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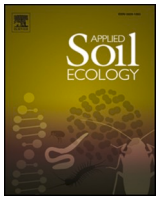

Drivers of the geographical distribution of nematode-based indices across Europe☆

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ABSTRACT

Nematode-based indices (NBIs) are widely used as indicators of soil health, reflecting key aspects of soil functioning. However, their spatial variability at the European scale remains poorly understood, limiting their integration into soil health policies. This study examines the geographical distribution of the Structure Index and Enrichment Index across seven European environmental zones, identifies the soil-forming factors shaping these patterns, and assesses whether these relationships vary across zones.

For this purpose, a pan-European nematode dataset was assembled spanning arable land, agricultural grasslands, natural grasslands, and forests. Structural equation modelling was applied to assess the role of the soil-forming factors: climate, topography, parent material and organisms, as well as indicators of disturbance: extreme weather events and land use intensity.

Our findings reveal clear variation in both indices across environmental zones. For the Structure Index, land use effects overrode natural environmental variability, while the Enrichment Index showed increased variability in arable systems. While all soil-forming factors showed relationships with the NBIs, model performance was low. This suggests that key factors were missing, however, disturbance factors did emerge as a key driver. Additionally, the relationship between NBI and environmental drivers varied substantially across zones, emphasizing the need for region-specific approaches.

These results highlight the importance of accounting for biogeographical context when interpreting NBIs as indicators for soil health. To enable their effective integration into soil health assessment and policy, future efforts should focus on harmonized sampling, improved data coverage, and the inclusion of ecologically relevant drivers, especially those capturing disturbance.

1. Introduction

Soil biota play a major role in the regulation of soil functions (i.e., nutrient cycling, carbon regulation, water regulation, disease suppression, and primary productivity) (Creamer et al., 2022). The intensification of agricultural land use has decreased belowground biodiversity and abundance, posing a threat to long-term soil functionality (Tsiafouli et al., 2015). Recognizing these risks, the European Commission is currently defining a Soil Monitoring Directive that aims to restore and maintain soil health across Europe by 2050 (European Commission, 2023). The Directive will outline proposed indicators for the assessment of soil health, with thresholds defined at Member State level to define soil health status. Standard soil health assessments predominantly focus on physical-chemical parameters, while soil biological parameters are often overlooked (Bünemann et al., 2018). This approach yields a limited view on soil health, as soil physical-chemical properties do not provide insight into belowground biological processes. The incorporation of soil biological indicators in large-scale monitoring assessments is challenging due to the lack of data to guide the selection of appropriate indicators and their interpretation. Therefore, it is imperative to obtain robust, spatially relevant data to support the interpretation of soil biological indicators, guide the selection of appropriate indicators, and inform the development of thresholds.

A major challenge in obtaining robust, spatially relevant data is the high spatial variability of soil biological indicators at continental and global scales (Eisenhauer et al., 2022). This spatial variability is, in part, defined by the response of biological communities to variations in environmental properties such as landform, climate and soil characteristics (Phillips et al., 2019; Potapov et al., 2023; Van den Hoogen et al., 2020). Understanding this response, known as the biogeography of soil organisms, is essential to effectively apply biological communities as indicators of soil health (Eisenhauer et al., 2021). While our knowledge of which environmental factors are important drivers of the spatial distribution of biological soil properties remains limited, we do have an extensive understanding of their relationship with soil physical-chemical properties. At the base of this understanding is Jenny's theory on soil formation, which states that soil characteristics at any given location result from an interplay of climate, topography, organisms, parent material, and time (Jenny, 1941). This paper asks the question if these soil-forming factors can also be utilized to improve our understanding of the biogeography of biological indicators of soil health.

1.1. Nematodes as soil health indicators

The selection of appropriate soil health indicators is constrained by the spatial distribution of soil organisms, as the suitability of organisms is limited to areas where they are naturally abundant (Pulleman et al., 2012). Nematodes, however, are ubiquitous, allowing them to be assessed across diverse environmental conditions (Yeates, 2004). They exhibit significant functional diversity, and shifts in their community composition have been linked to both land management practices and environmental changes, making them responsive indicators of soil health (Du Preez et al., 2022).

The functional diversity of nematodes can be categorized based on their feeding habits and ecological strategies. Nematodes occupy various trophic levels in the soil food web, playing vital roles in bacterial and fungal grazing, meso-fauna predation, and plant regulation through herbivory (Bilgrami and Gaugler, 2004). Therefore, their abundance and activity also reflects the presence of organisms to which they are trophically linked, providing further insight into soil food-web dynamics (Decraemer and Hunt, 2006; Yeates, 2010). Additionally, they adopt diverse ecological strategies, classified along the colonizer-persister (c-p) scale. Colonizers (r-strategists) grow rapidly, have short lifespans, and dominate in disturbed environments, whereas persisters (K-strategists) grow slowly, reproduce less, and thrive in stable soil ecosystems with complex soil food webs (Bongers, 1990).

Building on these ecological roles Bongers (1990) developed a set of nematode-based indices (NBIs) to assess soil food-web dynamics. By combining feeding strategies with c-p classification, nematodes are grouped into functional guilds, whose relative abundance is used to compute a range of NBIs. The most commonly used NBIs are the Structure Index (SI) and the Enrichment Index (EI) (Du Preez et al., 2022). The SI reflects the successional maturity of the soil community and the extent to which it is stressed by disturbance. As the soil food-web recovers from disturbance events, its complexity increases, which is reflected by higher SI values (Ferris et al., 2001). The EI is influenced by the abundance of enrichment-opportunist nematodes, which respond to elevated nutrient availability. Nutrient pulses can result from external inputs such as manure, but disturbances can also drive nutrient release through enhanced decomposition of organic matter (Ferris et al., 2001).

1.2. Functional biogeography of nematodes

Global and national studies on the biogeography of nematodes have shown that large-scale drivers such as climatic gradients or

environmental properties, can play an important role in understanding nematode distribution (Nielsen et al., 2014; Song et al., 2017; van den Hoogen et al., 2019). These studies have, however, primarily focused on total abundance and taxonomic diversity. These metrics do not always directly correlate with soil functions, as they overlook the significant functional diversity among nematode species. In contrast, NBIs account for this diversity and provide a more functionally relevant assessment of soil health (Du Preez et al., 2022; Kouser et al., 2021). Research on the spatial distribution of NBIs across multiple ecosystems or environmental zones underscores the need to calibrate these indices based on environmental conditions (Neher et al., 1998; Neher et al., 2005). Therefore, this study aims to improve our understanding of the spatial distribution of NBIs across Europe and their relationship with soil-forming factors.

To date, no studies have examined the biogeography of NBIs across Europe, however, potential drivers of NBI distribution at this scale can be inferred from the studies on nematode diversity and abundance. These studies have identified that soil organic carbon and vegetation are key driving factors influencing nematode abundance and diversity (Nielsen et al., 2014; Song et al., 2017; van den Hoogen et al., 2019). These properties are closely tied to nutrient availability, which creates favorable conditions for nematodes. Consequently, it can be hypothesized that these drivers positively influence both the SI and EI. Furthermore, as nematodes inhabit the water film surrounding soil particles, soil moisture likely serves as a critical direct driver of their functional diversity (Yeates, 2004). Other soil-forming factors, such as topography, climate and parent material may indirectly influence NBIs through their effects on soil moisture, organic carbon, and vegetation (Bennett et al., 2020; Celik et al., 2022; Kakhani et al., 2025; Yin et al., 2023). Chemical properties account for only a limited share of the spatial variation in NBIs, indicating that additional drivers likely contribute to the observed patterns (Neher and Campbell, 1994). Standard soil-forming factors do not account for disturbance, including natural events such as extreme weather and anthropogenic impacts like intensive land use. Ecological theory suggests that both the SI and EI respond to such factors. The SI tends to decline with increasing disturbance, whereas land-use intensity, often linked to nutrient enrichment through fertilization, may positively influence the EI (Cesarz et al., 2017; Puissant et al., 2021; Yan et al., 2018; Zhou et al., 2022). Therefore, incorporating disturbance indicators into the classical framework of soil-forming factors, may further improve our understanding of NBI distribution.

Regional studies on NBI spatial distribution have resulted in contrasting conclusions regarding the relationship between soil-forming factors and NBIs. For example, Tsiafouli et al. (2017) discovered that altitude has a stronger effect on NBIs than vegetation in a Greek region characterized by meadows and forested hills, whereas in Russia's Karelia region, which shares similar land cover, the primary driver for spatial variation in NBIs was vegetation (Matveeva and Sushchuk, 2016). This suggests that the relationship between NBIs and soil-forming factor may vary depending on regional environmental conditions.

1.3. Aims

This paper aims to provide an overview of the geographical distribution of nematode-based indices (NBIs) and their driving factors across Europe. To achieve this, we examine the differences in the Structure Index (SI) and Enrichment Index (EI) across seven European environmental zones (EEZs). Additionally, we assess the influence of soil-forming factors on this distribution, further expanding the standard framework by incorporating indicators of disturbance. Finally, we evaluate whether the drivers of NBI distribution differ among the seven environmental zones.

2. Materials and methods

For this study, we compiled a large dataset of community studies across Europe, further referred to as the NemEu database (Fig. 1). The data was provided by 28 nematologists and were originally collected over a time span of 45 years (1975–2020), covering a spatial extent of 21 countries across a range of land uses (Fig. 2a). This has resulted in a database of 1568 locations (2936 observations). The NemEu dataset is the largest nematode dataset available for European soils and was initially compiled as part of the dataset published by Van den Hoogen et al. (2020). However, unlike the Van den Hoogen et al. (2020) dataset which focuses on nematode feeding groups, this paper utilizes data to genus level to facilitate the calculation of the SI and EI. Further studies were gathered from other European nematode studies, in collaboration with the EUdaphobase project (Burkhardt et al., 2014). A dataset of this extent does present some limitations, such as the inconsistent sampling and extraction methodologies applied and the long time period over which data has been collected. However, this dataset also presents a unique opportunity to study spatial patterns of nematode functional diversity at a continental level.

2.1. Materials

2.1.1. Preparation of NemEU database

Data contributors were asked to provide metadata including date, season and year of sampling, land use type, site description, sampling depth, geographic coordinates, and any associated publications.

The first step in the cleaning of the metadata was the harmonization of the coordinates from the different studies included. All coordinates were converted to the coordinate reference system WGS 84, with the units in decimal degrees.

Reported land use types varied widely, therefore, we reclassified land use into five categories: forest and shrubland, natural grassland, agricultural grassland, arable, or other. Observations classified as "other" were excluded from the final dataset (Table 1). When multiple observations per site had different reported land use types, we selected only the observations corresponding most closely to the CORINE Land Cover classification (CORINE Land Cover) of the year nearest to the sampling year.

Sampling efforts covered all four seasons (Table 1). Sampling season was inferred from the sampling date when not explicitly reported. Seasons were defined as winter (December–February), spring (March–May), summer (June–August), and autumn (September–November). If samples were collected across multiple seasons at the same location, we retained only one season's observations, prioritizing spring, followed by autumn, summer and winter, based on the most common sampling times for nematode studies.

Sampling depth varied across the different studies (Table 1). To ensure that as many sites as possible could be included, we defined an overall sampling depth of 0–30 cm. In cases where separate observations were made at multiple depths per site, only the sampling depth closest to 20 cm was considered, as this depth is expected to capture the full nematode community (Sohlenius and Sandor, 1987).

After metadata cleaning, all observations missing information on coordinates, land use type, sampling season or sampling year were removed from the final dataset. In addition, we excluded samples collected from the rhizosphere specifically as well as samples from polluted areas.

Finally, the NBIs were calculated (see section 2.1.3.), after which all observations were averaged per unique location, including samples that were taken at the same site across multiple years.

2.1.2. Stratification by climatic conditions

To enable grouping of the sampling sites by climatic conditions, the sites were classified using the environmental stratification framework produced by Metzger et al. (2005). They produced a classification of European environmental zones (EEZ) by stratifying Europe according to a range of biophysical variables such as oceanicity, climatic properties and topography. In some EEZ there were too few observations to ensure

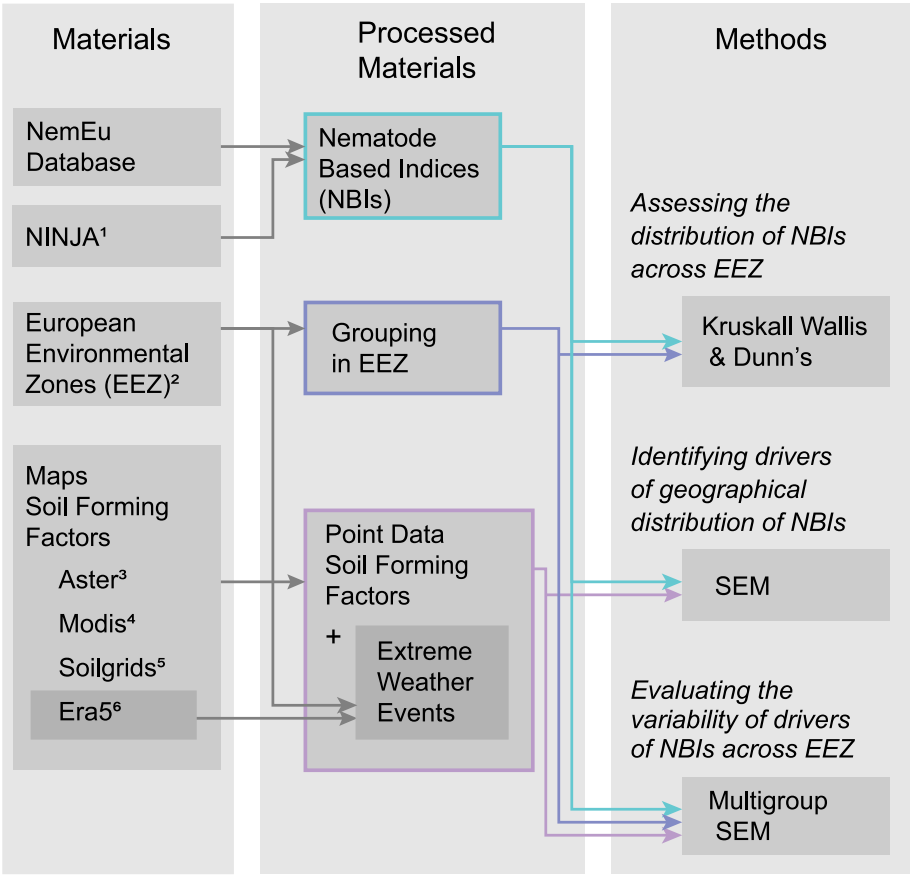

Fig. 1. Schematic overview of methods showing; 1) the data materials used in the study; 2) the steps taken to process the materials prior to analysis; 3) the statistical analyses performed for each of the research aims. [1](Sieriebriennikov et al. (2014), [2](Metzger et al., 2005), [3](NASA/METI/AIST/Japan Spacesystems, 2018), [4](Didan, 2021), [5](Poggio et al., 2021), [6](Muñoz Sabater, 2019).

Table 1
Overview of sample size per land use type, sampling season and sampling depth.

Land use type		Sampling season		Sampling depth	
Arable	335	Winter	214	≤5 cm	314
Agricultural grassland	302	Spring	554	≤10 cm	429
Natural grassland	180	Summer	331	≤20 cm	442
Forest and Shrubs	428	Autumn	146	≤30 cm	60

the robustness of the statistical analyses, therefore, we applied the following three adjustments: 1) Zones with less than 10 sampling sites were excluded, i.e. the Alpine North, Nemoral and Anatolian zones. 2) Zones than included >10 but <50 sites were clustered with adjacent climatic zones which demonstrated similar climatic conditions. The following climatic zones were combined; Continental with Pannonian zone; Mediterranean mountains with Alpine south; and Mediterranean north with Mediterranean south. 3) The border of the Boreal zone was extended to allow for the inclusion of a large number of sampling sites in the Russian Karelia region. These adjustments resulted in seven reclassified EEZs, ranging from north to south: Boreal (BOR), Atlantic north (ATN), Atlantic Central (ATC), Continental and Pannonian (COPA), Lusitanian (LUS), Mediterranean Mountains and Alpine South (MMAS) and Mediterranean North and South (MTNS) (Fig. 2a, Fig. 2b).

2.1.3. Nematode indices calculations

Nematode INdicator Joint Analysis (*NINJA*) (Sieriebriennikov et al., 2014) was used to calculate SI and EI, according to Ferris et al. (2001). Out of 302 taxonomic groups in the NemEu database, 54 were not recognized by *NINJA*. Following consultation with *Nemaplex* (Nemaplex.UCDavis.edu; Accessed (05/07/2024) and expert recommendations, the names of 47 taxa were updated according to the most current taxonomic classifications and 7 taxa were removed because they were identified as insect parasites or species inhabiting freshwater or marine environments.

2.1.4. Environmental datasets

We used global and European environmental maps to collect spatiotemporal data on a range of drivers representing soil-forming factors (Table 2). The selection of drivers that could explain variation in the NBIs was literature driven and based on the ecological theory underpinning the NBIs. When multiple data products were available, we chose maps that encompassed all selected sampling locations, prioritizing those with the finest spatial resolution. Whenever possible, we avoided the use of maps that were modelled using digital soil maps as input. Where needed, maps were reprojected to the WGS84 coordinate references system and resampled to 250 m resolution.

2.1.4.1. Soil and terrain data. We extracted elevation data from the *ASTER* product *ASTGTMv003* and subsequently used these values to assess ruggedness. We calculated the topographic ruggedness index from the 8 cells adjacent to the sampled cell (NASA/METI/AIST/Japan Spacesystems and U.S./Japan ASTER Science Team, 2018). The elevation and ruggedness maps were then resampled at 250 m resolution to align with the vegetation and soil property maps. Soil organic matter content and texture data were extracted from *Soilgrids 2.0* (Poggio et al., 2021). Point data was extracted for soil depths 0–5, 5–15 and 15–30 cm after which a weighted average was calculated to obtain an estimate for 0–30 cm depth.

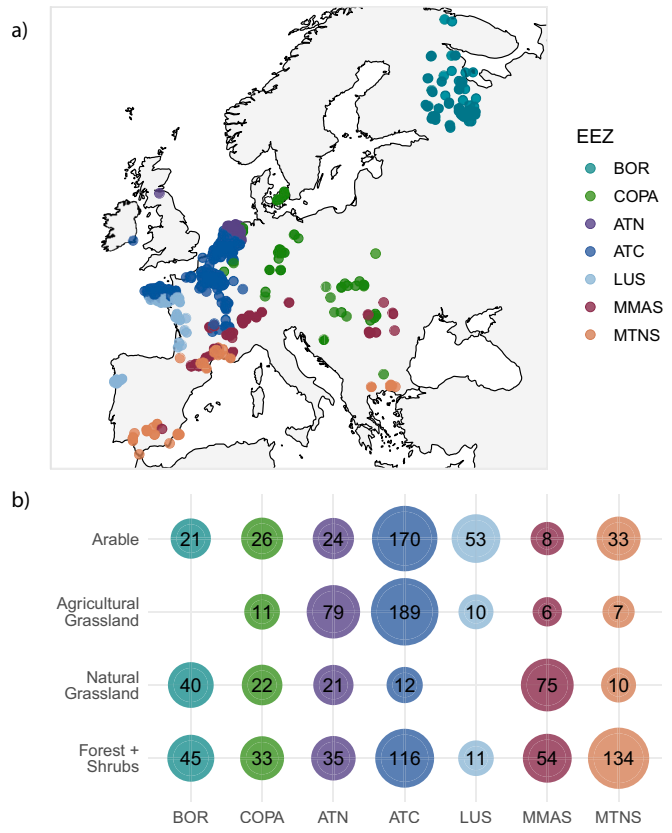

Fig. 2. (a) Geographical distribution and (b) sample size across different land use types of sampling points for each reclassified environmental zone; BOR – Boreal, COPA – Continental and Pannonian, ATN – Atlantic North, ATC - Atlantic Central, LUS – Lusitanian, MMAS - Mediterranean Mountains and Alpine South, MTNS – Mediterranean North and South.

2.1.4.2. Vegetation and land use intensity. Vegetation cover data was used to obtain an estimate of yearly biomass production. We extracted enhanced vegetation index (EVI) data from the *Modis* product *MOD13Q1 v061* for the years 2001 to 2019, at a resolution of 250 m (Didan, 2021). An estimate of yearly biomass production was then obtained by averaging the values for each 16-day time point over the included years, after which the area under the curve of the averaged values was calculated using trapezoid interpolation.

In addition to vegetation cover, we included land use type data to estimate local disturbances resulting from land use intensity. Land use information was sourced from the NemEu database metadata. To avoid including categorical drivers in the model, land use types were reassigned to a land use intensity gradient, as follows: 1 - forest and shrubs, 2 - natural grassland, 3 - agricultural grassland, and 4 - arable land.

2.1.4.3. Meteorological data and extreme weather events. Climate data on precipitation, air temperature and soil moisture were sourced from *Era5 land monthly averages* (Muñoz Sabater, 2019). To ensure comparability between weather effects and vegetation effects, we used a time range consistent with the available vegetation data. Specifically, we included the years 2000–2019 and calculated the average of all recorded values within this period. Due to the coarse resolution of the *Era5* land products, some sampling locations were covered by a sea mask. We used the nearest-neighbor approach to get a value estimate for these sites.

We used *Era5* land monthly time series for precipitation (P) and temperature (T) to determine the occurrence of extreme weather events compared to the regional average within the EEZ (Muñoz Sabater, 2019). The total number of extreme low and high events for T and P were used as a proxies for regional disturbance due to the occurrence of extreme T and P events within the EEZ. First, the average time series (1965–2020) of all pixels within each EEZ was calculated, after which we detrended the EEZ average time series according to Zscheischler et al. (2013). Then, we identified the 5th (extreme low) and 95th percentiles (extreme high) values of the P and T anomaly time series, for each EEZ. These values were considered the threshold for the occurrence of an extreme event, within a specific EEZ. Next, for each sampling location we detrended the complete time series and counted the occurrences where the anomaly value exceeded the 5th or 95th percentile

Table 2
Overview of selected environmental drivers of nematode-based indices.

soil forming factor	variable	product	years	original resolution	unit	original projection	source
Topography	Ruggedness	Elevation	–	250 m	–	Regular latitude-longitude grid	ASTGTMv003[1]
Topography	Elevation	Elevation	–	250 m	m	Regular latitude-longitude grid	ASTGTMv003[1]
Climate	Temperature	Air temperature at 2 m	2000–2019	9 km	k	Gaussian grid	ERA5_Land (monthly composite)[2]
Climate	Precipitation	Precipitation	2000–2019	9 km	m	Gaussian grid	ERA5_Land (monthly composite)[2]
Parent Material	Clay Content	Clay content (0–5, 5–15, 0–30 cm)	–	250 m	%	Goode's homolosine	Soilgrids 2.0[3]
Climate and Parent Material	Soil Moisture	Volumetric soil moisture (0–7 cm)	2000–2019	9 km	m^3 m^{-3}	Gaussian grid	ERA5_Land (monthly composite) [2]
Organism	Soil Carbon	Soil organic carbon content (0–5, 5–15, 0–30 cm)	–	250 m	dg kg^{-1}	Goode's homolosine	Soilgrids 2.0[3]
Organism	Vegetation	Enhanced vegetation index	2001–2019	250 m	(–)	Sinusoidal	MOD13Q1 v061 (16-daily composite)[4]
Disturbance	Temp Extremes	Air temperature at 2 m	1975–2019	9 km	count	Gaussian grid	ERA5_Land (monthly composite)[2]
Disturbance	Prec Extremes	Precipitation	1975–2019	9 km	count	Gaussian grid	ERA5_Land (monthly composite)[2]
Disturbance	Land Use Intensity	Land use type			(–)		metadata NemEu

[1] (NASA/METI/AIST/Japan Spacesystems and U.S./Japan ASTER Science Team, 2018).
[2] (Muñoz Sabater, 2019).
[3] (Poggio et al., 2021).
[4] (Didan, 2021).

of P and T, for the respective EEZ during the ten years prior to sampling.

2.2. Methods

2.2.1. Comparison of NBIs across environmental zones

The NBIs were checked for normality, and due to the violation of this assumption we used a non-parametric approach, the Kruskal-Wallis test, to assess whether the NBIs differed significantly across land use types. Next, we applied the Kruskal-Wallis test within each land use type to compare NBI values across EEZs. For both the land use type and EEZ we applied Dunn's post-hoc test to make pairwise comparisons (Dunn, 1961; Kruskal and Wallis, 1952).

2.2.2. Modelling the effect of soil-forming factors

The relationship between soil-forming factors and NBIs was tested by constructing a structural equation model (SEM) which was tested separately for each NBI. SEM was chosen because soil-forming factors are known to interact with each other, and a SEM can yield insights into how this network of interactions affects nematode functional diversity (Eisenhauer et al., 2022).

2.2.2.1. Hypothesis model. To avoid overcomplicating the model, a simplified structure with two layers of hypothesized drivers was developed (Fig. A1). The lower layer includes drivers hypothesized to directly affect the NBIs while also mediating the effects of other soil-forming factors: i.e., soil moisture, soil carbon, and vegetation. The upper layer has two groups. The first group includes drivers hypothesized to have only an indirect effect through the mediators: i.e., ruggedness, elevation, temperature, precipitation, and clay content. The second group includes disturbance factors hypothesized to affect NBIs both directly and indirectly through the mediators: i.e., land-use intensity and extreme weather events.

2.2.2.2. Modelling the effect of soil-forming factors using a non-nested SEM. The hypothesis model was first tested using a non-nested structure, wherein the regression coefficients remain identical across all environmental zones. This allows for the assessment of the relationship between the soil-forming factors and NBIs across all data points irrespective of environmental zone.

We applied the d-separation (*d-sep*) test approach as outlined by (Shipley, 2000), which tests the independence claims between variables that are not directly connected according to the hypothesized model structure. If the hypothesis model is rejected, the identification of violated independence claims can guide the construction of alternative hypothesis models, where violated claims are removed by adding relationships between the implicated variables. The *d-sep* approach also allows for the implementation of non-parametric or linearized alternatives when assumptions for linear regression are not met.

After specifying the hypothesis model, we assessed for each regression included in our hypothesized structure the following model assumptions: linearity, collinearity, homoscedasticity, and normality of residuals. Where the model assumptions were not met, the regression type was adjusted accordingly. Next, we identified all independence claims implied by our hypothesized causal structure and computed individual *p*-values for each claim. These *p*-values were combined using Fisher's *C*-statistic, followed by a χ^2 test to determine whether the observed data supported the hypothesized model structure.

In case the initial hypothesized model was rejected ($p < 0.05$), we refined the model iteratively. We first calculated the total Akaike Information Criterion (*AIC*), which is the sum of the *AIC* values for all regressions models within the hypothesized SEM. Next, the rejected independence claims were ranked in ascending order based on their *p*-values. Beginning with the independence claim having the lowest *p*-value, we introduced the direct relationship between implicated variables, thereby removing the violated independence claim, and recalculated the total *AIC* of this adjusted model. If Δ total *AIC* was > -3, the adjusted model was retained, otherwise, we reverted to the previous model, without making further adjustments (Shipley, 2013). This procedure was repeated sequentially for each remaining rejected independence claim, proceeding by ascending *p*-value until all previously rejected independence claims had been evaluated. The final adjusted model structure was then re-evaluated using the same χ^2 test based approach.

The hypothesized SEM model contains four regression models (for Soil Moisture, Soil Carbon, Vegetation and SI or EI). We applied a standard multiple regression model and standardized all drivers prior to the analysis using *Z*-score standardization. After testing for model assumptions, we found that no adjustments were needed. Beta regression, a generalized linear model designed for proportional outcome variables, could be an appropriate choice given that the SI and EI range from 0 to 100 (Ferrari and Cribari-Neto, 2004). However, our analysis showed that linear regression analysis consistently produced predictions within this range, indicating that this method was also valid. We chose linear regression for its interpretability and to facilitate the comparison with other drivers in the SEM that were predicted using a linear regression.

The original hypothesis model (Fig. A1) was rejected for both the SI and EI. For the SI, the model was accepted after adding a direct effect of ruggedness. For the EI, the model structure was supported after adding direct effects of ruggedness, precipitation, texture and elevation. Therefore, the only independence claim left in the adjusted model was between temperature and the EI.

2.2.2.3. Modelling the effect of soil-forming factors using a nested SEM. We applied the multigroup SEM approach developed by Douma and Shipley (2021) to assess whether the relationship between soil-forming factors and NBIs differed across environmental zones. We applied the same approach and tested the same hypothesis model as for the non-hierarchical SEM, but all regression coefficients were allowed to vary across environmental zones. Similar to the non-hierarchical SEM we assessed which independence claims were violated. When evaluating the Δ total *AIC* after model adjustments, independence claims were removed within a specific EEZ, with the regression slopes in other EEZs constrained to zero using dummy variables.

For the SI, this approach resulted in the addition of direct effects for elevation in the Continental and Pannonian, elevation and temperature in the Atlantic Central, and precipitation in the Mediterranean north and south. For the EI, direct effects were incorporated for temperature in the Boreal zone, ruggedness in the Continental and Pannonian, all hypothesized indirect effects in the Atlantic Central zone, temperature in the Mediterranean mountains and Alpine south, and elevation and precipitation in the Mediterranean north and south.

To summarize the effects of each driver across environmental zones, we present both direct and indirect effects. The direct effect is represented by the regression coefficient between the standardized driver and the NBI. Indirect effects were calculated by first computing pathway-specific effects as the product of regression coefficients along each causal pathway linking the driver to the NBI, and then taking the sum of these effects.

2.2.3. Software and packages

All statistical analyses were conducted in R v4.3.2 (R Core Team, 2024), with contributing packages *terra* v1.7–78 (Hijmans, 2024), *geosphere* v1.5–18 (Hijmans, 2022) and *pracma* v2.4.4 (Borchers, 2023) for processing of spatial data (section 2.1.4). Dunn's post-hoc tests (section 2.2.1) were performed with *FSA* (Ogle et al., 2023). Structural equation modelling (Section 2.2.2) used base R functions, with model assumption checks via *performance* (Lüdecke et al., *2021)*. Code is available at: https://git.wur.nl/mani001/nemeu_sem

3. Results

3.1. Comparison of NBIs across EEZ

The EI and SI are presented in a two-dimensional graph, which provides insights into the soil food web status (Fig. 3a). Low values for both indices indicate a degraded system, while high EI with low SI reflects nutrient enrichment with limited food-web complexity. Conversely, low EI with high SI suggests a depleted state with a structured food-web, whereas high values for both indices represent a well-structured system in nutrient-rich conditions (Du Preez et al., 2022).

Analysis of the distribution of the nematode community structure revealed NBI differences between the land use types (EI: $p < 0.001$, SI: $p < 0.001$) (Fig. 3a). Independent of EEZ, NBIs of samples from arable lands were predominantly observed in the upper left quadrant, representing an enriched and disturbed state (Fig. 3a). Statistical testing confirmed that EI was significantly higher in arable land (median = 65) than in all other land use types (43 ≤ median ≤ 48) (Fig. 3b) and that the SI was significantly lower in arable fields (median = 44) and agricultural grasslands (median = 45) compared to natural grassland (median = 66) and forest and shrubs (median = 57) (Fig. 3c). The agricultural grassland sites were generally positioned near the center of the four quadrants for EI (Fig. 3a). In contrast, natural grasslands and forests and shrubs were predominantly positioned in the lower right quadrant, suggesting that food webs in these non-agricultural systems were mostly mature but nutrient-limited (Fig. 3a). Among all land use types, forests were the least nutrient enriched (median = 43), having a lower EI than all other land use types (48 ≤ median ≤ 65) (Fig. 3b), whereas natural grasslands had the highest SI (Med = 66), significantly higher than all other land use types (44 ≤ median ≤ 57) (Fig. 3c).

For the SI, an interaction between land use type and EEZ was observed, meaning that differences in SI per EEZ were only apparent for

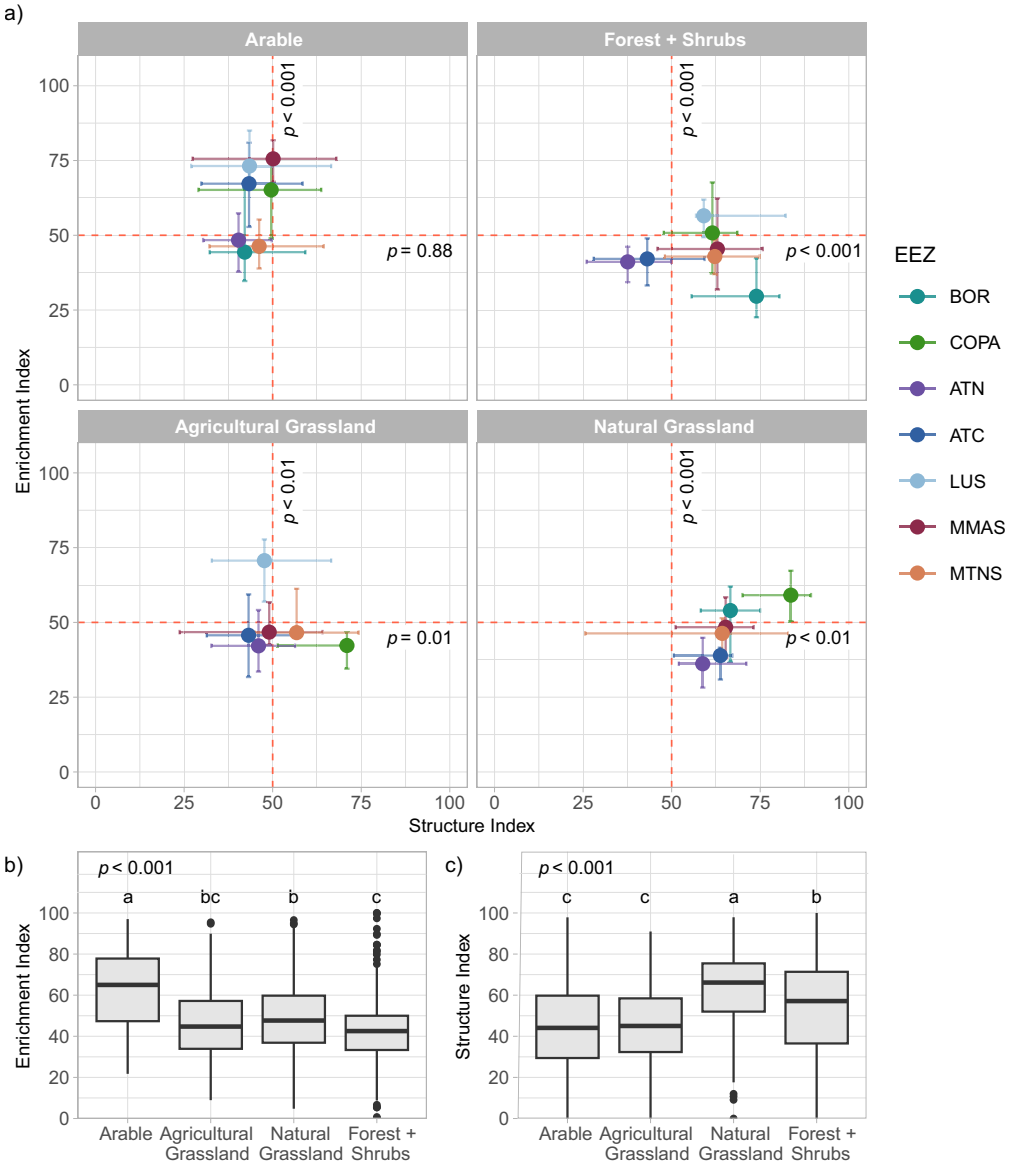

Fig. 3. Kruskal-Wallis comparison of nematode-based indices (a) across European environmental zones within each land use type and (b, c) between land use types. The points represent the median and the error bars represent the 25th and 75th percentile. The *p*-values on the y- and x-axis of figure a) represent the Kruskal-Wallis comparison across EEZ for the Enrichment Index and Structure Index, respectively. The *p*-values at the top of figures b) and c) represent the outcome of the Kruskal-Wallis test comparing land use types and boxplots marked with the same letter are not significantly different from each other according to Dunn's post-hoc test. BOR – Boreal, COPA – Continental and Pannonian, ATN – Atlantic North, ATC - Atlantic Central, LUS – Lusitanian, MMAS - Mediterranean Mountains and Alpine South, MTNS – Mediterranean North and South.

the non-agricultural land use types, whereas, SI values did not significantly differ between EEZs for either agricultural land use type. In arable fields, no significant EEZ differences were detected (40 ≤ median ≤ 50) (Fig. 3a). In agricultural grasslands, initial differences were observed (43 ≤ median ≤ 71, $p = 0.01$) (Fig. 3a), but Dunn's post-hoc test revealed no significant differences between EEZ pairs (Fig. A2a). In non-agricultural land uses, SI differed significantly between EEZs, with patterns varying by land use type. In natural grasslands ($p < 0.01$), the warmer, drier Continental and Pannonian zone had the highest SI (median = 84) (Fig. 3a). SI values in this zone were significantly higher than in the cooler, wetter Atlantic North (median = 59), Atlantic Central (median = 64) and high-altitude Mediterranean Mountains and Alpine South (median = 65) (Fig. A2a). In forests and shrublands ($p < 0.001$), SI values were low for the Atlantic zones, whereas the cold and dry Boreal zone had the highest SI (Fig. 3a). The SI was lowest in the Atlantic North (median = 38), significantly differing from all other zones (59 ≤ median ≤ 74) except the Atlantic Central (median = 43), which in turn was significantly lower than the Continental (median = 61) as well as the Boreal and both Mediterranean zones (62 ≤ median ≤ 74) (Fig. A2a). Overall, patterns in SI values were largely inconsistent across the non-agricultural land use types, with only a few recurring trends. The Atlantic zones consistently exhibited lower SI values, suggesting weaker

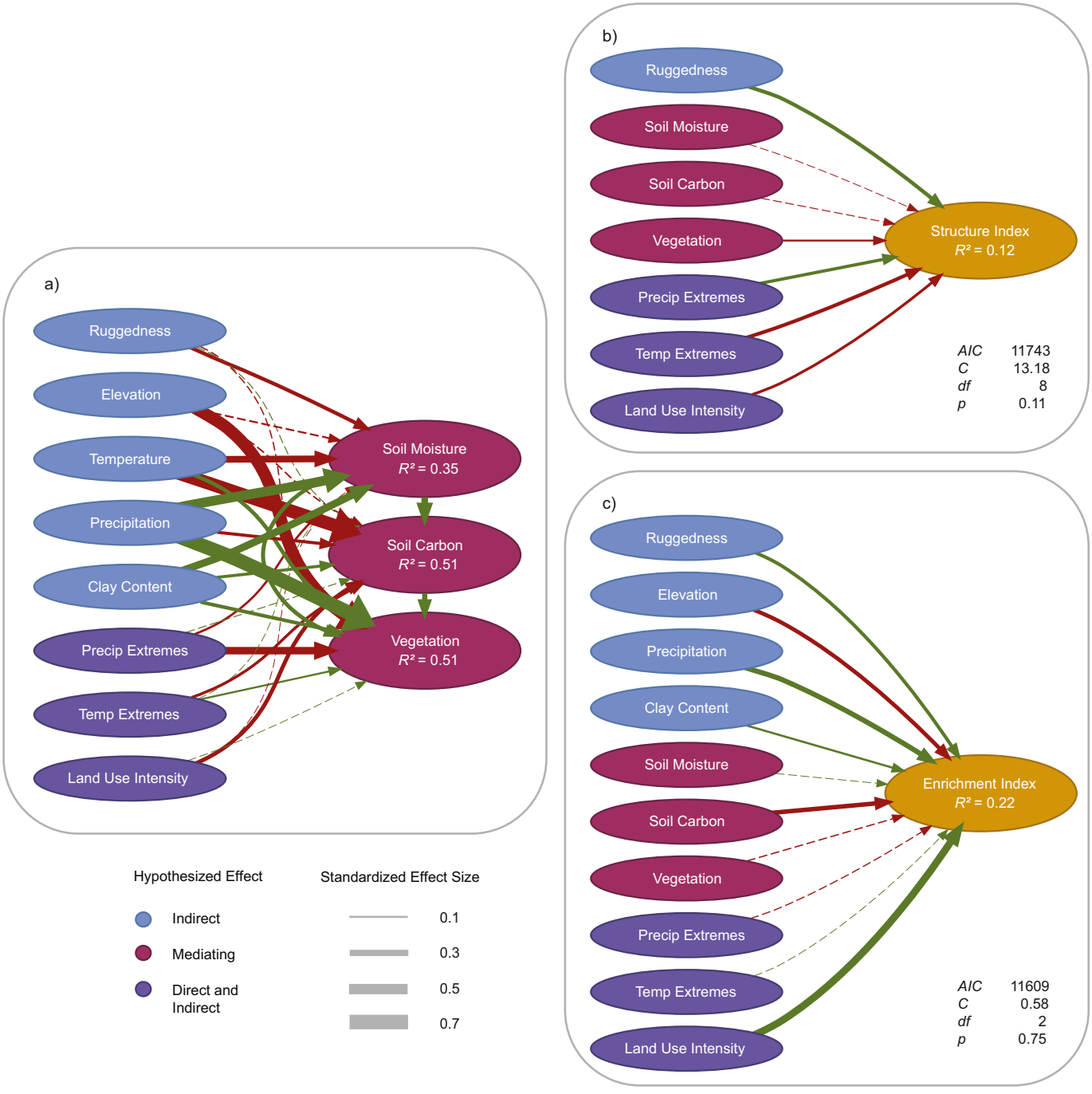

Fig. 4. SEM representing the effect of soil-forming factors on (a) mediating drivers, (b) Structure Index and (c) Enrichment index. Arrow thickness indicates the standardized regression coefficient, with green arrows representing positive relationships and red arrows negative ones. Dashed arrows denote non-significant effects ($p > 0.05$). *AIC* represents the sum of the *AIC* values from all four regression models in the SEM, *C* is Fisher's *C*-statistic based on the combined *p*-values of the independence claims, and *p* is the *p*-value according the χ^2 test of *C* with *df* degrees of freedom.

soil food-web structure in these regions. In contrast, SI values for the Boreal and Continental and Pannonian zones were relatively high, indicating a more developed soil food-web structure in these zones.

For the EI, significant differences between EEZs were observed for both agricultural and non-agricultural land use types (Fig. 3a). In arable land ($p < 0.001$), two distinct clusters emerged. The high EI cluster consists of the Continental Pannonian, Atlantic Central, Lusitanian, and Mediterranean Mountains and Alpine South (65 ≤ median ≤ 76), whereas the lower cluster included the Atlantic North, Mediterranean North and South and Boreal zones (44 ≤ median ≤ 48). Within the high cluster, the Atlantic Central (median = 67) and Lusitanian zones (median = 73), characterized by milder climates, had significantly higher EI values than all EEZs in the low cluster (Fig. A2b). Although the mountainous zone had the highest EI values (median = 76), this estimate was relatively unreliable due to limited observations (n = 6) (Fig. 2b). Within the lower cluster, the Mediterranean zone (Med = 46) exhibited significantly lower EI values than all EEZs in the high cluster (Fig. A2b). In agricultural grasslands ($p < 0.01$), EI values were relatively consistent across EEZs, except for the Lusitanian zone (median = 71), where EI was significantly higher than in the cooler, North (median = 42) and Central Atlantic zones (median = 46) (Fig. A2b). In non-agricultural land use types, EI patterns also varied widely. For natural grasslands ($p < 0.001$), EI values were particularly low in the Atlantic zones (Fig. 3a). Both the Atlantic North (median = 36) and Atlantic Central (median = 39) exhibited significantly lower EI values than the Continental Pannonian zone (median = 59), while the Atlantic North was also significantly lower than the Boreal (median = 54) and mountainous zones (median = 48) (Fig. A2b). In forests and shrublands ($p < 0.001$), the Boreal zone (median = 30) had notably low EI values (Fig. 3a), significantly lower than all other EEZs (42 ≤ median ≤ 57) except the Atlantic North (median = 41) (Fig. A2b). Overall, EI values exhibited inconsistent patterns across land use types, though some broad regional trends emerged. The Lusitanian and Continental Pannonian regions, characterized by warmer, more temperate climates, frequently had higher EI values, suggesting greater nutrient availability and microbial activity. In contrast, the northern Atlantic regions generally showed lower EI values, reflecting limited nutrient enrichment in these cooler environments.

3.2. Modelling the effect of soil-forming factors using a non-nested SEM

The tested SEM examined the direct and indirect pathways through which soil-forming factors influence NBIs, structured into two layers (Fig. 4). The upper layer assessed how soil-forming factors (topography, climate, parent material, organism and disturbance) shape key mediating drivers (soil moisture, vegetation, and soil carbon). The lower layer evaluated how these mediators, along with disturbance factors drive NBIs.

The upper layer of the SEM captured the relationships between soil-forming factors and mediating drivers reasonably well ($0.35 < R^2 < 0.51$), aligning with classical soil-forming factor dynamics (Fig. 4a). While numerous significant relationships were observed, the most pronounced effects were seen in topography, climate, parent material, and disturbance factors. Elevation had a strong negative effect on vegetation ($\beta = -0.60$, $p < 0.001$), suggesting that higher altitudes limit plant growth. Climate factors were key drivers, with temperature negatively affecting soil carbon ($\beta = -0.63$, $p < 0.001$) and precipitation positively influencing soil moisture ($\beta = 0.46$, $p < 0.001$) and vegetation cover ($\beta = 0.68$, $p < 0.001$). Finally, within the disturbance category, precipitation extremes strongly reduced vegetation cover ($\beta = -0.36$, $p < 0.001$), while land-use intensity negatively impacted soil carbon ($\beta = -0.19$, $p < 0.001$).

With a low predictive power ($R^2 = 0.12$), the SI model indicated weak direct relationships with the soil-forming factors (Fig. 4b). Moreover, several observed effects were challenging to interpret within classical pedological and ecological contexts. Topography stood out, with ruggedness positively affecting the SI ($\beta = 0.18$, $p \leq 0.001$), an unexpected result given that rugged landscapes are typically erosion-prone, potentially limiting soil food-web stability. Mediating factors played a minor role, with only vegetation having a significant but weak effect ($\beta = -0.09$, $p = 0.005$). The indirect impact of climate, parent material, and organism factors was therefore also limited. Disturbance factors emerged as the strongest driver, with extreme precipitation events increasing the SI ($\beta = 0.15$, $p < 0.001$), while extreme temperature events ($\beta = -0.17$, $p < 0.001$) and land-use intensity ($\beta = -0.13$, $p < 0.001$) had negative effects.

The model performance for EI remained relatively low ($R^2 = 0.22$) but was slightly higher than for SI (Fig. 4c). Furthermore, the hypothesized model structure, in which environmental effects are mediated through soil moisture, vegetation, and soil carbon, was largely unsupported, as only temperature did not have a direct effect on the EI independent of the mediators. Significant relationships were observed across all soil-forming factors, though some were difficult to explain. Topography influenced EI through both ruggedness and elevation, with ruggedness having a positive effect ($\beta = 0.16$, $p \leq 0.001$) and elevation a negative effect ($\beta = -0.19$, $p < 0.001$). Climate effects were limited to precipitation, which had a positive impact ($\beta = 0.24$, $p < 0.001$). Unexpectedly, soil carbon negatively influenced EI ($\beta = 0.21$, $p < 0.001$). Among disturbance factors, only land-use intensity emerged as a significant driver ($\beta = 0.35$, $p < 0.001$), likely reflecting nutrient enrichment through fertilization.

3.3. Modelling the effect of soil-forming factors using a nested SEM

To evaluate whether the relationship between soil-forming factors and NBIs varies between environmental zones, the same hypothesized model structure (Fig. A1) was tested using a nested SEM. The model performance improved substantially, with the R^2 increasing to 0.27 for SI and 0.43 for EI. Additionally, model fit metrics indicated a stronger explanatory power, as the *AIC* decreased significantly, despite the penalty for estimating additional parameters (Table 3). For SI, the *AIC* dropped from 12,090 to 9643, while for EI, it declined from 11,993 to 9643.

We assessed the key drivers of SI and EI across EEZs, by calculating the effects of all drivers with a direct relationship in the adjusted model, as well as the indirect effects of all the soil-forming factors through the proposed mediators (vegetation, soil carbon, and soil moisture). Similar to the non-nested model, the results did not support a strong mediating role for these drivers, as most indirect effects were close to zero, suggesting that soil-forming factors primarily exerted direct rather than mediated effects (Fig. 5).

The relationships between soil-forming factors and the SI varied considerably across EEZs, with different drivers dominating in each region (Fig. 5a). In the Boreal zone ($R^2 = 0.21$), SI was influenced only by land use intensity ($\beta = -0.23$, $p = 0.03$). In the Continental Pannonian zone ($R^2 = 0.38$), topography, climate, organism and disturbance factors were important drivers. Elevation ($\beta = 0.59$, $p = 0.003$) and soil moisture ($\beta = 0.41$, $p = 0.04$) had positive effects, while soil carbon had a negative effect ($\beta = -0.53$, $p = 0.009$). In addition, temperature

Table 3
Model fit statistics for non-nested versus nested SEM.

	Index	*AIC*	*C*	*df*	*p*	R^2
Non-Nested	Structure	11,743	13.18	8	0.11	0.12
	Enrichment	11,609	0.58	2	0.75	0.22
Nested	Structure	9513	71.06	62	0.20	0.27
	Enrichment	9227	40.67	50	0.82	0.43

AIC represents the sum of the *AIC* values from all four regression models in the SEM, *C* is Fisher's *C*-statistic based on the combined *p*-values of the independence claims, and *p* is the *p*-value from the χ^2 test of the *C* with *df* degrees of freedom.

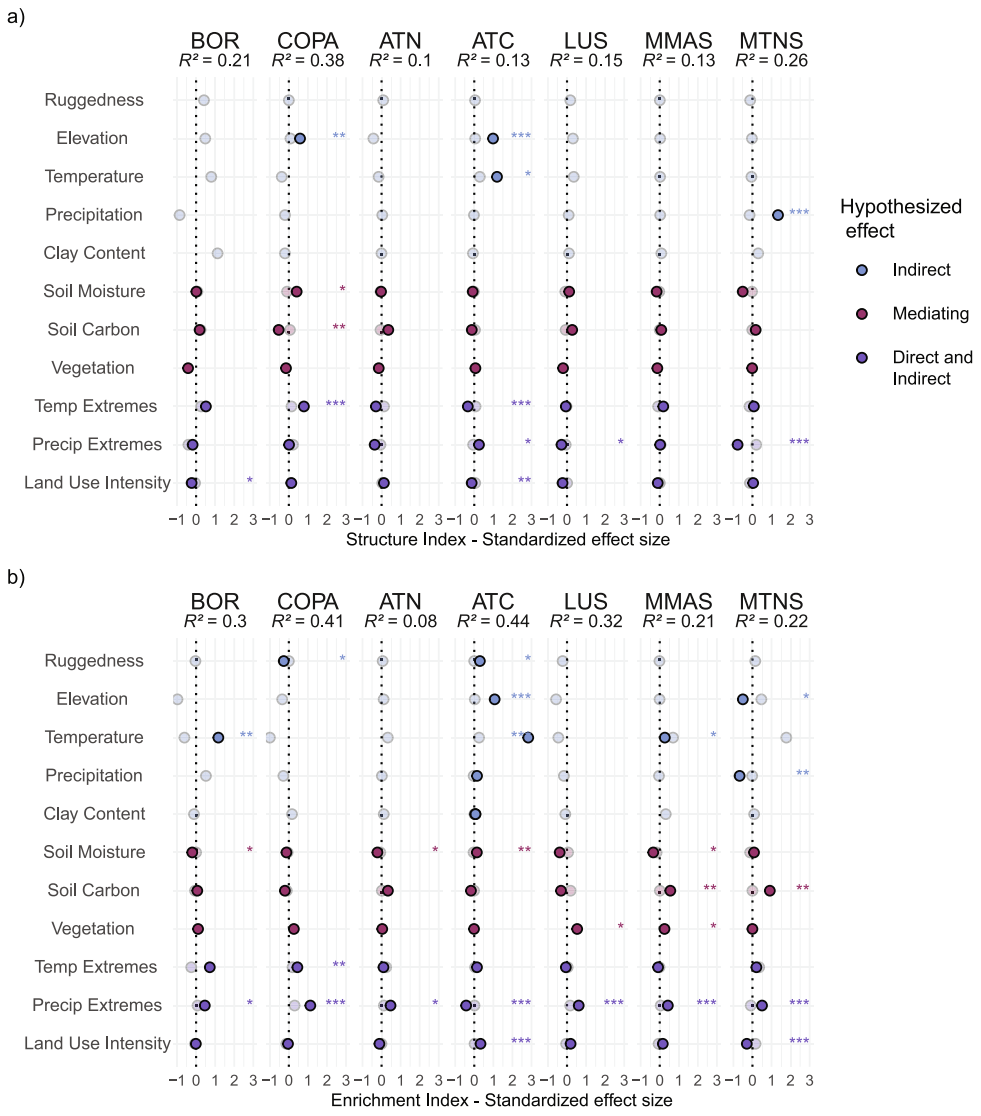

Fig. 5. Nested SEM representing the effect of soil-forming factors on (a) Structure Index and (b) Enrichment index within European environmental zones Solid points represent standardized regression coefficients of the direct effects on the nematode index, and transparent points represent the total indirect effect. The significance levels of the direct effects are denoted as: *** ($p < 0.001$), ** ($p < 0.01$) and * ($p < 0.05$). BOR – Boreal, COPA – Continental and Pannonian, ATN – Atlantic North, ATC - Atlantic Central, LUS – Lusitanian, MMAS - Mediterranean Mountains and Alpine South, MTNS – Mediterranean North and South.

extremes had a positive effect ($\beta = 0.79$, $p < 0.001$). In the Atlantic North, Atlantic Central, and Lusitanian zones ($R^2 = 0.10$, $R^2 = 0.13$, and $R^2 = 0.15$, respectively), model predictions were low. However, in the Atlantic Central zone, significant effects of topography and climate factors did occur. SI was positively influenced by elevation ($\beta = 0.98$, $p < 0.001$) and temperature ($\beta = 1.19$, $p = 0.01$). Disturbance factors also affected SI, with temperature extremes ($\beta = -0.34$, $p < 0.001$), precipitation extremes ($\beta = 0.25$, $p = 0.01$), and land use intensity ($\beta = -0.14$, $p = 0.005$) all exerting significant effects. In the Lusitanian zone, disturbance factors also had an effect through precipitation extremes ($\beta = -0.29$, $p = 0.04$). In the Mediterranean Mountains and Alpine South zones ($R^2 = 0.13$), no clear relationships between SI and soil-forming factors were observed. Lastly, in the Mediterranean North and South zone, climate and disturbance factors emerged as the key drivers. Precipitation had a positive effect ($\beta = 1.34$, $p < 0.001$), while precipitation extremes had a negative effect ($\beta = -0.78$, $p < 0.001$). Overall, disturbance factors were the only drivers that appeared consistently across multiple EEZs.

The drivers of EI also varied widely across EEZs, with climate, organism, and disturbance factors playing distinct roles in each region (Fig. 5b). In the Boreal zone ($R^2 = 0.3$), EI was primarily influenced by climatic and disturbance factors, with temperature ($\beta = 1.17$, $p = 0.006$) having a positive effect and soil moisture ($\beta = -0.2$, $p = 0.02$) a negative effect. In addition, precipitation extremes had a positive effect ($\beta = 0.46$, $p = 0.02$). In the Continental Pannonian zone ($R^2 = 0.41$), topography and disturbance were key factors, with ruggedness ($\beta = -0.27$, $p = 0.03$) negatively affecting EI, while temperature extremes ($\beta = 0.45$, $p = 0.009$) and precipitation extremes ($\beta = 1.13$, $p < 0.001$) had positive effects. In the Atlantic North, model performance was particularly low ($R^2 = 0.08$), but significant effects of climate and disturbance factors were observed through soil moisture ($\beta = -0.22$, $p = 0.02$) and precipitation extremes ($\beta = 0.47$, $p = 0.03$). The Atlantic Central zone ($R^2 = 0.44$) showed significant effects from topography, climate, and disturbance factors, with ruggedness ($\beta = 0.29$, $p = 0.03$), elevation ($\beta = 1.07$, $p < 0.001$), temperature ($\beta = 2.8$, $p < 0.001$), soil moisture ($\beta = 0.14$, $p = 0.009$), and land use intensity ($\beta = 0.33$, $p < 0.001$) having positive effects, while precipitation extremes ($\beta = -0.43$, $p < 0.001$) had a negative effect. In the Lusitanian zone ($R^2 = 0.32$), EI was driven by organism and disturbance factors, with both vegetation ($\beta = 0.53$, $p = 0.03$) and precipitation extremes ($\beta = 0.61$, $p < 0.001$) having a positive

effect on the EI. In the Mediterranean Mountains and Alpine South (R^2 = 0.21), climate, organism and disturbance factors were dominant, with temperature (β = 0.27, p = 0.03), soil carbon (β = 0.56, p = 0.002), vegetation (β = 0.25 and p = 0.03) precipitation extremes (β = 0.43, p = 0.001) all contributing positively and soil moisture (β = −0.34, p = 0.02) contributing negatively. Lastly, in the Mediterranean North and South (R^2 = 0.22), topography, organisms, and disturbance were key factors. Elevation ($\beta = -0.5, p = 0.02$) and precipitation ($\beta = -0.67, p = 0.004$) had negative effects, while soil carbon ($\beta = 0.91, p = 0.003$) and precipitation extremes ($\beta = 0.5, p < 0.001$) had positive effects. Land use intensity also showed a negative effect ($\beta = -0.3$, $p < 0.001$). Overall, disturbance factors had the most consistent effect on EI across EEZs, but in contrast to SI, topography, climate, and organism factors also played a more widespread role across different EEZs.

4. Discussion

This study provides the first large-scale assessment of the geographical distribution of the SI and EI, across Europe, examining how soil-forming factors and disturbance influence these indices across different environmental zones. Our results highlight the dominant influence of land use on NBIs, with intensive management reducing the SI while increasing EI. While NBIs varied across EEZs, land use effects overrode natural environmental differences for SI in arable fields. Traditional soil-forming factors proved insufficient to explain NBI distribution, while disturbance factors emerged as key drivers within the model. Allowing relationships to vary across EEZs enhanced model performance, which demonstrates that NBI-environment interactions are region-specific.

4.1. Strong influence of land use type on EI and SI

Our results show that land use strongly influences NBIs, with EI being higher in arable fields whereas SI is higher in non-agricultural land use types. These findings align with Bongiorno et al. (2019), who observed higher EI in intensively managed arable fields across Europe, attributing this to nutrient release from tillage rather than organic amendments. Similarly, Puissant et al. (2021) found a positive effect of inorganic fertilization on EI. These studies also reported a negative effect of tillage on the SI, aligning with our observation that land use intensity suppresses soil food-web stability (Bongiorno et al., 2019; Puissant et al., 2021). Additionally, Morrien et al. (2017) reported that food-web complexity improves in natural areas following arable land abandonment, reinforcing the conclusion that intensive agriculture decreases soil food-web structure and may impair ecosystem functioning. These results demonstrate the application of NBIs as effective soil health indicators, when assessing land management intensity. However, NBIs have also been shown to be significantly influenced by land use type and this context should be taken into consideration when utilizing these metrics.

4.2. Land use intensity overrides environmental differences for SI but not EI

We observed significant differences in SI and EI between EEZs, however, these patterns varied depending on land use type. In arable fields, the SI remained constant across EEZs, indicating that the intensive land management practices applied in arable farming override naturally occurring environmental variability. Consistent with these findings, Li et al. (2020) found that naturally occurring differences in nematode diversity across climatic zones were obscured by land use in agricultural grasslands.

In contrast, EI exhibited more pronounced differences between EEZs in arable fields. A clustering pattern emerged, with temperate zones more frequently appearing in the high cluster, while regions with more extreme climates were more common in the low cluster. This could be due to more favorable conditions for nutrient availability in temperate zones, which would be in accordance with the findings of Siles et al. (2023), who observed higher microbial biomass in temperate regions. However, interestingly, they found that these differences were less pronounced in agricultural land compared to natural land. The observed variation in arable fields may stem from a climate-disturbance interaction, in which agricultural disturbance increases nutrient release, and temperate climates further amplify this effect. Alternatively, the clustering may reflect more intensive nutrient management practices in temperate agricultural systems (De Vries et al., 2022). Overall, we found a clear interaction between land use and environmental zone, with this interaction differing depending on the index considered. For the SI, our results suggest that interpretation of the SI as soil health indicator must be contextualized within EEZ specifically for non-managed land use types, whereas, for the EI there is a need for such contextualization in both managed and non-managed land use types.

4.3. Patterns of SI and EI across EEZs vary among non-agricultural land use types

We found variation in both indices across EEZs for natural grasslands as well as forests and shrubs, though few consistent patterns emerged. Contrary to expectations that extreme environments support less complex and more disturbance-prone food webs (Wall and Virginia, 1999), we found that SI remained high in some regions with extreme climatic conditions. Studies on extreme environments support this pattern, showing that in desert, tundra, Arctic, and Antarctic ecosystems, SI can remain high under extreme but stable conditions (Darby et al., 2007; Kudrin et al., 2019; Peneva et al., 2009). This suggests that soil food webs can develop stability even in harsh environments, provided that disturbance remains minimal.

Conversely, low SI and EI values were observed in fertile temperate regions, such as the Atlantic zone, despite their favorable climatic conditions. One possible explanation is land management differences across EEZs, as forests in the Atlantic region are often young, heavily managed, or established on depleted soils, which may suppress SI and EI despite otherwise favorable conditions. This underscores the need to separate geographic and anthropogenic influences to accurately interpret the biogeography of NBIs.

4.4. EI and SI are more driven by disturbance factors than by soil-forming factors

Our findings indicate that traditional soil-forming factors, typically used to predict physical-chemical soil properties, are insufficient to adequately explain variations in NBIs across Europe. Although significant associations were found between all soil-forming factors and NBIs, the overall explained variance was notably low, especially for the SI (R^2 = 0.12) compared to the EI (R^2 = 0.22). Potapov et al. (2023), who used SEM to predict global collembola distribution, reported similar predictive performance for diversity and functional metrics (species richness: R^2 = 0.20, community metabolism: R^2 = 0.17) but higher performance for abundance metrics (density: R^2 = 0.36, biomass: R^2 = 0.40). Similarly, nematode-focused studies using machine learning reported limited predictive accuracy for nematode richness (R^2 = 0.12) (Köninger et al., 2023), and high predictive accuracy for nematode feeding group abundance ($0.79 \leq R^2 \leq 0.9$) (van den Hoogen et al., 2019).These findings suggest that functional and diversity-based metrics, such as NBIs, are inherently more difficult to predict using traditional soil-forming factors than abundance-based metrics.

We initially hypothesized that soil organic carbon, vegetation, and soil moisture would be key mediators of NBI distribution, shaping nematode communities by influencing resource availability and habitat conditions (Nielsen et al., 2014; Song et al., 2017; van den Hoogen et al., 2019). However, our results did not support this hypothesis. Instead, disturbance factors, specifically extreme weather events and land use intensity, played a stronger role in shaping NBIs than classical soil-

forming factors. Similarly, Dee et al. (2025) integrated disturbance risks into ecosystem service assessments and found them to be critical factors. These findings, along with our results, suggest that incorporating novel spatial indicators, such as extreme weather events and land use practices, could enhance predictions of NBI distribution.

4.5. Key drivers of SI and EI vary across EEZ

Our results show that the relationships between soil-forming factors and NBIs varied substantially across environmental zones, with some factors exerting opposing effects depending on the region. This supports findings by Shao et al. (2023) who found that dominant climatic drivers of nematode diversity shift across latitudes, with temperature playing a larger role in temperate forests and precipitation in tropical forests. The importance of specific drivers appeared to depend on their ecological relevance within each zone. In some cases, drivers typically considered moderate within a zone, such as elevation and temperature in the Atlantic Central, emerged as major contributors. In contrast, in other zones, it was the dominant or extreme drivers that shaped NBI patterns, such as temperature in the Boreal zone and precipitation in the Mediterranean North and South. This suggests that different mechanisms may underlie NBI responses across environmental zones, underscoring the need for region-specific interpretations when using NBIs to assess soil health.

4.6. Limitations, recommendations, and outlook

NBIs have shown promise as indicators for soil health assessment due to their strong link to soil functioning (Du Preez et al., 2022; Ruess, 2024). However, this large-scale assessment of nematode NBIs across Europe reveals that significant challenges remain before they can be effectively applied at the continental scale.

Working with a large, compiled database of studies from across Europe presented several challenges, particularly in achieving consistency and representativeness. The uneven distribution of sampling sites within and across EEZs, combined with variability in sampling methods, complicated both the modelling of patterns and the interpretation of results at a continental scale. In addition, limited information on land management practices made it challenging to disentangle the influence of land use from geographical patterns in nematode communities. These factors likely constrained our ability to capture ecological variability and assess broader trends with confidence. Although we aimed to address these issues through careful data selection, this approach could only mitigate variability to a limited extent and remained constrained by the availability and quality of existing data.

These limitations, highlight the need for further research, accordingly, we propose several recommendations to guide future efforts. First, additional efforts to integrate nematode community datasets would allow for stricter data selection without compromising sample size, thereby enhancing the robustness of continental-scale analyses. However, our results also underscore the importance of representative, pan-European sampling campaigns using uniform methods, ensuring balanced coverage of different land uses and environmental zones within Europe (Orgiazzi et al., 2018). In addition, exploring alternative modelling approaches, such as machine learning methods, that can accommodate complex hierarchical structures, non-linear relationships, and interaction effects may yield more accurate predictions of NBI geographical distribution patterns (Wadoux et al., 2020). These methods also offer the advantage of handling a broader range of predictors than SEM, making them well-suited for incorporating and testing novel indicators. Incorporating disturbance factors, such as extreme weather events, along with more detailed land use data including pesticide use, tillage, irrigation and pollution, could further improve model performance and enhance our understanding of spatial patterns of NBIs (Bongiorno et al., 2019; Campos-Herrera et al., 2022; Laasli et al., 2024; Puissant et al., 2021). Lastly, we focused on the SI and EI, however, there are many more indices such as the maturity index or the channel index that can further give insight into soil health and soil multifunctionality, therefore we recommend that further studies also consider additional NBIs (Du Preez et al., 2022).

Our findings underscore the importance of incorporating context-specific information when using NBIs to assess soil health. Although NBIs offer valuable insights into soil food-web structure and functioning, their considerable variability across EEZs raises questions about their suitability for large-scale monitoring efforts. With biogeographical patterns of NBIs still unclear, these indices may be more effectively applied at local or regional scales, where they can be interpreted relative to site-specific reference values. This consideration may also extend to other biological indicators, which frequently exhibit similarly context-dependent responses to land management and climatic variability in agricultural systems (Lauber et al., 2008).

Nematode trophic groups and total abundance are among the soil health indicators proposed in the Soil Monitoring and Resilience Directive, which aims to incorporate soil biodiversity into a pan-European monitoring framework (European Commission, 2023). Our findings suggest that the geographical distribution of these abundance-based metrics may be easier to predict than NBIs. Therefore, they may be indeed better suited than NBIs for establishing threshold values at the Member State level and could offer a more practical option for large-scale soil health assessments.

However, despite their practicality, abundance metrics do not capture soil ecological functions as effectively as NBIs (Du Preez et al., 2022; Ruess, 2024). Therefore, further research is needed to determine whether the spatial variability of NBIs can be understood well enough to support their large-scale application. This would require uniform sampling protocols across regions and land use types, a stronger focus on region-specific relationships between NBIs and environmental drivers, and the integration of metrics that capture both anthropogenic and natural disturbance factors.

5. Conclusions

This study highlights the dominant role of land use in shaping NBIs, with intensive management reducing SI and increasing EI. In arable systems, land use not only suppressed SI but also overrode natural environmental gradients between EEZs. In contrast, EI in arable land exhibited greater regional variability, with higher values observed in temperate zones compared to areas with more extreme climates. In non-agricultural land use types, both indices varied across environmental zones, though without consistent patterns, likely due to complex interactions between environmental and anthropogenic factors.

Traditional soil-forming factors commonly used to predict physical-chemical soil properties were insufficient to explain NBI distributions, particularly for SI. In contrast, extreme weather events and land use intensity, indicators of disturbance, emerged as key drivers of both SI and EI. This underscores the need to move beyond conventional predictors and incorporate more ecologically relevant variables in large-scale assessments of soil biological indicators. Additionally, the relationships between NBIs and environmental drivers varied substantially across environmental zones, reinforcing the importance of region-specific analyses.

Together, these findings demonstrate that NBIs are sensitive and functionally relevant indicators of soil health. However, their large-scale application remains constrained by spatial variability and the limited explanatory power of standard environmental drivers. Future efforts should focus on expanding data coverage using harmonized sampling protocols and integrating detailed land management and disturbance metrics. Improving our understanding of NBI spatial patterns will be essential to assess their suitability for inclusion in continental-scale soil monitoring frameworks.

CRediT authorship contribution statement

Doina Thais Constance Mani: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Vera Leatitia Mulder:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Carmen Vazquez Martin:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Stefan Geisen:** Writing – review & editing, Methodology, Data curation. **Raquel Campos-Herrera:** Writing – review & editing, Methodology, Data curation. **Andrea Čerevková:** Writing – review & editing, Methodology, Data curation. **Simone Cesarz:** Writing – review & editing, Methodology, Data curation. **Marcel Ciobanu:** Writing – review & editing, Methodology, Data curation. **Sofia R. Costa:** Writing – review & editing, Methodology, Data curation. **Ron de Goede:** Writing – review & editing, Methodology, Data curation. **Nico Eisenhauer:** Writing – review & editing, Methodology, Data curation. **Louise Jackson:** Writing – review & editing, Methodology, Data curation. **Daria Sergeevna Kalinkina:** Writing – review & editing, Methodology, Data curation. **Alexey Kudrin:** Writing – review & editing, Methodology, Data curation. **Elizaveta Mikhailovna Matveeva:** Writing – review & editing, Methodology, Data curation. **Juha Mikola:** Writing – review & editing, Methodology, Data curation. **Christian Mulder:** Writing – review & editing, Methodology, Data curation. **Peter Nagy:** Writing – review & editing, Methodology, Data curation. **Branimir Njezic:** Writing – review & editing, Methodology, Data curation. **Juan Emilio Palomares-Rius:** Writing – review & editing, Methodology, Data curation. **Vlada Peneva:** Writing – review & editing, Methodology, Data curation. **Iuliana Popovici:** Writing – review & editing, Methodology, Data curation. **Liliane Ruess:** Writing – review & editing, Methodology, Data curation. **Sara Sánchez-Moreno:** Writing – review & editing, Methodology, Data curation. **Marie Sünnemann:** Writing – review & editing, Methodology, Data curation. **Anna Alekseevna Sushchuk:** Writing – review & editing, Methodology, Data curation. **Mette Vestergård:** Writing – review & editing, Methodology, Data curation. **Cécile Villenave:** Writing – review & editing, Methodology, Data curation. **Lieven Waeyenberge:** Writing – review & editing, Methodology, Data curation. **Jakob Wallinga:** Writing – review & editing, Supervision, Conceptualization. **Rachel Creamer:** Writing – review & editing, Supervision, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT (OpenAI) in order to refine writing style, improve clarity and restructure paragraphs. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

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

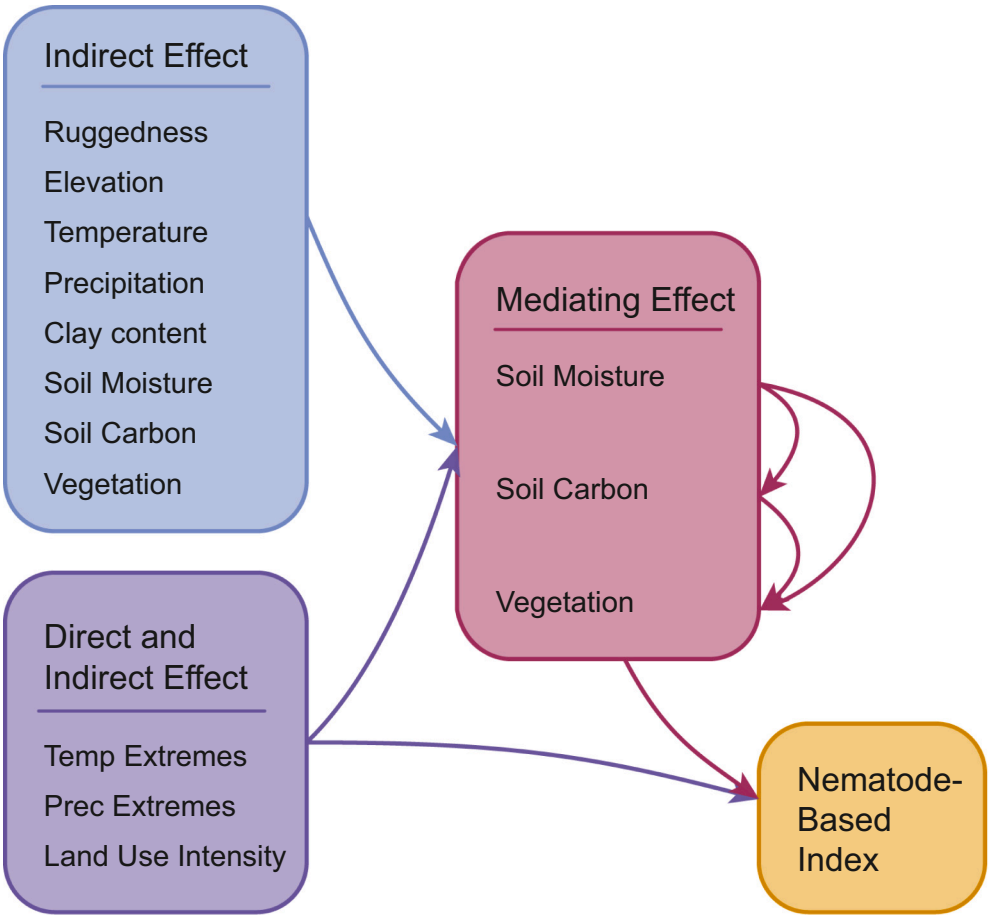

Fig. A1. Overview of the initial hypothesis model that was tested using SEM All drivers under *Indirect Effect* were hypothesized to have an indirect effect on the nematode-based index through each of the drivers under *Mediating Effect*. All drivers under *Direct and Indirect* were hypothesized to have a direct effect as well as an indirect effect through each of the drivers under *Mediating Effect*.

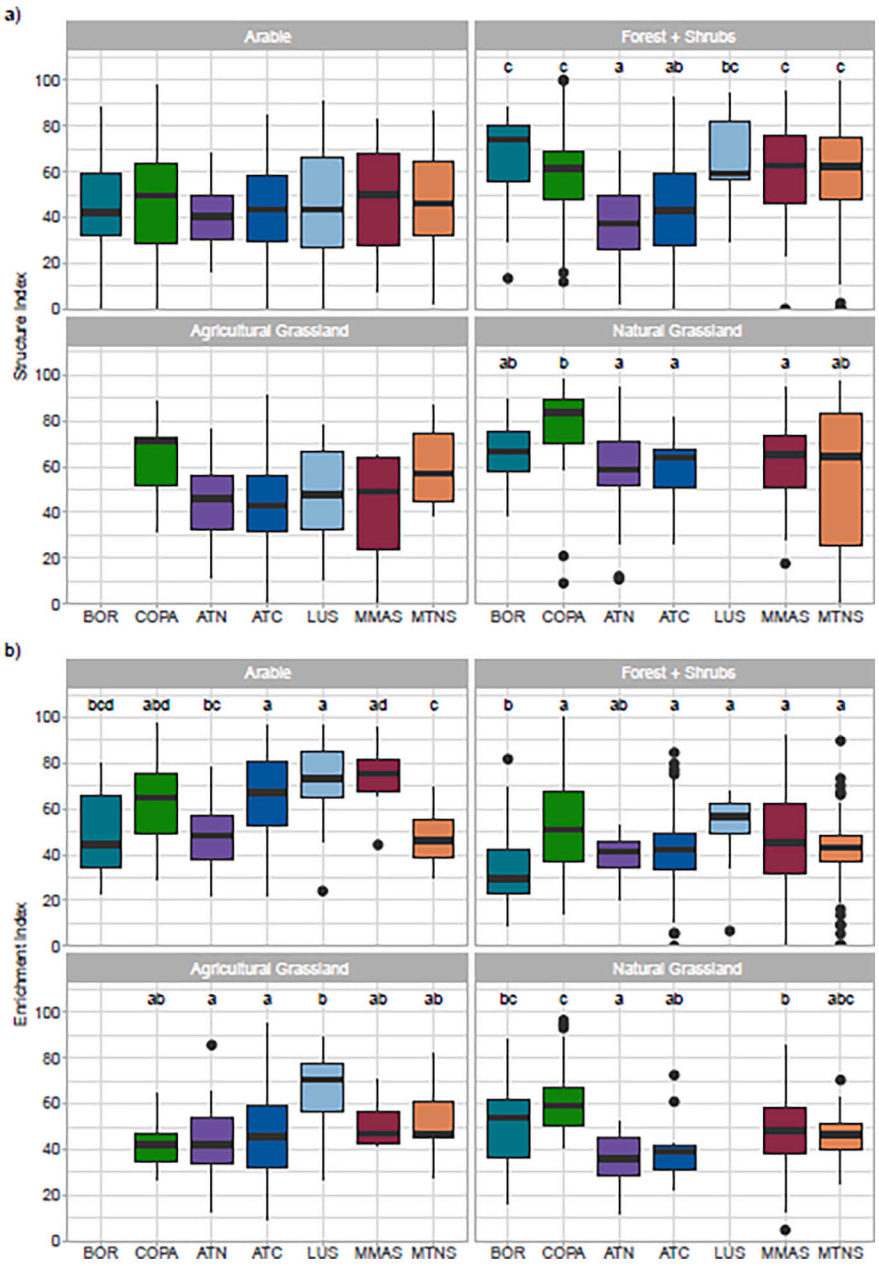

Fig. A2. Dunn's Posthoc test comparing the (a) Structure and (b) Enrichment Index across European environmental zones within each land use. Groups with identical letters are not significantly different from each other.

Data availability

Data will be made available trough 4TU.ResearchData under DOI: 10.4121/f78a7a49-486a-49af-b702-379313022890

References

Bennett, A.C., Penman, T.D., Arndt, S.K., Roxburgh, S.H., Bennett, L.T., 2020. Climate more important than soils for predicting forest biomass at the continental scale. Ecography 43, 1692–1705.

Bilgrami, A.L., Gaugler, R., 2004. Feeding behaviour. In: Gaugler, R., Bilgrami, A.L. (Eds.), Nematode Behaviour. CABI, Wallingford, UK, pp. 91–126.

Bongers, T., 1990. The maturity index - an ecological measure of environmental disturbance based on nematode species composition. Oecologia 83, 14–19.

Bongiorno, G., Bodenhausen, N., Bünemann, E.K., Brussaard, L., Geisen, S., Mäder, P., Quist, C.W., Walser, J.C., de Goede, R.G.M., 2019. Reduced tillage, but not organic matter input, increased nematode diversity and food web stability in European long-term field experiments. Mol. Ecol. 28, 4987–5005.

Borchers, H., 2023. _pracma: practical numerical math Functions_. R package version 2 (4), 4.

Bünemann, E.K., Bongiorno, G., Bai, Z.G., Creamer, R.E., De Deyn, G., de Goede, R., Fleskens, L., Geissen, V., Kuyper, T.W., Mäder, P., Pulleman, M., Sukkel, W., van Groenigen, J.W., Brussaard, L., 2018. Soil quality - a critical review. Soil Biol. Biochem. 120, 105–125.

Burkhardt, U., Russell, D.J., Decker, P., Döhler, M., Höfer, H., Römbke, J., Trog, C., Vorwald, J., Wurst, E., Xylander, W.E.R., 2014. The Edaphobase project of GBIF-Germany – a new online soil-organism zoological data warehouse. Appl. Soil Ecol. 83, 3–12.

Campos-Herrera, R., Palomares-Ruis, J.E., Blanco-Pérez, R., Rodríguez-Martín, J.A., Landa, B.B., Castillo, P., 2022. Irrigation modulates entomopathogenic nematode community and its soil food web in olive groves under different agricultural managements. Agric. Ecosyst. Environ. 337, 108070.

Celik, M.F., Isik, M.S., Yuzugullu, O., Fajraoui, N., Erten, E., 2022. Soil moisture prediction from remote sensing images coupled with climate, soil texture and topography via deep learning. Remote Sens-Basel 14, 5584.

Cesarz, S., Ciobanu, M., Wright, A.J., Ebeling, A., Vogel, A., Weisser, W.W., Eisenhauer, N., 2017. Plant species richness sustains higher trophic levels of soil nematode communities after consecutive environmental perturbations. Oecologia 184, 715–728.
CORINE Land cCover, CORINE land cover 1990-2018, European Union's Copernicus Land Monitoring Service information.
Creamer, R.E., Barel, J.M., Bongiorno, G., Zwetsloot, M., 2022. The life of soils: integrating the who and how of multifunctionality. Soil Biol. Biochem 166, 108561.
Darby, B.J., Neher, D.A., Belnap, J., 2007. Soil nematode communities are ecologically more mature beneath late- than early-successional stage biological soil crusts. Appl. Soil Ecol. 35, 203–212.
Decraemer, W., Hunt, D.J., 2006. Structure and classification. In: Perry, R.N., M.M. (Eds.), Plant nematology. CABI, Wallingford, UK, pp. 3–32.
Dee, L.E., Miller, S.J., Helmstedt, K.J., Boersma, K.S., Polasky, S., Reich, P.B., 2025. Quantifying disturbance effects on ecosystem services in a changing climate. Nat Ecol Evol 9, 436–447.
Didan, K., 2021. MODIS/Terra Vegetation Indices 16-Day L3 Global 250m SIN Grid V061 in: Center, NASA (EOSDIS Land Processes Distributed Active Archive Center (Ed.).
Douma, J.C., Shipley, B., 2021. A multigroup extension to piecewise path analysis. Ecosphere 12.
Du Preez, G., Daneel, M., De Goede, R., Du Toit, M.J., Ferris, H., Fourie, H., Geisen, S., Kakouli-Duarte, T., Korthals, G., Sanchez-Moreno, S., Schmidt, J.H., 2022. Nematode-based indices in soil ecology: application, utility, and future directions. Soil Biol. Biochem. 169.
Dunn, O.J., 1961. Multiple comparisons among means. J. Am. Stat. Assoc. 56, 52–64.
Eisenhauer, N., Bender, S.F., Calderón-Sanou, I., de Vries, F.T., Lembrechts, J.J., Thuiller, W., Wall, D.H., Zeiss, R., Bahram, M., Beugnon, R., Burton, V.J., Crowther, T.W., Delgado-Baquerizo, M., Geisen, S., Kardol, P., Krashevska, V., Martínez-Muñoz, C.A., Patoine, G., Seeber, J., Soudzilovskaia, N.A., Steinwandter, M., Sünnemann, M., Sun, X., van der Heijden, M.G.A., Guerra, C.A., Potapov, A., 2022. Frontiers in soil ecology—insights from the world biodiversity forum 2022. J. Sustain. Agric. Environ. 1, 245–261.
Eisenhauer, N., Buscot, F., Heintz-Buschart, A., Jurburg, S.D., Küsel, K., Sikorski, J., Vogel, H.-J., Guerra, C.A., 2021. The multidimensionality of soil macroecology. Glob. Ecol. Biogeogr. 30, 4–10.
European Commission, 2023. Proposal for a Directive Soil Monitoring and Resilience (Soil Monitoring Law), Brussels.
Ferrari, S., Cribari-Neto, F., 2004. Beta regression for modelling rates and proportions. J. Appl. Stat. 31, 799–815.
Ferris, H., Bongers, T., De Goede, R.G.M., 2001. A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. Appl. Soil Ecol. 18, 13–29.
Hijmans, R., 2022. geosphere: spherical Trigonometry. R package version 1, 5–18.
Hijmans, R., 2024. terra: spatial data Analysis. R package version 1, 7–78.
van den Hoogen, J., Geisen, S., Routh, D., Ferris, H., Traunspurger, W., Wardle, D.A., de Goede, R.G.M., Adams, B.J., Ahmad, W., Andriuzzi, W.S., Bardgett, R.D., Bonkowski, M., Campos-Herrera, R., Cares, J.E., Caruso, T., de Brito Caixeta, L., Chen, X., Costa, S.R., Creamer, R., da Cunha, Mauro, Castro, J., Dam, M., Djigal, D., Escuer, M., Griffiths, B.S., Gutierrez, C., Hohberg, K., Kalinkina, D., Kardol, P., Kergunteuil, A., Korthals, G., Krashevska, V., Kudrin, A.A., Li, Q., Liang, W., Magilton, M., Marais, M., Martin, J.A.R., Matveeva, E., Mayad, E.H., Mulder, C., Mullin, P., Neilson, R., Nguyen, T.A.D., Nielsen, U.N., Okada, H., Rius, J.E.P., Pan, K., Peneva, V., Pellissier, L., Pereira, Carlos, da Silva, J., Pitteloud, C., Powers, T.O., Powers, K., Quist, C.W., Rasmann, S., Moreno, S.S., Scheu, S., Setala, H., Sushchuk, A., Tiunov, A.V., Trap, J., van der Putten, W., Vestergard, M., Villenave, C., Waeyenberge, L., Wall, D.H., Wilschut, R., Wright, D.G., Yang, J.I., Crowther, T.W., 2019. Soil nematode abundance and functional group composition at a global scale. Nature 572, 194–198.
Jenny, H., 1941. Factors of Soil Formation: A System of Quantitative Pedology. Dover Publications, Dover Publications, New York.
Kakhani, N., Taghizadeh-Mehrjardi, R., Omarzadeh, D., Ryo, M., Heiden, U., Scholten, T., 2025. Towards explainable AI: interpreting soil organic carbon prediction models using a learning-based explanation method. Eur. J. Soil Sci. 76, e70071.
Köninger, J., Ballabio, C., Panagos, P., Jones, A., Schmid, M.W., Orgiazzi, A., Briones, M. J., 2023. Ecosystem type drives soil eukaryotic diversity and composition in Europe (vol 29, pg 5706, 2023). Glob. Chang. Biol. 29, 5706–5719.
Kouser, Y., Shah, A.A., Rasmann, S., 2021. The functional role and diversity of soil nematodes are stronger at high elevation in the lesser Himalayan Mountain ranges. Ecol. Evol. 11, 13793–13804.
Kruskal, W.H., Wallis, W.A., 1952. Use of ranks in one-criterion variance analysis. J. Am. Stat. Assoc. 47, 583–621.
Kudrin, A., Konakova, T.N., Taskaeva, A., 2019. Communities of soil nematodes of various tundra Phytocenoses differing in the development level of the shrub layer. Russ. J. Ecol. 50, 526–534.
Laasli, S.-E., Lahlali, R., Dababat, A.A., Paulitz, T., Assouguem, A., Ullah, R., Bari, A., İmren, M., Yüksel, E., Kenfaoui, J., Kiarie, L., Iraqi, D., Mokrini, F., 2024. Soil health in Moroccan olive agroecosystems: the bioindication role of terrestrial nematode dynamics. Heliyon 10, e40715.
Lauber, C., Strickland, M., Bradford, M., Fierer, N., Lauber, C.L., Strickland, M.S., Bradford, M.A., Fierer, N., 2008. The influence of soil properties on the structure of bacterial and fungal communities across land-use types. Soil biol Biochem 40: 2407-2415. Soil Biol. Biochem. 40, 2407–2415.
Li, X.P., Zhu, H.M., Geisen, S., Bellard, C., Hu, F., Li, H.X., Chen, X.Y., Liu, M.Q., 2020. Agriculture erases climate constraints on soil nematode communities across large spatial scales. Glob. Chang. Biol. 26, 919–930.
Lüdecke, D.B.-S., Mattan, S., Patil, Indrajeet, Waggoner, Philip, Makowski, Dominique, 2021. Performance: an R package for assessment, comparison and testing of statistical models. Journal of Open Source Software 6 (60).
Matveeva, E.M., Sushchuk, A.A., 2016. Features of soil nematode communities in various types of natural biocenoses: effectiveness of assessment parameters. Biol. Bull. 43, 474–482.
Metzger, M.J., Bunce, R.G.H., Jongman, R.H.G., Mücher, C.A., Watkins, J.W., 2005. A climatic stratification of the environment of Europe. Glob. Ecol. Biogeogr. 14, 549–563.
Morrien, E., Hannula, S.E., Snoek, L.B., Helmsing, N.R., Zweers, H., de Hollander, M., Soto, R.L., Bouffaud, M.L., Buee, M., Dimmers, W., Duyts, H., Geisen, S., Girlanda, M., Griffiths, R.I., Jorgensen, H.B., Jensen, J., Plassart, P., Redecker, D., Schmelz, R.M., Schmidt, O., Thomson, B.C., Tisserant, E., Uroz, S., Winding, A., Bailey, M.J., Bonkowski, M., Faber, J.H., Martin, F., Lemanceau, P., de Boer, W., van Veen, J.A., van der Putten, W.H., 2017. Soil networks become more connected and take up more carbon as nature restoration progresses. Nat Commun 8.
Muñoz Sabater, J., 2019. ERA5-Land monthly averaged data from 1950 to present., in: (CDS), Copernicus Climate Change Service (C3S) Climate Data Store (CDS) (Ed.).
NASA/METI/AIST/Japan Spacesystems, U.S./Japan ASTER Science Team, 2018. ASTER Global Digital Elevation Model V003 (NASA EOSDIS Land Processes DAAC).
Neher, D.A., Campbell, C.L., 1994. Nematode communities and microbial biomass in soils with annual and perennial crops. Appl. Soil Ecol. 1, 17–28.
Neher, D.A., Easterling, K.N., Fiscus, D., Campbell, C.L., 1998. Comparison of nematode communities in agricultural soils of North Carolina and Nebraska. Ecol. Appl. 8, 213–223.
Neher, D.A., Wu, J., Barbercheck, M.E., Anas, O., 2005. Ecosystem type affects interpretation of soil nematode community measures. Appl. Soil Ecol. 30, 47–64.
Nielsen, U.N., Ayres, E., Wall, D.H., Li, G., Bardgett, R.D., Wu, T.H., Garey, J.R., 2014. Global-scale patterns of assemblage structure of soil nematodes in relation to climate and ecosystem properties. Glob. Ecol. Biogeogr. 23, 968–978.
Ogle, D.H.D., C, J., Wheeler, A.P., Dinno, A., 2023. FSA: simple fisheries stock assessment Methods. R package version 0 (9), 5.
Orgiazzi, A., Ballabio, C., Panagos, P., Jones, A., Fernández-Ugalde, O., 2018. LUCAS soil, the largest expandable soil dataset for Europe: a review. Eur. J. Soil Sci. 69, 140–153.
Peneva, V., Lazarova, S., Elshishka, M., Makarova, O., Penev, L., 2009. Nematode assemblages of hair-grass (Deschampsia spp.) microhabitats from polar and alpine deserts in the Arctic and Antarctic.
Phillips, H., Guerra, C., Bartz, M., Briones, M., Brown, G., Crowther, T., Ferlian, O., Gongalsky, K., van den Hoogen, J., Krebs, J.J., Orgiazzi, A., Routh, D., Schwarz, B., Bach, E., Bennett, J., Brose, U., Decaëns, T., König-Ries, B., Loreau, M., Schmidt, O., 2019. Global distribution of earthworm diversity. Science 366, 480–485.
Poggio, L., de Sousa, L.M., Batjes, N.H., Heuvelink, G.B.M., Kempen, B., Ribeiro, E., Rossiter, D., 2021. SoilGrids 2.0: producing soil information for the globe with quantified spatial uncertainty. Soil 7, 217–240.
Potapov, A.M., Guerra, C.A., van den Hoogen, J., Babenko, A., Bellini, B.C., Berg, M.P., Chown, S.L., Deharveng, L., Kovác, L., Kuznetsova, N.A., Ponge, J.F., Potapov, M.B., Russell, D.J., Alexandre, D., Alatalo, J.M., Arbea, J.I., Bandyopadhyaya, I., Bernava, V., Bokhorst, S., Bolger, T., Castaño-Meneses, G., Chauvat, M., Chen, T.W., Chomel, M., Classen, A.T., Cortet, J., Cuchta, P., Manuela de la Pedrosa, A., Ferreira, S.S.D., Fiera, C., Filser, J., Franken, O., Fujii, S., Koudji, E.G., Gao, M.X., Gendreau-Berthiaume, B., Gomez-Pamies, D.F., Greve, M., Tanya Handa, I., Heiniger, C., Holmstrup, M., Homet, P., Ivask, M., Janion-Scheepers, C., Jochum, M., Joimel, S., Jorge, B.C.S., Jucevica, E., Ferlian, O., de Oliveira, L.C.I., Klauberg, O., Baretta, D., Krab, E.J., Kuu, A., de Lima, E.C.A., Lin, D.M., Lindo, Z., Liu, A., Lu, J.Z., Luciañez, M.J., Marx, M.T., McCary, M.A., Minor, M.A., Nakamori, T., Negri, I., Ochoa-Hueso, R., Palacios-Vargas, J.G., Pollierer, M.M., Querner, P., Raschmanová, N., Rashid, M.I., Raymond-Léonard, L.J., Rousseau, L., Saifutdinov, R. A., Salmon, S., Sayer, E.J., Scheunemann, N., Scholz, C., Seeber, J., Shveenkova, Y. B., Stebaeva, S.K., Sterzynska, M., Sun, X., Susanti, W.I., Taskaeva, A.A., Thakur, M. P., Tsiafouli, M.A., Turnbull, M.S., Twala, M.N., Uvarov, A.V., Venier, L.A., Widenfalk, L.A., Winck, B.R., Winkler, D., Wu, D.H., Xie, Z.J., Yin, R., Zeppelini, D., Crowther, T.W., Eisenhauer, N., Scheu, S., 2023. Globally invariant metabolism but density-diversity mismatch in springtails. Nat. Commun. 14.
Puissant, J., Villenave, C., Chauvin, C., Plassard, C., Blanchart, E., Trap, J., 2021. Quantification of the global impact of agricultural practices on soil nematodes: a meta-analysis. Soil Biol. Biochem. 161, 108383.
Pulleman, M., Creamer, R., Hamer, U., Helder, J., Pelosi, C., Pérès, G., Rutgers, M., 2012. Soil biodiversity, biological indicators and soil ecosystem services—an overview of European approaches. Curr. Opin. Environ. Sustain. 4, 529–538.
R Core Team, 2024. _R: A Language and Environment for Statistical Computing_. R Foundation for Statistical Computing, Vienna, Austria.
Ruess, L., 2024. Nematodes and their Trophic Interactions in the Soil Microbiome: Understanding and Utilising Soil Microbiomes for a more Sustainable Agriculture.
Shao, Y., Wang, Z., Liu, T., Kardol, P., Ma, C., Hu, Y., Cui, Y., Zhao, C., Zhang, W., Guo, D., Fu, S., 2023. Drivers of nematode diversity in forest soils across climatic zones. Proc. R. Soc. B Biol. Sci. 290, 20230107.
Shipley, B., 2000. A new inferential test for path models based on directed acyclic graphs. Struct. Equ. Model. Multidiscip. J. 7, 206–218.
Shipley, B., 2013. The AIC model selection method applied to path analytic models compared using a d-separation test. Ecology 94, 560–564.
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.
Siles, J.A., Vera, A., Díaz-López, M., García, C., van den Hoogen, J., Crowther, T.W., Eisenhauer, N., Guerra, C., Jones, A., Orgiazzi, A., Delgado-Baquerizo, M.,

Bastida, F., 2023. Land-use- and climate-mediated variations in soil bacterial and fungal biomass across Europe and their driving factors. Geoderma 434.
Sohlenius, B., Sandor, A., 1987. Vertical distribution of nematodes in arable soil under grass (Festuca pratensis) and barley (Hordeum distichum). Biol. Fertil. Soils 3, 19–25.
Song, D.G., Pan, K.W., Tariq, A., Sun, F., Li, Z.L., Sun, X.M., Zhang, L., Olusanya, O.A., Wu, X.G., 2017. Large-scale patterns of distribution and diversity of terrestrial nematodes. Appl. Soil Ecol. 114, 161–169.
Tsiafouli, M.A., Bhusal, D.R., Sgardelis, S.P., 2017. Nematode community indices for microhabitat type and large scale landscape properties. Ecol. Indic. 73, 472–479.
Tsiafouli, M.A., Thebault, E., Sgardelis, S.P., de Ruiter, P.C., van der Putten, W.H., Birkhofer, K., Hemerik, L., de Vries, F.T., Bardgett, R.D., Brady, M.V., Bjornlund, L., Jorgensen, H.B., Christensen, S., D' Hertefeldt, T., Hotes, S., Hol, W.H.G., Frouz, J., Liiri, M., Mortimer, S.R., Setala, H., Tzanopoulos, J., Uteseny, K., Pizl, V., Stary, J., Wolters, V., Hedlund, K., 2015. Intensive agriculture reduces soil biodiversity across Europe. Glob. Chang. Biol. 21, 973–985.
Van den Hoogen, J., Geisen, S., Wall, D.H., Wardle, D.A., Traunspurger, W., de Goede, R. G.M., Adams, B.J., Ahmad, W., Ferris, H., Bardgett, R.D., Bonkowski, M., Campos-Herrera, R., Cares, J.E., Caruso, T., de Brito Caixeta, L., Chen, X., Costa, S.R., Creamer, R., da Cunha, E.C.J.M., Dam, M., Djigal, D., Escuer, M., Griffiths, B.S., Gutierrez, C., Hohberg, K., Kalinkina, D., Kardol, P., Kergunteuil, A., Korthals, G., Krashevska, V., Kudrin, A.A., Li, Q., Liang, W., Magilton, M., Marais, M., Martin, J.A. R., Matveeva, E., Mayad, E.H., Mzough, E., Mulder, C., Mullin, P., Neilson, R., Nguyen, T.A.D., Nielsen, U.N., Okada, H., Rius, J.E.P., Pan, K., Peneva, V., Pellissier, L., da Silva, J.C.P., Pitteloud, C., Powers, T.O., Powers, K., Quist, C.W., Rasmann, S., Moreno, S.S., Scheu, S., Setala, H., Sushchuk, A., Tiunov, A.V., Trap, J., Vestergard, M., Villenave, C., Waeyenberge, L., Wilschut, R.A., Wright, D.G., Keith, A.M., Yang, J.I., Schmidt, O., Bouharroud, R., Ferji, Z., van der Putten, W.H., Routh, D., Crowther, T.W., 2020. A global database of soil nematode abundance and functional group composition. Sci Data 7, 103.
De Vries, W.R.m., P.F.A.M., Kros, J., Voogd, J.C., Schulte-Uebbing, L.F., 2022. Impacts of Nutrients and Heavy Metals in European Agriculture. Current and Critical Inputs in Relation to Air, Soil and Water Quality. ETC-DI.
Wadoux, A.M.J.C., Minasny, B., McBratney, A.B., 2020. Machine learning for digital soil mapping: applications, challenges and suggested solutions. Earth Sci. Rev. 210.
Wall, D.H., Virginia, R.A., 1999. Controls on soil biodiversity: insights from extreme environments. Appl. Soil Ecol. 13, 137–150.
Yan, D., Yan, D., Song, X., Yu, Z., Peng, D., Ting, X., Weng, B., 2018. Community structure of soil nematodes under different drought conditions. Geoderma 325, 110–116.
Yeates, G., 2004. Ecological and behavioural adaptations. In: Gaugler, R., Bilgrami, A.L. (Eds.), Nematode Behaviour. CABI, Wallingford, UK, pp. 1–24.
Yeates, G.W., 2010. Nematodes in ecological webs. In: Encyclopedia of Life Sciences (ELS). John Wiley & Sons Ltd., Chichester, UK, pp. 1–11.
Yin, C., Chen, X., Luo, M., Meng, F., Sa, C., Bao, S., Yuan, Z., Zhang, X., Bao, Y., 2023. Quantifying the contribution of driving factors on distribution and change of net primary productivity of vegetation in the Mongolian plateau. Remote Sens-Basel 15, 1986.
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.
Zscheischler, J., Mahecha, M.D., Harmeling, S., Reichstein, M., 2013. Detection and attribution of large spatiotemporal extreme events in earth observation data. Ecol Inform 15, 66–73.