



Shrub alters the spatial patterns of nematode taxonomic and functional diversity on the Qinghai-Tibet Plateau

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Abstract

Background and aims Shrub effect with climate change is known to alter alpha diversity of organism groups at the taxonomic level, but how it influences the beta diversity of soil organisms, particularly functional level, remains poorly understood. Here, we investigated the abundant nematode fauna to assess the shrub effects on alpha and beta diversity at both

taxonomic and functional level in sites on the Qinghai-Tibet Plateau.

Methods We collected three functional traits (i.e., diet, body mass and life-history) associated with resource acquisition, dispersal ability, reproduction and the rate of nutrient utilization. We calculated the functional alpha and beta diversity of nematode communities under shrubs and open spaces using kernel density n-dimensional hypervolumes and combined it with taxonomic diversity to disentangle the spatial patterns and community assembly of nematode communities.

Results Shrubs significantly increased taxonomic richness, but not functional richness. However, shrubs reshaped broad-scale nematode functional richness and ecological indices along climatic gradients. Shrubs significantly decreased the taxonomic and functional beta diversities of nematode communities, generating biota homogenization. The parallel changes of taxonomic and functional beta diversities were driven by distinct processes. Replacement dominated taxonomic beta diversity variation, while richness difference dominated functional beta diversity variation.

Conclusion Our findings show that shrubs were able to filter functional traits and limit the dispersal of species assemblages that exhibit such traits, thus causing taxonomic and functional homogenization of soil nematodes on the Qinghai-Tibet Plateau. Our findings advance understanding of the spatial patterns

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of belowground communities for taxonomic and functional aspects.

Keywords beta diversity · Functional diversity · Hypervolumes · Shrub effect · Soil fauna · Soil nematode

Introduction

Shrub encroachment due to intensive anthropogenic climate change has significantly altered the diversity and composition of above- and belowground communities around the globe (Collins et al. 2018). Previous studies documented diversity “hotspots” and “coldspots” of shrub effects on plants, which are probably the best-described group (Eldridge et al. 2011; Hao et al. 2021). By contrast, little is known about how shrubs affect belowground biodiversity, particularly its functional diversity (Chen et al. 2021). The general patterns and mechanisms of soil community diversity and functional traits responses to shrub effect remain elusive. Therefore, quantifying the general patterns and mechanisms of soil community diversity and functional trait responses to shrub effect is key to understand species assembly rules, evolutionary dynamics and ecosystem functioning and for advancing our knowledge on safeguarding biodiversity.

As an essential component of belowground community, soil nematodes are the most abundant and functionally diverse group of fauna globally (Franco et al. 2019). Nematode communities display a wide range of functional traits, spanning orders of magnitude of body size, varying considerably in life history traits, and distributing in multiple trophic levels in soil food webs (Li et al. 2020; Zhang et al. 2023). These functional traits characterize differences in resource acquisition strategies, determining the responses of nematodes to environmental changes (Bhaskar et al. 2014). Therefore, it is anticipated that functional traits are more sensitive than species diversity and can provide insights into potential changes in ecosystem function in response to shrub effect (Cadotte et al. 2011). However, our understanding of how belowground taxonomic and functional diversity respond to global environmental changes remains elusive given that soil community is a “black box” of highly redundant species.

Soil nematode community generally changes with environment changes. Shrub effect due to climate change could have large effects on nematode taxonomic and functional spatial patterns. Shrubs can positively affect soil nematode taxonomic and functional diversity because their canopy can provide microhabitats, namely in the form of high resource availability, secure oviposition and shelter for soil nematodes (Wang et al. 2019). Shrubs could mitigate the negative effects of temperature on functional richness because their canopy can moderate solar radiation and regulate extreme climatic factors for soil nematodes (Hao et al. 2021). However, shrubs with greater height, stronger woody stems, and denser canopies can intercept and redistribute precipitations, therefore possibly amplifying positive effects of precipitation on functional richness (Aranibar et al. 2004; Weber-Grullon et al. 2022). These aforementioned mechanisms would determine how shrub influences the spatial patterns of nematode taxonomic and functional richness along climate gradients.

In addition to investigating the spatial patterns of alpha diversity within sites, it is also important to assess beta diversity (the change of genera composition among sites) in terms of taxonomic and functional aspects (Liu et al. 2021). Taxonomic and functional beta diversities can both be partitioned into two different components: replacement (some genera disappear and are replaced by others) component and richness difference (species gain and loss) component (Cardoso et al. 2014). The replacement component usually occurs among communities with dispersal limitation and small ecological drift, while richness difference component often occurs among communities with selective extinction or colonization along environmental gradients. These can provide insight into the processes that maintain biodiversity. The presence of shrubs is an irreversible process with potential effects on the taxonomic and functional beta diversity of soil nematode communities (Xiao et al. 2023). On the one hand, shrub exacerbates habitat patchiness, redistributing nematode functional traits and species assemblages, thus limiting nematode dispersal (Trentanovi et al. 2013). On the other hand, compared to open space, shrubs are more stable habitats in the face of environmental disturbance, which could limit the range of potential colonizers by favoring or excluding particular functional attributes (Siegwart Collier and Mallik 2010; Wardhaugh

et al. 2012). These processes would alter the replacement and richness difference components, resulting in changes in taxonomic and functional beta diversities.

In this study, to comprehensively assess the shrub effects on nematode biogeographic patterns, we investigate nematode alpha and beta diversities in terms of taxonomic and functional aspects across a 1200 km × 1200 km area with widespread shrubs on the Qinghai-Tibet Plateau. We tested the following hypotheses: (1) shrubs increase taxonomic and functional alpha diversity and alter their spatial patterns along climatic gradients, and (2) shrubs decrease the taxonomic and functional beta diversity of nematode communities in a pattern of biotic homogenization through replacement and richness difference of taxonomic and functional forms.

2. Materials and methods

2.1. Study site and experimental setup

As it is the highest (average elevation of 4000 m above sea level) and largest plateau in the world, north of the Himalaya, the Qinghai-Tibet Plateau is highly sensitive to climate change (Chen et al. 2020). With global climate change, the Qinghai-Tibet Plateau has experienced rapid increase in temperature and precipitation, resulting in the expansion of shrub ranges (Brandt et al. 2013; Li et al. 2020; Yang et al. 2021).

In July and August 2020, samples were collected from 31 sites across a 1200 km × 1200 km area with widespread shrub on the Qinghai-Tibet Plateau (91°02'E-103°10'E, 29°37'N-39°12'N). The distance between any two sites was > 30 km (Figure S1). This 1.5 million km² area provided wide variation in precipitation and temperature over long distances. MAP (mean annual precipitation) ranges from 252 to 656 mm and MAT (mean annual temperature) ranges from -4.0 to 3.8°C. Rainfall in the study region is mainly concentrated between May and September (the growing season) and the peaks of the growing season are in mid-August. MAT and MAP data of the sampling sites were obtained from the global Worldclim dataset (<http://www.worldclim.org>; 30 arc-s or c.1 km at the equator). Extracted data were processed in ArcGIS software v10.3 using the spatial analysis tool (ESRI).

We sampled soils from both directly under and outside shrub canopies (5 m outside) in the herbaceous plant interspace in areas where shrubs were widely distributed. At each site, we set up a 50 m × 50 m quadrat and randomly selected five well-developed shrubs with similar sizes, at least 5 m from one another. We set up a 30 cm × 30 cm subplot beneath each selected shrub for soil sampling. Furthermore, we randomly established five subplot of the same size (30 cm × 30 cm) in adjacent open spaces served as controls, at least 5 m away from the shrub canopy.

2.2. Soil nematode

After removing litter and rocks, we collected soil cores (15 cm depth) using a soil auger (4 cm diameter) in each subplot. All soil samples were individually placed in plastic bags, which were sealed, and stored at 4°C for transportation to the laboratory at Lanzhou University. In the lab, soil nematodes were extracted from 50 ml subsamples of fresh soil using the improved Baermann wet funnel technique (Wang et al. 2018). Extracted nematodes were observed under 100×inverted microscope (Olympus CX43) to identify nematodes to genus level (Andriuzzi et al. 2020). The number of nematodes was expressed as individuals per 100 g of dry soil (Table S1). We pooled the data from all subplots within the same treatment at each site.

2.3. Functional traits

We collected functional traits from the database of Nematode Ecophysiological Parameter (<http://nemalex.ucdavis.edu>). We used three traits to characterize functional diversity: (a) diet: bacterivore, fungivore, herbivore, omnivore, and predator; (b) life-history: c-p value ranges from 1 to 5; (c) body mass (μg): the mass averaged across species in a given genus. These traits that have been shaped by large-scale evolutionary and ecological processes represented trophic structure, life cycles, and nutrient cycling, all traits we hypothesized are influenced by shrub cover. Body mass was Box-Cox transformed as needed to approach normality before analysis.

2.4. Soil and plant properties

In each subplot, all herbaceous plants were identified at the species levels to calculate plant richness (PR). Moreover, plant total biomass was clipped (clipped down to about 1 cm above the ground) at each subplot. Plant total biomass (PB, g/m^2) was determined gravimetrically by drying the plant samples for 48 h at 75 °C.

Soil moisture (SM, %) was determined gravimetrically by drying the soil samples for 48 h at 105 °C. After drying and sieving the soil samples, we measured other soil physical and chemical properties. Soil pH was measured with a pH electrode (PHSJ-3 F, China), and soil electrical conductivity (EC, S/m) was measured using a conductivity meter (Model DJS-1 C, China), both in 1: 5 soil-water ratios. Soil organic matter (SOC, g/kg) was measured with the wet oxidation method (Wang et al. 2019). Soil total nitrogen (TN, g/kg) and total phosphorus (TP, g/kg) were both digested with concentrated H_2SO_4 at 375°C for 3.75 h, respectively; then nitrogen was measured using the semi-micro Kjeldahl method, and phosphorus was analysed using the molybdenum antimony colorimetric method, using an automatic chemical analyser (SmartChem 200, AMS, Italy). Both soil nitrate nitrogen (NO, g/kg) and ammonium nitrogen (NH, g/kg) were obtained from 2 M KCl extracts, also measured using the automatic chemical analyser (SmartChem 200, AMS, Italy). Soil available phosphorus (AP, mg/kg) was measured by the molybdenum blue method after extraction with 0.5 mol L^{-1} NaHCO_3 at pH 8.5 (Wang et al. 2019).

2.3. Data analysis

2.3.1 Taxonomic and functional diversity

Taxonomic richness was assessed using the number of genera within a community. Taxonomic beta diversity and its two components (replacement and richness difference) were calculated using pairwise dissimilarity matrices based on the Jaccard dissimilarity.

We used multidimensional kernel density hypervolumes for calculating the functional diversity using *kernel.build* function in the ‘BAT’ package (Laliberté and Legendre 2010; Mammola and Cardoso 2020). Firstly, we used Gower distance to quantify the functional distances between nematodes. We then

used principal coordinate’s analysis (PCoA) based on this functional distance, and used the first four PCoA axes (81.17% explained variance) to construct hypervolumes using a Gaussian kernel estimator and a default bandwidth for each axis. Finally, we quantified the total volume of the functional hyperspace as functional richness (Laliberté and Legendre 2010). Functional beta diversity (the difference between functional hyperspaces) and its two components (functional replacement and richness difference) based on Jaccard dissimilarity. Moreover, we evaluated the functional contribution of each taxon within each community to the functional richness.

To comprehensively understand the nematode function, we assessed nematode ecological indices using NINJA (Nematode Indicator Joint Analysis, <https://shiny.wur.nl/ninja/>) web, including maturity index, channel index, basal index, structure index, enrichment index, structure footprint, enrichment footprint.

2.3.2 Statistical analysis

To assess the general patterns and mechanisms of soil nematode diversity, we used different approaches for alpha and beta diversity. We used generalized linear mixed models (GLMM) to determine the shrub effects on taxonomic and functional richness using *glmmTMB* function in the ‘glmmTMB’ package, with the shrubs as fixed effects and sites as random effect (Brooks et al. 2017). We used generalized linear models (GLM) to determine the effects of climatic factors on taxonomic and functional richness. To control for spatial autocorrelation, distance-based Moran’s eigenvector maps (dbMEM eigenfunctions, originally called PCNM) were computed, and the spatial eigenfunctions (dbMEMs) were used for estimation of the intercept of the GLM model using *pcnm* function in the ‘vegan’ package (Dixon 2003). The GLMM and GLM were used for count data (taxonomic richness) and the dispersion of GLMM and GLM was checked and adjusted using the generalized Poisson distribution (genpois) family. The GLMM and GLM with beta family were used for proportional data (functional richness) ranging between 0 and 1. Multiple comparisons were analyzed using Tukey’s HSD test, corrected using a false discovery rate (Benjamini and Hochberg 1995). We used Random

Forest analysis to identify the main predictors of taxonomic and functional richness using the *randomForest* function in the ‘randomForest’ package (Liaw and Wiener 2007). Through bootstrap aggregation (also known as out-of-bag or OOB cases), it combines multiple classification trees rather than relying on single regression. The importance of each predictor was computed for each tree and averaged over 5,000 trees, and determined by increase in the log of the mean square error (InMSE). The significance of the importance of each predictor on taxonomic and functional richness was assessed using the *rfPermute* function in the ‘rfPermute’ package. Moreover, Pearson correlation analyses were used to determine the relationship between nematode ecological indices and environmental factors.

Considering that beta diversity was calculated as the distance between nematode communities and the data were not independent, we used the Wilcoxon signed-rank test to test the shrub effects on taxonomic and functional beta diversity. The rate of distance-decay of the nematode communities was calculated as the slope of ordinary least-squares regression on the relationship between geographic distance (ln transformed) and taxonomic and functional beta diversity (ln transformed). The significance of the relationship between taxonomic and functional beta diversity and geographical distance under shrubs and open spaces was assessed by distance-based redundancy analysis (db-RDA) using the *capscale* function in ‘vegan’ package. We performed variation partitioning analysis (Borcard et al. 1992) to decompose the variation in taxonomic and functional beta diversity among soil factor, climate factor and spatial factor (dbMEMs) using the *varpart* function in ‘vegan’ package. We excluded the variables with strong multicollinearity (variance inflation factor > 10). Further, we used stepwise forward selection with permutation tests to identify the significant subsets ($P < 0.05$) of variables for each set of predictors under shrubs and in open spaces to quantify the relative contribution of climate, plant, soil and spatial factors to taxonomic and functional beta diversity and its two components. The environment effect (climate, plant, and soil factors) signifies the sole impact of selection, the spatial effect is often considered to represent the influence of dispersal (Zhou and Ning 2017).

Results

3.1 Taxonomic and functional richness

Shrubs significantly increased taxonomic richness ($P=0.001$), but had no significant effects on functional richness (Fig. 1a, b). The functional contribution analysis showed that shrubs significantly increased the functional contributions of nematode genera *Dorylaimus* ($P=0.034$) and *Coomansus* ($P=0.041$), which represent the largest body sizes, *K*-strategies, and higher trophic functional traits (Figure S2a, b).

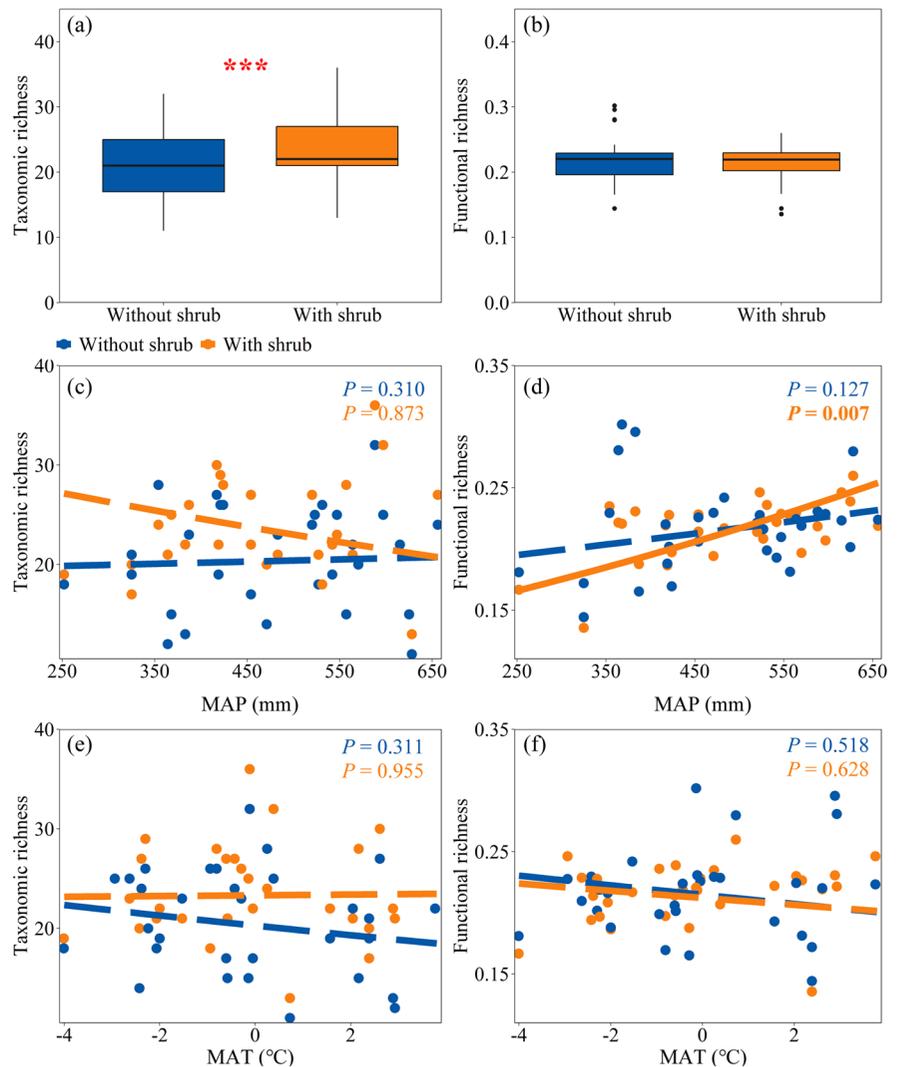
Shrubs had no significant effects on broad-scale taxonomic richness along climatic gradients (Fig. 1c, e), but reshaped precipitation gradients of functional richness (Fig. 1d). Functional richness significantly increased ($P < 0.001$) with MAP under shrub, but remained fairly constant in open space (Fig. 1d). The functional contribution of *Acrobeloides* (Diet=bacterivore, C-P=2, body size=0.223) and *Mononchus* (Diet=predator, C-P=4, body size=4.337) significantly increased ($P=0.008$ and $P=0.038$) with MAP (Figure S2d, e).

Alongside changes in richness, nematode function may change in their ecological indices with shrub and temperature (Fig. 2 and Figure S3). Shrub significantly increased ($P=0.023$) structure footprint, but not other ecological indices of nematode community (Figure S3). Maturity index ($P=0.008$) and structure index ($P=0.013$) significantly decreased with MAT under shrub, but remained constant in open space (Fig. 2). However, basal index ($P=0.029$) and enrichment footprint ($P=0.032$) significantly increased with MAT under shrub (Fig. 2), but remained constant in open space. Enrichment index significantly increased under shrub ($P < 0.001$) and in open space ($P=0.034$), while channel index and structure footprint were unaffected by MAT (Fig. 2).

3.2 Taxonomic and functional beta diversity

Shrubs significantly decreased the taxonomic ($P < 0.001$) and functional ($P < 0.001$) beta diversity (Fig. 3a, d). However, the parallel changes of taxonomic and functional beta diversity were driven by distinct processes. Replacement dominated the taxonomic beta diversity variation, while richness difference dominated the functional beta diversity

Fig. 1 The spatial patterns of soil nematode taxonomic and functional richness. (a) Shrub effects on taxonomic richness; (b) Shrub effects on functional richness; (c) The mean annual precipitation (MAP) pattern of taxonomic richness for shrubs (orange points and line) and open space (blue points and line); (d) The mean annual temperature (MAT) pattern of taxonomic richness; (e) The MAP pattern of functional richness; (f) The MAT pattern of functional richness. Asterisks indicate a significant difference between open space and sites with shrubs at 0.001 (***) significance levels. The solid line represents a significant relationship, while the dotted line represents a non-significant relationship



variation. Shrubs significantly decreased ($P=0.035$) the taxonomic replacement, but not taxonomic richness difference (Fig. 3b, c). However, shrubs had no significant effects on functional replacement, but significantly decreased ($P<0.001$) functional richness difference (Fig. 3e, f).

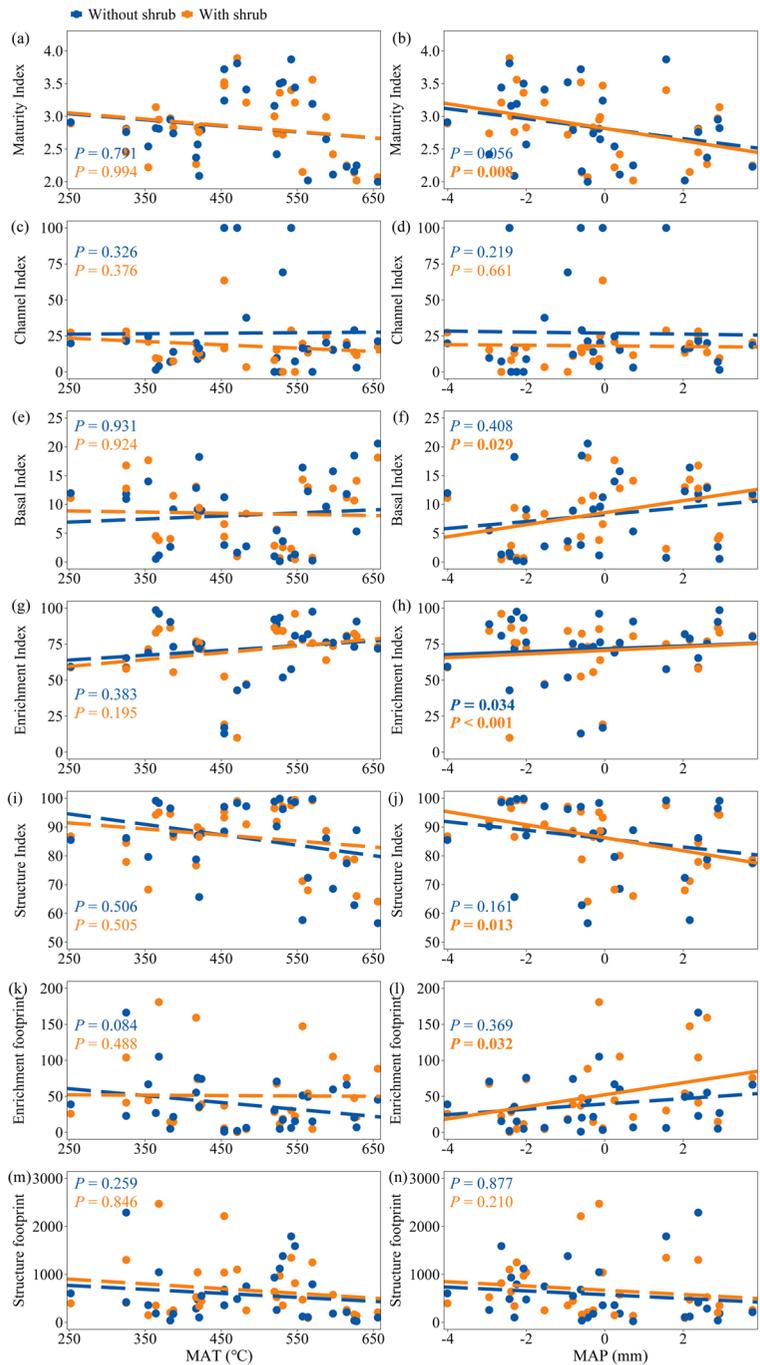
Taxonomic and functional beta diversity versus geographic distance for each pairwise set of samples displayed significant distance-decay relationships (Fig. 4a, d). Taxonomic replacement significantly increased with geographic distance under shrubs ($P=0.001$) and in open spaces ($P=0.007$), while taxonomic richness difference remained constant under shrubs and in open spaces (Fig. 4b, c). Functional replacement and richness difference components

significantly increased with geographic distance under shrubs ($P=0.002$), but remained constant in open spaces (Fig. 4e, f).

3.3 Drivers of taxonomic and functional diversity

The random forest analysis showed no significant determinants for taxonomic richness for observations in open spaces, while plant biomass ($P=0.049$) significantly affected taxonomic richness under shrubs (Figure S4a, b). However, soil available phosphorus ($P=0.010$) significantly affected functional richness in open spaces, whereas MAP ($P=0.009$) and soil electrical conductivity ($P=0.019$) significantly affected the functional richness under shrubs

Fig. 2 The spatial patterns of soil nematode ecological indices. (a) and (b): The mean annual precipitation (MAP) and The mean annual temperature (MAT) pattern of maturity index for shrubs (orange points and line) and open space (blue points and line); (c) and (d): channel index; (e) and (f): basal index; (g) and (h): enrichment index; (i) and (j): structure index; (k) and (l): enrichment footprint; (m) and (n): structure footprint. The solid line represents a significant relationship, while the dotted line represents a non-significant relationship



(Figure S4c, d). Moreover, nematode ecological index indices were only significantly ($P < 0.05$) affected by soil factors (total nitrogen, total phosphorus, available phosphorus, electrical conductivity, pH, soil moisture) in open space, but were significantly ($P < 0.05$) affected by a combination of climate, plant and soil

factors (available phosphorus, electrical conductivity, pH, plant biomass, plant richness, MAT) under shrubs (Figure S5 and Figure S6).

Variation partitioning analysis showed that climate ($P = 0.008$) and spatial ($P < 0.001$) factors significantly explained the variation in taxonomic beta

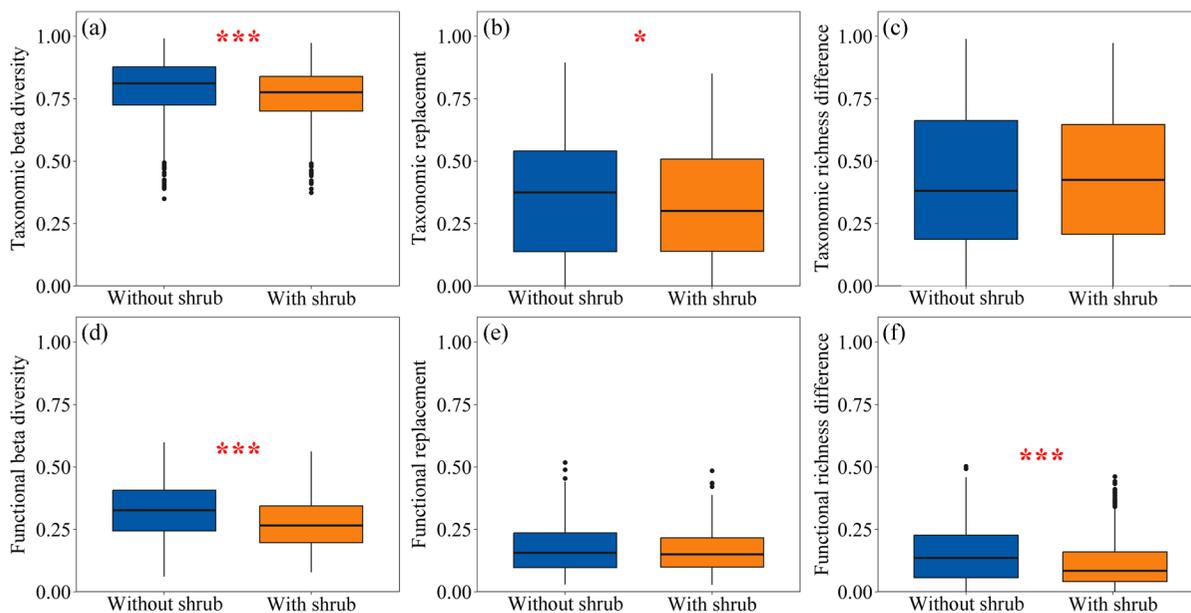


Fig. 3 Shrub effects on taxonomic and functional beta diversity and its two components. (a): Taxonomic beta diversity; (b): Taxonomic replacement component; (c): Taxonomic richness difference component; (d): Functional beta diversity;

(e): Functional replacement component; (f): Functional richness difference component. Asterisks indicate a significant difference between open space and sites with shrubs at the 0.05 (*) or 0.001 (***) significance levels

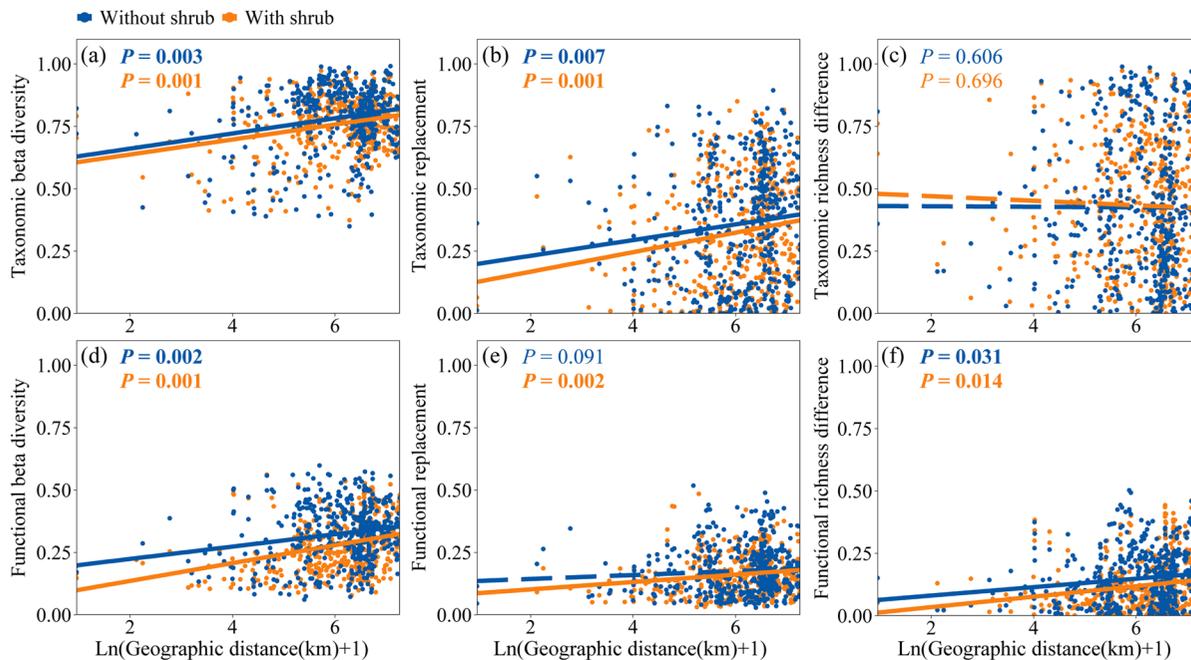


Fig. 4 Distance-decay curves of beta diversity for shrubs and open space. (a): Taxonomic beta diversity; (b): Taxonomic replacement component; (c): Taxonomic richness difference component; (d): Functional beta diversity; (e): Functional

replacement component; (f): Functional richness difference component. The solid line represents a significant relationship, while the dotted line represents a non-significant relationship

diversity in open space, whereas soil ($P=0.005$), climate ($P=0.014$), plant ($P<0.001$), and spatial ($P<0.001$) factors significantly explained the variation in taxonomic beta diversity under shrub (Fig. 5a, b). Moreover, climate ($P=0.017$), plant ($P=0.029$), and spatial ($P<0.001$) factors significantly explained the variation in functional beta diversity in open space, whereas soil ($P=0.003$), climate ($P<0.001$), and spatial ($P<0.001$) factors significantly explained the variation in functional beta diversity under shrub (Fig. 5c, d). Furthermore, climate, soil, and plant factors explained the variation in replacement and richness difference components of both taxonomic and

functional aspects under shrub compared with open space (Figure S7 and Figure S8).

4. Discussion

4.1 Shrubs alter the spatial patterns of taxonomic and functional alpha diversity along climatic gradients

Contrary to first hypothesized, shrubs only increased nematode taxonomic richness, whereas functional richness remained unchanged. Random forest analysis indicated that nematode diversity associated was

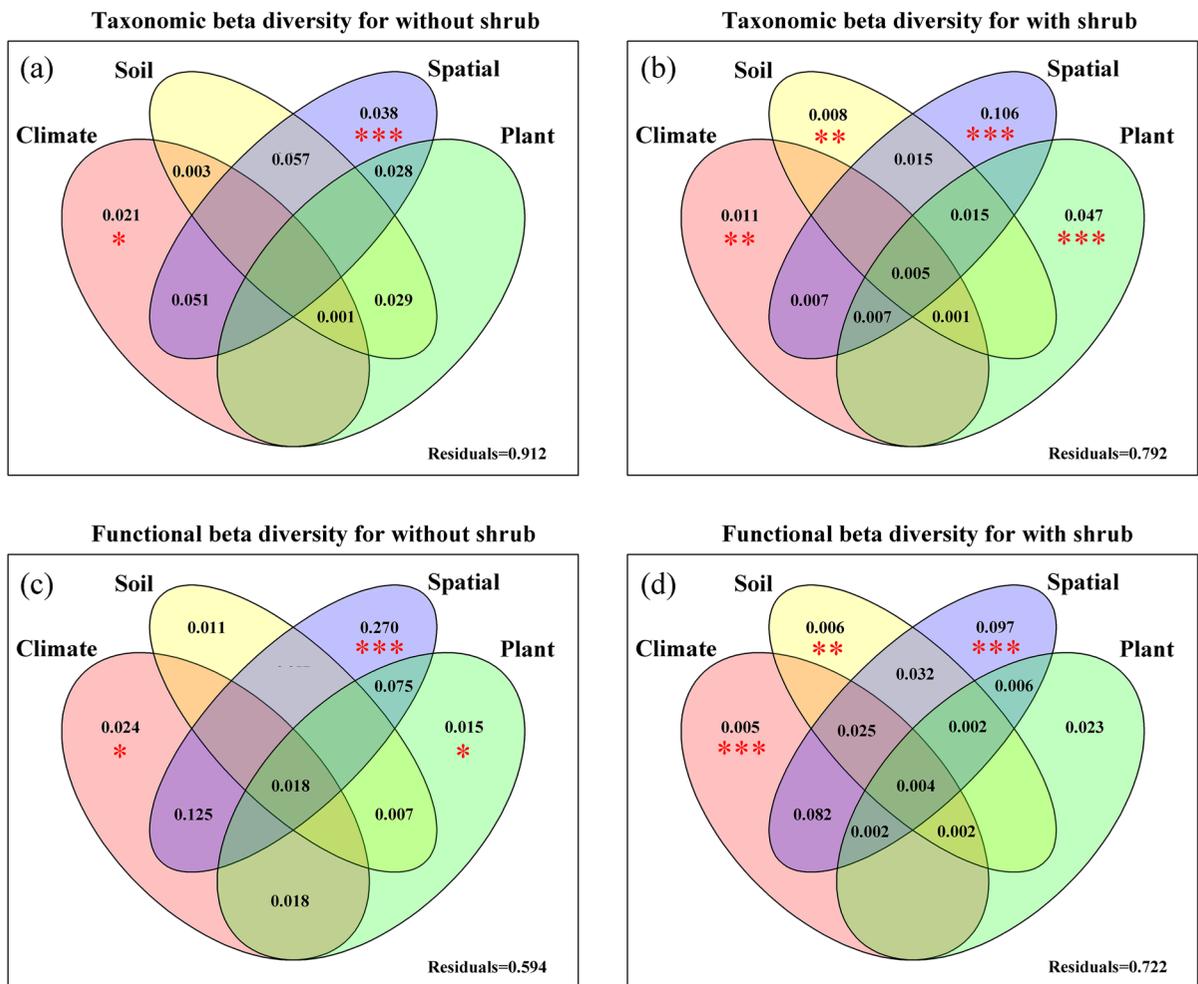


Fig. 5 Variation partitioning analysis of the variation in taxonomic and functional beta diversity explained by soil factor, climate factor and spatial factor. (a): Variation in taxonomic beta diversity for open space; (b): Variation in

taxonomic beta diversity for shrub; (c): Variation in functional beta diversity for open space; (d): Variation in functional beta diversity for shrub. The values in the Venn diagram intersections are adjusted R-squares

closely related to soil and plant factors (Figure S4). Shrubs, functioning as high-biomass and high-impact species in grassland ecosystems, can foster favorable microhabitats characterized by mild soil properties and high plant resource availability, which facilitate colonization by nematode species (Hortal et al. 2015; Wang et al. 2019). However, although shrubs increased the functional contribution of nematodes with larger sizes, *K*-strategies, and higher trophic functional traits, the functional richness response to shrubs remained constant. The mechanisms behind functional richness are complex: shrubs are associated with higher functional richness at mesic sites but with lower functional richness at arid sites compared to nearby open space, leading to unchanged functional richness (Fig. 1d). Similarly to other studies, the collapse of positive effects is typically driven by response of species to a decrease in resources, and therefore the positive effect generally switches to negative effect in highly stressed conditions when nematodes are competing for precipitation (Armas et al. 2011; Michalet et al. 2014). Since active nematodes require water films or water-filled pores, mesic soils have more habitable space for nematodes with larger sizes and longer life strategies than arid soils (Andriuzzi et al. 2020). Therefore, in mesic sites, we suggest that shrubs can provide high resource availability, further promoting species coexistence with different functional traits. However, in arid conditions, when water limitations exceed the benefits of enhanced resources from shrubs, the facilitative shrub effects on nematode functional richness could shift to competition (Michalet et al. 2014).

Furthermore, we used nematode ecological indices to disentangle the direction of functional diversity of nematode community. Shrub only significantly increased nematode structure footprint which may have a regulatory function in the food web (Fig. 2). Shrubs with complex roots are conducive to the ambush-hunting strategy of omnivore and predator soil fauna, in that this physical architecture tends to attract nematodes with longer C-P value, larger body, and higher trophic levels (Hodson et al. 2014). Therefore, shrub can increase nematode structure footprint and affect nematode function through bottom-up effects, which showed complex ecological communities with many trophic connections under shrubs (Biederman and Boutton 2009; Ferris 2010; Xie et al. 2021; Cui et al. 2023). These results point

to the crucial role that the presence of shrub has in biodiversity conservation, increasing nematode function, and maintaining the complexity of soil food web structure on the Qinghai–Tibet Plateau under future change scenarios.

Our finding showed that shrubs amplify the positive effects of MAP on functional richness. Shrubs with higher height, stronger woody stems and denser canopies can intercept and redistribute precipitation, thus promoting shrub growth and plant biomass, which results in high energy availability to the soil food web, therefore amplifying positive effects of MAP on functional richness (Aranibar et al. 2004; Weber-Grullon et al. 2022). We detected an asynchrony of changes in taxonomic and functional alpha diversity response to shrub, indicating that most nematode genera have similar ecological functions. Moreover, functional richness being more sensitive to shrubs than taxonomic richness indicates that functional diversity can reflect the processes that influence the survival and reproduction of nematodes, which can provide more powerful information on ecosystem functioning.

Moreover, shrubs enhanced the spatial patterns of nematode ecological indices along temperature gradients. Shrub amplified the negative effects of MAT on maturity and structure index and positive effects of MAT on basal and enrichment index and enrichment footprint. On the one hand, numerous studies show that climate warming can induce the encroachment of shrub, particularly at higher altitudes (Eldridge et al. 2011). A possible explanation is that the sensitivity of shrub and root activity to temperature may have amplified the sensitivity of nematode function to temperature (Eldridge et al. 2011). On the other hand, nematodes with higher trophic levels, longer generation time, and larger bodies are more sensitive to temperature than other nematodes (Franco et al. 2019). Moreover, increased MAT may affect the reproductive rate of omnivore and predator nematode, decreasing the abundance and biomass of omnivore and predator nematode, which could lead to the negative effects on maturity index and structure index of nematode community (Cui et al. 2023). Therefore, the increased MAT may decrease the predation-prey rate, increasing the abundance and biomass of lower trophic level nematode, and therefore basal and enrichment index and enrichment footprint of nematode community. Taken together, the presence of

shrub will amplify the response of nematode function to climate change, highlighting that climate changes with consequent shrub effects can reshuffle the soil nematode function and therefore ecosystem functioning on the Qinghai–Tibet Plateau.

Parallel responses of taxonomic and beta diversity responses to shrubs are driven by distinct processes

As advanced by our second hypothesis, shrub can decrease the taxonomic and functional beta diversity of soil nematodes in a pattern of important taxonomic and functional homogenization. Biotic homogenization is commonly found for aboveground community following plant invasion, while fewer studies focus on the soil community, particularly at functional levels (Zhang et al. 2019; He et al. 2022).

We partitioned beta diversity and found that the shrub effects on taxonomic and functional homogenization were driven by distinct processes. The replacement component contributes to variation in taxonomic beta diversity, whereas the richness difference component drives variation in functional beta diversity (Fig. 3). Shrub exacerbates habitat patchiness, which redistributes nematode functional traits and species assemblages (Trentanovi et al. 2013). Shrubs can limit the range of potentially successful nematodes by favoring or excluding functional traits underlying their survival therein, maintaining the stability of certain nematode functional traits in spatial variation and making nematode functional traits more similar, ultimately resulting in functional homogenization through decreasing the richness difference component (Xiao et al. 2023). However, the taxonomically distinct nematodes exhibit similar functional traits, so that shrub can limit (or constrain) the dispersal of nematode assemblages whose functional traits benefited from shrub, leading to taxonomic homogenization through decreasing the replacement component (Xiao et al. 2023).

Moreover, we found robust evidence for distance-decay relationships of functional and taxonomic beta diversity. The distance-decay slope was steeper under shrub than in open space, which may favour biotic and functional homogenization under shrubs. As a result, biotic and functional homogenization lead to a narrowing of ecological niches in the community, making nematodes more responsive to environmental change and therefore accelerating the spatial turnover

of species and function within the nematode community (He et al. 2022).

The variance partitioning analysis results showed that explanation of functional beta diversity using climate, soil, plant and spatial variables was higher than that of taxonomic beta diversity. This is yet more evidence that functional beta diversity is more sensitive to environmental changes than taxonomic diversity. Spatial factors explained a larger fraction of variation in taxonomic and functional beta diversity than climate, plant, and soil factors. This suggests that stochastic processes such as dispersal limitation are the main driver of variation in species and function of soil nematode community on the Qinghai–Tibet Plateau (Xiong et al. 2021). Furthermore, shrubs mitigate the spatial effects on functional beta diversity and amplify the effects of soil, climate, and plant factors on taxonomic and functional beta diversity, which further supports that selection may play a dominant role in driving the variation in taxonomic and functional beta diversity responses to shrubs. Shrubs can create effective environmental conditions that filter certain functional traits to reconstruct communities on the Qinghai–Tibet Plateau. We further speculate that climate changes with consequent shrub effects may affect the nematode communities and biogeochemical cycles they support, threatening the critical role of Qinghai–Tibet Plateau in global carbon cycling and climate change regulation. However, it is not clear whether taxonomic and functional homogenization of nematode communities also occurs at phylogenetic level and/or other organism groups. Therefore, it is necessary in the future to monitor the taxonomic, functional, and phylogenetic diversity of multiple organism group at large scales on the long-term and large scales.

5. Conclusion

We quantified the ecological processes of shrub effects that drive alpha and beta diversity of nematode soil communities in terms of taxonomic and functional aspects. Our study suggests that shrubs increase nematode diversity and amplify the response of nematode function to climate changes. Climate changes with consequent shrub effects will reshuffle the soil nematode function and ecosystem services that they support. Moreover, shrubs are able to filter certain functional traits and limit the dispersal of species assemblages that exhibit these traits, thus

causing taxonomic and functional homogenization of soil nematode communities, with ecosystem functioning of Qinghai–Tibet Plateau possibly facing future restructuring under climate change. Our findings provide valuable and timely information to understand how shrub affects taxonomic and functional aspects of belowground biodiversity, and produce a more precise picture of the responses of nematode communities to climate change.

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Data availability The data that support the findings of this study are openly available in figshare at <https://doi.org/10.6084/m9.figshare.22057109.v2>.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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