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Research article

Consequences of natural vegetation conversion to cropland in semiarid regions: Evidence from soil multifunctionality indicators

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ABSTRACT

The effects of converting primary land cover for agricultural use on litter composition and soil quality indicators remain insufficiently explored in semiarid regions. Shedding light onto this matter is therefore vital for optimizing soil performance and ecosystem services in these types of regions. To address this, the present study examined a wide range of litter and soil physical, chemical, and biological properties in natural sites (a forest and a rangeland) and in the respective agricultural lands (F-A and R-A, respectively) in northern Iran. In each site, three 1-ha plots were selected and, in each plot, four composite samples of litter and soil, were collected during the summer season. Soil sampling was also conducted in the autumn season to study the seasonal variation of soil microclimate and biological features. Our results showed that litter accumulation in the natural forest and rangeland sites was about 1.6 times greater than in the F-A and R-A sites. This greater accumulation was associated with improvements in soil physical properties (including lower bulk density, higher porosity, and greater stability), along with a 1.5–2-fold increase in the contents of essential nutrients (N, P, K, Ca, and Mg) in the primary sites. Soil microbial biomass carbon and nitrogen were 13–21% and 29–37% lower, respectively, in the agricultural area compared to the natural forest and rangeland sites. Furthermore, the conversion of the surveyed forest and rangeland to agricultural land (F-A and R-A) led to a significant decrease in soil enzyme activities (i.e., urease, acid phosphatase, and arylsulfatase) by approximately 51 %, 55%, and 17%. Land conversion also resulted in a reduction in fine root biomass by 30% and 40%, as well as in coarse root biomass by 64% and 84%, respectively. Likewise, the population of soil organisms decreased significantly, between 30 and 80%, together with the microbial abundance in the agricultural site with a history of rangeland being about 60% lower than in the natural forest. Moreover, most of the targeted soil faunal groups were affected by the season, registering a reduction in their densities during the summer compared to the autumn season. Overall, the higher input of better-quality organic matter in the forest and rangeland areas appears to be a key factor in the improved soil physical traits and fertility indicators in these natural habitats. These features are expected to boost soil biological indicators including microbial activity and biomass, enzyme activities, and the overall density of soil fauna. Conversely, a noticeable decline across all these indicators was observed in agricultural lands. This study highlights the importance of preserving primary vegetation to protect soil quality and biodiversity; as well as, the use of adapted trees and shrub species for potential restoration programs to conserve soil resources.

1. Introduction

Since many ecosystem services are supported and provided by soil, maintaining soil quality is essential for preserving these functions and services, which are crucial for improving human well-being (Kooch et al. 2024a, 2024b). In recent years, the conversion of natural land to agricultural use due to population growth and the ever-increasing demand for food has become a significant concern (Long et al., 2024; Ali et al.,

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2025). Such land-use transformations profoundly alter soil properties and functions by modifying abiotic (e.g., moisture and temperature) and biotic (e.g., vegetation composition and biodiversity) factors, ultimately threatening soil fertility and the delivery of key ecosystem services. Consequently, these alterations raise serious global concerns regarding soil fertility, ecosystem stability, and long-term environmental sustainability (Davari et al., 2020; Mganga et al., 2024). To mitigate these challenges, a comprehensive understanding of soil responses to land-use changes is essential for developing sustainable land management strategies. Evaluating soil quality and its vulnerability or resilience to degradation thus represents a fundamental step toward maintaining soil productivity and ecosystem services (Zeraatpisheh et al., 2020; Kooch et al. 2023a, 2023b). This is crucial given the current global context marked by rising food demands, climate change, and water scarcity (Gomiero, 2016). In this regard, it is of paramount importance to monitor representative indices for assessing soil quality and deterioration, as well as soil resistance to degradation in response to changes in land management (Zahedifar, 2023). Alongside these indicators, the quantity and quality of organic matter inputs, largely determined by vegetation type and land-use practices are particularly important, as they supply energy and nutrients to soil organisms and play a key role in regulating soil fertility and biological activity (Aulakh et al., 2022). Therefore, assessing the characteristics of the organic layer provides valuable insights into how the conversion of natural ecosystems into agricultural lands influences nutrient availability and soil functioning, offering a critical link between vegetation dynamics and soil processes (Usharani et al., 2019).

Soil quality refers to its capacity to function effectively within ecological and land-use limits, while supporting biological productivity and providing ecosystem services (Parsapour et al., 2024). This concept has emerged from two perspectives: one that examines the influence of anthropogenic soil management, and another one that focuses on the inherent properties of the mineral soil layer (Bünemann et al., 2018; El Behairy et al., 2024). Assessing soil quality involves evaluating various parameters, including physical, chemical, and biological properties, which are essential for sustaining plant growth and healthy ecosystems (Ahmed et al., 2021; Wu et al., 2021). Healthy soils, in addition to facilitating root growth, play a vital role in water infiltration and retention, nutrient cycling, and carbon sequestration, thereby enhancing biological activity and promoting efficient gas exchange (Adhikari and Hartemink, 2016; Ali et al., 2025). In this context, soil physical properties are fundamental for supporting and regulating key soil functions. While some properties remain fairly stable over time, others are highly responsive to environmental conditions and management practices (Schoenholtz et al., 2000). Moreover, changes in land use can significantly impact chemical parameters such as pH, nitrogen and organic matter content, which are crucial for maintaining soil fertility and health, as well as plant growth (Usharani et al., 2019). Accordingly, numerous studies have focused on soil physical and chemical properties to examine the effects of land-use and vegetation changes on soil quality (Getachew et al., 2012; Fentie et al., 2020; Feng et al., 2022). Soil is a conservative environment so the effect of land use changes may not be observable immediately, but at the same time, soil properties may vary substantially in a decade's time (Frouz, 2023). Likewise, soil biota is considered another key contributor for soil functionality, given its rapid response to a wide range of impacts; and its role in vital biogeochemical processes including organic matter decomposition and nutrient cycling (Philippot et al., 2021; Rutigliano et al., 2023; Kooch et al., 2024c). As such, there has been a growing emphasis on integrating soil biological indicators to broaden our knowledge about how land use management may influence soil resources (Horáková et al., 2020; Long et al., 2024).

Past research has shown that human intervention and the removal of the primary vegetation cover, resulting from the conversion of natural ecosystems into other land use, has had an irreversible impact on the soil ability to fulfill its functions and provide essential ecosystem services (Zahedifar, 2023; Ota et al., 2024; Gao et al., 2025). Because soil functions and related ecosystem services depend on the interaction of physical, chemical, and biological properties, assessing changes in these dimensions is crucial for understanding how land use/cover transformations influence soil system. However, although the effects of land cover change on soil physical and chemical properties have been extensively investigated (e.g., Buruso et al., 2023; Zarei et al., 2025), comparatively less attention has been given to soil biological properties, despite their high sensitivity to environmental disturbances and their fundamental role in regulating soil functions and services (Rutigliano et al., 2023). This oversight is especially pronounced in semi-arid ecosystems, despite the growing recognition of their importance. To fulfil this knowledge gap, the present study simultaneously evaluates a comprehensive set of physical, chemical, and biological indicators, with a particular emphasis on biological characteristics, aiming to assess the long-term effects of land cover change on soil health in a semi-arid region of northern Iran. By focusing on the consequences of land degradation, this research seeks to provide insight into how such changes impact soil functional indicators which are necessary for sustaining diverse ecosystem services (Davis et al., 2023). Building on prior research, when natural land is converted for agricultural use, it often results in the loss of vegetative cover, leaving the soil surface exposed (Hua et al., 2024). On the contrary, maintaining the vegetation cover contributes to soil protection by providing shade and adding litter; in other words, vegetation forms a protective layer on the soil surface that moderates harsh climatic conditions and reduces erosion across various spatial and temporal scales. Indeed, the presence of dense vegetation serves as a protective shield for the soil, preventing the loss of essential macro- and micronutrients required for plant growth and energy flow (Geetha et al., 2021). Consequently, forest dynamics influenced by natural succession and human activity can alter soil fauna communities through shifts in plant species composition, vegetation structure, litter quality, and micro environmental conditions (Yang and Chen, 2009). Additionally, soil nutrient availability has been identified as a key driver of soil biological properties (Singh et al., 2020). In light of this, the hypotheses of this study were formulated as follows: Converting forests and rangelands into agricultural fields with the removal of woody species is likely to reduce both the quantity and quality of organic matter inputs (hypothesis 1). A decline in woody species and vegetation density due to land use changes is expected to negatively impact soil stability and nutrient cycle (hypothesis 2). Reduced organic matter input and adverse environmental conditions (low soil moisture and high temperature), along with lower soil fertility are key limiting factors for soil biota activity in agricultural lands with forest and rangeland histories (hypothesis 3). Therefore, in a broader perspective, we asked in what way does land-use change affect soil quality and ecosystem sustainability, providing a scientific foundation for improved land management strategies amidst ever-increasing environmental challenges.

2. Materials and methods

2.1. Study area

This study examined the mountainous portion of Kinj, located in the Kojoor district of Mazandaran Province in northern Iran (see Fig. 1A). Geospatially, the research location is around 35°30′ N latitude and 51°38′ E longitude. It boasts a typical altitude of 1500-1600 m above sea level (asl), receives an annual average precipitation of 365 mm, and exhibits a potential annual evaporation rate of 1300 mm. The minimum and maximum temperatures in January and August were recorded at 6 °C and 24 °C, respectively (Fig. 1B). The general slope of the region is between 5 and 10 percent. A substantial portion of the natural vegetation in this region consists of forest ecosystems predominantly characterized by *Zelkova carpinifolia* (Pall.) K. Koch., *Quercus macranthera* Fisch. and C.A.Mey and *Ulmus minor* Mill. species, alongside rangeland vegetation composed of diverse shrub species including *Rhamnus pallasii* Fisch, *Prunus spinosa* L. and *Berberis integerrima* Bunge. Approximately

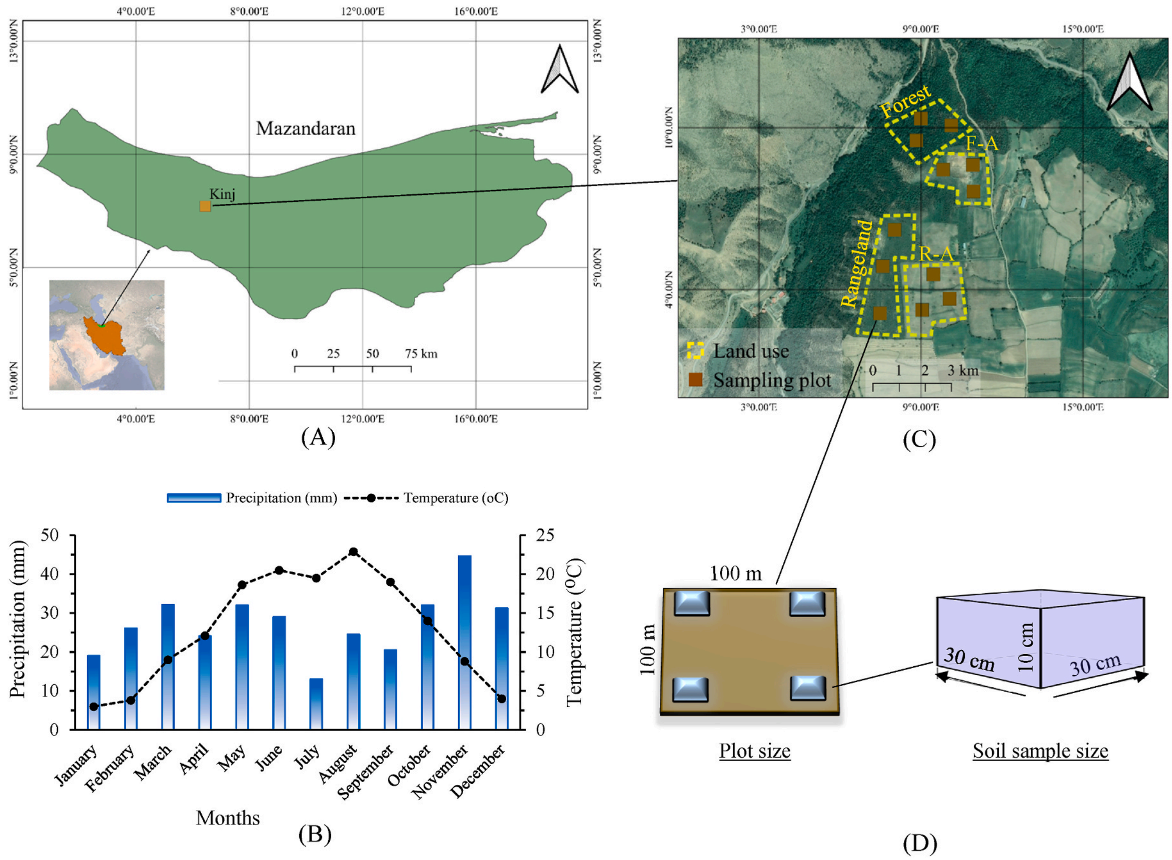

Fig. 1. Study area located in Mazandaran province, north of Iran (A), climate diagram of monthly temperatures and precipitation for the period 1993–2023 (B), and land uses: forest, rangeland, agricultural land with history of forest (F-A), and agricultural land with history of rangeland (R-A) (C). Schematic representation of the experimental design of soil sampling (D).

more than 30 years ago, local communities transformed sections of these natural habitats into agricultural lands, which is currently utilized for wheat (*Triticum aestivum* L.) cultivation. In summary, the land covers analysed in this research include: forest, rangeland, agricultural land with forest history (F-A), and agricultural land with rangeland history (R-A).

2.2. Sample collection

Taking into account preliminary research (Yang et al., 2021), the study sites were selected to be as similar as possible in terms of altitude and slope aspect. The study employed a paired-site design across with four land-use types: (1) a natural forest (serving as contrast plots), (2) a cropland converted from forest, (3) a natural rangeland (serving as contrast plots), and (4) a cropland converted from rangeland. Within each land-use type, three replicate 1-ha plots (100 m × 100 m) were established with at least 600 m spacing to avoid pseudo replication (Fig. 1C and see the details in Table 1). Within each site the experimental plots were located at a distance of about 6 to 8 km apart from the plots of the other land cover types (to prevent edge effects between habitats. In each plot, four litter and four soil (0–10 cm depth) samples (30 cm × 30 cm quadrats; Fig. 1D) were collected using a square metal frame during summer. Soil sampling was repeated (in different plots) in autumn to capture seasonal effects on microclimate and biological properties. This resulted in 48 litter samples (4 land-use types × 3 plots × 4 quadrats) and 96 soil samples (4 land-use types × 3 plots × 4 quadrats × 2 seasons). Samples were transported to the laboratory; a fraction of the samples was stored at 4 °C for biological analyses, while another fraction was air-dried and sieved (<2 mm) for physical and chemical analyses.

2.3. Laboratory analyses

2.3.1. Litter and soil physicochemical indicators

The thickness of the organic layer, from the surface of the organic material to the top of the mineral soil, was measured using a tape measure (Dechoum et al., 2015). Total litter carbon was assessed through dry combustion, and the content of other macronutrients (N, P, K, Ca, and Mg) was determined by mineralization techniques, using acid digestion with concentrated sulfuric acid, as outlined by Sun et al. (2022). The clod and pycnometer methods were employed to calculate the soil bulk density and particle density, as described by Blake and Hartge (1986) and Plaster (1985), respectively. The formula [1- (bulk density/particle density)] was applied to calculate soil porosity (Pires et al., 2014). The stability of soil aggregates, as well as the percentage of macro- and microaggregates were analysed following the techniques of Pojasok and Kay (1990), and Cambardella and Elliott (1992). Soil particle size distribution (texture) was measured using the hydrometer method (Bouyoucos, 1962). The samples were oven-dried for 24 h at 105 °C to determine the soil moisture content (Evett et al., 2009). The soil temperature was measured *in-situ* using a digital thermometer (Dostmann, Ottersberg, Germany) (Zancan et al., 2006).

An Orion Ionalyzer Model 901 pH reader and an Orion Ionalyzer Model 901 EC reader were used to measure the pH and the electrical conductivity (EC) of the soil in a 1:2.5 soil/water solution, respectively.

Table 1
Description of land covers at the Kinj region, northern Iran.

Land cover [a]	Dominant species	Tree density (ind. ha^{-1})	Mean ± standard error		Coverage (%)	Coverage (%) of co-dominant species	Physiographic characteristics		
			d.b.h*** (cm)	Height (m)			Altitude (m)	Slope (%)	Aspect
Forest	*Zelkova carpinifolia* (Pall.) K. Koch.	145	52.18 ± 7.56	18.78 ± 0.94	45	*Bromus danthoniae* Trin. (8)	1520-1543	5-8	North
	Quercus macranthera Fisch. and C.A.Mey	109	39.11 ± 5.82	12.23 ± 0.75	19	*Xanthium spinosum* L. (8) *Berberis integerrima* Bunge. (6)			
	Ulmus minor Mill.	87	21.09 ± 4.94	11.65 ± 0.82	17	*Medicago minima* L. (5) *Rhamnus pallasii* L. (<5) *Asteragalus gossypinus* Fisch. (<5) *Crataegus melanocarpa* M. B. (<5)			
Rangeland	*Rhamnus pallasii* Fisch. and C.A.Mey	-	-	-	42	*Asteragalus gossypinus* Fisch. (7)	1585-1593	6-9	North
	Prunus spinosa L.	-	-	-	22	*Teucrium polium* L. (<5)			
	Berberis integerrima Bunge.	-	-	-	15	*Medicago minima* L. (<5) *Crataegus melanocarpa* M. B. (<5)			
Agriculture**	*Triticum aestivum* L.	-	-	-	84	*Phalaris minor* Retz. (<5) *Avena fatua* L. (<5) *Convolvulus arvensis* L. (<5) *Lathyrus annuus* L. (<5)	1540-1559	6-8	North

[a] In the four corners of each of the 1-ha sample plots (see Fig. 1d), a macro plot of 400 m^2 (20 × 20m) was considered to determine the characteristics of the woody covers. Also, in the four corners of each of these macro plots, micro plots of 4 m^2 (2 × 2 m) were set up to assess the herbaceous cover (Kooch and Noghre, 2020). ** Moldboard plowing (10 cm) is applied every spring season. ***Diameter at the breast height (1.3 m).

The Walkley-Black protocol (Allison, 1975) was used for assessing soil organic carbon; while the soil organic matter (SOM) content was estimated as SOM = organic %C × 1.724 (Ezeigbo et al., 2013). The aggregate size distribution was performed using the wet sieving method with mesh sizes of 0.25 and 0.50 mm (Six et al., 2000). Micro- and macro-aggregate sizes varied between 0.05 and 0.25 mm and between 0.25 and 0.50 mm, respectively. To determine the total amount of soil nitrogen, the semi-micro Kjeldahl approach (Bremner and Mulvaney, 1982) was adopted. By combining carbon and nitrogen concentrations with bulk density values, soil carbon and nitrogen stocks were calculated (Sariyildiz et al., 2015). To estimate the amount of organic matter stratification, the total organic matter content from the upper layer was divided by that present in the bottom layer (Franzluebbers and Stuedemann, 2009). The Blair et al. (1995) method was used to calculate the soil carbon management index (CMI). Both particulate organic carbon (POC) and nitrogen (PON) were quantified following the physical fractionation method (Cambardella and Elliott, 1992). Dissolved organic-C (DOC) and -N (DON) in soil were computed using the method recommended by Jones and Willett (2006). Standard laboratory methods were used to determine the soil available content of P, K, Ca, and Mg (Bower et al., 1952; Homer and Pratt, 1961). Soil NH_4^+ and NO_3- contents were colorimetrically measured in 2 M KCl extracts (1:5, w/v) at 645 and 420 nm, respectively (Li et al., 2014).

2.3.2. Soil biological indicators

Basal respiration (BR) was measured as CO_2 evolution from soil samples for a three-day incubation period at 25 °C (Alef, 1995). Substrate-induced respiration (SIR) was assessed by mixing the soil samples with 1% (w/w) glucose, and the CO_2 production rate was also determined after three days of incubation (Anderson and Domsch, 1990). Microbial biomass carbon and nitrogen (MBC and MBN) were determined by the fumigation-extraction approach (Brookes et al., 1985). Enzymatic activities including urease, acid phosphatase, arylsulphatase, and invertase were measured based on the methodology proposed by Alef and Nannipieri (1995). Root biomass was determined by separation of the fine (diameter <2 mm) and coarse roots (diameter >2 mm); and then oven-dried at 70 °C to reach a constant weight (Neatrour et al., 2005). A hand-sorting method was used to sample earthworms followed by their classification into epigeic, anecic, and endogeic (Jeffery et al., 2010). Acarina and Collembola were extracted from the soil samples employing a customized Tullgren funnel as indicated by Hutson and Veitch (1987). Nematode extraction was performed using a customized cotton–wool filtration technique (Liang et al., 2009). After the extraction technique, soil protozoa were quantified using a microscope (Mayzlish and Steinberger, 2004). Bacteria and fungi were quantified by serial dilution-plating on nutrient agar and potato dextrose agar, respectively (Wollum, 1983).

2.4. Statistical analysis

By using the Kolmogorov-Smirnov and Levene tests, respectively, the data normality and homogeneity were examined. To compare the properties of the organic layer and the soil samples across the various land uses under study, one-way analysis of variance (ANOVA) was employed. The seasonal and land use related changes in soil biota, as well as in soil moisture, temperature and N mineralization were assessed by a two-way ANOVA. The Duncan test ($P < 0.05$) was applied for multiple comparisons of parameters' mean values amongst the various land uses. The software program SPSS v23 was used for all statistical calculations. Figures related to soil biota were created using OriginPro 2024b software. Following the methodology outlined by McCune and Mefford (1999), a principal component analysis (PCA) was utilized to explore the relationships between soil variables within the targeted land uses by using PC-Ord version 5.0. A structural equation model (SEM) was also constructed with Amos 20.0 to test the influence of land use on litter and soil properties. In addition, Gephi 0.9.7 software program was employed to create and visualise a network model with regards to land-use changes, as described by Bastian et al. (2009) and Cherven

(2015).

3. Results

3.1. Land use-induced alterations in litter quality and soil physicochemical attributes

The type of land cover affected differently most of the litter properties, except for the contents of C, K and Mg. An increased litter thickness was observed in the natural forest site, which was approximately 3-times greater compared to the agricultural site with rangeland history. Likewise, the largest amounts of N and Ca were reported for the litter samples collected in the forest site, being approximately 50% higher than those in the agricultural one with rangeland history. A similar trend was reported for P content, while the litter samples from the agricultural land were characterised by the highest C to N ratio (Table 2).

The majority of the soil physical characteristics, with the exception of three variables (particle density, macro/micro-aggregate ratio and silt content), exhibited statistically significant differences under the various land use conditions. In this regard, the soil bulk density in both R-A and F-A sites increased by 0.27 and 0.21 g cm^{-3}, respectively compared to the natural land use (forest). Likewise, the soil samples from the natural forest and rangeland sites exhibited a higher porosity (around 20%). The conversion of natural habitat to agricultural land (R-A) also resulted in a significant decrease in soil aggregate stability, with a reduction of about 1.3 times; as well as, in a reduction of around 33% in both macro- and microaggregate values. However, the macro/micro- aggregate ratio remained unchanged. The agricultural site (R-A) was characterised by a 28% higher sand content in comparison with the natural forest. Conversely, the forest site contained the highest clay content, which was approximately 24% greater than in the agricultural areas. Silt content remained relatively unaffected by the land use changes (Table 3).

In the case of the chemical properties, soil pH in the natural forest site was approximately 0.7 units higher than in the agricultural ones, with more acidic conditions in the R-A and F-A sites. Total soil N showed a 1.4-fold decrease in the agricultural site compared to the natural forest habitat. In addition, the conversion of forest and rangeland lands to agricultural use led to a 50-60% decrease in POC, PON, DOC, and DON contents. A similar trend was recorded for the total concentration of P, K, Ca and Mg, showing a decrease of 40-50% due to agricultural conversion. As a result, the abovementioned soil properties were ranked as follows: forest > rangeland > F-A > R-A (Table 3).

3.2. Variation in soil biological indicators across land use types

All the biological parameters with the exception of basal respiration and invertase varied significantly among land uses. The highest SIR levels were found in the natural rangeland habitat, showing a 30% increase compared to the R-A site. Furthermore, the conversion of the natural forest and rangeland to agricultural land resulted in reductions of microbial biomass carbon (MBC) by 21% and 13%, and microbial biomass nitrogen (MBN) by 37% and 29%, respectively. The proportion of carbon to nitrogen in microbial biomass under the various land uses changed significantly, with the lowest and highest values in the forest and the R-A sites, respectively. Urease, acid phosphatase and arylsulfatase reached their higher activities in the forest habitat, followed by the natural rangeland and the agricultural sites (forest > rangeland > F-A > R-A). Coarse and fine root biomass measurements showed significant variations under the different land uses, with values in the forest site being 2- and 3-times higher, respectively. The conversion of forest and rangeland to agricultural land was accompanied by a 30% and 40% reduction in the fine root biomass, and a 64% and 84% decrease in the coarse root biomass, respectively (Table 3).

Neither the land-use change nor the seasonal variations showed a significant effect on the soil N mineralization rate (Fig. 2). However, the results of the two-way ANOVA analysis revealed that the land use type had a significant impact on the abundance and biomass of most of the targeted soil organisms. Such effects were dependent on the season in the case of the density and biomass of epigeic earthworms, as well as for the densities of collembola, nematode and protozoa (Table 4). Specifically, the highest earthworms 'density and biomass were recorded in the forest site (Fig. 3A–H). The same trend was observed for other soil faunal groups including acarina, collembola, nematodes and protozoa reaching their highest densities in the natural forest, particularly in the autumn season. Similarly, microbial populations were more abundant in the natural forest followed by the rangeland and the agricultural land uses (Fig. 4A–H). Both bacteria and fungi were also affected by seasonal changes, with higher values in summer than in autumn (Fig. 4E and F). Regarding the microclimatic properties, soil moisture was higher in the forest site (28.06%) than in the agricultural one (R-A; 20.06%), whilst the R-A site was 4 °C warmer. Moreover, the highest soil moisture and the lowest soil temperature were recorded during the autumn season regardless of the land use (Fig. 4G and H). Overall, the land use had a prominent effect on soil properties based on the two-way ANOVA results indicating that the conversion of natural sites for agricultural use contributed to a larger extent than the seasonal changes to explaining the shifts in the number (33.44 %) and biomass (35.73 %) of earthworms, as well as in the population of acarina (42.70 %), collembola (64.88 %), nematodes (42.49 %), protozoa (34.85 %), fungi (57.78 %), bacteria (55.12 %), and moisture (34.07 %); while, temperature was more influenced by the season (33.20 %) than by the land use type (19.74 %) in the surveyed region (Fig. 5).

3.3. Relationships among land use types, litter and soil indicators

The correlations between the land use types, the litter properties and the soil variables were depicted in a PCA plot (Fig. 6). Four distinct clusters referring to each land use type were differentiated along the two components that accounted for 38.84% and 10.50 % of the overall variance. The natural sites (forest and rangeland) clustered on the negative side of the first axis, whilst the agricultural land uses

Table 2
Mean value (±standard error; number of samples = 12) of the litter properties across the studied land uses.

Litter properties	Land use				Summary ANOVA	
	Forest	Rangeland	F-A	R-A	F test	*P*- value
Thickness (cm)	9.09 ± 0.48 a	5.28 ± 0.95 b	5.47 ± 0.70 b	3.12 ± 0.33 c	14.017	***0.000***
C (%)	35.53 ± 2.94 a	38.03 ± 2.52 a	40.88 ± 1.17 a	43.64 ± 2.42 a	2.212	0.100
N (%)	2.15 ± 0.13 a	1.84 ± 0.15 a	1.20 ± 0.08 b	1.05 ± 0.04 b	21.486	***0.000***
C/N	17.56 ± 2.32 b	25.39 ± 5.37 b	35.55 ± 2.35 a	42.45 ± 2.87 a	10.013	***0.000***
P (%)	4.05 ± 0.11 a	3.77 ± 0.09 ab	3.46 ± 0.13 b	3.06 ± 0.15 c	11.248	***0.000***
K (%)	2.23 ± 0.23 a	1.94 ± 0.06 a	2.08 ± 0.13 a	1.78 ± 0.12 a	1.606	0.202
Ca (%)	2.43 ± 0.15 a	1.61 ± 0.10 b	1.33 ± 0.14 bc	1.11 ± 0.04 c	23.817	***0.000***
Mg (%)	0.81 ± 0.05 a	0.73 ± 0.05 a	0.69 ± 0.03 a	0.63 ± 0.03 a	2.703	0.057

Different letters in each line indicate significant differences ($P < 0.05$ by Duncan test) among the different land uses. Bold and italic values indicate significant statistical differences. Land uses: forest, rangeland, agricultural land with history of forest (F-A), and agricultural land with history of rangeland (R-A).

Table 3
Mean value (±standard error; number of samples = 12) of the soil properties across the studied land uses.

Soil properties		Land use				Summary ANOVA	
		Forest	Rangeland	F-A	R-A	F test	*P*-value
Physical properties	Bulk density (g cm^{-3})	1.08 ± 0.05 b	1.16 ± 0.02 b	1.29 ± 0.04 a	1.35 ± 0.03 a	16.080	***0.000***
	Particle density (g cm^{-3})	2.63 ± 0.04 a	2.65 ± 0.04 a	2.67 ± 0.05 a	2.62 ± 0.06 a	0.137	0.937
	Porosity (%)	0.58 ± 0.01 a	0.58 ± 0.01 a	0.51 ± 0.01 b	0.48 ± 0.01 b	10.154	***0.000***
	Aggregate stability (%)	67.82 ± 2.74 a	66.55 ± 2.91 ab	58.79 ± 2.41 bc	51.84 ± 3.01 c	7.148	***0.001***
	Macro-aggregate (g kg^{-1})	36.75 ± 2.02 a	28.92 ± 1.09 b	24.92 ± 2.43 b	24.58 ± 1.92 b	8.570	***0.000***
	Micro-aggregate (g kg^{-1})	55.75 ± 2.24 a	46.17 ± 3.99 b	37.83 ± 1.23 c	37.42 ± 1.75 c	11.665	***0.000***
	Macro/micro-aggregate ratio	0.66 ± 0.04 a	0.67 ± 0.05 a	0.66 ± 0.06 a	0.68 ± 0.08 a	0.024	0.995
	Sand (%)	18.50 ± 0.73 c	20.67 ± 1.20 bc	23.33 ± 1.09 ab	25.67 ± 1.51 a	7.099	***0.001***
	Silt (%)	44.33 ± 1.89 a	44.50 ± 1.53 a	44.58 ± 1.84 a	46.33 ± 1.87 a	0.273	0.845
	Clay (%)	37.17 ± 1.68 a	34.83 ± 1.10 ab	32.08 ± 0.83 b	28.00 ± 0.80 c	11.473	***0.000***
Chemical properties	pH (1:2.5 H_2O)	6.98 ± 0.09 a	6.66 ± 0.21 ab	6.27 ± 0.11 b	6.26 ± 0.12 b	5.572	***0.002***
	EC (dSm^{-1})	0.29 ± 0.00 a	0.27 ± 0.02 a	0.24 ± 0.01 a	0.24 ± 0.01 a	2.366	0.084
	Organic C (%)	2.91 ± 0.32 a	2.71 ± 0.23 a	2.97 ± 0.35 a	3.22 ± 0.40 a	0.390	0.761
	C in Macro-aggregate (g kg^{-1})	2.80 ± 0.29 a	2.71 ± 0.29 a	2.98 ± 0.24 a	3.15 ± 0.28 a	0.505	0.681
	C in Micro-aggregate (g kg^{-1})	2.77 ± 0.29 a	2.88 ± 0.27 a	2.74 ± 0.25 a	2.94 ± 0.27 a	0.119	0.949
	Cmacro/Cmicro ratio	1.08 ± 0.12 a	1.03 ± 0.13 a	1.27 ± 0.19 a	1.28 ± 0.24 a	0524	0.668
	C stock (Mg ha^{-1})	31.50 ± 3.34 a	31.81 ± 3.25 a	38.67 ± 4.76 a	43.20 ± 5.23 a	1.789	0.163
	OM stratification ratio	1.38 ± 0.13 a	1.23 ± 0.16 a	1.27 ± 0.17 a	1.25 ± 0.18 a	0.171	0.915
	Carbon management index	587.20 ± 87.14 a	494.58 ± 70.32 a	749.89 ± 186.4 a	930.14 ± 272.9 a	1.204	0.319
	Particulate organic C (mg kg^{-1})	3.39 ± 0.29 a	2.62 ± 0.20 b	1.76 ± 0.30 c	1.40 ± 0.24 c	11.891	***0.000***
	Dissolved organic C (mg kg^{-1})	39.97 ± 2.92 a	32.39 ± 3.10 ab	28.63 ± 2.48 bc	22.51 ± 2.22 c	7.284	***0.000***
	Total N (%)	0.34 ± 0.02 a	0.31 ± 0.02 ab	0.27 ± 0.03 bc	0.24 ± 0.01 c	3.669	***0.019***
	N in Macro-aggregate (g kg^{-1})	0.36 ± 0.03 a	0.34 ± 0.04 a	0.30 ± 0.03 a	0.27 ± 0.02 a	1.407	0.253
	N in Micro-aggregate (g kg^{-1})	0.22 ± 0.02 a	0.20 ± 0.02 a	0.18 ± 0.02 a	0.15 ± 0.01 a	1.652	0.191
	Nmacro/Nmicro ratio	2.09 ± 0.47 a	3.86 ± 2.20 a	2.28 ± 0.55 a	2.13 ± 0.33 a	0.523	0.669
	N stock (Mg ha^{-1})	3.71 ± 0.25 a	3.67 ± 0.28 a	3.54 ± 0.45 a	3.25 ± 0.21 a	0.434	0.730
	Particulate organic N (mg kg^{-1})	0.41 ± 0.06 a	0.31 ± 0.04 ab	0.22 ± 0.02 bc	0.16 ± 0.02 c	6.763	***0.001***
	Dissolved organic N (mg kg^{-1})	22.55 ± 1.64 a	17.71 ± 1.15 b	12.50 ± 1.03 c	10.57 ± 1.30 c	17.142	***0.000***
	C/N ratio	9.35 ± 1.77 a	8.87 ± 0.82 a	13.04 ± 2.59 a	13.54 ± 1.54 a	1.822	0.157
	Particulate organic C/N ratio	10.44 ± 1.66 a	10.77 ± 1.82 a	8.26 ± 1.45 a	10.97 ± 2.14 a	0.490	0.691
	Dissolved organic C/N ratio	1.87 ± 0.18 a	1.95 ± 0.27 a	2.36 ± 0.21 a	2.37 ± 0.28 a	1.179	0.328
	Available P (mg kg^{-1})	31.99 ± 2.51 a	25.49 ± 1.56 b	20.38 ± 1.47 c	17.23 ± 1.21 c	13.391	***0.000***
	Available K (mg kg^{-1})	326.08 ± 7.53 a	293.83 ± 6.83 b	243.25 ± 12.67 c	201.33 ± 13.34 d	27.381	***0.000***
	Available Ca (mg kg^{-1})	232.25 ± 16.63 a	182.25 ± 13.29 b	181 ± 9.55 b	117.25 ± 12.08 c	12.852	***0.000***
	Available Mg (mg kg^{-1})	42.25 ± 1.70 a	37.00 ± 2.23 b	29.67 ± 1.39 c	27.58 ± 1.32 c	15.715	***0.000***
Biological properties	Basal respiration (mg CO_2 g^{-1} day^{-1})	0.25 ± 0.02 a	0.29 ± 0.02 a	0.22 ± 0.03 a	0.20 ± 0.03 a	1.830	0.156
	Substrate induced respiration (mg CO_2 g^{-1}day^{-1})	1.04 ± 0.05 ab	1.23 ± 0.06 a	0.97 ± 0.08 b	0.90 ± 0.07 b	3.874	***0.015***
	Microbial biomass C (mg kg^{-1})	324.77 ± 30.23 a	275.70 ± 14.00 ab	254.21 ± 21.5 b	238.19 ± 18.15 b	2.977	***0.042***
	Microbial biomass N (mg kg^{-1})	40.67 ± 2.44 a	31.57 ± 0.47 b	25.43 ± 1.35 c	22.42 ± 1.47 c	25.459	***0.000***
	Microbial biomass C/N ratio	8.01 ± 0.20 c	8.75 ± 0.45 bc	9.99 ± 0.56 b	10.61 ± 0.42 a	4.473	***0.008***
	Urease (μg NH_4^+–N g^{-1} 2 h^{-1})	20.28 ± 1.41 a	15.17 ± 1.17 b	14.12 ± 1.05 b	10.50 ± 0.38 c	14.167	***0.000***
	Acid phosphatase (μg PNP g^{-1} h^{-1})	319.5 ± 35.41 a	185.17 ± 11.16 b	196.83 ± 20.93 b	140.67 ± 13.30 b	11.761	***0.000***
	Arylsulfatase (μg PNP g^{-1} h^{-1})	90.5 ± 3.39 a	85.58 ± 4.46 a	75.58 ± 5.28 ab	70.08 ± 6.47 b	3.411	***0.026***
	Invertase (μg glucose g^{-1} 3 h^{-1})	103 ± 6.03 a	103.92 ± 6.05 a	91.75 ± 7.01 a	87.17 ± 4.56 a	1.928	0.139
	Fine root biomass (mg m^{-2})	62.64 ± 5.01 a	50.51 ± 5.36 ab	43.88 ± 4.07 b	30.43 ± 2.07 c	9.643	***0.000***
	Coarse root biomass (kg ha^{-1})	1489.33 ± 58.83 a	713.00 ± 50.03 b	529.50 ± 43.33 c	109.08 ± 10.84 d	167.661	***0.000***

Different letters in each line indicate significant differences ($P < 0.05$ by Duncan test) among the different land uses. Bold and italic values indicate significant statistical differences. Land uses: forest, rangeland, agricultural land with history of forest (F-A), and agricultural land with history of rangeland (R-A). EC: electrical conductivity; OM: organic matter.

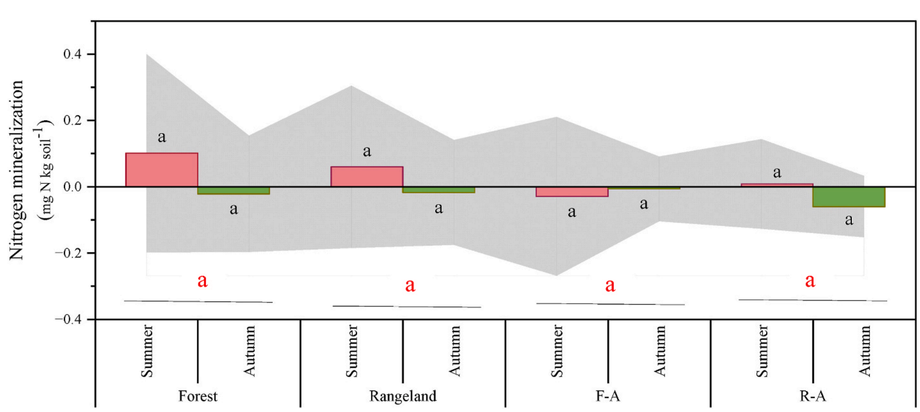

Fig. 2. Mean value (± standard error with gray background; number of samples = 12) of nitrogen mineralization in the two seasons under the different land uses: forest, rangeland, agricultural land with history of forest (F-A), and agricultural land with history of rangeland (R-A).

Table 4
The two-way analysis of variance of soil N mineralization, fauna and microclimate in the two seasons (autumn and summer) under the different land uses.

Source	Dependent Variable	Sum of Squares	df	Mean Square	F test	*P*- value
Land use	N mineralization	0.070	3	0.023	0.629	0.598
	Epigeic density	15.865	3	5.288	11.907	***0.000***
	Anecic density	7.708	3	2.569	7.373	***0.000***
	Endogeic density	1.917	3	0.639	3.551	***0.018***
	Earthworm density	61.865	3	20.622	16.973	***0.000***
	Epigeic biomass	2296.457	3	765.486	11.763	***0.000***
	Anecic biomass	1046.175	3	348.725	6.674	***0.000***
	Endogeic biomass	341.243	3	113.748	4.375	***0.006***
	Earthworm biomass	9257.704	3	3085.901	17.838	***0.000***
	Acarina density	2779493918	3	926497972.8	72.294	***0.000***
	Collembola density	662476768.9	3	220825589.6	129.047	***0.000***
	Total nematode	704634.615	3	234878.205	78.038	***0.000***
	Total protozoa	698700.458	3	232900.153	42.401	***0.000***
	Total fungi	31.057	3	10.352	46.813	***0.000***
	Total bacteria	5.116	3	1.705	39.73	***0.000***
	Moisture	1018.572	3	339.524	31.309	***0.000***
	Temperature	407.218	3	135.739	12.839	***0.000***
Season	N mineralization	0.091	1	0.091	2.429	0.123
	Epigeic density	11.344	1	11.344	25.542	***0.000***
	Anecic density	0.167	1	0.167	0.478	0.491
	Endogeic density	1.521	1	1.502	8.337	***0.005***
	Earthworm density	6.510	1	6.51	5.359	***0.023***
	Epigeic biomass	1364.966	1	1364.966	20.974	***0.000***
	Anecic biomass	5.985	1	5.985	0.115	0.736
	Endogeic biomass	280.303	1	280.303	10.781	***0.001***
	Earthworm biomass	513.005	1	513.005	2.965	0.089
	Acarina density	2571053851	1	2571053851	200.618	***0.000***
	Collembola density	117500786.9	1	117500786.9	68.665	***0.000***
	Total nematode	361989.844	1	361989.844	120.271	***0.000***
	Total protozoa	634400.167	1	634400.167	115.497	***0.000***
	Total fungi	3.050	1	3.050	13.79	***0.000***
	Total bacteria	0.344	1	0.344	8.023	***0.006***
	Moisture	998.718	1	998.718	92.097	***0.000***
	Temperature	684.748	1	684.748	64.766	***0.000***
Land use × Season	N mineralization	0.066	3	0.022	0.594	0.621
	Epigeic density	7.698	3	2.566	5.778	***0.001***
	Anecic density	0.417	3	0.139	0.399	0.754
	Endogeic density	0.583	3	0.194	1.081	0.362
	Earthworm density	9.698	3	3.233	2.661	0.053
	Epigeic biomass	949.231	3	316.41	4.862	***0.004***
	Anecic biomass	37.449	3	12.483	0.239	0.869
	Endogeic biomass	135.163	3	45.054	1.733	0.166
	Earthworm biomass	914.036	3	304.679	1.761	0.16
	Acarina density	31712903.87	3	10570967.96	0.825	0.484
	Collembola density	90501668.69	3	30167222.9	17.629	***0.000***
	Total nematode	326717.031	3	108905.677	36.184	***0.000***
	Total protozoa	188165.667	3	62721.889	11.419	***0.000***
	Total fungi	0.188	3	0.063	0.284	0.837
	Total bacteria	0.045	3	0.015	0.351	0.789
	Moisture	17.891	3	5.964	0.55	0.650
	Temperature	40.32	3	13.44	1.271	0.289

Bold and italic values indicate significant statistical differences.

characterised by lower levels of biological activity and soil fertility appeared along the positive side of the first component. The structural equation and network models that were constructed using both the litter and soil properties exhibited a significant correlation (greater than 0.5) with the PCA components (see Table 5). The results of the structural equation model fitting indicate that the SEM model aligns well with the empirical data. A summary of eight widely used goodness-of-fit indices for SEM is present, all of which are within acceptable thresholds, further validating the model's fit (Table 6). According to the SEM analysis, the type of land use had a more indirect effect on the soil biological properties; while the litter properties exerted a more direct impact on the soil physical and chemical properties, affecting the biological properties in an indirect manner (Fig. 7). Based on the network model, both lines and arrows represent the interactions between multiple variables, and the width of the lines indicates how strong these impacts are. he measured variables were grouped into modules based on their degree of influence as indicated by the node sizes (circles). The module known as M1, which is associated with land use changes, exhibited the highest degree of influence and is therefore represented by the largest node in the network model. The second most influential group pertained to the litter characteristics; and the subsequent modules were represented by collembola and earthworms, respectively. From M1 to M7 (that is related to seasonal changes), the influence of each module progressively decreased (Fig. 8).

4. Discussion

4.1. Land use–driven changes in litter and soil properties

The density and type of vegetation cover are major determinants of the amount and the characteristics of organic matter entering the soil surface, which through the processes of substrate deposition and rhizodeposition, plays a crucial role in shaping soil quality (Lohbeck et al., 2015; Alvafritz and Hertel, 2024). In line with previous works (Li et al., 2015; Maes et al., 2019; Pereira et al., 2022), we found that alterations in the litter quantity and quality under the various land covers was

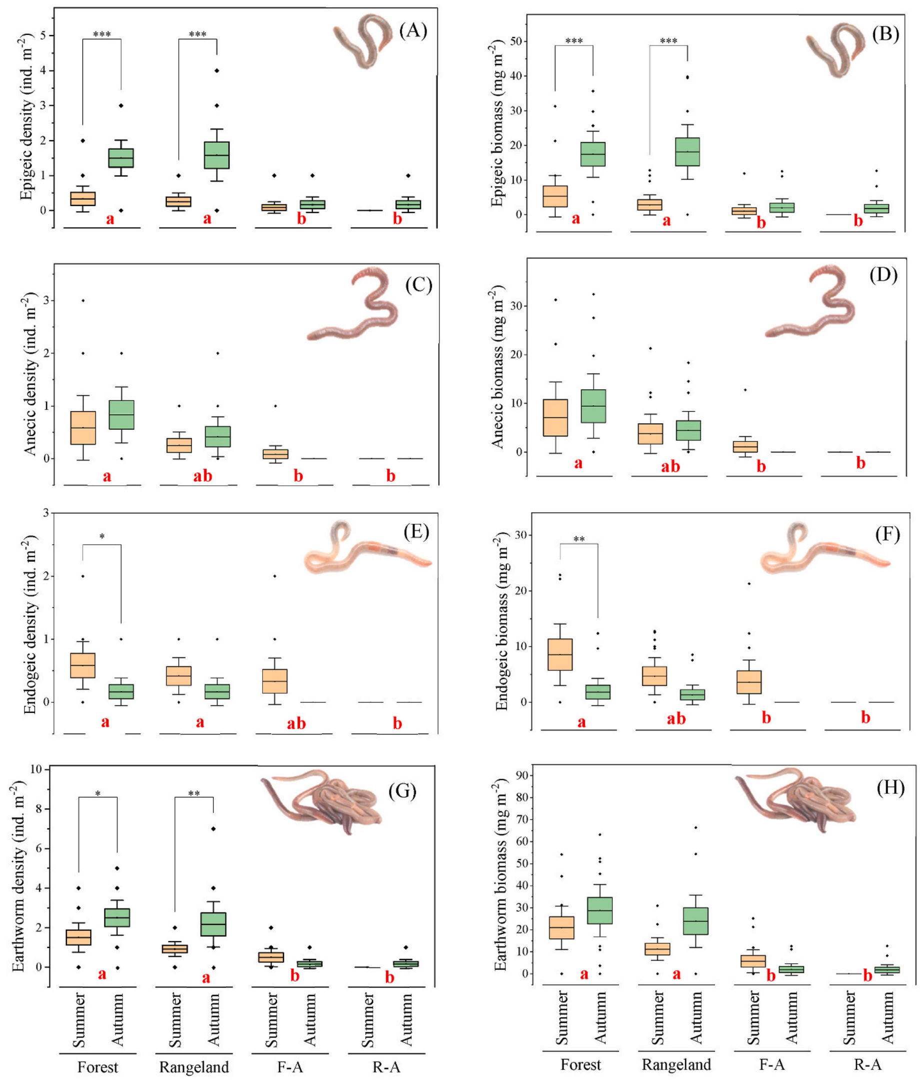

Fig. 3. Box plots illustrating soil earthworm activity in the two seasons under the different land uses: forest, rangeland, agricultural land with history of forest (F-A), and agricultural land with history of rangeland (R-A). The boxes denote interquartile range with mean as a black line and whiskers extending to the most extreme points. Different letters indicate significant differences ($P < 0.05$ by Duncan test) between land uses (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

accompanied by concomitant changes in the litter thickness and nutrient contents (N, P, and Ca). The greater litter thickness in the surveyed natural forest and rangeland areas, when compared to the other habitats for agricultural use, can be explained by the higher density and diversity of woody species, as a result of the increased litter input from these species (Kartalaei et al., 2023). Consistent with our findings, previous studies (Hättenschwiler, 2005; Laganière et al., 2010; Randriamananjara et al., 2025) demonstrated that the presence of diverse tree and plant species in forest ecosystems contributes to a more variable nutrient composition in leaf litter. This feature may lead to elevated concentrations of essential nutrients such as N, P, and K compared to agricultural lands, which often consist of a single crop species. Furthermore, the increased interactions among plants, soil, and microorganisms within natural ecosystems enhance nutrient uptake capabilities (Dotaniya and Meena, 2015) and facilitate the accumulation of these nutrients in plant tissues, ultimately resulting in higher nutrient concentrations in the leaf litter.

In line with our study, significant alterations in the soil physical properties as a consequence of land use changes have been well-documented in previous studies (Feng et al., 2022; Yu et al., 2022). The additional input of organic material into the soil under primary vegetation, especially in the forest land, accompanied by an increase in nutrient availability, alterations in the microclimate of the soil surface (temperature and moisture), and a boost in SOM lowered the bulk density of the soil while enhancing its porosity and aggregate stability (Usharani et al., 2019; Aulakh et al., 2022). Nonetheless, in the agricultural lands, tillage operations reduce organic material input leading to a decrease in soil porosity and aggregate stability, while increasing soil bulk density. These changes are likely due to the mechanical disturbance of the soil and the reduced penetration of organic matter, as observed by Haghighi et al. (2010), Sekucia et al. (2020), and Zi-zheng et al. (2023). Comparable findings have been reported by Fetene and Amera (2018) and Molla Fetene et al. (2022) indicating that a reduced clay content coupled with an increased sand level within the cultivated land can be related to the disruption of soil aggregates during plowing operations and the selective removal of clay particles through erosion processes. The substantial variation in soil moisture and temperature under the varying land use conditions can be attributed to alterations in the level of coverage and litter (Zhang et al., 2024). A high content of clay and organic matter in the soil, by increasing water retention capacity (Zhang et al., 2024), are key factors in enhancing soil moisture and reducing temperature values in the natural forest and rangeland areas.

Land use changes can also affect the density and type of vegetation,

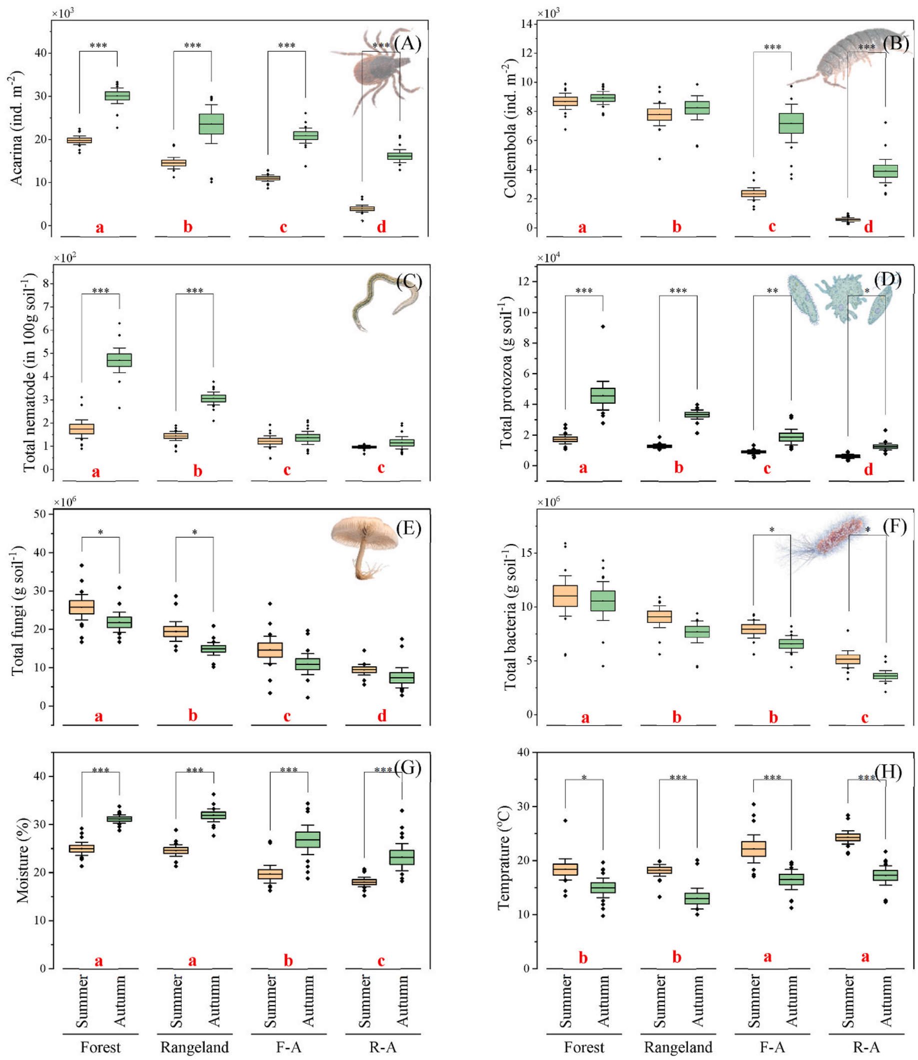

Fig. 4. Box plots illustrating soil fauna activity, moisture and temperature in the two seasons under the different land uses: forest, rangeland, agricultural land with history of forest (F-A), and agricultural land with history of rangeland (R-A). The boxes denote interquartile range with mean as a black line and whiskers extending to the most extreme points. Different letters indicate significant differences ($P < 0.05$ by Duncan test) between land uses (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

influencing the volume and quality of the entering organic material (Sun et al., 2024). This feature together with the shifts in soil microclimate can have an (in)direct impact on the chemical properties of the soil, mainly its nutrient content. Consistent with previous works (Fentie et al., 2020; Molla Fetene et al., 2022), the findings of the present study showed that the conversion of natural forests and rangelands into agricultural areas (F-A and R-A) diminished soil chemical quality indicators, including soil pH, as well as the contents of total N, K, P, Ca and Mg. The low concentration of P in the agricultural land could be attributed to the acidic soil pH and nutrient immobilization, whereas the higher levels of this element in the natural forest and rangeland are likely related to its release during mineralization processes (Selassie and Ayanna, 2013). Moreover, other macronutrients like K, P, Ca and Mg appeared in higher amounts in the surveyed forest area probably due to the high pH of the clay soil and the high volume of vegetation that lower the washing speed and favor the high accumulation of minerals (Jaleta Negasa, 2020; Molla Fetene et al., 2022). The elevated levels of POC and PON in the natural habitats compared to the agricultural environments are likely due to the existence of woody plant species, which boosts the amount of litter fall, improves soil pH, and drops the carbon-to-nitrogen ratio (Kartalaei et al., 2023; Kooch and Bayranvand, 2017). Furthermore, the variations in soil DOC and DON under the varying land uses could be attributed to differences in vegetation cover, which may influence the quantity and quality of organic inputs to the soil, as well as to the composition and activity of root systems (Sanji et al., 2020).

4.2. Responses of soil biological indicators to land-use change

Variations in land use, characterised by shifts in vegetation density and species composition, result in alterations in the volume and characteristics of organic materials production, as well as in changes in environmental conditions such as moisture, temperature, and nutrient availability. Altogether, it can have profound effects on soil fauna, flora, microbial communities, and ecosystem processes as supported by ours and previous research (Bakhshandeh et al., 2019; Liu et al., 2025). To this end, we observed that a reduced soil temperature and elevated moisture levels in the natural forested area created more optimal conditions for soil microbial biomass and activity. This is consistent with earlier works from Gschwend et al. (2021) and Christel et al. (2024). Moreover, variations in soil chemical properties, especially in pH, total N, and in other macronutrients may largely influence soil microbial activity (Horrigue et al., 2016; Rutigliano et al., 2023). In line with our results, Kooch et al. (2024a) (stated that the elevated soil SIR observed in the forest habitat can be ascribed to the abundant soil nutrients, the elevated moisture levels, and the substantial root biomass present in this environment. Indeed, extensive research has consistently demonstrated

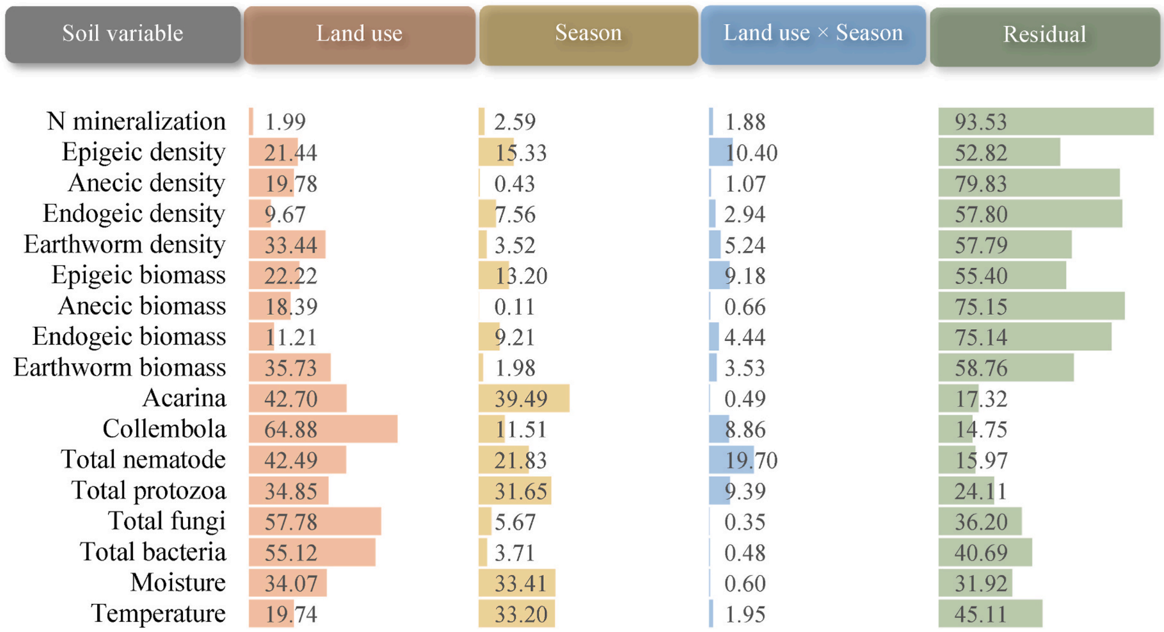

Fig. 5. Contribution (%) of independent single factors “land use”, “season” and the combination of both “land use × season” to variation of soil fauna, moisture, temperature and N mineralization by application of a two-way ANOVA test.

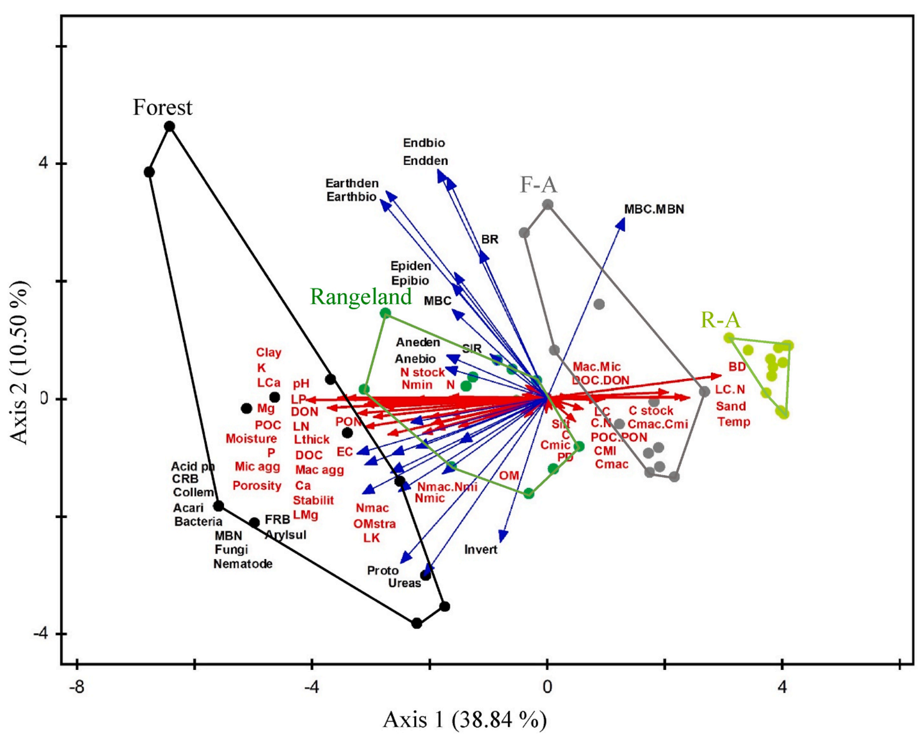

Fig. 6. Principal component analysis (PCA) comprising the land use types, as well as the litter properties, and the soil physicochemical and biological properties. The studied land uses were forest, rangeland, agricultural land with history of forest (F-A), and agricultural land with history of rangeland (R-A). The full names of the abbreviations are provided in Table 5.

that the soil physical and chemical traits are among the primary determinants of soil microbial community structure (Christel et al., 2024). Woody plant species, with their remarkable ability to expand root systems, also play a significant role in enhancing soil microbial biomass. Consequently, the alteration or removal of woody vegetation can profoundly impact the soil biological properties, particularly root biomass (including fine and coarse roots). The presence of woody species in natural areas, especially forests, is a key factor contributing to the higher root biomass compared to agricultural lands that are dominated by annual vegetation. Moreover, the higher diversity of woody plants in forests and rangelands may favor competition among plant root systems, leading to a greater root expansion and, subsequently, an increased fine and coarse root biomass. Additionally, the higher moisture content and nutrient availability in the soils of natural areas are other critical factors driving root expansion and biomass accumulation in these habitats (Azaryan et al., 2021).

Table 5
Correlation of the litter and soil properties with the first and second axis of the principal component analysis (PCA).

Litter and soil properties	Abbreviation	Axis 1	Axis 2	Soil properties	Abbreviation	Axis 1	Axis 2
Litter thickness	Lthick	−0.644**	0.059^{ns}	Available potassium	K	−0.799**	−0.026^{ns}
Litter carbon	LC	0.412**	0.115^{ns}	Available calcium	Ca	−0.575**	0.357*
Litter nitrogen	LN	−0.743**	0.070 ^{ns}	Available magnesium	Mg	−0.744**	−0.063 ^{ns}
Litter C/N ratio	LC. N	0.633**	−0.066 ^{ns}	Particulate organic carbon	POC	−0.719**	−0.070^{ns}
Litter phosphorus	LP	−0.648**	−0.011 ^{ns}	Particulate organic nitrogen	PON	−0.577**	0.228^{ns}
Litter potassium	LK	−0.255^{ns}	0.202 ^{ns}	POC/PON ratio	POC.PON	−0.054^{ns}	−0.249^{ns}
Litter calcium	LCa	−0.394**	0.121 ^{ns}	Dissolved organic carbon	DOC	−0.577**	0.033^{ns}
Litter magnesium	LMg	−0.771**	0.087 ^{ns}	Dissolved organic nitrogen	DON	−0.732**	0.248^{ns}
Bulk density	BD	0.724**	−0.132^{ns}	DOC/DON ratio	DOC.DON	0.262^{ns}	−0.315*
Particle density	PD	0.038^{ns}	0.237^{ns}	Nitrogen mineralization	Nmin	−0.184	0.194 ^{ns}
Porosity	Porosity	−0.620**	0.219^{ns}	Urease	Ureas	−0.598**	0.353*
Aggregate stability	Stability	−0.556**	0.057^{ns}	Acid phosphatase	Acid ph	−0.663**	−0.216^{ns}
Sand	Sand	0.587**	0.173^{ns}	Arylsulfatase	Arylsul	−0.436**	0.098^{ns}
Silt	Silt	0.117^{ns}	−0.141^{ns}	Invertase	Invertase	0-.296*	0.125 ^{ns}
Clay	Clay	−0.676**	0.005^{ns}	Epigeic density	Epiden	0.387**	−0.011 ^{ns}
Macro-aggregate	Mac agg	−0.563**	0.097^{ns}	Epigeic biomass	Epibio	0.410**	−0.017 ^{ns}
Micro-aggregate	Mic agg	−0.592**	0.141 ^{ns}	Anecic density	Aneden	−0.400**	−0.141^{ns}
Macro/Micro-aggregate ratio	Mac.Mic	−0.017^{ns}	−0.040^{ns}	Anecic biomass	Anebio	−0.400**	−0.117^{ns}
Soil moisture	Moisture	−0.728**	0.108^{ns}	Endogeic density	Endden	−0.441**	−0.358*
Soil temperature	Temp	0.632**	0.245 ^{ns}	Endogeic biomass	Endbio	−0.498**	−0.335*
Organic matter stratification ratio	OMstr	−0.039^{ns}	0.827**	Earthworm density	Earthden	−0.674**	−0.298*
pH	pH	−0.496**	0.246^{ns}	Earthworm biomass	Earthbio	−0.711**	−0.263 ^{ns}
Electrical conductivity	EC	−0.427**	−0.016^{ns}	Acarian density	Acarina	−0.925**	0.095 ^{ns}
Organic carbon	C	0.207^{ns}	0.807**	Collembola density	Collem	−0.924**	0.039 ^{ns}
Carbon in macro-aggregate	Cmac	0.221^{ns}	0.185^{ns}	Total nematode	Nematode	−0.537**	0.059^{ns}
Carbon in micro-aggregate	Cmic	0.059^{ns}	−0.061^{ns}	Total protozoa	Proto	−0.771**	0.128 ^{ns}
C macro/C micro-aggregate ratio	Cmac.Cmic	0.192^{ns}	0.206^{ns}	Total bacteria	Bacteria	−0.708**	0.158^{ns}
Carbon stock	C stock	0.399**	0.727**	Total fungi	Fungi	−0.767**	0.019^{ns}
Carbon management index	CMI	0.302*	0.627**	Basal respiration	BR	−0.319*	−0.168 ^{ns}
Total nitrogen	N	−0.499**	−0.284^{ns}	Substrate induced respiration	SIR	0.249*	−0.046^{ns}
Nitrogen in macro-aggregate	Nmac	−0.274 ^{ns}	0.235^{ns}	Microbial biomass carbon	MBC	0.403**	−0.055^{ns}
Nitrogen in micro-aggregate	Nmic	−0.334*	−0.122^{ns}	Microbial biomass nitrogen	MBN	0.787**	0.068^{ns}
N macro/N micro-aggregate ratio	Nmac.Nmic	−0.038 ^{ns}	0.121^{ns}	MBC/MBN	MBC.MBN	0.476*	−0.131 ^{ns}
Nitrogen stock	N stock	−0.208^{ns}	−0.345*	Coarse root biomass	CRB	−0.942**	0.040 ^{ns}
C/N ratio	C.N	0.382**	0.699**	Fine root biomass	FRB	−0.629**	0.110 ^{ns}
Available phosphorous	P	−0.676**	0.211 ^{ns}				

*$P < 0.05$, **$P < 0.01$, ns = not significant. Bold and italic values indicate significant statistical differences.

Table 6
Structural equation model (SEM) - summary statistics for model fit.

Fit index	Observed values	Recommended value
Chi-square/degrees of freedom (χ2/df)	4.064	≤3 or 3-5
Incremental fit index (IFI)	0.918	≥0.9
Comparative fit index (CFI)	0.914	≥0.9
Tucker Lewis index (TLI)	0.901	≥0.9
Parsimony comparative fit index (PCFI)	0.676	≥0.6
Parsimony normed fit Index (PNFI)	0.635	≥0.5
Root means square error of approximation (RMSEA)	0.083	≤0.08; ≤0.1
Normed fit index (NFI)	0.925	≥0.9

Enzymes associated with different nutrient cycles and that participate in different stages of degradation will not necessarily respond to land use changes in the same way (Wang et al., 2012). This was evident in the present study, where urease, acid phosphatase, and arylsulfatase activities declined significantly following the 30-year conversion of natural vegetation to cropland, while invertase activity remained unchanged. The pronounced reductions in urease and acid phosphatase, key enzymes in N and P cycling, are consistent with their dependence on soil organic carbon, total N, and available P, which are typically higher under natural vegetation (Wang et al., 2011; Cheng et al., 2013). Arylsulfatase showed a less accused reduction, likely reflecting its sensitivity to soil moisture and nutrient status (Guo et al., 2011). All in all, the differential sensitivity of the targeted enzyme activities likely reflects legacy effects of long-term land use changes, contributing to a time lag in microbial community functional adaptation (Shade et al., 2012; Louisson et al., 2023). The lower activities of N- and P-related enzymes align with reduced microbial biomass, labile organic fractions, and nutrient availability in converted lands, whereas C-acquiring enzymes like invertase often exhibit greater persistence as stabilized extracellular enzymes (Burns et al., 2013). This pattern suggests that N- and P-acquiring functions seem to respond more rapidly to the altered environment, while C-acquiring functions might exhibit a time lag, preserving characteristics of the original natural vegetation (Azaryan et al., 2021).

Furthermore, the more suitable microclimate conditions in the forest area in terms of soil moisture and temperature are expected to positively influence the abundance of soil fauna (Yang and Chen, 2009; Hua et al., 2024). The organic layer is known to provide habitat and food for the activity of soil organisms (Kooch et al., 2024a); as such, the fall of litter and the entry of more organic matter can be another plausible reason for the increase in the density of the targeted faunal groups in the forest lands. As stated by Yang and Chen (2009) and Kooch et al. (2018), the quality of organic matter also plays a significant role in this matter. As shown in Table 2, the organic layer in the natural forest was characterised by a higher nutrient content and a lower carbon-to-nitrogen ratio compared to the other land uses. Similar to soil acarina, collembolans also feed on plant debris in the soil surface, so the quality and quantity of the organic layer can influence their population. On the contrary, the loss of canopy cover and reduced vegetation density in the agricultural lands can create inappropriate conditions (i.e., high temperature and low humidity) negatively affecting the population of soil organisms. In fact, several authors pointed the importance of soil moisture in regulating soil acarina, collembola and earthworms' densities (Krab et al., 2015; Kooch et al., 2018; Kooch and Noghre, 2020). Soil nematode (Pan et al., 2022) and protozoa (Lin et al., 2017) communities have been found to be negatively affected by grazing, primarily due to soil

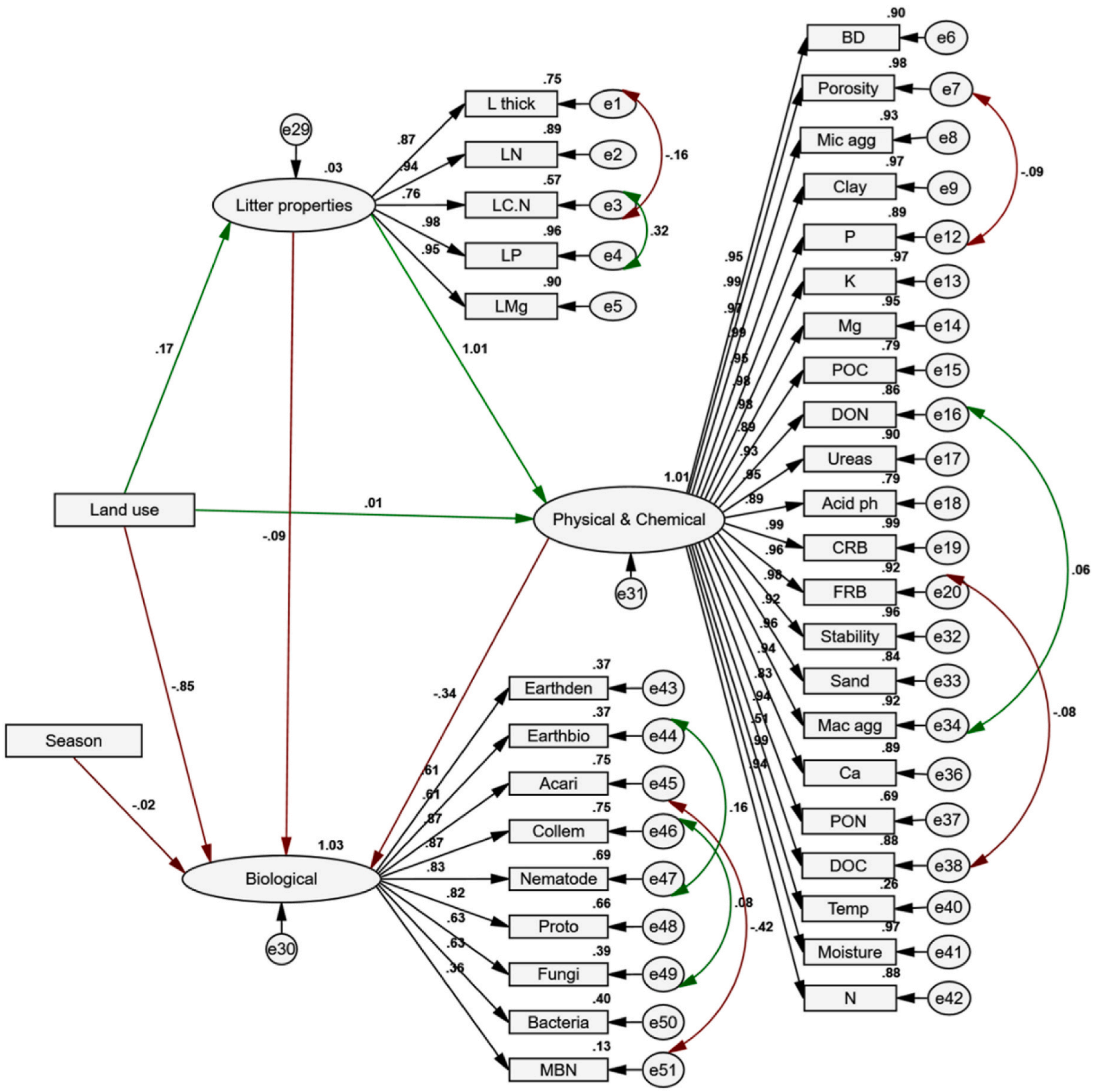

Fig. 7. Structural equation model (SEM) evaluating the direct and indirect effects of land use and season on the litter and soil properties. The numbers on the rectangular boxes and directions represent the standardized variance and the standardized regression weights, respectively. The full names of the abbreviations are provided in Table 5. CFI = 0.914, TLI = 0.901, IFI = 0.918, RMSEA = 0.083, PCFI = 0.676, CMIN/DF = 4.064, PNFI = 0.635. Details presented in Table 6.

compaction and lower soil moisture. In addition, Ma et al. (2022) showed that the decrease in humidity and increase in soil temperature create unfavorable conditions for bacterial and fungal populations. In this context, the significant variations in soil biota populations during summer and autumn across the studied land uses can be attributed to the notable fluctuations in soil moisture and temperature during these seasons. This highlights the interplay between soil microclimate conditions and biological activity in the studied land uses, particularly in response to seasonal changes.

Additionally, the physical and chemical characteristics of the soil can affect the populations of soil organisms (Singh et al., 2020). In natural sites, especially the forest, in which soil properties like the bulk density, porosity, aggregate stability and texture were more favorable, the studied groups of soil fauna showed a higher density in comparison with the agricultural sites. Moreover, earlier investigations (e.g., Singh et al., 2020; Liu et al., 2025) established soil pH and its variations as a crucial parameter regulating the activity of soil organisms. To that respect, higher pH levels were found in the forest site than in the agricultural lands (F-A, R-A); accordingly, earthworms' biomass and density as well as the population of soil acarina and collembola appeared in higher numbers in the forest land. Increased soil pH may also have a positive influence on the density of soil nematodes and protozoa (Lin et al., 2017; Pan et al., 2022), which is in line with our findings. Moreover, a higher nutrient availability as reported for the forest site can positively impact the density and activity of soil organisms (Bargali et al., 2019; Kartalaei et al., 2023). During autumn, a peak in abundance was recorded in the natural forest for most of the targeted faunal groups. This increase is likely related to the occurrence of favorable conditions during this season, such as fresh litter input, higher soil moisture, and cooler temperatures compared to the dry and warm summer. Taken together, these environmental factors create optimal conditions for the activity, reproduction, and survival of soil invertebrates, as underlined by Kooch et al. (2024a).

4.3. Interactions among land-use types, litter, and soil indicators: interpretation and insights

The analysis of soil variables across the varying land uses revealed

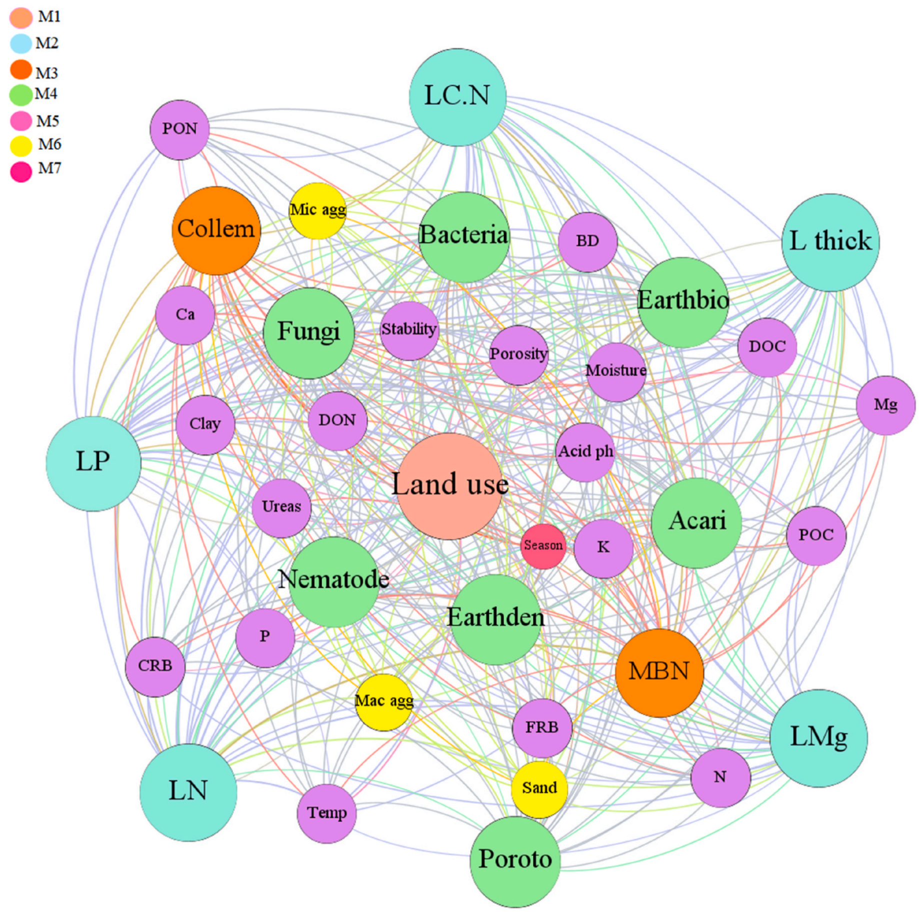

Fig. 8. A network model generated considering land use, season and thirty-six litter and soil properties. Each node (circle) represents a property, and each edge (connection) indicates significant correlations among properties across the soil samples. Node colors reflect the identified modules (groups), and the size and label of each node is proportional to the eigenvector centrality. The thickness of each edge (line) between two nodes is proportional to standardized regression weights. The size and the color density of the lines reflect the varying strength of relationship between the soil properties. The full names of the abbreviations are provided in Table 5.

that the distinct land cover types and management practices greatly influenced the studied soil quality indicators, as demonstrated by Mamabolo et al. (2024). In line with Gao et al. (2025), we quantitatively assessed the consequences of land use transformations on soil fertility indicators and soil biota in Iran's semi-arid regions. The findings of this study indicate that land use change has significant adverse effects on soil quality and can seriously compromise soil health. In particular, the reduction in organic matter inputs to the soil limits the availability of essential nutrients for plant growth and disrupts key nutrient-cycling processes. These impacts are largely attributed to the removal of vegetation cover (Haghighi et al., 2010). Furthermore, soil fauna and microbial communities, which play crucial roles in ecosystem functions underwent a decrease in terms of biomass and density following land-use conversion. Consequently, we cannot rule out that the microbial and enzymatic processes that underpin soil fertility and ecosystem services could be compromised. There are strong interactions between vegetation types, soil fertility characteristics, and biotic communities (Baligh et al., 2025). According to PCA output, significant changes in litter and soil characteristics were observed in the studied habitats. Overall, the natural forest was characterised by an increased organic matter input probably due to a high diversity and density of leaf cover, thereby favouring soil productivity, soil microbial biomass and activity. The results of the structural equation model (SEM) indicate that changes in soil biological characteristics are indirectly regulated by litter attributes as well as by the physical and chemical properties of the soil. The supply of organic inputs and plant residues, together with the diversity of vegetation cover, supports an active soil food web (Fu et al., 2017; Kooch et al., 2024a), thereby increasing the abundance and biomass of soil biota in forest ecosystems. The density and biomass of earthworms, collembolans, bacteria, fungi, nematodes, acarina, and protozoa were identified as key indicators of soil biological processes in the network model and showed a high sensitivity to land-use change, consistent with the findings of Piri et al. (2025). Overall, the results demonstrate statistically significant differences among land-use types and highlight the critical role of vegetation cover in promoting soil biological functioning and supporting sustainable land management.

4.4. Practical implications

This study emphasizes the importance of sustainable management and protection of natural vegetation in semiarid regions. Our findings provide evidence that the conversion of natural ecosystems into agricultural land has profound negative impacts on soil functions leading to a decrease in its quality. In this regard, the use of strategies to support the restoration of native vegetation, such as passive restoration and active planting of native vegetation could help to maintain soil health and prevent further degradation. Also, applying these findings to areas where land use change is unavoidable, the integration of agroforestry systems that combine native trees and agricultural crops could contribute to maintain soil quality, increase long-term agricultural productivity and promote sustainable management. Ultimately, this scientific outcome can help policymakers and natural resource managers to provide strategies to protect vegetation and improve soil performance in agricultural areas, while minimizing soil degradation and maintaining sustainable productivity. To this end, policy makers ought to come up with strategic plans to promote the use of native plants in the ecosystem restoration projects and train the farmers and other locals on the effectiveness of such strategies. These plans can be employed as viable and feasible solutions to enhance soil management and protect the natural resources in the semi-arid mountain areas.

4.5. Limitations of the research and recommendations

The findings of this study indicate that preserving native vegetation can help to reduce the negative impacts of ecosystem degradation and thus maintain soil quality and biodiversity in semi-arid ecosystems. However, due to the mountainous nature of the surveyed area, both the traffic and the access to the studied land use covers were not easily possible. In some cases, the regional conditions and environmental features involve a considerable number of restrictions and limitations for the researchers that should be taken into consideration within the experimental design. In particular, although similar studied sites were found to fulfil the purpose of the present work, the environmental and physiographic differences of these areas can be a limiting factor for the sampling campaign. In addition, the specific climatic conditions of these mountainous areas, which are often covered with snow during the cold season pose significant challenges for evaluating soil properties dynamics. In the future, research should specifically address long-term and multi-seasonal monitoring, including more precise measurements of soil properties and the use of more advanced tools to assess the impact of vegetation changes on soil biota and their functions through metagenomics and/or DNA barcoding. It is also recommended to consider time-series sampling designs in future studies to assess the possible time lags in the changes in soil enzymes in response to land-use transformations.

5. Conclusions

This study provides evidence about the impact of land-use change on soil properties and biological functions in the Alborz Mountains. The findings confirmed that natural ecosystems with dense vegetation cover, such as forests and rangelands, significantly increased litter input and contributed to improving soil physical properties and fertility. This is consistent with our first hypothesis. The shelter created by woody cover, together with an increased litter deposition are considered key factors positively affecting soil physical properties and soil fertility in the natural habitats, reinforcing our second hypothesis. On the contrary, the removal of woody species in the agricultural lands led to a reduced litter input, as well as changes in soil microclimate, and a decline in its physicochemical and biological properties. This was accompanied by a reduced microbial biomass and activity, a decrease in N- and P-related enzyme activities, along with a decline in root biomass and the density of distinct faunal groups in response to conversion of natural habitats into croplands, supporting our third hypothesis. In sum, the results of this study emphasize the importance of preserving natural ecosystems and show that the conversion of forests and rangelands to agricultural lands leads to a decrease in soil quality and damage to ecosystem services. To prevent and combat this, it is critical to implement sustainable land management practices that prioritise the conservation of natural ecosystems so as to maintain soil quality and enhance ecosystem services in a long-term. Restoration of native vegetation can also help to improve soil conditions in converted lands. In those cases where land-use change is unavoidable, the implementation of agroforestry systems aiming to reduce the intensity of agricultural activities, and returning plant residues to the field can contribute to reduce the abovementioned adverse effects on soil properties and ecosystem functions and help to maintain soil quality.

CRediT authorship contribution statement

Yahya Kooch: Writing – review & editing, Writing – original draft, Supervision, Software, Investigation, Conceptualization. **Mahmood Tavakoli:** Writing – original draft, Software, Investigation. **Fatemeh Heidari:** Writing – original draft, Software, Investigation. **María Gómez-Brandón:** Writing – review & editing. **Jan Frouz:** Writing – review & editing.

Declaration of competing interest

The authors declare that they have no conflict of interest.

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Data availability

Data will be made available on request.

References

Adhikari, K., Hartemink, A.E., 2016. Linking soils to ecosystem services—A global review. Geoderma 262, 101–111.
Ahmed, W., Wu, Y., Kidwai, S., Li, X., Zhang, G., Zhang, J., 2021. Spatial and temporal variations of nutrients and chlorophyll a in the Indus river and its deltaic creeks and coastal waters (Northwest Indian Ocean, Pakistan). J. Mar. Syst. 218, 103525. .
Alef, K., 1995. Estimating of soil respiration. In: Alef, K., Nannipieri, P. (Eds.), Methods in Soil Microbiology and Biochemistry. Academic Press, New York, pp. 464–470.
Alef, K., Nannipieri, P., 1995. Estimation of microbial activities. In: Methods in Applied Soil Microbiology and Biochemistry. Academic Press, London, pp. 193–270.
Ali, D., Hussain, A., Begum, F., Lin, C., Ali, S., Aitizaz Ahsan, W., Hussain, A., Hussain, F., 2025. Assessing the impact of land use and land cover changes on soil properties and carbon sequestration in the upper Himalayan region of Gilgit, Pakistan. Sustainable Chemistry One World 5, 100038, 5.
Allison, L.E., 1975. Organic carbon. In: Black, C.A. (Ed.), Methods of Soil Analysis. Madison, W. I. American Society of Agronomy, pp. 1367–1378. Part 2.
Alvafritz, L., Hertel, D., 2024. Impacts of land use history on leaf litter input, chemical composition, decomposition and related nutrient cycling in young and old secondary tropical lowland rainforests (Sumatra, Indonesia). Plant Soil 495, 359–370.
Anderson, T.H., Domsch, K.H., 1990. Application of eco-physiological quotients (qCO_2 and qD) on microbial biomasses from soils of different cropping histories. Soil Biol. Biochem. 22, 251–255. https://doi.org/10.1016/0038-0717(90)90094-G.
Aulakh, C.S., Sharma, S., Thakur, M., Kaur, P., 2022. A review of the influences of organic farming on soil quality, crop productivity and produce quality. J. Plant Nutr. 45, 1884–1905.
Azaryan, M., Abrari Vajari, K., Amanzadeh, B., 2021. Variations in humus and fine root properties related to development stages in a temperate natural Beech forest. Eur. J. For. Res. 140, 307–316.
Bakhshandeh, E., Hossieni, M., Zeraatpisheh, M., Francaviglia, R., 2019. Land use change effects on soil quality and biological fertility: a case study in northern Iran. Eur. J. Soil Biol. 95, 103119. .
Baligh, P., Honarjoo, N., Jalalian, A., Totonchi, A., 2025. Soil chemical and microbial properties affected by land use type in a unique ecosystem (Fars, Iran). Biomass Convers. Biorefinery 15, 29729–29739. .
Bargali, S.S., Padalia, K., Bargali, K., 2019. Effects of tree fostering on soil health and microbial biomass under different land use systems in the Central Himalayas. Land Degrad. Dev. 30, 1984–1998. .
Bastian, M., Heymann, S., Jacomy, M., 2009. Gephi: an open source software for exploring and manipulating networks. Proceedings of the international AAAI conference on web and social media 3, 361–362.
Blair, G.J., Lefroy, R.D., Lisle, L., 1995. Soil carbon fractions based on their degree of oxidation, and the development of a carbon management index for agricultural systems. Aust. J. Agric. Res. 46, 1459–1466. .
Blake, G.R., Hartge, K.H., 1986. Particle Density. Methods of Soil Analysis: Part 1 Physical and Mineralogical Methods, 5, pp. 377–382.
Bouyoucos, G.J., 1962. Hydrometer method improved for making particle size analyses of soils 1. Agron. J. 54, 464–465.
Bower, C.A., Reitemeier, R.F., Fireman, M., 1952. Exchangeable cation analysis of saline and alkali soils. Soil Sci. 73, 251–262.
Bremner, J.M., Mulvaney, C.S., 1982. Chemical and Microbiological Properties. Methods of Soil Analysis. Part II, 9. American Society of Agronomy: Soil Science Society of America, Madison, Wisconsin, pp. 595–624.

Brookes, P.C., Landman, A., Pruden, G., Jenkinson, D.S., 1985. Chloroform fumigation and the release of soil nitrogen: a rapid direct extraction method to measure microbial biomass nitrogen in soil. Soil Biol. Biochem. 17, 837–842.

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

Burns, R.G., DeForest, J.L., Marxsen, J., Sinsabaugh, R.L., Stromberger, M.E., Wallenstein, M.D., et al., 2013. Soil enzymes in a changing environment: current knowledge and future directions. Soil Biol. Biochem. 58, 216–234.

Buruso, F.H., Adimassu, Z., Sibali, L.L., 2023. Effects of land use/land cover changes on soil properties in Rib watershed, Ethiopia. Catena 224, 106977.

Cambardella, C.A., Elliott, E.T., 1992. Particulate soil organic-matter changes across a grassland cultivation sequence. Soil Sci. Soc. Am. J. 56, 777–783.

Cheng, F., Peng, X., Zhao, P., Yuan, J., Zhong, C., Cheng, Y., Cui, C., Zhang, S., 2013. Soil microbial biomass, basal respiration and enzyme activity of main forest types in the Qinling Mountains. PLoS One 8, e67353.

Cherven, K., 2015. Mastering Gephi Network Visualization. Packt Publishing Ltd.

Christel, A., Prevost-Bouré, N.C., Dequiedt, S., Saby, N., Mercier, F., Tripied, J., Comment, G., Villerd, J., Djemiel, C., Hermant, A., Blondon, M., 2024. Differential responses of soil microbial biomass, diversity and interactions to land use intensity at a territorial scale. Sci. Total Environ. 906, 167454. .

Davari, M., Gholami, L., Nabiollahi, K., Homaee, M., Jafari, H.J., 2020. Deforestation and cultivation of sparse forest impacts on soil quality (case study: west Iran, Baneh). Soil Tillage Reserch 198, 104504.

Davis, A.G., Huggins, D.R., Reganold, J.P., 2023. Linking soil health and ecological resilience to achieve agricultural sustainability. Front. Ecol. Environ. 21, 131–139.

Dechoum, M.S., Zenni, R.D., Castellani, T.T., Zalba, S.M., Rejmánek, M., 2015. Invasions across secondary forest successional stages: effects of local plant community, soil, litter, and herbivory on Hovenia dulcis seed germination and seedling establishment. J. Plant Ecol. 216, 823–833.

Dotaniya, M.L., Meena, V.D., 2015. Rhizosphere effect on nutrient availability in soil and its uptake by plants: a review. Proceedings of the National Academy of Sciences. India Section B: Biological Sciences 85, 1–12.

El Behairy, R.A., El Arwash, H.M., El Baroudy, A.A., Ibrahim, M.M., Mohamed, E.S., Kucher, D.E., Shokr, M.S., 2024. How can soil quality be accurately and quickly studied? A review. Agronomy 14, 1682. .

Evett, S.R., Schwartz, R.C., Tolk, J.A., Howell, T.A., 2009. Soil profile water content determination: spatiotemporal variability of electromagnetic and neutron probe sensors in access tubes. Vadose Zone J. 8, 926–941. .

Ezeigbo, O.R., Ukpabi, C.F., Abel-Anyebe, O., Okike-Osisiogu, F.U., Ike-Amadi, C.A., Agomoh, N.G., 2013. Physico-chemical properties of soil contaminated with refined petroleum oil in Eluama Community, Abia State, Nigeria. International Journal of Scientific Research and Management 1, 405–413.

Feng, Z., Wang, L., Peng, Q., Li, J., Liang, T., 2022. Effect of environmental factors on soil properties under different land use types in a typical basin of the North China Plain. J. Clean. Prod. 344, 131084. .

Fentie, S.F., Jembere, K., Fekadu, E., Wasie, D., 2020. Land use and land cover dynamics and properties of soils under different land uses in the tejibara watershed, Ethiopia. Sci. World J. 2020, 1479460. .

Fetene, E.M., Amera, M.Y., 2018. The effects of land use types and soil depth on soil properties of Agedit watershed, Northwest Ethiopia. Ethiopian Journal of Science and Technology 11, 39–56. .

Franzluebbers, A.J., Stuedemann, J.A., 2009. Soil-profile organic carbon and total nitrogen during 12 years of pasture management in the Southern Piedmont USA. Agriculture. Ecosystems & Environment 129, 28–36.

Frouz, J., 2023. Plant-soil feedback across spatiotemporal scales from immediate effects to legacy. Soil Biol. Biochem. 189, 109289.

Fu, X., Guo, D., Wang, H., Dai, X., Li, M., Chen, F., 2017. Differentiating between root- and leaf-litter controls on the structure and stability of soil micro-food webs. Soil Biol. Biochem. 113, 192–200. .

Gao, M., Hu, W., Li, M., Wang, S., Chu, L., 2025. Network analysis was effective in establishing the soil quality index and differentiated among changes in land-use type. Soil Tillage Res. 246, 106352. .

Geetha, K., Chaitanya, T., Padmaja, G., Krishna, A., 2021. Effect of different land use systems on soil properties. Pharm. Innov. 10, 1–6.

Getachew, F., Abdulkadir, A., Lemenih, M., Fetene, A., 2012. Effects of different land uses on soil physical and chemical properties in Wondo Genet area, Ethiopia. New York Science Journal 5, 110–118.

Gomiero, T., 2016. Soil degradation, land scarcity and food security: reviewing a complex challenge. Sustainability 8, 281.

Gschwend, F., Hartmann, M., Mayerhofer, J., Hug, A.S., Enkerli, J., Gubler, A., Meuli, R. G., Frey, B., Widmer, F., 2021. Site and land-use associations of soil bacteria and fungi define core and indicative taxa. FEMS (Fed. Eur. Microbiol. Soc.) Microbiol. Ecol. 97 fiab165.

Guo, P., Wang, C., Jia, Y., Wang, Q., Han, G., Tian, X., 2011. Responses of soil microbial biomass and enzymatic activities to fertilizations of mixed inorganic and organic nitrogen at a subtropical forest in East China. Plant Soil 338, 355–366.

Haghighi, F., Gorji, M., Shorafa, M., 2010. A study of the effects of land use changes on soil physical properties and organic matter. Land Degrad. Dev. 21, 496–502. .

Hättenschwiler, S., 2005. Effects of tree species diversity on litter quality and decomposition. In: Forest Diversity and Function: Temperate and Boreal Systems. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 149–164.

Homer, C.D., Pratt, P.F., 1961. Methods of Analysis for Soils, Plants and Waters. University of California, Agricultural Sciences Press, Berkeley, p. 309p.

Horáková, E., Pospíšilová, L., Vlček, V., Menšík, L., 2020. Changes in the soil's biological and chemical properties due to the land use. Soil Water Res. 15, 228–236.

Horrigue, W., Dequiedt, S., Prévost-Bouré, N.C., Jolivet, C., Saby, N.P., Arrouays, D., Bispo, A., Maron, P.A., Ranjard, L., 2016. Predictive model of soil molecular microbial biomass. Ecol. Indic. 64, 203–211. .

Hua, H., Sui, X., Liu, Y., Liu, X., Chang, Q., Xu, R., Li, M., Mu, L., 2024. Effects of land use type transformation on the structure and diversity of soil bacterial communities. Life 14, 252.

Hutson, B.R., Veitch, L.G., 1987. Densities of Collembola and Acarina in the soil and litter of three indigenous South Australian forests related to layer, site and seasonal differences. Aust. J. Ecol. 12, 239–261.

Jaleta Negasa, D., 2020. Effects of land use types on selected soil properties in central highlands of Ethiopia. Appl. Environ. Soil Sci. 2020, 7026929. https://doi.org/10.1155/2020/7026929. .

Jeffery, S., Gardi, C., Jones, A., Montanarella, L., Marmo, L., Miko, L., Ritz, K., Peres, G., Römbke, J., 2010. van der Putten. European Atlas of Soil Biodiversity. European Commission, Publications Office of the European Union, Luxembourg.

Jones, D.L., Willett, V.B., 2006. Experimental evaluation of methods to quantify dissolved organic nitrogen (DON) and dissolved organic carbon (DOC) in soil. Soil Biol. Biochem. 38, 991–999.

Kartalaei, Z.M., Kooch, Y., Tilaki, G.A.D., 2023. Litter and soil properties under woody and non-woody vegetation types: implication for ecosystem management in a mountainous semi-arid landscape. J. Environ. Manag. 348, 119238. .

Kooch, Y., Bayranvand, M., 2017. Composition of tree species can mediate spatial variability of C and N cycles in mixed beech forests. For. Ecol. Manag. 401, 55–64. .

Kooch, Y., Tavakoli, M., Akbarinia, M., 2018. Tree species could have substantial consequences on topsoil fauna: a feedback of land degradation/restoration. Eur. J. For. Res. 137, 793–805.

Kooch, Y., Parsapour, M.K., Wirth, S., 2023a. Soil functional indicators in different development stages of an oak (Quercus castaneifolia CA Mey.) stand. Appl. Soil Ecol. 189, 104922.

Kooch, Y., Parsapour, M.K., Nouraei, A., Kartalaei, Z.M., Wu, D., Gómez-Brandón, M., Lucas-Borja, M.E., 2023b. The effect of silvicultural systems on soil function depends on bedrock geology and altitude. J. Environ. Manag. 345, 118657.

Kooch, Y., Heidari, F., Haghverdi, K., Gómez-Brandón, M., Kartalaei, Z.M., 2024a. The type of land cover and management affect differently soil functional indicators in a semi-arid ecosystem. Appl. Soil Ecol. 202, 105553. .

Kooch, Y., Noghre, N., 2020. The effect of shrubland and grassland vegetation types on soil fauna and flora activities in a mountainous semi-arid landscape of Iran. Science of the total environment 703, 135497.

Kooch, Y., Nouraei, A., Wang, L., Wang, X., Wu, D., Francaviglia, R., Frouz, J., Parsapour, M.K., 2024b. Long-term landfill leachate pollution suppresses soil health indicators in natural ecosystems of a semi-arid environment. Chemosphere 367, 143647.

Kooch, Y., Haghverdi, K., Nouraei, A., Francaviglia, R., 2024c. Soil properties are affected by vegetation types in a semi-arid mountain landscape. Pedobiologia 102, 150932.

Krab, E.J., Cornelissen, J.H., Berg, M.P., 2015. A simple experimental set-up to disentangle the effects of altered temperature and moisture regimes on soil organisms. Methods Ecol. Evol. 6, 1159–1168.

Laganière, J., Pare, D., Bradley, R.L., 2010. How does a tree species influence litter decomposition? Separating the relative contribution of litter quality, litter mixing, and forest floor conditions. Can. J. For. Res. 40, 465–475.

Li, M., Zhou, X., Zhang, Q., Cheng, X., 2014. Consequences of afforestation for soil nitrogen dynamics in Central China. Agric. Ecosyst. Environ. 183, 40–46.

Li, Y., Li, B., Zhang, X., Chen, J.J., Zhan, F.D., Guo, X.H., Zu, Y.Q., 2015. Differential water and soil conservation capacity and associated processes in four forest ecosystems in Dianchi Watershed, Yunnan Province, China. J. Soil Water Conserv. 70, 198–206.

Liang, W., Lou, Y., Li, Q., Zhong, S., Zhang, X., Wang, J., 2009. Nematode faunal response to long-term application of nitrogen fertilizer and organic manure in Northeast China. Soil Biol. Biochem. 41, 883–890.

Lin, B., Zhao, X., Zheng, Y., Qi, S., Liu, X., 2017. Effect of grazing intensity on protozoan community, microbial biomass, and enzyme activity in an alpine meadow on the Tibetan Plateau. J. Soils Sediments 17, 2752–2762.

Liu, H.Q., Li, S.C., Li, H.J., Peng, Z.C., 2025. Soil pH Determining the Assembly Processes of Abundant and Rare Bacterial Communities in Response to Cultivation Modes in Lemon Farmlands. Plants 14 (12), 1852. https://doi.org/10.3390/plants14121852.

Lohbeck, M., Poorter, L., Martínez-Ramos, M., Bongers, F., 2015. Biomass is the main driver of changes in ecosystem process rates during tropical forest succession. Ecology 96, 1242–1252.

Long, X., Zhao, J., Li, J., Liao, X., Wang, J., Fu, Z., Zhang, W., Liu, X., Wang, K., 2024. Disturbance intensity shapes the soil micro-food web compositions and energy fluxes during seven-year land use changes. Soil Biol. Biochem. 194, 109424.

Louisson, Z., Hermans, S.M., Buckley, H.L., Case, B.S., Taylor, M., Curran-Cournane, F., Lear, G., 2023. Land use modification causes slow, but predictable, change in soil microbial community composition and functional potential. Environmental Microbiome 18 (1), 30.

Ma, L., Liu, L., Lu, Y., Chen, L., Zhang, Z., Zhang, H., Wang, X., Shu, L., Yang, Q., Song, Q., Zhang, J., 2022. When microclimates meet soil microbes: temperature controls soil microbial diversity along an elevational gradient in subtropical forests. Soil Biol. Biochem. 166, 108566.

Maes, S.L., Blondeel, H., Perring, M.P., Depauw, L., Brümelis, G., Brunet, J., Decocq, G., Den Ouden, J., Härdtle, W., Hédl, R., Heinken, T., 2019. Litter quality, land-use history, and nitrogen deposition effects on topsoil conditions across European temperate deciduous forests. For. Ecol. Manag. 433, 405–418. .

Mamabolo, E., Pryke, J.S., Gaigher, R., 2024. Soil macrofauna are important bioindicators of soil quality in agroecosystems under different management. Ecol. Indic. 167, 112723. .

Mayzlish, E., Steinberger, Y., 2004. Effects of chemical inhibitors on soil protozoan dynamics in a desert ecosystem. Biol. Fertil. Soils 39, 415–421.

McCune, B., Mefford, M.J., 1999. PC-ORD. Multivariate Analysis of Ecological Data, Version 4. Mjm Software Design, p. 233. Gleneden Beach, Oregon, USA.

Mganga, K.Z., Rolando, J., Kalu, S., Karhu, K., 2024. Microbial soil quality indicators depending on land use and soil type in a semi-arid dryland in Kenya. Eur. J. Soil Biol. 121, 103626. .

Molla Fetene, E., Getnet, K., Mekonnen, M., 2022. Land use change and its effect on selected soil properties in the northwest highlands of Ethiopia. Heliyon 8, e10157.

Neatrour, M.A., Jones, R.H., Golladay, S.W., 2005. Correlations between soil nutrient availability and fine-root biomass at two spatial scales in forested wetlands with contrasting hydrological regimes. Can. J. For. Res. 35, 2934–2941.

Ota, H.O., Mohan, K.C., Udume, B.U., Olim, D.M., Okolo, C.C., 2024. Assessment of land use management and its effect on soil quality and carbon stock in Ebonyi State, Southeast Nigeria. J. Environ. Manag. 358, 120889.

Pan, F., Yan, R., Zhao, J., Li, L., Hu, Y., Jiang, Y., Shen, J., McLaughlin, N.B., Zhao, D., Xin, X., 2022. Effects of grazing intensity on soil nematode community structure and function in different soil layers in a meadow steppe. Plant Soil 471, 33–46.

Parsapour, M.K., Kooch, Y., Hosseini, S.M., Alavi, S.J., 2024. Assessing soil microbial catabolic diversity in alder and oak plantations at varying developmental stages. Can. J. For. Res. (ja). (in press).

Pereira, L.C., Balbinot, L., Lima, M.T., Bramorski, J., Tonello, K.C., 2022. Aspects of forest restoration and hydrology: the hydrological function of litter. J. For. Res. 33, 543–552. .

Philippot, L., Griffiths, B.S., Langenheder, S., 2021. Microbial community resilience across ecosystems and multiple disturbances. Microbiol. Mol. Biol. Rev. 85, 10–1128. .

Pires, L.F., Brinatti, A.M., Saab, S.C., Cássaro, F.A.M., 2014. Porosity distribution by computed tomography and its importance to characterize soil clod samples. Appl. Radiat. Isot. 92, 37–45.

Piri, A.S., Kooch, Y., Hojjati, S.M., 2025. Changes in soil multifunctional properties in semi-arid environments are dependent on ecosystem health. Catena 254, 108978.

Plaster, E.J., 1985. Soil Science and Management. Delmar Publishers Inc, Albany, N.Y., p. 124

Pojasok, T., Kay, B.D., 1990. Assessment of a combination of wet sieving and turbidimetry to characterize the structural stability of moist aggregates. Can. J. Soil Sci. 70, 33–42.

Randriamananjara, M.A., Fenton, N.J., DesRochers, A., 2025. Understory vegetation diversity and composition in intensively managed plantations compared to extensively managed forests. N. For. 56, 5. https://doi.org/10.1007/s11056-024-10071-9.

Rutigliano, F.A., Marzaioli, R., Grilli, E., Coppola, E., Castaldi, S., 2023. Microbial, physical and chemical indicators together reveal soil health changes related to land cover types in the southern European sites under desertification risk. Pedobiologia 99, 150894.

Sanji, R., Kooch, Y., Rey, A., 2020. Impact of forest degradation and reforestation with Alnus and Quercus species on soil quality and function in northern Iran. Ecol. Indic. 112, 106132. .

Sariyildiz, T., Savaci, G., Kravkaz, I.S., 2015. Effects of tree species, stand age and land-use change on soil carbon and nitrogen stock rates in northwestern Turkey. iFor. Biogeosci. For. 9, 165. .

Schoenholtz, S.H., Van Miegroet, H., Burger, J.A., 2000. A review of chemical and physical properties as indicators of forest soil quality: challenges and opportunities. For. Ecol. Manag. 138, 335–356.

Sekucia, F., Dlapa, P., Kollár, J., Cerdá, A., Hrabovský, A., Svobodová, L., 2020. Land-use impact on porosity and water retention of soils rich in rock fragments. Catena 195, 104807.

Selassie, Y.G., Ayanna, G., 2013. Effects of different land use systems on selected physico-chemical properties of soils in Northwestern Ethiopia. J. Agric. Sci. 5, 112. .

Shade, A., Peter, H., Allison, S.D., Baho, D.L., Berga, M., Bürgmann, H., Huber, D.H., Langenheder, S., Lennon, J.T., Martiny, J.B.H., Matulich, K.L., Schmidt, T.M., Handelsman, J., 2012. Fundamentals of microbial community resistance and resilience. Front. Microbiol. 3, 417.

Singh, S., Sharma, A., Khajuria, K., Singh, J., Vig, A.P., 2020. Soil properties changes earthworm diversity indices in different agro-ecosystem. BMC Ecol. 20, 1–14.

Six, J., Paustian, K., Elliott, E.T., Combrink, C., 2000. Soil structure and organic matter I. Distribution of aggregate-size classes and aggregate-associated carbon. Soil Sci. Soc. Am. J. 64, 681–689.

Sun, Z., Tian, P., Zhao, X., Wang, Y., Wang, S., Fang, X., Wang, K., Liu, S., 2022. Temporal shifts in the explanatory power and relative importance of litter traits in regulating litter decomposition. Forest Ecosyst. 9, 100072. .

Sun, Y., Wang, X., Zhang, Y., Duan, W., Xia, J., Wu, J., Deng, T., 2024. Vegetation types can affect soil organic carbon and δ13C by influencing plant inputs in topsoil and microbial residue carbon composition in subsoil. Sustainability 16, 4538. .

Usharani, K.V., Roopashree, K.M., Naik, D., 2019. Role of soil physical, chemical and biological properties for soil health improvement and sustainable agriculture. J. Pharmacogn. Phytochem. 8, 1256–1267.

Wang, J.B., Chen, Z.H., Chen, L.J., Zhu, A.N., Wu, Z.J., 2011. Surface soil phosphorus and phosphatase activities affected by tillage and crop residue input amounts. Plant Soil Environ. 57, 251–257.

Wang, B., Xue, S., Liu, G.B., Zhang, G.H., Li, G., Ren, Z.P., 2012. Changes in soil nutrient and enzyme activities under different vegetations in the Loess Plateau area, Northwest China. Catena 92, 186–195.

Wollum, A.G., 1983. Cultural methods for soil microorganisms. Methods of soil analysis: part 2 chemical and microbiological properties 9, 781–802. https://doi.org/10.2134/agronmonogr9.2.2ed.c37.

Wu, Y., Zhang, Y., Dai, L., Xie, L., Zhao, S., Liu, Y., Zhang, Z., 2021. Hydrological connectivity improves soil nutrients and root architecture at the soil profile scale in a wetland ecosystem. Sci. Total Environ. 762, 143162.

Yang, X., Chen, J., 2009. Plant litter quality influences the contribution of soil fauna to litter decomposition in humid tropical forests, southwestern China. Soil Biol. Biochem. 41, 910–918.

Yang, X., Shao, M.A., Li, T., Gan, M., Chen, M., 2021. Community characteristics and distribution patterns of soil fauna after vegetation restoration in the northern Loess Plateau. Ecol. Indic. 122, 107236.

Yu, Q., Xu, L., Wang, M., Xu, S., Sun, W., Yang, J., Shi, Y., Shi, X., Xie, X., 2022. Decreased soil aggregation and reduced soil organic carbon activity in conventional vegetable fields converted from paddy fields. Eur. J. Soil Sci. 73, e13222.

Zahedifar, M., 2023. Assessing alteration of soil quality, degradation, and resistance indices under different land uses through network and factor analysis. Catena 222, 106807.

Zancan, S., Trevisan, R., Paoletti, M.G., 2006. Soil algae composition under different agro-ecosystems in North-Eastern Italy. Agric. Ecosyst. Environ. 112, 1–12.

Zarei, Z., Moosavi, A.A., Zarei, M., Nematollahi, M.A., 2025. Effect of land use change on some physical and chemical characteristics of soils in the northern half of Fars province. Iran. J. Soil Water Res. 56, 1161–1174.

Zeraatpisheh, M., Bakhshandeh, E., Hosseini, M., Alavi, S.M., 2020. Assessing the effects of deforestation and intensive agriculture on the soil quality through digital soil mapping. Geoderma 363, 114139.

Zhang, Z., Zhang, Y., Henderson, M., Wang, G., Chen, M., Fu, Y., Zeyu, D., Wanying, Z., Weiwei, H., Liu, B., 2024. Effect of land use type on soil moisture dynamics in the sloping lands of the Black soil (Mollisols) region of Northeast China. Agriculture 14, 1261.

Zi-zheng, D.E.N.G., Ming-jing, H.U.A.N.G., Wu-ping, Z.H.A.N.G., Guo-fang, W.A.N.G., 2023. Effects of conservation tillage on soil structure and bulk density under dryland. Chinese Journal of Soil Science 54, 46–55.