Science of the Total Environment 1020 (2026) 181545

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www elsevier com/locate/scitotenv

Research Paper

Fungal community structure and network connectivity as indicators of soil health under long-term land use

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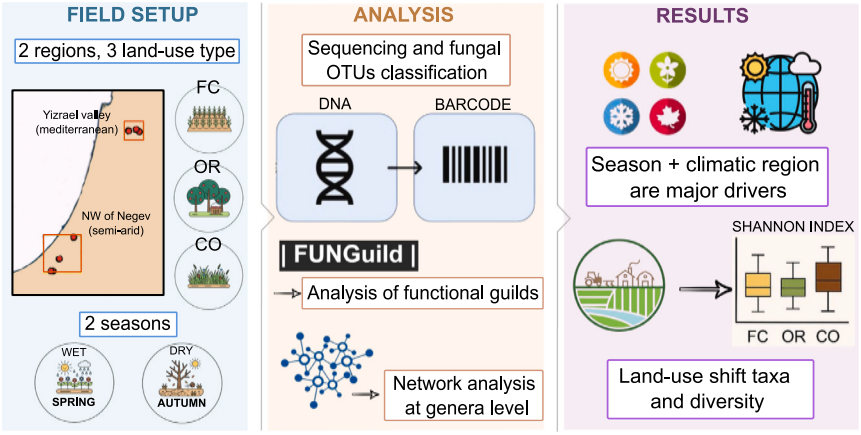
HIGHLIGHTS

- Soil fungi respond strongly to land use across climates and seasons.
- Orchard and control plots show highest fungal diversity and network complexity.
- Fungal composition is seasonally sensitive, especially in dry autumn periods.
- A stable core fungal community was detected across all treatments and regions.
- Network analysis reveals management impacts on soil fungal connectivity.

GRAPHICAL ABSTRACT



ARTICLE INFO

Keywords:
Land-use management
Soil fungal communities
Soil health indicators
Mediterranean and semi-arid regions

ABSTRACT

Agriculture practices induce profound changes in soil biological properties and soil functioning. However, we still lack an understanding of how soil fungal biodiversity responds to various practices. Metagenomic tools were used to investigate soil fungal communities and inferred ecological functions based on functional guild classification in response to the effect of climate region and land management. This study assessed how seasonal timing and long-term land management affect soil fungal communities, with the aim of exploring their potential as candidate indicators of soil biological status. We collected soil samples across two regions of Israel (Mediterranean north and semi-arid south), three land-use types—orchard (OR), field crops (FC), and non-cultivated control (CO)—and two seasons—autumn and spring. Abiotic parameters varied significantly by season, region, and depth, underscoring the importance of considering sampling time in soil assessment. Fungal community composition showed marked differences between land uses, suggesting sensitivity to long-term management. CO and OR soils consistently exhibited higher fungal diversity and network connectivity,

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https://doi.org/10.1016/j.scitotenv.2026.181545
Received 21 October 2025; Received in revised form 10 January 2026; Accepted 10 February 2026

while FC soils had lower richness and unique taxa. A stable core community of 10 genera was found across treatments. Functional guilds were dominated by saprotrophs, though specific taxa and guild contributions varied by management type and season. Overall, our results emphasize the importance of sampling timing and land-use history in shaping fungal communities and support the potential of fungal-based indicators for assessing soil status across agricultural systems.

1. Introduction

Changes in land use are an important human activity that affects the physical, chemical and biological properties of the soil. Soil biota communities with emphasis on microbial communities comprise a major portion of the agroecosystem and genetic diversity (Wagg et al., 2019) promoting diverse functionality such as nutrient cycling and supporting a broad range of ecosystem services (Carpenter et al., 2006; Ponge et al., 2013; van der Wal et al., 2009). The transfer of bacterially derived carbon and nitrogen through soil fauna further highlights the complexity of these food webs (Murray et al., 2009). Climatic region significantly impacts fungal diversity and community dynamics, primarily through changes in temperature, precipitation, and other abiotic factors. Mediterranean fungal communities, for example, are highly diverse due to moderate climatic conditions and seasonal rainfall, including saprotrophs, ectomycorrhizal fungi (ECM) and plant pathogens, with seasonal variations (Mora-Gómez et al., 2016; Orgiazzi et al., 2012; Martín-Pinto et al., 2023). Root-associated fungi exhibit the highest diversity and connectivity, aiding plant survival under extreme conditions (Zuo et al., 2021; Madouh et al., 2025; Wang et al., 2022). Land characteristics also significantly influence soil fungal communities, with effects varying by land use, soil type, and climatic region. Orchard soils often support structured microbial networks, and practices such as mulching or cover cropping can enhance fungal diversity, improving soil quality by increasing soil organic latter (SOM) and microbial connectivity (Liu et al., 2022; Xu et al., 2023). In addition, orchards, such as olive and apple orchards, harbor diverse fungal communities dominated by Ascomycota and Basidiomycota, including endophytes, pathogens, and mutualists such as mycorrhizae (Xu et al., 2023; Martins et al., 2021). In contrast, crop fields generally exhibit lower fungal diversity than uncultivated land due to biotic homogenization and the loss of rare fungi (Djemiel et al., 2023; Banerjee et al., 2024). Saprotrophs typically dominate, while mycorrhizal fungi are less abundant due to intensive soil management (Banerjee et al., 2024; Liu et al., 2022). Uncultivated land supports the highest fungal diversity with undisturbed ecosystems but lacks the enhanced nutrient cycling seen in managed systems (Djemiel et al., 2023; Banerjee et al., 2024). This land use is dominated by native saprotrophs, mycorrhizal fungi, and rare taxa adapted to natural conditions (Banerjee et al., 2024; Rosas-Medina et al., 2020). Changes in land use can alter the balance of functional fungal groups, potentially affecting ecosystem processes such as nutrient cycling and carbon sequestration (Brinkmann et al., 2019b; Xu et al., 2017). In this context, agroecological approaches emphasize the importance of maintaining soil biodiversity and ecosystem functions through diversified land-use systems, reduced chemical inputs, and context-specific management tailored to ecological and climatic conditions (Bocchi et al., 2022; Bocchi, 2023).

The overall objective of this study was to investigate whether different agroecological practices, climatic region, seasonality, and soil depth influence the diversity and taxonomic composition of soil fungal communities. We hypothesized that agroecological practices would be the main driver of the soil microbiota, while the autumn season, representing the dry period, would be associated with changes in the relative abundance of fungal phyla. To achieve this, we leveraged two long-term agricultural research plots that have maintained consistent land-use practices for over 15 years. These sites are located in two major agricultural regions of Israel: (a) the Jezreel Valley in the northern part of the country, and (b) the northwestern Negev Desert in the south. At each site, three distinct land-use types were defined for sampling: (1) orchard fields (OR), (2) field crops (FC), and (3) uncultivated control plots (CO).

Steinberger et al. (2022) used the same experimental setup to evaluate soil health through microbial activity and functional diversity metrics such as respiration, microbial biomass, and community level physiological profiling (CLPP), highlighting soil moisture and sampling season as important determinants of these indicators. Using the same site design and abiotic framework, the present study focuses on the fungal communities at the phylum and genus levels using ITS sequencing. This enables identification of fungal taxa associated with seasons and land-managements, inference of ecological guild structure, and characterization of community organization not available from CLPP-based indicators alone.

A deeper understanding of how land use and climatic zones interact to shape soil fungal communities is essential, as these microbial dynamics underpin key soil processes such as nutrient cycling, organic matter decomposition, and plant symbioses. Ultimately, insights into these interactions have critical implications for improving soil fertility, enhancing primary productivity, and guiding sustainable agricultural and economic development.

2. Methods

2.1. Soil sampling

Soil samples were collected from two notable agricultural areas in Israel: (i) The Jezreel Valley, located in the northern region of the country with a Mediterranean climate, renowned for its clayey soils and annual precipitation ranging from 420–470 mm (Service, 2021) (indicated with *N* in the following analysis); and (ii) the northwestern area of the Negev, a semi-arid desert zone in southern Israel, featuring clay-loam to sandy soils and annual precipitation levels ranging from 200–420 mm (Service, 2021) (indicated with *S* in the following analysis). Within each region, three specific and comparable sites were selected: Magen, Chavat HaShikmim and Talmey Yosef in region N and Ein Harod, Geva and Nir Yafe in the S region. For each one of these sites, three different land-use types were selected: orchards (OR), field crops (FC) and non-cultivated areas as control (CO). The different land-use types tested at each site were positioned as closely adjacent to each other as possible. Detailed descriptions of the selected plots are provided in Steinberger et al. (2022). At each sampling site, in order to accurately assess soil attribute variability, three pits (approximately 2 m in length, 0.6 m in width, and 1.2 m in depth) were excavated within each land-use area. In orchards where irrigation is conducted via a drip system, it is noted that the measured soil properties may be influenced by factors such as distance from the tree trunk and/or the drip irrigation line (Andreu et al., 1997). To address potential spatial variations resulting from irrigation, the pits within the orchards were dug from the tree trunks, at an angle of approximately 45 degrees from the tree row, towards the midpoint between two adjacent tree rows. Within each pit, four distinct depths were marked (1: 0–10 cm; 2: 10–30 cm; 3: 30–60 cm), and approximately 7 kg of disturbed soil samples (utilized for all other analyses) were collected along the pit walls at each designated soil layer, employing a soil core sampler and a garden scoop, respectively. From each disturbed soil sample, roughly 1 kg of freshly obtained soil was promptly sieved using a 2 mm sieve, sealed in a bag, and placed in a cooling box at 4 °C for biological analyses. The remaining disturbed soil samples were transported to the

laboratory, air-dried, ground, sieved through a 2 mm sieve and stored at room temperature for various additional chemical and physical analyses. Sampling expeditions were conducted during two seasons for both regions: fall (9-10/2016) and spring (2/2017 in the Negev and 2/2018 in the Jezreel Valley). Spring sampling was conducted in the same seasonal window (February) in both regions, but the campaigns occurred in different years due to logistical constraints. Sampling procedures, depths, and sample handling were identical across campaigns. In total, 324 soil samples were collected across two sampling seasons, two regions, three sites per region, three land-use types, three replicates, and three soil depths. These samples were individually placed in plastic bags, sealed, and stored in a cooling box at 4 °C until transportation to the laboratory. Upon arrival, they were maintained at 4 °C. From each of the 324 soil samples, five grams of soil were transferred to sterile test tubes and stored at −20 °C until DNA extraction.

2.2. Soil analyses: Abiotic analysis

The soil analyses included seven soil properties, soil moisture (SM), organic matter (OM), electric conductivity (EC), pH, total nitrogen (TN), organic carbon (OC), and the ratio between carbon and nitrogen (C:N) as described in Steinberger et al. (2022). SM was determined gravimetrically, as percentage of soil dry weight, by heating 5 g of soil in a muffling furnace at 105 °C for 24 h. OM was determined using the dry soil heated in a muffle furnace at 390 °C for 8 h. To compute soil pH, a filtered 1:2 soil and water mixture was subjected to an overnight incubation at room temperature, followed by shaking for 10 min at 160 rpm and another night in the incubator; finally, soil pH was determined with a pH electrode in the filtered supernatant. Soil EC was determined using an auto-ranging electrical conductivity/temperature electrode (TH2400, EI-Hamma) from a filtered 1:2 soil and distilled water mixture. Dried soil samples were used to determine the total C and N content by using a C:N analyzer (Flash EA 1112 series, Thermo). By subtracting the inorganic C as determined by a calcimeter from the total C, a measure of OC has been obtained. Finally, the ratios between organic carbon and nitrogen were computed.

Soil moisture (SM) and organic matter (OM) are important determinants of fungal growth and substrate availability, while electrical conductivity (EC) reflects salinity that can constrain microbial activity and community composition. Soil pH is a strong environmental factor for many fungal taxa, influencing nutrient availability and physiological tolerances. Total nitrogen (TN) and organic carbon (OC) represent fundamental resources associated with fertility, and the C:N ratio is a proxy for the relative balance of carbon versus nitrogen availability and organic matter quality. These variables were therefore used as abiotic predictors when interpreting patterns in fungal community structure across climatic regions, seasons, and land-use types. Additional details on these measurements can be found in Steinberger et al., 2022.

2.3. DNA extraction amplification and sequencing

Soil DNA was extracted from 0.5 g soil using an Exgene soil DNA mini kit from GeneAll (Seoul, Korea) and stored at −20C until PCR amplification. DNA was amplified using a SimpliAmpTM thermal cycler (Thermo Fisher Scientific, Walham, MA, USA), by mixing 12.5 μL HS Taq Mix Red (PCR Biosystems, London, UK), 9.5 μL ultrapure water, 1.0 μL extracted DNA, 1 μL CS1-ITS2 (ACACTGACGACATGGTTCTACAGCATCGATGAAGAACGCAGC), and 1 μL CS2-ITS4 (TACGGTAGCAGAGACTTGGTCTTCCTCCGCTTATTGATATGC). The thermal cycling program was set to: 95C for 2 min, followed by 40 cycles at 95 °C for 15 s, 50C for 30 s, 72C for 30 s, and after these cycles, 72C for 3 min. The amplified DNA was stored at −20C until sequencing. Sequencing (Miseq) was performed at the Hylabs Laboratory Ltd. (Rehovot, Israel; www.hylabs.co.il) sequencing facility using an Illumina sequencing platform (Illumina Inc., San Diego, CA, USA). Protocol PCR2: 2ul sample from PCR1 amplified sample containing CS1/CS2 adaptors was amplified for 10 cycles in 10ul using Fluidigm Access Array Barcode library according to manufacturer's protocol (2ul barcode per reaction). DNA was purified using Kapa Pure Beads at a ratio of 0.65X and quantified with qubit using Denovix DsDNA high sensitivity assay. DNA size and integrity was quantified by Tapestation using Agilent DNA screen tape and reagents.

2.4. Sequencing and analysis

Samples were run on a Miseq (Illumina) machine with 30 PhiX using MiSeq Reagent Kit v2 250PE. Demultiplexing was performed using bcl2fastq with default parameters allowing for 0 mismatch. Data was then mapped to PhiX using bowtie2 and unmapped reads were quantified, collected and examined using fastQC.

Demultiplexed reads were uploaded into CLC genomics workbench (Quigen), and analyzed using their ITS microbiome pipeline. The analysis workflow consists of quality filtration of the sequence data, and operational taxonomic unit (OTU) clustering was performed with default parameter settings. The adaptor sequence was removed and the reads with a quality score lower than 25 or length < 150 were discarded. The maximum number of acceptable ambiguous nucleotides was set to 2 and the length of the reads was fixed at 200–500bp. Chimeric sequences and singletons were detected and discarded. The remaining unique reads were used for OTU clustering, which was performed by alignment to the UNITE v7.2 database at 97 sequence similarity. After the removal of all reads that did not belong to the fungal kingdom, the data were normalized to 100 Fungal OTUs were categorized into trophic modes using FUNGuild (Nguyen et al., 2016).

2.5. Statistical analysis

The data were subjected to statistical analysis of variance to evaluate differences between means with different soil treatments (CO, OR, FC) and in different seasons (autumn–spring). Differences between seasons were assessed with a t-test using the statannotations package (v0.7.1) in Python (v3.11.2), while differences between pairs of treatments were evaluated with a Duncan's new multiple range test. Differences were considered statistically significant at p-value < 0.05.

We performed Principal Coordinates Analysis (PCoA) and Constrained Correspondence Analysis (CCA) (using the abiotic parameters, SITE, TREAT and Season as explanatory variables) on the phyla relative abundances using the vegan package (v2.7-0) in R (v4.4.2). The results of the PCoA and CCA were plotted using the ordiplot function from the vegan package. To assess the effect of the explanatory variables on the fungi community, a PERmutational Multivariate Analysis Of Variance (PERMANOVA) was performed using the anova.cca function in R. The Richness was computed simply as the number of different phyla or genera in a sample, while the Shannon's diversity index was calculated as

$$H' = -\sum_{i=1}^{N} p_i \ln p_i \quad (1)$$

where N is the number of observed phyla/genera in a sample and p_i is the relative abundance of the ith phylum/genus.

The network analysis was performed using the networkx package (v3.4.2) in Python, considering the genera as nodes; two genera nodes were connected by an edge if the Spearman's correlation coefficient r between their relative abundances was higher than a threshold ($r > 0.5$). Different conditions were compared (autumn/spring, north/south, and the three treatments) by computing a selection of network topology parameters: the number of edges and of nodes, the average degree and the average clustering coefficient. We also found the most connected taxa computing the degree centrality, which is the fraction of nodes connected to a given node, betweenness centrality. This centrality measure was computed using the networkx package in Python.

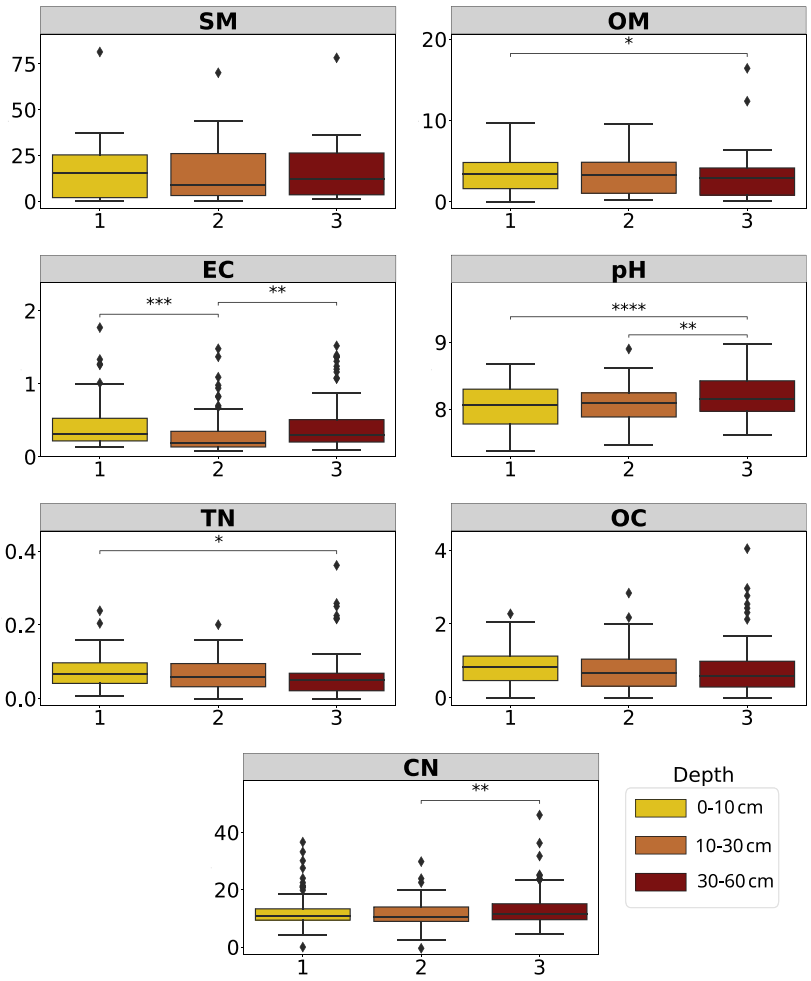

Fig. 1. Boxplots of the abiotic parameters at different depths (1: 0–10 cm, 2: 10–30 cm, 3: 30–60 cm). Significant differences between depths, assessed with ANOVA followed by a Duncan Test, are indicated with a bar over the couple of boxplots and a number of stars. Differences are considered statistically significant at p-value < 0.05 and are reported with the following legend: $10^{-2} < p < 5\ \ 10^{-2}$ (*), $10^{-3} < p < 10^{-2}$ (**), $10^{-4} < p < 10^{-3}$ (***), $p < 10^{-4}$ (****).

3. Results

3.1. Analysis of soils obtained from different land-use types closely adjacent for abiotic parameters

For all the samples we analyzed abiotic parameters including soil moisture (SM), organic matter (OM), electric conductivity (EC), pH, total nitrogen (TN), organic carbon (OC) and the ratio between C and N (C:N), across regions, land-use types, seasons, and depths(see Methods section for more details). These parameters are commonly used as indicators of soil status.

We first analyzed possible changes in soil samples obtained at 3 depths (0–10, 10–30 and 30–60 cm). For this analysis, data from all regions, land-use types, sites, and seasons were pooled in order to assess depth-related effects only. Some of the abiotic parameters depend on the depth, with electrical conductivity (EC) and pH displaying strong differences among depths, as shown in Fig. 1.

Seasonal variation in abiotic parameters across land-use types (CO, FC, and OR) and geographical regions (north and south) is shown in Fig. 2. Several parameters, including SM, EC, and pH, were significantly affected by seasonality; however, the magnitude and direction of these effects varied considerably among sites and land-use types.

The comparison between the two agroecological regions (Jezreel Valley, North; NW Negev, South) is shown in Fig. 3; values are pooled across the three sites within each region. Here it is evident that many abiotic parameters (SM, OM, TN, OC) are consistently higher in the northern region with respect to the southern region and these differences were only weakly influenced by season (autumn versus spring). Accordingly, Table 1 summarizes the average values and the associated standard errors of the abiotic parameters, with annotations that report the result of the Duncan Tests assessing differences across treatments. This Table reports significant differences between treatments in many cases; the strongest differences are found for SM, EC and TN and are more frequent in the north site with respect to the south. Therefore, overall, the abiotic parameters exhibit strong differences across conditions, reflecting a complex pattern.

3.2. Analysis of soils obtained from different land-use types closely adjacent for biotic parameters

From the same samples analyzed for abiotic parameters, we also analyzed the fungal community.Phylum-level community composition is reported as relative abundance, calculated as the proportion of reads (or OTU counts) assigned to each phylum out of the total fungal reads per sample (expressed as in the figures). Taxa that could not be assigned to a phylum are reported as unclassified/unassigned ('uni'). First, we did not observe any significant differences in phylum-level abundances across depths (Fig. 4). Consequently, data from all depths were averaged for subsequent analyses. Fig. 5a and Fig. 5b show respectively a stack plot and the boxplots of phyla abundances present as found in the soil in different seasons, geographical regions and land uses. There are some differences due to the site that depends on the

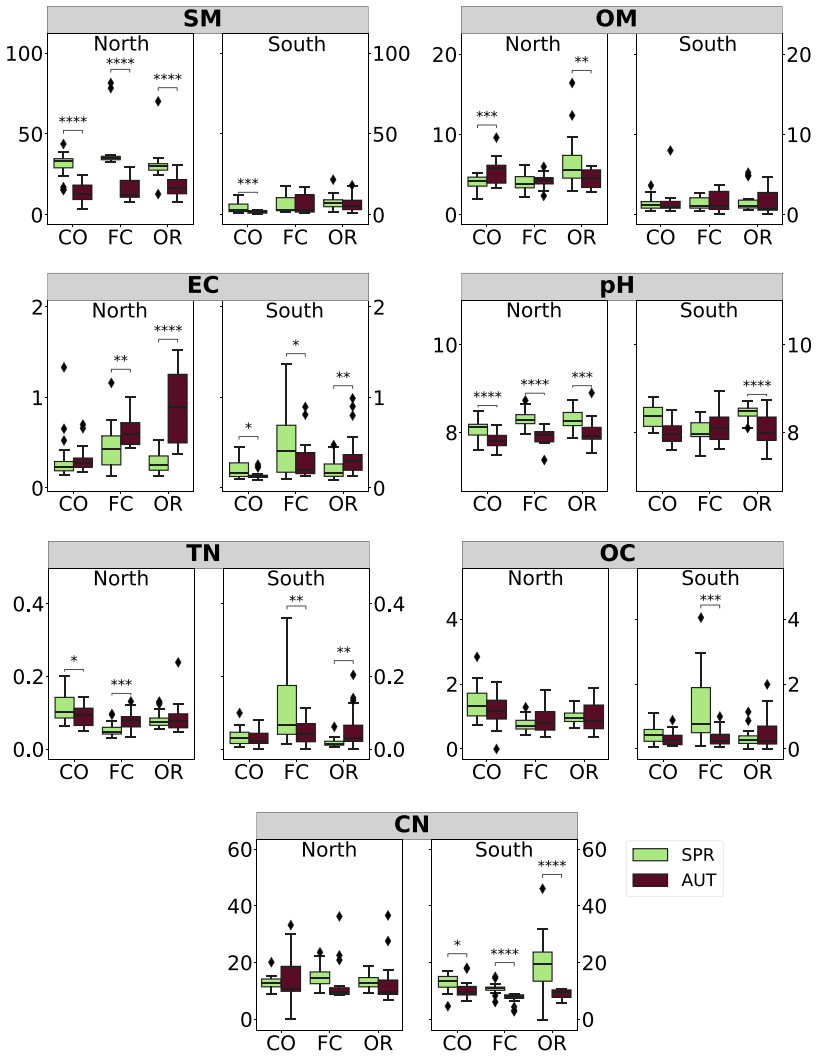

Fig. 2. Boxplots of the abiotic parameters in different seasons (spring and autumn), from different sites (north and south), and with different treatments of the soil (CO, FC, OR). Significant differences between seasons at fixed treatment, assessed with a t-test on the mean values of each abiotic parameter, are indicated with a bar over the couple of boxplots and a number of stars. Differences are considered statistically significant at p-value < 0.05 and are reported with the following legend: $10^{-2} < p < 5\ \ 10^{-2}$ (*), $10^{-3} < p < 10^{-2}$ (**), $10^{-4} < p < 10^{-3}$ (***), $p < 10^{-4}$ (****).

season, but in general, during spring we found a greater variety of phyla independent of the land use. Ascomycota, the most abundant phyla overall, is consistently more frequent in autumn compared to spring in the N (north), while the behavior is more complex in the S (south) site. In Table 2 we report the average values and the associated standard errors of the phyla abundances, annotated with the results of the Duncan Test to assess differences across treatments. Mortierellomycota and Basidiomycota are the phyla that are more affected by land use, with autumn being the season where the most significant differences are found. Then, we classified the genera in fungal guilds to gain insights on the functionality of the fungal biota across different conditions; Fig. 6a shows stackplots of the main guilds across different land use, season, and geographical regions. Saprotrophs consistently emerged as the most dominant guild, with only minor variations across conditions. Other frequently occurring guilds include Plant Pathogens and Endophytes. Overall, the composition and relative abundance of the major guilds remain consistent across all conditions. In order to understand better the function of these fungi, we analyzed the richness index, which is the simplest measure of biodiversity, at the level of genera and phyla, telling us how many different taxa are present in a community and Shannon's diversity Index, which measures how evenly the different taxa composing the community are distributed. As shown in Fig. 6b, significant differences are found between seasons in land non-cultivated (CO), especially in the N sites. These ecological indices vary moderately also across treatments (Table 3), with non-cultivated land (CO) and orchard fields (OR) being the types of land-use that most consistently show the highest degree of richness and diversity. Moreover, Venn diagrams were used to compare the fungal genera detected among the three soil treatments (CO, OR, FC) within each season-region group (Fig. 7). Across all conditions, we found a subset of genera consistently shared among treatments. This core fungal community is composed of ten genera, namely: *Alternaria Aspergillus Chaetomium Fusarium Humicola Mortierella Mycosphaerella Penicillium Plectosphaerella*, belonging mainly to the endophytes, saprotroph and plant pathogen guilds. The treatments with the highest richness of unique genera are OR in spring and CO in autumn, whereas FC consistently shows the lowest richness of unique genera across all conditions.

To gain deeper insights on the interaction and connectivity within a community, we performed network analysis at genera level, using Spearman's correlation coefficient to construct networks of genera across the different conditions. In Fig. 8 we show that in autumn the fungal genera are more connected, while the different land use leads to a different connectivity. In order to perform a quantitative comparison,

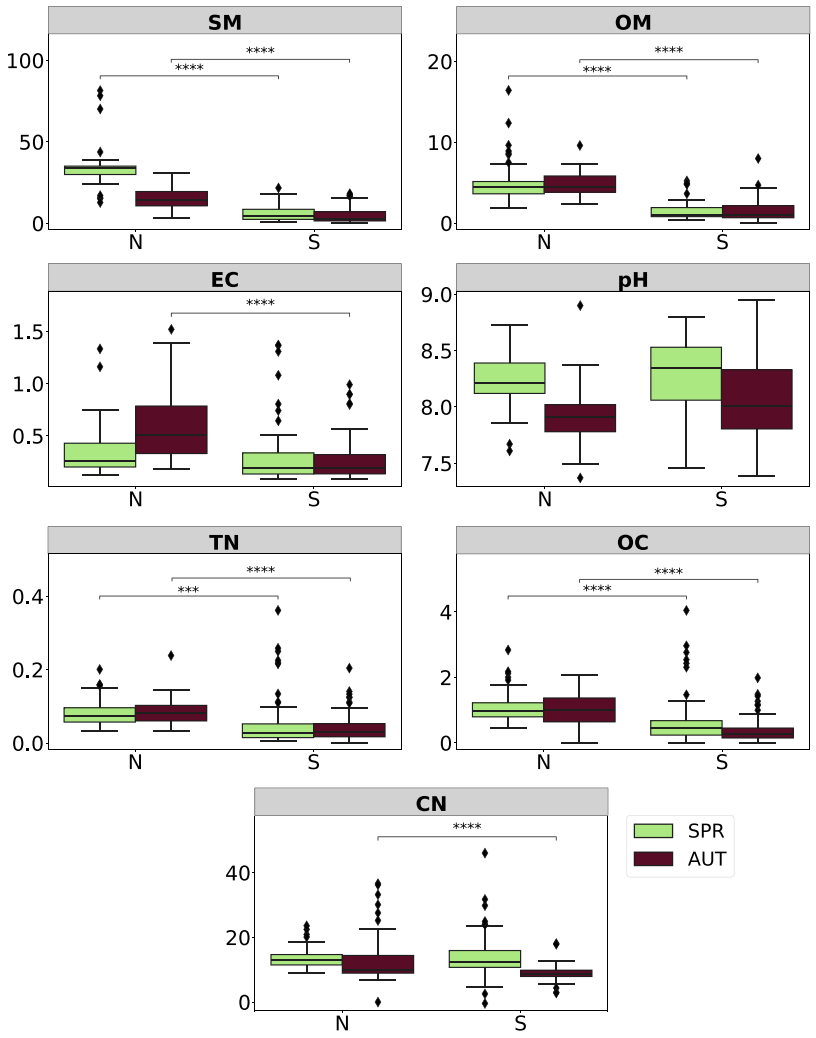

Fig. 3. Boxplots of abiotic parameters in different seasons (spring and autumn) and from different sites (north and south). Significant differences between sites at fixed season, assessed with a t-test on the mean values of each abiotic, are indicated with a bar over the couple of boxplots and a number of stars. Differences are considered statistically significant at p-value < 0.05 and are reported with the following legend: $10^{-2} < p < 5 \;\; 10^{-2}$ (*), $10^{-3} < p < 10^{-2}$ (**), $10^{-4} < p < 10^{-3}$ (***), $p < 10^{-4}$ (****).

we computed several global features of the network: the total number of nodes and edges, the average node degree, the clustering coefficient and the most connected taxa (based on the degree centrality); the results are shown in Table 4. In general, there are no significant differences in the global features of the networks across the various conditions, with the notable exception of the OR (orchard field) samples, whose genera network displays much higher number of edges and average degree. In other words, under this condition the network shows a higher degree of connectivity and more efficient communication between nodes, a typical feature of small-world networks. Finally, we carried out CCA analysis, which is a multivariate statistical technique that allows us to understand how one set of variables (explanatory variables) shapes the structure of another (response variables), followed by a PERMANOVA test that can identify the most important explanatory variables. Here we use the abiotic parameters together with season, geographical region, and land use as the explanatory variables and the phyla relative abundances as the response variables. As shown in Table 5, season, geographical site and land use significantly affect the phyla abundances. To a lesser extent, the soil moisture (SM) and pH parameters are important in determining the composition of the fungi community.

4. Discussion

This study provides important insights into how seasonal variation and land-use practices influence soil fungal communities across distinct agroecological zones. By integrating high-resolution metagenomic analysis with a temporally and spatially replicated sampling design, we were able to disentangle the independent and interactive effects of land-use intensity and climate variability on fungal community composition and dynamics. In addition to our previous paper (Steinberger et al., 2022) which provided the experimental platform and abiotic framework using microbial biomass (MB) and community level physiological profiling (CLPP), in the present paper we focused on fungal sequencing. Our findings reveal that land-use practices exert a stronger and more consistent influence on fungal community structure than climate, even across contrasting regions such as Mediterranean and semi-arid zones. This suggests that management intensity functions as a dominant ecological filter, shaping fungal assemblages regardless of regional climatic differences—supporting previous observations of reduced fungal diversity in intensively managed systems (Banerjee et al., 2024; Brinkmann et al., 2019a).

Seasonal variation significantly influenced fungal community composition, particularly the relative abundance of specific phyla during

Table 1
Soil abiotic parameters across different treatments. Significant differences found with a Duncan's multiple range test are indicated with letters; different letters within a row at fixed site and season denote a significant difference (p 0.05) between treatments. As an example, the code (CO a, FC a, OR b) indicates a significant difference between treatment CO and OR and between FC and OR, but no significant difference between CO and FC.

SITE	Season	TREAT	SM	OM	EC	pH
N	AUT	CO	13.51 ± 1.20 a	5.45 ± 0.35 b	0.32 ± 0.03 a	7.81 ± 0.04 a
		FC	14.30 ± 1.71	3.99 ± 0.31 a	0.63 ± 0.04 b	7.91 ± 0.04
		OR	17.61 ± 1.48 b	4.48 ± 0.24 a	0.89 ± 0.08 c	8.00 ± 0.06 b
	SPR	CO	30.96 ± 1.29 a	4.01 ± 0.17 a	0.30 ± 0.05 a	8.08 ± 0.04 a
		FC	38.23 ± 2.33 b	4.12 ± 0.19 a	0.44 ± 0.04 b	8.31 ± 0.04 b
		OR	30.68 ± 1.73 a	6.39 ± 0.57 b	0.28 ± 0.02 a	8.29 ± 0.04 b
S	AUT	CO	1.66 ± 0.19 a	1.42 ± 0.31	0.14 ± 0.01 a	8.00 ± 0.05
		FC	6.46 ± 1.19 b	1.59 ± 0.27	0.27 ± 0.04 b	7.43 ± 0.47
		OR	6.73 ± 1.07 b	1.60 ± 0.31	0.36 ± 0.05 b	8.07 ± 0.07
	SPR	CO	4.35 ± 0.62 a	1.32 ± 0.15	0.20 ± 0.02 a	8.06 ± 0.31
		FC	6.04 ± 1.13	1.32 ± 0.16	0.48 ± 0.09 b	7.69 ± 0.34
		OR	6.98 ± 1.03 b	1.58 ± 0.33	0.20 ± 0.02 a	8.44 ± 0.03
			TN	OC	CN	
SITE	Season	TREAT				
N	AUT	CO	0.09 ± 0.01	1.19 ± 0.12	14.55 ± 1.80	
		FC	0.08 ± 0.01	0.90 ± 0.09	12.35 ± 1.70	
		OR	0.08 ± 0.01	0.99 ± 0.10	12.49 ± 1.51	
	SPR	CO	0.11 ± 0.01 c	1.43 ± 0.09 c	12.90 ± 0.41 a	
		FC	0.05 ± 0.01 a	0.77 ± 0.04 a	14.86 ± 0.68 b	
		OR	0.08 ± 0.01 b	1.00 ± 0.04 b	12.97 ± 0.42 a	
S	AUT	CO	0.03 ± 0.01 a	0.31 ± 0.04	8.27 ± 1.09	
		FC	0.05 ± 0.01	0.35 ± 0.05	6.51 ± 0.62	
		OR	0.05 ± 0.01 b	0.51 ± 0.11	7.22 ± 0.78	
	SPR	CO	0.03 ± 0.01 a	0.41 ± 0.05 a	11.77 ± 0.85 a	
		FC	0.11 ± 0.02 b	1.18 ± 0.22 b	10.41 ± 0.58 a	
		OR	0.02 ± 0.01 a	0.32 ± 0.05 a	18.07 ± 2.14 b	

Table 2
Phyla relative abundances across different treatments, in different seasons (autumn and spring) and in different sites (north and south). Significant differences found with a Duncan's multiple range test are indicated with letters; different letters within a row at fixed site and season denote a significant difference (p 0.05) between treatments. As an example, the code (CO a, FC a, OR b) indicates a significant difference between treatment CO and OR and between FC and OR, but no significant difference between CO and FC.

SITE	Season	TREAT	Ascomycota	Mortierellomycota	uni	Basidiomycota
N	AUT	CO	0.75 ± 0.04	0.01 ± 0.01 a	0.04 ± 0.01 a	0.15 ± 0.04 b
		FC	0.78 ± 0.04	0.04 ± 0.01 a	0.11 ± 0.03 b	0.06 ± 0.02 a
		OR	0.79 ± 0.04	0.10 ± 0.03 b	0.04 ± 0.01 a	0.06 ± 0.03 a
	SPR	CO	0.51 ± 0.04	0.20 ± 0.04	0.01 ± 0.01 a	0.20 ± 0.04
		FC	0.50 ± 0.04	0.11 ± 0.03	0.18 ± 0.04 b	0.11 ± 0.02
		OR	0.59 ± 0.05	0.21 ± 0.05	0.02 ± 0.01 a	0.13 ± 0.03
S	AUT	CO	0.65 ± 0.03 a	0.07 ± 0.02 a	0.05 ± 0.01	0.19 ± 0.02 b
		FC	0.82 ± 0.03 b	0.06 ± 0.02 a	0.06 ± 0.01	0.03 ± 0.01 a
		OR	0.66 ± 0.03 a	0.20 ± 0.04 b	0.05 ± 0.01	0.02 ± 0.01 a
	SPR	CO	0.63 ± 0.05	0.22 ± 0.05 b	0.03 ± 0.01 a	0.09 ± 0.02 b
		FC	0.74 ± 0.04 b	0.08 ± 0.04 a	0.05 ± 0.01 b	0.07 ± 0.02
		OR	0.55 ± 0.04 a	0.26 ± 0.04 b	0.06 ± 0.01 b	0.03 ± 0.01 a
			Chytridiomycota	Glomeromycota	Mucoromycota	Rozellomycota
SITE	Season	TREAT				
N	AUT	CO	0.03 ± 0.02	<0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01
		FC	0.01 ± 0.01	<0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01
		OR	0.01 ± 0.01	<0.01 ± 0.01	<0.01 ± 0.01	0.01 ± 0.01
	SPR	CO	<0.01 ± 0.01 a	0.05 ± 0.01 b	0.02 ± 0.01 b	0.01 ± 0.01
		FC	0.04 ± 0.02 b	0.01 ± 0.01 a	0.01 ± 0.01	0.04 ± 0.02
		OR	0.01 ± 0.01	0.03 ± 0.01	<0.01 ± 0.01 a	0.01 ± 0.01
S	AUT	CO	0.01 ± 0.01	0.03 ± 0.01 b	<0.01 ± 0.01 a	<0.01 ± 0.01a
		FC	<0.01 ± 0.01	<0.01 ± 0.01 a	0.02 ± 0.01 b	0.01 ± 0.01 a
		OR	0.01 ± 0.01	<0.01 ± 0.01 a	0.01 ± 0.01 a	0.05 ± 0.02 b
	SPR	CO	<0.01 ± 0.01	0.02 ± 0.01	<0.01 ± 0.01 a	0.01 ± 0.01a
		FC	<0.01 ± 0.01	0.01 ± 0.01	0.06 ± 0.02 b	0.01 ± 0.01 a
		OR	0.01 ± 0.01	0.01 ± 0.01	<0.01 ± 0.01 a	0.09 ± 0.02 b

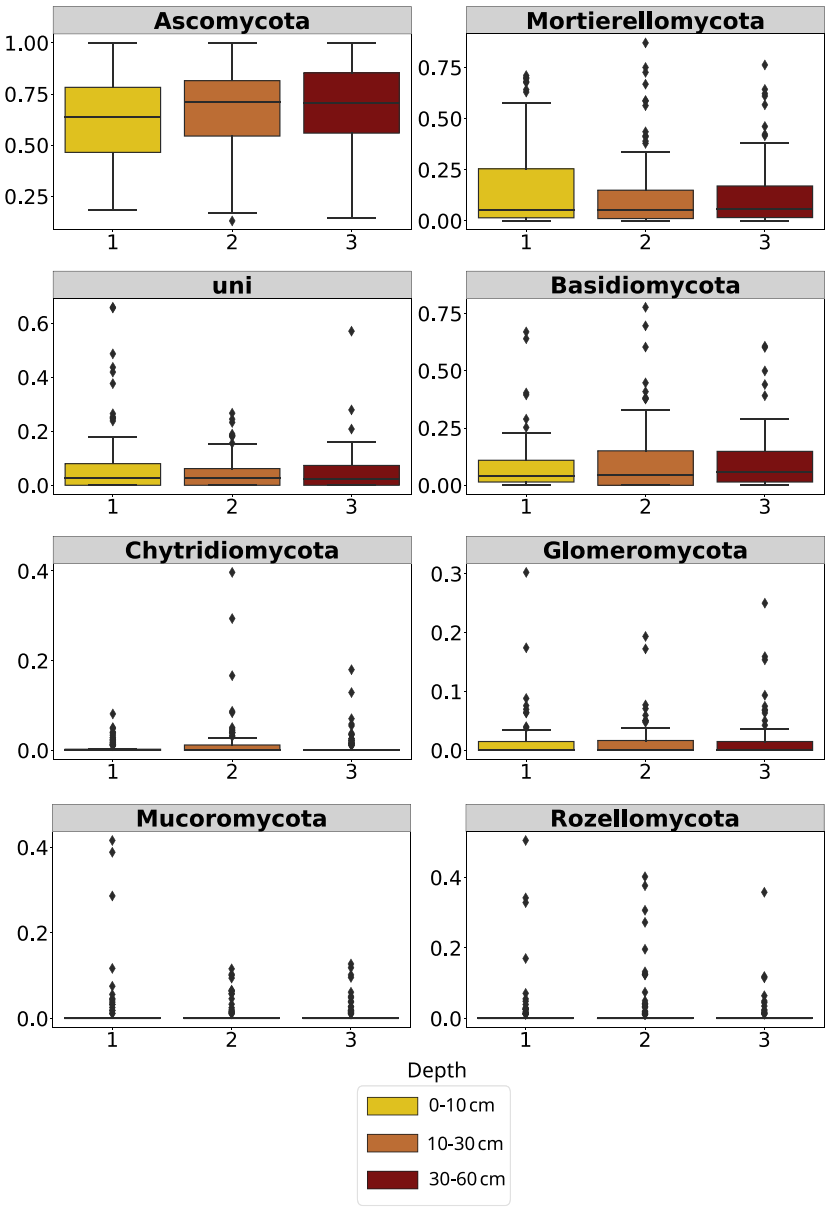

Fig. 4. Boxplots of phyla relative abundances at different depths (1: 0–10 cm, 2: 10–30 cm, 3: 30–60 cm). No significant differences are found across the three depths.

Table 3
Community richness and diversity indices across different treatments. Significant differences found with a Duncan's multiple range test are indicated with letters; different letters within a row at fixed site and season denote a significant difference (p 0.05) between treatments. As an example, the code (CO a, FC a, OR b) indicates a significant difference between treatment CO and OR and between FC and OR, but no significant difference between CO and FC.

SITE	Season	TREAT	Richness (phyla)	H' (phyla)	Richness (genera)	H' (genera)
N	AUT	CO	3.75 ± 0.37	0.63 ± 0.07	10.65 ± 0.70	1.91 ± 0.10 b
		FC	3.94 ± 0.42	0.62 ± 0.09	8.50 ± 1.06	1.48 ± 0.18 a
		OR	3.50 ± 0.30	0.54 ± 0.07	9.55 ± 0.65	1.68 ± 0.11
	SPR	CO	4.04 ± 0.24 a	0.94 ± 0.05	7.56 ± 0.51 a	1.34 ± 0.09
		FC	4.78 ± 0.22 b	1.04 ± 0.04 b	8.19 ± 0.53	1.54 ± 0.08
		OR	4.41 ± 0.25	0.85 ± 0.06 a	9.50 ± 0.77 b	1.50 ± 0.12
S	AUT	CO	4.87 ± 0.23 b	0.95 ± 0.05 b	10.91 ± 0.80	1.87 ± 0.10
		FC	3.58 ± 0.26 a	0.58 ± 0.07 a	10.42 ± 0.50	1.82 ± 0.08
		OR	4.48 ± 0.23 b	0.84 ± 0.05 b	10.96 ± 0.84	1.74 ± 0.12
	SPR	CO	4.33 ± 0.25 a	0.76 ± 0.07 a	10.44 ± 0.71	1.59 ± 0.12
		FC	4.17 ± 0.21 a	0.68 ± 0.07 a	9.71 ± 0.56	1.64 ± 0.09
		OR	5.00 ± 0.23 b	1.01 ± 0.05 b	9.35 ± 0.60	1.50 ± 0.10

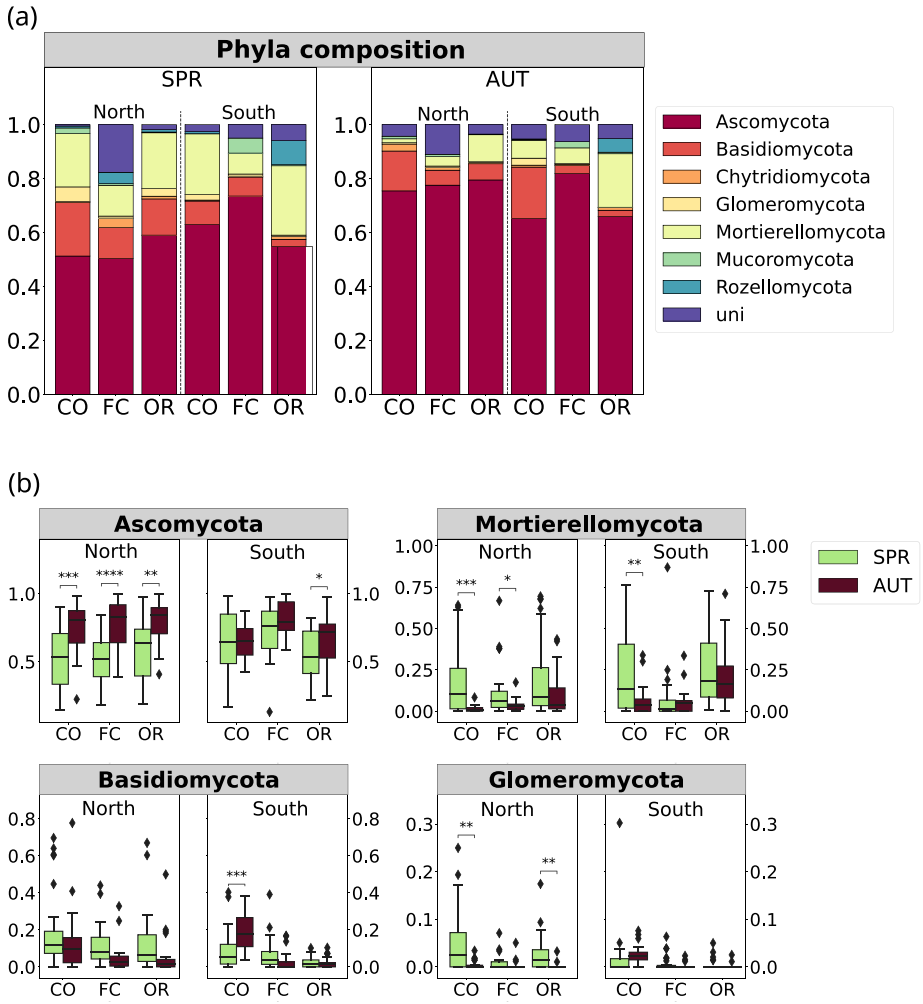

Fig. 5. (a) Stacked plots of relative abundance of each phyla and (b) boxplots of a selection of phyla relative abundances in different seasons (spring and autumn), from different sites (north and south), and with different treatments of the soil (CO, FC, OR). Significant differences between seasons at fixed treatment, assessed with a t-test on the mean values of each phyla abundance, are indicated with a bar over the couple of boxplots and a number of stars. Differences are considered statistically significant at p-value < 0.05 and are reported with the following legend: $10^{-2} < p < 5\ \ 10^{-2}$ (*), $10^{-3} < p < 10^{-2}$ (**), $10^{-4} < p < 10^{-3}$ (***), $p < 10^{-4}$ (****). In this picture, we report only the phyla abundances where significant differences were found.

Table 4
Statistics of the network analysis performed on the genera community over different seasons, different regions and different treatments. The number reported after the most connected taxa is the degree centrality.

	Node number	Edge number	Average degree	Average clustering coeff.	Most connected taxa
SPR	71	72	2.02	0.46	Hirsutella (0.071)
AUT	87	92	2.11	0.36	Keissleriella (0.070)
N	96	103	2.14	0.33	Powellomyces (0.073)
S	76	77	2.02	0.28	Rhinocladiella (0.066)
CO	87	84	1.93	0.27	Keissleriella (0.058)
FC	66	79	2.39	0.46	Bensingtonia (0.077)
OR	86	127	2.95	0.42	Schizothecium (0.106)

the dry autumn period. However, contrary to expectations of complete community turnover, our results indicate that fungal communities maintain a degree of taxonomic and functional stability across seasons. This finding highlights the importance of using high-resolution molecular tools, which can detect fine-scale taxon-level responses that may be missed by bulk diversity indices. In particular, transitional periods between dry and wet seasons revealed the most dynamic community shifts, likely driven by fluctuations in soil moisture and nutrient availability (Santalahti et al., 2016; Žifčáková et al., 2017). These patterns underscore the importance of timing in soil sampling protocols for accurate monitoring of microbial responses to environmental changes.

A novel aspect of this study is the application of fungal co-occurrence network analysis across different land-use systems and climatic contexts. Our findings show that orchard systems supported more complex, clustered, and highly connected fungal networks, indicative of greater ecological complexity and potential functional redundancy. In contrast, field crop systems displayed simplified networks, suggesting reduced biotic interactions and lower resilience to environmental disturbance. These structural differences provide mechanistic insights into how land-use intensity impacts not only community composition but also ecological stability and ecosystem functioning. The identification of a stable core fungal community shared across land uses, seasons, and

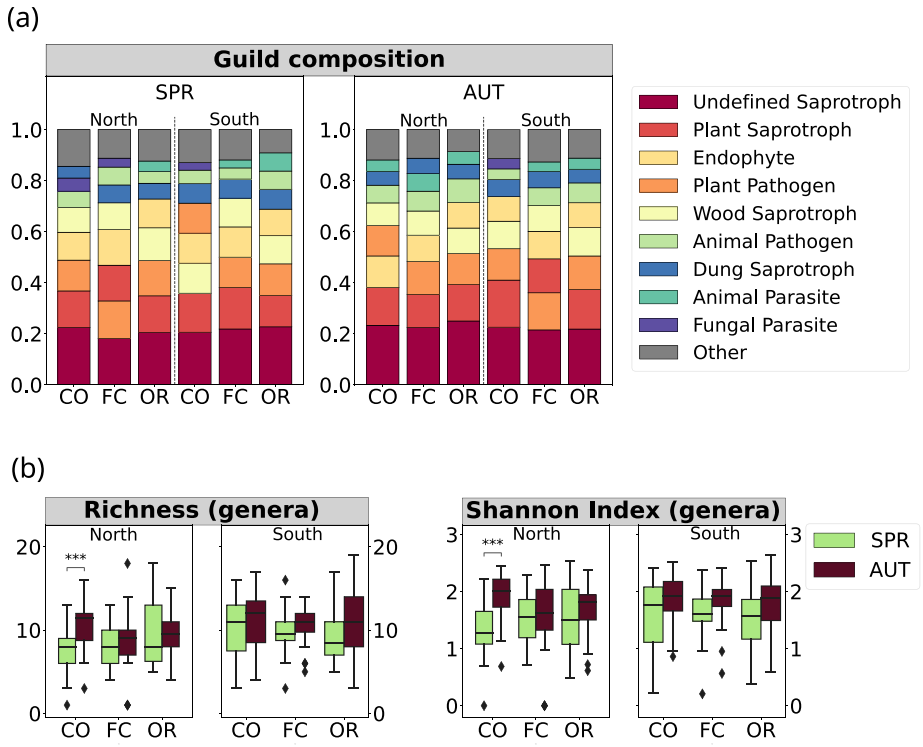

Fig. 6. (a) Distribution of fungal guilds and (b) boxplots of richness and Shannon's diversity index for genera community in different seasons (spring and autumn), from different sites (north and south), and with different treatments of the soil (CO, FC, OR). Significant differences between seasons at fixed treatment, assessed with a t-test on the mean values of each community index, are indicated with a bar over the couple of boxplots and a number of stars. Differences are considered statistically significant at p-value < 0.05 and are reported with the following legend: $10^{-2} < p < 5\ \ 10^{-2}$ (*), $10^{-3} < p < 10^{-2}$ (**), $10^{-4} < p < 10^{-3}$ (***), $p < 10^{-4}$ (****).

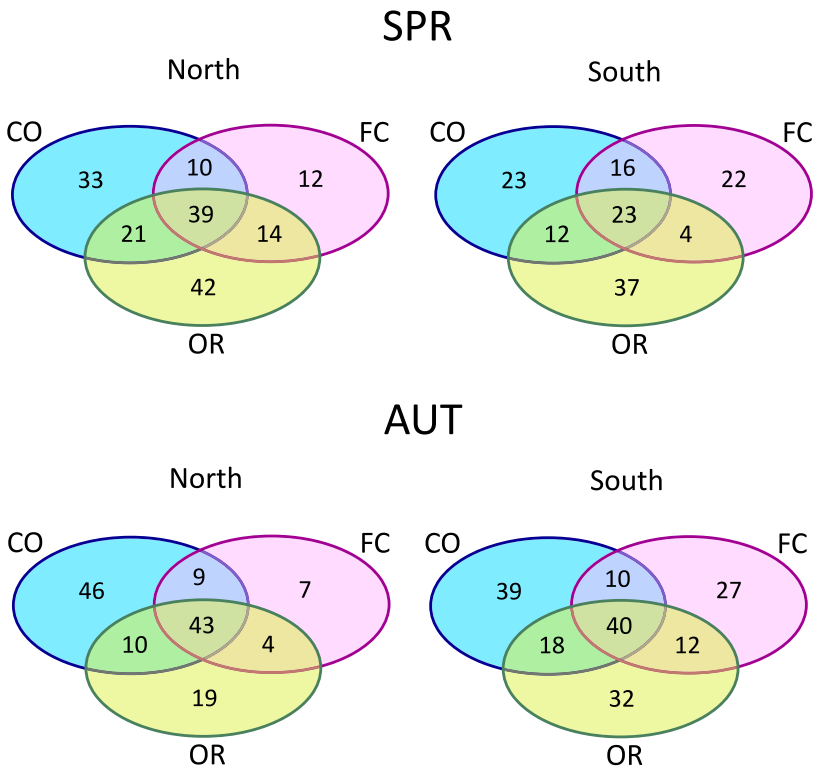

Fig. 7. Venn diagrams of the number of fungal genera shared or not shared across different treatments at fixed location and season.

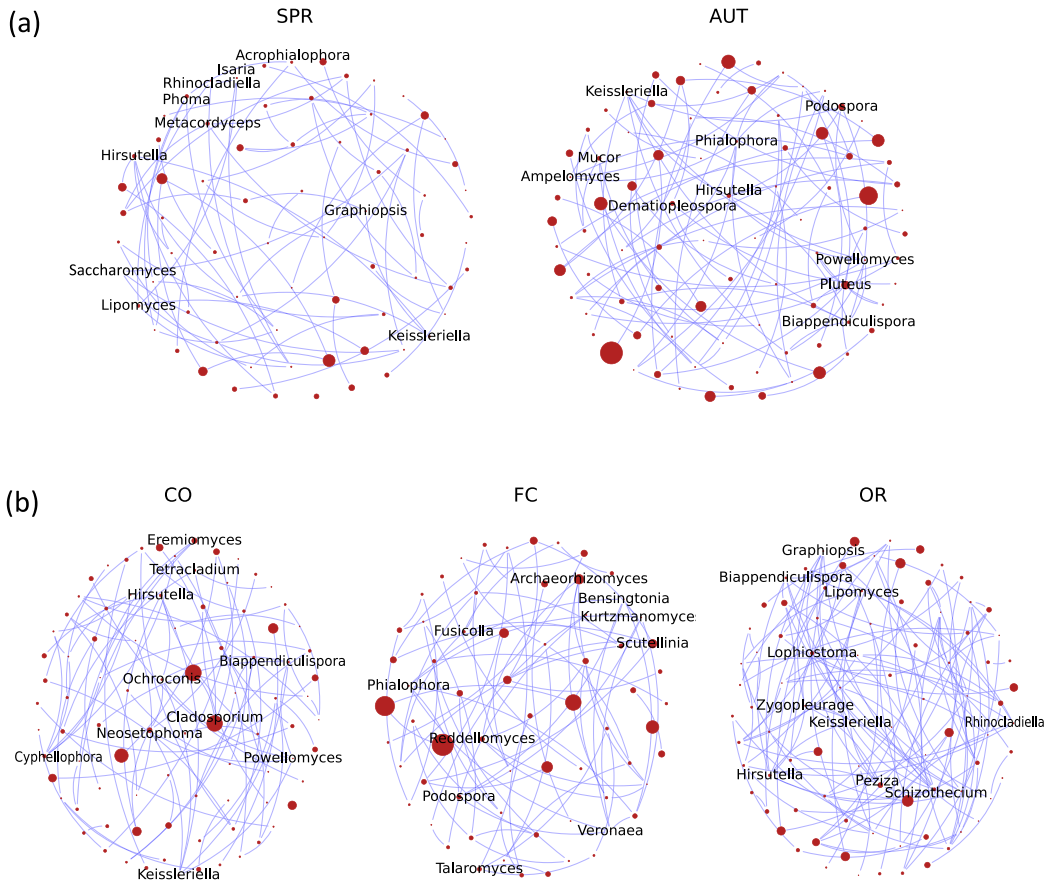

Fig. 8. Network analysis of the fungal genera in (a) two different seasons (spring and autumn) and (b) with three different treatments. The width of the edges and the size of the nodes are proportional respectively to the Spearman's correlation coefficient between the corresponding nodes and the relative abundance of the node. The labels of the ten most connected genera are displayed.

Table 5
Results of the ANOVA like permutation test for CCA to assess the importance of abiotic parameters, SITE, TREAT and Season in explaining the phyla relative abundances.

Factor	Df	Chi Square	F	Pr(>F)	Significance
SITE	1	0.012	4.145	0.001	****
TREAT	2	0.079	9.565	0.001	****
Season	1	0.037	8.906	0.001	****
S.M	1	0.010	2.656	0.024	*
OM	1	0.005	1.179	0.299	
EC-(ds/m)	1	1.106	1.068	0.354	
pH	1	0.023	5.602	0.002	***
TN-( )	1	0.005	1.289	0.259	
OC-( )	1	0.005	1.189	0.299	
C:N	1	0.007	1.700	0.096	

climatic zones is another significant contribution. Dominated by saprotrophic and endophytic taxa, this core likely plays a critical role in decomposition and plant-associated processes. The persistence of this core community under varied conditions suggests a potential benchmark for assessing soil health. Deviations from this core could serve as early indicators of soil degradation or recovery, enhancing the diagnostic power of fungal-based soil assessments. Given growing global demands for food, livestock, and biofuel (Schader et al., 2015), land resources face increasing pressure. Balancing these demands with climate mitigation goals requires a deeper understanding of the trade-offs between productivity, biodiversity, and ecosystem services such as carbon sequestration. Our findings support integrating fungal community metrics with other soil function indicators—such as carbon flux, nutrient cycling, and plant productivity—into comprehensive sustainability indices. These tools can improve the accuracy of soil health monitoring and inform land-use decision-making under variable environmental conditions (Nannipieri et al., 2012). This research contributes to the evidence base advocating for agroecological transitions in agriculture. By demonstrating the responsiveness of fungal communities to land use and seasonality, we emphasize the need for systems that enhance ecological integrity alongside yield. Practices such as perennial cropping, organic amendments, and reduced soil disturbance promote fungal diversity and ecosystem resilience and should be prioritized in sustainable land management, especially in climate-vulnerable regions. In conclusion, this study advances fungal ecology towards an applied framework for soil health assessment. Fungal community structure, connectivity, and resilience respond predictably to long-term management across climatic gradients. Future research should scale this

approach to broader landscapes and link microbial indicators to agricultural outcomes, supporting evidence-based policy for sustainable and resilient food systems.

5. Conclusion

Balancing land use with climate mitigation is a growing challenge as global demand for food, livestock, and fuel intensifies pressure on land resources (Schader et al., 2015). Effective land-use strategies must consider trade-offs between productivity, biodiversity, and carbon sequestration. This study emphasizes the critical role of soil fungal communities as sensitive and integrative indicators of soil health across varied climatic regions and long-term agricultural systems. Using metabarcoding, soil property data, and network analysis, the study reveals that land-use history and management intensity primarily shape fungal community structure, while seasonal timing notably affects species composition and abundance. Perennial, low-disturbance systems—especially orchards—consistently showed higher fungal diversity, stronger network connectivity, and more stable communities compared to intensively managed field crops, which exhibited lower diversity and simplified biotic networks due to frequent disturbance. These patterns were consistent across Mediterranean and semi-arid climates, confirming the robustness of fungal indicators in diverse environments. Seasonal variation, particularly during dry periods, significantly influenced fungal phyla, underlining the need to time soil sampling carefully for accurate microbial assessments. A stable core fungal community found across all land uses provides a functional baseline for identifying deviations from healthy soil conditions. The findings support integrating fungal metrics with other ecological indicators like carbon flux, nutrient cycling, and plant productivity into a multidimensional soil health index. Long-term studies are recommended to evaluate the stability and predictive power of these indicators. The study also contributes to the agroecological transition movement by highlighting how fungal sensitivity to land use and seasonality underscores the importance of agricultural designs that support not only productivity but also ecological integrity. Practices such as perennial cropping, organic inputs, and reduced soil disturbance enhance fungal diversity and are key to sustainable land management. Future research should investigate how agroecological practices at different spatial scales influence microbiome function, providing science-based tools to guide land-use policies and the development of resilient food systems. Overall, fungal community metrics offer a promising addition to conventional soil monitoring, helping to inform sustainable agricultural strategies under growing environmental pressures.

CRediT authorship contribution statement

Yosef Steinberger: Writing – review & editing, Supervision, Methodology, Funding acquisition, Data curation, Conceptualization. **Tirza Doniger:** Methodology, Investigation, Data curation. **Edoardo Marchi:** Writing – original draft, Formal analysis. **Gil Eshel:** Methodology, Investigation, Data curation. **Stefano Bocchi:** Writing – review & editing, Supervision. **Stefano Zapperi:** Writing – original draft, Visualization, Supervision, Methodology. **Caterina A.M. La Porta:** Writing – review & editing, Writing – original draft, Supervision, Formal analysis.

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

During the preparation of this work the author(s) used [ChatGPT] in order to improve the language. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Yosef Steinberg reports financial support was provided by Israeli Ministry of Agriculture and Rural Development (Grant No. 20-03-0001). If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

CAMLP and SB acknowledge funding from the HORIZON-MISS-2024-SOIL-01-01 project Soil Health Living Lab Network for Combating Desertification in the Mediterranean. Long-term sampling, laboratory work, and field support were funded by the Israeli Ministry of Agriculture and Rural Development (Grant No. 20-03-0001) and the Israeli Ministry of Science and Technology. This work also benefited from a long-standing collaboration between Italian and Israeli researchers, which has been essential to achieving the integrative data analysis and broad understanding of soil system structure and function presented in this study.

Appendix A. Supplementary data

Supplementary Figure 1: Multivariate Analysis of Fungal Community Structure.

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.scitotenv.2026.181545.

Data availability

Data will be made available on request.

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