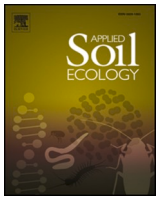
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Predicted effects of climate change on the spatial distribution of soil nematodes at a regional scale

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ABSTRACT

Soil biodiversity is essential for the provision of ecosystem services, yet the response of belowground communities to climate change remains unclear and poorly integrated into conservation policies. In soil, nematodes are recognized as bioindicators of soil health and function. In this study, we aimed to assess the current distribution and potential shifts in nematode communities across the North of Portugal, considering the climate forecasts. A total of 406 soil samples were collected throughout the region in different land-use types (agriculture, forests, pastures and urban areas), in a stratified sampling design, from which soil nematodes were extracted and identified through morphological characters. Species distribution models were created using ensemble approaches to predict their distribution under current and future climate conditions.

Our results show that slope, agriculture cover and precipitation were the most important drivers of nematode distributions. Model projections under three future climate Shared Socioeconomic Pathways (SSP1, SSP3, SSP5) for 2041–2070 suggest a decline in nematode richness in 58.10% of the region, particularly in the northwest. Trophic groups responded differently: omnivores, fungivores and herbivores substantially reduced their distribution, while bacterivores expanded their range. Results suggest that protected areas buffer species loss and foster richness gain across all climate scenarios, although their effectiveness remains uncertain. This study highlights the importance of protecting belowground communities and their functions in the face of climate change. Integrating soil biodiversity into policy planning will contribute to build resilient ecosystems under global change.

1. Introduction

Soils represent one of the most complex and biologically diverse environments on Earth, including microbes, fungi, nematodes, and larger soil animals that interact in complex ecological networks. (Bardgett and van der Putten, 2014; Guerra et al., 2020). Soil biodiversity plays an important role in maintaining essential ecosystem functions, such as organic matter decomposition, plant productivity, nutrient cycling and pathogen regulation (Bardgett and van der Putten, 2014; Wall et al., 2015; Guerra et al., 2021), which are key for human health and of high economic importance worldwide (Holzman, 2012). In the sphere of soil biodiversity, nematodes serve as useful indicators of soil health and disturbance due to their widespread distribution and abundance across all habitats containing water and organic carbon sources, under a variety of climatic conditions (Bongers and Ferris, 1999). These organisms occupy every trophic level within the soil food web (Bongers and Bongers, 1998), including bacterivores, fungivores, omnivores, and predators (as free-living nematodes), as well as herbivores (Yeates et al., 1993). Taken together, nematodes intervene in all soil processes, and the analysis of nematode assemblages allows for the assessment of soil biodiversity functionality, such as the activity of decomposition pathways and soil nutrient status (Bongers et al., 1997) as well as the regulation services and herbivory pressure (Ferris, 2010). Herbivorous nematodes have been mostly studied in agriculture-related

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research fields (Archidona-Yuste et al., 2021; Yang et al., 2021; Yeates and Bongers, 1999), although they are widely represented in all land-use types (Carvalho et al., 2025). Currently, these organisms are also used to assess the effects of global change and land-use intensification, highlighting their importance in understanding overall soil ecosystem health and functioning (Renčo et al., 2020; Siebert et al., 2020; Zhou et al., 2022).

Little knowledge is available on the distribution and main drivers of soil biodiversity. Several broader scale studies defy the long-standing view that belowground biodiversity follows the common patterns of aboveground organisms, suggesting that these are regulated by different mechanisms (Opik et al., 2006; Decaens, 2010; Nielsen et al., 2014). A recent study on the patterns of global nematode abundance showed larger densities of these organisms in sub-Arctic regions rather than in temperate and tropical regions (van den Hoogen et al., 2019). These findings stress that reliable assessments of the changes in soil biodiversity as well as their soil ecological impacts are lacking and, as a result, the instruments for policymakers rely mostly on soil chemistry and physical soil impacts, such as erosion (Guerra et al., 2021). As ecological assessments on soil biodiversity remain limited, the projected climate changes are likely to further influence the soil biota patterns.

In its latest report, the Intergovernmental Panel on Climate Change (IPCC) considers that global warming will continue to increase in almost all considered scenarios and development pathways according to the level of greenhouse gas emissions (IPCC, 2023). As climate predictions point to rapid changes in temperature and precipitation patterns, soil biodiversity distribution patterns may be altered. In fact, temperature and precipitation are reported across several studies as important drivers for soil organisms and community assemblages (van den Hoogen et al., 2019), whereas plant disease pressures are likely to change due to expected variation in humidity and soil moisture (Singh et al., 2023). However, climate change can also indirectly affect soil biota by altering plant composition and distribution, which are linked by key ecological processes, including primary production, decomposition, and nutrient cycling (Bardgett and Wardle, 2003; Wardle et al., 2004; Bardgett and van der Putten, 2014). Given the importance of soil bacteria for nutrient cycling, changes in community patterns could translate into causal effects on other soil organisms, e.g. nematodes, and whole ecosystems (Mod et al., 2021). To mitigate the impacts of climate change on soil communities, the establishment of conservation areas and further inclusion of soil organisms in policy agendas have been suggested as key strategies (Cameron et al., 2019; Geisen et al., 2019; European Union, 2024). Current protected areas do not fully target soil biota and its functions, mainly addressing aboveground biodiversity, such as plants and birds, and food production (Guerra et al., 2021). Some studies reported that protected areas have no significant effects on soil communities (Ciobanu et al., 2019) and are currently inefficient in effectively reducing threats to soil biodiversity (Cameron et al., 2019). However, significant beneficial effects of protected areas have been reported on the regulation service provided by soil organisms in the North of Portugal (Duarte et al., 2024).

Recent advancements in ecological modelling allow for a clearer understanding of belowground biodiversity distributions, drivers and dynamics. Species distribution models (SDM) have been widely used to assess species distribution patterns, including the potential proliferation of invasive species (Peterson, 2003; Guisan and Thuiller, 2005). These tools have numerous different applications, such as quantifying the environmental niche of species (Austin et al., 1990; Vetaas, 2002), and modelling species assemblages, including biodiversity and composition, based on individual species predictions (Guisan and Theurillat, 2000), as well as to assess the impact of climate change and other environmental changes on species distributions (Zeiss et al., 2023). It involves the prediction of the current distribution of a given species and the projection of how this distribution may shift in response to anticipated climate change (Thuiller, 2004). A particular approach combines Shared Socioeconomic Pathways (SSP) with Representative Concentration Pathways (RCP). Whilst the former model estimates the direction of several socioeconomic factors (e.g. economic growth, population demographics), the latter describes different levels of greenhouse gases and other radiative forcings (Pörtner and Roberts, 2022).

In this study, we aimed to investigate the distribution and potential future changes in nematode communities across the heterogeneous landscape of the North of Portugal. Specifically, the objectives were to: (i) assess the current spatial distribution of nematode taxa in relation to key environmental drivers, including land-use types, climate, and soil properties; (ii) evaluate the influence of climate factors on nematode diversity and functional groups; (iii) project future changes in nematode distributions under varying climate scenarios of SSP and identify potential impacts on soil biodiversity; and (iv) compare the predicted changes in nematode communities within and outside protected areas and understand the implications for soil biodiversity conservation and ecosystem function under future climate and land-use conditions.

2. Material and methods

2.1. Area of study and soil sampling

The North of Portugal was selected as our area of study, covering approximately 21,515 km^2 (Fig. 1). This is a highly heterogeneous region, subject to a wide array of pressures, land-use types and different environmental conditions (Cano-Diaz et al., 2023; Duarte et al., 2024; Carvalho et al., 2025).

In order to obtain a fair representation of the environmental conditions of the North of Portugal, 406 soil samples were collected using a hierarchical stratified random sampling scheme with a 20 × 20 km grid applied across the entire area of study (Fig. 1). In each grid cell, 6 different land-use types were sampled in the same day between September and December 2021: annual and perennial agriculture, native and exotic forests, pastures and urban areas. At each site, a composite soil sample was collected from 9 soil cores down to 10 cm depth taken with a hori-hori knife from a 900 m^2 area. Soil cores were mixed in a plastic bag, after removal of plant material and large stones, and used to fill a 100 mL plastic container with soil, which was transported in a refrigerated box to the laboratory and kept at 5 °C in the dark and processed within the following up to 45 days.

2.2. Nematode occurrence data

Nematodes were extracted from 100 mL soil samples using the tray method, an adaptation of the Baermann funnel (Whitehead and Hemming, 1965), for 72 h. Nematodes were identified based on their morphological characters following diagnostic keys (Goodey, 1963; Mai et al., 1996; Ferris, 2011). Nematodes were identified to family or up to genus level (some free-living nematodes, herbivore nematodes), according to the resolution needed to assign them into the correct functional groups.

2.3. Environmental variables

Climate factors (such as mean annual temperature and precipitation), location attributes (such as slope), land cover types (including forest and agricultural cover and proximity to urban areas), and soil chemical and physical properties (such as soil nitrogen, pH, clay and silt content) were obtained per sample site (Supplementary Table S1). Most environmental variables were obtained from existing public datasets in raster format. However, soil phosphorus, pH, organic carbon, and clay and silt content (%) were measured directly from the soil samples: Soil organic carbon was analysed using the Walkley & Black chromic acid wet oxidation method (Nelson and Sommers, 1996; FAO, 2020). Soil pH was measured potentiometrically in a soil-to-water suspension with a ratio of 1 part soil to 2.5 parts water (by mass/volume). Extractable phosphorus was assessed using the modified Egner-Riehm method

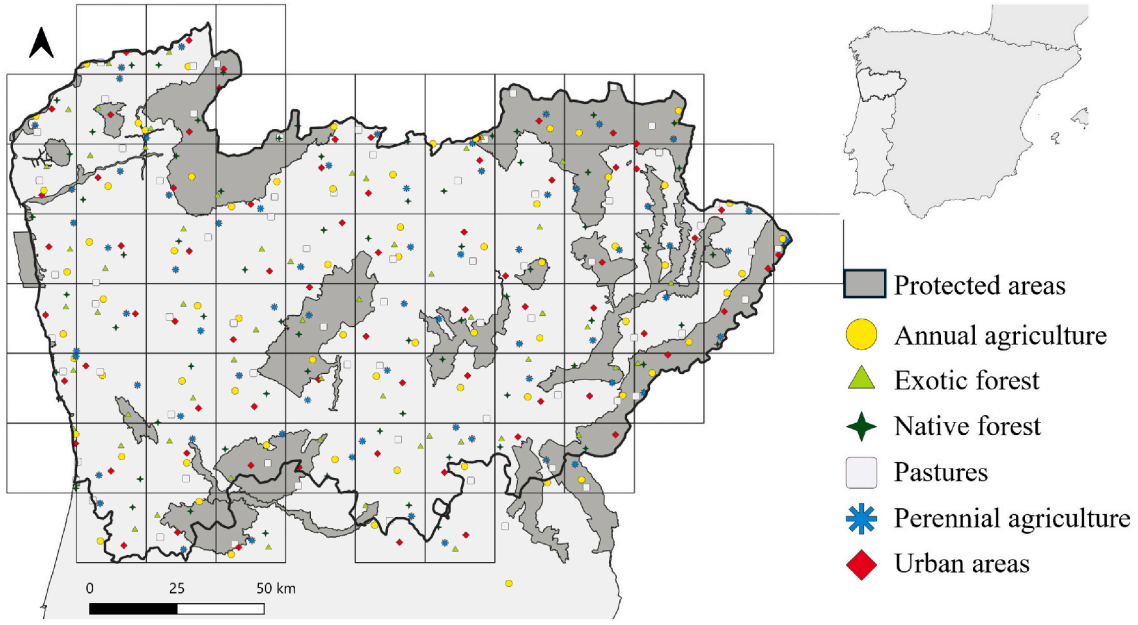


Fig. 1. Distribution of the 406 soil samples collected throughout the North of Portugal, within protected and non-protected areas, in 6 different land-use types: native and exotic forests (70 and 57 samples, respectively), pastures and urban areas (71 samples each), and annual and perennial agriculture (70 and 67 samples, respectively).

(Egner et al., 1960), with a lactate-acetate solution filtered and measured by molecular absorption spectrophotometry. The content of clay and silt (%) was determined through particle-size distribution, quantifying silt ($0.02 > Ø > 0.002$ mm) and clay ($Ø < 0.002$ mm) according to the International Union of Soil Science recommendations (Atterberg Scale). All environmental variables present in the raster format (retrieved from available datasets) were transformed following a z-score transformation and reprojected or resampled onto a 1 km grid system and into WGS84, as necessary. In the case of environmental rasters of pH, nitrogen, SOC, clay and silt content, these were standardized with respective mean and standard deviation from determined values from soil sampling, as these provide direct observations of local soil conditions rather than interpolated estimates, while preserving the relative spatial gradients of the original raster layers. To avoid multicollinearity among the environmental variables, values were extracted, and correlated variables were sequentially removed using the variable inflation factor (VIF) ≥ 5 criterion (Fox and Weisberg, 2019). Additionally, based on our previous screening for the same study region (Carvalho et al., 2025), elevation, temperature extremes and seasonality were not retained, as these were consistently highly correlated with mean annual temperature and redundant with other temperature predictors at this spatial extent.

2.4. Model fitting

To estimate current and future distributions of the different nematode taxa, ensemble species distribution models were developed in R software (R Core Team, 2022), running efficiently up to 10 single classification models on presences/pseudo-absences, with the *biomod2* package (Thuiller et al., 2022). A pseudo-absence dataset was generated, using nematode taxa occurrences as presences. To avoid overfitting, only taxa with ≥15 occurrences, i.e. 33 nematode taxa, were selected for the analysis, and the Top 10 most important predictors were selected among the environmental variables present in Supplementary Table S1, following a similar workflow used in Zeiss et al. (2023). This variable screening was performed with MaxEnt, which was used here as a preliminary and standardized approach to reduce the predictor stack before ensemble modelling. This algorithm was selected because it provides a suitable balance between predictive performance and computational efficiency (Elith et al., 2006; Hernandez et al., 2006; Valavi et al., 2021). This procedure allowed a consistent ranking of predictors across taxa, whereas averaging across all algorithms would have greatly increased computational time.

To find the most important predictors, the *biomod2:get_variables_importance* function was used, which calculates the *Pearson* correlation between the standard predictions and those with the variable randomly permuted (Thuiller et al., 2016). Higher values of variable importance signify a stronger influence of the variable on the model. The 10 environmental variables with the highest average permutation importance were selected: NDVI, mean annual precipitation, slope, mean annual temperature, agriculture cover, nitrogen, soil copper, wind speed, soil moisture and clay and silt content. Once the main environmental drivers for nematode taxa distribution were determined, these predictors were then applied in each final individual species distribution model to assess their potential distribution.

For each taxon, a ratio of 3 pseudo-absences per presence was used in the models and replicated 10 times (Barbet-Massin et al., 2012), derived from a generated pseudo-absence dataset. We used 10-fold cross-validation (80:20%, 5 repetitions), and True Skill Statistic (TSS) to improve model performance for ensemble modelling (Allouche et al., 2006), these being combined by each combination of repetition datasets and pseudo-absence. Additionally, the weight of single models was assigned according to their evaluation score, meaning that models with higher accuracy are more important for predictions.

To assess the main drivers of each taxon distribution, the same procedure to find the Top 10 most important variables was followed, and *biomod2:get_variables_importance* was used to estimate the relative variable importance.

2.5. Current and future projections

Prediction maps originated from best-rated ensemble models (maximizing TSS) were generated with a model-specific threshold for each taxon, converting the derived probabilities into binary predictions. To calculate predicted taxa richness (or number of taxa per grid cell), derived maps containing the binary predictions were summed.

To assess the potential effect of future climate conditions on nematode distribution, the nematode distributions were reprojected for the same environmental variables except for mean annual temperature and mean annual precipitation. These future predictions were obtained from CHELSA 2.1 global climate models GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1–2-HR, MRI-ESM2–0 and UKESM1–0-LL (Karger et al., 2021), for the time period of 2041–2070, and for three shared-socioeconomic pathways (SSP) combined with representative concentration pathways (RCP: SSP1– "sustainable path" RCP 2.6; SSP3 – "regional rivalry" with RCP 7.0; and the most negative case scenario, the SSP5 – "fossil-fuelled development" with RCP 8.5 (Pörtner and Roberts, 2022). All remaining environmental variables were kept constant across scenarios to isolate the climate effects on nematode distribution. For each global climate model and taxon, four different projections were obtained: current distribution and each of the shared socioeconomic pathways. All predictions were averaged across the global climate models. The current and future ranges of mean annual temperature and precipitation across the region, including protected areas, are summarised in Supplementary Fig. S1.To compare the potential change of distribution under each SSP with the current distribution, the *biomod2:BIOMOD_RangeSize* function was used, which computes the number of grid cells lost, stable or gained, and relative proportion, for a species across the area of study. It was then possible to determine which taxa are potentially going to be affected by the change in temperature and precipitation conditions, but also to gain insight into how whole trophic groups may be affected. By calculating the difference of predicted richness in each grid cell among the layers, we were able to evaluate the potential loss or gain of species along the entire North of Portugal and, more specifically, compare the loss or gain of species between designated protected areas and areas with no conservation status.

3. Results

3.1. Nematode dataset

A total of 44 different nematode taxa were found in the 406 soil samples across the North of Portugal (Supplementary Table S2). Among them, 10 taxa of bacterivores, 7 fungivores, 6 omnivores, two predators and 19 herbivore taxa. The fungivores Aphelenchoididae and the bacterivores Cephalobidae and Panagrolaimidae were the nematode taxa with the highest incidence throughout the soil samples, whilst the rarest nematodes found comprised the herbivore *Longidorus* and the omnivore Nordiidae with one occurrence and Bunonematidae with two occurrences.

The mean taxa richness was 14.57 (SD = 3.54), with a minimum of 5 and a maximum of 26 taxa.

3.2. Importance of environmental factors on nematode distribution

Slope, agriculture cover and mean annual precipitation were the most important variables for the modelling distribution of the 33 nematode taxa (Fig. 2A). On the contrary, mean annual temperature, clay + silt content and wind speed contributed the least to the distribution modelling. However, the variable contribution varied according to nematode trophic groups (Fig. 2B-E). For example, for fungivores, our results show agriculture cover, NDVI and mean annual precipitation as more important than temperature and wind speed (Fig. 2B), whilst bacterivores were dependent on slope, NDVI and soil nitrogen conditions and less on moisture and climate factors such as temperature and wind speed (Fig. 2C). The distribution of herbivores was conditioned by slope, agriculture cover and precipitation with smaller effects of soil properties such as texture (clay + silt content), copper and wind speed (Fig. 2D). As for omnivores and predators, our results indicate different conditions affect their distribution, as the former is dependent on slope, agriculture cover and NDVI (Fig. 2E), and the latter is dependent on values of precipitation and soil properties such as nitrogen and moisture (Fig. 2F).

Strong and moderate linear correlations were found between environmental drivers and the occurrence of free-living nematode taxa (Fig. 3). The strongest relationship was found regarding NDVI and the fungivore *Tylencholaimus* ($\rho = 0.76$), also being strongly correlated with predators Mononchidae and Tripylidae ($\rho = 0.49$ and $\rho = 0.55$) and the bacterivores Teratocephalidae and *Wilsonema*. Agriculture cover was strongly correlated with the fungivores Aphelenchidae, but also with the omnivores Aporcelaimidae, Leptonchidae, and Dorylaimidae. The bacterivores Alaimidae and *Wilsonema*, fungivores Tylenchidae and

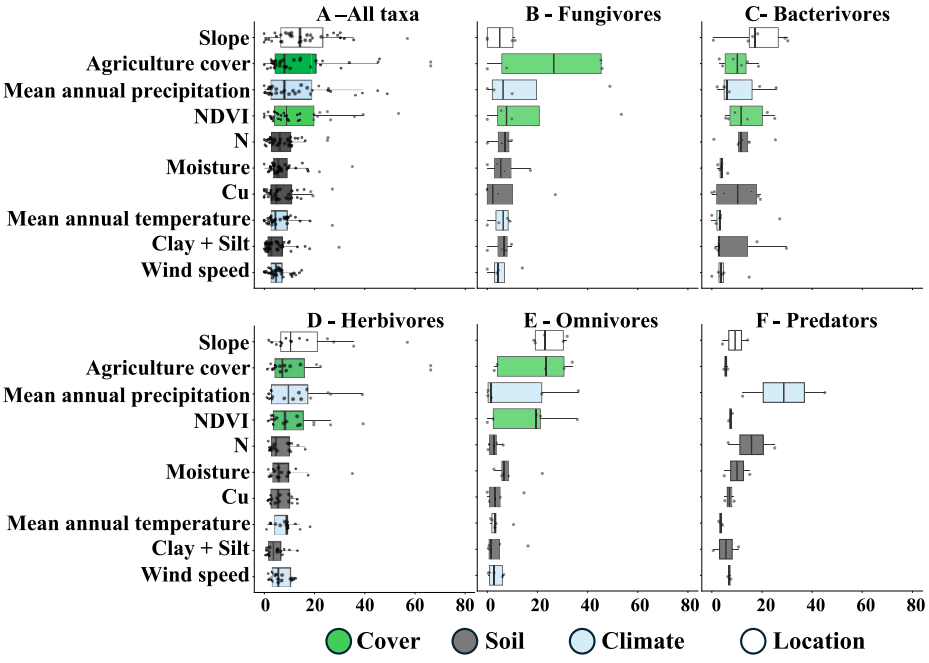


Fig. 2. Boxplot of the importance of the variables to species distribution models of 33 nematode taxa and each trophic group using ensemble models: (A) All nematode taxa (33), (B) Fungivores ($n = 4$), (C) Bacterivores ($n = 6$), (D) Herbivores ($n = 16$), (E) Omnivores ($n = 5$) and (F) Predators ($n = 2$).

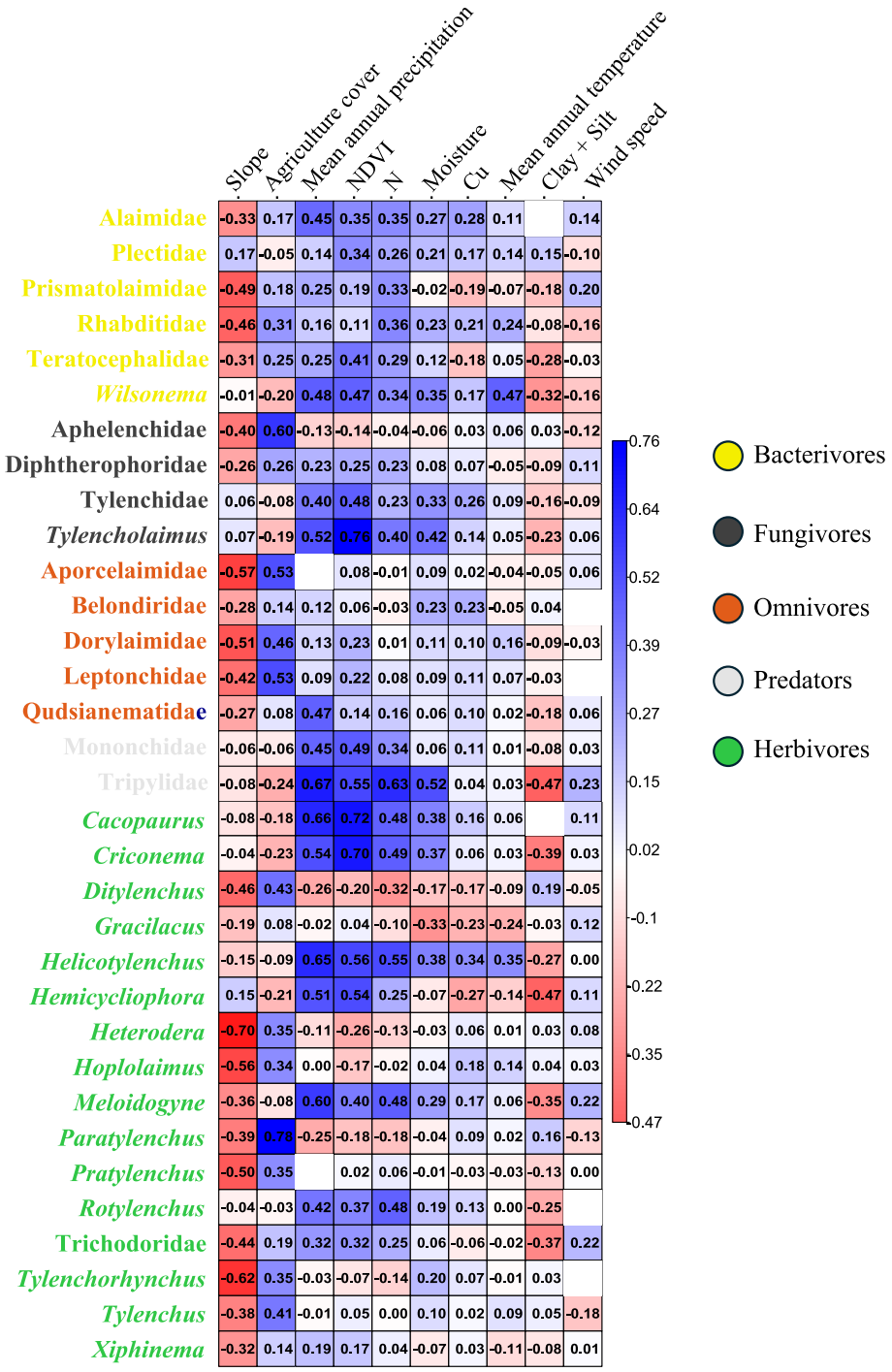


Fig. 3. *Pearson* correlations between the probability of presence of 17 free-living and 16 herbivore nematode taxa, resulting from species model distribution, and environmental variables, across the North of Portugal. Empty squares correspond to non-significant correlations ($p > 0.05$).

Tylencholaimus, omnivores Qudsinematidae and predators Mononchidae and Tripylidae were positively correlated with precipitation, especially Tripylidae with a strong correlation ($\rho = 0.67$). However, temperature did not seem to influence free-living nematodes, except for *Wilsonema* ($\rho = 0.47$). Similarly, Trypilidae was the only taxon largely affected by soil moisture, with a positive correlation score of 0.5, and *Tylencholaimus*, to a lesser extent, with a 0.42 score. Moreover, both Tripylidae and *Tylencholaimus* seemed to be influenced by soil nitrogen, with Tripylidae being highly correlated ($\rho = 0.67$). Slope, as the most important variable for the distribution modelling, had an overall negative linear relationship to the probability of occurrence of free-living nematode taxa, with strong correlation with omnivores Aporcelaimidae ($\rho = -0.57$) and Dorylaimidae ($\rho = -0.51$), and the bacterivores Prismatolaimidae ($\rho = -0.49$) and Rhabditidae ($\rho = -0.46$). None of the free-living nematode taxa were highly positively or negatively correlated with wind speed.

Mainly positive correlations were found between the occurrence of herbivore nematode taxa and environmental drivers (Fig. 3), except for soil clay and silt content for *Cacopaurus* and *Hemicycliophora*, with correlation scores of -0.43 and -0.47, respectively, while slope was strongly correlated with the occurrence of *Heterodera* ($\rho = -0.70$), *Tylenchorhynchus* ($\rho = -0.62$), *Hoplolaimus* ($\rho = -0.56$), *Pratylenchus* ($\rho = -0.50$), *Ditylenchus* and *Trichodoridae* ($\rho = -0.46$ and $\rho = -0.44$,

respectively). The strongest positive relationship (ρ = 0.78) found was between agriculture cover and the herbivore *Paratylenchus*. Precipitation was mainly positively correlated with: *Cacopaurus* and *Helicotylenchus* (ρ = 0.66 and ρ = 0.65, respectively), *Meloidogyne* (ρ = 0.60), *Criconema* (ρ = 0.54), *Hemicycliophora* (ρ = 0.51) and *Rotylenchus* (ρ = 0.42). Our results also showed NDVI as strongly correlated with several herbivore taxa, namely *Cacopaurus* (ρ =0.72), *Criconema* (ρ = 0.70), *Helicotylenchus* (ρ = 0.56) and *Hemicycliophora* (ρ =0.54). In addition, soil nitrogen shared mainly a strong correlation of 0.55 with *Helicotylenchus*, *Criconema* (ρ = 0.49), and a correlation score of 0.48 with *Cacopaurus, Meloidogyne* and *Rotylenchus*.

3.3. Distribution and richness change across climate scenarios

The mean predicted nematode taxa richness for the entire North of Portugal under current environmental conditions was 14.90 (SD =7.68). Under climate conditions for the timeframe of 2041–2070 within the shared socio-economic pathways SSP1, SSP3, and SSP5, the mean taxa richness was predicted as 13.48 (SD = 6.74), 13.01 (SD = 6.35), and 12.85 (SD = 6.20), respectively. All three climate scenarios consistently predict a loss of nematode taxa in 58.10% of the region, while a gain is projected in 13.44% of the land area, mostly in the southeast (Fig. 4).

The predicted taxa richness derived from 33 species distribution models in the North of Portugal suggests areas with a higher incidence of nematode taxa, especially in the west (Fig. 4A). On the other hand, the south and south-east of the region are predicted to have lower richness of nematode taxa. The same pattern was found for the number of taxa in the different shared socioeconomic pathways (Supplementary Fig. S2). The western part of the region still had the highest taxa richness, however, this is projected to decline under future climatic scenarios (SSP1, SSP3, and SSP5). Moreover, the uncertainty in predicted taxa richness, expressed in standard deviation across the 5 global climate models, increased from SSP1 to SSP5 (Supplementary Fig. S3). The change in richness between current and future climate conditions showed a progressive trend according to the SSP, with the loss of taxa being most pronounced under the climate conditions of SSP5 (Supplementary Fig. S4). Similarly to Supplementary Fig. S2 and S3, a major loss of nematode taxa was evident in the western part of the region, up to more than 7 different taxa. However, an increment in species richness was predicted in the eastern part of the region throughout all climate scenarios.

Regarding the change of distribution of nematodes, omnivores were the most negatively affected trophic group, whilst bacterivore nematodes mostly benefited from the shift of climate conditions (Fig. 4C and Supplementary Table S3). The effect on the different trophic groups follows a similar trend for each shared socioeconomic pathway, although more evident in SSP5, with bacterivores having positive range change (%) whilst herbivores, omnivores, predators and fungivores all lose distribution span. For SSP1, our results estimated an increase in the mean range distribution of 3.86% for bacterivores. On the other hand, a

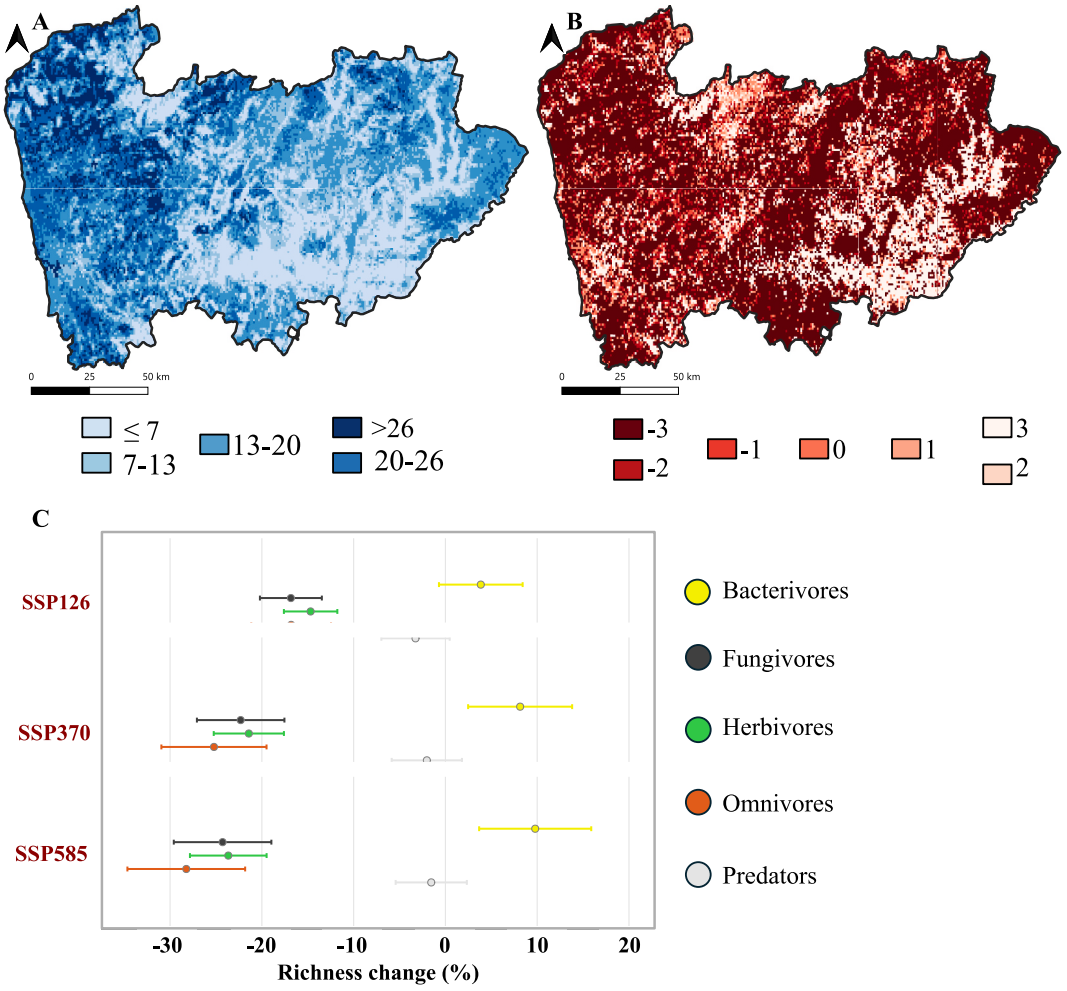


Fig. 4. Predicted changes in nematode taxa richness in the North of Portugal under different climate scenarios for 2041–2070. A) Predicted nematode taxa richness in current environmental conditions. B) Agreement across the shared socioeconomic pathways on the predicted gain or loss (>5%) in the distribution of nematode taxa in the North of Portugal. Values range from −3 (loss predicted in all scenarios) to 3 (gain predicted in all scenarios). C) Mean percentage of range change distribution of different nematode trophic groups for each shared socioeconomic pathway.

decrease of 16.83% range change for fungivores, 14.69% for herbivores, 16.81% for omnivores and 3.26% for predators was predicted. Regarding predictions within SSP3, bacterivores will increase 8.14% of their range distribution, while fungivores (22.31%), herbivores (21.42%), omnivores (25.22%) and predators (2.02%) will all lose distribution. In the worst climate scenario, SSP5, there was a similar trend but with more accentuated distribution change than in other scenarios, with bacterivores increasing their distribution by 9.78%. Omnivores will be the most affected trophic group with 28.23% loss distribution, followed by herbivores with 23.66%, fungivores with 24.28% and predators decreasing 1.54% of their distribution area.

Our results predict areas with a protected status to have fewer negative impacts on nematode taxa richness across all scenarios (Table 1). For the sustainability scenario (SSP1), predictions suggest 61.82% of the area will decline in the number of taxa, however, this value represented 12.03% less than the predicted value for non-protected areas. For SSP3, these values increased to 65.29% in protected areas and to 79.5% in non-protected areas and, in the worst scenario, the difference was 66.72% for protected areas and 80.62% for non-protected areas. The percentage of area predicted to gain taxa was also affected by the conservation status, as the values are larger in protected areas than in non-protected areas, across all scenarios. Whilst protected areas were predicted to gain species in 33.54% for SSP1, 30.8% for SSP3 and 29.8% for SSP5, in non-protected areas these percentages amount to 22.71, 17.83 and 10.06%, respectively, for the same shared socioeconomic pathways.

4. Discussion

4.1. Environmental drivers of nematode distribution

According to our models, slope, agricultural cover and mean annual precipitation are important drivers of nematode distribution at a regional level (Fig. 2A). Slope and aspect have been widely studied for the effect on soil properties, influencing nutrient availability and microbial activity (Sidari et al., 2008; Zhang et al., 2011). Significant effects of slope on nutrient distribution were reported in forest ecosystems, highlighting its role in shaping spatial patterns of soil characteristics across different landscape positions (Tsui et al., 2004). Mean annual temperature was not identified as a main driver of nematode distribution in our findings. The inclusion of seasonal and extreme temperature metrics in the region could better capture region constraints, as these are reported across several studies as important drivers (Verschoor et al., 2001; Bhusal et al., 2015). This may also help explain the weak pairwise correlation between probability of presence of most taxa and temperature (Fig. 3). Unlike the modelling framework applied to nematode taxa, these correlations assume simple linear relationships, which may not adequately capture more complex responses, as well as temperature effects that may vary among taxa. In addition, the same set of predictors across all nematode taxa was used to ensure comparability and standardization, although it may have not accounted for taxon-specific ecological responses.

Wind speed had low relative importance in our models (Fig. 2). However, its ecological relevance is documented as an important mechanism of nematode dispersal pathway (Ptatscheck et al., 2018), hence it is expected to influence nematode diversity. Our models are based on the assumption of static land use over time, as potential land-use trajectories were not included in the modelling framework. Land-use change induces functional shifts on nematode communities (Afzal et al., 2023; Yang et al., 2026), thus these findings should be interpreted as the expected response to climate change. Anthropogenic activities such as agriculture are consistently described in the literature as the main drivers of soil biota (Veresoglou et al., 2015; Geisen et al., 2019). With increasing land-use intensification, soils become more depleted and eroded, resulting in a loss of soil biodiversity and the functions it performs, while enhancing the incidence of pathogens. In our results, agriculture cover favoured the occurrence of nematodes belonging to different trophic groups, such as the fungivores Aphelenchidae, the omnivores Aporcelaimidae, Dorylaimidae and Leptonchidae (Fig. 3), and herbivores *Ditylenchus, Paratylenchus* and *Tylenchus* (Fig. 3). These associations most likely reflect the type of agriculture in the region, as annual crops are abundant in the east, e.g. maize crops, whilst perennial crops such as vines and fruit trees are more present throughout the west (INE, 2023). Annual crops seem to promote the abundance of bacterivores, whilst herbivores are greatly enhanced in perennial crops, as suggested following assessments on soil quality and disturbance in different cropping systems (Diale et al., 2023). In this study, bacterivore nematode occurrence was highly dependent on NDVI and soil nitrogen content (Fig. 2C). Since bacterivores are often associated with enriched soils with high microbial activity, their abundance increases in environments subjected to fertilization and disturbances leading to rapid decomposition. The strong influence of ecosystem type on nematode assemblages is widely reported (Neher, 2010; Zhang et al., 2012), hence, it is expected that nematode occurrence varies according to the type of ecosystem most representative of the region. The strong association of predatory taxa with NDVI in this study supports this; in this region, the NDVI is highly correlated with forest cover. Given the longer life span and greater sensitivity of predators and omnivores to disturbance (Bongers and Bongers, 1998), ecosystems with lower levels of anthropogenic influence foster their presence and abundance. In contrast, it is well documented that bacterivores and herbivores can thrive in highly managed ecosystems (Bongers et al., 1997; Li et al., 2022). Considering current climate projections point to rapid shifts in temperature and precipitation patterns, it is imperative to address how soil biological communities may respond to these alterations.

4.2. Changes in terrestrial biodiversity patterns

Our findings predict a decline in soil biodiversity driven by changing climate conditions in 58.10% of the land across all scenarios (Fig. 4B), although it becomes more pronounced as climate predictions grow more extreme (Fig. S2). The relative stability in the projected predator distribution across climate scenarios (Fig. 4C), despite marked shifts in other trophic groups, may reflect broader ecological tolerance or the absence of trophic dependencies in the species distribution models. This highlights a key limitation of these modelling approaches, as they do not account for biotic interactions, potentially leading to ecologically misleading projections. Moreover, predatory nematodes are expected to be sensitive to reduced soil moisture because larger-bodied taxa depend on thicker water films for movement and feeding (Wallace, 1968). Most importantly, these nematodes depend on habitat stability and prey availability (Lejoly et al., 2026), which according to our findings, are expected to decline overall (Fig. 4C). In addition, past studies on the effects of climate change on nematode communities also suggest shifts in predator-prey balance (Franco et al., 2019: Homet et al., 2023).

The threat of biodiversity loss is more relevant in the northwest of the region. Here, climate conditions significantly differ from the eastern

Table 1
Percentage of area predicted to experience gain or loss of nematode taxa in protected and non-protected areas in the North of Portugal under different Shared Socioeconomic Pathways (SSP) scenarios. SSP1, SSP3, and SSP5 represent future climatic conditions for 2041–2070 under the Shared Socioeconomic Pathways 1, 3, and 5, respectively. 'Loss (%)' refers to the proportion of pixels where species richness is projected to decrease, while 'Gain (%)' refers to the proportion of pixels where species richness is projected to increase under each scenario.

	Protected areas			Non-protected areas		
	SSP1	SSP3	SSP5	SSP1	SSP3	SSP5
Loss (%)	61.82	65.29	66.72	73.85	79.50	80.62
Gain (%)	33.54	30.80	29.80	22.71	17.83	17.06

areas, with higher precipitation regularity and milder temperatures, as it is close to the coastal zone. In fact, comparisons between current climate conditions and forecasts for 2041–2070 indicate a foreseeable increase in temperature in the east, along with a decrease in precipitation in the northwest. As our predictions suggest, nematode richness is particularly higher in areas with larger precipitation levels, which might explain the pattern of projected loss of soil biodiversity in the northwest. As seen in Supplementary Fig. S4, projected gains of nematode taxa are projected predominantly in northeastern Portugal, meaning environmental conditions for soil communities might improve. Lately, considerable effort has been put into research to understand how and which climate factors will affect soil biodiversity. Nematode communities are greatly regulated by precipitation across grasslands according to a regional-scale study assessing patterns of soil biodiversity in the Mongolian plateau (Chen et al., 2015). Still, the response to water availability may differ between nematode trophic groups (Homet et al., 2023). Given the crucial role of soil nematodes in nutrient dynamics and the regulation of soil organism populations (Neher, 2001; Ferris, 2010), shifts in terrestrial biodiversity dynamics might result in unpredictable and potentially detrimental outcomes. As fundamental soil processes, e.g. decomposition, are mediated by soil organisms, changes in the structure of soil communities may alter the rate of processes that drive these biogeochemical processes (Schimel and Gulledge, 1998). Furthermore, the extent to which a function may change if terrestrial communities undergo such transformations remains uncertain (Singh et al., 2010).

Bacterivores might be the main beneficiary of climate change (Fig. 4C and Supplementary Table S3), with a distribution change between 3.86 and 9.78%, from SSP1 to SSP5. Additionally, we predict that fungivore distribution will decrease, possibly leading to a more predominant decomposition pathway towards a bacterial-dominated energy channel. Given that bacteria are more opportunistic and responsive to nutrient availability compared to fungi, it helps to explain our findings (Chen et al., 2015). However, realistically, the effects on terrestrial biodiversity will result from the interplay of multiple global change factors. The interaction between reduced precipitation, elevated CO_2 and warming modify the energy channels leading to a bacterial-dominated energy channel, and decrease the ratio of carbon to phosphorus-acquiring enzymes, authors found in a grassland field experiment in North America (Thakur et al., 2019). Also, temperature and elevated CO_2 is reported to drive microbial biomass changes, possibly due to higher root growth and exudation. Furthermore, the direct effects of temperature and precipitation on plant communities are well-established, significantly influencing their composition and dynamics at regional scales (O'Brien, 1998; Kreft and Jetz, 2007; Cleland et al., 2013). Climate change might alter the dynamics of plant-pathogen interaction, which in turn could negatively affect the resistance of the plant to various pathogens and risk the outbreak of new plant diseases, increasing their distribution (Singh et al., 2023). However, our results suggest that the distribution of herbivores will significantly decline by 14.69% in SSP1 and 23.81% in SSP5 (Fig. 4C and Supplementary Table S3). But this could be attributed to the indirect effects of climate change. A broad scale study of 1.350 European plants estimated 27–42% plant species loss and 45–63% turnover per pixel due to changes in climate conditions (Thuiller et al., 2005). As the distribution patterns of herbivores are highly dependent on plant composition, it is expected that their spatial occurrence might be similarly affected. The effect of warming on nematode community composition, leading to an increased percentage of herbivores, is reported in a two-year rice paddy field experiment in China, which manipulated temperature and CO_2 levels (Wang et al., 2019). However, these changes were influenced by the rice growth stage. Such environmental shifts could lead to a lack of horizontal control by competition (Brinkman et al., 2005; Piśkiewicz et al., 2007; Costa, 2024). Still, plant disease suppression is strongly influenced by top-down effects of predatory soil organisms, including omnivore and predator nematodes, tardigrades and microarthropods (Piśkiewicz et al., 2007; Bardgett and van der Putten, 2014).

With increasingly severe climate projections, we predict that shifts in precipitation and temperature patterns will lead to a loss of spatial distribution for omnivores, ranging from 16.81% to 28.23% in the North of Portugal (Fig. 4C and Supplementary Table S3). Considering the beneficial contribution of these higher trophic groups to disease control and suppressiveness, these findings may imply a loss of regulation functions on soils. These organisms are typically larger-bodied taxa with slower metabolic and reproduction rates, making them especially sensitive to ecosystem alterations (Bongers and Bongers, 1998; Kladivko, 2001). As environmental conditions for these groups become less favourable, food webs are disrupted, leading to changes in soil biota and functionality (Geisen et al., 2019). Although different components of soil biodiversity are expected to be affected to varying degrees, the overall structure of food webs is likely to shift due to interactions among terrestrial diversity components, resulting in altered soil functioning. Hence, effective mitigation strategies that concern the protection of soil biodiversity and related ecosystem services are imperative.

Our findings suggest that protected areas help mitigate the impacts of climate change, with species loss ranging from 61.82 to 66.72% of the land area, depending on the climate scenario (Table 1), while in non-protected areas, this loss range increases from 73.85 to 80.62%. Additionally, when species gains occur with climate change, they constitute a larger percentage of land in protected areas compared to non-protected areas (from 29.80 to 33.54% in protected areas and from 17.06 to 22.71% in non-protected areas). This could be an indicator that conservation areas, albeit not designed to target soil biodiversity (Cameron et al., 2019; Guerra et al., 2021), gather favourable socio-environmental conditions that might enhance the resilience of soil communities. Under the Portuguese legal framework for nature conservation, protected areas may impose constraints on land management and activities potentially harmful to natural habitats and biota, such as soil alteration, vegetation removal or reconversion, land use change, hydrological modification, construction and road opening (República Portuguesa, 2008). More specifically, in Peneda-Gerês National Park, regulation restricts intensive agricultural, livestock and silvo-pastoral systems, where common habitats include oak forests, riverine woodlands and peat bogs (ICNF - Instituto da Conservação da Natureza e das Florestas, 2017). Previous research in this study region suggests that it may also be mediated by habitat quality and structure, as nematode functional diversity was associated with soil organic carbon and soil moisture (Duarte et al., 2024). Although Supplementary Fig. S1 indicates that protected and non-protected areas overlap in their climatic ranges, the mean annual temperature range suggests slightly lower extremes within protected areas. Thus, the lower percentage losses in protected areas may be partly influenced by their spatial distribution along climatic gradients. The lack of positive effects of conservation areas on soil biodiversity is widely reported (Ciobanu et al., 2019; Guerra et al., 2019). However, our own previous studies in the North of Portugal revealed a larger regulation service of soil communities in forests within protected areas than in non-protected areas (Duarte et al., 2024). While our results strongly suggest that protected areas can buffer climate change impacts, the specific mechanisms driving this resilience remain unclear and warrant further investigation, particularly regarding habitat heterogeneity and land-use history. It seems important to assess which conservation strategies are producing positive effects belowground and to clarify their mechanisms.

Overall, our findings highlight the critical importance of protecting soil biodiversity and maintaining ecosystem functions under the threat of climate change. The shifts in biodiversity patterns in our results, including changes in soil nematode distribution and the likely effects on nutrient cycling and disease control, underscore the complexity of climate-induced impacts on terrestrial ecosystems. Given their sensitivity to environmental changes, nematode communities represent valuable indicators of soil health. Their inclusion in the upcoming Soil Monitoring and Resilience Directive (European Commission, 2024),

albeit as optional indicators, further supports their use in future monitoring frameworks. Protected areas are here projected to provide considerable resilience to soil communities in the face of climate change, thus, there is a clear need for the development of comprehensive conservation policies that specifically target belowground organisms. Moving forward, effective climate adaptation and mitigation strategies must prioritize the protection of soil biodiversity, ensuring the stability of ecosystem functions that underpin human and environmental well-being.

CRediT authorship contribution statement

Rui P. Carvalho: Writing – original draft, Methodology, Formal analysis. **A. Carolina Duarte:** Writing – review & editing, Methodology. **Carlos A. Guerra:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Susana Mendes:** Writing – review & editing, Methodology. **Concha Cano-Diaz:** Writing – review & editing, Methodology. **Sofia R. Costa:** Writing – review & editing, Supervision, Conceptualization.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2026.107229.

Data availability

The data that support the findings of this study are openly available in figshare at https://doi.org/10.6084/m9.figshare.30364405.

References

Afzal, S., Nesar, H., Imran, Z., Ahmad, W., 2023. Change in land-use from natural forest impacts functional composition and metabolic footprint of soil nematode community in Western Himalayas. Acta Ecol. Sin. 43, 842–852. https://doi.org/10.1016/j.chnaes.2022.12.004.

Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J. Appl. Ecol. 43, 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x.

Archidona-Yuste, A., Wiegand, T., Eisenhauer, N., Cantalapiedra-Navarrete, C., Palomares-Rius, J., Castillo, P., 2021. Agriculture causes homogenization of plant-feeding nematode communities at the regional scale. J. Appl. Ecol. 58, 2881–2891. https://doi.org/10.1111/1365-2664.14025.

Austin, M.P., Nicholls, A.O., Margules, C.R., 1990. Measurement of the realized qualitative niche: environmental niches of five Eucalyptus species. Ecol. Monogr. 60, 161–177. https://doi.org/10.2307/1943043.

Barbet-Massin, M., Jiguet, F., Albert, C.H., Thuiller, W., 2012. Selecting pseudo-absences for species distribution models: How, where and how many? Methods Ecol. Evol. 3, 327–338. https://doi.org/10.1111/j.2041-210X.2011.00172.x.

Bardgett, R.D., van der Putten, W.H., 2014. Belowground biodiversity and ecosystem functioning. Nature 515, 505–511. https://doi.org/10.1038/nature13855.

Bardgett, R.D., Wardle, D.A., 2003. Herbivore-mediated linkages between aboveground and belowground communities. Ecology 84, 2258–2268. https://doi.org/10.1890/02-0274.

Bhusal, D.R., Tsiafouli, M.A., Sgardelis, S.P., 2015. Temperature-based bioclimatic parameters can predict nematode metabolic footprints. Oecologia 179, 187–199. https://doi.org/10.1007/s00442-015-3316-4.

Bongers, T., Bongers, M., 1998. Functional diversity of nematodes. Appl. Soil Ecol. 10, 239–251. https://doi.org/10.1016/S0929-1393(98)00123-1.

Bongers, T., Ferris, H., 1999. Nematode community structure as a bioindicator in environmental monitoring. Trends Ecol. Evol. 14, 224–228. https://doi.org/10.1016/S0169-5347(98)01583-3.

Bongers, T., van der Meulen, H., Korthals, G., 1997. Inverse relationship between the nematode maturity index and plant parasite index under enriched nutrient conditions. Appl. Soil Ecol. 6, 195–199. https://doi.org/10.1016/S0929-1393(96)00136-9.

Brinkman, E., Duyts, H., Putten, W., 2005. Consequences of variation in species diversity in a community of root-feeding herbivores for nematode dynamics and host plant biomass. Oikos 110, 417–427. https://doi.org/10.1111/j.0030-1299.2005.13659.x.

Cameron, E.K., Martins, I.S., Lavelle, P., Mathieu, J., Tedersoo, L., Bahram, M., Gottschall, F., Guerra, C.A., Hines, J., Patoine, G., Siebert, J., Winter, M., Cesarz, S., Ferlian, O., Kreft, H., Lovejoy, T.E., Montanarella, L., Orgiazzi, A., Pereira, H.M., Eisenhauer, N., 2019. Global mismatches in aboveground and belowground biodiversity. Conserv. Biol. 33, 1187–1192. https://doi.org/10.1111/cobi.13311.

Cano-Diaz, C., Zeiss, R., Carvalho-Santos, C., Carvalho, R.P., Costa, S.R., Duarte, A.C., Fernandes, P., Guerra, A.C., 2023. Mapping socio-environmental pressures to assess Portuguese soil vulnerability. Appl. Geogr. 161, 103103. https://doi.org/10.1016/j.apgeog.2023.103103.

Carvalho, R.P., Guerra, C., Cano-Díaz, C., Mendes, S., Costa, S.R., 2025. Distribution of plant-parasitic nematode communities across land-use types in the north of Portugal. Appl. Soil Ecol. 206, 105852. https://doi.org/10.1016/j.apsoil.2024.105852.

Chen, D., Cheng, J., Chu, P., Hu, S., Xie, Y., Tuvshintogtokh, I., Bai, Y., 2015. Regional-scale patterns of soil microbes and nematodes across grasslands on the Mongolian plateau: relationships with climate, soil, and plants. Ecography 38, 622–631. https://doi.org/10.1111/ecog.01226.

Ciobanu, M., Eisenhauer, N., Stoica, I.A., Cesarz, S., 2019. Natura 2000 priority and non-priority habitats do not differ in soil nematode diversity. Appl. Soil Ecol. 135, 166–173. https://doi.org/10.1016/j.apsoil.2018.12.009.

Cleland, E., Collins, S., Dickson, T., Farrer, E., Gherardi, L., Hallett, L., Hobbs, R., Hsu, J., Turnbull, L., Suding, K., 2013. Sensitivity of grassland plant community composition to spatial vs. temporal variation in precipitation. Ecology 94, 1687–1696. https://doi.org/10.1890/12-1006.1.

Costa, S.R., 2024. Ecology. In: Perry, Roland N., Moens, Maurice, Jones, John T. (Eds.), plant nematology, 3rd edition. Centre for Agriculture and Bioscience International (CABI), pp. 316–344. https://www.cabidigitallibrary.org/doi/10.1079/9781800622456.0000.

Decaens, T., 2010. Macroecological patterns in soil communities. Glob. Ecol. Biogeogr. 19, 287–302. https://doi.org/10.1111/j.1466-8238.2009.00517.x.

Diale, P., Lobe, P., Schulte auf'm Erley, G., Höppner, F., Schrader, S., 2023. Nematode abundances and community diversity under energy crop (maize and sainfoin) cultivation in annual and perennial cropping systems. Biomass Bioenergy 175, 106844. https://doi.org/10.1016/j.biombioe.2023.106844.

Duarte, A.C., Guerra, C.A., Cano-Díaz, C., Zeiss, R., Carvalho-Santos, C., Carvalho, R.P., Costa, S.R., 2024. Effects of protected areas on soil nematode communities in forests of the north of Portugal. Biodivers. Conserv. 33, 73–89. https://doi.org/10.1007/s10531-023-02732-6.

Egner, H., Riehm, H., Domingo, W.R., 1960. Investigations on the chemical soil analysis as a basis for assessing the soil nutrient status II: chemical extraction methods for phosphorus and potassium determination. K Lantbruksakad Ann. 26, 199–215.

Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T., Zimmermann, N.E., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29, 129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x.

European Commission, 2024. Proposal for a directive of the European Parliament and of the Council on a Soil Monitoring and Resilience (Soil Monitoring Law). https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CONSIL:ST_14954_2023_INIT.

European Union, 2024. Regulation (EU) 2024/1991 of the European Parliament and of the Council of 24 June 2024 on nature restoration. https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX%3A32024R1991.

Ferris, H., 2011. Key to Families (and Subfamilies) of Plant and Soil Nematodes. http://nemaplex.ucdavis.edu/Taxadata/Famkey.htm.

Ferris, H., 2010. Form and function: metabolic footprints of nematodes in the soil food web. Eur. J. Soil Biol. 46, 97–104. https://doi.org/10.1016/j.ejsobi.2010.01.003.

Food and Agriculture Organization of the United Nations (FAO), 2020. Standard operating procedure for soil organic carbon. Walkley-Black method: titration and colorimetric method. Rome. https://openknowledge.fao.org/handle/20.500.14283/ca7471en.

Zhou, J., Wu, J., Huang, J., Sheng, X., Dou, X., Lu, M., 2022. A synthesis of soil nematode responses to global change factors. Soil Biol. Biochem. 165, 108538. https://doi.org/10.1016/j.soilbio.2021.108538.

Fox J., Weisberg S. 2019. A companion to applied regression, 3rd edition. Sage, thousand oaks. https://socialsciences.mcmaster.ca/jfox/books/companion/.

Franco, A.L.C., Gherardi, L.A., de Tomasel, C.M., Andriuzzi, W.S., Ankrom, K.E., Shaw, E. A., Bach, E.M., Sala, O.E., Wall, D.H., 2019. Drought suppresses soil predators and promotes root herbivores in Mesic, but not in xeric grasslands. Proc. Natl. Acad. Sci. USA 116, 12883–12888. https://doi.org/10.1073/pnas.1900572116.

Geisen, S., Wall, D., Putten, Wim, 2019. Challenges and opportunities for soil biodiversity in the Anthropocene. Curr. Biol. 29, R1036–R1044. https://doi.org/10.1016/j.cub.2019.08.007.

Goodey, T., 1963. Soil and Freshwater Nematodes: a Monograph. Rewritten by J.B. Goodey. Methuen, Co. Ltd. 544. doi:https://doi.org/10.1001/jama.1951.03670110105039.

Guerra, C.A., Pendleton, L., Drakou, E.G., Proença, V., Appeltans, W., Domingos, T., Pereira, H.M., 2019. Finding the essential: improving conservation monitoring across scales. Glob. Ecol. Conserv. 18, e00601. https://doi.org/10.1016/j.gecco.2019.e006.

Guerra, C.A., Heintz-Buschart, A., Sikorski, J., Chatzinotas, A., Guerrero- Ramírez, N., Cesarz, S., Beaumelle, L., Rillig, M.C., Maestre, F.T., Delgado-Baquerizo, M., Buscot, F., Overmann, J., Patoine, G., Phillips, H.R.P., Winter, M., Wubet, T., Küsel, K., Bardgett, R.D., Cameron, E.K., Eisenhauer, N., 2020. Blind spots in global soil biodiversity and ecosystem function research. Nat. Commun. 11, 3870. https://doi.org/10.1038/s41467-020-17688-2.

Guerra, C.A., Bardgett, Richard, Caon, Lucrezia, Crowther, Thomas, Delgado-Baquerizo, Manuel, Montanarella, Luca, Navarro, Laetitia, Orgiazzi, Alberto, Singh, Brajesh, Tedersoo, Leho, Vargas, Ronald, Briones, Maria, Buscot, Francois, Cameron, Erin, Cesarz, Simone, Chatzinotas, Antonis, Cowan, Donald, Djukic, Ika, Hoogen, Johan, Eisenhauer, Nico, 2021. Tracking, targeting, and conserving soil biodiversity. Science 371, 239–241. https://doi.org/10.1126/science.abd7926.

Guisan, A., Theurillat, J.-P., 2000. Equilibrium modeling of alpine plant distribution: how far can we go? Phytocoenologia 30, 353–384. https://doi.org/10.1127/phyto/30/2000/353.

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8, 993–1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x.

Hernandez, P.A., Graham, C.H., Master, L.L., Albert, D.L., 2006. The effect of sample size and species characteristics on performance of different species distribution modelling methods. Ecography 29, 773–785. https://doi.org/10.1111/j.0906-7590.2006.04700.x.

Holzman, D.C., 2012. Accounting for nature's benefits: the dollar value of ecosystem services. Environ. Health Perspect. 120, 152–157. https://doi.org/10.1289/ehp.120-a152.

Homet, P., Ourcival, J.-M., Gutiérrez, E., Domínguez-Begines, J., Matías, L., Godoy, O., Gómez-Aparicio, L., 2023. Short- and long-term responses of nematode communities to predicted rainfall reduction in Mediterranean forests. Soil Biol. Biochem. 179, 108974. https://doi.org/10.1016/j.soilbio.2023.108974.

ICNF - Instituto da Conservação da Natureza e das Florestas, 2017. Áreas Protegidas. https://icnf.pt/. Accessed 06 Fev 2026.

INE, 2023. In: Instituto Nacional de Estatística, IP – Portugal (Ed.), Estatísticas da produção vegetal. https://www.ine.pt/xportal/xmain?xpid=INE&xpgid=ine_indicadores&indOcorrCod=0000021&contexto=bd&selTab=tab2&xlang=pt. accessed in 07/10/2024.

IPCC, 2023. Climate change 2023: synthesis report. Contribution of working groups I, II and III to the sixth assessment report of the intergovernmental panel on climate change [Core writing team, H. Lee and J. Romero (eds.)]. IPCC, Geneva, Switzerland, pp. 67–89. https://doi.org/10.59327/IPCC/AR6-9789291691647.

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P., Kessler, M., 2021. Climatologies at high resolution for the earth's land surface areas. EnviDat. https://doi.org/10.16904/envidat.228.v2.1.

Kladivko, E.J., 2001. Tillage systems and soil ecology. Soil Tillage Res. 61, 61–76. https://doi.org/10.1016/S0167-1987(01)00179-9.

Kreft, H., Jetz, W., 2007. Global patterns and determinants of vascular plant diversity. Proc. Nat. Acad. Sc. U. S. A 104, 5925–5930. https://doi.org/10.1073/pnas.0608361104.

Lejoly, J.D.M., Mason-Jones, K., Veen, G.F.C., 2026. A soil food web approach to integrate soil fauna into multitrophic biogeochemistry. Commun. Earth Environ. 7, 322. https://doi.org/10.1038/s43247-026-03322-4.

Li, X., Liu, T., Li, H., Geisen, S., Hu, F., Liu, M., 2022. Management effects on soil nematode abundance differ among functional groups and land-use types at a global scale. J. J. Anim. Ecol. 91, 1770–1780. https://doi.org/10.1111/1365-2656.13744.

Mai, W., Mullin, P., Lyon, H., Loeffler, K., 1996. Plant-Parasitic Nematodes: A Pictorial Key to Genera, 5th ed. Cornell Univ Pr. https://doi.org/10.7591/9781501728419.

Mod, H., Buri, A., Yashiro, E., Guex, N., Malard, L., Pinto-Figueroa, E., Pagni, M., Hirzel, H., Meer, J., Guisan, A., 2021. Predicting spatial patterns of soil bacteria under current and future environmental conditions. ISME J. 15, 1–14. https://doi.org/10.1038/s41396-021-00947-5.

Neher, D.A., 2001. Role of nematodes in soil health and their use as indicators. J. Nematol. 33, 161–168 https://pubmed.ncbi.nlm.nih.gov/19265875/.

Neher, D.A., 2010. Ecology of plant and free-living nematodes in natural and agricultural soil. Annu. Rev. Phytopathol. 48, 371–394. https://doi.org/10.1146/annurev-phyto-073009-114439.

Nelson, D.W., Sommers, L.E., 1996. Total carbon, organic carbon and organic matter. In: Bartels, J.M., et al. (Eds.), Methods of Soil Analysis: Part 3 Chemical Methods, 3rd edn, SSSA Book Series, pp. 961–1010. https://doi.org/10.2136/sssabookser5.3.c34. Madison.

Nielsen, U.N., et al., 2014. Global-scale patterns of soil nematode assemblage structure in relation to climate and ecosystem properties. Glob. Ecol. Biogeogr. 23, 968–978. https://doi.org/10.1111/geb.12177.

O'Brien, E.M., 1998. Water–energy dynamics, climate, and prediction of woody plant species richness: an interim general model. J. Biogeogr. 25, 379–398 http://www.jstor.org/stable/2846224.

Opik, M., Moora, M., Liira, J., Zobel, M., 2006. Composition of root-colonizing arbuscular mycorrhizal fungal communities in different ecosystems around the globe. J. Ecol. 94, 778–790. https://doi.org/10.1111/j.1365-2745.2006.01136.x.

Peterson, A.T., 2003. Predicting the geography of species invasions via ecological niche modeling. Q. Rev. Biol. 78, 419–433. https://doi.org/10.1086/378926.

Piśkiewicz, A., Duyts, H., Berg, M., Costa, S., Putten, W., 2007. Soil microorganisms control plant ectoparasitic nematodes in natural coastal foredunes. Oecologia 152, 505–514. https://doi.org/10.1007/s00442-007-0678-2.

Pörtner, H.-O., Roberts, D.C., 2022. IPCC AR6 Report–Working Group II: Climate Change 2022: Impacts. Impacts, Adaptation and Vulnerability. Cambridge University Press, p. 3056. https://doi.org/10.1017/9781009325844.

Ptatscheck, C., Gansfort, B., Traunspurger, W., 2018. The extent of wind-mediated dispersal of small metazoans, focusing nematodes. Sci. Rep. 8, 6814. https://doi.org/10.1038/s41598-018-24747-8.

R Core Team, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. https://www.R-project.org/.

Renčo, M., Gömöryová, E., Čerevková, A., 2020. The effect of soil type and ecosystems on the soil nematode and microbial communities. Helminthologia 57, 129–144. https://doi.org/10.2478/helm-2020-0014.

República Portuguesa, 2008. Establishes the legal framework for the conservation of nature and biodiversity and revokes decrees-Laws Nos. 264/79, of august 1, and 19/93, of January 23, article 43.°. https://diariodarepublica.pt/dr/detalhe/decreto-lei/142-2008-454502.

Schimel, J.P., Gulledge, J., 1998. Microbial community structure and global trace gases. Glob. Chang. Biol. 4, 745–758. https://doi.org/10.1046/j.1365-2486.1998.00195.x.

Sidari, M., Ronzello, G., Vecchio, G., Muscolo, A., 2008. Influence of slope aspects on soil chemical and biochemical properties in a Pinus laricio forest ecosystem of Aspromonte (southern Italy). Eur. J. Soil Biol. 44, 364–372. https://doi.org/10.1016/j.ejsobi.2008.05.

Siebert, J., Ciobanu, M., Schädler, M., Eisenhauer, N., 2020. Climate change and land use induce functional shifts in soil nematode communities. Oecologia 192, 281–294. https://doi.org/10.1007/s00442-019-04560-4.

Singh, B., Bardgett, R., Smith, Pete, Reay, D., 2010. Microorganisms and climate change: terrestrial feedbacks and mitigation options. Nat. Rev. Microbiol. 8, 779–790. https://doi.org/10.1038/nrmicro2439.

Singh, B., Delgado-Baquerizo, M., Egidi, E., Guirado, E., Leach, J., Liu, H., Trivedi, P., 2023. Climate change impacts on plant pathogens, food security and paths forward. Nat. Rev. Microbiol. https://doi.org/10.1038/s41579-023-00900-7.

Thakur, M.P., Del Real, I.M., Cesarz, S., Steinauer, K., Reich, P.B., Hobbie, S., Eisenhauer, N., 2019. Soil microbial, nematode, and enzymatic responses to elevated CO2, N fertilization, warming, and reduced precipitation. Soil Biol. Biochem. https://doi.org/10.1016/j.soilbio.2019.04.020.

Thuiller, W., 2004. Patterns and uncertainties of species range shifts under climate change. Glob. Chang. Biol. 10, 2020–2027. https://doi.org/10.1111/j.1365-2486.2004.00859.x.

Thuiller, W., Lavorel, S., Araújo, M., Sykes, M., Prentice, I., 2005. Climate change threats to plant diversity in Europe. Proc. Natl. Acad. Sci. USA 102, 8245–8250. https://doi.org/10.1073/pnas.0409902102.

Thuiller, W., Georges, D., Engler, R., Breiner, F., 2016. biomod2: Ensemble Platform for Species Distribution Modeling. https://cran.r-project.org/web/packages/biomod2/biomod2.pdf.

Thuiller, W., Georges, D., Gueguen, M., Engler, R., Breiner, F., Lafourcade, B., Patin, R., 2022. biomod2: ensemble platform for species distribution modeling. R package version 4.1–2. https://CRAN.R-project.org/package=biomod2.

Tsui, C.-C., Chen, Z.-S., Hsieh, C.-F., 2004. Relationships between soil properties and slope position in a lowland rain forest of southern Taiwan. Geoderma 123, 131–142. https://doi.org/10.1016/j.geoderma.2004.01.

Valavi, R., Guillera-Arroita, G., Lahoz-Monfort, J.J., Elith, J., 2021. Predictive performance of presence-only species distribution models: a benchmark study with reproducible code. Ecol. Monogr. 42 (e01), 486. https://doi.org/10.1002/ecm.1486.

van den Hoogen, J., Geisen, S., Routh, D., Ferris, H., Traunspurger, W., Wardle, D.A., Crowther, T.W., 2019. Soil nematode abundance and functional group composition at a global scale. Nature 572, 194–198. https://doi.org/10.1038/s41586-019-1418-6.

Veresoglou, S.D., Halley, J.M., Rillig, M.C., 2015. Extinction risk of soil biota. Nat. Commun. 6, 8862. https://doi.org/10.1038/ncomms9862.

Verschoor, B.C., De Goede, R.G.M., De Hoop, J.-W., De Vries, F.W., 2001. Seasonal dynamics and vertical distribution of plant-feeding nematode communities in grasslands. Pedobiologia 45, 213–233. https://doi.org/10.1078/0031-4056-00081.

Vetaas, O.R., 2002. Realized and potential climate niches: a comparison of four Rhododendron tree species. J. Biogeogr. 29, 545–554. https://doi.org/10.1046/j.1365-2699.2002.00694.x.

Wall, D.H., Nielsen, U.N., Six, J., 2015. Soil biodiversity and human health. Nature 528, 69–76. https://doi.org/10.1038/nature15744.

Wallace, H.R., 1968. The dynamics of nematode movement. Annu. Rev. Phytopathol. 6, 91–114. https://doi.org/10.1146/annurev.py.06.090168.000515.

Wang, J., Li, M., Zhang, X., Liu, X., Li, L., Shi, X., Hu, H., Pan, G., 2019. Changes in soil nematode abundance and composition under elevated [CO2] and canopy warming in a rice paddy field. Plant Soil 445, 425–437. https://doi.org/10.1007/s11104-019-04330-4.

Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Seťälä, H., Van Der Putten, W.H., Wall, D. H., 2004. Ecological linkages between aboveground and belowground biota. Science 304, 1629–1633. https://doi.org/10.1126/science.1094875.

Whitehead, A.G., Hemming, J.R., 1965. A comparison of some quantitative methods of extracting small vermiform nematodes from soil. Ann. Appl. Biol. 55, 25–38. https://doi.org/10.1111/j.1744-7348.1965.tb07864.x.

Yang, B., Banerjee, S., Herzog, C., Ramírez, A., Dahlin, P., Van der Heijden, M., 2021. Impact of land use type and organic farming on the abundance, diversity, community composition and functional properties of soil nematode communities in vegetable farming. Agric. Ecosyst. Environ. 318, 107488. https://doi.org/10.1016/j.agee.2021.107488.

Yang, X., Schädler, M., Eisenhauer, N., Schlüter, S., Wu, M., Blagodatskaya, E., Wang, X., 2026. Trait-based responses of soil nematode communities to land use and climate change. J. Appl. Ecol. 63, e70297. https://doi.org/10.1111/1365-2664.70297.

Yeates, G.W., Bongers, T., 1999. Nematode diversity in agroecosystem. Agric. Ecosyst. Environ. 74, 113–135. https://doi.org/10.1016/S0167-8809(99)00033-X.

Yeates, G.W., Bongers, T., De Goede, R.G.M., Freckman, D.W., Georgieva, S.S., 1993. Feeding habits in soil nematode families and genera – an outline for soil ecologists. J. Nematol. 25, 315–331. https://pmc.ncbi.nlm.nih.gov/articles/PMC2619405/.

Zeiss, R., Briones, M., Mathieu, J., Lomba, Â., Dahlke, J., Heptner, L.-F., Salako, G., Eisenhauer, N., Guerra, C., 2023. Climate effects on the distribution and conservation of commonly observed European earthworms. Conserv. Biol. 38. https://doi.org/10.1111/cobi.14187.

Zhang, M., Liang, W.J., Zhang, X.K., 2012. Soil nematode abundance and diversity in different forest types at Changbai Mountain, China. Zool. Stud. 51, 619–626. http://zoolstud.sinica.edu.tw/default.htm.

Zhang, S., Chen, D., Sun, D., Wang, X., Smith, J.L., Du, G., 2011. Impacts of altitude and position on the rates of soil nitrogen mineralization and nitrification in alpine meadows on the eastern Qinghai–Tibetan Plateau, China. Biol. Fertil. Soils. 48, 393–400. https://doi.org/10.1007/s00374-011-0634-5.