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RESEARCH ARTICLE

Spatial patterns and ecological drivers of soil nematode β -diversity in natural grasslands vary among vegetation types and trophic position

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Abstract

1. Understanding biogeographic patterns of community assemblages is a core objective in ecology, but for soil communities these patterns are poorly understood. To understand the spatial patterns and underlying mechanisms of β -diversity in soil communities, we investigated the β -diversity of soil nematode communities along a 3,200-km transect across semi-arid and arid grasslands.
2. Spatial turnover and nested-resultant are the two fundamental components of β -diversity, which have been attributed to various processes of community assembly. We calculated the spatial turnover and nested-resultant components of soil nematode β -diversity based on the β -partitioning framework. Distance matrices for the dissimilarity of soil nematode communities were computed using the 'Sørensen' method. We fitted negative exponential models to compare the distance decay patterns in nematode community similarity with geographic distance and plant community distance in three vegetation types (desert, desert steppe and typical steppe) and along the whole transect. Variation partitioning was used to distinguish the contribution of geographic distance and environmental variables to β -diversity and the partitioned components.
3. Geographic distance and environmental filtering jointly drove the β -diversity patterns of nematode community, but environmental filtering explained more of the variation in β -diversity in the desert and typical steppe, whereas geographic distance was important in the desert steppe. Nematode community assembly was explained more by the spatial turnover component than by the nested-resultant component. For nematode feeding groups, the β -diversity in different vegetation types increased with geographic distance and plant community distance, but the nested-resultant component of bacterial feeders in the desert ecosystem decreased with geographic distance and plant community distance.
4. Our findings show that spatial variation in soil nematode communities is regulated by environmental processes at the vegetation type scale, while spatial processes

mainly work on the regional scale, and emphasize that the spatial patterns and drivers of nematode β -diversity differ among trophic levels. Our study provides insight into the ecological processes that maintain soil biodiversity and biogeographic patterns of soil community assemblage at large spatial scales.

KEYWORDS

grassland ecosystem, soil community, spatial turnover, trophic position, vegetation type, β -diversity

1 | INTRODUCTION

Disentangling the possible mechanisms behind the biogeographic patterns of biotic communities is a major challenge in ecological research (Vellend, 2010). While the distribution patterns of above-ground organisms are well documented (Eisenhauer, 2016; Svenning et al., 2011), the spatial patterns and ecological processes that drive the variation of soil organisms are far less well understood, partly due to the high species richness that is inherent in below-ground subsystems (Bardgett & van der Putten, 2014; Fierer et al., 2009).

Variation in species composition among habitats of different geographic regions is frequently expressed as β -diversity (Svenning et al., 2011; Vellend, 2010), and this can provide insight into the processes that maintain biodiversity. At the global scale, the mismatch area between above-ground and below-ground biodiversity covered more than a quarter of the terrestrial surface (Cameron et al., 2019), implying different mechanisms for regulating above-ground and soil biodiversity. However, the limited knowledge of biogeographic patterns of the below-ground subsystem impedes our understanding of the spatial patterns of soil biodiversity. Community assembly can be regulated by deterministic processes (e.g. species sorting, environmental filtering and biotic interactions) and/or by stochastic processes (e.g. dispersal limitation due to geographic barriers, birth and death rates, and dispersal abilities), and these two processes individually or jointly influence the spatial distribution of biotic communities (Dini-Andreote et al., 2015; Ellwood et al., 2009; Langenheder & Székely, 2011). Environmental and spatial gradients can strongly influence β -diversity of soil organisms (Fierer & Jackson, 2006). Therefore, differences in environmental conditions or vegetation types on a regional scale can lead to different regulatory mechanisms for spatial patterns of soil biodiversity. However, the relative importance of environmental (i.e. environmental filtering) and spatial processes (dispersal limitation) for determining the spatial patterns of soil biodiversity is still controversial (Jiao et al., 2019).

The β -diversity partitioning approach proposed by Baselga (2010) can be used to examine the role of different drivers of biogeographic patterns of soil communities in different spatial scales (Andrew et al., 2012; Gianuca et al., 2017; Speed et al., 2013). Previous studies have indicated that the species turnover process (i.e. the changes in species composition among two assemblages) and the nested-resultant process (i.e. the assemblage at a given site being a subset of the regional assemblage) of community β -diversity varied among

ecosystem types, local species pools and among different spatial scales (Baselga et al., 2013; Gianuca et al., 2017; Hill et al., 2017). For instance, spatial turnover is often high in producers due to their dependence on nutrient availability in the local environment (Bengtson et al., 2007; Wang et al., 2014), which may, in turn, have bottom-up effects on plant feeders and microbial feeders in soil. The nested component can point out the relevance of spatial processes such as dispersal limitation in structuring the community (Baselga et al., 2012). Therefore, the β -diversity partitioning approach can be used to quantify the different biogeographic patterns in the diversity of soil communities.

In the terrestrial ecosystem, high plant diversity is often closely correlated with high habitat heterogeneity and therefore with a higher potential for specialization of functional groups of soil organisms (Eisenhauer et al., 2011; Kreft & Jetz, 2007). However, the composition and β -diversity of soil community assemblages are not only constrained by bottom-up processes but also by top-down trophic influences (Caruso et al., 2011; Si et al., 2016). These interactions among plant, plant feeder and their predator interactions strongly impact diversity distribution (Ohlmann et al., 2018). Previous work has shown that spatial species turnover decreases with increasing trophic levels (Zalewski et al., 2018), which implies that β -diversity of different trophic levels may have different influence mechanisms and biogeographic patterns. Meanwhile, the interactions among trophic levels are different under different environmental conditions due to habitat preferences (Martinez-Almoyna et al., 2019). Therefore, delineating the regulation of plant community on β -diversity for different trophic levels in different vegetation types is important to reveal the underlying mechanisms of the biogeographic patterns of below-ground biodiversity.

Grassland ecosystems play a critical role in biodiversity conservation and carbon sequestration of terrestrial ecosystems, and are an ideal platform to disentangle the mechanisms that shape the biogeographic patterns of soil communities (Lorenz & Lal, 2018; Wang et al., 2017). We conducted a field survey along a grassland transect in the arid and semi-arid regions of northern China. As soil nematodes occupy different trophic levels in the soil food web (Wardle et al., 2004), they are good model organisms to investigate how β -diversity varies among trophic levels. Along the grassland transect, we determined the composition of soil nematode communities across three natural vegetation types (desert, desert steppe and typical steppe) from west to east of the transect. We first examined the potential influence of environmental and spatial processes on

the variation of soil nematode communities across the three vegetation types and along the whole transect, then we partitioned the components of β -diversity to examine the principal drivers of nematode community composition and how they vary among nematode feeding groups. We test the following hypotheses: (a) In the typical steppe and desert steppe, the environmental filtering effect (spatial turnover component) will be more important than the dispersal limitation effect (nested-resultant component), while the reverse will be true in the desert ecosystem, since the harsh environment conditions in the desert ecosystem will lead to stronger filtering effect (Pen-Mouratov & Steinberger, 2005). (b) Variations among soil nematodes of different trophic levels (β -diversity) will increase with increasing geographic distance and with plant community distance, since the variations in space/plant community distance are closely related to the variation in the soil microbial community at the same level (Thakur et al., 2015; Wang et al., 2017), and this can have trophic cascading effects on soil nematode feeding groups.

2 | MATERIALS AND METHODS

2.1 | Study area and sampling sites

The experiment was set up along a 3,200-km transect from west to east, across Xinjiang Uygur Autonomous Region, Gansu province, and the Inner Mongolia Autonomous Region in northern China (91°15'E–120°28'E, 39°51'N–50°30'N). The transect was established in arid and semi-arid grasslands of northern China in August 2012. The main vegetation types from west to east in this region are desert, desert steppe and typical steppe (Wang et al., 2017). A total of 50 sampling sites (14 in desert, 18 in desert steppe, and 18 in typical steppe; Table S1) were selected across the gradient.

Mean annual temperatures (MAT) along the transect range from -2.88°C to 9.17°C , and mean annual precipitation (MAP) varies from 38 to 435 mm. MAT and MAP data of the sampling sites were obtained from the global Worldclim dataset (<http://www.worldclim.org>; Hijmans et al., 2005). Extracted data were processed in ArcGIS software v9.3 using the spatial analysis tool (ESRI). The spatial geographic coordinates and elevation data of each sampling site were recorded with a handheld GPS unit (eTrex Venture, Garmin). Representative soil types of this region include Aeolian sandy soil, grey desert soil, brown calcareous soil, chestnut soil and chernozem (Luo et al., 2016). *Reaumuria*, *Nitraria* and *Suaeda* are the dominant plant genera in the desert ecosystem, *Stipa*, *Allium* and *Eragrostis* are dominant in the desert steppe, and *Leymus*, *Stipa* and *Cleistogenes* are dominant in the typical steppe.

2.2 | Soil and plant sampling

At each site, we selected two main plots of $50\text{ m} \times 50\text{ m}$ each that were located approximately 1,000 m apart. There were five subplots ($1\text{ m} \times 1\text{ m}$) within each main plot (Figure S1). In each subplot

($1\text{ m} \times 1\text{ m}$), the above-ground plant biomass was clipped, and then the plant material was sorted to species level (Luo et al., 2016; Wang et al., 2019). Plant biomass was then oven-dried at 65°C for 24 hr and above-ground community biomass was calculated. After removing plant litter and stones from the soil surface, five soil cores (2.5 cm diameter) were collected at 0–10 cm depth and then mixed so that there was one composite sample for each subplot in the field. Composite soils were sieved through a 2.0-mm mesh to remove roots and rocks in the lab. After gentle homogenization, the fresh soil samples were separated into two subsamples: one was preserved for soil physiochemical analysis and the other was kept at 4°C in a refrigerator for nematode analysis. Since some samples got lost during processing, and because some samples where nematodes could not be identified properly due to poor quality were removed, a total of 384 samples were included in this study, with each site having 4–10 replicate samples.

The basic soil properties of each vegetation type are listed in Table S1. Soil pH- H_2O was measured after adding 10 g fresh soil to 25 ml of water. Total organic carbon (TOC) and total nitrogen (TN) were measured using an automatic elemental analyser (Vario MACRO cube, Elementar Analysensysteme GmbH). Total phosphorus (TP) in the soil was determined colorimetrically (800 nm) on a spectrophotometer (Carry500, Varian Company; Wang et al., 2020). Soil moisture (SM) content was determined after drying the soil at 105°C for 48 hr.

Soil nematodes were extracted from 100 g fresh soil using a modified cotton-wool filter method (Oostenbrink, 1960; Townshend, 1963). At least 100 specimens per sample were randomly selected and identified to genus level (Ahmad & Jairjuri, 2010; Bongers, 1994; Li et al., 2017). If the total number of nematodes was <100 , all of them were identified. The number of nematodes was expressed as individuals per 100 g dry soil. All recorded genera were classified into four main feeding groups (bacterial feeders, fungal feeders, omnivores/predators and plant-parasites) according to Yeates et al. (1993) and the Nemaplex database (<http://nemaplex.ucdavis.edu/>) (Table S2).

2.3 | Partitioning β -diversity of nematodes

β -Diversity and its two components of the nematode community in each of the three vegetation types and across the whole transect were calculated following the method of Baselga (2010). The Sørensen dissimilarity (β_{sor}) was additively partitioned into two separate components, the Simpson dissimilarity (β_{sim} , spatial turnover component; representing compositional changes due to species turnover) and the nestedness dissimilarity (β_{sne} , nested-resultant component; representing differences in genera richness between two communities):

$$\beta_{\text{sor}} = \frac{b + c}{2a + b + c},$$

$$\beta_{\text{sim}} = \frac{\min(b, c)}{a + \min(b, c)},$$

$$\beta_{sne} = \frac{|b - c|}{2a + b + c} \times \frac{a}{a + \min(b, c)}.$$

Here, a is the number of shared genera between two communities, b is the number of genera that occur in the first community but not in the second, c is the number of genera that occur in the second community but not in the first and $\min(b, c)$ is the minimum number of exclusive genera of two communities (for subplot, main plot and between each two sites). The β -ratio index was calculated as the proportion of the nested-resultant component to the total dissimilarity (β_{sne}/β_{sor}). Hence, a β -ratio <0.5 indicates that β -diversity is determined mainly by the spatial turnover processes, and a β -ratio >0.5 indicates that the nested-resultant pattern is the dominant component (Dobrovolski et al., 2012). All metrics used for the dissimilarity matrices (β_{sor} , β_{sim} and β_{sne}) of the nematode communities were based on presence/absence data.

2.4 | Statistical analyses

To obtain an overview of the distribution patterns of β -diversity, we calculated the total β -diversity and its two partitioned components for each site by averaging the β -diversity between subplots within each site. The β -diversity (β_{sor}) and partitioned components (β_{sim} and β_{sne}) were displayed along the grassland transect using the thin-plate spline method (Figure 1). To determine the correlation of nematode β -diversity with the plant community and soil properties at the main plot level and site level, we merged the presence/absence data of subplots on different scales. For main plot level, we merged all the subplots in each main plot, and then calculated the β -diversity between the two main plots within each site. For site level, we merged all subplots in each site, and then calculated the β -diversity between each pair of two sites. Plant community and soil property data were merged and distance was calculated in the same way. Soil data were merged by calculating the average of soil variables (SM, pH, TOC, TN and TP).

To examine the relationships between nematode community diversity, geographic distance and plant community composition within vegetation types and along the whole transect, we calculated the β -diversity and partitioned components between the subplots in each vegetation type and across the whole transect. We calculated geographic distances and plant community distances based on the 'Euclidean' and 'Sørensen' metric respectively. Then, we fitted a negative exponential model to describe the distance decay in nematode community similarity (NCS, 1–community dissimilarity) with geographic distance and plant community distance (community dissimilarity) in each vegetation type and along the whole transect (Figure 2). Previous work has shown that this is a good model to describe distance decay patterns at large spatial scales (Gómez-Rodríguez & Baselga, 2018; Nekola & McGill, 2014). We calculated the untransformed geographic distance based on the latitude and longitude of each

sampling site. The decay rates (regression slopes) of community similarity with an observed distance were considered as a measurement of the pattern of β -diversity (Condit et al., 2002). We evaluated those decay models using the goodness-of-fit with computed pseudo- r^2 values ($1 - \text{model deviance}/\text{null deviance}$). To assess whether the decay parameters (slopes and intercepts) differed in the three sets of nematode β -diversity for the three vegetation types and the whole transect, we bootstrapped the slopes and intercepts of the fitted models based on 999 permutations (Figure 3) and carried out a one-way ANOVA. We used the same method to analyse the relationships between diversity of nematode feeding groups, geographic distance and plant community composition within vegetation types and along the whole transect (Figures 4 and 5).

To quantify the relative importance of the explanatory factors that shape nematode communities along the entire transect and in each vegetation type, we performed variance partitioning analysis (VPA) to determine the proportion of variation (%) explained by the environmental variables and geographic distance (Figure 6; Figures S3 and S4). We assessed the contribution of the unique and combined fractions associated with three sets of environmental predictors: climatic variables (MAP and MAT), soil variables (SM, pH, TOC, TN and TP), and plant variables (species richness, above-ground biomass and community composition). A principal component analysis based on the plant community data was performed, and then we used plant richness, biomass and sample scores of the first six axes (PC1–PC6, accounted for 80%–97% of total variation) of the plant community as the set of plant variables. We implemented a step-wise forward selection in the Monte Carlo permutation test to find the significant subsets ($p < 0.05$) for each set of predictors across the whole transect. Then, we standardized the selected datasets to create the climatic, soil and plant matrices to estimate the effects of the environmental factors on the variation in the total nematode community (β_{sor}) and two decomposed components (β_{sim} and β_{sne}). The same approaches were carried out after spatial variables were included in the analysis for the nematode feeding groups in each vegetation type and along the whole transect. To represent the spatial variation, the principal coordinates of the neighbour matrices (PCNM) eigenfunctions were determined based on Moran's spatial autocorrelation analysis (Dray et al., 2006). The positive spatial eigenvalues (PCNMs) from a truncated distance matrix were used as spatial variables (Borcard & Legendre, 2002). The significance for the constraint fractions of interest was determined using a permutation test based on a distance-based redundancy analysis (db-RDA), and the adjusted R^2 criterion was computed with 999 permutations.

To visualize the patterns of nematode and plant community composition in two dimensions, we used non-metric multidimensional scaling (NMDS; Austin, 2013; Figure S5). The Kruskal's stress criterion was estimated to evaluate the goodness-of-fit for the final ordination model (Kruskal, 1964). The β -ratio was based on the average

of the β -ratio of the subplots within each vegetation types and whole transect (Figure S6).

All statistical analyses were conducted in R v3.5.1 (R Development Core Team, 2019). Pairwise community dissimilarity matrixes and negative exponential models were constructed using the BETAPART v1.5.1 package (Baselga et al., 2018). Spatial interpolation was implemented using the FIELDS v8.4-1 package (Nychka et al., 2019). NMDS and VPA were implemented in the VEGAN v2.5-2 package (Oksanen et al., 2018). Forward selection was performed using the PACKFOR v0.0-8 package (Dray et al., 2013). PCNM analysis was carried out in the PCNM v0.0-8 package (Dray et al., 2006). For visualization of the data, we used the GGLOT2 v3.1.1 package (Wickham et al., 2019).

3 | RESULTS

3.1 | Spatial patterns of nematode β -diversity in different vegetation types

The total β -diversity (β_{sor}) within sites (average of the dissimilarity between subplots within each site) decreased gradually from the west to the east along the grassland transect (Figure 1). The β -diversity between sites and between main plots was mainly regulated by plant community and soil variables respectively (Figure S2). The β -diversity of the nematode community showed similar patterns for the spatial variation along geographic distance and plant community distance (Figure 2). Significant differences in mean parameters were also detected for each vegetation type (ANOVA, $p < 0.001$ in all cases), and the slopes were significantly steeper for the whole transect than for three vegetation types separately (Figure 3). Variation partitioning analysis revealed that the combined effects of environmental and spatial variables played a dominant role in generating nematode β -diversity, with spatial variables accounting for a larger proportion of the explained variation (Figure S3; Table S3). Environmental filtering explained more of the variation in β -diversity in the desert and typical steppe, whereas geographic distance was important in the desert steppe (Figure 6).

In a further analysis where we excluded the effects of spatial distance, all three sets of predictors jointly influenced the nematode β -diversity in the whole grassland transect, with relatively higher pure effects from the composition of the plant community than from the soil parameters (β_{sor} , $p < 0.001$; Figure S4). We found a significant effect of plant community composition on nematode β -diversity in the typical steppe and desert (11% and 11% for β_{sor} respectively), with a higher contribution from plant factors in the typical steppe (combined effects) than in the desert steppe (5.3% for β_{sor} ; Figure S4). The effects of soil and climatic variables were also stronger in typical steppe and desert than in desert steppe. Nematode communities among different vegetation types were separated in the ordination of the NMDS, with more variation among individual samples from the desert ecosystem than from the desert steppe and the typical steppe (Figure S5).

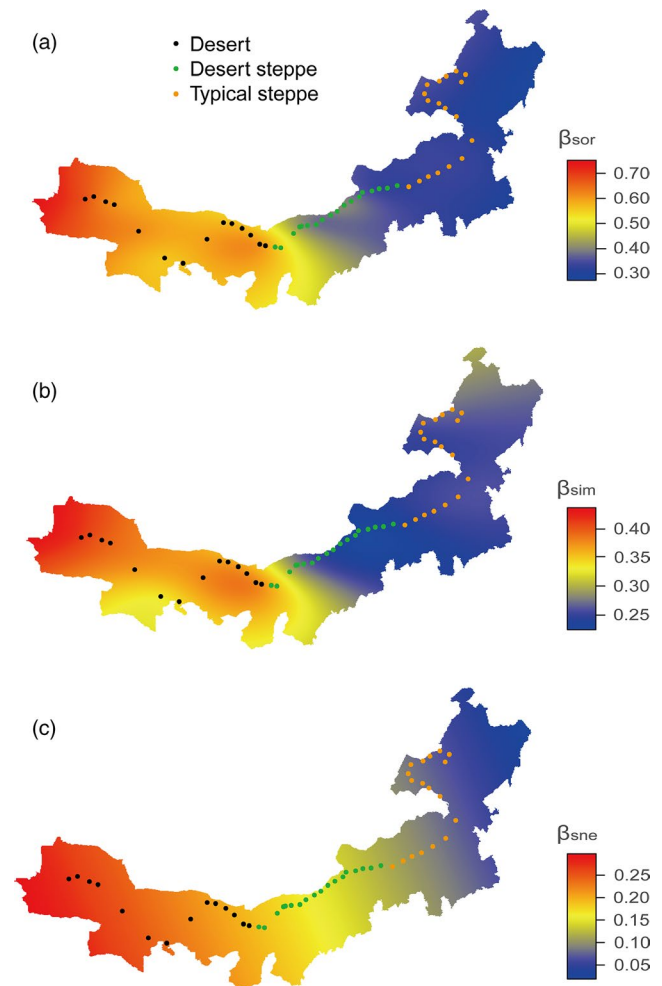


FIGURE 1 Geographic interpolations of different components of community dissimilarity (averaging the β -diversity between subplots within each site) of soil nematodes. (a) β_{sor} (the total community dissimilarity), (b) β_{sim} (the spatial turnover component dissimilarity) and (c) β_{sne} (the nested-resultant component dissimilarity) in the three vegetation types

3.2 | Spatial variation of β -diversity among nematode feeding groups

For nematode feeding groups, the variation patterns of β -diversity among feeding groups differed significantly along geographic distance and plant community distance. The largest variation among nematode communities (NCSsor) was found for the whole transect both when examined over geographic distance ($p < 0.001$; Figure 4) and over plant community distance ($p < 0.001$; Figure 5).

Across the grassland transect, the slope of the plant-parasites (slope: $M = -0.90$, $SD = 0.31$; intercepts: $M = 0.91$, $SD = 0.03$) was significantly steeper than that of the other feeding groups along plant community distance (Figure S7). Omnivores/predators displayed the flattest slopes along geographic distance (slope: $M = -0.00013$, $SD = 0.000089$; $p < 0.001$) and plant community distance for the whole transect (slope: $M = -0.26$, $SD = 0.16$; $p < 0.001$; Figure S7).

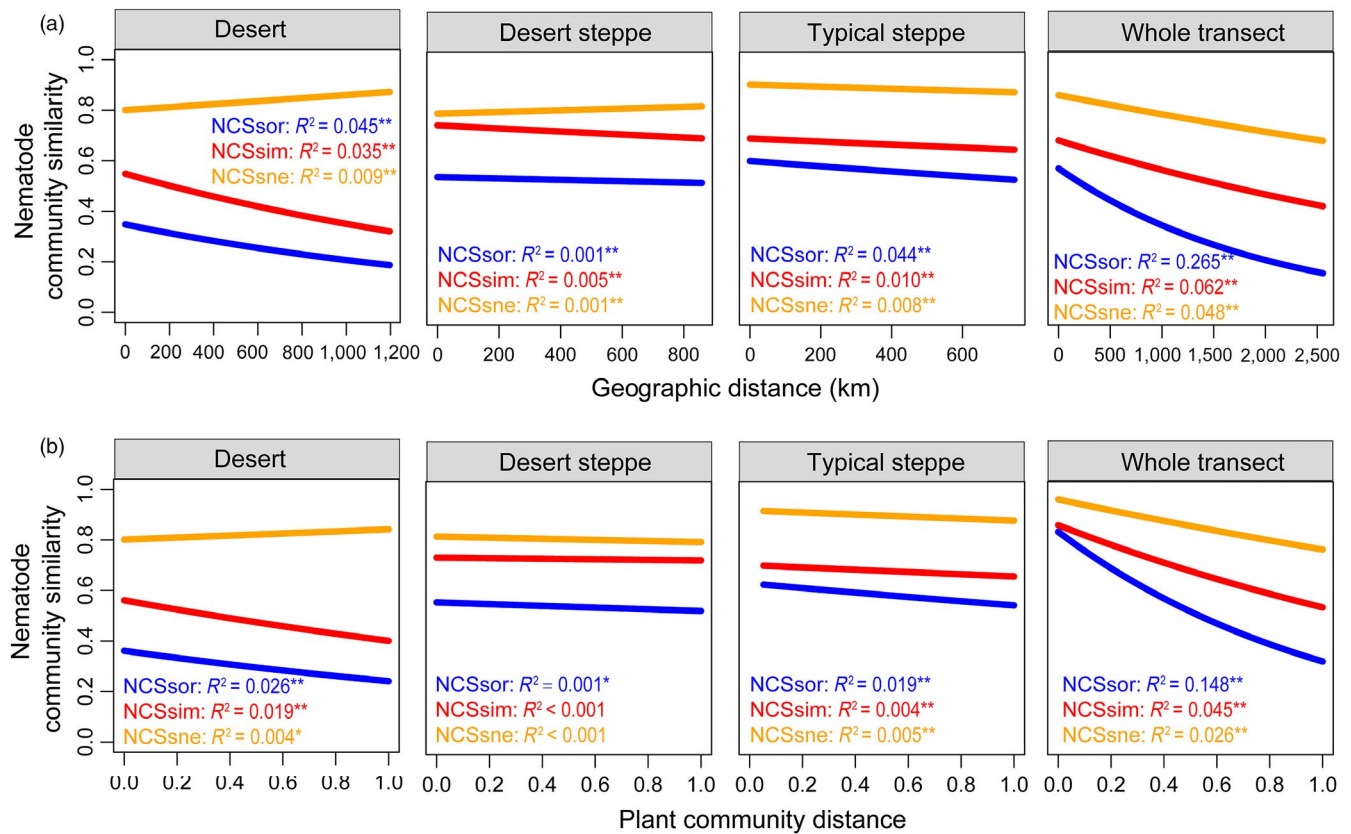


FIGURE 2 Patterns of nematode community similarity along (a) geographic distance and (b) plant community distance for each of three vegetation types and for the whole transect. The significance of the relationship (* $p < 0.05$; ** $p < 0.01$) is represented for the patterns of NCSsor (1 – the total nematode community dissimilarity), NCSsim (1 – the spatial turnover component dissimilarity) and NCSsne (1 – the nested-resultant component dissimilarity)

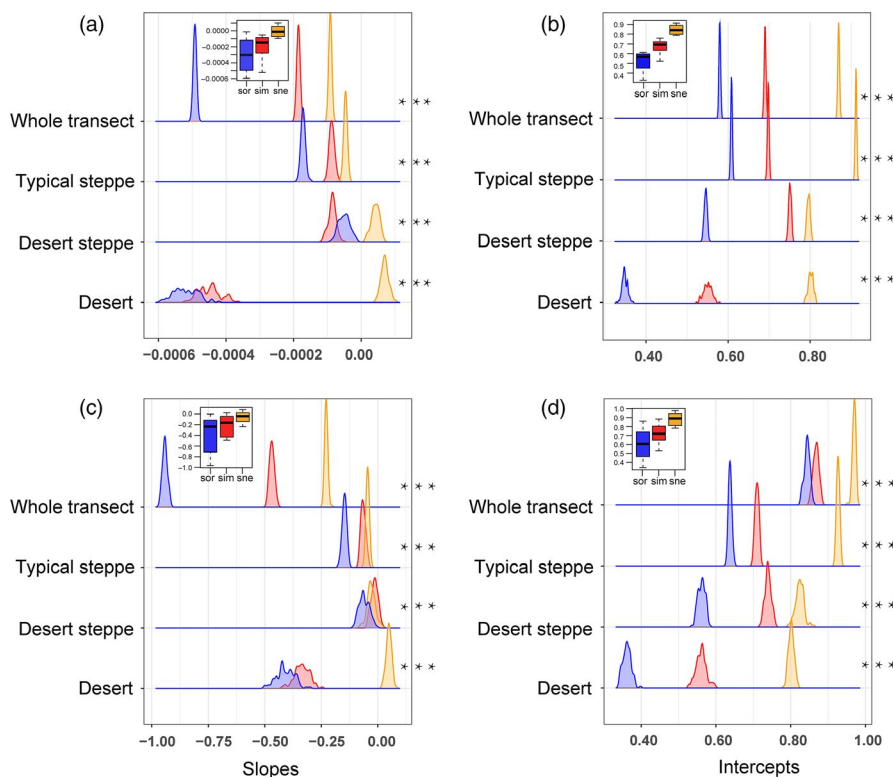


FIGURE 3 Bootstrapped distributions of the slopes (a, c) and intercepts (b, d) describing the distance decay patterns across geographic distance (a, b) and plant community distance (c, d) for the total β -diversity (blue), the spatial turnover component (red) and the nested-resultant component (yellow) for each of the three vegetation types and for the whole transect. The insets represent the bootstrapped distributions of the mean parameter values in the different vegetation types. The significant differences (***) among the three sets of nematode β -diversity parameters are shown

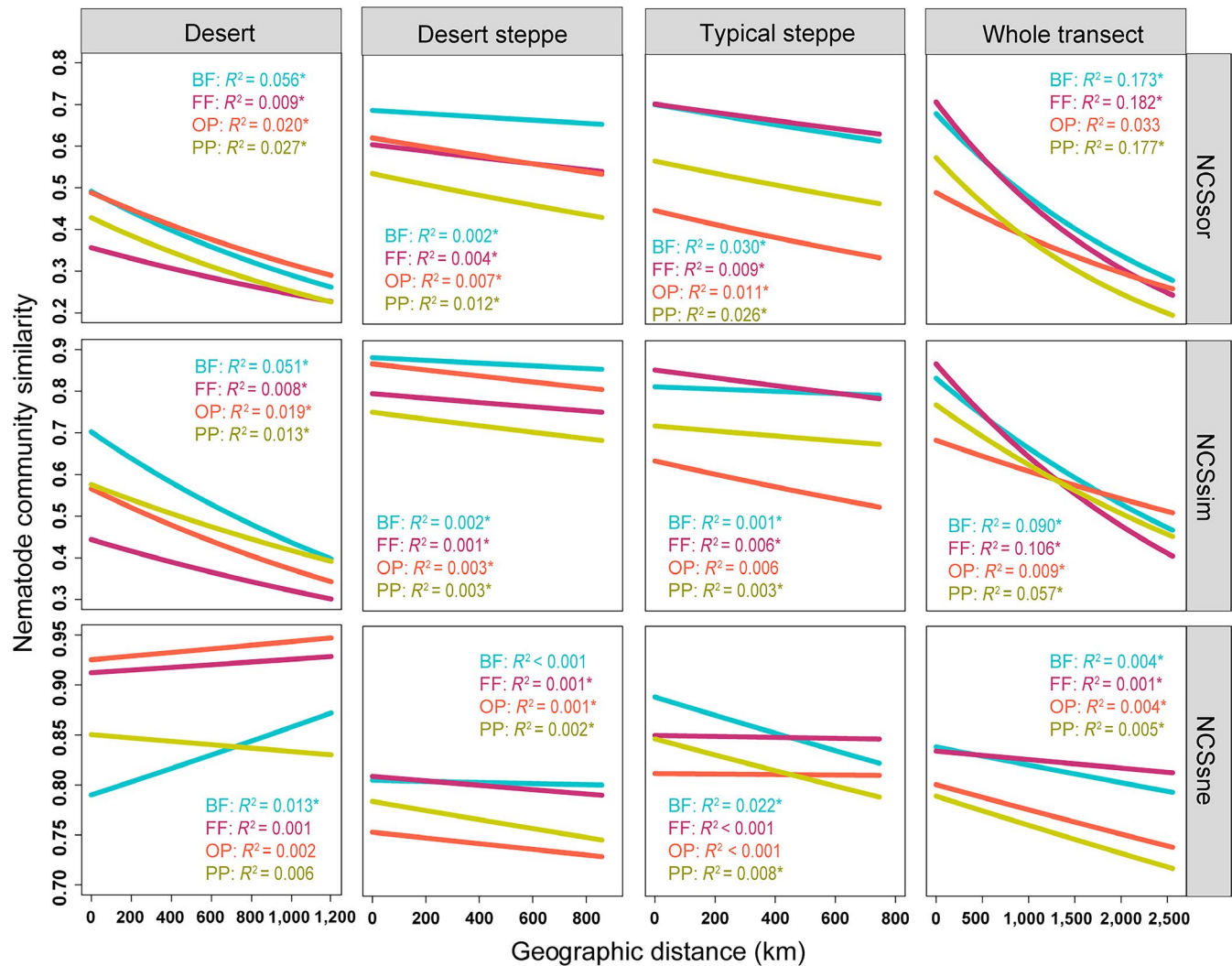


FIGURE 4 Relationship between nematode community similarity and geographic distance for different feeding groups in each of the three vegetation types and for the whole transect. The significance of the relationship ($*p < 0.05$) is marked for the patterns of NCSsor (1 – the total nematode community dissimilarity), NCSsim (1 – the spatial turnover component dissimilarity) and NCSsne (1 – the nested-resultant component dissimilarity). BF, bacterial feeders; FF, fungal feeders; OP, omnivores/predators; PP, plant-parasites

3.3 | Partitioning of β -diversity along the grassland transect

The diversity pattern of soil nematodes along the whole grassland transect was mainly explained by the spatial turnover component (β_{sim}), but the relative contribution of the nested-resultant component was higher in the desert steppe than in the desert and typical steppe (Figure S6). The combined effects of the environmental and spatial variables (significant PCNMs) both explained 35% of the variation of the spatial turnover component and the nested-resultant component ($p < 0.001$; in all cases; Figure S7). In a further analysis where we excluded the effects of spatial distance, a total of 30% and 27% of the variation in spatial turnover (β_{sim} , $p < 0.001$), and nested-resultant components (β_{sne} , $p < 0.001$) were explained by the measured environmental variables (Figure 6). We subsequently compared the separated components of the parameter from the bootstrapped distributions in the different vegetation types. The slopes of the spatial turnover component

(ANOVA, $p < 0.001$; $M = -0.00021$) were significantly steeper than those for the nested-resultant component ($M = -0.000025$) across the geographic distance (Figure 2), and the intercepts of the total β -diversity ($M = 0.61$, $SD = 0.08$) were significantly lower than those of the spatial turnover ($M = 0.79$, $SD = 0.07$) and the nested-resultant components ($M = 0.82$, $SD = 0.02$; Figure 3). The lowest values of slopes and intercepts across both geographic distance and plant community distance were observed for the nested-resultant component (Figures 2 and 3).

Interestingly, we found a positive relationship between the similarity of the nested-resultant component (NCSsne) and geographic distance and plant community distance in the desert ecosystem ($p < 0.05$; Figure 2a). For the community similarities of the spatial turnover (NCSsim; pseudo- $r^2 = 0.062$), and the nested-resultant components (NCSsne; pseudo- $r^2 = 0.048$), the steepest slopes were all detected across the geographic distance when compared with those across the plant community distance (Figure 2a,b).

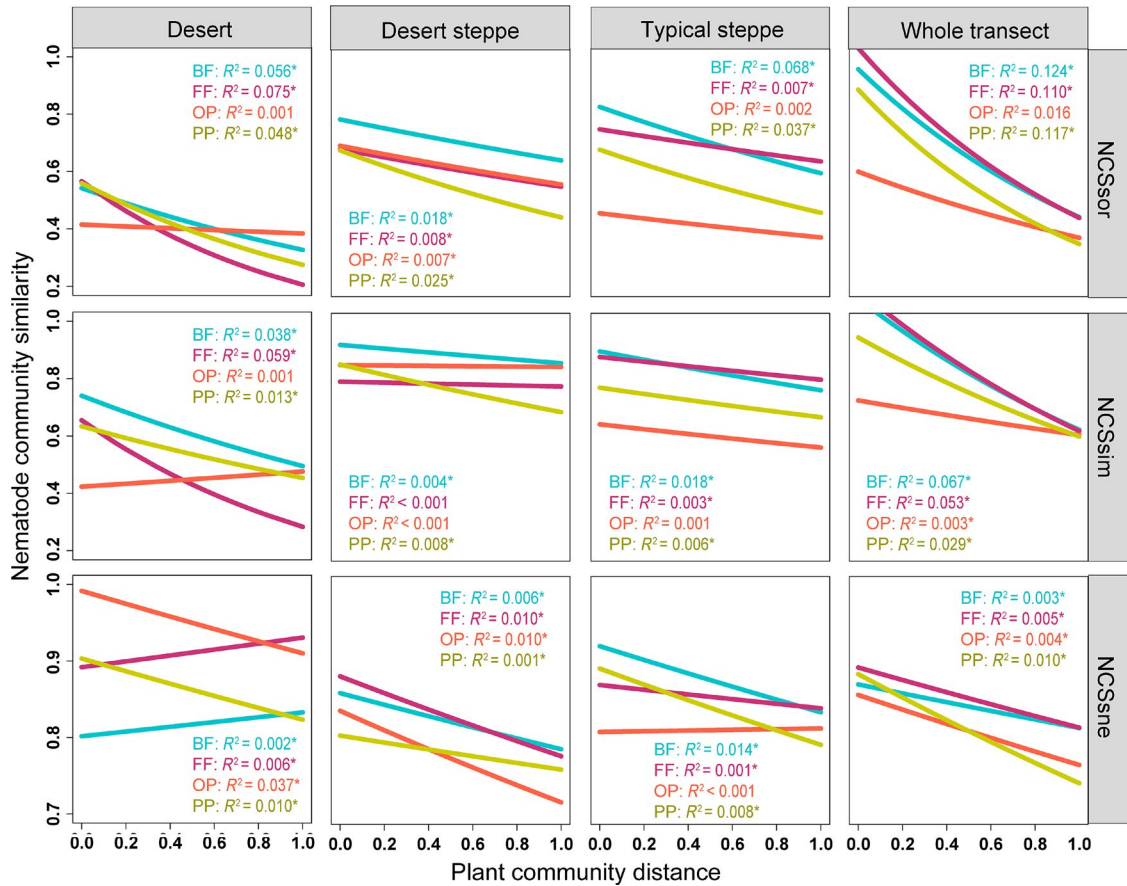


FIGURE 5 Relationship between nematode community similarity and plant community distance for different feeding groups in each of the three vegetation types and for the whole transect. The significance of the relationship (* $p < 0.05$) is marked for the patterns of NCCSor (1 – the total nematode community dissimilarity), NCCsim (1 – the spatial turnover component dissimilarity) and NCCsne (1 – the nested-resultant component dissimilarity). BF, bacterial feeders; FF, fungal feeders; OP, omnivores/predators; PP, plant-parasites

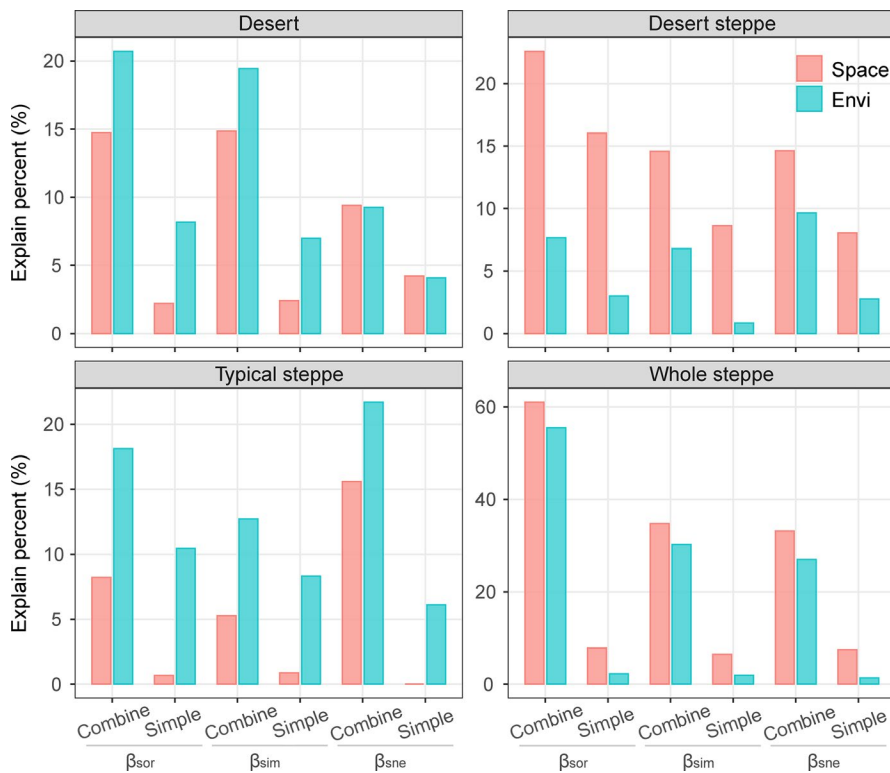


FIGURE 6 Variance partitioning of the soil nematode community based on distance-based redundancy analysis (db-RDA) for β_{sor} (the total community dissimilarity), β_{sim} (the spatial turnover dissimilarity) and β_{sne} (the nested-resultant component dissimilarity). The explained percentages of combined effect and simple effect for space (geographic distance) and envi (environmental variables) are displayed separately. All selected subsets of the explanatory variables were obtained from forward selection (999 permutations; $\alpha < 0.05$)

When the bootstrapped distributions of parameters (slopes and intercepts) were compared in the desert ecosystem, the slopes of the nested-resultant component of the bacterial feeders (pseudo- $r^2 = 0.013$; $M = 0.000081$) showed a weak upward trend with increasing geographic distance ($p < 0.001$; Figures 4 and 5). The slopes of the nested-resultant component of the bacterial feeders (pseudo- $r^2 = 0.002$; $M = 0.0038$) and the fungal feeders (pseudo- $r^2 = 0.006$; $M = 0.043$) displayed similar patterns with an increase in plant community distance (ANOVA, $p < 0.001$; Figures 4 and 5). Thus, the nested-resultant patterns (NCSsne) of microbivorous nematodes in the desert ecosystem increased with geographic distance.

4 | DISCUSSION

We investigated the spatial patterns of soil nematode communities along a temperate grassland gradient. Our results show that the β -diversity of soil nematodes varies among vegetation types and among trophic levels of nematodes in the grassland ecosystems. The spatial distance and environmental filtering jointly explained the variation in nematode β -diversity, with a greater contribution from the environmental filtering for the typical steppe and desert, while the contribution from geographical distance was larger in the desert steppe. In comparison with the nested-resultant component, spatial turnover was the dominant process that determined the total β -diversity of the nematode community across the whole transect.

4.1 | Drivers of nematode β -diversity among vegetation types

In contrast to our first hypothesis, we found that the environment filtering was important in the desert and typical steppe, but not in the desert steppe. The soil, plant and climate factors varied obviously in the typical steppe, so these environmental factors have a greater impact on the spatial distribution of nematode communities. Nematodes live in the water film in the soil pores. Therefore, the moisture content in the soil determines the spread of soil nematodes (Xiong et al., 2020). In the desert steppe, low SM limited the movement of nematodes. At the same time there is only limited variation in soil and plant factors in this ecosystem, leading to a greater influence of spatial factors on nematode dissimilarity. In the desert ecosystem, although the spread of nematodes has been limited, the nutritional demands of the nematodes are more pressing due to the patchy distribution of the above-ground vegetation in the arid region (Luo et al., 2018). As a result, the composition of the nematode community is mainly determined by the nutrients supplied by plants and present in the soil in the small areas that are vegetated, which may explain the higher β -diversity of nematodes in the desert ecosystem. The results obtained from all sets of the measured environmental drivers (excluding geographic effects) confirm this. Plant community and soil variables contributed most

(combined effects) to the variation among nematode communities in the desert and typical steppe.

4.2 | Partitioning β -diversity of nematodes among vegetation types

The spatial turnover component was the dominant factor explaining nematode β -diversity over the whole transect and in the three vegetation types separately. However, we did not find that the nested-resultant component was important in the desert ecosystem. There was more variation in nematode β -diversity (mean bootstrapped slopes) along geographic and plant community distances in the whole transect than in the individual vegetation types as expected, which suggests that the driving factors influencing the spatial patterns of the nematode communities in the individual vegetation types differ from those at the larger spatial scale. We should note that the explanatory power of the negative exponential model that is presented was relatively low, especially for the individual vegetation type. However, our findings show that geographic distance explained a larger fraction of variation in total nematode β -diversity than measured environmental variables over the whole grassland transect. This suggests that stochastic processes are the main driver of variation in nematode communities across this temperate grassland.

In our study, the nested-resultant component of soil nematode β -diversity increased with increasing geographic distance and plant community distance in the desert ecosystem, which is contrary to the inference of neutral theory, that is a distance decay relationship in biogeographic patterns (Morlon et al., 2008; Soininen et al., 2007) and to that reported in other studies on soil community similarity and geographic or environmental gradients (Anderson et al., 2011; Green & Bohannan, 2006). The limited dispersal capacity of soil nematodes and their adaptation to dry conditions may be the main reasons for this spatial pattern (Placella et al., 2012). The pattern that we observed could be an artefact but could also potentially be explained by strong environmental filtering caused by local environmental stresses, such as drought. Possibly, these environmental effects may have filtered out some non-competitive species, such as drought-sensitive species (Chase, 2007) so that only a selected subset of nematode species remained.

4.3 | Drivers of nematode β -diversity among different trophic levels

Our results highlight that the β -diversity and its two components varied greatly among the three vegetation types and depended on the trophic position of the soil nematodes. A recent meta-analysis also concluded that patterns of β -diversity components depended on the trophic status or biological traits of the functional groups (e.g. dispersal type, body size; Soininen et al., 2017). This may be

because focal trophic groups formed different feeding habits and life-history traits in the local environment, which could affect the colonization process to a new region. According to Chase (2010), interspecific relationships (e.g. competition, predation and parasitism) affect the construction of soil communities through resource constraints. Thus, we assume that the diversity patterns of soil nematode communities are associated with soil conditions and with the composition of the plant community in each vegetation type as this could alter the community of the plant feeders directly, and other trophic levels indirectly via the impacts of plants on soil nutrient conditions.

Interestingly, there was a weak relationship between the nested-resultant component of bacterial feeders and geographic distance or plant community distance in the desert ecosystem, consistent with the findings of Carvalho et al. (2010) who studied spider assemblages over a spatial gradient in the Mediterranean region. At large spatial scales, the extinction and recolonization dynamics induced by climatic history are likely to result in an increase of nestedness pattern (Baselga et al., 2012; Dobrovolski et al., 2012). In our study, we inferred that the nested-resultant processes may not vary with longitudinal extent owing to the complex colonization and extinction processes. Several studies have shown that the underlying mechanisms for the nested-resultant patterns were habitat nested, selective extinction and selective colonization (Dobrovolski et al., 2012; Ulrich & Fiera, 2009). We inferred that the rates of colonization or extinction of bacterial feeders and fungal feeders may be responsible for the observed patterns. Our study shows that variation in the lower trophic levels of the nematode community is not always linked to patterns of higher trophic levels. Hence, it is important to study biogeographic patterns from a multi-trophic perspective to better understand the underlying mechanisms of soil biodiversity.

5 | CONCLUSIONS

We quantified the ecological processes that drive nematode β -diversity across a large spatial scale. The spatial diversity patterns we observed for soil nematodes did not always follow the distance decay relationship at the regional scale, presenting a challenge to the traditional ecological theories. The spatial turnover and nested-resultant components of nematode β -diversity varied across different spatial scales and also varied between nematode feeding groups. Our findings on the biogeographic patterns of soil organisms provide insight into the spatial patterns of below-ground assemblages and the ecological processes that drive these patterns.

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AUTHORS' CONTRIBUTIONS

X.H., X.W. and Q.L. conceived the ideas and designed the research; C.W., X.W. and X.L. collected the data; D.X., S.F. and Y.L. analysed the data; D.X., Q.L., Y.L., T.M.B. and W.L. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Nematode data for this study are deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.6wwpzgmxr> (Xiong et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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