



Relative importance of altitude shifts with plant and microbial diversity to soil multifunctionality in grasslands of north-western China

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Abstract

Background and aims Above- and belowground biodiversity determines the capacity of ecosystems to provide multiple functions simultaneously (i.e., multifunctionality), while their relative importance along environmental gradients remains unclear. Our

objective of this study was to investigate how plant and microbial diversity along an altitudinal gradient affected soil multifunctionality in grasslands.

Methods The effects of plant and microbial (including bacteria, fungi and archaea) diversity on soil multifunctionality were estimated along a 2300 m altitudinal gradient across six grassland types in the Tianshan Mountain, China. The soil multifunctionality was calculated based on 12 parameters related to carbon, nitrogen, phosphorous cycling, and soil nutrient status.

Results The relative importance of plant and microbial diversity to soil multifunctionality shifted at an altitude of 1900 m while threshold for each soil

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function varied along altitudinal gradient. At low altitudes (<1900 m), plant species richness showed a robust positive effect and had a more substantial impact on soil multifunctionality than microbial diversity. Altitude had a significant effect on plant species richness via indirect means by altering soil moisture. At high altitudes (>1900 m), soil multifunctionality was influenced by a combination of plant and microbial diversity. Similarly, fungal richness was positively associated with soil multifunctionality, while archaeal richness had the opposite effect.

Conclusion The effect of plant and soil microbial diversity on soil multifunctionality was mediated by altitude in grasslands, which can guide the restoration efforts aimed to maximize soil multifunctionality in grassland ecosystems.

Keywords Plant species richness · Soil microbial diversity · Soil multifunctionality · Altitude

Introduction

Understanding the relationship between biodiversity and the simultaneous maintenance of multiple ecosystem functions (i.e., multifunctionality) has been a core topic in ecology over the past decades (Gamfeldt et al. 2008; Isbell et al. 2011; Soliveres et al. 2016). A large number of studies have revealed that ecosystem multifunctionality could be directly determined by both plant species richness and microbial diversity (Hector and Bagchi 2007; Delgado-Baquerizo et al. 2016; Li et al. 2021). Plant species richness is strongly connected to ecosystem functioning (Jing et al. 2015), as diverse plant communities have a higher chance of containing species that are well adapted to a particular environment. Soil microbes also play a key role in maintaining ecosystem functions by promoting decomposition, nutrient cycling, and resource availability (Wagg et al. 2019; Delgado-Baquerizo et al. 2020). With the advent of 21st century, biodiversity and functionality research has shifted from solely focusing on single trophic level transitions to investigating biodiversity-multifunctionality interactions across multiple trophic levels. This shift stimulate to investigate the roles of plant and soil microbial diversity on soil multifunctionality (Valencia et al. 2018; Schuldt et al. 2018). Global climate change

and associated various environmental conditions are critically affecting biodiversity and have diverse ecological consequences. Hu et al. (2021) reported an aridity driven shift in biodiversity–soil multifunctionality relationships. However, the extent to which these relationships changed and their relative impacts influenced by other environmental gradients especially altitude shift at spatial scales remained largely unknown. These limitations affect our predictions and understanding for the impact of relative altitude shift with changing plant and soil microbial biodiversity to soil multifunctionality.

It is reported that plant and soil microbial diversity have the relative importance on ecosystem functioning along the environmental gradient (Delgado-Baquerizo et al. 2019). A recent study found that in less arid regions, soil multifunctionality was mostly affected by the positive effect of plant species richness while in arid regions it was mostly controlled by microbial diversity (Hu et al. 2021). In natural ecosystems, plant species richness, microbial diversity and the degree of aridity were co-varied along altitudinal gradient and are completely related to soil multifunctionality (Körner 2007; Malhi et al. 2010). It indicates that the relative importance of plant and microbial diversity on soil multifunctionality also regulated by altitude shifts. Altitudinal gradients are among the most powerful phenomena for ‘natural experiments’ of testing ecological and evolutionary responses of microbes to geophysical influences (Körner 2007). Altitudinal gradients caused the regular shifts in environmental factors (e.g., moisture and temperature) leading to water and heat redistribution and complex adaptations to changes in the vertical distribution of vegetation (Malhi et al. 2010).

In low-altitude regions, adequate hydrothermal conditions are suitable for plant growth (Hautier et al. 2009). The consequent resources input to soils through plant exudates are considered the major regulators of soil multifunctionality (Petchey and Gaston 2002; Bai et al. 2007). In high-altitude regions, plant growth is limited by the temperature while microbes are relatively cold-tolerant as organic matter and nutrient transformation have been controlled by these microorganisms (Xu et al. 2014). Based on these reasons, an increasing number of studies have reported that plant richness and microbial diversity generally respond nonlinearly to environmental gradients due to the variation in thresholds (Berdugo et al. 2020; Hu

et al. 2021). It indicates that variations in thresholds between plant species richness and microbial diversity played an important role in regulating soil multifunctionality along an altitudinal gradient.

Soil functions are essential for regulating global biogeochemical cycles, such as soil carbon, nutrient cycling and storage (Bardgett and van der Putten 2014; Manning et al. 2018; Crowther et al. 2019). Therefore, it is important to understand the impact of biodiversity on soil functions. The soil multifunctionality index aggregates various soil functions into a single index in contrast to a single soil function. Hence, soil multifunctionality index provides the opportunity to interpret the simultaneous response of multiple soil functions to estimate the overall impact of treatments on ecosystems (Delgado-Baquerizo et al. 2017; Zheng et al. 2019). Previously, the soil multifunctionality index was calculated to represent multiple functions that regulate soil biogeochemical cycles (Maestre et al. 2016; Crowther et al. 2019). Currently, soil multifunctionality is frequently used to investigate the biodiversity and ecosystem functions.

The Tianshan Mountains, which lie in the vicinity of Eurasia, are one of the seventh largest mountain ranges in the world. Previous independent studies in this area have revealed that climate, plant species richness, microbial diversity and soil function changed differently with increasing altitude. It provides us an ideal system to examine the relative importance of plant and microbial diversity on soil multifunctionality. On the basis of these investigations, we evaluated plant species richness, microbial diversity (soil archaea, bacteria, and fungi richness), soil chemical properties, and 12 soil functions at 34 sites across 6 grassland types along 2300 m altitudinal gradient. We tended to address the following scientific questions: First, how individual soil function changes along altitudinal gradient? Second, how plant species richness and microbial diversity vary along altitudinal gradient? Third, how do altitude, species richness and microbial diversity affect soil multifunctionality in terms of relative importance and influencing pathways? We predicted that (1) along the altitudinal gradient, soil individual function showed a nonlinear response and (2) in the low-altitude region plant species showed the more richness and the higher importance to soil multifunctionality, while at high-altitude region the soil microbial diversities

showed well-established communities which are highly important to soil multifunctionality. (3) Different altitudes will cause changes in physical and chemical factors in different areas affecting plant species and microbial diversity which will further affect soil multifunctionality.

Materials and methods

Field survey and sampling

Soil samples and plant community characteristics were collected from 34 sites along an altitudinal gradient from 780 to 3100 m in Tianshan Mountain, Xinjiang Uygur Autonomous Region, China (Fig. S1). These sites encompassed six main steppe types, i.e., alpine meadow, mountain meadow, temperate meadow steppe, temperate steppe, temperate desert steppe, and temperate desert. The dominant plant species are *Carex* spp., *Artemisia* spp., and *Polygonum* spp. (alpine meadow); *Bromus* spp., and *Poa* spp. (mountain meadow); *Stipa* spp., and *Phlomis* spp. (temperate meadow steppe); *Stipa* spp., *Leymus* spp., and *Cleistogenes* spp. (temperate steppe); *Anabasis* spp., *Kalidium* spp., and *Seriphidium* spp. (temperate desert steppe and temperate desert).

The longitude, latitude, and altitude information were recorded using a hand-held GPS unit (eTrex Venture; Garmin, Olathe, KS, USA). Climate attributes, including the mean annual temperature (MAT) and mean annual precipitation (MAP), of each sampling site were obtained from a national climate database (<http://data.cma.cn>). This information is provided in Supplementary Table 1.

Field sampling was conducted during the wet season (June to September) when biological activity and productivity were maximal. Briefly, a 100 m × 100 m survey area was first set up randomly in each sample plot. After recording the longitude, latitude and altitude, three standard 1 m × 1 m quadrats ($n=3$) were then randomly selected along the diagonals in the survey area. Collectively, 102 plant and soil samples were collected from 34 sites. Site-level grasses and dwarf shrubs were harvested to estimate plant species richness. Site selection was based on two principles. First, we selected all grassland types occurring along the altitudinal gradient. Second, each selected grassland type had no grazing disturbances,

pest and disease infestations, and well-grown plants. Corresponding soil cores (500 g of mixed soil sample at 0–10 cm depth) were also randomly collected per 1-m² plot. Following field sampling, the soil was sieved (<2 mm mesh) and separated into two parts: one part was immediately frozen at -20 °C for characterizing soil microbial diversity, and the other part was temporarily stored at 4 °C for soil enzymes and chemical analyses. The soil moisture content was determined gravimetrically after drying in an oven at 105 °C to a constant weight. Soil pH was measured in a 1:2.5 soil/water ratio solution with a compound electrode (PE-10, Sartorius, Germany).

Measurement of soil functions

Soil total carbon and total nitrogen were quantified with an Elemental Analyzer 3000 (Euro Vector, Italy) following standard protocol. The soil inorganic carbon content was determined based on volumetric measurements by a Calcimeter 08.53 (Eijkelkamp, The Netherlands), and the soil organic carbon content was calculated from the total soil carbon minus the soil inorganic carbon. Soil available phosphorus was assessed following a 0.5 M NaHCO₃ extraction. Flame spectrophotometry was used to determine soil available potassium (Sarker et al. 2018). The activity of extracellular soil enzymes (including α -1,4-glucosidase, β -1,4-glucosidase, β -1,4-xylosidase, N-Acetyl-glucosaminidase, L-leucine aminopeptidase, β -D-cellobiosidase, and phosphatase) was measured in 1 g of soil by fluorometry (Saiya-Cork et al. 2002; DeForest 2009).

Assessment of soil multifunctionality

Soil multifunctionality was assessed by commonly used multifunctionality techniques of averaging method and multiple-threshold approach (Jing et al. 2015; Hu et al. 2021). Twelve soil functions were included in this study and these soil functions represented a wide range of ecosystem services. It includes the stocks and active fractions of nutrients e.g., soil total carbon, total nitrogen, available phosphorus, and available potassium. In addition, soil extra-cellular enzymes i.e., α -1,4-glucosidase, β -1,4-glucosidase (starch degradation), N-Acetyl-glucosaminidase (chitin degradation), L-leucine aminopeptidase (peptides degradation), β -D-cellobiosidase (cellulose degradation),

β -1,4-xylosidase (xylan degradation), and phosphatase (phosphorus mineralization) were evaluated to partially characterize soil nutrient cycling processes. Overall, these soil functions served as a good indicator for the processes underlying of nutrient cycling, biological productivity, and the build-up of nutrient pools (Jax 2010). In the averaging method, the soil functions were normalized and standardized using the Z score transformation and averaged to obtain the soil multifunctionality index for each field site. The averaged multifunctional index provided a simple and intuitively interpretable amount of the ability of an ecosystem to provide multiple functions simultaneously, but it did not allow for potential constraint of substitution between different functions (Byrnes et al. 2014; Manning et al. 2018). In practice, different functions could not be used as substitutes, which means that a decrease in one function cannot be compensated by an increase in another (Gamfeldt et al. 2008). To solve this problem, we need to evaluate whether multiple functions are simultaneously performing at high levels and the multiple-threshold approach was used. The multiple-threshold approach calculated the number of functions in each ecosystem that reach a certain threshold. This threshold is normally some percentage of the maximum observed value of each function. However, it is often difficult to accurately select the appropriate threshold value. Consequently, we plotted the range of threshold between 0% and 100% to evaluate the effect of diversity on multifunctionality. We selected this approach in order to examine the change of the shape of the fitted curve at different thresholds, rather than evaluating the statistical evidence for any single curve (Byrnes et al. 2014). The maximum value is necessarily to measure to control the potential artifacts arising from the data, while the selection of the highest attainable value from a function is necessarily a single observation, which could also be an outlier due to observation error, process noise, or other factors. Here, we calculated the mean of the $n+1$ as a highest measurement for each function across all richness levels in plot values where n is the smallest sample size of each richness treatment level (Byrnes et al. 2014; Perkins et al. 2015). We assessed the soil multifunctionality using this maximum value which is the mean of thirty-five highest observations for each function ($n=34$). Combining these two approaches to measure multifunctionality performance we can better determine the relationship between biodiversity and multifunctionality (Byrnes et al. 2014).

Amplicon sequencing and microbial data processing

Soil DNA was extracted using a MoBio PowerSoil DNA Isolation Kit (Mobio Laboratories, Solana Beach, CA, USA) according to the manufacturer's protocol. The primers 338 F (5'-ACTCCTACGGGAGGCAGCAG-3') and 806R (5'-GGACTACH VGGGTWTCTAAT-3'), ITS5F (5'-GCATCGATGAAGAACGCAGC-3') and ITS1R (5'-TCCTCCGCTTATTGATATGC-3'), and 524F10extF (5'-TGYCAGCCGCCGCG GTAA-3') and Arch958RmodR (5'-YCCGGCGTTGAVTCCAATT-3') were used for bacteria (Caporaso et al. 2011), fungi (Yang et al. 2022), and archaea (Wang et al. 2022), respectively, in high-throughput sequencing based on an Illumina MiSeq System (Roche, Switzerland).

The obtained sequencing data were analyzed with the UPARSE pipeline. Clean reads were obtained by merging the forward and reverse reads, and the merged sequences were truncated to 420, 240 and 420 bp for bacteria, fungi, and archaea, respectively. The low-quality sequences and singletons were filtered. The "unnoise3" command was used to identify and correct sequencing errors and remove chimeras. Then, the obtained sequences were clustered at a 97% threshold for further study. Taxonomic identification was performed based on the RDP classifier with default databases.

Metrics of plant and soil microbial diversity

The total number of plant species (plant species richness), observed archaeal OTUs (soil archaeal richness), observed bacterial OTUs (soil bacterial richness), and observed fungal OTUs (soil fungal richness) were used to represent the biodiversity. The FUNGuild tool was employed to further divide the fungal OTUs into saprotrophs, pathogens, and symbiont trophic modes based on the taxonomic classification of the fungi (Nguyen et al. 2016). We also defined the soil microbial diversity index, calculated by averaging the standardized values of archaeal, bacterial, and fungal richness, to represent the overall changes in soil microbial diversity (Wagg et al. 2014).

Statistical analyses

In order to improve the normality of the residuals, all soil functions and plant species richness were transformed by \log_{10} -transformation. To investigate how individual soil function changes along an altitudinal

gradient, we used linear and nonlinear [quadratic and generalized additive models (GAMs)] regressions and selected the model with the lower AIC value (Fig. 1). Each of these models produced a different point that described the point at which the altitudinal gradient changes (i.e., the threshold) to justify the shift in the nonlinear relationship that being assessed. The regression coefficient and significance were determined for the pre- and post- threshold regions (Table S2).

An analysis of variance based on the type-I sum of squares in a linear mixed-effects model was employed to test the relationships between the multiple biotic variables (plant species richness and the soil microbial diversity index), altitude, and soil multifunctionality by considering section location as a random term (Table S3). The sampling site is located on the northern slopes of the Tianshan Mountains. According to previous studies (Li et al. 2022) this section has been divided into east, middle and west, which have distinct environmental differences. Sampling sites within a given region have ecological similarities. The linear mixed-effects models were performed using the R package "lme4". In addition, marginal (variance explained by fixed factors) and conditional (variance explained by fixed and random factors) R^2 values were calculated using the R package "piecewiseSEM". The variance inflation factor (VIF) was used to evaluate the risk of multi-collinearity, and variables with $VIF < 10$ were selected in all cases. For example, there is a strong collinear relationship between altitude and MAP and MAT, so we made it clear in the SEM analysis that in addition to the two factors of MAT and MAP, only the altitude was retained. Nonlinear changes in the standardized coefficients of biodiversity were obtained by a linear mixed-effects model (Table S3). The standardized coefficients of each fixed term were then bootstrapped with moving-window analysis within each subset window ($N=500$ independent simulations), which was matched to the altitude value across the 34 sites. Ultimately, we fitted linear and nonlinear regressions to the bootstrapped coefficients of biodiversity along altitude applying packages "parallel" and "lme4" in R, and identified the altitudinal gradient thresholds for variations in biodiversity coefficients (Hu et al. 2021). For the calculation of the standardized coefficients of the mixed linear model, we followed the three principles: First, all independent variables were standardized, i.e., each independent variable was subtracted

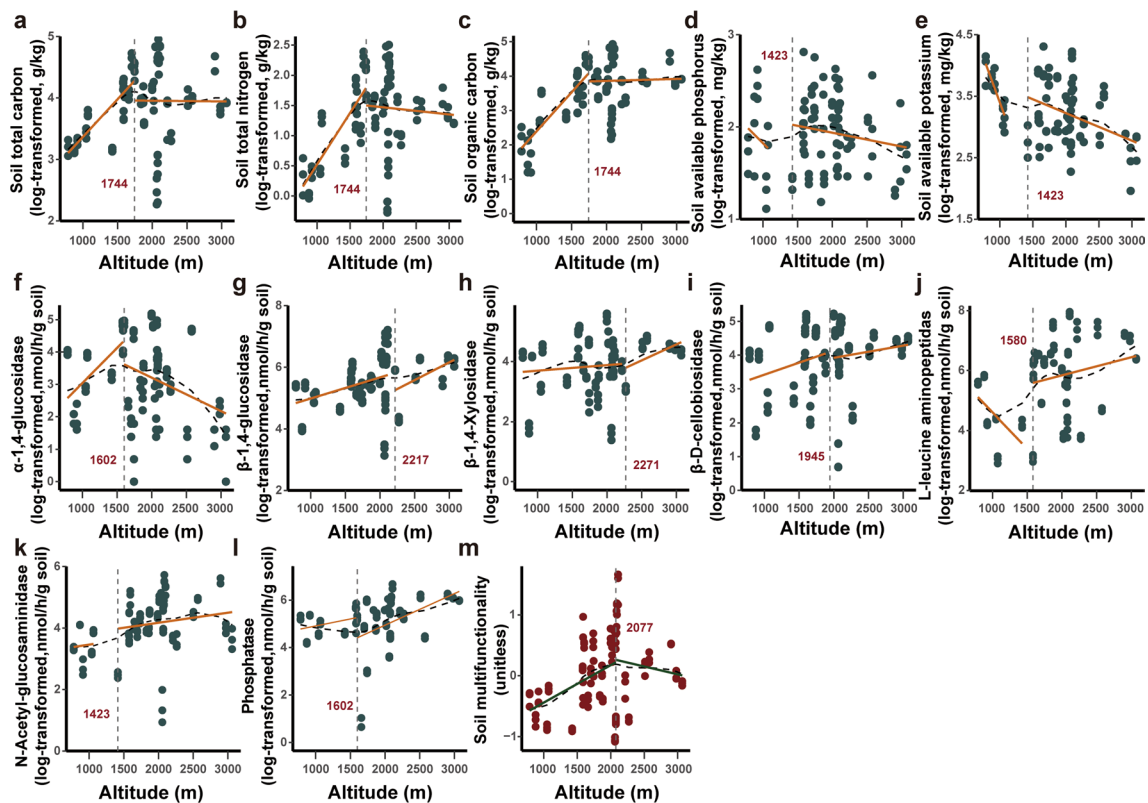


Fig. 1 Nonlinear responses of individual soil functions and multifunctionality to increasing altitudinal. Nonlinear responses of soil total carbon (a), soil total nitrogen (b), soil organic carbon (c), soil available phosphorus (d), soil available potassium (e), α -1,4-glucosidase (f), β -1,4-glucosidase (g), β -1,4-Xylosidase (h), β -D-cellobiosidase (i), L-leucine aminopeptidase (j), N-Acetyl-glucosaminidase (k), Phosphatase (l)

from its mean and divided by its standard deviation. Second, we performed a linear regression on the standardized independent variables to obtain the regression coefficients. Third, we divided the regression coefficient by the standard deviation to obtain the standardized coefficient. We assessed the significance of the biodiversity bootstrapped standardized coefficients at 95% confidence intervals for each subset window to further support the altitude thresholds identified here. All boxplots were drawn using the “ggplot2” package in R. Then, we used an unpaired two-sided Mann-Whitney U-test to compare the slope evaluated before and after each threshold, visualized by the “ggplot2” package. Nonlinear regressions were a better fit to the data and there was a possibility that thresholds were present. Therefore, we explored the

and soil multifunctionality (m) to altitude, and their respective altitude thresholds. The black and blue dashed lines indicate the nonlinear trends fitted by quadratic or generalized additive models (GAMs). The grey dashed lines and red inset numbers represent the identified altitude thresholds. The orange and green solid lines denote the linear fit at both sides of each aridity threshold

presence of thresholds only when nonlinear models were a better fit for the data. We used the “*chngpt*” and “*gam*” packages in R to fit segmented/step/segmented and GAM regressions, respectively, and the *segmented* package was used to fit segmented regressions with two thresholds (Berdugo et al. 2020). The presence of an altitude threshold means that once an altitudinal level is reached, a given variable changes its value (i.e., discontinuous threshold) or its relationship with the altitudinal gradient (i.e., continuous threshold) abruptly. The Akaike information criterion (AIC) was also used to choose the best threshold model and the corresponding threshold.

After the altitude thresholds were determined, ordinary least squares (OLS) regression was employed to elucidate the relationship between each

above- and belowground biodiversity component at high and low altitudes and soil multifunctionality. Moreover, using the “*multifunc*” package in *R*, the relationships between biodiversity and soil multifunctionality were analyzed by multiple threshold approach. In addition, partial linear regression and general linear models (GLMs) assume that biodiversity and/or abiotic effects are additive and not interactive. We had fitted the structural equation models (SEMs) to infer the relative importance of abiotic (altitude, soil pH, and soil moisture content) and biotic (plant, archaeal, bacterial, and fungal richness) factors on soil multifunctionality. A prior model based on the known effects or relationships among the predictors of soil multifunctionality was established first, and all abiotic and biotic data were normalized. These data sets were fitted to the model and tested for their overall fit using maximum likelihood estimation methods. Before modeling, bivariate correlations were checked between all variables to ensure that a linear model was appropriate ($r < 0.8$). Finally, the chi-squared test (χ^2), degrees of freedom (df), comparative fit index (CFI), probability level (P) and root mean square error of approximation (RMSEA) were calculated. Where the fit was deemed good when $\chi^2/df \leq 2$, $0.05 < P \leq 1.00$, $CFI \leq 1.00$, $0 \leq RMSEA \leq 0.05$ (Schermelleh-Engel et al. 2003). SEM models were performed with the software AMOS 22.0. All statistical analyses were performed using *R* version 4.1.2.

Results

Trends of individual soil function with increasing altitude

With increasing altitude, individual soil functions exhibited a nonlinear regression but varied in their response trends and thresholds. Remarkably, soil total carbon, total nitrogen, organic carbon, α -1,4-glucosidase, β -1,4-glucosidase and phosphatase increased in the pre-threshold altitude region, with thresholds ranging from 1602 to 2217 m (Fig. 1a–c, f, g, l). Available potassium, L-leucine aminopeptidase and N-Acetyl-glucosaminidase exhibited a negative correlation with increasing altitude at pre-threshold altitude (Fig. 1e, j, k). At the post-threshold altitude region, soil available phosphorus, available potassium, α -1,4-glucosidase and β -1,4-Xylosidase gradually diminished

with increasing altitudinal gradient, while β -1,4-glucosidase and phosphatase increased significantly (Fig. 1d–h, l). In general, soil multifunctionality also exhibited a unimodal pattern with increasing followed by decreasing along the altitudinal gradient (Fig. 1m and Table S2). Similarly, strong and positive effects of altitude on soil multifunctionality were observed when using the multiple-threshold approach (Fig. S2).

Relationship between biodiversity and soil multifunctionality along an altitudinal gradient

As predicted, plant species richness and the soil microbial diversity index showed the varied effects on soil multifunctionality and were both non-linear throughout the altitudinal gradient (Fig. 2 and Table S3). The threshold for the soil microbial diversity index (1945 m) lagged behind the threshold for plant species richness (1845 m), indicating that plant richness is more sensitive to changes in altitude (Fig. 2a). The positive effect of plant species richness on soil multifunctionality diminished sharply at an altitude of 1845 m (Fig. 2a). Again, these results were evidenced by the significant bootstrap coefficient for plant species richness at lower altitudes (Fig. 2c). In contrast, the slope of the relationship between microbial diversity indices and soil multifunctionality changed abruptly at an altitude of 1945 m, showing a sharp decline (Fig. 2a, b). Plant species richness had a stronger influence on soil multifunctionality than the microbial diversity index at low altitudes. The effect of plant species richness on soil multifunctionality diminished with increasing altitude, while the effect of microbial diversity on soil multifunctionality increased gradually. As the biodiversity-soil multifunctionality relationship clearly shifted at an altitude of approximately 1900 m, the altitudinal gradients were further divided into two groups (i.e., sites with altitudes < 1900 m and > 1900 m) to represent low- and high- altitude regions.

The effect of plant and microbial diversity on soil multifunctionality in low- and high- altitude regions

Soil multifunctionality was positively ($P < 0.05$) correlated with plant species richness (Fig. 3a, black line) but had no significant correlation with the soil microbial diversity index (Fig. 3b) across the altitudinal gradient (considering both low- and high-altitude

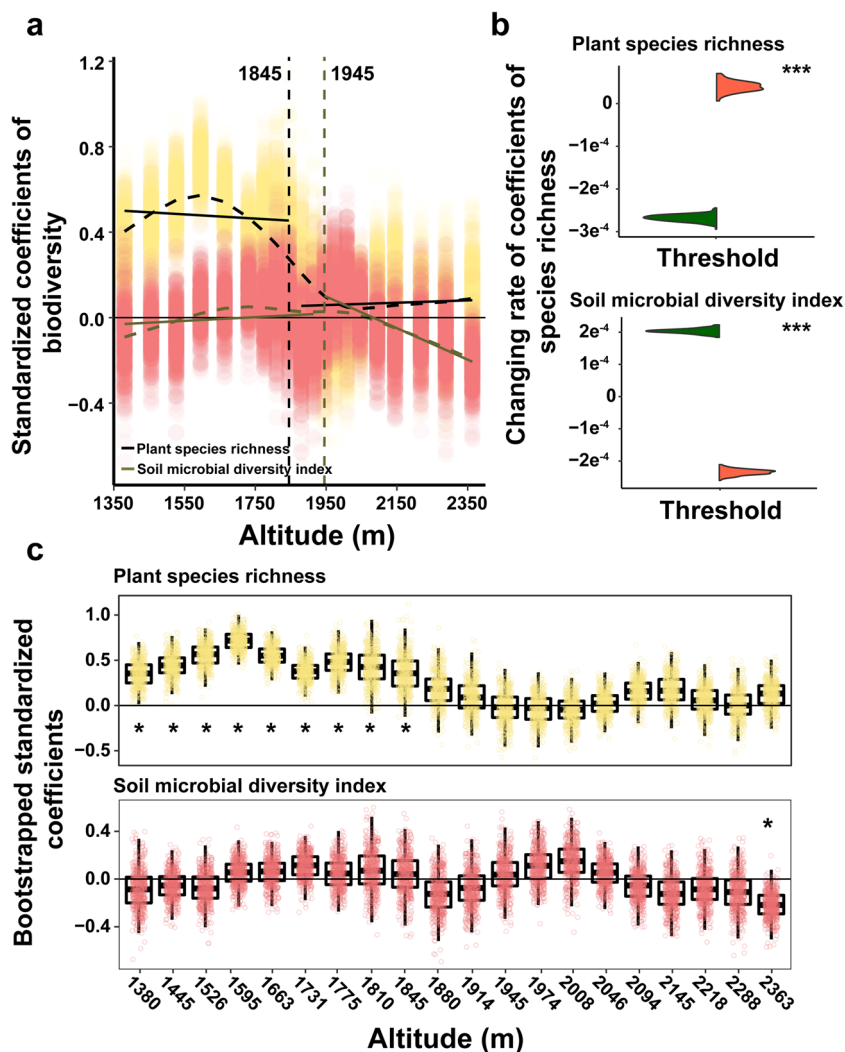


Fig. 2 Nonlinear changes in the relationships between biodiversity and soil multi-functionality along an altitudinal gradient. Nonlinear changes in standardized coefficients of biodiversity (**a**) were obtained from a linear mixed-effects model (Table S3) throughout a moving subset window along an altitudinal gradient. The dots indicate the bootstrapped coefficients of the fixed terms shown for each subset window, and the dashed lines denote the nonlinear trend fitted. In **a**, the vertical dashed lines and inset numbers represent the altitudinal thresholds identified, and the solid lines represent the linear fit on both sides of each altitudinal threshold. Violin diagrams show bootstrapped slopes (**b**) of the two regressions existing on each side of the altitudinal threshold found for plant species rich-

ness and the soil microbial diversity index in (**a**) (dark green represents the regression before the threshold, and orange represents the regression after the threshold). Significant differences before and after the threshold were determined using an unpaired two-sided Mann-Whitney U-test, and the significance level was $P < 0.001^{***}$. Boxplots (**c**) demonstrate the distribution of bootstrapped standardized coefficients corresponding to those in (**a**) for each subset window ($N = 500$ independent simulations). Boxplots show the median (center line) and 25th and 75th percentiles of each distribution. Asterisks indicate significant values of coefficients with 95% confidence intervals (one-sided $P \leq 0.05$)

regions). Nevertheless, when we investigated the effects of microbial richness on soil multifunctionality at higher resolution, we found that soil multifunctionality decreased with archaeal richness ($P < 0.05$)

but increased with fungal richness ($P < 0.05$) (Fig. 3c and e, black line) across the altitudinal gradient. Similarly, analysis with the multiple-threshold and the linear mixed-effects models exhibits the same results

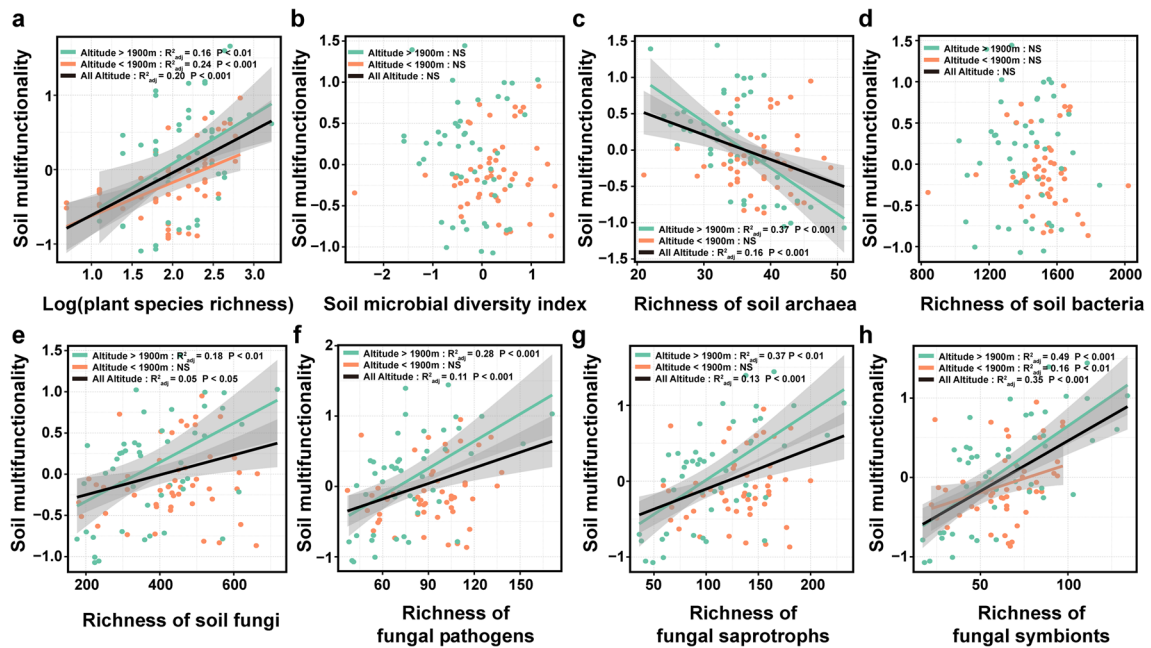


Fig. 3 Relationships between plant and microbial diversity and soil multi-functionality. Relationships between plant species richness (a), the soil microbial diversity index (b), soil archaeal richness (c), soil bacterial richness (d), soil fungal richness (e), the richness of fungal pathogens (f), the richness of fungal saprotrophs (g), the richness of fungal symbionts (h)

(Fig. S3 and Table S3). In low-altitude regions, plant species richness and fungal symbiont richness had a positive ($P < 0.05$) effect on soil multifunctionality, while the other factors had no effect (Fig. 3a, h, orange line). In high-altitude regions, the richness of plants, total fungi, fungal pathogens, fungal saprotrophs, and fungal symbionts exhibited a positive ($P < 0.05$) relationship with soil multifunctionality (Fig. 3a, e–h, green line), while archaeal richness had the opposite effect (Fig. 3c, green line). Overall, soil microbial richness at high altitudes had a greater impact on soil multifunctionality than at low altitudes. But the soil microbial diversity index was not enough related to soil multifunctionality, suggested some limitations that fungi had a significant positive effect on soil multifunctionality at high altitude, while archaea had a negative effect, which cancelled each other out. As high moisture and low temperature accumulated high organic matter stock that support soil biota with low metabolic activity, which may reduce the impact of soil microbial richness on soil multifunctionality at high altitudes.

and soil multi-functionality at sites with altitudes < 1900 m and > 1900 m, as well as across all field sites. Lines represent the fitted linear OLS model. Solid lines denote statistically significant (two-sided $P \leq 0.05$) relationships. Shaded areas represent the 95% confidence interval of the regression lines

The multiple-threshold approach was employed to further validate the effect of biodiversity on soil multifunctionality (Fig. 4). In the low-altitude regions, the relationship between plant species richness and soil multifunctionality peaked at the threshold of 53% (T_{mde}) with a slope of 0.51 (R_{mde}), indicating that an increase of at least ~2 plant species at this time improved 1 soil function [Fig. 4a (a), (e)]. The maximum possible effect of plant richness on soil multifunctionality (P_{mde}) at low altitudes was 72%. Moreover, the effect of plant species richness on the number of functions surpassing different thresholds of multi-functionality was mainly positive, whereas a large proportion of the belowground diversity (soil archaeal, bacterial, and fungal richness) effect was negative (Fig. 4a). The highest T_{mde} , R_{mde} and P_{mde} indicated that the promotion effect of plant species richness on soil multifunctionality was strongest in low-altitude regions (Table S4). In high-altitude regions, the T_{mde} of fungal richness associated with soil multifunctionality was 16% [Fig. 4b (l), (p)]. The realized maximum effect of fungal diversity on soil multifunctionality was 0.01 (R_{mde}), which demonstrated that

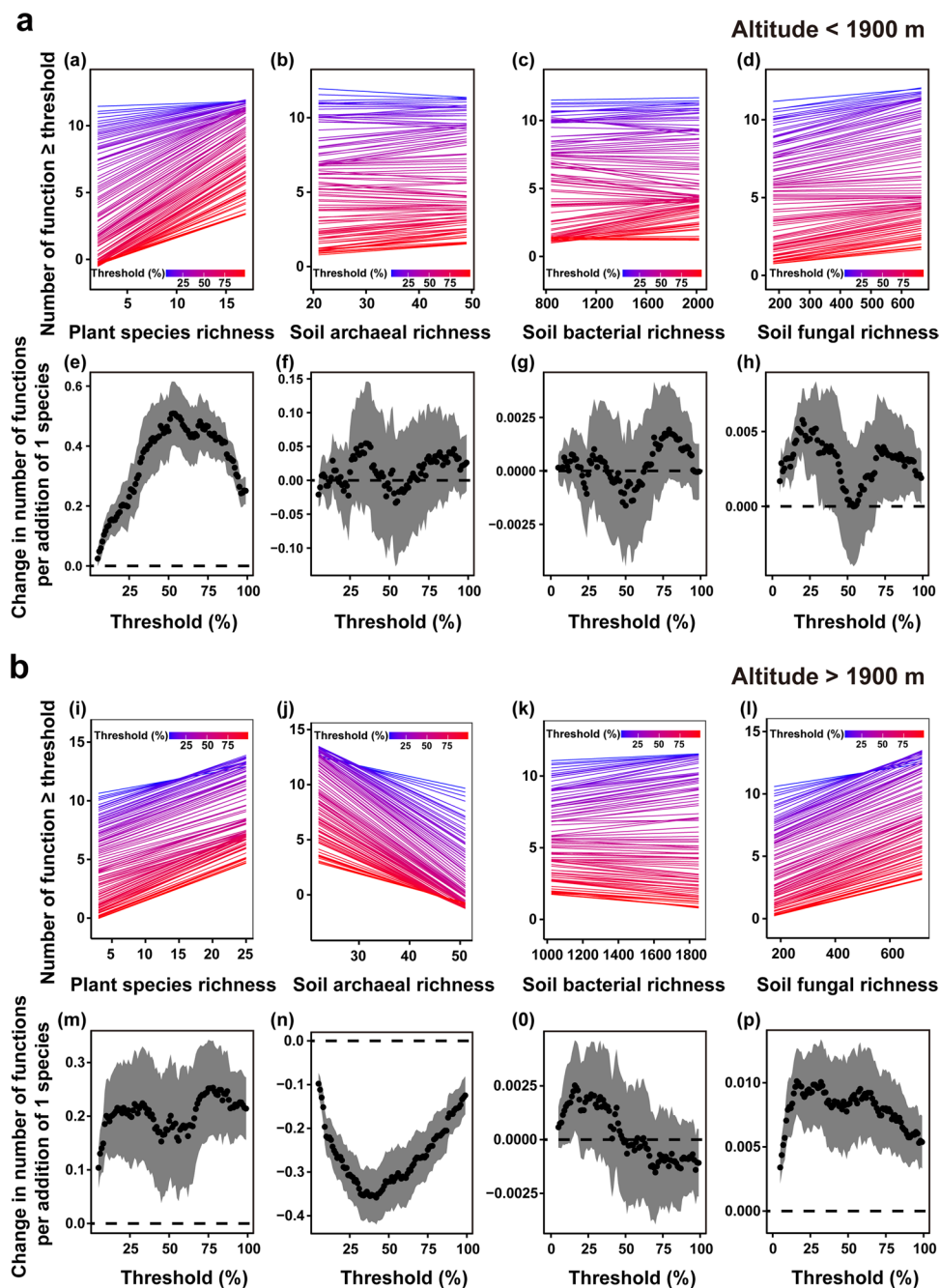


Fig. 4 Relationship between plant and microbial diversity and soil multi-functionality based on the multi-threshold approach with all samples. Relationships between plant and microbial diversity and the number of functions above a threshold of the maximum observed function across the full range from 0–100%. Colors indicate different thresholds, as shown in the legend (blue=low, red=high), with cooler colors denoting

lower thresholds and warmer colors denoting higher thresholds. (e–h, m–p) The slope of the relationship between species richness and the number of functions at or above a threshold of the maximum observed functions. The dashed line and shaded area indicate the slope and the 95% confidence interval of the regressions

the improvement of 1 function required approximately 100 fungal species in high-altitude regions (Table S4). In addition, plant species richness and fungal richness had a significant effect on the maintenance of multiple soil functions operating at higher performance levels compared with bacterial richness (Fig. 4b). The positive effect of plant richness on soil multifunctionality was significantly stronger at low altitudes than at high altitudes (Table S4).

The effect of biodiversity and abiotic factors on soil multifunctionality in low- and high- altitude regions

We fitted SEMs to infer the direct and indirect effects of biotic (plant species richness, soil archaeal, bacterial, and fungal richness) and abiotic (altitude, soil pH, and soil moisture content) factors on soil multifunctionality in low- and high-altitude regions (Fig. 5). In low-altitude regions, the influence of altitude on soil multifunctionality was mediated through soil moisture content, plant species richness, and fungal richness (Fig. 5a). Fungal richness indirectly enhances soil multifunctionality by increasing plant species richness, while plant species richness and soil moisture content have direct contributing effects on soil multifunctionality (Fig. 5a). In high-altitude regions, archaeal richness was influenced by a combination of altitude and soil moisture content, which negatively affected soil multifunctionality (Fig. 5b). Soil fungal richness exhibited a direct positive impact on soil multifunctionality in high-altitude regions (Fig. 5b). Under this circumstance, altitude directly or indirectly (via soil moisture content) affected plant species richness, resulting in a positive effect of plant species richness on soil multifunctionality (Fig. 5b). At both high and low altitudes, there was a clear effect of increased plant species richness on soil multifunctionality owing to improved moisture, showing the importance of moisture to plant species richness.

Discussion

As we predicted, all soil functions and multifunctionality responded in a nonlinear manner to increasing altitude. Our study found that the relative importance of plant species richness and microbial diversity to soil multifunctionality shifted at the altitude of 1900 m at Tianshan Mountain. Contrary to our

predictions, plant species richness had a significant positive effect on soil multifunctionality across the entire altitudinal gradient. Particularly, soil multifunctionality below 1900 m was mostly driven by plant species richness, while above 1900 m it was determined by combination of plant, fungal and archaeal richness. This phenomenon could be explained by following reasons.

Plant species richness improved soil multifunctionality in low- and high- altitude regions

Theories and empirical studies provide evidence that changes in precipitation and temperature have a significant impact on soil microbial diversity, plant communities, and the various ecosystem services (Castro et al. 2009; Pasari et al. 2013). Climate warming and the following reduced moisture strongly filtered the existing microbial species, which may also result in the loss of biodiversity (Guo et al. 2019; Wu et al. 2022). A suitable environment increased the biotope space available to plant species, enhancing the potential for niche complementarity among species and resource inputs to soil, thus further strengthening the positive impact of plant richness on soil multifunctionality (Maestre et al. 2012). The SEMs supports this mechanism, and we similarly found that moisture conditions indirectly act on soil multifunctionality through strong effects on plant and microbial richness (Fig. 5). Despite the grass layer was low and simple in structure and a short growing period with slow root turnover at high altitudes (Cui et al. 2015), while the adequate moisture promoted the positive effect of plant species richness on soil multifunctionality (Fig. 5b).

Biodiversity can further change the availability of various resources and soil functions through resources turnover (Delgado-Baquerizo et al. 2020), which may be another reason for plant richness and also enhancing soil multifunctionality. Plant species richness had stronger effects on soil multifunctionality at low altitudes (Figs. 2, 3 and 4). A possible reason is that the higher dry matter content and protein content of grass populations at lower altitudes (Han 2007) enhance net primary production thus increasing litter input into the soil and stimulating soil nutrient cycling and plant turnover rates (Hooper and Vitousek 1998; Ma et al. 2010; Valencia et al. 2018), and ultimately enhancing soil multifunctionality. Furthermore, approximately

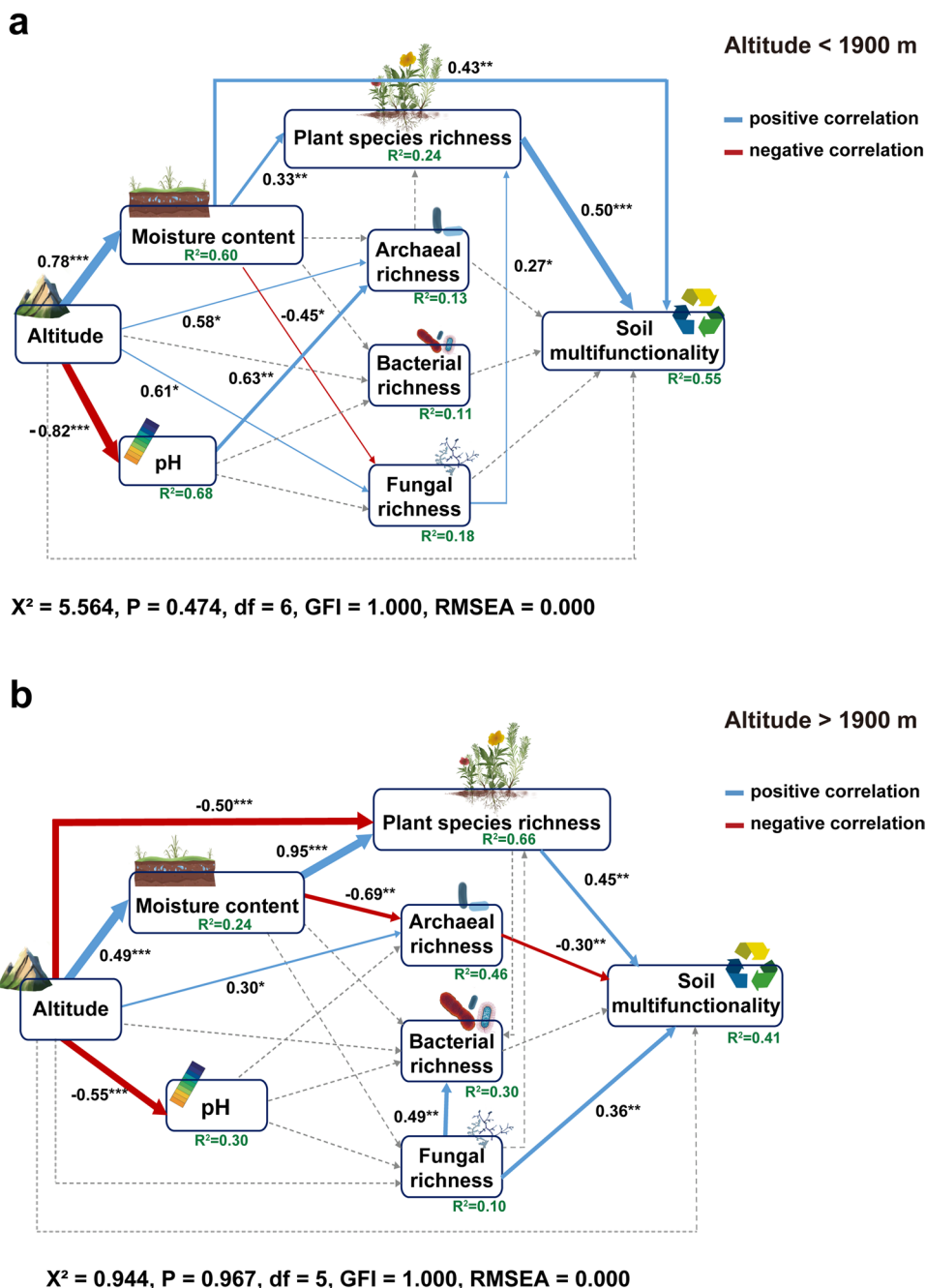


Fig. 5 Structural equation models (SEMs) of altitude, soil properties, and biodiversity as predictors of soil multi-functionality. Solid blue arrows represent positive paths ($P < 0.05$), solid red arrows represent negative paths ($P < 0.05$) and dotted grey arrows represent nonsignificant paths ($P > 0.05$). The

arrow's thickness is proportional to the magnitude of the standardized path coefficients and indicative of the strength of the relationship. Asterisks indicate the significance level of each coefficient: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. R^2 is the proportion of variance explained by the model

5–10% of the carbon absorbed by plants in photosynthesis is excreted into the soil via the roots, and root exudates also contain important signaling molecules with important multi-trophic effects (Brzostek et al. 2013; Cros et al. 2019). Increased plant species richness promotes the input of root exudates into the soil, while symbiotic fungi associated with plants can stimulate plant productivity by supplying limiting nutrients (e.g., phosphorus) to the plants (van der Heijden et al. 2008; Makhalanyane et al. 2015).

The impacts of microbial diversity on soil multifunctionality are enhanced in high-altitude regions

In our study, it was found that when the altitude exceeds 1900 m, the grassland type transitions from temperate steppe to alpine meadow, which has characteristics of low temperature and abundant precipitation (Han 2007). The vegetation in alpine meadow ecosystems was small sized and dense, making it difficult for other species to invade and providing a high degree of stability (Zhou et al. 2006).

In nature, the links between soil microbial diversity and multifunctionality are mostly caused by environmental factors that have the same effect on both parts (Chen et al. 2022). Under natural ecosystems microbial community has greater resistance to harsh environmental conditions as compared to individual microbe (Wang et al. 2014). By integrating our results, it was found that the role of microbial diversity (archaeal, and fungal richness) in soil multifunctionality became more important at high altitudes than at low altitudes (Figs. 2, 3, 4 and 5). A study on a global scale found that soil fungal decomposers thrived in colder and wetter soils with relatively high soil carbon contents (Feng et al. 2022). In high-altitude regions, low temperature cannot satisfied the rapid soil nutrient cycling or turnover rates (Peng et al. 2020); thus, higher microbial diversity, particularly that of fungi, is required to rapidly breakdown organic matter from complex and recalcitrant polymers (e.g., cellulose and lignin) into simple and labile materials (Eastwood et al. 2011; Li et al. 2019). It is corroborated that all fungal functional groups (fungal diversity of pathogens, saprotrophic organisms and symbionts) were positively associated with soil multifunctionality at high altitudes (Fig. 3). An investigation at high altitude demonstrated that soil

acidification associated with pedogenesis reduced the soil organic carbon decomposition (Jing et al. 2015), and resulted in high organic matter accumulation and our soil organic carbon results (Fig. 1c) are coherent with these findings. The wetter ecosystem in high altitude and hotter environment in low altitude directly affect the belowground biodiversity (Delgado-Baquerizo et al. 2019). Further, the combination of high temperatures and dry conditions can result in abrupt reductions in extracellular cellulolytic enzyme activities (A´Bear et al. 2014). Under these circumstances, the effect of soil microbial diversity on soil multifunctionality is not relatively important. This is consistent with our results that fungal richness significantly showed positive affects to soil multifunctionality at higher altitudes but has no effect at lower altitudes (Figs. 3, 4 and 5).

Compared to bacteria and fungi, archaea do not tend to be involved in litter decomposition (Buée et al. 2009; Siles and Margesin 2016). Under cold environments, archaea utilized their specific metabolic pathways (e.g., methanogenesis and chemolithoautotrophic ammonia oxidation) to decompose organic and inorganic carbon and nitrogen compounds into the air (Cavicchioli 2006), which may negatively affect the soil multifunctionality. Similarly, the cold conditions at high altitudes drive the abundance of soil microorganisms with slow metabolic rates which reduced the dominance and performance of the fast metabolic rate bacterial taxa (Crowther et al. 2019). So it becomes less important on soil multifunctionality as compared to the fungi, which is coherent with our result (Fig. 4b). In conclusion, fungal diversity positively impacted soil multifunctionality, and archaeal diversity had a contrasting effect, highlighting that the contribution of different soil microbial taxa to multiple soil functions was also different at high altitudes. In addition, this site-specific and interactive dataset of plant and microbial diversity on soil multifunctionality would laid the foundation and provide the basic data for developing altitude-specific biodiversity conservation strategies in future at the Tianshan Mountains. In high altitude, scientist should consider microbial communities more precisely, while plants species should be considered along the altitude gradient for improving their conservation and to mitigate the negative impacts of climate change and human activities on soil functions and grassland ecosystem services.

Conclusions

We found the relative importance of plant species and soil microbial diversity to soil multifunctionality along an altitudinal gradient. It laid the foundation dataset for developing altitude-specific biodiversity conservation strategies in future to mitigate the negative impacts of climate change or human activities on soil functions and grassland ecosystem services. At lower and higher altitudes, plant species richness emerged as a dominant factor in enhancing soil multifunctionality, while microbial diversity gained the prominence at higher altitudes. Low altitudes have suitable hydrothermal conditions, which increased plant diversity and productivity. Low temperature and high humidity conditions in high-altitude regions accelerated the microbial-mediate nutrient cycling and promoted plant growth. At this point, plant and microbial diversity become equally important for soil multifunctionality. Overall, the relative importance of aboveground and belowground biodiversity to soil multifunctionality changes with altitude. This means that plants and microbes need to be treated differently when developing diversity conservation strategies for regions at different altitudes.

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Data availability The bacterial, fungal and archaeal sequences obtained in this study are available at the NCBI Sequence Read Archive (<http://www.ncbi.nlm.nih.gov/Traces/sra/>) under the accession numbers SRP386704, SRP388269 and SRP388202, respectively.

Declarations

Availability of analysis scripts Scripts employed in the analyses are available upon request.

Competing interest The authors declare that they have no conflicting financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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