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Biodiversity co-variation patterns in a range of soil organism taxa across highly contrasting ecosystems

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ABSTRACT

Soil biodiversity as a critical component of terrestrial ecosystems and their functioning varies across spatial scales and environmental conditions. However, it remains unclear whether and how biodiversity patterns co-vary among different soil taxa across ecosystems.

In this study, we compared diversity patterns of plants, earthworms, nematodes, bacteria, and fungi, as five major groups of soil organisms, across six strongly contrasting ecosystems ranging from mountain peatland to crop fields, including within-ecosystem variation in soil moisture. We hypothesized co-variation in taxonomic richness (alpha diversity) and composition (beta diversity) of multiple groups of soil organisms across ecosystems, moisture conditions and spatial scales.

In partial contrast to our initial hypothesis, co-variation in the taxonomic richness among these groups was limited, though significant positive associations were found among bacteria, fungi, and earthworms across all sites. Plant diversity showed distinct associations with soil organism diversity, particularly with earthworms and bacteria, highlighting above–belowground biodiversity linkages. Beta diversity showed substantial co-variation among all soil organism groups, reflecting a spatial coupling of their communities that was influenced by differences in soil moisture conditions. These patterns were more pronounced in near-natural and no-till agroecosystems compared to conventional agricultural systems. Our results highlight that ecosystem type shapes broad-scale taxonomic richness, while local soil moisture critically influences soil biodiversity and spatial community composition, emphasizing the multi-scale drivers of soil biodiversity.

1. Introduction

Soil biodiversity is a critical component of terrestrial ecosystems, contributing to essential ecosystem functions such as the regulation of nutrient cycling and carbon dynamics (Wall et al., 2012; Bardgett and Van Der Putten, 2014; Eisenhauer et al., 2017; Guerra et al., 2020). This diversity encompasses a wide range of organisms, including plants, soil fauna, and microorganisms, each playing distinct yet interrelated roles across various spatial and temporal scales (Bardgett and Van Der Putten, 2014). Plants, earthworms, nematodes, bacteria, and fungi have been

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shown to be particularly important in structuring soil food webs and influencing community dynamics across multiple spatial scales (Berg and Bengtsson, 2007; Brussaard et al., 2007; Morriën, 2016). Plants, as primary producers, are at the bottom of the soil food web by contributing most of the organic matter to soils (Cebrian and Lartigue, 2004), while earthworms act as ecosystem engineers, modifying soil structure and other properties such as organic matter content and its distribution (Lavelle et al., 1997; Lavelle and Spain, 2001; Blouin et al., 2013). Nematodes, along with bacterial and fungal communities, drive much of the nutrient cycling, and are thus at the interface of soil fauna and primary producers, playing an essential role in biodiversity dynamics (Bardgett and Van Der Putten, 2014; Trap et al., 2016; van den Hoogen et al., 2019; Zhang et al., 2024).

All these organisms interact within a complex soil ecological network, the determinism of which remains poorly understood (Potapov et al., 2023). Key abiotic drivers such as soil moisture, temperature, and nutrient availability significantly affect the spatial distribution of soil community composition and diversity. The different groups of soil organisms differ in their sensitivity and range of tolerance to variability in these abiotic factors, adding to the complexity of soil community responses to environmental gradients (Siebert et al., 2019). Biotic interactions are a further component influencing spatial patterns and dynamics of diversity. For example, plant-derived resources have a direct effect on the diversity and structure of the heterotrophic soil fauna and microbial communities (Korboulewsky et al., 2016; Fujii et al., 2020) and different trophic guilds of nematodes feeding either on bacteria, fungi, or plant roots depend on these groups of organisms for their growth and reproduction (Yeates et al., 1993). However, the extent to which soil food webs are structured across different spatial scales remains largely unexplored (Liu et al., 2020). Surprisingly little is known about how composition and diversity co-vary among different groups of soil organisms across various types of ecosystems, spatial scales, and environmental gradients (Maraun et al., 2003; Eisenhauer et al., 2012). This is despite the fact that such knowledge is critical to anticipate changes in soil biodiversity in the current context of land-use and climate change. Ecosystem-type independent general patterns of soil biodiversity may also provide the possibility for relatively easy to determine proxies for soil biodiversity with the increasing need for ecosystem monitoring and assessment.

Human activities are likely to have a profound impact on the composition and diversity of soil biological communities (De Vries et al., 2013). The simplification or alteration of sources of organic matter in agroecosystems, compared to near-natural ecosystems, can lead to reduced soil biodiversity, biotic homogenization, and potentially weaker resilience to climate fluctuations (De Vries et al., 2012; Tsiafouli et al., 2015). The increasing frequency and intensity of extreme climatic events pose further risks, potentially accentuating biodiversity loss, decline in abundance of certain taxa, and shifts in community composition, which may result in a loss of soil organism functional diversity (Maestre et al., 2015; Cavicchioli et al., 2019; Guerra et al., 2021). Flooding, droughts and subsequent soil rewetting, for example, can impose significant stress on various organism groups, from plants to microorganisms (Schimel, 2018). Understanding how human activities and climate change-induced variations in water regimes influence soil organism diversity is therefore crucial for predicting ecosystem responses and ensuring sustainable management practices (Dubrovský et al., 2014).

To estimate variation and shifts in communities across ecosystems and environmental conditions requires assessments beyond alpha diversity, that characterizes the richness and diversity of soil communities within a given site or spatial scale. Rather, beta diversity has emerged as a key metric for understanding how biodiversity changes across different spatial scales, environmental gradients, or disturbance regimes. Beta diversity explicitly takes into account the composition of the communities (e.g. the identity of the species), and quantifies the difference in composition across different sites (Soininen et al., 2018). It provides valuable insights into both near-natural ecosystems and intensively managed ecosystems such as agroecosystems, as it integrates across the effects of land use, habitat fragmentation, and environmental heterogeneity on biodiversity. High beta diversity at a given site underlies ecosystem stability and resilience, while its decline may reveal biotic homogenization and a loss of functional diversity, with significant implications for ecosystem services and functioning (Mori et al., 2018). Beta diversity also reflects the influence of abiotic factors, such as soil moisture, and of biotic interactions, which vary across ecosystems. Distinct patterns in beta diversity may help us better understand how certain taxa could serve as indicators of biodiversity changes, aiding conservation and monitoring efforts. Distinguishing between turnover, i.e. the replacement of species, and nestedness, i.e. the subset of species occurring in different communities, may further provide insight into the underlying processes shaping biodiversity patterns and community assembly (Mori et al., 2018). While turnover is often driven by environmental differences or disturbances, and tends to dominate at local and regional scales where communities respond to distinct ecological filters, nestedness is often a result of habitat degradation or species loss (Baselga, 2010, 2012).

In this study, we aim to assess how the diversity and composition of different groups of soil organisms, with a focus on plants, earthworms, nematodes, fungi and bacteria, co-vary and to what degree such covariation differs across spatial scales. Specifically, we explore whether the contrasting environmental conditions in agroecosystems, compared to near-natural ecosystems, are associated with distinct patterns of covariation in the diversity and composition of different soil organism groups. We also examine whether changes in diversity caused by varying moisture conditions across different ecosystem types are correlated among different groups of soil organisms. We expected that the diversity of plants, implying biochemical diversity of rhizodeposits influencing soil organic matter chemistry, should favor more diverse soil bacterial and fungal, nematode, and earthworm communities. As such, we hypothesized that taxonomic richness and community composition of the different groups of organisms co-vary spatially. We further anticipated that soil moisture conditions would modulate above-belowground diversity relationships, with the nature of these couplings varying according to organism groups and moisture conditions. Moderate moisture differences might sustain positive co-variations among organism groups through shared resource and habitat conditions, while extreme moisture levels (drought or waterlogging) would act as strong environmental filters disrupting these associations. Specifically, we hypothesized that in excessively wet conditions, fauna (earthworms, nematodes) would show reduced diversity due to hypoxia, while microbial diversity (bacteria, fungi) might increase due to enhanced moisture availability. Conversely, under drier conditions, plant-fauna diversity couplings might be maintained through plant-mediated mechanisms supporting soil fauna diversity, whereas microbial communities would likely exhibit drought-adapted compositions. These expectations reflect the different physiological and ecological tolerances of organism groups to soil moisture stress.

By examining these patterns, our research seeks to improve our understanding of the relationships among different soil biodiversity components, providing essential insights for biodiversity conservation and sustainable ecosystem management.

2. Material and methods

2.1. Study areas and design

Six study sites were selected in the Occitanie region, France, to encompass a gradient of land-use intensity from near-natural ecosystems to agroecosystems (Fig. 1). The three near-natural ecosystems included a Mediterranean oak forest, a mountain peatland, and a temperate riparian forest. **The three near-natural habitats were chosen to represent highly contrasting environmental and ecological conditions,**

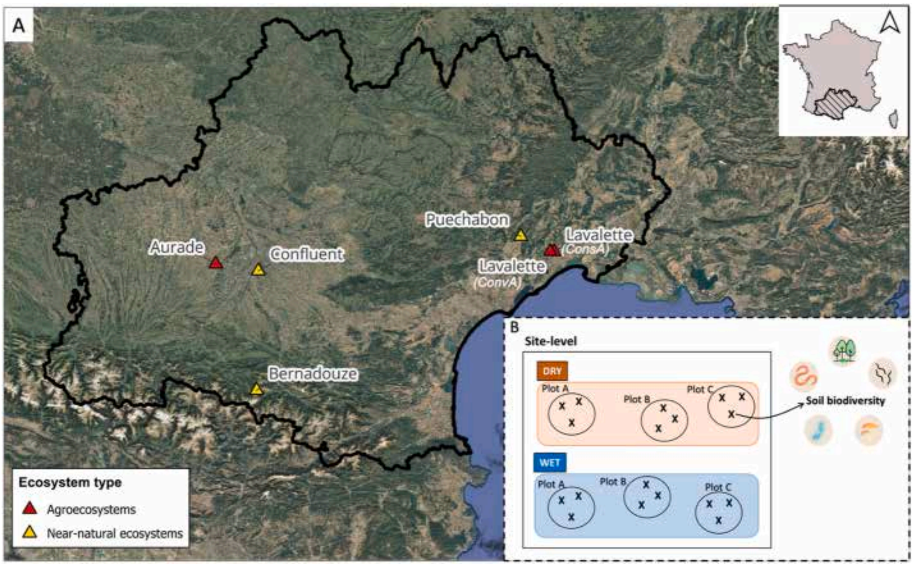

Fig. 1. (A) Geographic location of the study sites in southern France, representing agroecosystems (red triangles) and near-natural ecosystems (yellow triangles). The sites include Auradé, Confluent, Lavalette (ConvA and ConsA, conventional and conservation agriculture respectively), Puéchabon, and Bernadouze. (B) Schematic representation of the sampling experimental design with the two site-specific extremes in soil moisture (dry and wet). Each of these humidity conditions includes three plots (A, B, C), each with three sampling points located in close proximity (3 m). Soil biodiversity (plants and their roots, earthworms, nematodes, bacteria, fungi) is assessed at each sampling point. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

spanning variations in environmental constraints, soil types, vegetation structure, and successional stages, allowing us to examine how soil biodiversity varies along these gradients, with each habitat offering unique soil properties and microclimates that drive soil biodiversity. The three agroecosystems comprised a temperate crop field and two Mediterranean crop fields, the latter under contrasting soil management practices (conventional tillage and conservation agriculture). This distinction resulted in a total of six study sites, spanning a broad gradient of land-use intensity and soil moisture conditions.

The Mediterranean oak forest at Puéchabon has been instrumented since 2001 as part of several national and international research infrastructures (ICOS https://meta.icos-cp.eu/resources/stations/ES_FR-Pue, AnaEE RI, OSU OREME) with continuous monitoring of water and carbon budgets along with meteorological and soil variables. The mountain peatland of Bernadouze, is a long term monitoring site (OHM Homme Milieu, SNO Tourbières, https://deims.org/708c9dcd-6757-4bb8-b849-3cc5666252f2) for water and carbon budgets (Rosset et al., 2020; Garisoain et al., 2024). The temperate riparian forest is part of a nature reserve at the confluence of the Garonne and Ariège rivers, characterized by periodic flooding and fluctuating groundwater levels (RNR Confluence Garonne-Ariège, 2024). The temperate crop field at Auradé (temperate conventional agriculture hereafter) has followed a wheat/rapeseed/wheat/sunflower crop rotation since 2004, with the recent introduction of winter cover crops (ICOS https://meta.icos-cp.eu/resources/stations/ES_FR-Aur). Within the Mediterranean crop field at Lavalette (OSU OREME), two management systems were considered as distinct study sites: conventional tillage (Mediterranean conventional agriculture hereafter) and no-till conservation agriculture (Mediterranean conservation agriculture).

Together, these six sites covered a wide range of ecosystem types, climatic conditions, soil properties and land-use intensities (Table 1, Table B 1), allowing examination of how soil biodiversity responds to contrasting environmental conditions. The classification into "dry" and "wet" plots was based on long-term monitoring of soil water content or intrinsic experimental setups (e.g., rain exclusion and irrigation). We additionally installed soil humidity sensors (TMS-4 data loggers, TOMST, Prague, Czech Republic, Wild et al., 2019) at all sampling plots at time of sampling and measured soil humidity over the course of one year. The variability in soil moisture within these sites was driven by either experimental manipulation or natural hydrological dynamics. At Puéchabon (Mediterranean oak forest), a long-term rainfall exclusion experiment, implemented since 2003, reduces precipitation by 25–30 % to simulate drier conditions (Limousin et al., 2009; Gavinet et al., 2019). At Lavalette (Mediterranean crop field), soil moisture is influenced by contrasting irrigation practices in each of the two management regimes (conventional and conservation agriculture). In contrast, at Bernadouze (mountain peatland), Confluent (temperate riparian forest), and Auradé (temperate conventional agriculture), soil moisture variability arises from contrasting topography. These sites are monitored for multiple years with continuous data collection of climatic and soil variables. Based on this monitoring, six plots were identified within each site (three in comparatively wetter and three in comparatively drier conditions, see sampling design description below). This classification integrates multiple temporal and spatial variations in soil moisture records, taking into account parameters such as topography, distance from the river, and depth of the water table, in addition to quantitative data from soil moisture loggers (Fig. B 1).

Although variable among sites, individual plots were on average at a distance of about 50 m (maximum range between 10 m and 200 m). Within each site, six plots were established at the extremes of the site-specific soil moisture gradient, three representing comparatively wetter conditions and three representing drier conditions (Fig. 1). Each plot contained three sampling points (1 m^2 each) spaced approximately 3 m apart, resulting in 18 sampling points per site and 108 across all sites.

2.2. *Data collection*

Data on soil organism diversity were collected between 28 March 2022 (Lavalette) and 10 June 2022 (Bernadouze), following the sequence of sites: Lavalette (ConvA) – Lavalette (ConsA) - Puechabon - Confluent - Auradé – Bernadouze. Sampling was aligned with the site-specific phenological spring, defined by leaf outbreak of deciduous woody species to assure sampling at the same phenological period at all sites. Sampling was conducted under generally mild and favorable weather conditions for soil biodiversity sampling typical of Spring following a relatively mild Winter. While daily variations in weather (e.

Table 1

Environmental and soil properties of the six study sites (including two management types at the Lavalette site). Mean annual precipitation (MAP), mean annual temperature (MAT); Soil texture is represented by proportions of sand, silt and clay.

Site	GPS coordinates	Climate type	Ecosystem type	Land use	Drivers of within-site variation in soil moisture	Altitude (m a.s.l.)	MAP (mm)	MAT (°C)	Soil pH	Soil bulk density (g. cm-3)	Soil C/N	Soil organic matter (g/kg)	Sand (g/kg)	Silt (g/kg)	Clay (g/kg)
Auradé (Temperate conventional agriculture)	43°32′58.7"N 1°06′22.0"E	Mediterranean, hot and dry summer (Csa)	Agroecosystem	Conventional agriculture	Topography	250	668	13.1	6.4 ± 0.55	1.3 ± 0.09	9.2 ± 0.42	18.2 ± 3.13	202 ± 65	498 ± 66	300 ± 58
Lavalette (Mediterranean conventional agriculture)	43°38′42.7"N, 3° 52′ 28.1"E	Mediterranean, hot and dry summer (Csa)	Agroecosystem	Conventional agriculture	Irrigation	38	745	14.7	8.5 ± 0.04	1.5 ± 0.07	9.4 ± 0.99	15.0 ± 2.10	363 ± 88	438 ± 58	200 ± 31
Lavalette (Mediterranean conservation agriculture)	43°38′42.7"N, 3° 52′ 28.1"E	Mediterranean, hot and dry summer (Csa)	Agroecosystem	Conservation agriculture	Irrigation	38	745	14.7	8.5 ± 0.05	1.8 ± 0.06	10.4 ± 0.81	20.7 ± 3.59	354 ± 101	442 ± 68	205 ± 35
Puéchabon (Mediterranean oak forest)	43°44′29’’N, 3°35′45’’E	Transitional Mediterranean, warm summer (Cfb)	Near-natural ecosystem (Evergreen broadleaf forest - EBF)	Unmanaged forest	Rain exclusion	270	967	13.5	7.6 ± 0.17	0.82 ± 0.08	18.7 ± 3.27	176 ± 50	282 ± 66	517 ± 81	201 ± 49
Bernadouze (Mountain peatland)	42°48′09.3"N 1°25′25.7"E	Sub-alpine, warm summer (Cfb)	Near-natural ecosystem (Minerotrophic peatland)	Extensive grazing	Elevation above the water table	1343	1478	7.5	5.1 ± 0.8	0.12 ± 0.04	26.6 ± 11.6	749 ± 186	–	–	–
Confluent (Temperate riparian forest)	43°31′24.1"N 1°25′07.4"E	Transitional Mediterranean, warm summer (Cfb)	Near-natural ecosystem	Natural reserve	Proximity to and elevation above the Garonne River	145	660	14.4	7.9 ± 0.08	0.86 ± 0.18	12.6 ± 0.97	63.0 ± 14.9	237 ± 164	505 ± 113	259 ± 62

g., sunny or rainy days) can influence soil fauna activity, particularly for earthworms, conditions during our sampling were consistently humid across sites, minimizing potential biases in organism representation.

At each sampling point (1 m^2), a soil monolith (25 × 25 cm, 0–20 cm depth) was collected from the center of the vegetation survey area to assess earthworm organism communities, which can have significant vertical activity. Four cylindrical soil cores (5.3 cm in diameter, 0–10 cm depth) were taken 5 cm away from each side of the monolith to quantify soil bulk density and physicochemical properties, and to characterize soil microbial (bacteria, fungi) and nematode communities. The 0–10 cm layer was chosen because it corresponds to the biologically most active topsoil horizon, where most microorganisms and fine roots occur. An additional soil core (5 cm in diameter to a depth of 5 cm) was taken at each sampling point to determine soil water content at field capacity. All sampling procedures followed international standard protocols for soil parameters and the specific groups of soil organisms to ensure comparability of biodiversity and soil measurements with other databases globally. Prior to monolith and core extractions, surface litter was carefully removed from the topsoil layer.

2.2.1. *Soil properties*

The soil cores specifically sampled to determine soil water content at field capacity were covered with lids on both sides immediately after sampling and transported to the laboratory. Fresh weight at sampling was measured before the cores were placed in a water bath for 12h. The water saturated cores were then placed with a lid on top on a water-filled sand bath and drained for 48 h to reach field capacity, reweighed and then dried at 105 °C to constant weight and weighed again.

2.2.2. *Vegetation survey*

At each sampling point, we started with the identification of all plant species within the sampling plot area of 1 m^2. Identification was performed at the species levels for almost all individuals except for rare cases where seedlings could only be identified at the genus or family level. We visually estimated total plant cover (in %), as well as cover of each individual species (Dengler, 2023). Relative species abundance was calculated based on proportion of total species-level cover values. For plot- and site-level considerations we averaged the percentage cover values obtained at the sampling point level.

2.2.3. *Earthworm sampling*

Earthworms were extracted manually from one half (vertical split) of the soil monoliths and placed in a vial containing soil for transport. In the laboratory, earthworms were counted, weighed and identified based on Bouché (1972).

2.2.4. *Nematode community sampling and identification*

Nematodes were extracted using the Oostenbrink direct cottonwood filter method (Townshend, 1963) using a 16 cm diameter and 2 cm deep PVC “Petri dish”-Baermann device from 100 g of fresh soil samples for 48h at 25 °C in the dark. Extracted nematodes were then counted under a stereomicroscope and around 200 individuals per sample were randomly selected and identified at the genus or family level with a compound microscope. Taxa were then assigned to trophic groups as described by Yeates et al. (1993). Nematode genus abundance was calculated as number of nematodes per kg of dry soil.

2.2.5. *Microbial soil community*

For microbial community analysis, all samples were sieved to 2 mm and immediately frozen for molecular analyses upon return from the field.

In order to characterize diversity of bacterial and fungal communities, total soil genomic DNA was extracted from 500 mg of soil with the FastDNA SPIN™ kit for soil (MP Biomedicals Santa Ana, CA, USA) as described by Tournier et al. (2015). DNA was quantified using PicoGreen fluorescence (Molecular Probes, Paris, France) and kept at −20 °C until amplification.

Bacterial and fungal community diversity were assessed by sequencing the V3–V4 region of the 16S rDNA and the internal transcribed spacer ITS2 of the nuclear ribosomal RNA on a MiSeq Illumina sequencer. Sequencing was performed by ADNId laboratory Qualtech group (https://www.adnid.fr/) (Montpellier, France) as described in Brondani et al. (2022). Primers and PCR conditions are described in Appendix B (Appendix B, Table B 2).

DNA amplification was performed by PCR in a total volume of 15 μl containing 1X master mix, Type-it Microsatellite PCR Kit (Qiagen, Hilden, Germany), 0.13 μM of each primer and 2 μl of genomic extracted DNA. PCR amplifications were verified by electrophoresis migration on a 1.5 % agarose gel. PCR products were purified using the Agencourt® AMPure® XP kit (Beckman Coulter, Italy, Milano). Each PCR product was tagged using the Nextera XT DNA Library Prep Kit (Illumina Inc., San Diego, CA) in a second PCR reaction. Tagged PCR products were purified using the Agencourt® AMPure® XP kit (Beckman Coulter, Italy, Milano) and quantified with the Tecan Nanoquant spectrometer. Equal amounts of DNA for each sample were pooled and then cleaned using the Agencourt® AMPure® XP kit (Beckman Coulter, Italy, Milano). The DNA library was controlled on Fragment analyzer from Advanced Analytical and quantified using SYBR Green-Quantitative Polymerase Chain Reaction on real-time PCR. The DNA library was finally sequenced on an Illumina Miseq instrument with 2 × 250-bp technology and V2 chemistry (Illumina Inc., San Diego, California, USA). For bacterial and fungal community analysis, sequences were clustered using SWARM with a distance of 1, which is a distance-based method rather than a percentage similarity threshold. Although this approach is similar to generating Amplicon Sequence Variants (ASVs), we refer to these clusters as OTUs throughout the manuscript for consistency. Illumina sequencing data were analyzed as described in Brondani et al. (2022). The raw data are available under the bioproject PRJEB106611 (Table B 2).

2.3. *Diversity indices*

Organisms were identified to the highest possible taxonomic resolution, which varied by group according to common practice, such discrepancies are inevitable given the wide range of organisms considered here. Plants and earthworms were identified to the species level, nematodes to the genus level and bacteria and fungi to operational taxonomic units (OTU). At each sampling point, we calculated relative abundance for each taxon as well as total species, genus, or OTU richness. To assess patterns at broader spatial scales, we aggregated these measures at the plot and ecosystem levels by calculating mean relative abundance across all sampling points within each spatial unit. As taxonomic identification was based on different taxonomic identification levels, we use the term taxonomic richness throughout. We also calculated the Shannon diversity index using the *vegan* package (Oksanen et al., 2022).

We calculated a multidiversity index following the procedure of Beaumelle et al. (2023), using the standardized richness of the five soil organism groups. Specifically, for each group, we computed a z-score of taxonomic richness and averaged these values to obtain a single multidiversity index (Allan et al., 2014).

To assess spatial associations between organism groups and compare beta diversity partitioning, we first calculated beta diversity using presence/absence data to ensure consistency across taxa, excluding abundance. We used the Sørensen dissimilarity index (β_{SOR}) to quantify total compositional variation ($\beta_{SOR} = \beta_{SIM} + \beta_{SNE}$), where β_{SIM} represents turnover, and β_{SNE} accounts for nestedness-resultant dissimilarity, measured on a normalized scale from zero to one.

2.4. *Statistical analyses*

For each organism group, mean taxonomic richness and Shannon diversity were computed per site and per site x soil moisture condition. Pairwise post-hoc comparisons were performed between sites following a Kruskal-Wallis test to identify significant differences between groups; significant groupings are indicated by letters on the boxplots. To evaluate the differences in mean diversity metrics based on soil moisture across sites, Wilcoxon rank-sum tests were conducted separately for each organism group and each site. Detailed results of these tests are provided in appendix A.

We performed additive diversity partitioning to decipher the proportional contributions of diversity relative to each spatial level in the spatially hierarchical sampling design. We decomposed gamma diversity into alpha diversity and five successive beta diversity components corresponding to increasing spatial scales: dissimilarities in species composition among sampling points within a plot (β_1), among plots within a soil moisture condition (β_2), among soil moisture conditions within a site (β_3), among sites within an ecosystem type (agroecosystem or near-natural ecosystem) (β_4), and among ecosystem types within the region (β_5). These analyses were performed using the *vegan* package with 1000 randomizations to test the significance of each component. This approach was applied to both taxonomic richness and Shannon diversity to evaluate how biodiversity is structured across scales. While beta diversity in taxonomic richness reflects dissimilarities in species composition, beta diversity in Shannon diversity accounts for both species composition and relative abundances, capturing differences in community structure across spatial scales. A final level distinguished agroecosystems (Mediterranean and Temperate agriculture) from near-natural ecosystems (mountain peatland, Mediterranean oak forest, and temperate riparian forest). According to our experimental design, we performed a beta diversity partitioning at two spatial scales: among sites (β_4), separately for each organism group, and between wet and dry soil moisture conditions within each site (β_3), also separately for each group. We partitioned the total beta diversity (β_{SOR}) into turnover (β_{SIM}) and nestedness (β_{SNE}) components by applying the function *beta.multi()* from the *betapart* package (Baselga and Orme, 2012).

Standardized mean difference effect sizes (Hedges' g) were calculated based on average differences between taxa diversity (separately for multidiversity index, taxonomic richness, and Shannon diversity index) under the different soil moisture conditions (wetter versus drier) (Gibbons et al., 1993; Cohen, 2013; Hedges and Olkin, 2014). The Hedges' g effect size represents a standardized mean difference corrected for positive bias, i.e. the raw mean difference is divided by the pooled standard deviation of the two groups. It was calculated using the *cohen.d()* function from the *effize* package.

We applied partial correlation networks to examine associations among taxa based on alpha and beta diversity metrics. Separate networks were constructed for alpha diversity and for beta diversity, ensuring independent analyses of community structure and compositional variation. Alpha diversity networks were built using taxonomic richness and Shannon diversity indices, while beta diversity networks were based on pairwise compositional dissimilarity using the *beta.pair()* function with the Sørensen dissimilarity index. The advantages of building partial correlation networks include that they do not require a priori knowledge of the structure (Harris, 2016) and that correlations can be graphically represented and analyzed to reveal key inter-dependencies and highly connected variables (Friedman et al., 2008). Networks were inferred using the Graphical Lasso method (Least Absolute Shrinkage and Selection Operator, LASSO) implemented in R package *bootnet* (Epskamp et al., 2018), which estimates partial correlations while controlling for the influence of other variables (Epskamp and Fried, 2018). A regularization penalty was applied to limit the number of parameters, with the tuning parameter selected using the Extended Bayesian Information Criterion (EBIC). Networks were visualized as undirected weighted graphs (i.e., there is an association, but the direction is not determined), where nodes represent diversity metrics for each taxon and edges indicate significant (undirected) partial correlation coefficients (Ohlmann et al., 2018; Pedersen, 2024). To ensure robustness, we implemented a bootstrap procedure with the CorStability() function and only interpreted edges with stability values > 0.5 (Epskamp and Fried, 2018; Epskamp et al., 2018). The strength centrality measure (i.e., the sum of absolute edge weights) was used to assess the relative influence of each taxon in the network. To explore diversity associations at different spatial scales, three sets of networks were constructed. The first set provided a global perspective by integrating all sampling points across sites. The second set focused on site-specific relationships, with separate networks for each site. The third set targeted beta diversity under contrasting soil moisture conditions, with one network capturing associations between the wet and dry points within each site and another comparing beta diversity within similar moisture conditions (either wet or dry points). Edges in the networks reflect taxon associations, with positive edges indicating co-variation in diversity metrics or beta diversity patterns, and negative edges suggesting opposing trends (Bhushan et al., 2019). Non-significant associations were excluded. Details on network accuracy assessment, tuning parameter selection, and stability analyses are provided in the Appendix. For all these analyses we followed the procedure provided by Montoya-Sánchez et al. (2023).

All analyses were performed with R software version 4.3.3 (R Core Team, 2022).

3. Results

3.1. Alpha diversity patterns: correlations between groups and influence of soil moisture

Across all sites, we recorded 122 plant species, 15 earthworm species, 92 nematode genera, 9377 fungal OTUs, and 50,353 bacterial OTUs. Taxonomic richness markedly differed among the six study sites (Fig. A1), with the mountain peatland hosting the highest plant richness, while fungal and bacterial richness peaked in the temperate riparian forest ($p < 0.05$). Nematode richness was highest in Mediterranean sites, and earthworm richness was generally low but slightly higher in the temperate ecosystems. Overall, we observed the same patterns for the Shannon diversity index (Fig. A 2).

Taxonomic richness was influenced by soil moisture conditions across sites. The number of nematode genera was higher in drier conditions, whereas wetter conditions favored higher bacterial and fungal OTU richness ($p < 0.05$; Fig. A 2, Fig. A 3). This pattern was consistent for Shannon diversity for bacteria only, with higher bacterial OTU diversity observed under wetter compared to drier conditions (Appendix A: Fig. A 2, Fig. A 3). To further characterize the magnitude of these shifts in taxonomic richness, we examined the effect sizes. Overall, we found no effect of the comparatively drier conditions on the multidiversity index, i.e. considering all five taxonomical groups together, across the six different sites (Fig. 2A). However, drier conditions had a negative impact on the multidiversity index in the peatland, but a positive one in the temperate riparian forest (Fig. 2A). When breaking down these effect sizes on taxonomic richness by soil organism group and per site, drier conditions had, in general, negative effects on the number of taxonomic units compared to wetter conditions (Fig. 2B). Drier conditions exhibited lower fungal richness across all sites except in the riparian and the Mediterranean oak forests. Bacterial communities showed site-specific effects varying between neutral to negative responses to drier conditions. For nematodes and earthworms, we observed higher taxonomic richness under drier, compared to wetter conditions, in the temperate riparian forest. In contrast, plant and nematode richness in the peatland were lower under drier conditions. Similar patterns were observed using the Shannon diversity index (see Fig. A 5). Effect size of soil moisture was never significant in the Mediterranean oak forest.

Across all sites, we found significant correlations between taxonomic richness of the different soil organism groups (Fig. 4, Table A 1). There were significant positive correlations between bacteria and fungi

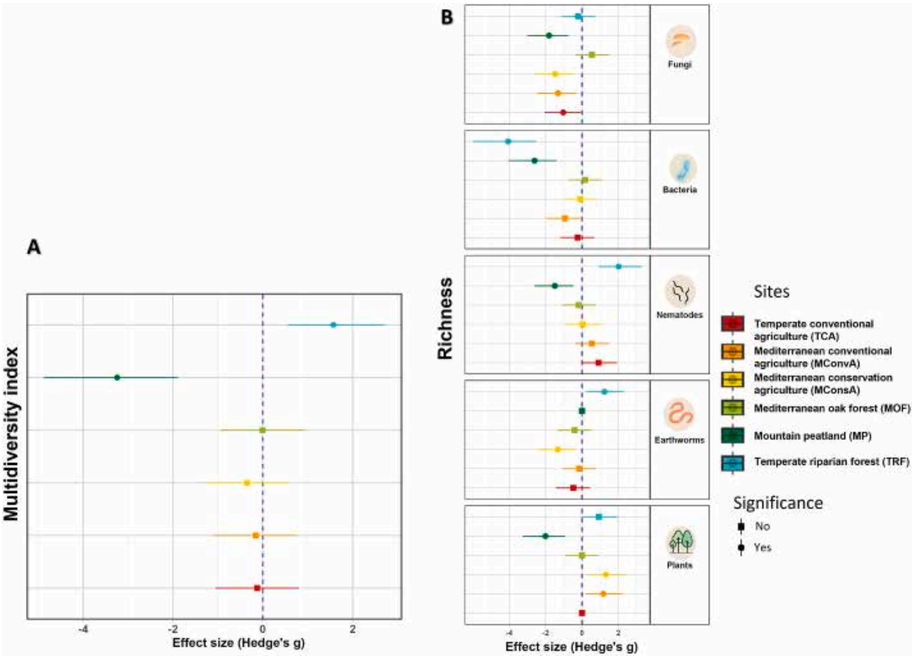

Fig. 2. Hedges's effect size of soil moisture conditions (wetter versus drier) on (A) multidiversity index and (B) taxonomic richness across ecosystems and soil organism groups. Positive or negative effect sizes indicate positive or negative effect of drier sites on diversity, respectively. Significant differences between soil moisture conditions are highlighted in purple. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

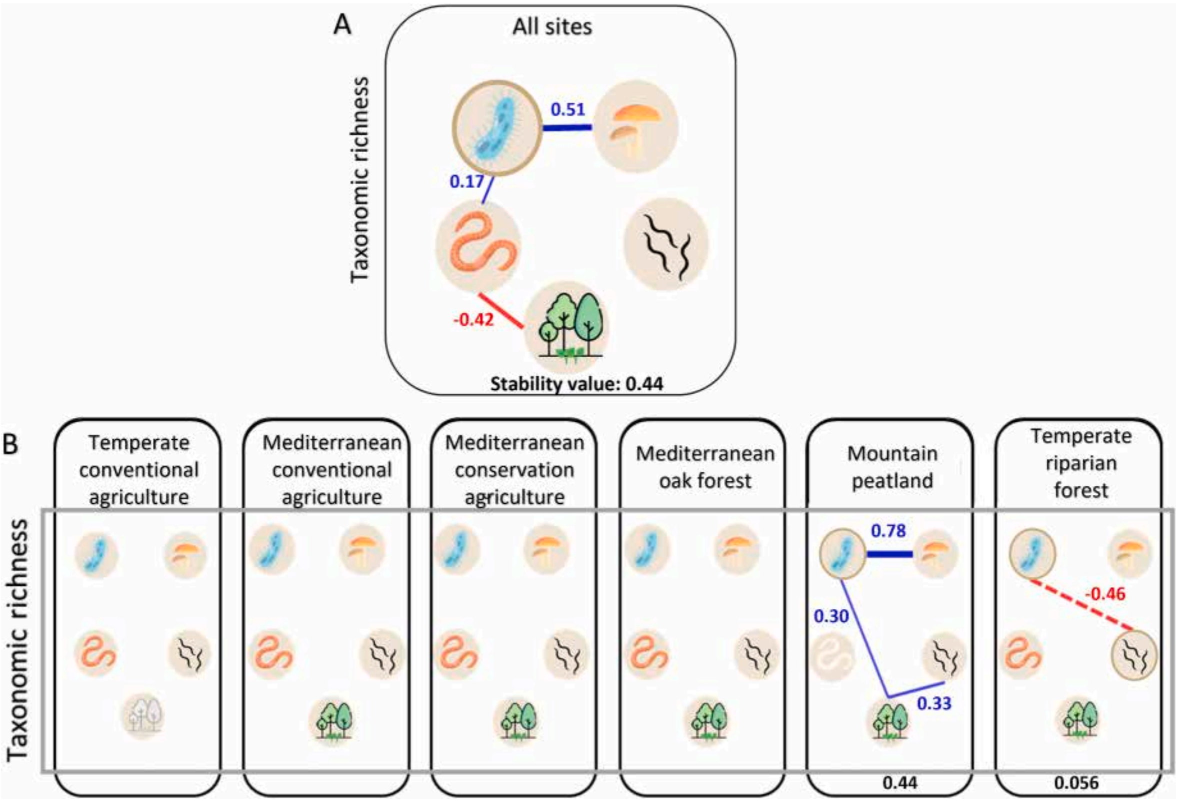

Fig. 3. Taxonomic richness co-variations between soil organism groups (i.e. plants, earthworms, nematodes, fungi and bacteria) across all sites (A) and within each site (B). In panel (A), the global co-variation network illustrates the significant partial correlations between taxonomic richness for different soil organism groups when all sites are considered together. Positive correlations are represented by blue lines and negative correlations by red lines. Panel (B) shows the site-specific co-variation networks, highlighting how the relationships between soil organism groups vary among the study sites. The dashed lines represent associations with network stability values below 0.25. Stability values for each network are displayed below the corresponding graphs. Taxa with the highest strength centrality values in the networks are highlighted with a thicker border. Additional details on network stability and strength centrality values are provided in appendix A Tables A 1 and A 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

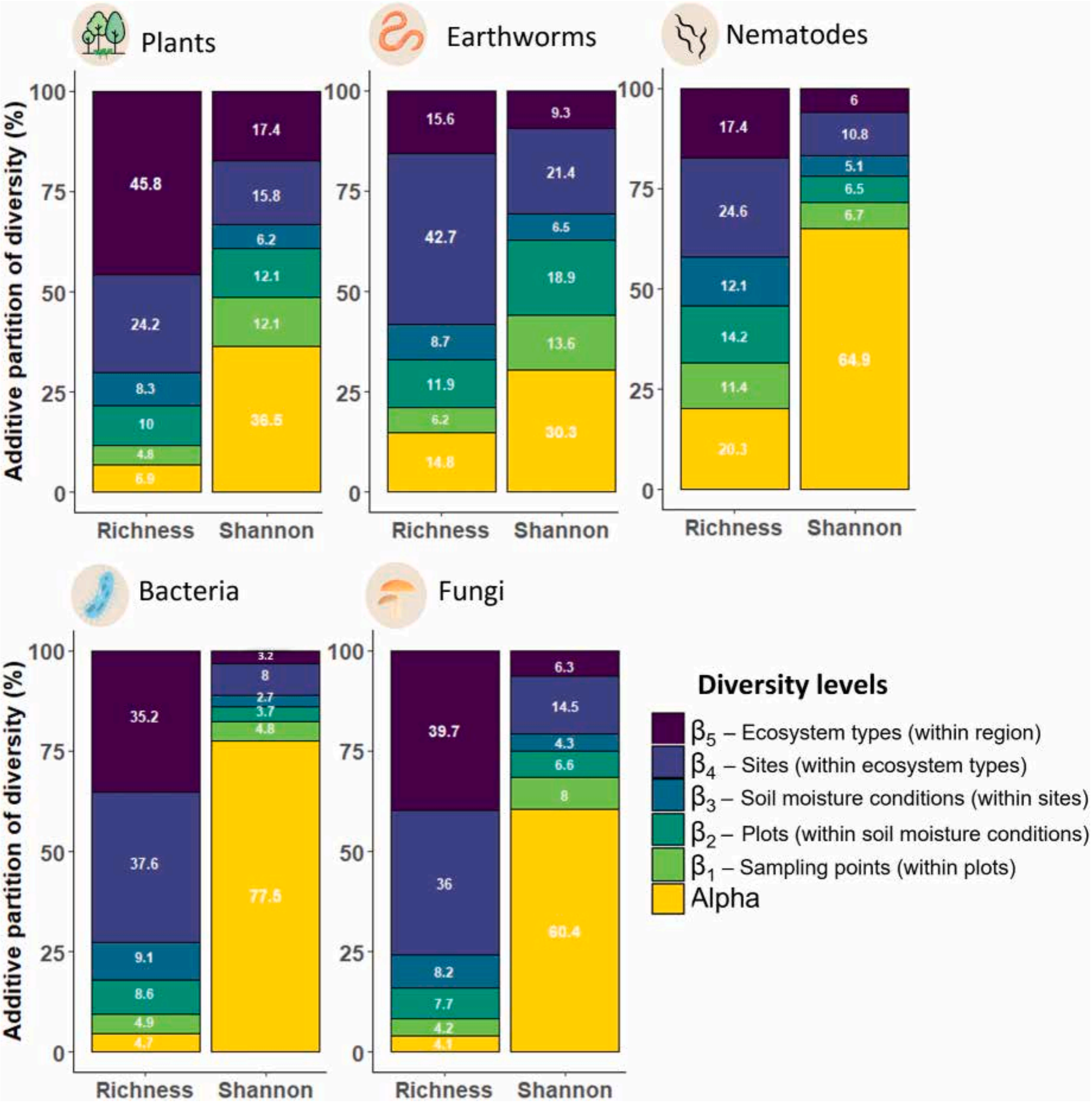

Fig. 4. Additive partitioning of diversity into alpha and beta components (for five soil organism groups, presented for both taxonomic richness and Shannon diversity indices. Each bar illustrates the percentage contribution of different levels of diversity to the overall observed diversity, referred to as total gamma diversity. Alpha represents the contribution of diversity at the sampling point (alpha diversity). The components of β-diversity indicate varying spatial scales, from lowest to highest: β_1 represents diversity among sampling points within plots, β_2 among plots within different soil moisture conditions, β_3 among soil moisture conditions within sites, β_4 among sites within ecosystem types, and β_5 among ecosystem types within the entire region.

richness and also between bacteria and earthworm richness. In contrast, a negative correlation was detected between earthworm and plant species richness. When accounting for environmental covariates such as soil pH and soil organic matter (SOM) through additional analyses (Supplementary Figures A 6 and A 7), we observed distinct groupings: plants and earthworms were more closely associated with SOM, while bacteria and nematodes were linked to soil pH, with a notable negative correlation between soil pH and SOM. When each site was analyzed separately, we found relatively few significant relationships in only two sites (Fig. 4, Table A 1) and none when we added pH and SOM (stability value < 0.25), probably due to limited statistical power with relatively low intra-site replication. In the mountain peatland we found positive correlations between fungal and bacterial richness, between plant and bacterial richness, and between nematode and plant richness. In the temperate riparian forest, the network had a low stability value (<0.25) suggesting that the negative relationship between nematode and bacterial richness should be interpreted with caution (Table A 2). No significant correlation between taxonomic richness was found in the agroecosystems and in the Mediterranean oak forest (see Fig. A 8 for detailed results on Shannon diversity index, Tables A 1, A 3).

3.2. Diversity partitioning

The additive partitioning of diversity showed that patterns of soil biodiversity across spatial scales were relatively consistent among groups of organisms, despite a few notable differences (Fig. 4). Across all groups, broad-scale β-diversity components (β_4 and β_5, corresponding to β-diversity between sites and between ecosystem types respectively) accounted for most of the taxonomic richness, particularly in plants, fungi, and bacteria (with $\beta_4 + \beta_5$ ranging from 70.0 % to 75.7 %), and to a slightly lesser extent in earthworms ($\beta_4 = 42.7$ %, $\beta_5 = 15.6$ %). In contrast, nematode diversity was more evenly partitioned across spatial

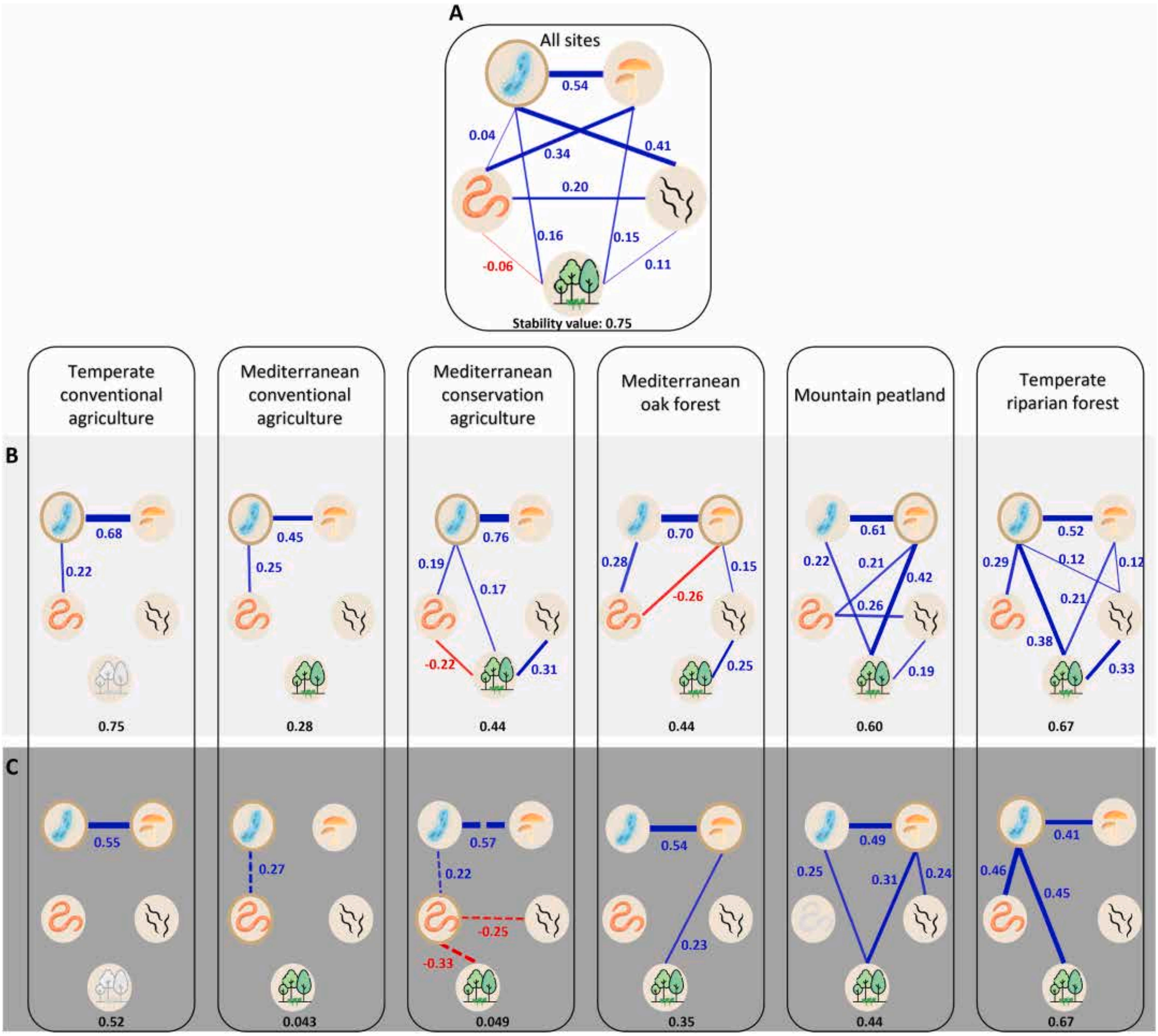

Fig. 5. Co-variations in taxonomic composition (beta diversity measured using the Sørensen dissimilarity index) between soil organism groups (i.e. plants, earthworms, nematodes, fungi and bacteria) across all sites (A) across all sampling points ($n = 18$) within each site (B), and between points under wet versus dry conditions ($n = 9$ for each humidity conditions, C). In panel C, earthworms were not included in mountain peatland due to the absence of species in dry conditions, preventing β-diversity calculations between wet and dry. Edge thickness is proportional to partial correlation coefficients, with blue edges indicating positive correlations (i.e., greater similarity in the composition of one taxon corresponds with greater similarity in another taxon) and red edges indicating negative correlations (i.e., greater dissimilarity in one taxon corresponds with similar community composition in another taxon). The length of the edges is not meaningful. Nodes are transparent when a group of organisms is absent. The dashed lines represent associations with network stability values below 0.25. Stability values for each network are displayed below the corresponding graphs. Taxa with the highest strength centrality values in the networks are highlighted with a thicker border. Additional details on network stability and strength centrality values are provided in appendix A Tables A 1, A 4 and A 5. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

scales, with alpha diversity contributing moderately (20.3 %) and β-components showing balanced contributions (each between 11.4 % and 24.6 %). However, Shannon diversity patterns differed notably from those of taxonomic richness, with a stronger contribution of local-scale variation across most organism groups. For bacteria, fungi, and nematodes, alpha diversity (diversity at each sampling point) represented the largest share of gamma diversity (77.5 %, 60.4 %, and 64.9 %, respectively), indicating relatively homogeneous communities across space but substantial variation in species evenness at the sampling point. In contrast, alpha diversity contributed less to overall diversity in plants (36.5 %) and earthworms (30.3 %), where larger-scale components, particularly variation among sites (β_4) and between ecosystem types (β_5), accounted for a substantial proportion of diversity. Intermediate spatial levels (β_1–β_3) had lower and more variable contributions across all taxa.

Most of the β_4 (dissimilarities in species composition among sites from the same ecosystem type) and β_3 (dissimilarities in species composition among soil moisture conditions within sites) diversity components resulted from taxa turnover (Fig. A 9). The mean total beta diversity among sites varied from 0.50 (nematodes) to 0.96 (plants) showing high dissimilarities among sites. For all soil organism groups, turnover dominated the total beta diversity ranging from 70 % for earthworms to 91 % for plants. Nestedness was highest for earthworms, accounting for 11 % of the total beta diversity across sites (Fig. A 9). When analyzing sites separately, the $\beta_{\text{Soil moisture}}$ associated with the two contrasting soil moisture conditions at each site showed differences depending on the organism groups. For instance, in agroecosystems, earthworms had a relatively higher contribution to species nestedness compared to other groups, while for nematodes, beta diversity was consistently dominated by species turnover across different sites (Fig. A 9).

3.3. *Between- and within-site co-variations patterns in community composition across soil organism groups*

Graphical Lasso analysis of beta diversity across all sites highlighted significant co-variations in the taxonomic composition of soil organism groups. Strong positive associations were observed between fungi and bacteria, earthworms and fungi, as well as bacteria and nematodes, reflecting shared spatial dissimilarity patterns (Fig. 5A–Table A 1). In other words, when fungal communities are more similar between two points (i.e., low beta diversity), bacterial communities also tend to be more similar. Conversely, higher spatial dissimilarity in fungal communities corresponds to higher dissimilarity in bacterial communities, highlighting parallel spatial structuring processes across these groups. In contrast, plants and earthworms exhibited a negative association (Fig. 5A–Table A 1).

When Graphical Lasso networks were analyzed separately for each site, considering all 18 sampling points (two moisture conditions each with three plots and three sampling points per plot) (Fig. 5B), a recurring pattern emerged: bacteria-fungi and bacteria-earthworm associations were consistently observed across most sites, except in the mountain peatland for the bacteria-earthworm association, which likely is simply because of essentially no earthworm presence in this ecosystem type. In agroecosystems, the networks were more complex in the no-till site (Mediterranean conservation agriculture) compared to tilled agroecosystems, as well as in natural systems. Specifically, the number of associations was higher in Mediterranean conservation agriculture (5 associations), Mediterranean oak forest (5), mountain peatland (6), and temperate riparian forest (7), compared to tilled agroecosystems such as Mediterranean conventional agriculture (2) and Temperate conventional agriculture (2) (Fig. 5B–Table A 4). The centrality of soil organism groups, as indicated by strength values (the sum of all correlations involving a given soil organism group), varied across sites (Table A 4). Bacteria had the highest strength values in most of the sites (values = 1.09 to 1.45 Table A 4) making them the most central group, except in Mediterranean oak forest and mountain peatland, where fungi exhibited the highest strength values (1.22 and 1.47 respectively; Table A 4).

Graphical Lasso networks were also constructed to analyze co-variations in the taxonomic composition of soil organism groups across contrasting moisture conditions (wet vs. dry) within each site (Fig. 5C). Compared to the site-specific networks including all sampling points, the number of significant associations was generally lower for wet-dry contrasts. For example, networks displayed only one association in Temperate conventional agriculture against two in networks including all points, two against five in Mediterranean oak forest, four against seven in mountain peatland, and three against seven in temperate riparian forest. At the Mediterranean agriculture sites, networks exhibiting low stability values (<0.25), indicating limited consistency of the relationships in these contexts (Table A 5). Despite lower network stability for Mediterranean agriculture sites, a recurrent pattern was observed across all other sites: with a consistent positive association between bacteria and fungi, while associations involving soil fauna or plants were generally absent or limited. Bacteria and fungi were the most central groups in networks from Temperate conventional agriculture, while bacteria dominated in temperate riparian forest and fungi were the most central in mountain peatland and Mediterranean oak forest (Fig. 5C–Table A 5). Furthermore, the strength of recurrent associations, such as bacteria-fungi, was generally weaker under wetter versus drier conditions within each site compared to the site-specific networks.

4. Discussion

With a focus on the five distinct groups of soil organisms, plants, earthworms, nematodes, fungi and bacteria, our study explored whether their diversity co-varies and how this variation is spatially structured. We chose to address this question across highly contrasting ecosystems to search for general patterns independent of obvious ecosystem-type-specific patterns. A secondary goal was to explore the possibilities of a generally applicable proxy to evaluate soil biodiversity without the need to characterize multiple groups of organisms in detail. In partial contrast to our initial hypothesis, co-variation in the taxonomic richness among these groups was limited, suggesting that it may not be sufficient to characterize the taxonomic richness of one particular, possibly more easily to determine, group of organisms to draw conclusions about the taxonomic richness of other groups. On the other hand, when considering spatial differences in community composition (i.e. beta diversity), substantial co-variation was observed across all soil organism groups, indicating significant connections in the spatial organization of multiple soil organism communities. As expected, these co-variation patterns were stronger in near-natural ecosystems and in no-till agricultural system than in conventional agricultural systems. Ecosystem type (near-natural vs. agroecosystems) influenced taxonomic richness at a broader scale, while local soil moisture conditions played a critical role in shaping the spatial composition of soil biodiversity at finer spatial scales. These findings underscore how both ecosystem type and small-scale environmental conditions act as significant determinants of specific aspects of soil biodiversity.

4.1. *Weak co-variations in alpha diversity among groups of soil organisms*

As a result of our selection of highly contrasting sites in terms of land use and climate, it was not surprising that taxa composition showed little overlap across sites, reflecting the role of site-specific characteristics and historical factors in shaping soil communities (Maravalhas and Vasconcelos, 2020; Liu et al., 2024). Limited overlap in community composition across sites was a strength of our study when testing for co-variation in richness among different groups of organisms, independent of species identity. The generally positive co-variation in taxonomic richness we observed between bacteria and fungi, and to a lower degree between earthworms and bacteria, suggests relatively coherent richness patterns among these three groups at large spatial scales across vastly different ecosystems and environmental conditions covered with our study. This result is consistent with studies showing that earthworms can influence microbial diversity and composition directly by eating soil and indirectly by altering soil structure and nutrient cycling (Nechitaylo et al., 2010; Koubová et al., 2015; de Menezes et al., 2018). Earthworm-driven changes in soil aeration, porosity, and moisture dynamics may create favorable conditions for microbial communities, which could explain the co-variation observed here (Homet et al., 2021; Ganault et al., 2024). However, nematode richness showed little or no co-variation with microbial or earthworm richness. While nematodes are known to interact with soil microbes, particularly as bacterial and fungal grazers, their response patterns appear more context-dependent and less predictable (Pereira et al., 2024). Their relatively independent variation across sites and conditions may reflect specific trophic interactions, microhabitat preferences, or resilience to environmental filtering not shared with the other groups studied. More surprising was the negative relationship between earthworms and plants across all sites. This pattern was the result of the particular situation at two of our sites. At the time of sampling the temperate conventional agricultural site was essentially without plants, as it typically occurs for some part of the year in conventionally managed croplands. At the same time, there was a relatively high earthworm richness at this same site. This pattern may have been influenced by the timing of sampling, which occurred during the bare soil period in agricultural fields just before sowing crops. During this period plants are sparse or almost completely absent (in conventional agriculture involving ploughing), highlighting the importance of considering phenological stages when interpreting α-diversity relationships. The second site was the mountain peatland, where plant species richness was high, but earthworms were almost absent. This illustrates the limitations of our approach comparing vastly different ecosystems. Interestingly, when considering soil pH and SOM as additional factors, we observe that while these environmental variables show expected relationships with biodiversity patterns (e.g., positive pH-bacteria correlation as documented by Fierer, 2006), they do not substantially alter our main conclusions regarding taxonomic richness co-variations. The co-variation of soil pH and organic matter with distinct soil organism groups across sites suggests that these environmental variables interact in complex ways to shape biodiversity patterns, potentially mediating some of the α-diversity associations we observe. However, the persistence of bacteria-fungi co-variation even after accounting for these environmental factors supports our interpretation of biological interactions playing a key role in structuring these communities. Our data on alpha diversity demonstrate the significant influence of soil moisture, in shaping taxonomic richness. However, the effect of soil moisture conditions was rarely homogeneous among groups of soil organisms, which illustrates general differences in soil moisture dependencies among broad groups of organisms. Only the mountain peatland showed a consistent pattern of decreasing taxonomic richness in drier conditions for four groups of soil organisms concurrently, plants, nematodes, fungi and bacteria. This pattern likely reflected the common sensitivity of these organisms adapted to stable, water-saturated conditions, to fluctuating soil humidity, with particularly dry conditions during summer (e.g., Toberman et al., 2008; Hillgén et al., 2024) and linked soil moisture variations to shifts in microbial communities and enzyme activities, and carbon and nitrogen cycling in peatlands (Xu et al., 2021). At other sites, groups of soil organisms were influenced in different ways by soil moisture conditions, displaying positive, negative, or neutral patterns. For instance, in the temperate riparian forest, nematode and earthworm richness increased under drier conditions, likely due to reduced flooding stress, while fungal richness remained stable and bacterial richness declined. These contrasting patterns suggest that certain groups, like macrofauna, may benefit from alleviated anoxic stress, whereas microbial communities remain tightly constrained by moisture-dependent nutrient cycling (Annala et al., 2022). In the Mediterranean agroecosystem, dryness negatively affected fungal and nematode richness, but had neutral or weak effects on other groups. Drought in these soils may limit decomposition, oxygen availability and organic matter decomposition (Franco et al., 2019; Biryol et al., 2024), creating patchy microhabitats. Contrary to previous studies, no taxonomic richness of any group of organisms has increased or decreased significantly with drier conditions in the Mediterranean oak forest. This is possibly due to the presence of taxa adapted to fluctuating moisture in forest litter (Richard et al., 2011; Shahin et al., 2013) and the buffering effect of perennial vegetation. These contrasting patterns highlight that soil organism responses to moisture conditions are highly context-dependent. Within a given site, some taxa are constrained by abiotic limitations (e.g., microbial groups in peatlands), while others benefit from alleviated stress (e.g., earthworms in riparian zones). In many cases, changes in vegetation composition under drier conditions may indirectly drive changes in microbial and faunal communities via shifts in rhizosphere interactions (Maestre et al., 2015; Franco et al., 2019). For instance, drought-tolerant plants may host microbial taxa adapted to low-moisture conditions, which may influence herbivore and bacterivorous or fungivorous nematode populations (Castro et al., 2010; Naylor and Coleman-Derr, 2018; Biryol et al., 2024). Differences in sampling depth among organism groups may also contribute to the observed patterns. Moisture in shallow soil layers is typically more variable (Meng and Sun, 2023; Li et al., 2024) and may exert stronger short-term control on microorganisms and nematodes sampled in the 0–10 cm layer, whereas earthworms sampled at deeper layers (0–20 cm) may experience less variable and more favorable moisture conditions. Nonetheless, it remains unclear whether this organism-specific sampling could result in a methodological bias or rather adequately represents organism-specific differences in size and mobility within the soil.

Collectively, these findings emphasize that the impact of dryness varied not only across taxa but also depending on local site characteristics and underscore the critical role of local hydrological context in mediating soil biodiversity responses.

4.2. *The spatial structure of co-variation in soil biodiversity*

The spatial variation in soil organism diversity reflects a complex interplay between ecosystem type and local environmental conditions, a pattern observed across all groups of soil organisms. Ecosystem type emerged as a key determinant of taxonomic richness, suggesting that broad spatial scales capture key environmental drivers shaping biodiversity. This is in line with studies showing sharp community transitions across ecosystem boundaries (Miyashita et al., 2014). In contrast, within-ecosystem variation played a more prominent role for nematodes and earthworms, possibly due to their greater sensitivity to local microhabitats and spatially heterogeneous resources (van den Hoogen et al., 2019).

Beta diversity associations revealed positive co-variations among bacterial and fungal, bacterial and nematode, and fungal and earthworm community compositions. These associations may result from shared responses to environmental gradients, parallel ecological filtering, or direct or indirect biotic interactions (Medina-Sauza et al., 2019; Thakur and Geisen, 2019; Pelaez-Sanchez et al., 2024). For instance, the positive bacterial-fungal association, which was observed across both ecosystem types and at all sites, may reflect shared environmental influences or direct biotic interactions due to their complementary roles in different soil processes (Van Der Heijden et al., 2008; Hartmann and Six, 2023). Indeed, fungi facilitate bacterial dispersal and resource availability by decomposing recalcitrant organic matter, releasing substrates that fuel bacterial activity (Bahram et al., 2018) and creating microhabitats that sustain bacterial diversity (Bahram et al., 2018; Deveau et al., 2018). This relationship may be sufficiently robust that it is also observed in agroecosystems despite their frequent disturbances. In contrast, the relationships among other groups of soil organisms appear to be more fragile in more disturbed agroecosystems, perhaps through reduced interaction complexity as disturbance-tolerant species dominate, potentially weakening interactions density. This fragmentation may impair essential soil functions, such as organic matter decomposition and nutrient cycling (Yang et al., 2021). Interestingly, beta diversity co-variation between bacteria and nematodes was positive and relatively robust when assessed across all sites, but absent in five of the sites and very weak in temperate riparian forest when analyzed at the site level. This suggests that local conditions may modulate their community composition co-variation. These co-variation patterns among soil organism groups may have functional implications, as taxa with complementary roles in decomposition, nutrient cycling, or organic matter turnover could influence ecosystem processes. Although the present study did not focus on diversity-function linkages, the observed structuring of beta diversity suggests potential links between community composition and soil processes. This was particularly true in near-natural ecosystems, suggesting that comparatively low levels of disturbance may favor similar beta diversity patterns across distinct groups of soil organisms. However, near-natural ecosystems themselves are environmentally highly heterogeneous. These environmental contrasts are reflected in the structure of beta-diversity networks observed in our results, with the riparian forest showing a more extensive network of associations than the mountain peatland or the Mediterranean oak forest. The Mediterranean forest with the simplest network among the three natural ecosystems is characterized by a coarse-textured soil within a rocky matrix, severe summer drought, the mountain peatland by cool and humid conditions, and the riparian forest by often waterlogged soils near the Garonne river. These differences likely shape both local environmental filtering and the potential for co-occurrence among taxa, potentially explaining the observed variation in network complexity in the studied natural ecosystems.

Similar to the switch from near-natural ecosystems to agroecosystems, contrasting soil moisture conditions further disrupted these patterns, decreasing associations between soil fauna and plants or between bacteria and nematodes. This loss of spatial co-variation may be the result of disturbance due to more extreme soil moisture conditions. For example, plants may reduce rhizodeposition under more constrained soil moisture conditions such as in drier areas (Preece and Peñuelas, 2016), but also under more frequent anoxic conditions, such as in the wetter part in the temperate riparian forest, which limits the provision of critical resources for soil fungi and bacteria and the soil food web that they sustain (Wagg et al., 2019). Although the bacterial-fungal association remained stable across sites and moisture conditions, increasing drought frequency could further destabilize these interactions, favoring drought-adapted fungi while reducing functionally specialized bacterial taxa (De Vries and Shade, 2013; de Vries et al., 2018). Such shifts may decouple bacterial-fungal networks, ultimately weakening microbial-mediated soil processes essential for ecosystem resilience (Ali, 2023).

At the site level, beta diversity was mainly driven by species turnover rather than nestedness. The only small contribution of nestedness to beta diversity further suggests that few species are ubiquists. This aligns with findings that more intensive land use, for example through planting monocultures or through frequent tillage, shifts community composition towards disturbance-tolerant or generalist taxa, often resulting in taxonomic homogenization rather than diversity loss (Villarreal-Barajas and Martorell, 2009; Tsiafouli et al., 2015). Moist sites, like the temperate riparian forest and the mountain peatland, exhibited pronounced community composition variations, i.e. higher beta diversity between wetter and drier conditions than at the other sites. This may result from threshold effects with temporarily completely water-saturated soils in these two ecosystems requiring particular adaptive traits from soil organisms during prolonged anoxic conditions. For certain groups of soil organisms, such as earthworms, the nestedness component of beta diversity sometimes exceeded turnover, reflecting habitat filtering or local extinctions under changing conditions. In contrast, the Mediterranean oak forest showed no significant community composition shifts in response to soil moisture variations. This stability might reflect adaptations of resident taxa to naturally fluctuating moisture levels that were not sufficiently profoundly modified by additional rain exclusion. Rather than changes in overall diversity, variations in abundance, functional group composition, or seasonal shifts may play a more significant role in shaping these communities (Richard et al., 2011; Homet et al., 2023).

These patterns can be better understood by considering life history traits and dispersal abilities across groups of soil organisms. Earthworms, nematodes, fungi and bacteria, featuring highly contrasting mobility, exhibit different patterns of diversity across scales. Relatively less mobile organisms may show higher beta diversity at finer spatial scales, reflecting more localized community shifts. In contrast, organism groups with higher dispersal capacity may exhibit greater turnover at larger scales (Soininen et al., 2018). Furthermore, intermediate trophic levels, such as predatory and bacterivorous nematodes, may exhibit weak correlations with prey or resource groups, reflecting combined top-down and bottom-up influences rather than absence of ecological interactions (Coleman et al., 2014). This variation in beta diversity components across groups of soil organisms supports the idea that dispersal limitations and ecological traits, such as substrate specificity and resource availability, play a significant role in shaping community structure at different scales (Litchman, 2015; Liu et al., 2022).

5. Conclusions and future research directions

The diversity of five major groups of soil organisms across an exceptionally broad range of ecosystems varied largely independently, suggesting that it may be difficult to conclude about general soil biodiversity patterns based on a detailed assessment of a particular group of organisms. Nevertheless, we found that plant diversity was linked to soil biodiversity, particularly through its associations with earthworms and bacteria, underscoring that above- and belowground communities shared spatial and environmental processes. In addition, the positive correlations between taxonomic richness of fungi and bacteria, and to a lesser degree with earthworms across all ecosystems indicate that there may be some general principles in soil biodiversity patterns at large spatial scales. This opens promising avenues for further studies inquiring general patterns in soil biodiversity. However, despite the complementary expertise needed and the labour-intensive nature of the work involved, our results suggest that more generalizable patterns may only be found via larger sampling effort, including a larger spectrum of ecosystem types or a larger gradient of soil moisture. Moreover, more robust patterns would likely emerge from higher temporal (within and across years) and spatial (within and across ecosystem types) replication of sampling. Considering additional soil invertebrate groups such as micro- and macro-arthropods would also increase the generality of such findings.

Nonetheless, the consideration of how communities vary in taxonomic composition across space (beta diversity) revealed substantial co-variation across all groups of soil organisms, suggesting that the spatial organization of biodiversity in contrasting groups of soil organisms are structured in similar ways. This has substantial implications for the general understanding of how soil biodiversity is organized in space and for management and conservation strategies.

Notwithstanding the rather qualitative nature of the contrasted soil moisture conditions we evaluated with our study, our data suggest a strong influence of soil moisture on the spatial structuring of soil biodiversity. This indicates that ongoing climate change may modify the relationships in biodiversity among groups of soil organisms and their spatial structure with likely consequences for ecosystem properties. Experimental approaches would be needed to understand these changes and their consequences in more mechanistic detail. Additionally, soil moisture emerged as a key local environmental driver, influencing both biodiversity patterns and the strength of associations among taxa.

Future research should aim to disentangle the relative contributions of environmental filtering, biotic interactions, and stochastic processes in shaping soil biodiversity at multiple spatial scales. In particular, the role of soil moisture gradients in structuring beta diversity warrants further investigation in the context of global climate change scenarios. Experimental approaches manipulating soil moisture across spatial and temporal scales could provide valuable insights into the resilience of soil communities and develop effective strategies for its conservation and management.

CRediT authorship contribution statement

Axelle Tortosa: Writing – review & editing, Writing – original draft, Investigation, Formal analysis. **Grégoire T. Freschet:** Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization. **Jean Trap:** Writing – review & editing, Writing – original draft, Validation, Supervision, Investigation, Formal analysis, Data curation, Conceptualization. **Alain Brauman:** Writing – review & editing, Methodology, Investigation. **Yvan Capowiez:** Writing – review & editing, Methodology, Investigation. **Sylvain Coq:** Writing – review & editing,

Validation, Methodology, Investigation. **Jim Félix-Faure:** Methodology, Investigation, Data curation. **Nathalie Fromin:** Writing – review & editing, Validation, Methodology, Investigation, Data curation. **Laure Gandois:** Writing – review & editing, Resources, Investigation. **Maritxu Guiresse:** Resources. **Raoul Huys:** Writing – review & editing, Resources, Investigation, Data curation. **Antoine Lecerf:** Writing – review & editing, Visualization, Validation, Resources, Project administration, Investigation, Funding acquisition, Data curation, Conceptualization. **Jean-Marc Limousin:** Writing – review & editing, Resources, Investigation. **Alexandru Milcu:** Writing – review & editing, Validation, Investigation. **Johanne Nahmani:** Writing – review & editing, Validation, Investigation. **Agnès Robin:** Validation, Resources, Methodology, Investigation, Data curation. **José Miguel Sánchez-Pérez:** Resources, Investigation. **Sabine Sauvage:** Resources, Investigation. **Tiphaine Tallec:** Resources. **Claire Wittling:** Resources, Methodology, Investigation. **Stephan Hattenschwiler:** Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2026.110093.

References

Ali, Arshad., 2023. Biodiversity–ecosystem functioning research: Brief history, major trends and perspectives. Biological Conservation 285, 110210. https://doi.org/10.1016/j.biocon.2023.110210.

Allan, E., Bossdorf, O., Dormann, C.F., Prati, D., Gossner, M.M., Tscharntke, T., Blüthgen, N., Bellach, M., Birkhofer, K., Boch, S., Böhm, S., Börschig, C., Chatzinotas, A., Christ, S., Daniel, R., Diekötter, T., Fischer, C., Friedl, T., Glaser, K., Hallmann, C., Hodac, L., Hölzel, N., Jung, K., Klein, A.M., Klaus, V.H., Kleinebecker, T., Krauss, J., Lange, M., Morris, E.K., Müller, J., Nacke, H., Pašalić, E., Rillig, M.C., Rothenwöhrer, C., Schall, P., Scherber, C., Schulze, W., Socher, S.A., Steckel, J., Steffan-Dewenter, I., Türke, M., Weiner, C.N., Werner, M., Westphal, C., Wolters, V., Wubet, T., Gockel, S., Gorke, M., Hemp, A., Renner, S.C., Schöning, I., Pfeiffer, S., König-Ries, B., Buscot, F., Linsenmair, K.E., Schulze, E.-D., Weisser, W. W., Fischer, M., 2014. Interannual variation in land-use intensity enhances grassland multidiversity. Proceedings of the National Academy of Sciences 111, 308–313. https://doi.org/10.1073/pnas.1312213111.

Annala, M.J., Lehosmaa, K., Ahonen, S.H.K., Karttunen, K., Markkola, A.M., Puumala, I., Mykrä, H., 2022. Effect of riparian soil moisture on bacterial, fungal and plant communities and microbial decomposition rates in boreal stream-side forests. Forest Ecology and Management 519, 120344. https://doi.org/10.1016/j.foreco.2022.120344.

Bahram, M., Hildebrand, F., Forslund, S.K., Anderson, J.L., Soudzilovskaia, N.A., Bodegom, P.M., Bengtsson-Palme, J., Anslan, S., Coelho, L.P., Harend, H., Huerta-Cepas, J., Medema, M.H., Maltz, M.R., Mundra, S., Olsson, P.A., Pent, M., Põlme, S., Sunagawa, S., Ryberg, M., Tedersoo, L., Bork, P., 2018. Structure and function of the global topsoil microbiome. Nature 560, 233–237. https://doi.org/10.1038/s41586-018-0386-6.

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

Baselga, A., 2012. The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. Global Ecology and Biogeography 21, 1223–1232. https://doi.org/10.1111/j.1466-8238.2011.00756.x.

Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography 19, 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x.

Baselga, A., Orme, C.D.L., 2012. Betapart: an R package for the study of beta diversity. Methods in Ecology and Evolution 3, 808–812. https://doi.org/10.1111/j.2041-210X.2012.00224.x.

Beaumelle, L., Giffard, B., Tolle, P., Winter, S., Entling, M.H., Benítez, E., Zaller, J.G., Auriol, A., Bonnard, O., Charbonnier, Y., Fabreguettes, O., Joubard, B., Kolb, S., Ostandie, N., Reiff, J.M., Richart-Cervera, S., Rusch, A., 2023. Biodiversity conservation, ecosystem services and organic viticulture: a glass half-full. Agriculture, Ecosystems & Environment 351, 108474. https://doi.org/10.1016/j.agee.2023.108474.

Berg, M.P., Bengtsson, J., 2007. Temporal and spatial variability in soil food web structure. Oikos 116, 1789–1804. https://doi.org/10.1111/j.0030-1299.2007.15748.x.

Bhushan, N., Mohnert, F., Sloot, D., Jans, L., Albers, C., Steg, L., 2019. Using a gaussian graphical model to explore relationships between items and variables in environmental psychology research. Frontiers in Psychology 10, 1050. https://doi.org/10.3389/fpsyg.2019.01050.

Biryol, C., Trap, J., Prévosto, B., Dupouyet, S., Baldy, V., Santonja, M., 2024. Managing both overstory and understory vegetation mitigates the impact of drought on soil nematode communities in a Mediterranean pine forest. Applied Soil Ecology 202, 105585. https://doi.org/10.1016/j.apsoil.2024.105585.

Blouin, M., Hodson, M.E., Delgado, E.A., Baker, G., Brussaard, L., Butt, K.R., Dai, J., Dendooven, L., Peres, G., Tondoh, J.E., Cluzeau, D., Brun, J.-J., 2013. A review of earthworm impact on soil function and ecosystem services. European Journal of Soil Science 64, 161–182. https://doi.org/10.1111/ejss.12025.

Bouché, M.B., 1972. Lombriciens De France. Ecologie Et Systématique, Annales De Zoologie. INRA Editions.

Brondani, M., Plassard, C., Ramstein, E., Cousson, A., Hedde, M., Bernard, L., Trap, J., 2022. Morpho-anatomical traits explain the effects of bacterial-feeding nematodes on soil bacterial community composition and plant growth and nutrition. Geoderma 425, 116068. https://doi.org/10.1016/j.geoderma.2022.116068.

Brussaard, L., Pulleman, M.M., Ouédraogo, É., Mando, A., Six, J., 2007. Soil fauna and soil function in the fabric of the food web. Pedobiologia 50, 447–462. https://doi.org/10.1016/j.pedobi.2006.10.007.

Castro, H.F., Classen, A.T., Austin, E.E., Norby, R.J., Schadt, C.W., 2010. Soil microbial community responses to multiple experimental climate change drivers. Applied and Environmental Microbiology 76, 999–1007. https://doi.org/10.1128/AEM.02874-09.

Cavicchioli, R., Ripple, W.J., Timmis, K.N., Azam, F., Bakken, L.R., Baylis, M., Behrenfeld, M.J., Boetius, A., Boyd, P.W., Classen, A.T., Crowther, T.W., Danovaro, R., Foreman, C.M., Huisman, J., Hutchins, D.A., Jansson, J.K., Karl, D.M., Koskella, B., Mark Welch, D.B., Martiny, J.B.H., Moran, M.A., Orphan, V.J., Reay, D. S., Remais, J.V., Rich, V.I., Singh, B.K., Stein, L.Y., Stewart, F.J., Sullivan, M.B., van Oppen, M.J.H., Weaver, S.C., Webb, E.A., Webster, N.S., 2019. Scientists' warning to humanity: microorganisms and climate change. Nature Reviews Microbiology 17, 569–586. https://doi.org/10.1038/s41579-019-0222-5.

Cebrian, J., Lartigue, J., 2004. Patterns of herbivory and decomposition in aquatic and terrestrial ecosystems. Ecological Monographs 74, 237–259. https://doi.org/10.1890/03-4019.

Cohen, J., 2013. Statistical Power Analysis for the Behavioral Sciences, second ed. Routledge, New York. https://doi.org/10.4324/9780203771587.

Coleman, D.C., Zhang, W., Fu, S., 2014. Toward a holistic approach to soils and plant growth. In: Dighton, J., Krumins, J.A. (Eds.), Interactions in Soil: Promoting Plant Growth. Springer, Netherlands, Dordrecht, pp. 211–223. https://doi.org/10.1007/978-94-017-8890-8_11.

Deveau, A., Bonito, G., Uehling, J., et al., 2018. Bacterial–fungal interactions: ecology, mechanisms and challenges. FEMS Microbiology Reviews 42 (3), 335–352. https://doi.org/10.1093/femsre/fuy008.

de Vries, F.T., Griffiths, R.I., Bailey, M., Craig, H., Girlanda, M., Gweon, H.S., Hallin, S., Kaisermann, A., Keith, A.M., Kretzschmar, M., Lemanceau, P., Lumini, E., Mason, K. E., Oliver, A., Ostle, N., Prosser, J.I., Thion, C., Thomson, B., Bardgett, R.D., 2018. Soil bacterial networks are less stable under drought than fungal networks. Nature Communications 9, 3033. https://doi.org/10.1038/s41467-018-05516-7.

De Vries, F.T., Liiri, M.E., Bjørnlund, L., Bowker, M.A., Christensen, S., Setälä, H.M., Bardgett, R.D., 2012. Land use alters the resistance and resilience of soil food webs to drought. Nature Climate Change 2, 276–280. https://doi.org/10.1038/nclimate1368.

De Vries, F.T., Shade, A., 2013. Controls on soil microbial community stability under climate change. Frontiers in Microbiology 4. https://doi.org/10.3389/fmicb.2013.00265.

De Vries, F.T., Thébault, E., Liiri, M., Birkhofer, K., Tsiafouli, M.A., Bjørnlund, L., Bracht Jørgensen, H., Brady, M.V., Christensen, S., De Ruiter, P.C., d'Hertefeldt, T., Frouz, J., Hedlund, K., Hemerik, L., Hol, W.H.G., Hotes, S., Mortimer, S.R., Setälä, H., Sgardelis, S.P., Uteseny, K., Van Der Putten, W.H., Wolters, V., Bardgett, R.D., 2013. Soil food web properties explain ecosystem services across European land use systems. Proceedings of the National Academy of Sciences 110, 14296–14301. https://doi.org/10.1073/pnas.1305198110.

de Menezes, A.B., Prendergast-Miller, M.T., Macdonald, L.M., Toscas, P., Baker, G., Farrell, M., Wark, T., Richardson, A.E., Thrall, P.H., 2018. Earthworm-induced shifts in microbial diversity in soils with rare versus established invasive earthworm populations. FEMS Microbiology Ecology 94. https://doi.org/10.1093/femsec/fiy051 fiy051.

Dengler, J., et al., 2023. Should we estimate plant cover in percent or on ordinal scales? Vegetation Classification and Survey 4, 131–138. https://doi.org/10.3897/vcs.98379.

Dubrovský, M., Hayes, M., Duce, P., Trnka, M., Svoboda, M., Zara, P., 2014. Multi-GCM projections of future drought and climate variability indicators for the Mediterranean region. Regional Environmental Change 14, 1907–1919. https://doi.org/10.1007/s10113-013-0562-z.

Eisenhauer, N., Antunes, P.M., Bennett, A.E., Birkhofer, K., Bissett, A., Bowker, M.A., Caruso, T., Chen, B., Coleman, D.C., Boer, W. de, Ruiter, P. de, DeLuca, T.H., Frati, F., Griffiths, B.S., Hart, M.M., Hättenschwiler, S., Haimi, J., Heethoff, M., Kaneko, N., Kelly, L.C., Leinaas, H.P., Lindo, Z., Macdonald, C., Rillig, M.C., Ruess, L., Scheu, S., Schmidt, O., Seastedt, T.R., Straalen, N.M. van, Tiunov, A.V., Zimmer, M., Powell, J.R., 2017. Priorities for research in soil ecology. Pedobiologia 63, 1–7. https://doi.org/10.1016/j.pedobi.2017.05.003.

Eisenhauer, N., Reich, P.B., Isbell, F., 2012. Decomposer diversity and identity influence plant diversity effects on ecosystem functioning. Ecology 93, 2227–2240. https://doi.org/10.1890/11-2266.1.

Epskamp, S., Borsboom, D., Fried, E.I., 2018. Estimating psychological networks and their accuracy: a tutorial paper. Behavior Research Methods 50, 195–212.

Epskamp, S., Fried, E.I., 2018. A tutorial on regularized partial correlation networks. Psychological Methods 23, 617–634. https://doi.org/10.1037/met0000167.

Fierer, N., et al., 2006. The diversity and biogeography of soil bacterial communities. Proceedings of the National Academy of Sciences 103 (3), 626–631. https://doi.org/10.1073/pnas.0507535103.

Franco, A.L.C., Gherardi, L.A., De Tomasel, C.M., Andriuzzi, W.S., Ankrom, K.E., Shaw, E.A., Bach, E.M., Sala, O.E., Wall, D.H., 2019. Drought suppresses soil predators and promotes root herbivores in mesic, but not in xeric grasslands. Proceedings of the National Academy of Sciences 116, 12883–12888. https://doi.org/10.1073/pnas.1900572116.

Friedman, J., Hastie, T., Tibshirani, R., 2008. Sparse inverse covariance estimation with the graphical lasso. Biostatistics 9, 432–441. https://doi.org/10.1093/biostatistics/kxm045.

Fujii, S., Berg, M.P., Cornelissen, J.H.C., 2020. Living litter: dynamic trait Spectra predict Fauna composition. Trends in Ecology & Evolution 35, 886–896. https://doi.org/10.1016/j.tree.2020.05.007.

Ganault, P., Nahmani, J., Capowiez, Y., Fromin, N., Shihan, A., Bertrand, I., Buatois, B., Milcu, A., 2024. Earthworms and plants can decrease soil greenhouse gas emissions by modulating soil moisture fluctuations and soil macroporosity in a mesocosm experiment. PLoS One 19, e0289859. https://doi.org/10.1371/journal.pone.0289859.

Garisoain, R., Jacotot, A., Delire, C., Binet, S., Le Roux, G., Gascoin, S., Rosset, T., Gogo, S., Granouillac, F., Payre-Suc, V., Gandois, L., 2024. Mountain peatlands and drought: carbon cycling in the pyrenees amidst global climate change. Journal of Geophysical Research: Biogeosciences 129. https://doi.org/10.1029/2024JG008041 e2024JG008041.

Gavinet, J., Ourcival, J., Limousin, J., 2019. Rainfall exclusion and thinning can alter the relationships between forest functioning and drought. New Phytologist 223, 1267–1279. https://doi.org/10.1111/nph.15860.

Gibbons, R.D., Hedeker, D.R., Davis, J.M., 1993. Estimation of effect size from a series of experiments involving paired comparisons. Journal of Educational Statistics 18, 271. https://doi.org/10.2307/1165136.

Guerra, C.A., Delgado-Baquerizo, M., Duarte, E., Marigliano, O., Görgen, C., Maestre, F. T., Eisenhauer, N., 2021. Global projections of the soil microbiome in the Anthropocene. Global Ecology and Biogeography 30, 987–999. https://doi.org/10.1111/geb.13273.

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

Harris, D.J., 2016. Inferring species interactions from co-occurrence data with Markov networks. Ecology 97, 3308–3314. https://doi.org/10.1002/ecy.1605.

Hartmann, M., Six, J., 2023. Soil structure and microbiome functions in agroecosystems. Nature Reviews Earth & Environment 4, 4–18. https://doi.org/10.1038/s43017-022-00366-w.

Hedges, L.V., Olkin, I., 2014. Statistical Methods for meta-analysis. Academic Press.

Hillgén, O., Palviainen, M., Laurén, A., Könönen, M., Ojala, A., Pumpanen, J., Peltomaa, E., 2024. Subtle changes in topsoil microbial communities of drained forested peatlands after prolonged drought. Environmental Microbiology Reports 16, e70041. https://doi.org/10.1111/1758-2229.70041.

Homet, P., Gómez-Aparicio, L., Matías, L., Godoy, O., 2021. Soil fauna modulates the effect of experimental drought on litter decomposition in forests invaded by an exotic pathogen. Journal of Ecology 109, 2963–2980. https://doi.org/10.1111/1365-2745.13711.

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

Korboulewsky, N., Perez, G., Chauvat, M., 2016. How tree diversity affects soil fauna diversity: a review. Soil Biology and Biochemistry 94, 94–106. https://doi.org/10.1016/j.soilbio.2015.11.024.

Koubová, A., Chroňáková, A., Pižl, V., Sánchez-Monedero, M.A., Elhottová, D., 2015. The effects of earthworms *Eisenia* spp. on microbial community are habitat dependent. European Journal of Soil Biology 68, 42–55. https://doi.org/10.1016/j.ejsobi.2015.03.004.

Lavelle, P., Bignell, D., Lepage, M., Wolters, V., Roger, P., Ineson, P., Heal, O., Dhillion, S., 1997. Soil Function in a Changing World: the Role of Invertebrate Ecosystem Engineers.

Soil organisms. In: Lavelle, P., Spain, A.V. (Eds.), 2001. Soil Ecology. Springer, Netherlands, Dordrecht, pp. 201–356. https://doi.org/10.1007/0-306-48162-6_3.

Li, N., Skaggs, T.H., Ellegaard, P., Bernal, A., Scudiero, E., 2024. Relationships among soil moisture at various depths under diverse climate, land cover and soil texture. Science of The Total Environment 947, 174583. https://doi.org/10.1016/j.scitotenv.2024.174583.

Limousin, J.M., Rambal, S., Ourcival, J.M., Rocheteau, A., Joffre, R., Rodriguez-Cortina, R., 2009. Long-term transpiration change with rainfall decline in a Mediterranean Quercus ilex forest. Global Change Biology 15, 2163–2175. https://doi.org/10.1111/j.1365-2486.2009.01852.x.

Litchman, E., 2015. Microbial resource utilization traits and trade-offs: implications for community structure, functioning, and biogeochemical impacts at present and in the future. Frontiers in Microbiology 6.

Liu, C., Li, X., Mansoldo, F.R.P., An, J., Kou, Y., Zhang, X., Wang, J., Zeng, J., Vermelho, A.B., Yao, M., 2022. Microbial habitat specificity largely affects microbial co-occurrence patterns and functional profiles in wetland soils. Geoderma 418, 115866. https://doi.org/10.1016/j.geoderma.2022.115866.

Liu, J., Wu, A., Yin, R., Xu, Z., You, C., Zhang, L., Xu, L., Xu, H., Wang, L., Li, H., Liu, S., Liu, Y., Tan, B., 2024. Tree species-mediated soil properties shape soil fauna community structure more strongly in the soil layer: evidence from a common garden experiment. Applied Soil Ecology 203, 105640. https://doi.org/10.1016/j.apsoil.2024.105640.

Liu, L., Zhu, K., Wurzburger, N., Zhang, J., 2020. Relationships between plant diversity and soil microbial diversity vary across taxonomic groups and spatial scales. Ecosphere 11, e02999. https://doi.org/10.1002/ecs2.2999.

Maestre, F.T., Delgado-Baquerizo, M., Jeffries, T.C., Eldridge, D.J., Ochoa, V., Gozalo, B., Quero, J.L., García-Gómez, M., Gallardo, A., Ulrich, W., Bowker, M.A., Arredondo, T., Barraza-Zepeda, C., Bran, D., Florentino, A., Gaitán, J., Gutiérrez, J. R., Huber-Sannwald, E., Jankju, M., Mau, R.L., Miriti, M., Naseri, K., Ospina, A., Stavi, I., Wang, D., Woods, N.N., Yuan, X., Zaady, E., Singh, B.K., 2015. Increasing aridity reduces soil microbial diversity and abundance in global drylands. Proceedings of the National Academy of Sciences 112, 15684–15689. https://doi.org/10.1073/pnas.1516684112.

Maraun, M., Martens, H., Migge, S., Theenhaus, A., Scheu, S., 2003. Adding to 'the enigma of soil animal diversity': fungal feeders and saprophagous soil invertebrates prefer similar food substrates. European Journal of Soil Biology 39, 85–95. https://doi.org/10.1016/S1164-5563(03)00006-2.

Maravalhas, J.B., Vasconcelos, H.L., 2020. Ant diversity in neotropical savannas: hierarchical processes acting at multiple spatial scales. Journal of Animal Ecology 89, 412–422. https://doi.org/10.1111/1365-2656.13111.

Medina-Sauza, R.M., Álvarez-Jiménez, M., Delhal, A., Reverchon, F., Blouin, M., Guerrero-Analco, J.A., Cerdán, C.R., Guevara, R., Villain, L., Barois, I., 2019. Earthworms building up soil Microbiota, a review. Frontiers in Environmental Science 7. https://doi.org/10.3389/fenvs.2019.00081.

Meng, T., Sun, P., 2023. Variations of deep soil moisture under different vegetation restoration types in a watershed of the Loess Plateau, China. Scientific Reports 13, 4957. https://doi.org/10.1038/s41598-023-32038-0.

Miyashita, T., Amano, T., Yamakita, T., 2014. Effects of ecosystem diversity on species richness and ecosystem functioning and services: a general conceptualization. In: Nakano, S. -ichi, Yahara, T., Nakashizuka, T. (Eds.), Integrative Observations and Assessments. Springer, Japan, Tokyo, pp. 29–47. https://doi.org/10.1007/978-4-431-54783-9_2.

Montoya-Sánchez, V., Kreft, H., Arimond, I., Ballauff, J., Berkelmann, D., Brambach, F., Daniel, R., Grass, I., Hines, J., Hölscher, D., Irawan, B., Krause, A., Polle, A., Potapov, A., Sachsenmaier, L., Scheu, S., Sundawati, L., Tscharntke, T., Zemp, D.C., Guerrero-Ramírez, N., 2023. Landscape heterogeneity and soil biota are central to multi-taxa diversity for oil palm landscape restoration. Communications Earth & Environment 4, 1–9. https://doi.org/10.1038/s43247-023-00875-6.

Mori, A.S., Isbell, F., Seidl, R., 2018. Β-diversity, community assembly, and ecosystem functioning. Trends in Ecology & Evolution 33, 549–564. https://doi.org/10.1016/j.tree.2018.04.012.

Morriën, E., 2016. Understanding soil food web dynamics, how close do we get? Soil Biology and Biochemistry 102, 10–13. https://doi.org/10.1016/j.soilbio.2016.06.022.

Naylor, D., Coleman-Derr, D., 2018. Drought stress and root-associated bacterial communities. Frontiers in Plant Science 8, 2223. https://doi.org/10.3389/fpls.2017.02223.

Nechitaylo, T.Y., Yakimov, M.M., Godinho, M., Timmis, K.N., Belogolova, E., Byzov, B. A., Kurakov, A.V., Jones, D.L., Golyshin, P.N., 2010. Effect of the earthworms Lumbricus terrestris and Aporrectodea caliginosa on bacterial diversity in soil. Microbial Ecology 59, 574–587. https://doi.org/10.1007/s00248-009-9604-y.

Ohlmann, M., Mazel, F., Chalmandrier, L., Bec, S., Coissac, E., Gielly, L., Pansu, J., Schilling, V., Taberlet, P., Zinger, L., Chave, J., Thuiller, W., 2018. Mapping the imprint of biotic interactions on β-diversity. Ecology Letters 21, 1660–1669. https://doi.org/10.1111/ele.13143.

Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., Caceres, M.D., Durand, S., Evangelista, H.B.A., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M.O., Lahti, L., McGlinn, D., Ouellette, M.-H., Cunha, E.R., Smith, T., Stier, A., Braak, C.J.F.T., Weedon, J., 2022. Vegan: Community Ecology Package.

Pedersen, T.L., 2024. Ggraph: an Implementation of Grammar of Graphics for Graphs and Networks.

Pelaez-Sanchez, S., Schmidt, O., Frouz, J., Čápová, K., Courtney, R., 2024. Effects of earthworms on microbial community structure, functionality and soil properties in soil cover treatments for mine tailings rehabilitation. European Journal of Soil Biology 120, 103603. https://doi.org/10.1016/j.ejsobi.2024.103603.

Pereira, T.J., De Santiago, A., Bik, H.M., 2024. Soil properties predict below-ground community structure, but not nematode microbiome patterns in semi-arid habitats. Molecular Ecology 33, e17501. https://doi.org/10.1111/mec.17501.

Potapov, A., Lindo, Z., Buchkowski, R., Geisen, S., 2023. Multiple dimensions of soil food-web research: history and prospects. European Journal of Soil Biology 117, 103494. https://doi.org/10.1016/j.ejsobi.2023.103494.

Preece, C., Peñuelas, J., 2016. Rhizodeposition under drought and consequences for soil communities and ecosystem resilience. Plant and Soil 409, 1–17. https://doi.org/10.1007/s11104-016-3090-z.

Richard, F., Roy, M., Shahin, O., Sthultz, C., Duchemin, M., Joffre, R., Selosse, M.-A., 2011. Ectomycorrhizal communities in a Mediterranean forest ecosystem dominated by Quercus ilex: seasonal dynamics and response to drought in the surface organic horizon. Annals of Forest Science 68, 57–68. https://doi.org/10.1007/s13595-010-0007-5.

RNR Confluence Garonne-Ariège, 2024. Bilan D'Activités 2023 - RNR Confluence Garonne-Ariège.

Rosset, T., Binet, S., Antoine, J.-M., Lerigoleur, E., Rigal, F., Gandois, L., 2020. Drivers of seasonal- and event-scale DOC dynamics at the outlet of mountainous peatlands revealed by high-frequency monitoring. Biogeosciences 17, 3705–3722. https://doi.org/10.5194/bg-17-3705-2020.

Schimel, J.P., 2018. Life in dry soils: effects of drought on soil microbial communities and processes. Annual Review of Ecology, Evolution, and Systematics 49, 409–432. https://doi.org/10.1146/annurev-ecolsys-110617-062614.

Shahin, O., Paul, N.M.-S., Rambal, S., Joffre, R., Richard, F., 2013. Ectomycorrhizal fungal diversity in Quercus ilex Mediterranean woodlands: variation among sites and over soil depth profiles in hyphal exploration types, species richness and community composition. Symbiosis 61, 1–12. https://doi.org/10.1007/s13199-013-0252-0.

Siebert, J., Sünnemann, M., Auge, H., Berger, S., Cesarz, S., Ciobanu, M., Guerrero-Ramírez, N.R., Eisenhauer, N., 2019. The effects of drought and nutrient addition on soil organisms vary across taxonomic groups, but are constant across seasons. Scientific Reports 9, 639. https://doi.org/10.1038/s41598-018-36777-3.

Soininen, J., Heino, J., Wang, J., 2018. A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. Global Ecology and Biogeography 27, 96–109. https://doi.org/10.1111/geb.12660.

Thakur, M.P., Geisen, S., 2019. Trophic regulations of the soil microbiome. Trends in Microbiology 27, 771–780. https://doi.org/10.1016/j.tim.2019.04.008.

Toberman, H., Freeman, C., Evans, C., Fenner, N., Artz, R.R.E., 2008. Summer drought decreases soil fungal diversity and associated phenol oxidase activity in upland Calluna heathland soil. FEMS Microbiology Ecology 66, 426–436. https://doi.org/10.1111/j.1574-6941.2008.00560.x.

Tournier, E., Amenc, L., Pablo, A.L., Legname, E., Blanchart, E., Plassard, C., Robin, A., Bernard, L., 2015. Modification of a commercial DNA extraction kit for safe and rapid recovery of DNA and RNA simultaneously from soil, without the use of harmful solvents. MethodsX 2, 182–191. https://doi.org/10.1016/j.mex.2015.03.007.

Townshend, J., 1963. A Modification and Evaluation of the Apparatus for the Oostenbrink Direct Cottonwool Filter Extraction Method.

Trap, J., Bonkowski, M., Plassard, C., Villenave, C., Blanchart, E., 2016. Ecological importance of soil bacterivores for ecosystem functions. Plant and Soil 398, 1–24. https://doi.org/10.1007/s11104-015-2671-6.

Tsiafouli, M.A., Thébault, E., Sgardelis, S.P., Ruiter, P.C. de, Putten, W.H. van der, Birkhofer, K., Hemerik, L., Vries, F.T. de, Bardgett, R.D., Brady, M.V., Bjornlund, L., Jørgensen, H.B., Christensen, S., Hertefeldt, T.D., Hotes, S., Hol, W.H.G., Frouz, J., Liiri, M., Mortimer, S.R., Setälä, H., Tzanopoulos, J., Uteseny, K., Pižl, V., Stary, J., Wolters, V., Hedlund, K., 2015. Intensive agriculture reduces soil biodiversity across Europe. Global Change Biology 21, 973–985. https://doi.org/10.1111/gcb.12752.

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., Mauro da Cunha Castro, J., Dam, M., Djigal, D., Escuer, M., Griffiths, B.S., Gutiérrez, C., Hohberg, K., Kalinkina, D., Kardol, P., Kergunteil, A., Korthals, G., Krashevska, V., Kudrin, A.A., Li, Q., Liang, W., Magilton, M., Marais, M., Martín, 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., Carlos Pereira da Silva, J., Pitteloud, C., Powers, T. O., Powers, K., Quist, C.W., Rasmann, S., Moreno, S.S., Scheu, S., Setälä, H., Sushchuk, A., Tiunov, A.V., Trap, J., van der Putten, W., Vestergård, M., Villenave, C., Waeyenberge, L., Wall, D.H., Wilschut, R., Wright, D.G., Yang, J., 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.

Van Der Heijden, M.G.A., Bardgett, R.D., Van Straalen, N.M., 2008. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecology Letters 11, 296–310. https://doi.org/10.1111/j.1461-0248.2007.01139.x.

Villarreal-Barajas, T., Martorell, C., 2009. Species-specific disturbance tolerance, competition and positive interactions along an anthropogenic disturbance gradient. Journal of Vegetation Science 20, 1027–1040. https://doi.org/10.1111/j.1654-1103.2009.01101.x.

Wagg, C., Schlaeppi, K., Banerjee, S., Kuramae, E.E., van der Heijden, M.G.A., 2019. Fungal-bacterial diversity and microbiome complexity predict ecosystem functioning. Nature Communications 10, 4841. https://doi.org/10.1038/s41467-019-12798-y.

Wall, D.H., Bardgett, R.D., Behan-Pelletier, V., Herrick, J.E., Jones, T.H., Six, J., Strong, D.R., Putten, W.H. van der, Ritz, K., 2012. Soil Ecology and Ecosystem Services. OUP Oxford.

Wild, J., Kopecký, M., Macek, M., Šanda, M., Jankovec, J., Haase, T., 2019. Climate at ecologically relevant scales: a new temperature and soil moisture logger for long-term microclimate measurement. Agricultural and Forest Meteorology 268, 40–47. https://doi.org/10.1016/j.agrformet.2018.12.018.

Xu, Z., Wang, S., Wang, Z., Dong, Y., Zhang, Y., Liu, S., Li, J., 2021. Effect of drainage on microbial enzyme activities and communities dependent on depth in peatland soil. Biogeochemistry 155, 323–341. https://doi.org/10.1007/s10533-021-00828-1.

Yang, T., Lupwayi, N., Marc, S.-A., Siddique, K.H.M., Bainard, L.D., 2021. Anthropogenic drivers of soil microbial communities and impacts on soil biological functions in agroecosystems. Global Ecology and Conservation 27, e01521. https://doi.org/10.1016/j.gecco.2021.e01521.

Yeates, G.W., Bongers, T., De Goede, R.G., Freckman, D.W., Georgieva, S.S., 1993. Feeding habits in soil nematode families and genera—an outline for soil ecologists. Journal of Nematology 25, 315.

Zhang, C., Wright, I.J., Nielsen, U.N., Geisen, S., Liu, M., 2024. Linking nematodes and ecosystem function: a trait-based framework. Trends in Ecology & Evolution S0169534724000399. https://doi.org/10.1016/j.tree.2024.02.002.