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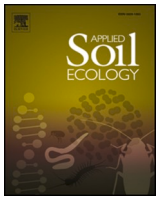

Research paper

Distribution of plant-parasitic nematode communities across land-use types in the North of Portugal

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ABSTRACT

Plant-parasitic nematodes pose a significant threat to agriculture globally, yet, while much is known about their local effects, the large-scale distribution and primary drivers are still unknown. Our objective was to investigate the influence of land-use and other environmental factors in the distribution of plant-parasitic nematodes at regional scale. A comprehensive soil sampling campaign was conducted in the North of Portugal, covering diverse land-use types, geography and climate. A total of 406 soil samples were taken from six different land-use types: annual and perennial agriculture, pastures, urban areas, and exotic and native forests. Plant-parasitic nematodes were extracted and identified to genus level through morphological characters analysis and edaphoclimatic data was obtained from our analysis and from various European datasets. Taxonomic and functional diversity indices were calculated to evaluate the impact of land-use and environmental factors on community structure. Additionally, species distribution models using ensemble of machine learning algorithms were created to predict the potential distribution of plant-parasitic nematodes. Our findings revealed that pastures had significantly more diverse plant-parasitic nematode communities, with higher alpha diversity, biomass, and herbivory footprint. Meanwhile, forests had the lowest diversity, but more heterogeneous communities within sites. The influence of environmental factors such as soil properties, land cover, and climate on the distribution of plant-parasitic nematodes could not be established. However, the potential distribution of different genera can differ according to environmental variables. Our findings provide valuable insights into the distribution patterns of plant-parasitic nematodes in northern Portugal, which can inform future land-use planning and management strategies.

1. Introduction

Soil nematodes are the most abundant animals on Earth, accounting for an estimated four-fifths of all animals on land, and feature all the trophic levels of the soil food web (van den Hoogen et al., 2019). Free-living nematodes can be assigned through their trophic group into bacterivores, fungivores, omnivores and predators (Yeates et al., 1993), and all soilborne herbivores are plant-parasitic nematodes that feed on plant roots, having protrusible stylets to pierce plant cells for feeding, with varying degrees of specialisation. These herbivores account for approximately 83 megatones of fresh biomass worldwide (van den Hoogen et al., 2019), and their ecological interactions with their hosts ultimately affect plant performance and distribution (Neher, 2010; Bardgett and van der Putten, 2014; Dietrich et al., 2020). Although they occur in all environments colonised by plants, including natural and semi-natural systems, plant-parasitic nematodes have been traditionally studied in agroecosystems due to their direct economic impact on crop yields. Altogether, plant-parasitic nematodes parasite virtually all crops causing an estimated $125 billion loss annually, representing 14 % of the crop yield in the world (Mesa-Valle et al., 2020). This generalisation does not account for activity of plant-parasitic nematodes that is often unnoticed, mostly due to these soil-borne pathogens being small and causing nonspecific aboveground symptoms on the plants. According to their life strategy and feeding behaviour, plant-parasitic nematodes are classified as ecto-, semi-*endo*- and endoparasites (Yeates et al., 1993). Ectoparasitic nematodes develop their entire life cycle outside the host,

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migrating through soil and using their stylet to feed on roots. The semi-endoparasitic nematodes partially penetrate the host plant to feed at a stage of their life cycle, albeit having migratory stages. Such nematodes, including *Rotylenchus* and *Helicotylenchus* spp., may occur in high densities, feeding on roots of diverse plants of agriculture importance. Finally, endoparasitic nematodes include both migratory endoparasites, e.g. *Pratylenchus* and *Ditylenchus* spp., that migrate through the plant tissues causing lesions, and sedentary endoparasites, such as root-knot nematodes and cyst nematodes, *Meloidogyne* and *Heterodera/Globodera* spp., respectively. These genera occupy the respective first and second position on the list of the most economically important plant-parasitic nematodes in crops worldwide (Jones et al., 2013). Feeding on the cytoplasm of living plant cells, the juveniles of these nematodes establish a close interaction with their hosts, inducing through several complex changes in cellular morphology and physiology, the formation of multinucleate feeding cells, which become the exclusive source of nutrients for these nematodes (Quentin et al., 2013). Also importantly, plant-parasitic nematodes predispose plants to be attacked by a suite of opportunistic pathogens like fungi (Back et al., 2002; Castillo et al., 1998; Jones et al., 2013; Wheeler et al., 2019).

Nematodes have developed several different life strategies ranging from colonizers to persisters (r to K-strategists) on a scale of 1–5 (cp-scale). Colonizers produce many small eggs and rapidly exploit nutrient-enriched habitats in contrast to persisters, which rarely react in these conditions and have a low reproduction rate and a long life span. The combination of nematode life strategy with their feeding group results in the concept of nematode 'guilds' with application on establishment of several indices (Bongers and Bongers, 1998; Bongers and Ferris, 1999). More recently, the metabolic activity of nematodes in the community has been introduced as a tool to assess the nature and magnitude of ecosystem functions and has been used in different spatial scale studies (Ferris, 2010; Ferris et al., 2012; Hu et al., 2016). Biomass and metabolic footprints may be more appropriate for evaluating soil energy channels and nutrient allocation to various food web levels than abundance, as these refer to matter and energy flows in the ecosystem (Ciobanu et al., 2015).

Given the growing impact of land-use changes and increased agricultural intensification, as drivers of biotic homogenization and shifts in ecological communities (including plant-parasitic nematodes), significant alterations to the diversity of these communities are expected to occur (Archidona-Yuste et al., 2021). And, for these reasons, large-scale assessments of the diversity, distribution and density of plant-parasitic nematodes related to the conversion of more natural systems into different degrees of land-use intensity, whether agricultural or urban areas, are of utmost importance for the design of future and successful management strategies of these nematodes.

The overall aims of our work were i) to describe the spatial distribution, abundance and diversity of plant-parasitic nematode communities across different land-use types, at a regional scale; and ii) to assess to which extent land-use shapes plant-parasitic nematode communities; and iii) to evaluate the influence of environmental variables on communities of plant-parasitic nematodes.

2. Material and methods

2.1. Area of study and soil sampling

The study was conducted in the North of Portugal and covered an area of approximately 21,515 km^2 (Fig. 1). This region is a highly heterogeneous one with a wide variety of environmental conditions and land-use types that is subject to an extensive array of pressures that range from invasive species and land-use change to forest fires and contamination (Carmo et al., 2011; Vicente et al., 2013; De la Fuente and Beck, 2018; Bragança et al., 2019; Cano-diaz et al., 2023; Duarte et al., 2024). In northern Portugal, the mountainous landscape is predominantly characterized by Cambisols and Regosols, with granite and schist being the dominant geological formations (Ramos et al., 2017). In order to obtain a representative sampling on a regional scale, the entire area of study was overlaid by a 20 km grid on a hierarchical stratified random sampling scheme. For each grid cell, six random sites were sampled within the same day with each site corresponding to a specific major land-use type: annual and perennial agricultural crops (70 and 67 samples, respectively), pastures (71 samples), urban areas (71 samples) (Fig. 1) and both exotic and native forest systems (57 and 70 samples, respectively). Although the land-use allocation was not proportional to land cover size, but rather similarly within each grid cell, this sampling

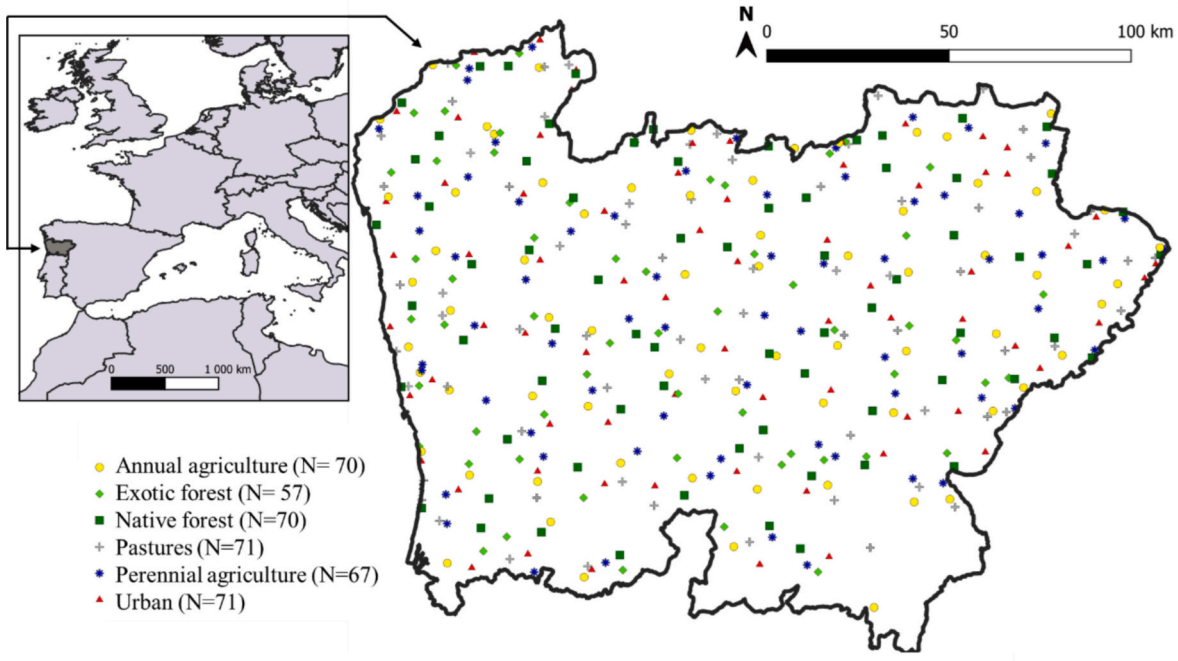

Fig. 1. Distribution of the 406 sampling sites across the North of Portugal. Sampled land-use types include: annual and perennial agriculture, exotic and native forests, pastures, and urban green parks.

design allowed to homogeneously survey the entire area (Vos et al., 2000). And, with the multiple land-use sites in each square it was possible to appropriately represent the different habitats, pressures and drivers within the regional environmental gradient (Guerra et al., in rev.).

Soil sampling was performed, in a systematic and randomized manner, in the Autumn, between September and December 2021, a period characterized as a warm and dry year in the region, following Soil BON Field Sampling Protocol (Guerra et al., 2021) and covering all land-use types in a given grid square. At each sampling site, a soil sample composed of 9 soil cores (approximately 250 mL soil each, 2.25 L total soil) was collected across a homogeneous area of 900m^2 (30x30m) to account for the local heterogeneity of soils, and GPS coordinates were retrieved. All soil cores were extracted using a hori-hori (5 cm diameter) knife down to 10 cm depth, combined in a plastic bag and mixed after removal of stones or plant material larger than ca. 1 cm. A 120 mL plastic container was filled with 100 mL soil and transported in a refrigerated box to the laboratory for nematode extraction. The remainder dried at 60 °C for the rapid drying of large volume of soil prior to physical-chemical properties according to standard protocols (below) and storage. Soil for nematode extraction was kept at 5 °C in the dark and treated within the next 45 days.

Taken together, the soil sampling strategy allowed to investigate the plant-parasitic nematode diversity in the soil and their functions, as well as the interplay between soil communities and their spatial distribution and soil properties, shedding light on the ecological dynamics that underpin soil health and biodiversity.

2.2. Environmental variables and space coverage

Several complementary environmental variables covering climate (e.g. mean annual temperature and precipitation), location (e.g. slope), land cover (e.g. forest and agricultural cover and distance to urban areas) and soil chemical and physical properties (e.g. soil organic nitrogen, pH, clay and silt content) were selected to provide an adequate characterization of the processes occurring in the area of study (Fig. 2; Supplementary Table S1). To resolve the possible resolution differences among the environmental variable rasters obtained from different datasets, we followed a data standardization process where all the environmental variables were reprojected to a common coordinate reference system (WGS84) and to a common 1 km^2 pixel size to ensure spatial alignment, using bilinear method as resampling strategy with the help of *raster* package in R (Hijmans, 2022). Whilst all environmental variables were retrieved from available datasets in raster format, approximately 1 kg of soil was sieved through a 2 mm mesh to determine.soil phosphorus, pH, soil organic carbon and clay and silt content (%). Soil organic carbon was determined based on the Walkley & Black chromic acid wet oxidation method (Nelson and Sommers, 1996; FAO, 2020). Soil pH was determined potentiometrically in a soil-to-water suspension, maintaining a ratio of 1 part soil to 2.5 parts water (by mass/volume). Extractable phosphorus was determined by the modified Egner-Riehm method (Egner et al., 1960), filtering a solution of lactate-acetate solution and measured by molecular absorption spectrophotometry. Clay and silt content (%) was determined through particle-size distribution, silt ($0.02 > Ø > 0.002$ mm) and clay ($Ø < 0.002$ mm), as recommended by the International Union of Soil Science (Atterberg Scale). Although all environmental raster values followed the same z-

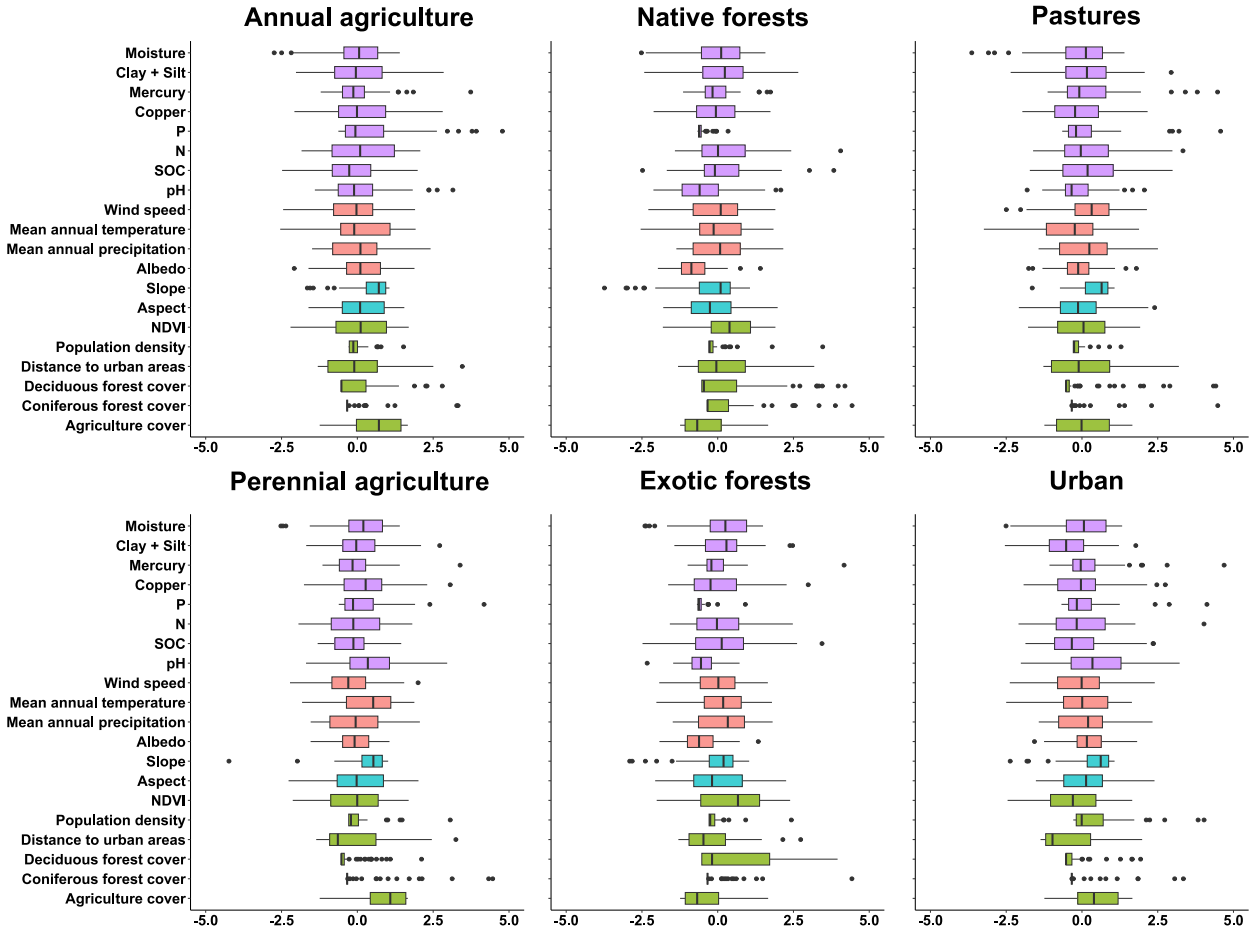

Fig. 2. Distribution of each of the environmental variables considered across the sampled sites in different land uses: annual and perennial agriculture, exotic and native forests, pastures, and urban areas.

score standardization, environmental rasters of soil organic carbon, pH, phosphorus and clay and silt content were standardized with respective mean and standard deviation derived from collected values to maintain scale and variability of the observed data.

Multicollinear variables were excluded, resulting in a final set of 20 environmental variables (Supplementary Table S1). Environmental variables discarded due to high correlation were aridity index, precipitation seasonality, temperature seasonality, forest cover, elevation, potential evapotranspiration and nitrogen deposition. Resulting environmental variables were subsequently used to assess the overall environmental space coverage and further analyses.

2.3. Nematode data collection and identification

Nematodes were extracted from the soil by the tray method, an adaptation of the Baermann funnel, with high extraction efficiency for plant parasitic nematodes (Whitehead and Hemming, 1965) and the ability to extract mobile stages of endoparasites such as *Heterodera*, *Meloidogyne* and *Pratylenchus* (Costa et al., 2012), in the Centre of Molecular and Environmental Biology. Soil was spread thinly (ca. 0.5 cm thick layer) and evenly on a kleenex sheet on a plastic grid inside the tray (22.5 × 15.5 × 6.5 cm – Length x Width x Height), that was then filled with sufficient water to flood the soil (ca. 300 mL). After 72 h, the nematode suspension collected. The nematode suspension collected in the tray was then concentrated by sieving through a 20 μm-pore sieve. Initially, the first 100–200 nematodes of the community were identified, in which plant-parasitic nematodes were identified whenever possible to genus level through analysis of their morphological characters at up to 200× magnification, following simple diagnostic keys (Goodey, 1963; Mai et al., 1996; Ferris, 2011), and all plant-parasitic nematodes present in samples were counted. Due to the extensive and exhaustive nature of the data collection and analysis process, replicates were not included in this study.

2.4. Statistical analysis

All statistical analyses were conducted using R software version 4.2.1 (R Core Team, 2022). In order to assess the overall coverage of the selected edaphoclimatic and land cover variables in the target region, we conducted a statistical multidimensional analysis with the selected variables. Being effective at finding outliers for multivariate data, the Mahalanobis distance was calculated in multidimensional space and centred with the known distribution based on the environmental variables observed at the sampled sites. This procedure allowed to calculate the distance of each point to the mean centre, represented as the mean of every variable in the multivariate data. The Mahalanobis distance follows a Chi-squared distribution with d degrees of freedom (number of dimensions, d = 20), the overall environmental coverage was estimated using Chi-square for the 20 dimensions, whereas outliers were estimated for a Chi-square of 0.975.

To ascertain the effect of land-use type on the community of plant-parasitic nematodes, metrics for alpha diversity and beta diversity were calculated based on the number of nematodes of each taxon found in our samples.

Alpha diversity, taxa richness and indexes of evenness and Shannon-Weiner, were calculated, which reflect loss or gain and regulation of genus dominance in each community in response to environmental activity and changes on land-use type, using the *vegan* software package in R (Oksanen et al., 2019). Beta diversity was calculated to analyse the difference in plant-parasitic nematode communities across the spatial scale of the area of study. Prior to beta diversity calculation, a distance matrix was computed with the Bray Curtis dissimilarity index from the nematode abundance matrix after Log transformation. Then, the multivariate homogeneity of group dispersion between different land-use type was compared using *betadisper* function (Anderson et al., 2006; Legendre and De Cáceres, 2013). With each land-use type as group centroids, the distances were tested for significance ($p < 0.05$) from each other with ANOVA. For functional diversity, plant-parasitic nematodes were assigned into functional guilds using the NINJA software (Sieriebriennikov et al., 2014) to calculate abundance, biomass and herbivory footprint. Other functional diversity metrics, that are based on the analogy of taxonomic diversity, were computed, such as functional richness - the amount of functional space filled by the community - and functional evenness - the regularity of the density distribution in the filled niche volume - using nematode biomass as a functional trait (Mason et al., 2005; Villéger et al., 2008). As they are independent from each other, these indices assess different components of the distribution of species in the functional niche. Both functional richness and functional evenness metrics were computed with biomass as functional trait using the *fundiversity* package in R (Grenié and Gruson, 2022), and adequately transformed to fulfil the normality assumption before post hoc analysis by LSD. To assess the adequacy of the sampling effort, a rarefaction curve analysis was conducted, with the help of *vegan* package, to assess if the sample size effectively captured the taxa diversity.

The selected environmental variables were subject to variation partitioning (Borcard et al., 1992; Legendre and Legendre, 2012), after standardization, to assess their unique and shared contributions to the plant-parasitic nematode community structure using *varpart* function embedded in *vegan* package in R.

2.5. Species distribution modelling

An ensemble species distribution modelling (SDM) approach was developed with the help of *biomod2* package in R software (Thuiller et al., 2022) for taxa with >50 occurrences (*Criconema*, *Ditylenchus*, *Gracilacus*, *Helicotylenchus*, *Heterodera/Globodera*, *Hoplolaimus*, *Meloidogyne*, *Paratylenchus*, *Pratylenchus*, *Rotylenchus*, Trichodoridae, *Tylenchorhynchus*, *Tylenchus*, *Xiphinema*) among the 406 samples for the entire area of study (a total of 14 plant-parasitic nematode taxa). Although descriptive and non-predictive modelling techniques embedded in vegan R package are useful tools in revealing community-level patterns, it lacks distribution capabilities. This approach was carried to provide insights into the potential distribution patterns and areas of high risk for these taxa as well as to account the most important environmental drivers of their distribution. Integrating vegan and species distribution models enables a comprehensive understanding of plant-parasitic nematode community structure and other individual parameters such as abundance and footprints, as well as facilitates the prediction of their potential distribution across the study area.

This tool enables the execution of 10 different classification models using either presence/absence or presence/pseudo-absence data. Consequently, our plant-parasitic nematode abundance dataset was then converted to the form of presence/pseudo-absence, where absences were treated as pseudo-absences together with a newly pseudo-absence generated across the area of study. For each taxon, the number of pseudo-absences generated exceeded the number of presences by a factor of three and was replicated 10 times (Barbet-Massin et al., 2012), with an input of environmental data from a stack of rasters containing the explanatory variables (previously standardized; Supplementary Table S1). To improve model predictive performance and accuracy, we conducted model training and evaluation using 10-fold cross-validation (5 repeats), which allows to validate the models on independent subsets of the dataset. Evaluation metrics *TSS* (true skill statistics) and *ROC AUC* (area under the ROC curve) were selected to the development of ensemble models and combined by each combination of pseudo-absence and repetition datasets, merging algorithms together. Also, probabilities from the selected models were weighted according to their evaluation scores, giving more importance to high rated models.

The output included, for each taxon, an estimation of environmental variable contribution and a raster with binary predictions (maximizing *TSS*). Variable importance was determined in *biomod2:get_variables_importance* function with a randomisation procedure, which

computes *Pearson* correlation between the standard predictions and predictions where the variable has been randomly permutated (Thuiller et al., 2009). Higher values of variable importance indicate stronger influence of the variable to the model. Average contribution of the environmental variables among the 14 plant-parasitic taxa was determined, as well as the top 5 most important for each individual taxa were identified as these encompass a significant portion of total contribution. Furthermore, to understand the relationship between the species occurrence and changes in environmental variables, response curves were developed with *bm_PlotResponseCurves* function, for the most economically important plant-parasitic taxa that we found: *Meloidogyne, Heterodera/Globodera, Pratylenchus, Ditylenchus* and *Xiphinema*. Predicted taxa richness was obtained by overlaying the maps of distribution of each respective taxon – stacked species distribution models – in QGIS software (version 3.22.12) with simple addition (taxa richness for given location correspond to the sum of plant-parasitic taxa predicted for same location). The coefficient of determination (R^2) between predicted and observed richness was determined to ensure robust comparisons between modelled predictions and actual observed data, thereby validating the accuracy of the SDM projections.

3. Results

3.1. Plant-parasitic nematode occurrence and diversity

A total of 19 different taxa (17 genera and two independent families) were recorded from the soil samples across all land-use types with 242,703 plant-parasitic nematodes being extracted (Supplementary Table S2). The abundance of plant-parasitic nematodes was affected by the type of land-use ($p < 0.05$) with soils in pastures having a significantly higher abundance, followed by urban areas and both types of agriculture (annual and perennial) and forest having fewer nematodes (Supplementary Table S3). The mean abundance of ectoparasitic nematodes was larger across land-uses than other feeding types, with the exception of annual agriculture (AGR), in which numbers of migratory endoparasites were higher, particularly due to large numbers of *Pratylenchus* spp. Most taxa occurred in all land-use types, whereas *Longidorus* were only detected in perennial agriculture (2 specimens in one sample) and *Hemicyclophora* were absent in perennial agriculture. The most abundant taxa were *Pratylenchus* and *Paratylenchus*, comprising >50 % of all plant-parasitic nematodes, and overall being the dominant genera. In pastures, urban areas, exotic forests and perennial agriculture, *Paratylenchus* was the most frequently observed taxon, whilst in annual agriculture, the plant-parasitic nematode community was dominated by *Pratylenchus* spp. followed by *Paratylenchus* spp.; the ectoparasitic *Gracilacus* was the most common genus present in native forests.

3.2. Diversity

Land-use type significantly affected the alpha-diversity and functional diversity of plant-parasitic nematode communities found in our soil samples across the North of Portugal (Fig. 3). Pasture areas had significantly more diverse communities, with a higher mean of taxa, followed by urban areas, whilst less diverse communities were found in forest soils (Fig. 3a and b). Differences in similarity of abundances of plant-parasitic nematodes in the different ecosystems were not found (Fig. 3c). Overall, significant differences in beta diversity were found among communities of each land-use type (Fig. 3d). Forest ecosystems harbour less similar community patterns than the rest of land-use types; this is shown by the higher values of distance to the centroids. Communities found in pasture and urban soils were more identical to each other with less variation ($p < 0.05$), followed by agricultural soil samples.

Nematode functional richness was significantly higher in pasture soils than in forest and annual agriculture soils, followed by perennial agriculture and urban soils, whilst forest ecosystems had a smaller amount of niche space occupied by plant-parasitic nematode taxa (Fig. 3e). The nematode functional evenness, or distribution of body mass within communities, was significantly higher in forest communities, especially in soils of native forests (Fig. 3f). These results suggest that despite their higher functional richness, the body mass of plant-parasitic nematode communities present in pastures is less regularly distributed.

The rarefaction curve analysis (Supplementary Fig. S1) suggests that the sampling effort nearly achieved sampling saturation, covering a significant portion of the taxa richness of plant-parasitic nematodes.

3.3. Environmental space coverage and effects of environmental on nematode community composition

The selected environmental variables used in the sampling design resulted in a representation of 92.53 % of environmental space coverage. However, regarding nematode community variation, only 13.92 % of the variance was explained from the sum of unique and joint fractions of the multiple environmental variables. This value of explained percentage is divided in unique and joint fractions of the datasets of variables used, namely land cover, climate, location and soil variables (Supplementary Table S1). Land cover variables had the highest explanatory contribution of all, with almost 6 % of the total variance, followed by soil variables at 1.27 % and by climate and location variables, making up almost 8 % of the variance in the community. Their joint fractions, which consist of the explained variance accountable from two or more datasets of variables, make up the rest of the total variance explained.

3.4. Species models distribution of plant-parasitic nematodes

The predicted map of PPN taxa richness (Fig. 4a), based on set environmental conditions, shows areas with highly suitable habitats across the North of Portugal, in particular areas of high population density in the West region and northern region. On the other hand, the East and Centre region of the area of study is projected as having less suitable environmental conditions for most plant-parasitic nematodes. Still, according to the predictive models, the importance of the environmental variables varied among taxa but overall, some variables had the highest contribution to the prediction of plant-parasitic nematode distribution (Fig. 4b). In fact, considering the mean percentage contribution of each variable for plant-parasitic nematode taxa distribution model, mean annual precipitation had the highest impact on the distribution of plant-parasitic nematodes, followed by slope, mean annual temperature, NDVI and human population density as the overall most important variables (Fig. 4b). These variables together with agriculture cover, aspect, nitrogen, albedo, moisture and soil phosphorus comprehend >70 % of the percent contribution of all variables. Although these percentage values are dependent on the variables used in the model, which add up to 100 %, it is possible to underline their importance over other variables, such as soil mercury, coniferous forest cover and soil organic carbon (Supplementary Table S4).

The predicted distribution of plant-parasitic nematodes with worldwide economic importance was both positive and negatively influenced by environmental conditions across the North of Portugal, according to the variability of the probability of occurrence of these taxa (Fig. 5). The occurrence of *Heterodera/Globodera* did not seem to be negatively affected by most of the environmental variables, excepting soil moisture, NDVI and soil phosphorus. As for *Ditylenchus* spp., higher percentage of agricultural crops at the expense of forest areas are beneficial to their occurrence, however, human population density together with soil moisture and higher values of soil copper are negatively correlated. The occurrence of species of *Meloidogyne* is favoured by higher values of precipitation, albedo and also, soil phosphorus, although it seems the rest of the variable do not affect to a great extent, whether positively or negatively. Regarding the probability of *Pratylenchus* spp. being found,

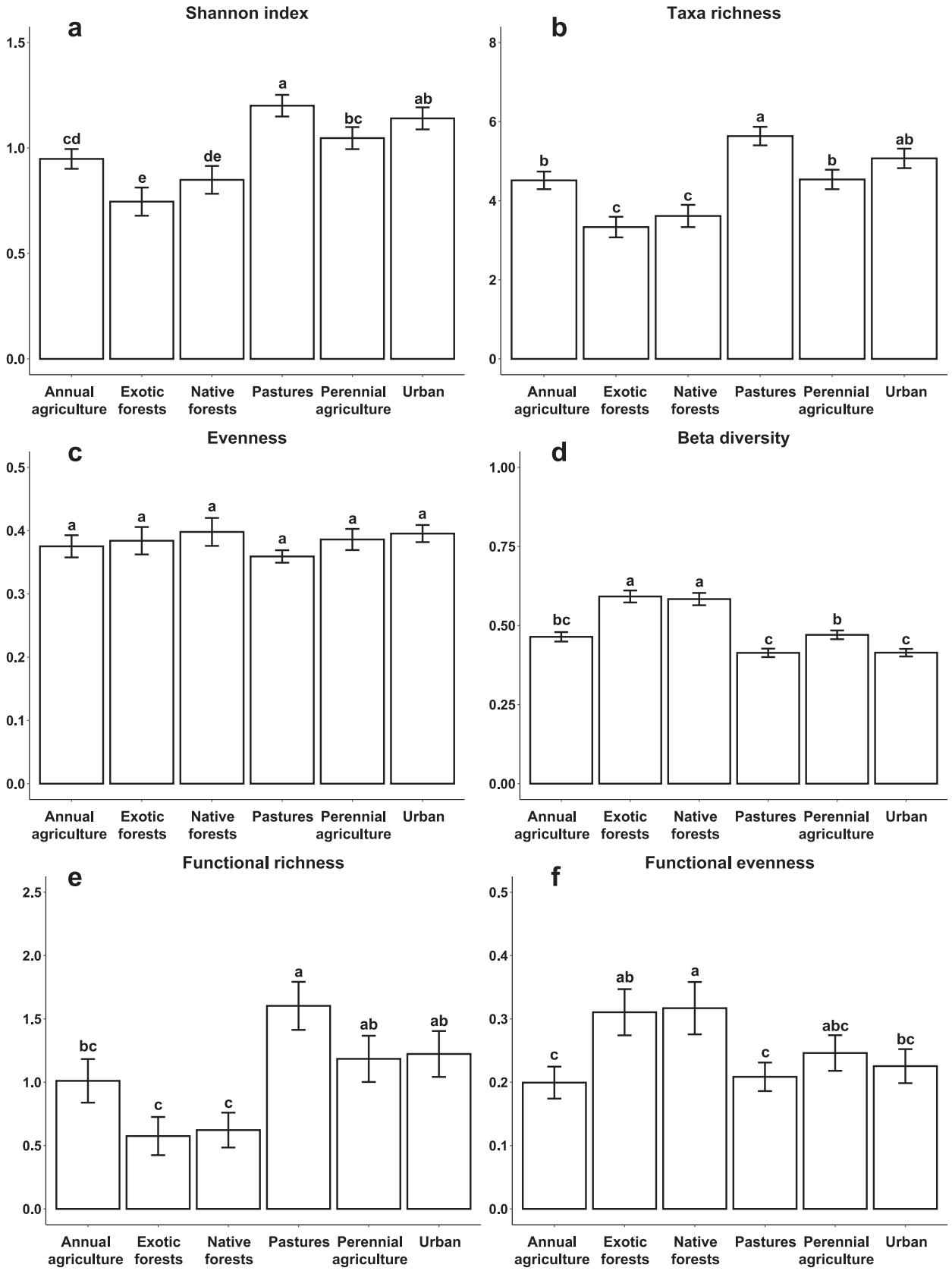

Fig. 3. Plant-parasitic nematode community diversity metrics of Shannon index, taxa richness, Evenness index, beta diversity (as variance of the homogeneity of group dispersion), and functional diversity calculated from soil samples of 100 mL collected across different land-use types. Values are means ± standard error and columns with different letters are statistically different according to LSD test ($p < 0.05$).

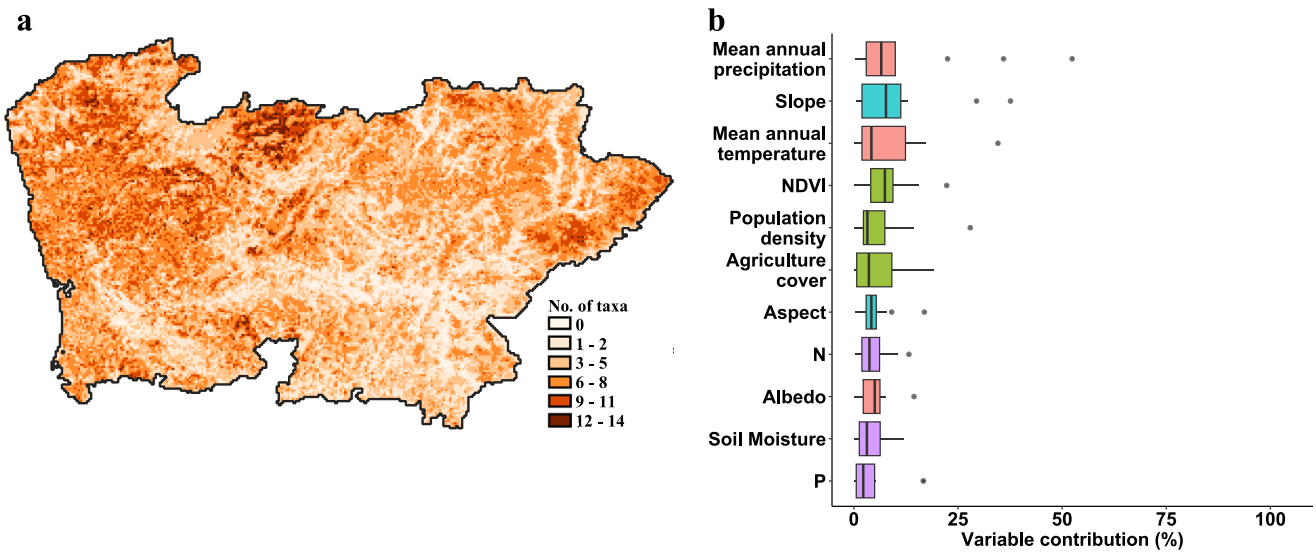

Fig. 4. Taxa richness of plant-parasitic nematodes (a) and contribution of the most important environmental variables (> 70 % contribution) to species distribution models of 14 taxa of plant-parasitic nematodes (b) using ensemble models.

our results suggest that higher values of precipitation, NDVI, and pH to some extent, maximize this probability, however, human population density and deciduous forest cover negatively affect it. *Xiphinema* spp. are more likely to be found in areas with higher values of NDVI and albedo, but also with increased areas of agriculture fields. SOC did not seem to be important for distribution of other plant-parasitic taxa, yet, for *Xiphinema* spp., it highly determines their occurrence. Clay and silt content did not affect most of the taxa, however, intermediate range values are more beneficial for *Ditylenchus*.

There was no apparent difference on the distribution pattern when segregated by feeding behaviour, excepting for semi-endoparasites (Supplementary Fig. S2). Predominantly, the West zone holds greater conditions for the various semi-endoparasite nematodes and, to some extent, the same applies for ectoparasites, although these nematodes likely occur in most of the region, especially in the northern-central area of the region, where environmental conditions are suitable for each of the ectoparasite species to occur. On the other hand, endoparasites seem highly generalists as these are predicted to occur almost throughout the entire region with no specific pattern. Furthermore, it is possible to highlight particular distribution patterns for each taxon (Fig. 6). Occurrence of most plant-parasitic nematode species was higher in the West region of the area of study, such as *Helicotylenchus* and Trichodoridae, whilst others such as *Xiphinema* and *Tylenchorhynchus* showed a wide distribution.

These models also estimate that forest ecosystems have poorer conditions for plant-parasitic nematodes, resulting in fewer taxa (Supplementary Table S5). The R^2 values between predicted richness and observed richness, for sampled locations, revealed that the species distribution models more efficiently predict the plant-parasitic nematode taxa in perennial agriculture and urban areas.

Ultimately, the mean values of performance of the models attested by Area under the ROC curve (AUC) and True skill statistic (TSS) for the 14 Plant-Parasitic nematode models based on different type of environmental variables were 0.896 and 0.766, respectively (Supplementary Table S6).

4. Discussion

4.1. Taxonomic and functional diversity

The taxonomic and functional analysis of the plant-parasitic nematode community revealed a variation in the impact of land-use type (Fig. 3 and Supplementary Table S2). Results show distinct community patterns as influenced by mechanisms inherent to the land-use type. At a taxonomic level, plant-parasitic nematode communities in pasture soils were more diverse, with higher taxa richness but also with higher biomass and herbivory footprint, reflecting a larger herbivory pressure in these systems. These results are in accordance with the more abundant and diverse plant-parasitic nematode communities in grasslands compared to those in both conventional and organic vegetable fields in Switzerland (Yang et al., 2021). In semi- and natural pastures in Spain, most common grasses and legumes were good hosts for the most prevalent plant-parasitic nematode species, which may explain their wide distribution (Talavera and Navas, 2002). On a functional level, higher functional richness in managed grasslands in comparison to shrubland/woodland has been reported (Sechi et al., 2018), although our results point to a higher regularity on species biomass distribution in forest ecosystems, especially native forests. This suggests the biomass of plant-parasitic nematodes tends to be uniform among forest communities, and may indicate comparable host resource availability (Fig. 3). Previous studies suggest that soil C:N ratio is correlated with functional diversity, with nematodes in soils with lower C:N ratio being more heterogeneous in body size, contrary to forest soils which generally have lower nutrient levels, as soil nematodes adapt better in nutrient-poor agroecosystems when fertilization levels are reduced (Mulder and Maas, 2017). This may explain plant-parasitic nematode communities in pastures or annual agriculture having lower functional evenness (Supplementary Table S2). Also, Pothula et al. (2019) reported higher abundance of cp4 and cp5 nematodes in forest soils than disturbed ecosystems. Considering that a larger proportion of cp4 and cp5 nematodes were found in forest soils than in other land-use types (Supplementary Fig. S3), it contributed to more uniform communities body mass-wise (Mulder and Maas, 2017). This has often been described as a result of a pattern of species invasions, loss of native species or change in species richness through time, so changes in functional diversity might not be a consequence of changes in taxonomic diversity (Olden and Rooney, 2006). Although most forests in the North of Portugal are managed to some extent and being subject to distinct pressures, they provide long-term stable conditions than agriculture where soil management is more frequent regularly tilled, fertilized and exposed to a wide array of chemical inputs.

Land-use type significantly affected the variation of the plant-parasitic nematode community composition (Fig. 3d), where higher beta diversity reflects greater heterogeneity in plant-parasitic nematode communities, indicating that there are larger differences in community

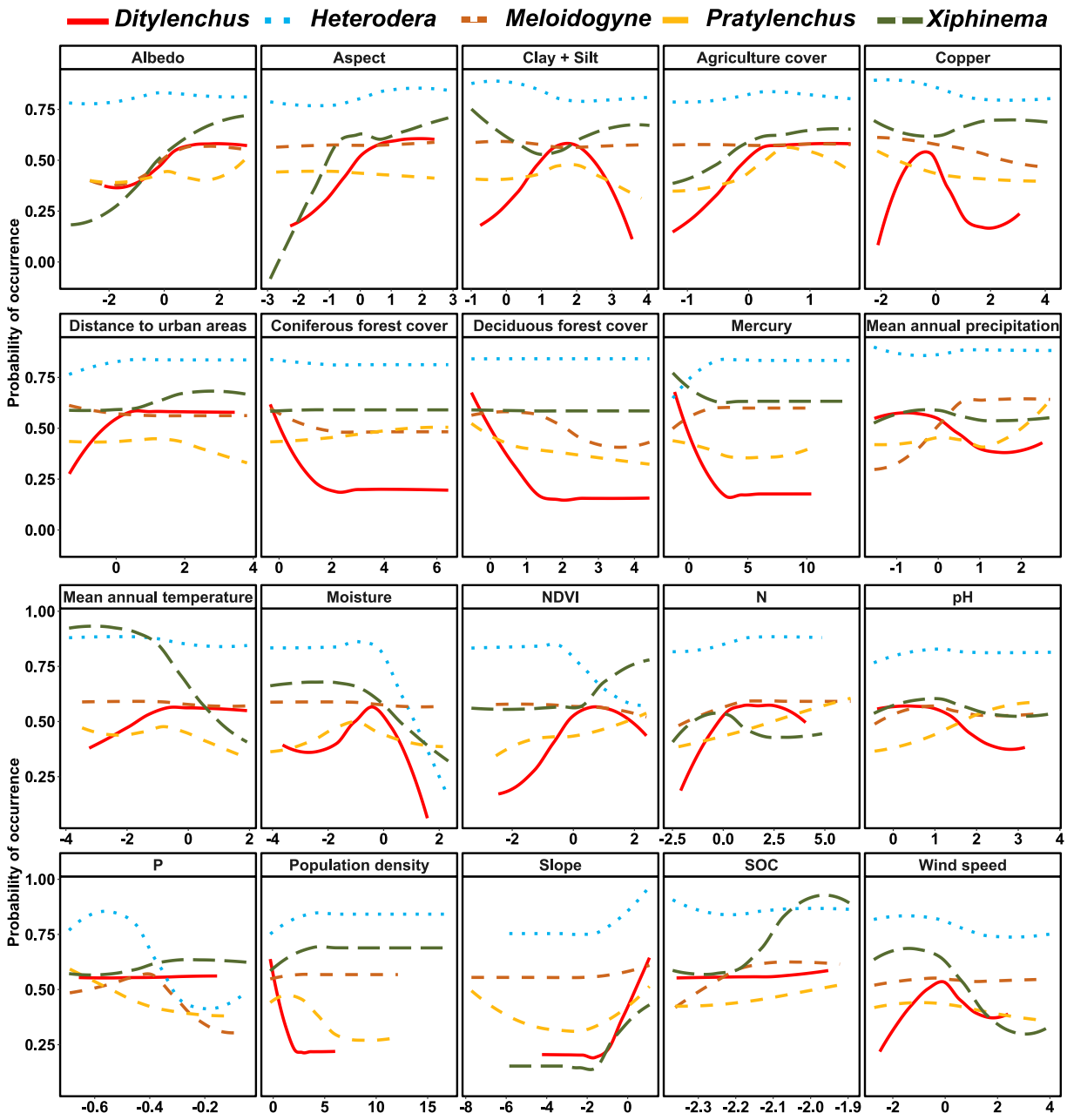

Fig. 5. Response curves of the probability of occurrence of *Ditylenchus*, *Heterodera*, *Meloidogyne*, *Pratylenchus* and *Xiphinema* for environmental variables used in species distribution models.

composition between different sites of each land-use type. Thus, the overall diversity of plant-parasitic nematode communities across the forest ecosystems was greater, with more spatial variation than agricultural fields and urban areas, when, in fact, agriculture and urbanization are considered major causes of biotic homogenization (Foster et al., 2009; Gossner et al., 2016). Still, a large fraction of the spatial variation in plant-parasitic nematode community composition in the North of Portugal remains unexplained as the set of variables used in the analysis explain ca 14 % of the total variation, with land cover accounting for most of the variation. Similar results are reported in the literature and attributed to a combination of stochastic and functional equivalence (Quist et al., 2019). Plant-parasitic nematodes may perform similar functions in communities which might lead to species competition for the same ecological niche share (Ettema, 1998). Archidona-Yuste et al. (2020) found similar figs. (89.7 %) of unexplained variation in plant-parasitic nematode communities of commercial olive orchards in Spain. These numbers might also be a result of omission of important variables and ecological gradients or attributed to spatial configuration and the strength of the environmental control (Smith and Lundholm, 2010). Also, in our case, the environmental variables were extracted from available international databases, which may not reflect the exact conditions in situ, as these have been produced from model predictions and thus, contain their own uncertainties.

The concept of functional redundancy in soil communities has been widely discussed in scientific literature (Andrén and Balandreau, 1999; Bardgett and van der Putten, 2014; Heemsbergen et al., 2004) albeit a greater plant-parasitic nematode diversity may promote competition and, therefore, contributes to disease suppression by horizontal control (Brinkman et al., 2004, 2005; Piśkiewicz et al., 2007). Despite plant-parasitic nematodes being considered an economic threat to the growth and vigour of most crops, knowledge of the implications of these soilborne organisms on natural systems and different land-use type,

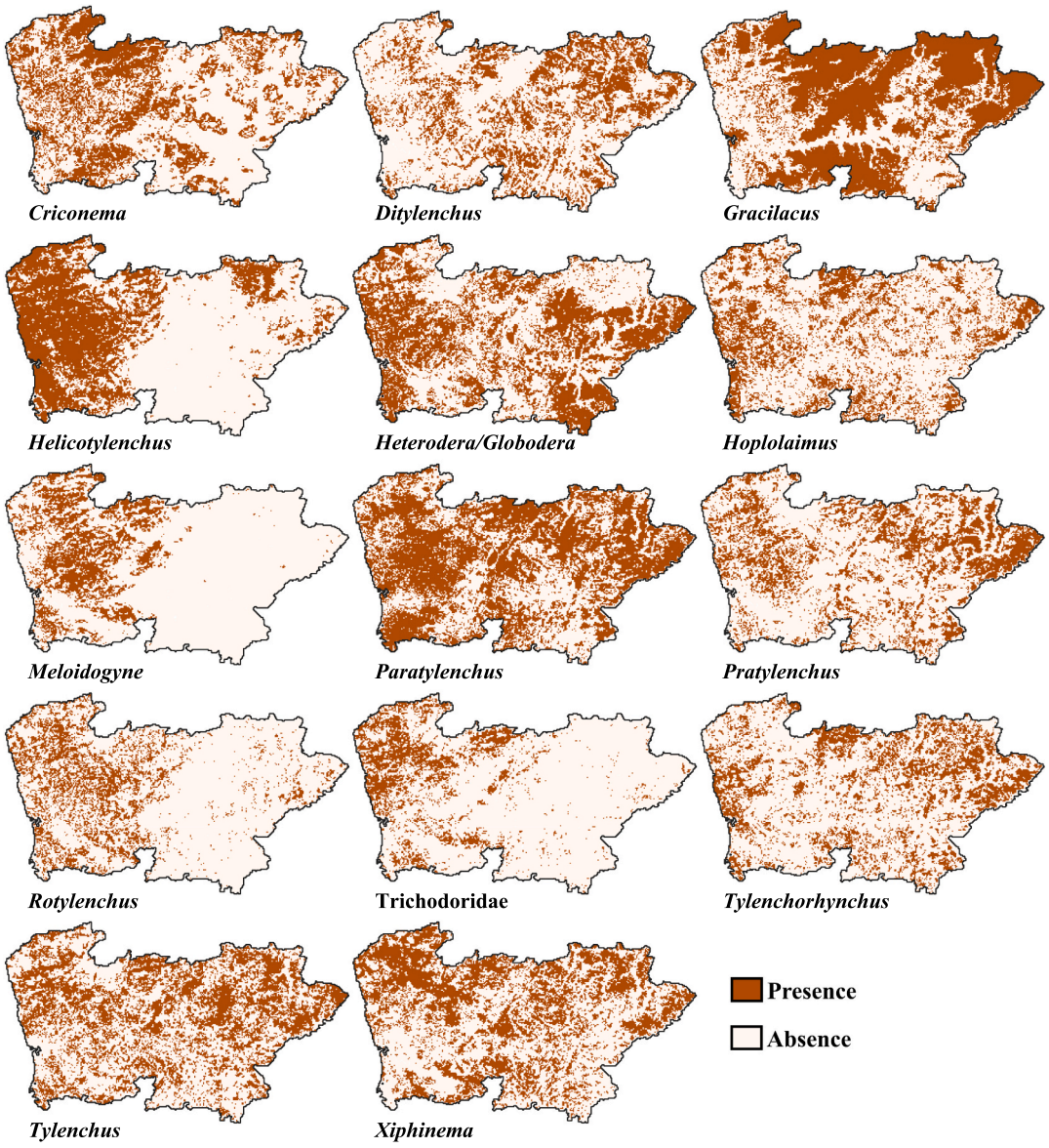

Fig. 6. Distribution map of plant-parasitic nematode taxa based on the species distribution modelling across the North of Portugal.

other than agriculture fields, are still scarce. However, beneficial functions of plant parasitic nematodes on ecosystem functioning have already been reported in the literature. For example, their natural role as regulation agents in plant succession (van der Putten et al., 1993; Bardgett et al., 1999), and, ultimately, the presence of herbivore nematodes in plant roots change the exudate composition leading to a flow of carbon and nutrients that increase microbial activity (Yeates et al., 1998; Tu et al., 2003).

Our results support previous findings and highlight the effect of land-use type on soil biodiversity providing understanding on the influence of land-use type shaping soil communities, threatening the provision of ecosystem functions.

4.2. Abundance of plant-parasitic nematodes

In a total of 19 different taxa found, species of *Pratylenchus* and *Paratylenchus* were the most abundant taxa comprising >50 % of all plant-parasitic nematodes. Both genera were previously reported in Portugal, where the root-lesion nematode *Pratylenchus* is considered a major problem in potato crops (Esteves et al., 2015). Considered one of the genera with most economic importance in agricultural systems worldwide (Jones et al., 2013) and being the most abundant plant-parasitic nematodes in our soil samples of annual agriculture, this is, therefore, a cause for concern among farmers. Still, other plant-parasitic nematode genera of economic importance were also present in our samples, such as the case of *Ditylenchus*, *Xiphinema* and the two most economically relevant groups of plant-parasitic nematodes worldwide: cyst nematodes *Heterodera/Globodera* and root-knot nematodes *Meloidogyne* spp. Although most of the species within the genus *Ditylenchus* are not plant parasites, some species cause significant damage to various crops globally (e.g., on rice in South-East Asia and potato tubers in Europe or groundnuts in South Africa (Jones et al., 2013)). The ecto-parasite *Xiphinema* was not found in high densities, neither it is suggested to be intimately to land-use type from our results, however, several species of *Xiphinema* are economically important in grapevine and fig, however, mostly due to their role as a vector of *Grapevine fanleaf virus* (GFLV) (Hewitt et al., 1958). Being a severe virus disease of grapevines across the globe (Andret-Link et al., 2004), the high density of vineyards in the Douro region, combined with the historical significance of grapevine cultivation in Portugal, highlights a potential threat to the viticulture industry. Despite this, root-knot nematodes and cyst nematodes are the most studied genera among plant-parasitic

nematodes due to their damage on crops worldwide and the difficulty in controlling their populations once they infest agricultural soils. Although some species are commonly widespread, land-use type influences their abundance (Supplementary Table S3). In this work, *Meloidogyne* and *Heterodera/Globodera* were more abundant in soil samples of pasture ecosystems, albeit this may happen due to commonly used yearly rotation of pasture with annual agricultural crops in which several sites had already been harvested when they were sampled. Further, more plant biomass resources may be available in pastures enhancing plant-parasitic nematode diversity due to more diverse plant communities with complementary host suitability (de Deyn et al., 2004). Both genera have been found widely distributed across the globe and considering their economic importance, this information might be useful for land management practices, considering, in our work, density and herbivory pressure of economically important plant-parasitic nematodes were suppressed in forest ecosystems (Supplementary Table S3).

The plant-parasitic nematode taxa found in our samples were present throughout almost all land-use types, making it challenging to establish a connection between their presence and the type of ecosystem. Furthermore, the soil sampling conducted exclusively in the autumn season, without seasonal replication, introduces a limitation to comprehensively understanding the dynamic shifts in plant-parasitic nematode populations over time. A study into the seasonal dynamics of plant-parasitic nematode taxa revealed fluctuations in both abundance and population structure in grasslands, mostly associated with seasonal shifts in soil temperature and moisture content (Verschoor et al., 2001). However, although analysis of the plant-parasitic nematode community as a whole provided a more direct measure of soil functions, these results reveal the relationship between land-use type and the occurrence and distribution of several plant-parasitic species.

4.3. *Effects of environmental conditions on nematode community structure and distribution*

Our approach of stacked species model distribution revealed precipitation, slope, temperature, NDVI and population density as the most important statistical predictors (Fig. 3b; Supplementary Table S4), comprising almost half of the average contribution among all variables. Precipitation was the most important variable on the average contribution across all 14 plant-parasitic genera. In a changing world where current climate projections are pointing to rapid climate change (Parmesan and Yohe, 2003; Kharin et al., 2007; Bronselaer et al., 2018) and a rise in land-use intensity (Popp et al., 2017; Titeux et al., 2016), global changes may have important implications on terrestrial biodiversity and ecosystem functions. Given that precipitation and temperature are important environmental drivers of plant-parasitic nematode distribution, it is possible that the current distribution of these soil-borne organisms could adjust in response to future climate change projections, although the impact of climate change was not tested. Furthermore, the shift in environmental conditions may possibly create more suited conditions for some species over others in certain areas, regulated by different set of conditions, which might be a concern for agriculture farmers in case of economically important species such as the root-knot nematode *Meloidogyne* or cyst nematodes *Heterodera/Globodera*. In fact, many studies already described the relationship between temperature and the life cycle of several plant-parasitic species, which might favour the spread range and density (Seshadri, 1964; Maleita et al., 2012). Just as temperature increases and precipitation patterns change, with reduced precipitation in summer and increased in spring and autumn (Schädler et al., 2019), shifts in plant communities are highly expected, thus affecting communities of soil biota and plant-soil feedback, anticipating consequences for ecosystem functioning (van der Putten et al., 2013). Previous studies have shown influence of altered precipitation and warming on soil biodiversity parameters and functions (Blankinship et al., 2011; van den Hoogen et al., 2019).

Plant-parasitic nematodes need plants to survive and complete their life cycle, hence it is expected that NDVI is an important driver of their occurrence, as this metric is an indicator of the density of vegetation. In fact, positive relationships have been found between NDVI and abundance of plant-parasitic nematodes across different land uses at global scale (Li et al., 2022). Additionally, plants are considered the major drivers of plant-parasitic nematodes at species level, as, for example, functional groups of plants have different rooting patterns that might be more beneficial for certain species of plant-parasitic nematode. Hence, we are aware the lack of data on plants in the sampled location is a major limitation that could further influence our results and comprehension.

Human population density is also a driver of plant-parasitic nematode occurrence across the region (Fig. 4b). As suggested in Li et al., 2022, human modified habitats may increase the abundance of plant-parasitic nematodes, which could possibly explain the reason that most plant-parasitic taxa are likely to occur in the Western part of the area of study (Fig. 4a). Here, the region is characterized by large urban areas with higher population density. Together with a more intensive agricultural management, the land-use intensity is higher and native forest ecosystems are scarce and fragmented, likely enhancing suitable conditions for plant-parasitic nematodes. Among the 14 plant-parasitic genera, it is possible to observe different distribution patterns (Fig. 6), mostly shaped by individual environmental requirements. Considering the predicted distribution of endoparasites (Supplementary Fig. S2), the most important plant-parasitic taxa due to their impact on crops worldwide, these seem highly adaptable species as our models expect a widespread occurrence almost throughout the entire region. Interestingly, the area of high suitability for plant-parasitic nematode taxa in the northern area of the region (Fig. 4) coincides with Barroso Agro-Sylvo-Pastoral System, a Globally Important Agricultural Heritage System as classified by the Food and Agriculture Organization of the United Nations (FAO, 2018). Community-based systems activities of agro-sylvo-pastoral activities persist in this area, creating an interconnection of agriculture, forestry and livestock pastoral production. The above-ground biodiversity and sustainability partly linked to landscape complexity of this system seems to be mirrored in belowground processes (Costa et al., 2021). Further studies should elucidate how the Barroso Agro-Sylvo-Pastoral systems create favourable conditions for establishment of several plant-parasitic nematodes. According to previous studies, edaphic conditions such as soil organic carbon and nutrient availability also play a crucial role in the establishment and distribution of nematodes, as has been assessed previously at global scale (Bardgett and van der Putten, 2014; van den Hoogen et al., 2019). However, it was not clear in our results, which could be attributed to various reasons. For example, soil organic carbon values retrieved from Global Soil Organic Carbon Map (FAO, 2022) correspond to a target depth of 30 cm and, whilst in our samples, we specifically gathered the topsoil of 10 cm. Furthermore, the higher variability in other environmental conditions across the area of study may have diminished the importance of soil organic carbon and other nutrients. Additionally, although some of the environmental variables have a broad time scale (e.g. precipitation and NDVI; Supplementary Table S1), our models take into consideration the presence records of the plant-parasitic taxa found during the autumn soil sampling. If seasonal changes in plant-parasitic nematode community patterns are expected, as aforementioned, the reliance on a single-time data might limit the comprehensive understanding of their distribution dynamics.

Despite these models not including inter-specific interactions such as predation, as they are modelled by the set environmental variables, predictive modelling is a useful tool to monitor progress towards meeting global biodiversity goals, and to support and decision-making for soil ecosystems.

5. Conclusions

The present work sets out to study the structural and functional changes of plant-parasitic nematode communities, spatially across the

region North of Portugal, in response to multiple land-use types. Simultaneously, this study allowed us to track and map the distribution of plant-parasitic nematodes and determine environmental conditions that contribute to their distribution. An insightful approach to understand the future projection of these organisms would be the use of a modelling framework using current and forecast climate data that would help perceive future implications for belowground biodiversity in such scale assessments. Considering the climate change forecasts and land-use intensification, large-scale studies monitoring soil biodiversity and functions would be of unparalleled importance to minimize ecological consequences.

CRediT authorship contribution statement

Rui P. Carvalho: Writing – original draft, Investigation, Conceptualization. **Carlos Guerra:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Concha Cano-Díaz:** Writing – review & editing. **Susana Mendes:** Writing – review & editing. **Sofia R. Costa:** Writing – review & editing, Supervision, Methodology, Conceptualization.

Declaration of competing interest

The authors declare that they have no 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.2024.105852.

Data availability

The authors are unable or have chosen not to specify which data has been used.

References

Anderson, M., Ellingsen, K., McArdle, B., 2006. Multivariate dispersion as a measure of beta diversity. Ecol. Lett. 9, 683–693. https://doi.org/10.1111/j.1461-0248.2006.00926.x.

Andrén, O., Balandreau, J., 1999. Biodiversity and soil functioning - from black box to can of worms? Appl. Soil Ecol. 13, 105–108. https://doi.org/10.1016/S0929-1393(99)00025-6.

Andret-Link, P., Hoffmann, C., Valat, L., Ritzenthaler, C., Demangeat, G., Vigne, E., Laval, V., Pfeiffer, P., Stussi-Garaud, C., Fuchs, M., 2004. Grapevine fanleaf virus: still a major threat to the grapevine industry. J. Plant Pathol. 86, 183–195.

Archidona-Yuste, A., Wiegand, T., Castillo, P., Navas-Cortés, Juan A., 2020. Spatial structure and soil properties shape local community structure of plant-parasitic nematodes in cultivated olive trees in southern Spain. Agric. Ecosyst. Environ. 287, 106688. https://doi.org/10.1016/j.agee.2019.106688.

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.

Back, M., Haydock, P., Jenkinson, P., 2002. Disease complexes involving plant parasitic nematodes and soilborne pathogens. Plant Pathol. 51, 683–697. https://doi.org/10.1046/j.1365-3059.2002.00785.x.

Barbet-Massin, M., Jiguet, F., Albert, C., 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., Cook, R., Yeates, G., Denton, C., 1999. The influence of nematodes on below-ground processes in grassland ecosystems. Plant and Soil 212, 23–33. https://doi.org/10.1023/A:1004642218792.

Blankinship, J., Niklaus, P., Hungate, B., 2011. A meta-analysis of responses of soil biota to global change. Oecologia 165, 553–565. https://doi.org/10.1007/s00442-011-1909-0.

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.

Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the spatial component of ecological variation. Ecology 73, 1045–1055. https://doi.org/10.2307/1940179.

Bragança, I., Lemos, P.C., Delerue-Matos, C., Domingues, V., 2019. Assessment of pyrethroid pesticides in topsoils in northern Portugal. Water Air Soil Pollut. 230, 166. https://doi.org/10.1007/s11270-019-4209-7.

Brinkman, E.P., Veen, J., Putten, W., 2004. Endoparasitic nematodes reduce multiplication of ectoparasitic nematodes, but do not prevent growth reduction of *Ammophila arenaria* (L.) Link (marram grass). Appl. Soil Ecol. 27, 65–75. https://doi.org/10.1016/j.apsoil.2004.02.004.

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.

Bronselaer, B., Winton, M., Griffies, S., Hurlin, W., Rodgers, K., Sergienko, O., Ronald, S., Russell, J., 2018. Change in future climate due to Antarctic meltwater. Nature 564, 53–57. https://doi.org/10.1038/s41586-018-0712-z.

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.

Carmo, M., Moreira, F., Casimiro, P., Vaz, P., 2011. Land-use and topography influences on wildfire occurrence in northern Portugal. Landsc. Urban Plan. 100, 169–176. https://doi.org/10.1016/j.landurbplan.2010.11.017.

Castillo, P., Mora-Rodríguez, M., Navas Cortés, J., Jiménez-Díaz, R., 1998. Interactions of *Pratylenchus thornei* and *fusarium oxysporum* f. sp. ciceris on chickpea. Phytopathology 88, 828–836. https://doi.org/10.1094/PHYTO.1998.88.8.828.

Ciobanu, M., Popovici, I., Zhao, J., Stoica, A., 2015. Patterns of relative magnitudes of soil energy channels and their relationships with environmental factors in different ecosystems in Romania. Sci. Rep. 5, 17606. https://doi.org/10.1038/srep17606.

Costa, S., Kerry, B., Bardgett, R., Davies, K., 2012. Interactions between nematodes and their microbial enemies in coastal sand dunes. Oecologia 170, 1053–1066. https://doi.org/10.1007/s00442-012-2359-z.

Costa, S.R., Sousa, J.N., Pascoal, C., 2021. Soil functioning relates to land use in a sustainably managed agro-sylvo-pastoral ecosystem. In: Keep soil alive, protect soil biodiversity. Global symposium on soil biodiversity, 19–22 April 2021 – Outcome document. Rome, Italy.

De la Fuente, B., Beck, P., 2018. Invasive species may disrupt protected area networks: insights from the pine wood nematode spread in Portugal. Forests 9, 282. https://doi.org/10.3390/f9050282.

de Deyn, G.B., Raaijmakers, C., Ruijven, J., Berendse, F., Putten, W., 2004. Plant species identity and diversity on different trophic levels of nematodes in the soil food web. Oikos 106, 576–584. https://doi.org/10.1111/j.0030-1299.2004.13265.x.

Dietrich, P., Roeder, A., Cesarz, S., Eisenhauer, N., Ebeling, A., Schmid, B., Schulze, E.-D., Wagg, C., Weigelt, A., Roscher, C., 2020. Nematode communities, plant nutrient economy and life-cycle characteristics jointly determine plant monoculture performance over 12 years. Oikos 129, 466–479. https://doi.org/10.1111/oik.06989.

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.

Esteves, I., Maleita, C., Abrantes, Isabel., 2015. Root-lesion and root-knot nematodes parasitizing potato. Eur. J. Plant Pathol. 141, 397–406. doi:141. https://doi.org/10.1007/s10658-014-0551-1.

Ettema, C., 1998. Soil nematode diversity: species coexistence and ecosystem function. J. Nematol. 30, 159–169.

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.
Ferris, H., 2011. Key to Families (and Subfamilies) of Plant and Soil Nematodes. http://nemaplex.ucdavis.edu/Taxadata/Famkey.htm. (Accessed 6 January 2022).
Ferris, H., Griffiths, B., Porazinska, D., Powers, T., Wang, K.-H., Tenuta, M., 2012. Reflections on plant and soil nematode ecology: past, present and future. J. Nematol. 44, 115–126.
Food and Agriculture Organization of the United Nations (FAO), 2018. Globally important agriculture heritage systems: combining agricultural biodiversity, resilient ecosystems, traditional farming practices and cultural identity. Food and Agriculture Organization of the United Nations 16–17. https://www.fao.org/3/i9187en/I9187EN.pdf.
Food and Agriculture Organization of the United Nations (FAO), 2020. Standard operating procedure for soil organic carbon. In: Walkley-Black method: titration and colorimetric method. Rome.
Food and Agriculture Organization of the United Nations (FAO), 2022. Global Soil Organic Carbon Map – GSOCmap v.1.6: Technical report. Rome. https://doi.org/10.4060/cb9015en.
Foster, D., Swanson, F., Aber, J., Burke, I., Brokaw, N., Tilman, D., Knapp, A., 2009. The importance of land-use legacies to ecology and conservation. BioScience 53, 77–88. https://doi.org/10.1641/0006-3568(2003)053[0077:TIOLUL]2.0.CO;2.
Goodey, T., 1963. Soil and Freshwater Nematodes: A Monograph. Rewritten by J.B. Goodey. Methuen, Co. Ltd., p. 544
Gossner, M., Lewinsohn, T., Kahl, T., Grassein, F., Boch, S., Prati, D., Birkhofer, K., Renner, S., Sikorski, J., Wubet, T., Arndt, H., Baumgartner, V., Blaser, S., Blüthgen, N., Börschig, C., Buscot, F., Diekötter, T., Jorge, L., Jung, K., Allan, E., 2016. Land-use intensification causes multitrophic homogenization of grassland communities. Nature 540, 266–269. https://doi.org/10.1038/nature20575.
Grenié, M., Gruson, H., 2022. Fundiversity: easy computation of alpha functional diversity indices. R package version 1.0.0. https://CRAN.R-project.org/package=fundiversity.
Guerra, A.C., Wall, D.H., Eisenhauer, N., 2021. Unearthing soil ecological observations: see supporting information as supplementary material. Soil Org. 93, 79–81. https://doi.org/10.25674/so93iss2id164.
Heemsbergen, D., Berg, M., Loreau, M., van Hal, J., Faber, J.H., Verhoef, H., 2004. Biodiversity effects on soil processes explained by interspecific functional dissimilarity. Science 306, 1018–1020. https://doi.org/10.1126/science.1101865.
Hewitt, W.B., Raski, D.J., Goheen, A.C., 1958. Nematode vector of soil-borne fanleaf virus of grapevines. Phytopathology 48, 586–595.
Hijmans, R., 2022. Raster: geographic data analysis and modeling. R package version 3.6–3. https://CRAN.R-project.org/package=raster.
van den Hoogen, J., Geisen, S., Routh, D., Ferris, H., Traunspurger, W., Wardle, D.A., Goede, R., Adams, B., Ahmad, W., Andriuzzi, W., Bardgett, R., Bonkowski, M., Campos-Herrera, R., Cares, J., Caruso, T., Caixeta, L., Chen, X., Costa, S., Creamer, R., 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.
Hu, N., Li, H., Tang, Z., Li, Z., Tian, J., Lou, Y., Li, J., Li, G., Hu, X., 2016. Community diversity, structure and carbon footprint of nematode food web following reforestation on degraded Karst soil. Sci. Rep. 6, 28138. https://doi.org/10.1038/srep28138.
Jones, J., Haegeman, A., Danchin, E., Gaur, S., Helder, J., Jones, M., Kikuchi, T., Manzanilla Lopez, R.H., Palomares-Rius, J., Wesemael, W., Perry, R., 2013. Top 10 plant-parasitic nematodes in molecular plant pathology. Mol. Plant Pathol. 46, 946–961. https://doi.org/10.1111/mpp.12057.
Kharin, V., Zwiers, F., Zhang, X., Hegerl, G., 2007. Changes in temperature and precipitation extremes in the IPCC ensemble of global coupled model simulations. J. Climate 20, 1419–1444. https://doi.org/10.1175/JCLI4066.1.
Legendre, P., De Cáceres, M., 2013. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. Ecol. Lett. 16, 951–963. https://doi.org/10.1111/ele.12141.
Legendre, P., Legendre, L., 2012. Chapter 10 - interpretation of ecological structures. In: Pierre, L., Louis, L. (Eds.), Developments in Environmental Modelling, vol. 24. Elsevier, pp. 521–624. https://doi.org/10.1016/B978-0-444-53868-0.50010-1.
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. 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 University Press. https://doi.org/10.7591/9781501728419.
Maleita, C., Curtis, Rosane, Abrantes, Isabel, 2012. Thermal requirements for the embryonic development and life cycle of *Meloidogyne hispanica*. Plant Pathol. 61, 1002–1010. https://doi.org/10.1111/j.1365-3059.2011.02576.x.
Mason, N.W.H., Mouillot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111, 112–118. https://doi.org/10.1111/j.0030-1299.2005.13886. X.
Mesa-Valle, C., Garrido-Cárdenas, J., Cebrian-Carmona, J., Talavera, M., Manzano-Agugliaro, F., 2020. Global Research on Plant Nematodes. Agronomy 10, 1148. https://doi.org/10.3390/agronomy10081148.
Mulder, C., Maas, R., 2017. Unifying the functional diversity in natural and cultivated soils using the overall body-mass distribution of nematodes. BMC Ecol. 17, 36. https://doi.org/10.1186/s12898-017-0145-9.
Neher, D., 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, third ed. SSSA Book Series, Madison, pp. 961–1010. https://doi.org/10.2136/sssabookser5.3.c34.
Oksanen, J., Blanchet, F.G., Friendly, M., Kind, R., Legendre, P., McGlinn, D.M., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2019. vegan: Community ecology package. https://CRAN.R-project.org/package=vegan.
Olden, J.D., Rooney, T.P., 2006. On defining and quantifying biotic homogenization. Glob. Ecol. Biogeogr. 15, 113–120. https://doi.org/10.1111/j.1466-822X.2006.00214.x.
Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42. https://doi.org/10.1038/nature01286.
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.
Popp, A., Calvin, K., Fujimori, S., Havlík, Petr, Humpenöder, F., Stehfest, E., Bodirsky, B., Dietrich, J., Doelmann, J., Gusti, M., Hasegawa, T., Kyle, P., Obersteiner, M., Tabeau, A., Takahashi, K., Valin, H., Waldhoff, S., Weindl, I., Wise, M., Vuuren, D., 2017. Land-use futures in the shared socio-economic pathways. Glob. Environ. Chang. 42, 331–345. https://doi.org/10.1016/j.gloenvcha.2016.10.002.
Pothula, S., Grewal, P., Auge, R., Saxton, A., Bernard, E., 2019. Agricultural intensification and urbanization negatively impact soil nematode richness and abundance: a meta-analysis. J. Nematol. 51, 1–17. https://doi.org/10.21307/jofnem-2019-011.
van der Putten, W.H., van Dijk, C., Peters, B.A.M., 1993. Plant-specific soil-borne diseases contribute to succession in foredune vegetation. Nature 362, 53–56. https://doi.org/10.1038/362053a0.
van der Putten, W., Bardgett, R., Bever, J., Bezemer, T., Casper, B., Fukami, T., Kardol, P., Klironomos, J., Kulmatiski, A., Schweitzer, J., Suding, K., Voorde, T., Wardle, D., 2013. Plant-soil feedbacks: the past, the present and future challenges. J. Ecol. 101, 265–276. https://doi.org/10.1111/1365-2745.12054.
Quentin, M., Abad, P., Favery, B., 2013. Plant parasitic nematode effectors target host defense and nuclear functions to establish feeding cells. Front. Plant Sci. 4, 53. https://doi.org/10.3389/fpls.2013.00053.
Quist, C., Gort, G., Mooijman, P., Brus, D., Elsen, S., Kostenko, O., Vervoort, M., Bakker, J., Putten, W., Helder, J., 2019. Spatial distribution of soil nematodes relates to soil organic matter and life strategy. Soil Biol. Biochem. 136, 107542. https://doi.org/10.1016/j.soilbio.2019.107542.
R Core Team, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. https://www.R-project.org/.
Ramos, T., Horta, A., Gonçalves, M., Pires, F., Duffy, D., Martins, J., 2017. The INFOSOLO database as a first step towards the development of a soil information system in Portugal. Catena 158, 390–412. https://doi.org/10.1016/j.catena.2017.07.020.
Schädler, M., Buscot, F., Klotz, S., Reitz, T., Durka, W., Bumberger, J., Merbach, I., Michalski, S., Kirsch, K., Remmler, P., Schulz, E., Auge, H., 2019. Investigating the consequences of climate change under different land-use regimes – a novel experimental infrastructure. Ecosphere 10, e02635. https://doi.org/10.1002/ecs2.2635.
Sechi, V., Goede, R., Rutgers, M., Brussaard, L., Mulder, C., 2018. Functional diversity in nematode communities across terrestrial ecosystems. Basic Appl. Ecol. 30, 76–86. https://doi.org/10.1016/j.baae.2018.05.004.
Seshadri, A., 1964. Investigations on the biology and life cycle of Criconemoides *Xenoplax Raski*, 1952 (Nematoda: Criconematidae). Nematologica 10, 540–562. https://doi.org/10.1163/187529264x00204.
Sieriebriennikov, B., Ferris, H., de Goede, R.G.M., 2014. NINJA: an automated calculation system for nematode-based biological monitoring. Eur. J. Soil Biol. 61, 90–93. https://doi.org/10.1016/j.ejsobi.2014.02.004.
Smith, T.W., Lundholm, J.T., 2010. Variation partitioning as a tool to distinguish between niche and neutral processes. Ecography 33, 648–655. https://doi.org/10.1111/j.1600-0587.2009.06105.x.
Talavera, M., Navas, A., 2002. Incidence of plant-parasitic nematodes in natural and semi-natural mountain grassland and the host status of some common grass species. Nematology 4, 541–552. https://doi.org/10.1163/156854102760290518.
Thuiller, W., Lafourcade, B., Engler, R., Araújo, M.B., 2009. BIOMOD – a platform for ensemble forecasting of species distributions. Ecography 32, 369–373. https://doi.org/10.1111/j.1600-0587.2008.05742.x.
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.
Titeux, N., Henle, K., Mihoub, J.B., Regos, A., Geijzendorffer, I.R., Cramer, W., Verburg, P., Brotons, L., 2016. Biodiversity scenarios neglect future land-use changes. Glob. Chang. Biol. 22, 2505–2515. https://doi.org/10.1111/gcb.13272.
Tu, C., Koenning, S., Hu, S., 2003. Root-parasitic nematodes enhance soil microbial activities and nitrogen mineralization. Microb. Ecol. 46, 134–144. https://doi.org/10.1007/s00248-002-1068-2.
Verschoor, B., de Goede, R.G.M., de Hoop, J.-W., de Vries, F., 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.
Vicente, J., Fernandes, R., Randin, C., Broennimann, O., Gonçalves, J., Marcos, B., Pôças, I., Alves, P., Guisan, A., Honrado, J., 2013. Will climate change drive alien invasive plants into areas of high protection value? An improved model-based regional assessment to prioritise the management of invasions. J. Environ. Manage. 131, 185–195. https://doi.org/10.1016/j.jenvman.2013.09.032.

Villéger, S., Mason, N., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaced framework in functional ecology. Ecology 89, 2290–2301. https://doi.org/10.1890/07-1206.1.

Vos, P., Meelis, E., Ter Keurs, W.J., 2000. A framework for the design of ecological monitoring programs as a tool for environmental and nature management. Environ. Monit. Assess. 61, 317–344. https://doi.org/10.1023/A:1006139412372.

Wheeler, D., Scott, J., Dung, J., Johnson, D., 2019. Evidence of a trans-kingdom plant disease complex between a fungus and plant-parasitic nematodes. PloS One 14, e0211508. https://doi.org/10.1371/journal.pone.0211508.

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.

Yeates, G.W., Bongers, T., De Goede, R.G.M., Freckman, S.S., Georgieva, 1993. Feeding habits in soil nematode families and genera – an outline for soil ecologists. J. Nematol. 25, 315–331.

Yeates, G.W., Saggar, S., Denton, C., Mercer, C., 1998. Impact of clover cyst nematode (*Heterodera Trifolii*) infection on soil microbial activity in the rhizosphere of white clover (*Trifolium Repens*) - a pulse-labelling experiment. Nematologica 44, 81–90. https://doi.org/10.1163/005225998X00082.