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Climate and edaphic factors drive soil nematode diversity and community composition in urban ecosystems

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ABSTRACT

Rapid urbanization profoundly affects global biodiversity. How urbanization modifies soil biodiversity and perturbs nematodes remains limited. Here, we investigated soil nematodes in four land-use types: Parks, residential areas, natural forests, and maize fields across 12 cities in China. Urban parks and surrounding forests had similar nematode richness exceeding that in urban residential areas and surrounding farmlands. Nematode communities in parks and residential areas were, however, more homogenous than in forests and farmlands. Variations in nematode assemblages in both core urban and urban surroundings were mainly due to taxa replacement, indicating that nematodes were spatially isolated in cities. Urban residential areas were colonized by the lowest number of specialists (i.e., with narrow niche width) and smaller body sizes. Urban parks, conversely, served as hotspots for soil nematodes in cities. Together, our results indicate that urbanization processes reduce nematode diversity, with e.g., 30% loss in residential areas compared to forests, and homogenize soil nematode communities.

1. Introduction

With increasing human population and housing, the demand for city space is growing and consubsequently urban areas are expanding (Seto et al., 2012). Urban expansion and associated land-cover changes drive habitat loss and threaten biodiversity (Beninde et al., 2015). Therefore, efforts are needed to harmonize anthropogenic activities with biodiversity conservation for the sustainable development of modern cities (Lambert and Donihue, 2020). Yet, we still lack an understanding of factors that shape urban biodiversity, for instance how urban biodiversity changes with urban expansion (Uchida et al., 2021) and the types of urban habitats, which is critical to the development of strategies for

biodiversity conservation in cities. This is particularly true for belowground biodiversity, which has only recently begun to be considered as an irreplaceable part of ecosystem health (Guerra et al., 2021; Wall et al., 2015).

Soils serve as habitat for the majority of terrestrial biodiversity (Bardgett and van der Putten, 2014; Orgiazzi et al., 2016). Free-living nematodes are among the most abundant and biodiverse invertebrate animals in soil (van den Hoogen et al., 2019). Moreover, they are highly diverse in terms of feeding guilds and occupy various trophic levels in soil food webs, driving multiple ecosystem functions, such as the processing of organic matter and the regulation of soil microbial populations (Yeates et al., 1993; Wan et al., 2022). Further, nematodes serve

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as bioindicators due to their high sensitivity to physicochemical changes in soil (Zhao and Neher, 2013). Globally, soil nematodes display distinct latitudinal diversity gradients, with highest diversity but lowest speciation rates at middle latitudes (Gong et al., 2021; Song et al., 2017; Wu et al., 2016). This supports the relevance of interactions between climate and soil abiotic factors in driving nematode diversity (Thakur et al., 2020), and both of these factors are vulnerable to urbanization (Kalnay and Cai, 2003; Lorenz and Lal, 2009). Until today, however, there are only few studies on the relationships between urbanization and soil nematode diversity across spatial scales.

Land-use change, which is particularly strong in urban areas, is regarded as the main driver of soil biodiversity loss (Schmidt et al., 2017; Tóth et al., 2020). Effects of land-use changes are supposed to be particularly strong in cities and consequently are likely to negatively impact soil nematodes. Variations in soil conditions due to land-use changes drive microbial carbon cycling (Malik et al., 2018), which likely also affects soil nematode communities in urban areas given that nematodes feed on soil microorganisms. Further, urbanization changes climatic factors, with local climate varying considerably between different land-use types within cities (Pielke, 2005). Climatic variables such as temperature increase nematode diversity in resource rich soils but decrease it in resource poor soils, and the latter typically applies for intensively managed soils (Siebert et al., 2019). As evidenced by other terrestrial organisms (Gardi et al., 2013; Thakur et al., 2022), the effects of climatic variables may aggravate those of land-use changes (Peters et al., 2019). Land-use change differentially impacts soil biodiversity depending on land-use types (van Asselen and Verburg, 2013). For example, land-use change from natural to agricultural systems increased bacterial diversity due to fertilization effects (Kim et al., 2021). Further, the effects of land-use change on soil biodiversity might be manifested by cascading effects of plant diversity, which is the predominant driver for soil biodiversity in natural ecosystems (Wen et al., 2020).

We investigated how urbanization associated land-use changes and climate variables interactively affect the diversity and community composition of soil nematodes. We took soil samples from four land-use types in rapidly expanding cities across China, i.e., core urban areas, which included parks and residential areas, and urban surrounding areas, which included farmlands and forest sites (Bai et al., 2014). We then investigated the role of climatic variables (temperature and precipitation) and land-use types in shaping soil nematode diversity and community composition. We hypothesized that (1) land-use changes strongly impact nematode diversity by reducing the richness and homogenizing the community composition in core urban areas compared to urban surrounding sites, and (2) climate variables, alone and interactively with land-use types, contribute to variations in nematode richness and community composition.

2. Materials and methods

2.1. Sampling design and soil collection

Soil samples were taken from 12 cities in China between May and August 2021 (Table S1). The cities were located in regions spanning from subtropical to temperate climates. In each city, we selected four land-use types: urban surrounding farmland, urban surrounding forest, urban park and urban residential sites. Each land-use type was replicated four times in each city. Urban surrounding forest (Mostly consist of natural or close to natural forests) and farmland (Most sites cultivated with maize) sites were located at the outskirt of each city, and urban parks and residential sites were located within cities and thus represented core urban sites. In each of the cities, the four sampling sites of each land-use type were separated by at least 1 km. At each sampling site, a plot (20 m × 20 m) was randomly established for soil sampling. In the plot, nine soil cores were randomly collected with an auger (diameter 5.5 cm, depth 0–10 cm) and mixed as a composite sample. In total, we collected 192 soil samples (12 cities × 4 land-use types × 4

replicates). Soil samples were transported to the laboratory on ice. An aliquot was stored at −20 °C for molecular analysis and another was air-dried for physicochemical analysis after passing through 0.2 mm mesh.

2.2. Determination of soil properties

Soil total carbon (TC), soil total nitrogen (TN) and soil total phosphorus (TP) were measured as soil variables representing resources for microorganisms and soil animals. Soil TC and TN were measured using an elemental analyzer (Elemental Analyzer System Vario Macro Cube, Langenselbold, Germany). Soil TP was measured by Inductively Coupled Plasma-Atomic Emission Spectrometry (ICPS-7500) using the triacid digestion-ICP-AES method. Soil pH was measured using a pH meter (PHS–3C., Shanghai Leici) after shaking a soil-water suspension (1:5 w/v) for 30 min. Soil moisture content was determined using 10 g of fresh soil dried at 105 °C for 48 h.

2.3. Soil DNA extraction and nematode amplicon sequencing

Each composite soil sample was thoroughly mixed and 10 g of this soil was then homogenized, genomic DNA was extracted from 0.5 g soil using the MP FastDNA spin kit for soil (MP Biomedicals, Solon, OH, USA) according to the manufacturer's instructions. The quality and quantity of the extracted DNA were certified with 1% agarose gel electrophoresis and Nanodrop-2000 spectrophotometer (NanoDrop Technologies Inc. Wilmington, DE, USA), respectively. The hypervariable V4 region of the 18S rDNA gene was chosen for amplicon sequencing using the universal eukaryotic primer pair NF1–F/18Sr2b-R (Porazinska et al., 2009). PCR amplification of the 18S rDNA gene was performed as follows: initial denaturation at 95 °C for 3 min, followed by 30 cycles of denaturing at 95 °C for 30 s, annealing at 55 °C for 30 s, extension at 72 °C for 30 s, and single extension at 72 °C for 10 min, and ended by holding at 4 °C. The PCR mixtures contained 4 μL 5 × TransStart FastPfu buffer, 2 μL dNTPs (2.5 mM), 0.8 μL forward primer (5 μM), 0.8 μL reverse primer (5 μM), 0.4 μL TransStart FastPfu DNA Polymerase, 10 ng template DNA and 20 μL ddH$_2$O. The PCR reactions were performed in triplicate and with a negative control replacing template DNA by ddH$_2$O. The PCR product was extracted from 2% agarose gel and purified using the AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, Union City, CA, USA) according to the manufacturer's instructions and quantified using Quantus™ Fluorometer (Promega, USA). Purified amplicons were pooled and sequenced on an Illumina MiSeq PE300 platform (Illumina, San Diego, USA) by Majorbio Bio-Pharm Technology Co. Ltd. (Shanghai, China).

2.4. Sequence data processing

Paired-end sequence data were joined and demultiplexed using Cutadapt (Martin, 2011). Then, the sequences <200 bp, average quality score <20 or ambiguous characters were discarded using UPARSE (Edgar, 2013). After chimeras and singletons were removed, closed reference operational taxonomic units (OTUs) were clustered based on 97% similarity using the script pick_closed_reference_OTU.py in QIIME (Caporaso et al., 2010). The taxonomy of the sequenced OTUs was assigned using SILVA v138 (Quast et al., 2013). The resulting OTUs were then filtered and the OTUs successfully assigned to "Nematode" were retained, which resulted in a rarefied 2300 sequences per sample for downstream analysis. A phylogenetic tree was constructed using the longest representative sequence for each nematode OTU using FastTree with default settings (Price et al., 2009). Subsequently, the body size for each nematode OTU was allocated according to the data collected from NEMAPLEX (http://nemaplex.ucdavis.edu/) and published papers with averaged genus (Aslani et al., 2022; Luan et al., 2020). The niche width of each nematode OTU was calculated based on the Levins' index (Levins, 1968) as implemented in the niche.width function of the spaa package (Zhang, 2016).

2.5. Statistical analyses

All the analysis and figures were generated using R 4.1.2 (R Core Team, 2022) except noted otherwise. In the analyses we used three categories of variables, i.e. climatic, urban and soil factors, to explore determinants of nematode richness and community composition. To quantify the impact of urbanization on soil nematodes, data including urban area, urban population size, population density, urbanization rate, proportion of green space and average green space per person for each city were assembled from https://www.mohurd.gov.cn/. For each sampling site, we extracted 19 climate variables from WorldClim version 2.1 (Fick and Hijmans, 2017). To reduce collinearity among urban and climatic variables, we calculated variance-inflation factors (VIFs) for each climate or urban variable using the vif function in the car package (Fox and Weisberg, 2018); only variables of a vif <4 were selected for further analysis (Gross, 2003). Of the urban variables, urban area, population density and urbanization rate were retained as explanatory variables; for the climatic variables, annual mean temperature, isothermality, annual mean precipitation and warmest quarter precipitation were retained (Fox and Monette, 1992). To quantify the contribution of each explanatory variable to variations in richness, a random forest (RF) analysis with 5000 permutations was performed to evaluate the most important factors using the R package rfPermute (Archer, 2020). To analyze variations in nematode community composition among land-use types, nonmetric multidimensional scaling (NMDS) was performed using metaMDS in the R package vegan (Oksanen et al., 2020). Homogenization effects were assessed using Bray-Curtis distance, with the effects getting greater by lower Bray-Curtis distance values. To further analyze variations in nematode community composition, beta diversity was partitioned into spatial species turnover and nestedness, representing the diversity resulting from species replacement and species loss, respectively (Baselga, 2010), using the R package adespatial (Dray et al., 2022). For each combination of land-use types, indicator species (OTU) analysis was performed using the R package indicspecies (De Cáceres and Legendre, 2009). The identified indicator OTUs were taken to represent specialists in the respective land-use types (Moore et al., 2021). The association between each indicator species and one or more of the land-use types was visualized using bipartite networks in the R package igraph (Csardi and Nepusz, 2006). For each environmental variable, threshold indicator taxa analyses were used for detecting key environmental variables and their threshold values were calculated in the R package TITAN2 (Baker et al., 2020). The sum of the indicator species scores was used to detect lower and upper thresholds for each environmental variable. To determine the direct and indirect effects of urbanization on soil nematodes, a partial least squares path model (PLS-PM) was constructed using the R package plspm (Sanchez et al., 2015). To build the model urban area, population density and urbanization rate were defined as the latent variable urban; annual mean temperature (BIO1), isothermality (BIO3), annual mean precipitation (BIO12) and warmest quarter precipitation (BIO18) were defined as latent variable climate; and total carbon (TC), total nitrogen (TN) and total phosphorus (TP) were defined as latent variable soil resource. We included the first axis from NMDS to represent the variation in nematode community composition in the PLS-PM.

3. Results

3.1. Nematode richness

The richness of nematodes in urban surrounding farmland and urban residential soils was significantly lower than in urban surrounding forest and urban park soils (Fig. 1A). Among the variables studied, climatic variables were the most important predictor of nematode richness explaining 44.3%, 34.6%, 31.4%, and 18.2% of the variation in urban residential, urban park, urban surrounding farmland and urban surrounding forest sites, respectively (Fig. 1B). Soil and urban variables

ranked as second and third predictors of nematode richness for urban surrounding forests, urban parks and urban residential sites. While in urban surrounding farmland soils, urban variables were more important than soil variables but still next to climatic variables (Fig. 1B). The species-area curve of nematode richness was significant for farmland and forest, but not for park and residential soils (Fig. S1).

3.2. Nematode community composition

Nematode community composition overlapped widely among land-use types (Fig. 2A). Beta diversity in urban surrounding forest and farmland significantly exceeded that in the urban park and residential sites, thus the communities were more homogenous in core urban than in urban surrounding sites (Fig. 2B). Variations in beta diversity in each of the land-use types were mainly due to turnover of species, which typically contributed >60% to the total beta diversity (Fig. 2C). Distance-decay relationships were significant in each of the four land-use types, with the slope decreasing in the order urban residential sites > urban park > urban surrounding forest > urban surrounding farmland (Fig. 2D). Moreover, species turnover in the urban surrounding forest increased with urban area, whereas it decreased in urban residential sites (Fig. S2).

3.3. Indicators and thresholds

Each land-use type was colonized by a subset of soil nematodes exclusively occurring in these land-use types ('indicator species'; Fig. 3A). Urban surrounding forest and urban park were inhabited by more nematode indicator species than urban surrounding farmland and urban residential soils. Urban surrounding forests and urban parks also shared a high number of indicator species. Most of the species in urban surrounding forests and urban parks tended to have larger body sizes and niche widths than in urban surrounding farmland and urban residential soils (Fig. 3A). The threshold analysis for nematode richness decreasing with urban area peaked at 473 km^2, whereas the threshold analysis for nematode richness increasing with urban area peaked at 1000 km^2 (Fig. 3B).

3.4. Pathways of urbanization effects

The partial least squares path model (PLS-PM) indicated that both climate and land use affect the richness and composition of urban soil nematode communities via a combination of direct and indirect effects (Fig. 4A). Direct effects of climate and land use only correlated with richness (positive) and composition (negative), respectively. Soil variables ranked as the most important variables for both richness and composition, with the standardized coefficients for soil resource based variables (soil C, N, and P concentrations) being strongly negative for richness and strongly positive for composition (Fig. 4B). Soil pH also positively correlated with community composition, whereas soil moisture correlated negatively with both richness and composition.

4. Discussion

The lack of significant difference in soil nematode richness between urban surrounding and core urban areas partially rejects our first hypothesis. However, lower nematode diversity in urban surrounding farmland compared to urban surrounding forests, and also between urban residential areas compared to urban parks support our assumption that soil nematode diversity declines with increasing human impacts. Potentially, similar levels of land-use changes in farmland and residential area resulted in comparable nematode richness. This suggests that land-use intensity, rather than land-use type is the main driver for the soil biodiversity. Our results indicate that in addition to anthropogenic disturbances, climatic factors are key determinants of soil nematode diversity across land-use types, supporting our second hypothesis. Soil
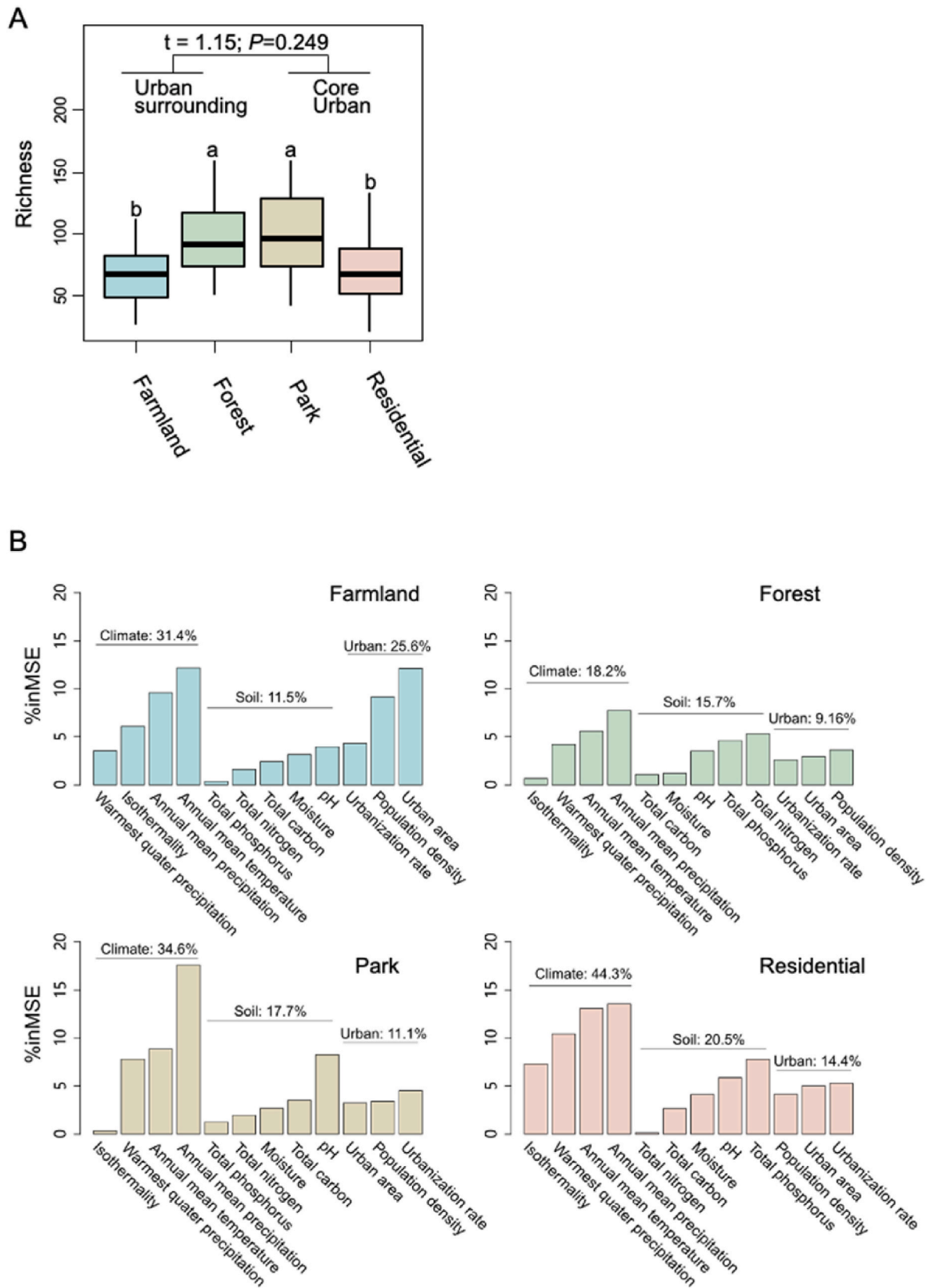
Fig. 1. Pattern and drivers of nematode richness in urban soils. Variations in nematode species richness among the four land-use types, i.e. urban surrounding farmland and forests, and urban park and residential sites (A), and relative importance of climatic, soil and urban variables to nematode richness in the four land-use types for nematode species richness (B). The relative importance of each driver (%inMSE) was derived from random forest analysis.
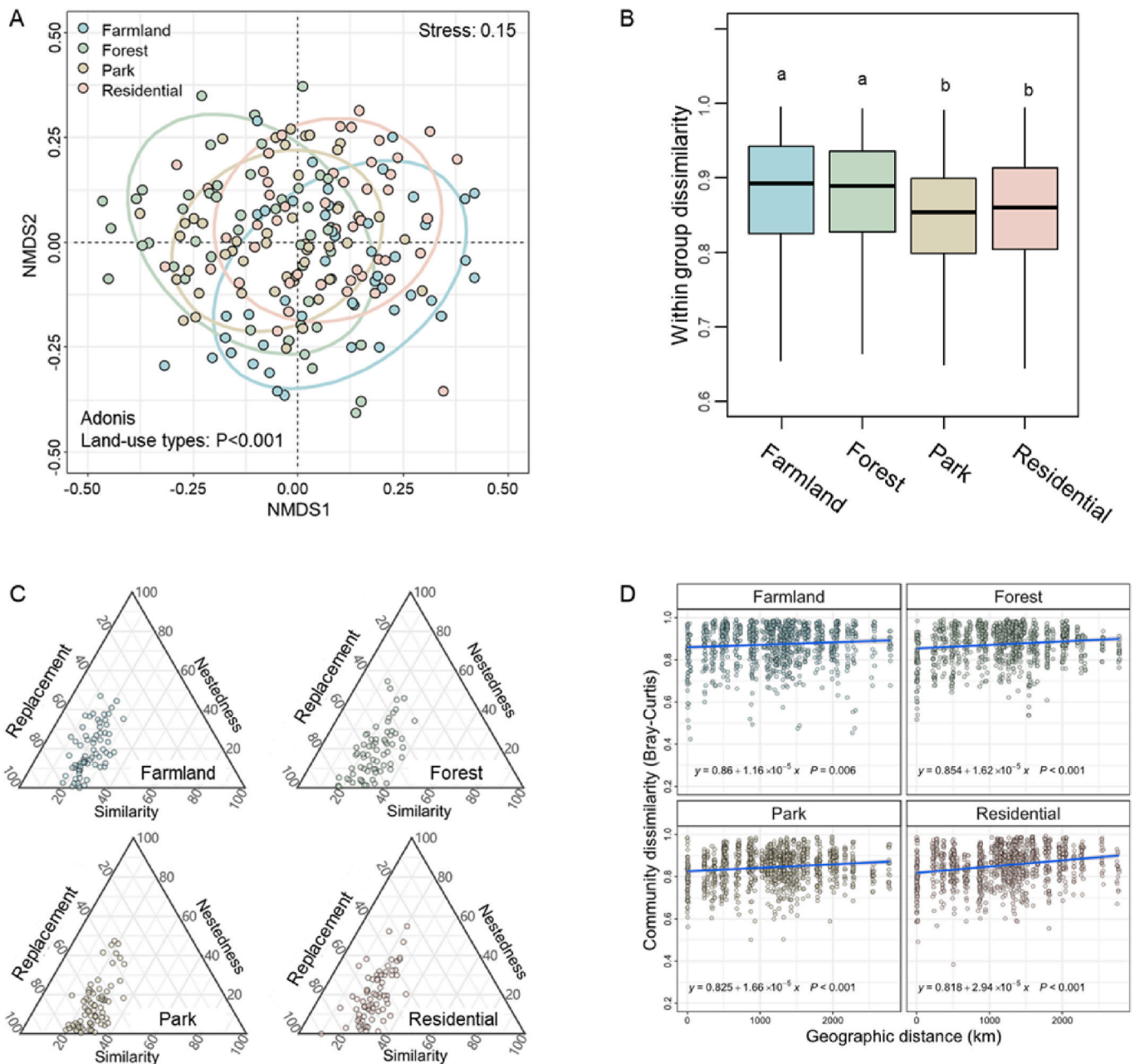
Fig. 2. Nematode community composition in urban soils. Variations in nematode community composition as indicated by non-metric multidimensional scaling (NMDS) (A). Differences within group dissimilarities of soil nematode communities between land-use types as indicated by distance-based permutational multivariate analysis of variance (Adonis); different letters indicate significant differences ($P < 0.05$) (B). Beta diversity (using Sørensen dissimilarity index) of soil nematode communities; each point represents a pair of sites; its position is determined by a triplet of values summing to 1 on similarity, turnover and nestedness (C). Distance-decay relationships of soil nematode community dissimilarity in the four land-use types (D).

resources are a major driver of nematode diversity. Moreover, SOC content determines soil microbes, which are the food source of microbivore nematodes and contribute to their diversity (Neilson et al., 2020; Song et al., 2017). Complementary to SOC, TN has been shown to strongly influences the abundance of opportunistic nematodes (Shaw et al., 2019). Other soil characteristics, such as pH, which was significantly higher in urban soils, may contribute to variations in nematode diversity. Soil texture is also an important determinant of soil animal diversity (Erktan et al., 2020), but was not investigated in this study. We obtained the body size of nematodes from the NEMAPLEX database for each nematode genus, which may have limitations as these data may not exactly match the true body size of nematode species in our samples.

Typically, species richness increases with area as suggested by the

species-area relationship (Lomolino, 2000), however, soil nematode communities may also be more detrimentally affected in larger cities due to stronger human impacts. As indicated by our results, nematode richness in both urban parks and residential areas was insensitive to city size, presumably reflecting that these artificial green spaces provide a similar number of niches for soil nematodes irrespective of the degree of urbanization (Lepczyk et al., 2017). Further, the diversity of soil nematodes in urban surrounding habitats may also be affected by the size of the city as larger cities may also be associated with stronger impacts on the city surrounding due to higher demand for agricultural products as well as more intensive recreational activities (Lin et al., 2019; Satterthwaite et al., 2010). In fact, in urban surrounding farmland soil nematode richness declined with city size, whereas this was not the case
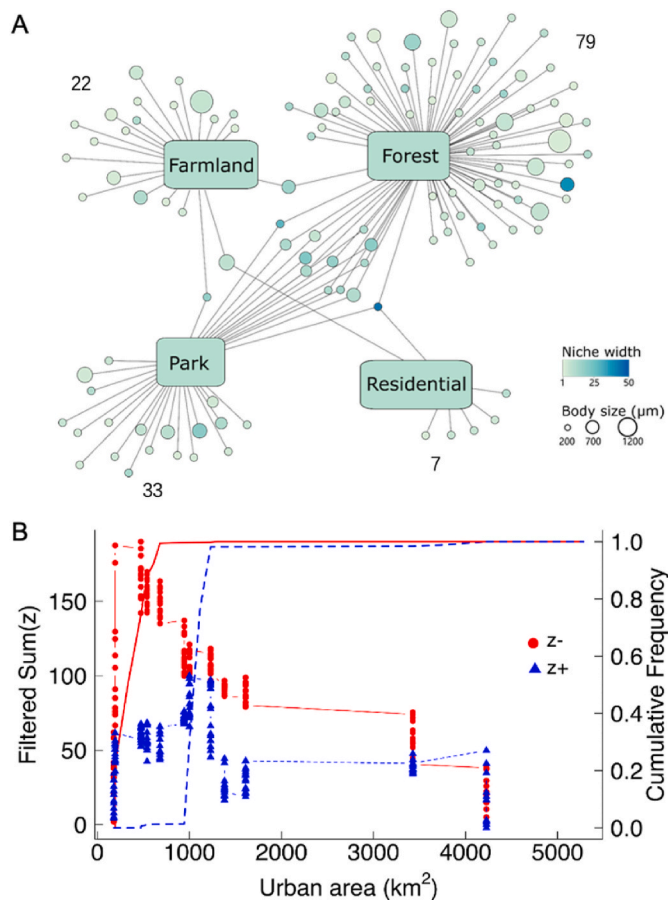
Fig. 3. Indicator species and threshold taxa in urban soils. For each land-use type; the values given with each land-use type correspond to the number of indicator species; the color of the circles indicates the niche width; the size of the circles indicates nematode body size (A). Threshold taxa analyses and community-level responses of nematode richness declining (z−; red dots) or increasing (z+; blue triangles) with increasing urban area (accumulated z-scores reflecting the magnitude of response) (B).

in urban surrounding forests. This further supports the notion that urban surrounding agricultural fields of larger cities are more intensively used and this detrimentally affects soil animal diversity. The fact that this was not the case in urban surrounding forests indicates that more recreational use of forests had minor effects on soil nematode communities. Overall, the results are consistent with our finding that nematode communities in the studied land-use systems were predominantly structured by abiotic factors. However, the detrimental effects of increased disturbance due to urbanization might have been mitigated by increased temperature in cities as urbanization has been found to favor thermophilic taxa (Piano et al., 2017). Potentially, the extinction risk of soil nematodes in cities is reduced due to higher temperature in urban greenspaces (Suggitt et al., 2018).

In addition to low soil nematode richness, urban residential areas contained fewer nematode specialists compared to the other land-use types. This reduction likely contributed to the homogenization of soil nematode communities in urban residential areas (Gossner et al., 2016). Also, it is in line with the negative correlation between turnover rates of nematode communities and the size of cities in urban residential areas, presumably reflecting that nematode specialists decline if cities get larger (Concepción et al., 2015). Further, nematode specialists in urban residential areas were characterized by smaller body size, again reflecting negative urbanization effects on habitat specialists (Magura et al., 2020). The threshold analysis for increasing nematode richness peaked at an urban area of 1000 km^2, whereas the threshold analysis for

decreasing nematode richness peaked at an urban area of 473 km^2. As the latter is greater than the average size of Chinese and global cities, this indicates that future urbanization processes are likely to be associated with a decline in soil nematode biodiversity across the world (Bai et al., 2014; Li et al., 2019). Our finding that nematode community composition is more homogenous in core urban sites than urban surrounding areas partially supports our first hypothesis. Similar results have been reported for plants (Pearse et al., 2018) and above-ground animals (McKinney, 2006) including birds (Proppe et al., 2013) and insects (Knop, 2016). However, little is known about the effects of urbanization on the spatial structure of soil organisms. Similar to above-ground taxa, earthworm communities were found to be homogenized in urban habitats, presumably due to human-facilitated dispersal (Tóth et al., 2020). Our study suggests that the same applies to soil nematode communities.

Moreover, our results showed that changes in soil nematode community composition were mainly due to the turnover of species rather than nestedness (Baselga, 2010). Interestingly, species turnover in urban surrounding forests increased with urban area, whereas it decreased in urban residential sites. This implies that the size of cities affects both nematode beta diversity in urban as well as urban surrounding soils, but that these effects are opposing. Presumably, the decline in turnover in urban residential areas with city size is due to species loss (Caula and Sanz D'Angelo, 2021). By contrast, the increase in turnover in urban surrounding forest with city size is likely due to increased spread of nematode species by agricultural but also recreational activities in the surroundings of larger cities. We found that factors associated with urbanization exceeded soil factors in explaining variations in soil nematode richness in urban surrounding farmland, whereas the opposite was true for urban surrounding forests, urban park and urban residential areas. This might serve as a warning that the influence of urbanization on soil biodiversity may reach beyond the urban area itself and in particular affect urban surrounding farmlands. Presumably, it reflects that urbanization is associated with increased management intensity of farmland surrounding the cities without affecting soil properties, but negatively affecting soil biodiversity. Adding to the effects of cities on surrounding farmland, on a global scale, urban expansion is predicted to result in a loss of 1.8–2.4% of farmland near cities by 2030 (Bren d'Amour et al., 2017). This compromises the increasing need for agricultural products with urbanization (Wang et al., 2021). Therefore, both increasing urban area as well as increasing management intensity of farmland threatens soil biodiversity (Pothula et al., 2019), which in the long-term may threaten the provisioning of agricultural goods to urban populations.

5. Conclusions

Urbanization reduces biodiversity and homogenizes soil nematode communities. Generally, changes in nematode richness were mainly driven by climatic variables and soil characteristics, i.e., mean annual temperature and soil organic carbon, respectively. Notably, our results indicate that urbanization not only affects nematode communities in urban residential areas, but also urban surroundings, with nematode richness in urban surrounding farmland declining with increased size of cities. These results highlight that greater attention is needed to devise protection strategies targeting at increasing the number of urban parks, but also strategies to protect soil biodiversity in urban surrounding areas, in particular the increasing urban surrounding farmland serving food for urban populations.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.
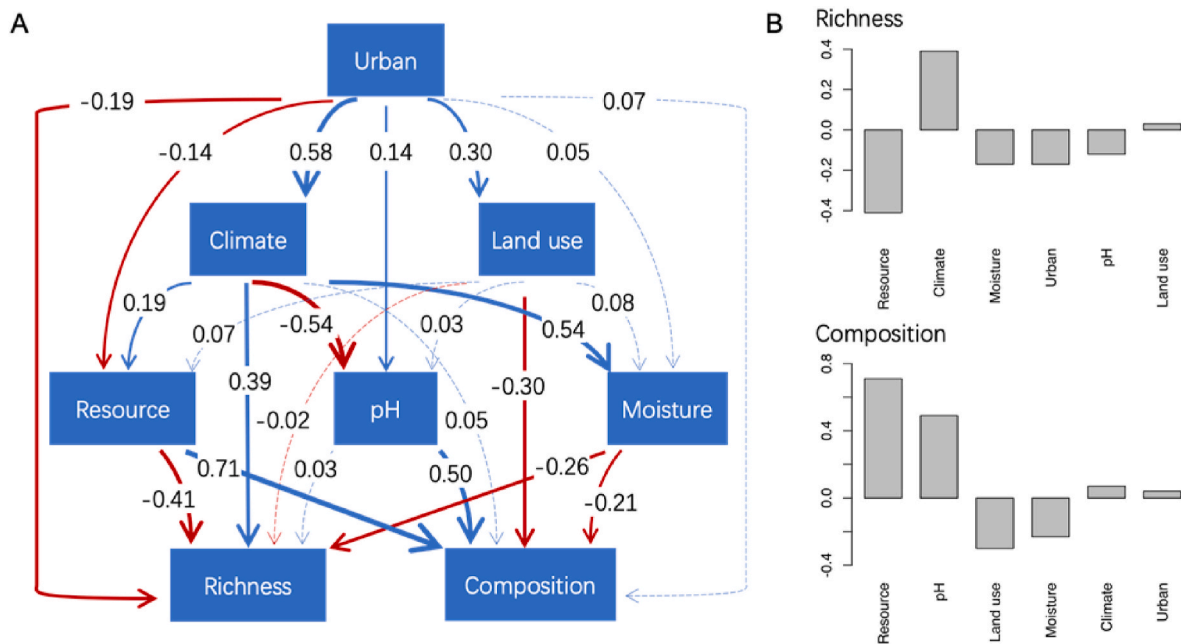
Fig. 4. Pathways of land-use and climatic variables on soil nematodes in urban soils. (A) Partial least squares path model (PLS-PM) on direct and indirect effects of climate and land-use related variables on soil nematode richness and community composition; the width of arrows is proportional to the strength of path coefficients (standardized coefficients); solid blue and red arrows indicate positive and negative relationships ($P < 0.05$), respectively; dashed arrows indicate non-significant relationship ($P > 0.05$). (B) Standardized total effects (direct plus indirect) of climate and land-use related variables from the PLS-PM model.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2023.109010.

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