strongly influenced beta diversity ($p = 0.001$). (iii) Tourism disturbance indirectly affected soil microbial functionality and ecological restoration capacity via alterations in fungal functional guilds. This study provides scientific references for sustainable ecological development in karst grasslands.

Karst landforms are a unique category of topographical features formed by the extended breakdown of carbonate minerals. These landscapes are distinguished by caves, peaks, and depressions, which are defining features of this geological formation. Karst regions, characterized by karst landforms, are regarded as some of the most diverse hydrogeological settings on the planet. These ecosystems are recognized as intricately linked to atmospheric, hydrospheric, and biospheric processes alongside human history and development[1]. The South China Karst has been recognized as a World Natural Heritage Site due to its unique features and representation of global humid tropical to subtropical karst landscapes. The principal landforms comprise tower-like karst (peak forest), cone-like karst (peak bush), and sword-like karst[2]. The region's geography is intricate and varied, and its natural environment is delicate. As a result, the region is distinguished by substantial natural resources, encompassing both groundwater and surface tourism assets. Nonetheless, due to the expansion of the global population and the swift advancement of tourism, the karst tourism region is increasingly affected by human activities[3]. Tourism interference is recognized as a significant anthropogenic impact on the biological environment of the karst tourism area[4–6]. The principal types of interference encompass trampling surface plants and soil by tourists, chemical pollution from abandoned garbage, and installing tourist facilities[7–9]. The detrimental impacts of these disturbances on the soil environment, such as the degradation of soil structure, nutrient depletion, and changes in microbial communities, have hindered the restoration of soil ecosystems in karst tourism regions and affected the ecological preservation of karst natural heritage[10,11].

Karst regions display pronounced ecological vulnerability stemming from their infertile soils, limited nutrient supply capacity, and proneness to erosion[12–17]. Consequently, the soil environment becomes pivotal for conservation strategies in these areas. It has been demonstrated that soil microorganisms exhibit a greater degree of responsiveness to the characteristics of the soil environment than plant factors[18–20]. Fungi play a crucial role in the material and energy cycles, especially in terrestrial environments. They are essential to biogeochemical cycles and are the principal global carbon and nutrient cycle sources[21,22]. Fungal activities have been shown to influence the composition of plant and animal populations and the pace of ecological processes. Moreover, they have demonstrated a substantial favorable effect on rehabilitating damaged soils by enhancing nutrient utilization efficiency and facilitating soil aggregate formation[23–27]. As a fundamental regulator of ecosystem function, the soil microbial community plays a crucial role in the stability and resilience of karst ecosystems through dynamic alterations in their structure and function[28–32]. The soil fungal population, an essential element of the microbial community, is crucial for ecosystem material cycling and functional maintenance.

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Furthermore, it illustrates substantial community dynamics in the disturbance response mechanism[33]. Thus, a comprehensive investigation of soil fungus in karst areas will furnish microbiological theoretical foundations for managing rocky desertification. Plus, it will clarify the biogeochemical cycling mechanisms specific to environmentally sensitive regions. This will provide a scientific foundation for the ecological restoration and sustainable management of karst natural assets[34,35].

Soil fungi, necessary for ecosystems, can significantly influence the functioning of subsurface ecosystems extensively[36–38]. Research has shown the crucial function of mycorrhizal fungi in regulating the carbon cycle, with ascomycetous mycorrhizal (AM) fungi displaying an essential capacity to reduce losses of both organic and inorganic resources[39]. Natural restoration reshapes soil fungal composition and activity, boosting nutrient cycling and carbon storage capacity[40]. Microbial diversity and complex network structures significantly strengthen key ecological processes like soil nitrogen cycling. These communities also provide predictive biomarkers of ecosystem functionality, supporting ecological integrity in karst tourism regions[41–43]. The existing literature indicates that variations in soil pH, a reduction in soil organic matter, changes in soil chemical composition, and shifts in the population and activity of soil microbes are affected to differing degrees by disturbances associated with tourism[34,44–47]. Despite considerable study by several experts on tourism disturbances, most studies have focused on the high-latitude plateau regions of China, particularly the Tibetan Plateau[48]. Research on disturbances in karst tourism zones is severely lacking[49–52]. This work holds substantial importance for the ecological rehabilitation of the Karst World Natural Heritage tourism region[16]. This study aims to analyze soil and soil fungus in a tourism region subjected to different intensities of tourism disturbance. This would facilitate the identification of the response mechanisms of grassland soil microorganisms to tourism disturbances, along with the main elements impacting the sustainable utilization of grassland tourism. The subsequent hypotheses were posited: (1) Tourism disturbance substantially impacts soil trace chemical element content and soil fungal structure; (2) varying intensities of tourism disturbance exert distinct effects on soil fungal diversity and abundance; and (3) SOC is the primary factor influencing soil fungi in karst tourism regions.

Methods

Overview of the study area

The study area is situated in the Baicaoping Ten Thousand Mu Grassland Tourism Area (104°27′27″E, 26°52′16″N), Weining County, Guizhou Province, China, at an average elevation of around 2600 m. The site is situated at the base of Zu'an Mountain, which has an elevation of 2817 m above sea level. The core area of the site covers approximately 120,000 mou, with the utilized area extending to 100,000 mou, resulting in a total area exceeding 400,000 mou. The study area exemplifies karst geomorphology, characterized by low latitude and high altitude, and features a relatively flat karst hilly mountain pasture landscape. This pasture is the largest of its type in southern China and serves a crucial function as a livestock base in the southwestern region of the country. The region's climate is categorized as a subtropical monsoon humid climate, characterized by a terrain elevation variation of 100–150 m, an average annual temperature of 9.5 °C, a total annual temperature of 2000 °C, an average annual precipitation of 890 mm, and approximately 1800 h of sunshine per year. Karst landforms heavily impact the region by exposing rock surfaces, promoting thin soil layer development, and limiting water retention capacity. The ecological fragility of the area is a significant concern. The thin soil layer is susceptible to degradation from overgrazing and human activities, which may increase the likelihood of rocky desertification. A preliminary investigation proved that the predominant vegetation in the study area includes white clover, dogbane, paintbrush, and various grass species, such as dandelion, which together form perennial miscellaneous grass meadows. The study area serves as a convergence point for the Yi and Miao ethnic groups, with a historical utilization of the grassland for grazing, resulting in the shortage of a grazing gradient in this research. The herders graze according to established customary practices. The primary types of tourism in this region consist of playgrounds, horseback riding, skating, and hiking. The survey data reveals that the annual tourist count in the study area before the epidemic was roughly 60,000 individuals.

Sample plot setting and sampling

This study aimed to examine the effects of different levels of tourism disturbance intensity on soil within a karst tourism region. Experimental sample plots were established in early August 2024, after which came the setup of study sample plots in mid-August. The degree of tourism interference is influenced by the proximity of tourism routes and the concentration of tourists. The observed variations in distances indicate the differential intensity levels of tourism activities. Distance proximity has been shown to have a positive causal relationship with the intensity of interference, while increased distance has been empirically demonstrated to result in diminished interference intensity[53]. The spatial distribution of tourist activities within the designated study area has been investigated. The predominant concentration of tourist activities has been ascertained within the core area, which is defined as the territory within a diameter of 0–100 m. A marked diminution in tourist interference has been observed in the areas extending beyond this radius. The research identified four categories of tourist interference intensity (Table 1): no tourist interference, light tourist interference, moderate tourist interference, and severe tourist interference[54]. The test sample plots were categorized into three groups: light tourism disturbance area (LD), medium tourism disturbance area (MD), and severe tourism disturbance area (SD), all maintaining uniform stand conditions. The no tourism disturbance (ND) area was the control (Fig. 1).

Six parallel sample plots, each measuring 10 m × 10 m, were established within each experimental sample plot. The distance from the sample plots to the boundary exceeded 10 m. The area of each sample plot was adequately large, and to mitigate spatial heterogeneity among the sample plots, sample squares were established within each plot. Soil samples from each sample square were collected employing the 5-point method. After removing the apoplastic layer from the soil surface, physical soil samples were collected using a ring knife in 0–10 cm depth increments, with each new depth set at 5 cm. Soil microbial assay samples were collected simultaneously using a microbial sampler. To address the problem of spatial heterogeneity, soil samples were collected from sampling sites at equal intervals and combined into a single replicate. A total of 24 samples were collected to assess the chemical properties of the soil, and an additional

Table 1 | Indicators for grading the intensity of tourism disturbances

Type of disturbance intensity	Distance range (from tourist routes)	Level of human activity	Vegetation coverage	Temperature
ND	No visitor areas	No tourist activity, grassland left in its natural state	>90%	16–22°
LD	60–100m	No visible signs of human activity, low number of tourists	60–90%	16–22°
MD	30–60m	Small amount of litter and signs of trampling, heavy foot traffic	30–60%	16–22°
SD	0–30m	Significant human activity, high levels of litter and trampling, high concentration of visitors	<30%	16–22°

ND no disturbance, *LD* light disturbance, *MD* moderate disturbance, *SD* severe disturbance.

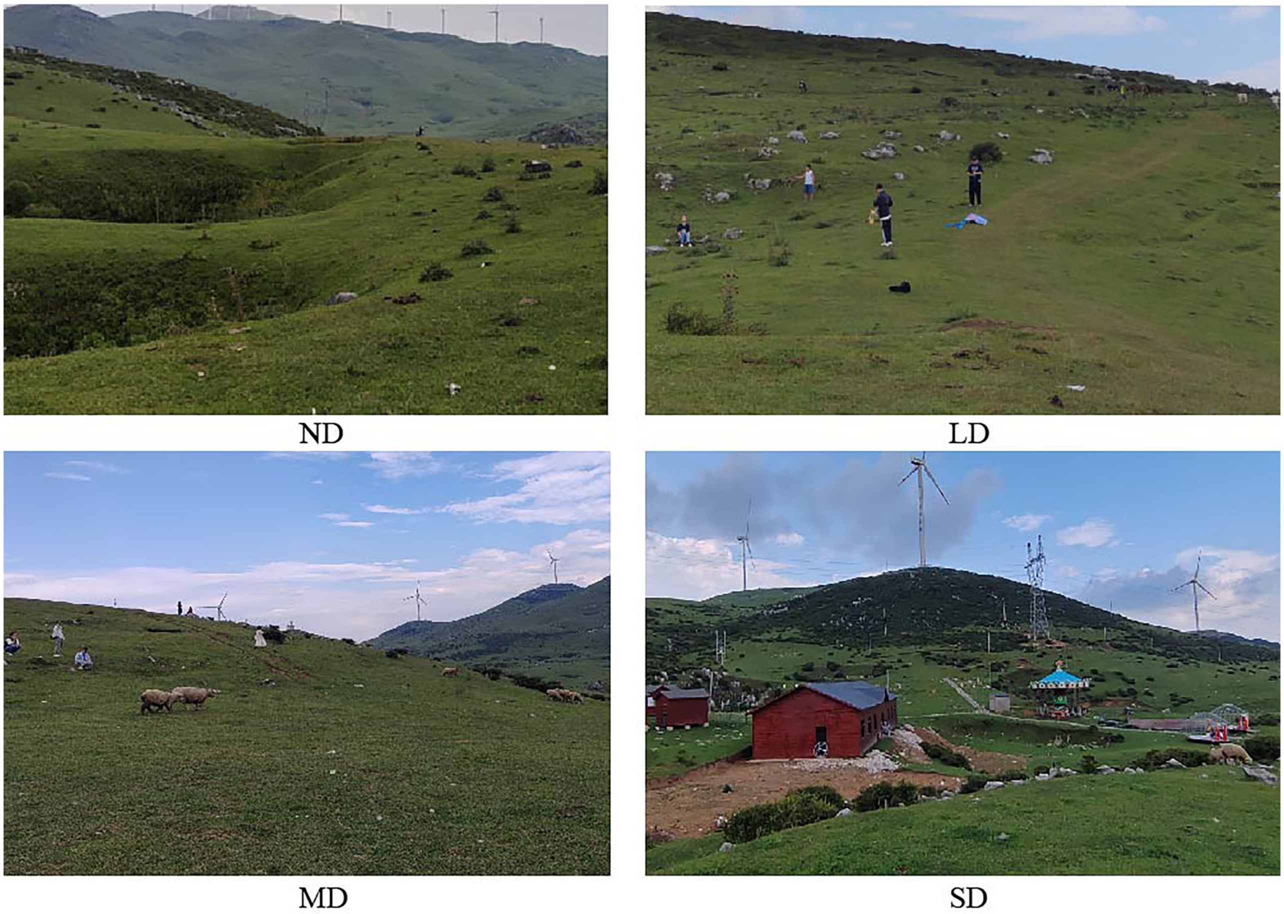


Fig. 1 | Live view of different tourism disturbance intensity in the study area. ND no disturbance, LD light disturbance, MD moderate disturbance, SD severe disturbance.

24 samples were received to evaluate the microbial properties of the soil. Samples were collected from four distinct sites. The initial samples were returned to the National Engineering Research Center of Karst Desertification Control to evaluate the soil's chemical properties. In contrast, the subsequent samples were stored in a dry ice foam box at −78.5 °C and forwarded to the Beijing Baimaike Company for analysis.

This study sought to mitigate environmental covariates, including temperature, during sampling according to the ranges specified in Table 1. Nevertheless, the uncontrollable outdoor environment seriously affected the sampling process, producing limited research data samples and individual data anomalies. This may lead to bias in the research data. This study utilizes a fixed spatial distance from major tourist routes as a spatial proxy variable to characterize the potential disturbance intensity of tourist activities. This distance gradient is hypothesized to reflect a trend of decreasing disturbance intensity from proximal to distal locations. Nevertheless, the current study did not directly assess indicators of real-time disturbance intensity. The observed changes along this gradient may be due to tourism disturbance or partially reflect the presence of other environmental factors, such as microclimate, that naturally vary with distance.

Determination of soil chemical properties

The soil samples collected were analyzed in the laboratory to assess their chemical properties. Soil pH was assessed using the electrode method, while soil organic carbon (SOC) was quantified through the potassium dichromate-external heating method. Total nitrogen (TN) was quantified utilizing the Kjeldahl method (FLOWSYS, SYSTEA, Italy). Soil alkali hydrolyzed nitrogen (AN) was assessed using the alkaline diffusion. Total phosphorus (TP) and available phosphorus (AP) in soil were quantified using the molybdenum-antimony colorimetric method (Specord 200 PLUS, Analytik, Germany). Total potassium (TK) and available potassium (AK) in soil were quantified using the flame photometric method (ICE3500, Thermo Fisher, USA).

DNA extraction, amplification, sequencing, and bioinformatics analysis

Genomic DNA was extracted from the samples utilizing the TGuide S96 Magnetic Soil/Fecal DNA Kit (Tengen Biotechnology (Beijing) Co., Ltd.) following the manufacturer's guidelines. The extracted DNA's quality and quantity were assessed via electrophoresis on a 1.8% agarose gel, followed by concentration and purity determination using a NanoDrop 2000 UV–Vis spectrophotometer (Thermo Scientific, Wilmington, USA). The Polymerase Chain Reaction (PCR) was employed to amplify fungal Internal Transcribed Spacer (ITS) gene fragments using the primer pairs ITS1F (CTTGGTCATTTAGAGGAAGTAA) and ITS2 (GCTGCGTTCTTCATCGATGC). Forward and reverse ITS primers were tagged with sample-specific Illumina index sequences to facilitate deep sequencing. The PCR was conducted in a total reaction volume of 10 μl, consisting of 5–50 ng of DNA template, 0. The subsequent components are necessary: 3 μl of forward primer (10 μM), 0.3 μl of reverse primer (10 μM), 5 μl of KOD FX Neo buffer, 2 μl of dNTP (2 mM each), 0.2 μl of KOD FX Neo, and ddH2O to a final volume of 20 μL. Following this, denaturation was performed at 95 °C for 30 s, succeeded by annealing at 50 °C for 30 s. Subsequently, an extension at 72 °C for 40 s was conducted, followed by a final step at 72 °C for 7 min. Amplification products were purified using an Omega DNA purification kit (Omega Inc., Norcross, GA, USA), and quantification was carried out with a Qsep-400 instrument (BiOptic, Inc., New Taipei City, Taiwan, ROC). Amplicon libraries underwent 2 × 250 bp paired-end sequencing utilizing an Illumina Novaseq 6000 (Beijing Biomarker Technologies Co., Ltd., Beijing, China)[55].

Table 2 | Soil chemical properties under different intensities of tourism disturbance

	pH	SOC (g kg^{-1})	TN (g kg^{-1})	TP (g kg^{-1})	TK (g kg^{-1})	AN (mg kg^{-1})	AP (mg kg^{-1})	AK (mg kg^{-1})
ND	5.11 ± 0.11a	13.87 ± 0.18a	9.25 ± 0.12a	1.86 ± 0.14a	8.37 ± 0.15a	774.94 ± 8.38a	1.31 ± 0.04a	213.67 ± 29.40ab
LD	5.58 ± 0.16b	10.62 ± 0.44b	7.92 ± 0.34b	1.56 ± 0.06b	11.59 ± 0.38b	723.59 ± 22.55ab	1.11 ± 0.09a	205.67 ± 30.42ab
MD	5.55 ± 0.04b	9.50 ± 0.21c	7.22 ± 0.15b	1.60 ± 0.02b	10.60 ± 0.09c	679.51 ± 8.78b	0.96 ± 0.11ab	156.50 ± 4.73a
SD	5.41 ± 0.05b	7.86 ± 0.46 d	6.13 ± 0.30c	1.59 ± 0.07b	12.06 ± 0.29b	579.15 ± 32.98c	0.63 ± 0.25b	331.83 ± 30.34b
One-way ANOVA								
P value	0.015	0.000	0.000	0.071	0.000	0.000	0.024	0.132

The mean values (mean ± standard deviation, $n = 6$) followed by different lowercase letters indicate significant differences between the treatment groups ($p < 0.05$). *SOC* soil organic carbon, *TN* total nitrogen, *TP* total phosphorus, *TK* total potassium, *AN* quick-acting nitrogen, *AP* effective phosphorus, *AK* quick-acting potassium, *ND* no disturbance, *LD* light disturbance, *MD* moderate disturbance, *SD* severe disturbance.

This study's bioinformatics analysis was executed using BMKCloud (http://www.biocloud.net/). The raw data were filtered using Trimmomatic (version 0.33), with filter parameters derived from the quality of individual nucleotides[56]. Primer sequences were identified and removed using Cutadapt (version 1.9.1)[57]. The PE reads acquired from the prior steps were compiled using USEARCH (version 10)[58], subsequently followed by the elimination of chimeric sequences through UCHIME (version 8.1)[59]. The high-quality reads produced by the previously mentioned steps were used in the subsequent analysis. USEARCH (version 10.0) is recommended for clustering sequences at a 97% similarity level, applying a default threshold of 0.005% of the total sequenced sequences to filter OTUs. The SILVA database (version 138.1)[60] was used for the classification and annotation of OTUs within the Naive Bayes classifier in QIIME[61], integrating a confidence threshold of 70% to prevent low-confidence annotations. Before conducting the diversity analysis, methods for calculating relative abundance were utilized, and data normalization was done using Python 2 software (matplotlib-v1.5.1 database). The research used BMKCloud (https://www.biocloud.net) to analyze sequencing data.

Analysis of data

The effects of varying disturbance intensities on soil properties, relative abundance at the fungal phylum and genus levels, and differences among functional taxon groups of fungi were analyzed using IBM SPSS Statistics 27 software. Data analysis was performed using one-way analysis of variance (ANOVA), the Kruskal-Wallis Test, and multiple comparisons. The Mothur software was installed to compute the Chao1, ACE, Shannon, and Simpson indices of alpha diversity using OTU data. The indices were designed to represent the richness and diversity of soil microbial communities. The composition of common and unique soil fungi at the phylum and genus levels in grassland samples subjected to varying intensities of tourism disturbance was analyzed using the Vegan package in R. PCoA analysis, based on Bray–Curtis distance measurements, along with a similarity test (ANOSIM), was employed to conduct a comparative analysis of the beta diversity of soil fungi in grasslands, considering different intensities of tourism disturbance. Redundancy analysis (RDA) was utilized to determine the relationship between specific environmental factors and soil microbial communities. This study assessed the relationships between environmental factors and the structure of soil fungal communities at both the phylum and genus levels. This was accomplished using Spearman correlation heatmaps from the Vegan package in R. The next step entailed determining the correlations between environmental factors and soil fungal community structure at both the phylum and genus levels, applying Spearman correlation heatmaps. The FUNGuild tool was employed for functional gene prediction of soil fungi.

Results

Soil chemical characteristics under different intensities of tourism disturbance

The influence of tourist disturbances, which vary in intensity, on soil chemistry in karst grasslands presents a complex issue. This study showed a gradual decrease in soil pH equivalent to increased disturbance intensity. The variation ranged from 4.93 to 6.29, with the mean fluctuating between 5.11 and 5.58. The lowest value was recorded in ND, while the highest was in LD, with the following hierarchy: LD > MD > SD > ND. In disturbed karst soils, greater disturbance intensity intensifies the soil acidification process (Table 2). SOC content ranged from 6.11 to 14.47 g kg—^{1}, with mean values spanning 7.86–13.87 g kg^{-1}. The highest SOC levels occurred under natural disturbance (ND). SOC content decreased significantly with increasing disturbance intensity, demonstrating a clear gradient pattern: ND > LD > MD > SD. Total nitrogen (TN) followed a similar trend to SOC, declining significantly with increasing disturbance intensity. In contrast, total phosphorus (TP) and total potassium (TK) demonstrated distinct response patterns. TP levels averaged between 1.86 and 1.56 g kg^{-1}, reaching their highest concentration under natural disturbance (ND) and their lowest under light disturbance (LD). This revealed the gradient pattern: ND > MD > SD > LD. Conversely, TK laid out a nadir under ND conditions, with its distribution pattern opposing TP's. The trends of alkaline dissolved nitrogen (Available nitrogen, AN) and quick-acting phosphorus (Available phosphorus, AP) aligned with those of SOC, both reflecting a decline as disturbance intensity increased. Ammonium nitrogen (AN) content ranged from 457.34 to 808.00 mg kg^{-1}. Mean values spanned 579.15–774.94 mg kg^{-1}, reaching maximum concentrations under natural disturbance (ND) and minimum concentrations under severe disturbance (SD). The variability of the analytical parameter could be seen by the range of AP content, which spanned from 0.07 mg kg^{-1} to 1.39 mg kg^{-1}. The AP content ranged from 0.07 mg kg^{-1} to 1.39 mg kg^{-1}., with a minimum mean value of 0.63 mg kg^{-1} in SD and a maximum mean value of 1.31 mg·kg^{-1} in ND. The mean values of available potassium (AK) vary from 156.50 mg·kg^{-1} to 331.83 mg kg^{-1}, with the highest value recorded in SD and the lowest in MD.

Soil fungal composition at various levels of tourist disturbance

1,845,374 raw sequence pairs were obtained from the high-throughput sequencing of 24 samples, resulting in 1,651,853 high-quality validated sequences after double-ended sequence quality control and splicing. The minimum number of Clean Reads for individual samples was 37,619, with an average output of 68,827 per sample. The samples exhibited a microbial taxa composition comprising 16 phyla, 52 orders, 119 families, 267 genera, and 627 species (Supplementary Table 1). Analysis using Venn diagrams revealed that OTU specificity and sharing were distinguishable among sample groups characterized by varying interference intensities (Supplementary Fig. 1). The four sample groups (SD, MD, LD, and ND) comprised 2196, 1767, 1829, and 1483 specific OTUs, respectively. A total of 124 OTUs were split within the four sample groups.

Analysis of species composition revealed that the top 10 most abundant fungal phyla in the samples were: *Ascomycota* (48.01%), *Basidiomycota* (28.22%), *Mortierellomycota* (14.43%), unclassified Fungi (6.35%), *Rozellomycota* (1.29%), *Chytridiomycota* (0.95%), *Glomeromycota* (0.53%), *Calcarisporiellomycota* (0.08%), *Mucoromycota* (0.05%), and *Kickxellomycota* (0.04%) (Fig. 2a). The top 10 most abundant fungal genera, in descending order of abundance, were unclassified *Ascomycota* (17.52%), *Mortierella* (14.39%), unclassified Fungi (6.35%), *Leohumicola* (5.13%), unclassified

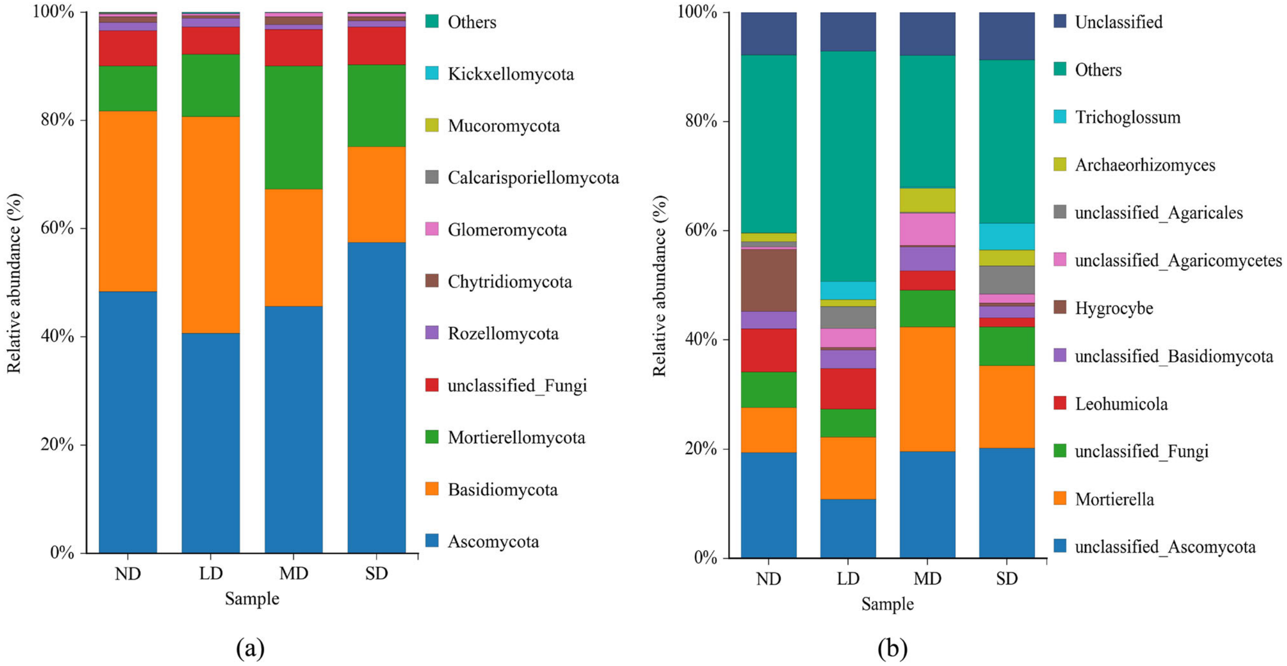


Fig. 2 | Soil fungal relative abundance under different levels of tourism disturbance. Relative abundance maps at the phylum (**a**) and genus (**b**) level for soil fungi. The horizontal axis denotes the sample names, whilst the vertical axis indicates the relative abundance percentages. The utilization of distinct colors signifies the classification of different species; the arrangement of stacked columns denotes the top ten taxonomic groups in terms of their relative abundance at each taxonomic level. ND no disturbance, LD light disturbance, MD moderate disturbance, SD severe disturbance.

Basidiomycota (3.26%), *Hygrocybe* (3.20%), unclassified *Agaricomycetes* (2.85%), unclassified *Agaricales* (2.58%), *Archaeorhizomyces* (2.54%), and *Trichoglossum* (2.12%) (Fig. 2b). *Ascomycota* and *Basidiomycota* were the predominant fungal phyla at the phylum level. In contrast, the predominant group within the fungal phylum was unclassified_*Ascomycota* alongside *Mortierella*. ANOVA stated that, at the phylum level, different levels of travel disturbance greatly impacted *Basidiomycota* ($p = 0.010$), *Mortierellomycota* ($p = 0.028$), and *Kickxellomycota* ($p = 0.039$) (Supplementary Table 2). A significant difference emerged between *Ascomycota* in the LD and SD groups ($p < 0.05$). Compared to ND, MD and SD drastically lowered the relative abundance of *Basidiomycota*. Additionally, MD notably increased the relative abundance of *Mortierellomycota*, while LD significantly improved the relative abundance of *Kickxellomycota* ($p < 0.05$). The relative abundance of *Mortierella* at the genus level was considerably affected by varying intensities of travel disturbance ($p = 0.028$). The relative abundance of other soil fungal genera was not significantly affected ($p > 0.05$) (Supplementary Table 2). A comparison of ND with MD significantly impacted the relative abundance of *Mortierella* and unclassified_*Agaricomycetes* ($p < 0.05$). The difference between MD and LD did not achieve statistical significance ($p > 0.05$). SD significantly decreased the relative abundance of *Leohumicola* ($p < 0.05$); however, the differences between LD and MD were not significant ($p > 0.05$).

Diversity of soil fungi under different degrees of disturbance from tourists

The species dilution curves indicated that the sequencing depth was adequate for the study, the data volume was adequate, and the sample diversity was successfully proven (Supplementary Fig. 2). Alpha diversity is a crucial ecological metric for evaluating species richness and diversity within individual samples. This metric quantifies the extent of biological diversity present within a community. The Chao1 and Ace indices are employed to assess species richness, which is defined as the count of species present in a specific sample. The Shannon and Simpson indices are applied to evaluate species diversity. The results of this study revealed notable differences in the alpha richness index across different levels of tourist disturbance intensity (Fig. 3). The MD treatment led to a noticeable enhancement in soil fungal diversity, as indicated by elevated Chao1 and ACE indices relative to the ND treatment ($p = 0.031$). No significant differences were found between the ND group and the LD and SD groups, nor between the LD group and the MD and SD groups ($p > 0.05$). The Shanno and Simpson indices showed no statistically significant variation in diversity among the three treatments versus ND ($p > 0.05$).

Beta diversity is an essential ecological metric that quantifies variety in species composition among different samples or settings. It illustrates the diversity of communities in spatial dimensions and their responses to environmental gradients. The research confirmed significant variations in fungal community structure, backed up by ANOSIM analysis, across different intensities of tourism disturbance. This finding indicates a substantial variation in community composition across different disturbance conditions ($R = 0.634$, $p = 0.001$). The PERMANOVA analysis confirmed this observation, meaning that 15.3% of the variation in community structure was attributable to differences in disturbance intensity ($p = 0.001$). Principal Coordinate Analysis (PCoA) elucidated this divergent characteristic (Fig. 4). The PCoA results indicated that the fungal community structure among the samples demonstrated significant separation based on varying travel disturbance intensities, highlighting notable differences in Beta diversity across the LD, MD, SD, and ND groups ($p = 0.001$).

Relationships between different environmental factors and soil fungi

A RDA was conducted to examine the soil fungal community structure, considering chemical environmental factors at both the phylum and genus levels. The RDA analysis results pointed out that the spatial differentiation of soil fungal community structure at both the phylum and genus levels was positively correlated with soil factors (Fig. 5). Heat map analysis of colonies with a relative abundance exceeding 1% elucidated the relationships between soil fungi and environmental factors. At the phylum level, significant positive correlations were found between SOC, TN, and AN with *Basidiomycota* ($p < 0.05$). Additionally, *Mortierellomycota* exhibited a significant negative correlation with SOC, AN, and AK while showing a

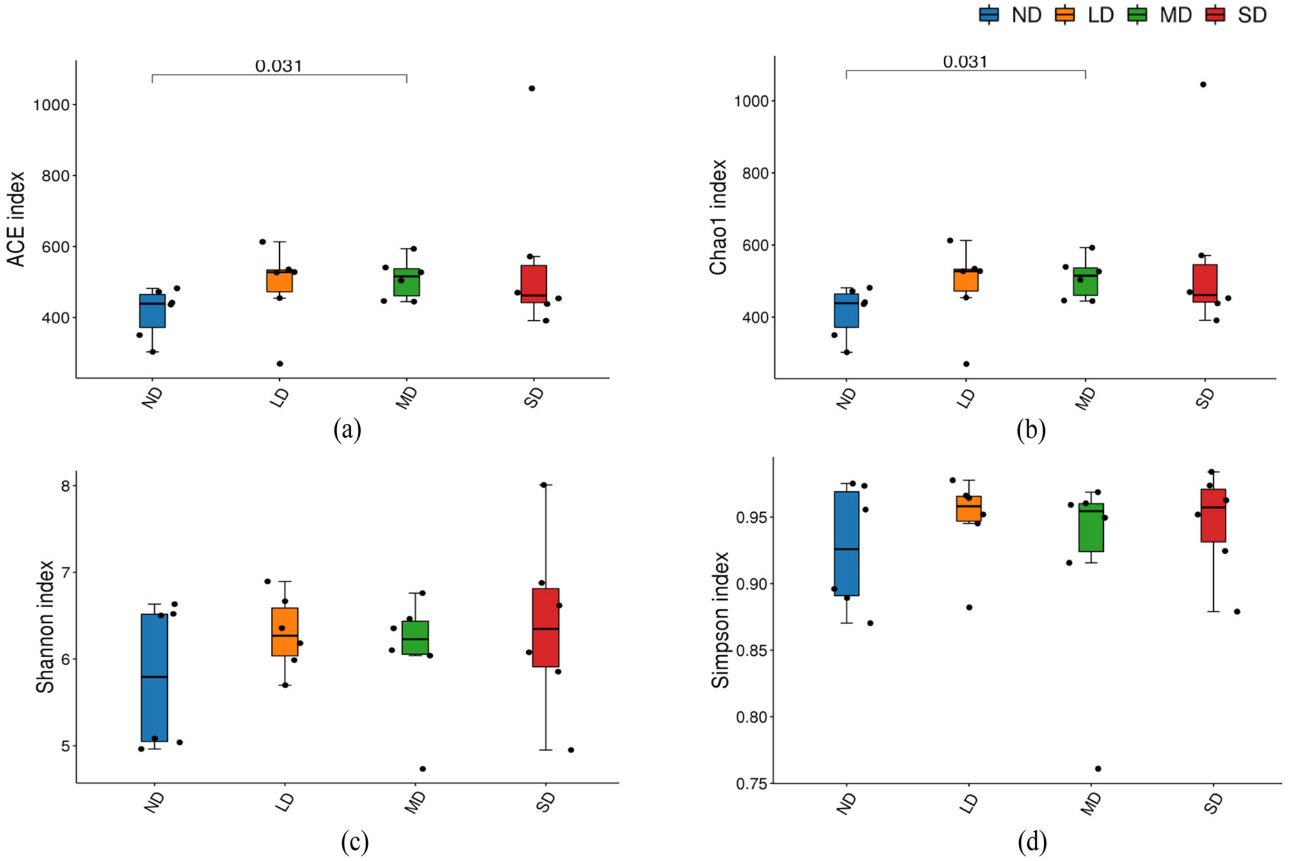


Fig. 3 | Alpha diversity index plots. **a** ACE index; **b** Chao1 index; **c** Shannon index; **d** Simpson index, ND no disturbance, LD light disturbance, MD moderate disturbance, SD severe disturbance.

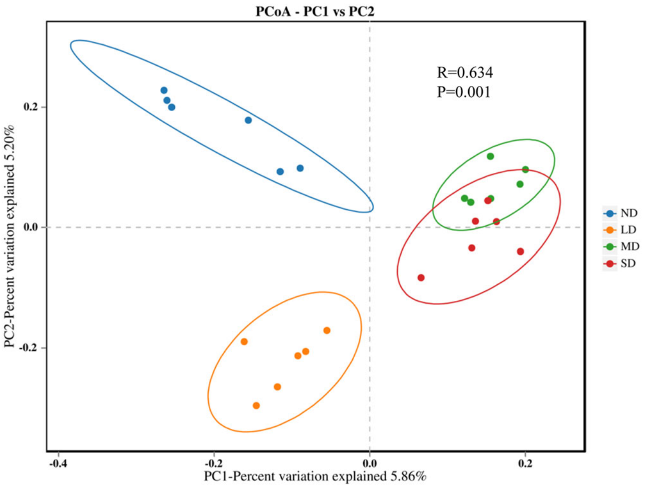


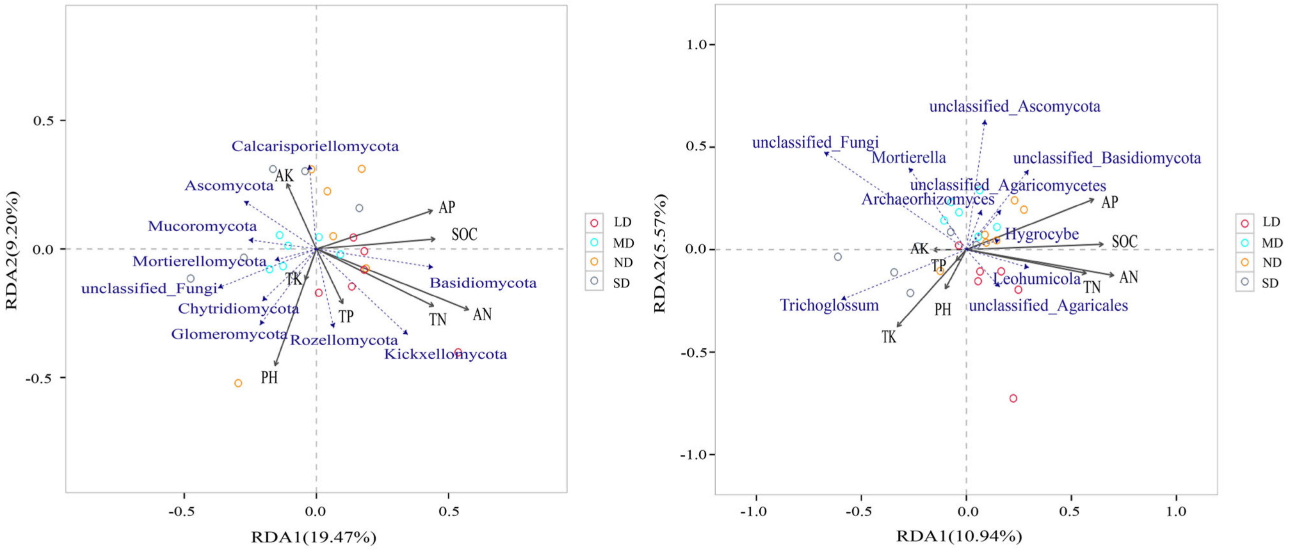
Fig. 4 | The following figure illustrates a Principal Coordinate Analysis (PCoA) plot of soil fungal communities. Each data point on the graph corresponds to a sample; different colors represent different groups of samples; oval circles indicate 95% confidence ellipses (i.e., if there were 100 samples in the sample group, 95 would fall within them). The horizontal coordinate is representative of the first principal component, whilst the percentage signifies the contribution of the first principal component to the sample variance. The vertical coordinate is representative of the second principal component, with the percentage denoting the contribution of the second principal component to the sample variance. ND no disturbance, LD light disturbance, MD moderate disturbance, SD severe disturbance.

significant positive connection with pH ($p < 0.05$) (Fig. 6a). At the genus level, pH showed a significant positive correlation ($p < 0.05$) with *Mortierella* and unclassified *Agaricomycetes* species. TK disclosed a significant positive correlation ($p < 0.01$) with *Trichoglossum* species, whereas AP presented a significant negative correlation ($p < 0.05$) with the same genus. Additionally, recognized negative correlations were identified between SOC, TN, and AN with the genus *Trichoglossum* ($p < 0.001$). Conversely, these parameters demonstrated significant positive correlations with *Leohumicola* ($p < 0.05$). SOC, AN, and AK showed significant negative correlations with *Mortierella* ($p < 0.05$). A negative correlation was observed between TP and the genus unclassified_*Ascomycota* ($p < 0.05$). A significant negative correlation exists between AK and the genus unclassified_*Agaricomycetes* ($p < 0.05$) (Fig. 6b).

The Monte Carlo ranking of environmental factors confirmed that AN ($p = 0.019$) was the main driver shaping the structure of soil fungal phyla communities. Its correlation with fungal communities was significantly greater than other factors, proving that nitrogen is the crucial element driving changes in fungal phyla communities (Supplementary Table 3). At the genus level, the effects of SOC ($p = 0.018$), TN ($p = 0.045$), AN ($p = 0.025$), and AP ($p = 0.047$) on soil fungal phyla were significant (Supplementary Table 3), emphasizing that SOC and nitrogen are the primary environmental factors changing the genus level of soil fungal communities.

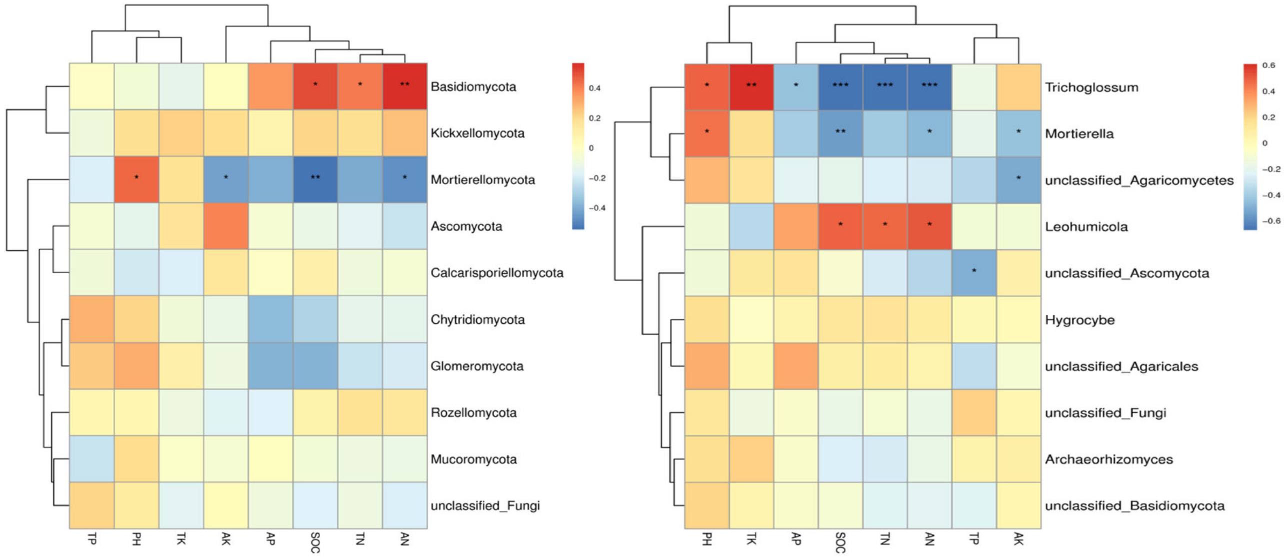
Analysis of potential functional groups of soil fungi

The research employed the FUNGuild tool to predict and assess the functional genes of soil fungi. The findings suggested that saprotrophic nutrients symbolized the most significant relative abundance within the functional group of nutrient types, comprising 67.92% of the total. This component showcased its maximum in the high disturbance strength (SD) treatment condition, whereas it was at its minimum in the non-disturbance (ND)



(a) (b)

Fig. 5 | Spatial relationships between environmental factors and soil fungal communities. The following figures illustrate the horizontal redundancy analysis (RDA) plots for phylum (**a**) and genus (**b**). The length of the arrow represents the strength of the environmental factor's influence on community changes. The longer the arrow, the greater the influence of the environmental factor. The angle between the arrow and the coordinate axis represents the correlation between the environmental and coordinate factors. The smaller the angle, the higher the correlation. The closer the sample point is to the arrow, the stronger the effect of the environmental factor on the sample. If the sample is located in the same direction as the arrow, it indicates a positive correlation between the environmental factor and the changes in the sample species community. If the sample is located opposite to the arrow, it indicates a negative correlation between the environmental factor and the changes in the sample species community. ND no disturbance, LD light disturbance, MD moderate disturbance, SD severe disturbance.



(a) (b)

Fig. 6 | Correlation between Environmental Factors and Soil Fungi. The following heat map illustrates the relative abundance of phylum (**a**) and genus (**b**) colonies that exceeds 1%. The left-hand clustering tree is the species clustering tree, the upper clustering tree is the sample clustering tree, and the middle section is the heatmap. The colors correspond to the legend, with red indicating positive correlation and blue indicating negative correlation; darker colors indicate higher correlation. If an asterisk (*) is present, it indicates significant correlation (** denotes $p < 0.05$, ** denotes $p < 0.001$, and *** denotes $p < 0.0001$). ND no disturbance, LD light disturbance, MD moderate disturbance, SD severe disturbance.

condition. The symbiotrophic group communicated an inverse relationship in relative abundance compared to the saprotrophic group, with peak abundance recorded in the ND treatment and minimal abundance in the SD treatment. The pathogenic trophic type constituted only 12.48% of the sample (Supplementary Table 4).

Subsequent analysis revealed that the twenty most abundant functional taxa are depicted in Fig. 7. The undefined saprotroph was significantly represented across all subgroups. The presence of undefined saprotrophs, symbiotrophs, and arbuscular mycorrhizal fungi (Botrytis cinerea) was elevated in the ND and LD subgroups. Conversely, soil saprotrophs and dung saprotrophs displayed greater amounts in the MD and SD subgroups. The ND subgroup carried an elevated presence of undefined saprotrophs and undefined biotrophs. The Plant Pathogen variable maintained greater significance in the LD and MD subgroups than in the other treatment

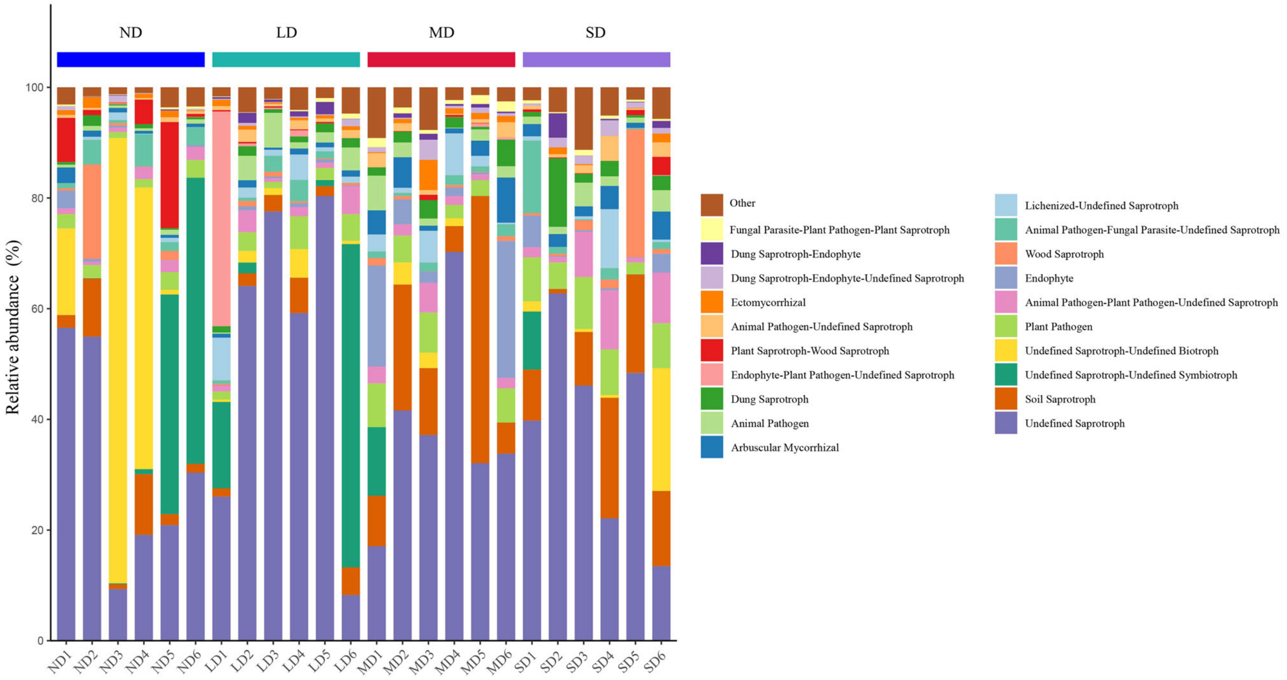


Fig. 7 | Functional genes predicting functional taxa. ND no interference, LD mild interference, MD moderate interference, SD severe interference.

Table 3 | Kruskal-Wallis test results for fungal functional guilds

Guild	*H*	df	*η*²	Asymptotic *p*	Monte Carlo *p*	99% CI for Monte Carlo *p*
Fungal Parasite-Plant Pathogen-Plant Saprotroph	13.673	3	0.363	0.003	0.001	[0.000,0.001]
Leaf Saprotroph	11.140	3	0.317	0.011	0.006	[0.004,0.008]
Dung Saprotroph-Undefined Saprotroph	9.805	3	0.290	0.020	0.039	[0.034,0.044]
Arbuscular Mycorrhizal	9.420	3	0.282	0.024	0.016	[0.012,0.019]
Plant Pathogen	9.113	3	0.275	0.028	0.020	[0.016,0.023]
Dung Saprotroph-Endophyte-Undefined Saprotroph	8.240	3	0.256	0.041	0.032	[0.028,0.037]
Lichenized-Undefined Saprotroph	7.934	3	0.248	0.047	0.037	[0.032,0.042]
Animal Pathogen	7.927	3	0.248	0.048	0.037	[0.033,0.042]
Endophyte	7.540	3	0.239	0.057	0.046	[0.040,0.051]
Soil Saprotroph	7.527	3	0.239	0.057	0.046	[0.041,0.051]

H Kruskal-Wallis test statistic, *df* Degrees of freedom, *η*² Eta-squared effect size, *CI* Confidence interval. Significant results (*p* < 0.05) highlighted in descending order of effect size (*η*²).

groups. The Kruskal-Wallis expressed significant intergroup variability ($p < 0.05$) among the categories of Fungal Parasite-Plant Pathogen-Plant Saprotroph, Leaf Saprotroph, and Dung Saprotroph-Undefined Saprotroph across different gradients of travel interference. The categories of Arbuscular Mycorrhizal, Plant Pathogen, Dung Saprotroph-Endophyte-Undefined Saprotroph, Lichenized-Undefined Saprotroph, Animal Pathogen, and other functional taxa highlighted significant intergroup variability ($p < 0.05$) (Table 3). No significant differences were observed in the remaining functional groups. Comparative analyses concluded significant variation in the relative abundance of Fungal Parasite-Plant Pathogen-Plant Saprotroph between ND and MD ($p < 0.001$), as well as between LD and MD ($p = 0.005$). The relative abundance of Leaf Saprotroph offered significant variation among LD-MD, LD-SD, ND-MD, and ND-SD ($p < 0.05$). No significant difference was observed between ND-LD and MD-SD ($p > 0.05$). Additionally, Dung Saprotroph-Undefined Saprotroph proved a statistically significant difference among ND-SD, MD-SD, and LD-SD ($p < 0.05$). The findings stated a statistically significant difference ($p < 0.05$) in Arbuscular Mycorrhizal (AM) levels among ND-MD, ND-SD, LD-MD, and LD-SD groups. No significant differences ($p > 0.05$) were noted among the other groups. Significant differences in Plant Pathogen and Dung Saprotroph-Endophyte-Undefined Saprotroph were noticed exclusively between the ND-SD and LD-SD groups ($p < 0.05$). The lichenized saprotroph displayed substantial distinctions in its composition among the ND-LD, ND-MD, and ND-SD categories ($p < 0.05$). A similar discrepancy was noted in the animal pathogen, practicing significant variation in its composition among the ND-LD, ND-MD, and ND-SD categories ($p < 0.05$) (Supplementary Table 5).

At the phylum level, *Ascomycota* emerged as the most dominant phylum in the Pathotroph, Saprotroph, and Symbiotroph categories, representing 78.87%, 51.22%, and 41.19%, respectively (Supplementary Fig. 3). This text targets to offer a thorough overview of the subject matter. At the genus level, *Marasmius* (15.59%), *Leohumicola* (19.52%), and *Lecythophora* (35.71%) were identified as the predominant phyla of pathogenic, saprotrophic, and symbiotic trophic genera, respectively (Supplementary Fig. 3).

Discussion

Soil's physical and chemical properties are crucial for assessing its quality. Changes in these properties significantly impact soil microbial diversity and functionality. These impacts directly relate to the stability and sustainability of soil ecological service functions[62]. In karst landscapes, soil conditions serve as key indicators of rocky desertification management effectiveness. Monitoring dynamic changes in soil physicochemical properties provides a valuable measure of soil ecological function characteristics[63–65]. This study presents findings that illustrate that tourism disturbance decisively impacts the chemical properties of the soil environment in a karst tourism area across multiple dimensions. The investigation indicates that pH, SOC, total nitrogen (TN), total potassium (TK), alkaline dissolved nitrogen (AN), and quick-acting phosphorus (AP) provide notable sensitivity to tourism disturbance, evidence of significant differences. The findings suggest that grassland ecosystems offer sensitivity and vulnerability to external disturbances[4,66–68]. The nutrient elements in the soil, specifically nitrogen (N), phosphorus (P), and potassium (K), stated significant variation patterns influenced by tourism activities[69–72]. It was found that SOC, TN, AN, and AP content decreased gradually with increasing disturbance intensity, suggesting that they may be sensitive indicators of the extent of external soil disturbance. The hypothesis suggests that varying levels of tourism disturbance may have led to changes in soil structure, affecting soil trace element content and limiting soil nutrient effectiveness, resulting in different degrees of response[73]. The present study's findings illustrate that severe disturbance can significantly limit soil nutrients, creating substantial variations in the concentrations of carbon (C), nitrogen (N), and phosphorus (P). These alterations may compromise the energy cycle of soil material. In light of increasing tourism development, it is required for karst tourism regions to improve the long-term, dynamic monitoring of soil environmental factors. Establishing a systematic scientific evaluation system for soil quality is essential for supporting the sustainable development of karst ecosystems[74,75].

In contrast, the increase in tourism disturbance aggravated the content of AK in the soil, showing the diversified response characteristics of environmental factors under different disturbance scenarios, reflecting the complex change mechanisms of soil nutrient elements in the context of tourism disturbance. This phenomenon reveals the complex mechanisms underlying soil nutrient element changes driven by tourism disturbance. These findings validate the initial hypothesis. Developing targeted resource management strategies for karst regions is essential to mitigate potential risks to ecosystem stability from tourism activities. These strategies should optimize the arrangement and intensity of tourism operations. This approach seeks to enhance the effectiveness of rocky desertification management, mitigate the risk of ecological recurrence of management outcomes, and offer both a theoretical foundation and practical support for achieving ecological health within World Natural Heritage sites[76,77].

The biological structure and diversity of soil are recognized as fundamental determinants of ecosystem functioning and are intrinsically linked to sustainable ecosystem productivity[78]. The present study demonstrates that, under varying levels of tourism disturbance, *Ascomycota* and *Basidiomycota* are the predominant fungal phyla, while unclassified_*Ascomycota* is the fungal genus group with the highest relative abundance. The analysis of variance shows that different levels of tourism disturbance profoundly impact *Basidiomycota* ($p = 0.010$), *Mortierellomycota* ($p = 0.028$), and *Kickxellomycota* ($p = 0.039$) at the phylum level. At the genus level, distinct degrees of tourism disturbance strongly affected the relative abundance of *Mortierella* ($p = 0.028$). At the same time, no significant effects were noted for the relative abundance of other soil fungal genera ($p > 0.05$). The genus *Leohumicola* showed a significant decline in relative abundance under high disturbance intensity ($p < 0.05$), consistent with prior research findings[79]. *Ascomycota* and *Basidiomycota* in karst ecosystems demonstrate a greater ability to endure environmental stress and optimize resource utilization, equated to other fungi, which may contribute to their dominance in soil[80]. Mild disturbance (LD) may promote the proliferation of predatory fungi, such as *Kickxellomycota*, potentially enhancing microbial interactions. The observed modifications in *Mortierellomycota* align with the moderate disturbance hypothesis, meaning that this group is influenced by moderate disturbance. It is hypothesized that the influence of MD may promote the mineralization of readily decomposable organic matter. This process can boost short-term nutrient turnover efficiency. High-intensity interference significantly affects *Leohumicola*, likely due to its reliance on a microenvironment abundant in organic matter. Meanwhile, soil compaction and organic matter destruction by SD may inhibit its growth. The severity of disturbance increases the degradation of soil fungi, including arbuscular mycorrhizal fungi, with their recovery being a prolonged and irreversible process[81]. Thus, its extraordinary reduced abundance indicates significant soil degradation, which is particularly relevant for evaluating nature reserves' tourism carrying capacity threshold. Consequently, rocky desertification management requires systematically assessing tourism disturbance impacts on key fungal groups (e.g., *Ascomycota*, *Basidiomycota*, unclassified *Ascomycota*, *Leohumicola*) and their ecological functions. Such assessment underpins the strategic optimization of microbial community structure regulation, ultimately enhancing the stability and resilience of soil ecological functions. Optimizing strategies for regulating microbial community structure is necessary to enhance soil ecological functions' stability and resilience.

Soil microbial diversity becomes a critical ecological indicator of ecosystem health and function, highlighting microbial community stability and sensitivity to environmental gradients[82,83]. Soil fungal communities in karst grassland ecosystems ensure ecological functions and material cycling, equally important functional regulators[41]. The analyses of Chao1 and Ace index concerning Alpha diversity indicators suggested that moderate tourism disturbance (MD) significantly enhanced the abundance of fungal communities ($p < 0.05$). This finding highlights how moderate tourism disturbance may significantly improve fungal diversity by increasing microhabitat heterogeneity to a moderate extent. The effects of insufficient or excessive disturbance on microbial diversity seemed limited. This finding supports the hypothesis of the moderate disturbance doctrine. The Shanno and Simpson indices showed no statistically significant difference ($p > 0.05$) in diversity among the three treatments relative to ND. This phenomenon can be attributed to the idea that moderate disturbances create microhabitats, which act as sites for the growth of rare species, consequently promoting an increase in opportunistic r-strategists. It is plausible that the low relative abundance of rare species led to no significant alteration in overall diversity. A notable difference in community structure was identified among the ND, LD, MD, and SD treatment groups, indicating that differing levels of tourism disturbance seriously affected the beta diversity of soil fungal communities ($p = 0.001$). The study demonstrated slight variance in most alpha diversity metrics, whereas beta diversity displays significant separation. This phenomenon seems to originate from functional redundancy within the fungal community, where distinct fungal groups may perform similar functions. As a result, alpha diversity remained stable, whereas renowned changes in beta diversity were detected. The findings indicate that karst ecosystems exhibit considerable sensitivity and diversity in response to external disturbances, particularly tourism activities, due to their structural and functional fragility[36,84]. The mechanisms identified suggest that tourism management should account for local peaks in species populations and the extensive and varied impacts of different disturbance intensities on soil fungal community composition, functional diversity, and ecosystem stability throughout the region[85]. Integrating microbial ecology research with ecological restoration techniques can provide a solid scientific foundation and practical guidelines for improving ecological restoration strategies, strengthening ecosystem functions, and achieving sustainable development in karst regions[86,87].

Soil-dwelling fungi play a crucial regulatory role in terrestrial ecosystems. The interaction between the structure and function of these communities and the cycling of soil nutrients varies significantly across different disturbance scenarios[88]. Research indicates that varying land use patterns strongly influence the diversity of soil fungal communities and the characteristics of functional taxa associations[89,90]. The regulatory mechanisms of environmental factors on soil fungal communities demonstrated notable heterogeneity across varying disturbance intensities[91,92]. The results of this study signal that the spatial differentiation of soil fungal communities at both the phylum and genus levels is significantly associated with soil physicochemical factors. AN ($p = 0.019$) was identified as a key variable influencing the distribution of fungal communities at the phylum level, highlighting the critical ecological function of nitrogen in regulating community structure within fungal phyla. The findings suggested significant effects of SOC ($p = 0.018$), TN ($p = 0.045$), AN ($p = 0.025$), and AP ($p = 0.047$) on the distribution of fungal communities at the phylum level. This finding indicates that SOC and nitrogen are the primary environmental factors shaping alterations in fungal community structure at the phylum level. This phenomenon can be attributed to tourism's heightened disruption of karst soil habitats, leading to changes in soil carbon and nitrogen ratios.

The alterations indirectly influence the composition of soil fungal communities via plant-soil-microbe interactions. Gao and other researchers also identified total nitrogen (TN) as the primary factor influencing soil fungal community structure[91]. This finding is consistent with the results of the current study. Yan et al. conducted a detailed investigation revealing that tufted mycorrhizal fungi in karst regions were significantly influenced by TN[93]. In non-karstic regions, nitrogen, as a key nutrient, influences the composition of soil fungal communities. These findings demonstrate the critical role of nitrogen and organic carbon in shaping the ecological function and structural stability of soil fungal communities. This provides fresh insights into the environmental mechanisms driving soil microbial ecological processes. Tourism disturbance significantly alters soil ecosystem functional dynamics, as evidenced by shifts in soil nitrogen and organic carbon levels. Consequently, karst desertification management must prioritize tourism disturbance, given its broad ecological impacts. Future research should investigate the long-term driving mechanisms of soil nitrogen and disturbance intensity on soil fungal communities and examine these communities' functional potential and dynamic response mechanisms through the integration of microecological techniques[94,95].

Functional prediction analysis (FUNGuild) indicated that saprotrophic fungi were predominant across all functional guilds. This pattern likely resulted from increased litter decomposition rates due to high-intensity tourism disturbance, suggesting negative impacts on soil environments in karst tourism zones. Tourism activities could elevate litter or necromass inputs, offering supplementary saprotroph substrates. Additionally, changes in SOC, TN, and AP may lead saprotrophs to raise the secretion of extracellular enzymes (such as cellulases and chitinases) to compete for recalcitrant organic matter in conditions of restricted carbon/nitrogen availability. Low availability of available phosphorus, a critical limiting nutrient for plants and microorganisms, may increase carbon allocation from plants to symbiotic fungi. Certain saprotrophs secrete acid phosphatases to mineralize organic phosphorus. Decreased AP levels may enhance the expression of phosphate-solubilising functional genes in these microbes, possibly improving their competitive advantage. This finding supports the "disturbance-resource availability" hypothesis, which asserts that physical disturbance increases resource availability in the short term and promotes saprophytic strategies. Long-term stabilization has been demonstrated to facilitate mutually beneficial symbiosis[96,97].

Changes in the functional groups of fungi supported this finding. ANOVA revealed significant intergroup variability ($p < 0.05$) among the following taxa: Fungal Parasite-Plant Pathogen-Plant Saprotroph, Leaf Saprotroph, Dung Saprotroph-Undefined Saprotroph, Arbuscular Mycorrhizal, Plant Pathogen, Dung Saprotroph-Endophyte-Undefined Saprotroph, Lichenized-Undefined Saprotroph, and Animal Pathogen. Further pairwise comparative analyses proved that the disturbance gradient likely acts as an ecological filter. Low-intensity issues may favor specialized functional guilds, such as mutualists or endophytes, to sustain ecological stability in karst tourism regions. In contrast, high-intensity disturbance regimes are prone to the predominance of biotrophic or pathogenic functional guilds. This dominance benefits the decomposition of organic matter and may undermine the resilience of soil ecosystems. Additionally, phylum *Ascomycota* may support this trophic pattern via genus-level functional differentiation, as proven by the prevalence of the saprotrophic genus *Leohumicola* in severely disturbed (SD) sites. Distinct disturbance regimes have multiple impacts on the control of karst rocky desertification. Tourism disturbance significantly alters the composition of functional fungal groups, triggering considerable changes in soil ecosystem functional dynamics[98]. There is a need to improve research on the connection between different functional fungal communities and ecosystem services in soil across various disturbance scenarios. This will establish a scientific foundation for the ecological restoration of karst landscapes and the sustainable management of tourism regions concerning climate change and human activities[99].

The "disturbance gradient" established in this study depends on spatial distance from tourist trails, which indicates actual disturbance intensity. Due to the lack of direct in situ measurements of disturbance magnitude, we cannot completely rule out the possibility that the observed variations in soil and fungal communities along the distance gradient may be triggered by environmental covariates inherently linked to spatial proximity, rather than solely by tourism disturbance itself. Thus, our conclusion that disturbance is the primary driver of microbial community shifts aligns with the disturbance hypothesis, though the confines of this spatial surrogate limit it. Future research requiring direct quantification of disturbance intensity will be crucial for rigorously certifying this causal relationship. Future research should focus on the long-term monitoring of karst ecosystems affected by tourism disturbance. This research will require comprehensive ecological quality assessments and thoroughly examining tourism area management grounded in ecological principles. This research aims to enhance the accuracy and systematic scientific foundation for the ecological restoration of the World Karst Natural Heritage.

Data availability

Sequence data supporting the findings of this study have been deposited in the NCBI database at https://www.ncbi.nlm.nih.gov/bioproject/PRJNA1283545.

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Y.C.: Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. YS: Supervision, Methodology, Resources, Investigation, Funding acquisition. X.C.: Writing – original draft, Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. S.W.: Writing – review & editing, Methodology, Formal analysis, Data curation. S.S.: Formal analysis, Supervision, Data curation.

Competing interests

The authors declare no competing interests.

Additional information

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