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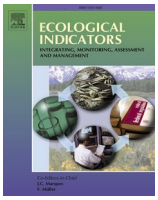

Soil functional indicators in a mountain forest-rangeland mosaic of northern Iran

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ABSTRACT

Soil plays an essential role in providing ecosystem services, especially in mountain ecosystems which are often considered as fragile and sensitive systems and commonly consist of a mosaic of forest and rangeland plant communities. The relationship between above-ground plant cover and the properties of soil organic and mineral layers in mountain areas are rarely studied. This research aimed to assess the effect of different land covers (i.e. forest, forest-rangeland ecotone, and rangeland) on soil functional indicators, i.e. fertility and biological activities, in the Hyrcanian region of northern Iran. We hypothesized that (i) the presence of tree cover enhances soil fertility and biological activities and creates hot spots (islands) of soil functional indicators especially in the topsoil, (ii) litter quality and organic matter fractions are the drivers for activities of soil organisms, nutrient cycles and transformation processes in mountain ecosystems. Litter (O-horizon including L, F and H layers) and mineral soil samples (in two separate depths of 0–10 cm and 10–20 cm) were taken using iron frames (30 × 30 cm). In total, 45 litter and 90 soil samples were transferred to the laboratory. Soil characteristic especially in the 0–10 cm depth, litter carbon (C), nitrogen (N) and C/N ratio were significantly affected by different land covers showing the maximum of soil organic C and microbial activity under forest. Our findings showed that the studied land covers, as well as litter and soil properties can be separated by PCA output. The first and second axes, accounted more than 50% of the explained variance in each of the studied soil depths. Soils with a better quality of litter (i.e. lower C/N ratio), higher values for organic matter fractions, soil fertility indicators and soil biological activities can be attributed to the forest. In contrast, positions of low soil fertility indicator values and biota abundance were imposed by forest-rangeland ecotone and rangeland. Although each land cover plays a prominent ecological role and takes its place in the evolutionary process, forests are essential because of their capacity to store and transform carbon and nutrients and to create hotspots identified by functional soil indicators. Based on our findings, soil functions decreased ranked in the order forest > forest-rangeland ecotone > rangeland, which can be assigned to the lower density of trees, and the amount of litter mass and litter quality. It

Abbreviations (see Fig.4): land covers, Litter and soil properties: F, Forest; E, Ecotone; R, Rangeland; Litter Lit C, Litter carbon; Lit N, Litter nitrogen; Lit CN, Litter carbon to nitrogen ratio); soil (BD, Bulk density; PD, Particle density; Porosity, Soil porosity; Mac Agg, Macro aggregate; Mic Agg, Micro aggregate; Stabilit, Soil stability; Sand, Soil sand; Silt, Soil silt; Clay, Soil clay; WC, Water content; Temp, Soil temperature; pH, Soil pH; EC, Electrical conductivity; C, Organic carbon; C mac, Carbon in macro aggregate; C mic, Carbon in micro aggregate; C seq, Carbon sequestration; POC, Particulate organic carbon; DOC, Dissolved organic carbon; N, Total nitrogen; N mac, Nitrogen in macro aggregate; N mic, Nitrogen in micro aggregate; N seq, Nitrogen sequestration; N min, Nitrogen mineralization; Ammon, Ammonium NitrateNitrate; PON, Particulate organic nitrogen; DON, Dissolved organic nitrogen; CN, Soil carbon to nitrogen ratio; P, Available phosphorous; K, Available potassium; Ca, Available calcium; Mg, Available magnesium; FRB, Fine root biomass; Epi Den, Epigeic density; Epi Bio, Epigeic biomass; Ane Den, Anecic density; Ane Bio, Anecic biomass; Endo Den, Endogeic density; Endo Bio, Endogeic biomass; Earth De, Earthworm density; Earth Bi, Earthworm biomass; Acarina, Acarina density; Collembo, Collembola density; Nematode, Total nematode; Protozoa, Protozoa density; Bacteria, Total bacteria; Fungi, Total fungi; BR, Basal respiration; SIR, Substrate induced respiration; MBC, Microbial biomass carbon; MBN, Microbial biomass nitrogen; MBC.MBN, Soil microbial biomass carbon to microbial biomass nitrogen; qCO_2, Soil metabolic quotient; MR, Microbial ratio; CAI, Carbon availability index UreaseUrease; Acid pho, Acid phosphatase; Aryl, Arylsulfatase; Invertas, Invertase.

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can be concluded that tree covers have a prominent role in increasing soil functions, which should be given special consideration in the restoration of degraded mountain ecosystems.

1. Introduction

Nowadays, questions about changes in land use and land cover and the associated impacts on terrestrial ecosystem functions are a central concern, which also makes the importance of protecting natural forests in the context of global climate change and global warming of great interest (Moniruzzaman et al., 2021). Changes in land use as one of the most important and influential factors for environmental change can contribute significantly to an increase in global atmospheric CO_2 concentrations and to the loss of ecosystem functions and services (Hosonuma et al., 2012; Singh et al., 2020). Therefore, understanding the impact of land use change on the environment and identifying the main causes is necessary to achieve the most appropriate land management strategy and maximum ecosystem benefits from transformed land while limiting further land use change (Montanarella and Panagos, 2021). The role of land cover in the functions of terrestrial ecosystems that determine primary production, organic matter stocks, and nutrient cycling is unquestionable and considerable (Acosta-Martinez et al., 2018; Mancini Teixeira et al., 2020). Changes in the type of vegetation cover can lead to a substantial variation in soil properties and thus to changes in soil fertility. In terrestrial ecosystems, soil as a natural component directly contributes to numerous ecosystem functions and services, including net primary production, climate and water regulation, nutrient cycling and carbon sequestration (Prescott and Grayston, 2013; Singh et al., 2018a). The composition of the above-ground plant community can effectively influence soil processes and functions through several factors, including microclimate change (buffering canopy temperature fluctuations and maintaining soil moisture), production of litter and root exudates, and provision of habitat or resources for macro- and microorganisms (Ushio et al., 2010; Putten et al., 2013). Understanding the influence of plant communities on soil's multiple functions is, therefore, of high importance and value. Accordingly, global interest in the assessment of land use change and the impact of land management on soil properties is increasing (Nath et al., 2018; Sheng Han and Lin, 2019). In this context, soil organisms are the most important indicators of soil quality and functions. The frequency and activity of these factors depend on the physico-chemical properties of the soil or soil types, the quantity and quality of organic residues, the type of vegetation cover (including species combinations, soil canopy structure and root architecture), land use processes, and climate (Xueyong et al., 2009). Furthermore, there is a general consensus on a direct and indirect relationship between soil microbial processes and virtually all higher-level terrestrial ecosystem functions (Singh et al., 2010; Delgado-Baquerizo et al., 2016). For example, forest to pasture conversion has significant impacts on the soil through the removal of long-standing forest vegetation and the farming practices that follow. This process leads to a disturbance of the balance between the availability of plant organic matter and decomposition by soil microorganisms (Don et al., 2011; Singh et al., 2017), which ultimately affects soil quality and functions (de Carvalho et al., 2016; Malik et al., 2018). Microorganisms play a central role in the cycles of carbon and of essential nutrients (N and P) (Burns et al., 2013). Through their immediate response to changes in soil conditions, the biological and biochemical properties of a soil can thus be assumed to be key indicators of soil quality and health (Nannipieri et al., 2012; Singh et al., 2017).

It has been demonstrated that changes in land use or land cover and subsequent land management practices have an impact on microbial and enzyme activities, particularly as a result of deforestation (Jourgholami et al., 2019; Xu et al., 2020), tillage (Raiesi and Beheshti, 2015; Maharjan et al., 2017) and fertilizer application (Saikia et al., 2019). Soil biological characteristics are considered suitable, preferential indicators for soil quality studies when compared to physical and chemical parameters, as they are sensitive to even minor changes in the soil environment (Shimamoto et al., 2018; Mendes et al., 2019). For example, the enzymatic activity of soil is reported to be a significant and sensitive indicator of soil quality and fertility, as the catalyzed release of nutrients directly affects the growth of plants and microorganisms (Medeiros et al., 2015; Acosta-Martinez et al., 2018; Kooch et al., 2018). Furthermore, the most important rationale for using enzymatic activities as a soil quality index is the close relationship with soil quality parameters such as soil organic matter (SOM) content, C and N transformation besides the potential to indicate trends of system changes more rapidly compared to other soil properties (Yao et al., 2020). Several studies show that enzyme activities can be considered the most sensitive indicators for detecting such changes caused by changes in management practices and climate change impacts (Kooch et al., 2018; Zarafshar et al., 2020). The study of changes in soil quality is therefore of great importance for identifying and assessing the impacts of different management practices in agriculture or natural resources, especially in case of conversion or reclamation of sites that were previously used as pasture or forest sites. Studies available so far reflect the short-term effects of management on soil quality and have provided a valuable basis for monitoring management practices in a wide range of regions to identify and prevent soil degradation, enable sustainable production and ultimately protect the environment (Rowe, 2012; Lavelle et al., 2016).

The evidence is abundant and convincing that there are complex relationships between land cover, the litter produced above and below ground and the resulting biological properties of the soil. The main objective of this study was to evaluate soil functional indicators (i.e. measurements of soil fertility and biological activities) in a forest-mountain mosaic in northern Iran. Our specific objectives were (i) to study the effects of different land cover types (i.e. forest, forest-edge ecotone and pasture) on properties of soil organic and mineral layers and (ii) to determine the driving forces of soil biota populations, microbial processes and nutrient cycles. We hypothesized that (i) the presence of tree cover increases soil fertility and biological activities and creates hot spots (islands) of soil functional indicators, especially in the topsoil, (ii) litter quality and organic matter fractions are the driving forces of soil organism activity, nutrient cycles and transformation processes in mountain ecosystems. We expect that the results will improve scientific approaches to better understand soil functions and the impacts of land use, especially in rarely studied and vulnerable mountain ecosystems and ultimately help to optimize land cover management and improve ecosystem services.

2. Materials and methods

2.1. Study area

With an area of 14100 ha, the Vaz watershed is located in the vicinity of Noor city, Mazandaran province, northern Iran (51° 55′ E to 52° 12 'E latitudes and 36° 12′ N to 36° 30 'N longitudes) (Fig. 1A). The region extends at an altitude range of 270–3350 m above sea level with slope ranges of 0–45%. Mean annual temperature is 11 °C (the average minimum temperature from December to March is below zero), and mean annual rainfall is 1200 mm with a dry season between May and August. According to the USDA Soil Taxonomy, the parent material is dolomite limestone that belongs to the upper Jurassic and lower Cretaceous periods. The soil is of the order Alfisoils, with a silty clay loam texture. In the area, vegetation types are strongly determined by altitude and distinguished mosaics of forest at low altitudes to rangeland at high altitudes (Salar, 2018).

2.2. Litter and soil sampling

In August 2019, following a field trip, sites with different land covers (i.e. forest, forest-rangeland ecotone and rangeland) were selected. These sites were never fertilized and had not been used for grazing. These sites have similar conditions in terms of physiographic characteristics (i.e. altitude range of 1800–2000 m above sea level and 10–19% range of slope with a northern aspect; see Table 1) and climatic conditions. To avoid pseudoreplication (see Hurlbert, 1984), each site was replicated three times (n = 3) within a distance of 4–7 km (see Fig. 1B). Within each site, an area 4-ha (200 m × 200 m) was regarded. Then, macro-plots (20 × 20 m) and micro-plots (2 × 2 m) were employed to record coverage of woody and herbaceous species (Mesdaghi, 2005), respectively (Fig. 1C and Table 1). In the central part of macro-plots (see Fig. 1C), litter (O-horizon including L, F and H layers) and soil samples (in two different depths of 0–10 cm and 10–20 cm) were taken using iron frames (30 × 30 cm area). In total, 45 litter and 90 soil samples were transferred to the laboratory. Litter thickness was measured with a ruler from the litter surface to the top of the mineral soil at the same places of soil sampling. Litter mass was measured by placing an iron frame on the ground and cutting around the edge with a knife. The litter within the frame was collected to the top of the mineral soil. All samples were washed, oven-dried at 105 °C for 48 h and weighed. The litter mass was measured as mass per unit area (kg m^{-2}) (Kooch et al., 2020a).

2.3. Laboratory analyses

2.3.1. Litter properties

Litter C and N contents were determined by dry combustion with an elemental analyser (Kooch et al., 2017a).

2.3.2. Soil physico-chemical properties

Bulk density was measured by the clod method (Plaster, 1985). Particle density was determined by pycnometer method (Blake and Hartge, 1986). Soil porosity was calculated based on bulk and particle density data (Pires et al., 2014). Soil texture was measured by the Bouyoucos hydrometer method (Bouyoucos, 1962). Water content was measured by drying soil samples at 105 °C for 24 h, and soil temperature was measured using a digital thermometer (Zancan et al., 2006). Aggregate size distribution was determined by wet sieving with mesh diameters of 0.25 and 0.50 mm (Cambardella and Elliott, 1992). Aggregate stability was determined by the Yoder method (Kemper and Rosenau, 1986).

Soil pH was determined using an Orion Ionalyzer Model 901 pH meter in a 1:2.5, soil: water solution. EC (Electrical Conductivity) was determined using an Orion Ionalyzer Model 901 EC meter in a 1:2.5 soil: water solution (Kooch et al., 2017a). Organic carbon was determined by the Walkley-Black technique (Allison, 1975), and the Micro-Kjeldahl technique was used to determine total nitrogen (Bremner and Mulvaney, 1982). Soil C and N sequestration in the studied soil depth were calculated using bulk density data, and the C and N contents (Kooch et al., 2012). Nitrogen mineralization was measured using a laboratory incubation procedure under controlled conditions (Robertson, 1999). Soil NH_4^+ and NO_3^- were extracted with a 2 M KCl solution (soil:solution, 1:5) and then filtered through a 0.45 μm filter. NH_4^+ and NO_3^- concentrations were determined in extracted solutions colorimetrically at 645 and 420 nm, respectively (Li et al., 2014). Available P was determined spectrophotometrically according to the Olsen method (Homer and Pratt, 1961). Available K, Ca, and Mg (by ammonium acetate extraction at pH 9) were determined with an atomic absorption spectrophotometer (Bower et al., 1952).

Particulate organic carbon (POC) and particulate organic nitrogen (PON) were measured by a physical fractionation method (Cambardella and Elliot, 1992). A total organic carbon (TOC) analyser (Shimadzu TOC-550A) was used to measure dissolved organic carbon (DOC) and dissolved organic nitrogen (DON). The difference between the total dissolved nitrogen reading and the combined NH_4^+ and NO_3^- values was calculated as DON (Jones and Willett, 2006). Each sample was cleared of fine roots (<2 mm diameter) and dried at 70 °C to a constant mass (Neatrour et al., 2005).

2.3.3. Soil biota

The earthworms were collected by hand sorting simultaneously with the soil sampling, and identified based on ecological categories (i.e., epigeic, anecic and endogeic) by external characteristics (Kooch et al., 2014b). Soil Acarina and collembola were extracted with the help of a modified Tullgren funnel as described by Hutson and Veitch (1987). Nematodes were extracted by a modified cotton–wool filter method (Liang et al., 2009). Following the extraction method, soil protozoa population densities were counted under a microscope (see Mayzlish and Steinberger, 2004). Bacteria and fungi were cultivated on nutrient agar (NA) and potato dextrose agar (PDA), respectively. 1 g of fresh soil was dispersed in 9 ml of distilled water (10^{-1} dilution). After shaking, 1 ml of the dilution was transferred aseptically into another 9 ml of distilled water repeatedly until final dilutions were obtained (10^{-1} to 10^{-7}). Dilutions 10^{-4} to 10^{-7} were inoculated on the NA plates as follows: 0.1 ml of a dilution was spread over the plate with a sterile plastic spreader and incubated at 26 °C for 1 week. Three treatments were prepared for each inoculated dilutions 10^{-3} to 10^{-5} were inoculated on the PDA plates following the same procedure. After incubation, the colonies were counted through visual observation (Kooch et al., 2020b).

2.3.4. Soil microbial and biochemical activities

Evolved CO_2 was measured in a 3-day incubation experiment at 25 °C in order to evaluate soil basal respiration (BR) (Alef, 1995). Glucose 1% was used as substrate and evolved CO_2 was detected after 72 h incubation to determine substrate-induced respiration (SIR) (Anderson and Domsch, 1990). The soil metabolic quotient, qCO_2 (BR:

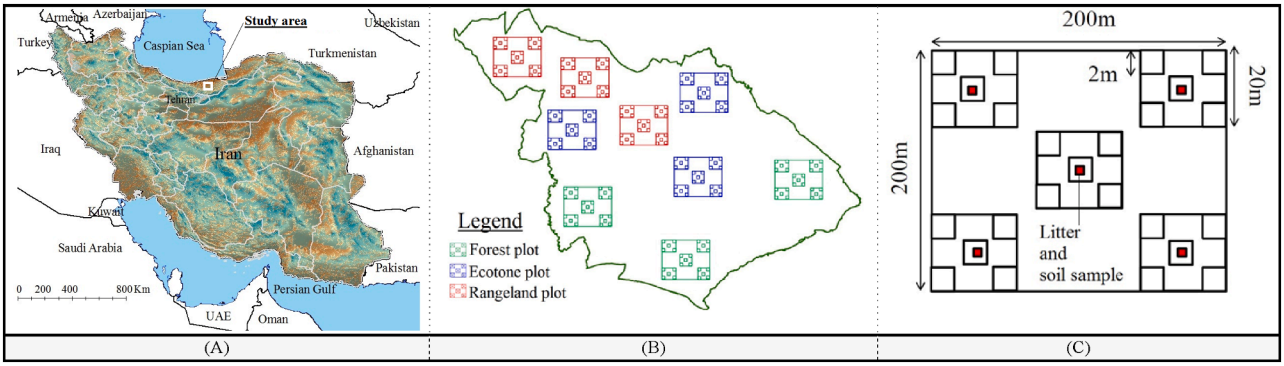

Fig. 1. Location of the study area in Northern Iran, Mazandaran Province (A), schematic representation of the spatially separated sites (B), and experimental layout and sampling design adopted for each studied site (C) (figures not to scale).

Table 1
Description of land cover types in the Vaz watershed, Mazandaran Province, northern Iran.

Land cover	Altitude (m)	Slope (%)	Slope aspect	Dominant woody plant	Canopy cover (%)	Number of trees (ha^{-1}) (Mean ± standard error)	Tree basal area (m^2 ha^{-1})(Mean ± standard error)	Dominant understory plant (>5%)	Litter mass (kg m^{-2})
Forest	1800–1900	10–15	North	*Fagus orientalis* Lipsky	42 ± 1.32	105 ± 9	9.67 ± 0.19	*Asperula odorata* L. (22%)	11.9–22.2
				Carpinus betulus L.	20 ± 1.45	87 ± 8	7.23 ± 0.22	*Euphorbia amygdaloides* L. (15%)	
				Fraxinus excelsior L.	15 ± 1.76	41 ± 6	4.12 ± 0.05	*Hypericum androsaemum* L. (10%)	
				Acer velutinum Boiss.	10 ± 1.45	25 ± 8	2.98 ± 0.07		
Ecotone	1850–1950	12–18	North	*Fagus orientalis* Lipsky	54 ± 2.25	122 ± 11	12.56 ± 1.27	*Hypericum androsaemum* L. (8%)	8.9–11.6
				Carpinus betulus L.	9 ± 2.42	32 ± 9	3.92 ± 0.35	*Euphorbia amygdaloides* L. (7%)	
				Crataegus microphylla C. Koch.	10 ± 2.19	–	–	*Medicago sativa* L. (14%)	
				Berberis integerrima Bunge.	9 ± 1.84	–	–	*Stachys laxa* Boiss. & Buhse. (10%)	
Rangeland	1900–2000	15–19	North	*Crataegus microphylla* C. Koch.	12 ± 2.15	–	–	*Stachys laxa* Boiss. & Buhse. (25%)	6.5–10.2
				Berberis integerrima Bunge.	11 ± 1.45	–	–	*Lolium prenne* L. (22%)	
				Ribes Uva – crispa L.	8 ± 1.49	–	–	*Teucrium polium* L. (18%)	
				Prunus spinosa L.	6 ± 1.02	–	–	*Asperula glomerata* (M. Bieb.) (8%)	

MBC; Anderson and Domsch, 1990), the microbial ratio or entropy (MBC:Organic C; Insam and Domsch, 1988) and the C availability index (BR: SIR; Cheng et al., 1996) were calculated based on the values of organic C, BR, SIR and MBC. Microbial biomass carbon (MBC) and nitrogen (MBN) were measured using the fumigation-extraction method (Brookes et al., 1985).

Urease activity (EC 3.5.1.5) was measured by incubating 5 g fresh soil sample with 2.5 ml of a 0.08 M urea solution for 2 h at 37 °C and finally, NH_4^+ was determined colorimetrically at 690 nm (Kandeler and Gerber, 1988). Acid phosphatase activity (EC 3.1.3.2) was measured by the method described by Tabatabai (1994). Briefly, a fresh soil sample of 1 g was placed in 50 ml test tube, to which one drop of toluene and 4 ml of modified universal buffer (pH 6.5) was added. The samples were incubated with p-nitrophenyl phosphatase for 1 h at 37 °C. After filtration, the yellow color intensity was measured by spectrophotometer at 400 nm. Arylsulphatase activity (EC 3.1.6.1) was assayed according to the method of Tabatabai and Bremmer (1970). Soil samples (1 g) were incubated for 1 h at 37 °C with 0.25 ml of toluene, 4 ml of 0.5 M acetate buffer (pH = 5.8) and 1 ml of p-nitrophenyl sulphate (PNPS) solution. The reaction was stopped by adding 1 ml of 0.5 M $CaCl_2$ and 4 ml of 0.5 M NaOH. The contents were mixed thoroughly and filtrated. Finally, the amount of p-nitrophenol released from PNPS hydrolysis in the soil suspension was measured at 400 nm. Invertase activity (EC 3.2.1.26) was determined by incubating 5 g soil with 15 ml of sucrose solution (1.2%) and 15 ml of 2 M acetate buffer (pH = 5.5) for 3 h at 50 °C according to Schinner and von Mersi (1990). The released reducing sugars were analyzed colorimetrically at 690 nm.

2.4. Statistical analysis

Data normality was checked by the Kolmogorov Smirnov test (data were normally distributed; p-value > 0.05), while the homogeneity of variances was tested using the Levene's test (variances were homogeneous; p-value > 0.05). One-way ANOVA with Duncan's test were performed to detect the effect of different land covers on litter and soil characteristics (0–10 cm and 10–20 cm). For all statistical analyses, SPSS v.20 software was used. Multivariate correlations were analyzed using a factor analysis based on principal components analyses (PCA) performed by PC-Ord version 5.0 (Mc Cune and Mefford, 1999). Data for land covers, litter and mineral soil (0–10 and 10–20 cm depths) properties were investigated with the aim to identify the samples that generate similar patterns. The two first components (PC1 and PC2) were selected for further interpretation of the results. In addition, heat plots (as a part of the PCA output) were produced to show hot spots (islands) of increased soil functioning.

3. Results

3.1. Litter and soil physico-chemical properties

The results of ANOVA indicated that there were significant differences (p-value < 0.05) in the litter and soil physico-chemical properties among different land covers (Fig. 2 and Table 2). The contents of litter C and N were significantly higher under the forest compared to ecotone and rangeland. In contrast, the forest showed the lowest litter C/N ratio in comparison with ecotone and forest (Fig. 2). Higher values of soil bulk density were found in rangeland than in ecotone and forest land covers. Soil porosity did not show statistically significant differences in the 0–10 cm depth under the studied land covers, while in the 10–20 cm depth, decreased ranked in the order of forest > ecotone > rangeland. Macro aggregate, micro aggregate and aggregate stability were significantly different among the studied land covers (forest > ecotone ≈

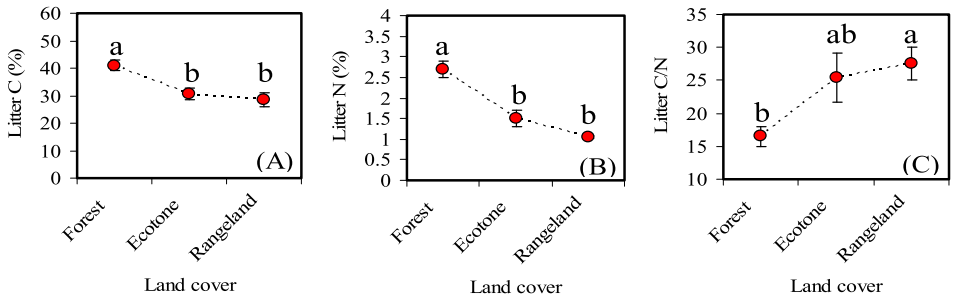

Fig. 2. Mean (±SE; n = 15) contents of litter carbon (*F* test = 9.549**), nitrogen (*F* test = 27.235**) and C/N ratio (*F* test = 4.667*) under different land covers. *P < 0.05, **P < 0.01.

rangeland) for both soil depths with higher variability found in the 0–10 cm layer than in 10–20 cm soil depth. Higher values for the sand fraction were present under rangeland, ecotone and forest, respectively, in both studied soil depths. The soil silt fraction was significantly ranked in the order of forest < ecotone < rangeland in the 0–10 cm depth (no significant changes in the 10–20 cm depth). Greater amounts of clay contents were found under forest (with significant changes in the 0–10 cm depth and without significant changes in the 10–20 depth) compared to ecotone and rangeland. At both soil depths, the forest cover had a higher water content than the ecotone and rangeland. Soil temperature showed significant changes (rangeland ≈ ecotone > forest in the 0–10 cm soil depth and rangeland > ecotone > forest in the 10–20 cm soil depth) among the land covers (Table 2). Based on the data from both studied soil depths, higher values for soil pH, organic C, C in macro-aggregates, and for C sequestration were found under forest compared to ecotone and rangeland covers. Whereas increased soil EC was found under forest ≈ ecotone than in rangeland cover. Values of soil C in micro-aggregates were found ranked in the order of forest > ecotone > rangeland, respectively. With higher values at 0–10 cm soil depth, soil POC, DOC, total N, N in macro- and mico-aggregates, as well as N sequestration and mineralization, ammonium, nitrate, PON and DON showed significant decrease in forest, ecotone and rangeland, respectively. The soil C/N ratio did not show statistically significant differences in 0–10 cm soil depth under the studied land covers. Whereas the highest soil C/N ratios in 10–20 cm soil depth were allocated to rangeland compared to ecotone and forest. Soil available nutrients (i.e. P, K, Ca and Mg) were decreased, ranked in the order of forest, ecotone and rangeland covers, respectively, with maximum values in 0–10 cm soil depth (Table 2).

3.2. Soil biota and biological activities

In 0–10 cm soil depth, significantly higher amounts of fine root biomass were found under forest than under ecotone and rangeland covers. Whereas, in 10–20 cm soil depth, fine root biomass was significantly different, ranked in the order of forest > ecotone ≈ rangeland. Highest earthworm activities (i.e., abundance and biomass) were observed under forest, ecotone and rangeland covers, respectively (Table 3). Among different ecological groups of earthworms, the epigeic had higher abundance in 0–10 cm soil depth, whereas endogeic and anecic had more activities in 10–20 cm soil depth (Table 3 and Fig. 3). At both studied soil depths, the populations of Acarina, collembola, nematode, protozoa, bacteria and fungi were declining along the order of forest, ecotone and rangeland covers, respectively. Soil microbial indices (i.e. BR, SIR, MBC and MBN) and enzyme activities (i.e. urease, acid phosphatase, arylsulfatase and invertase) also had higher values in the forest site, especially in 0–10 cm soil depth, compared to ecotone and rangeland covers. However, the stoichiometry of microbial indices (i.e. MBC/MBN, qCO_2, microbial ratio and CAI) showed different reactions in the studied soil depths in relation to the type of regional land covers (Table 3). Furthermore, the studied land covers, litter quality and soil properties could be separated by PCA output. The first and second axes accounted for more than 50% of the explained variance in each of the studied soil depths (38.34 and 12.37% for 0–10 cm soil depth and also 38.58 and 13.14% for 10–20 cm soil depth, respectively). Thus, soils with a better quality of litter (i.e. lower C/N ratio), higher values for organic matter fractions, soil fertility indicators and soil biological activities can be attributed to the forest cover. In contrast, positions of low soil fertility indicators and biota abundance were imposed by forest-rangeland ecotone and rangeland covers (Fig. 4). Based on heat plots of soil functional indicators under different land covers, forest ecosystems created hot spots of soil fertility and biological activities in the study area (Fig. 5).

4. Discussion

4.1. Soil fertility

One of the main components providing ecosystem stability is soil fertility, which shows notable changes under the influence of different land covers and land use systems. In Iran, most areas of mountain ecosystems, which are often considered as fragile and sensitive, are covered by a mosaic of forest and rangeland plant communities. Based on data from this study, the highest contents of soil organic C and N, as well as contents of P and K were found under forest compared to ecotone and rangeland covers (Table 2). In general, litter quality is the main influential factor on soil properties providing favorable conditions for producing increased SOM amounts. Furthermore, the availability of nutrients to microbes depends on compounds derived from dead leaves, roots and returned woody tissue, thus affecting amount and activity of soil microbial biomass and community structure (Chen et al., 2020; Cao et al., 2020). The land cover change affects these processes through variation of litter quantity and quality by different plant species (Bell et al., 2015). This issue can be directly related to the tree cover in the studied land and to different composition of plant species in the overstory and understory (Turbé et al., 2010; Liu et al., 2019). Due to the higher stand density in forest land cover, an increase in litter mass has been expected (Kerdraon et al., 2020). Dominant woody plants in the study area (i.e. *Fagus orientalis, Carpinus betulus*, *Fraxinus excelsior*, *Acer velutinum*, *Crataegus microphylla*, *Berberis integerrima*, *Ribes Uva – crispa* and *Prunus spinosa*) affect the quality of SOM due to the different qualities of their litter. However, according to previous research reports (Kooch and Bayranvand, 2019; Kooch and Noghre, 2020a, b), tree species (compared to shrubs and grasses) have a more effective role in changing soil organic layers (i.e. litters) due to the larger volume of plant debris that enters the soil. In the study area, all tree species are in deciduous form and differ in litter quality. *C. betulus*, *F. excelsior* and *A. velutinum* have a high quality of litter (higher concentration of nutrients with lower levels of C and C/N ratio) compared to *F. orientalis* with a low litter quality (lower concentration of nutrients with higher levels of C and C/N ratio) (Augusto et al., 2002; Kooch et al., 2017a, b; Kooch and Bayranvand, 2019; Majasalmi and Rautiainen, 2020). In addition, Aubert et al. (2003) pointed out that *C. betulus* litters generally

Table 2
Soil physico-chemical properties (mean ± standard error) under different land covers.

Land cover / soil properties	Depth (cm)	Forest	Ecotone	Rangeland	*F test*
Bulk density (g cm^{-3})	0–10	1.19 ± 0.03b	1.30 ± 0.04ab	1.38 ± 0.17a	5.005**
	10–20	1.25 ± 0.02b	1.34 ± 0.04ab	1.45 ± 0.02a	10.812**
Particle density (g cm^{-3})	0–10	2.37 ± 0.10	2.39 ± 0.02	2.40 ± 0.06	0.055 ns
	10–20	2.37 ± 0.05	2.39 ± 0.05	2.41 ± 0.03	0.140 ns
Porosity (%)	0–10	47.15 ± 4.63	45.36 ± 2.30	41.67 ± 2.84	0.672 ns
	10–20	46.83 ± 1.70a	43.20 ± 2.27ab	39.68 ± 1.43b	3.783*
Macro aggregate (%)	0–10	57.66 ± 2.52a	40.13 ± 1.82b	34.13 ± 1.91b	33.446**
	10–20	60.40 ± 3.81a	48.00 ± 3.30b	39.93 ± 2.27b	10.406**
Micro aggregate (%)	0–10	30.00 ± 2.52a	22.00 ± 1.29b	16.33 ± 0.96b	15.688**
	10–20	34.40 ± 3.90a	25.13 ± 2.52ab	18.80 ± 2.93b	6.106**
Aggregate stability (%)	0–10	69.82 ± 1.32a	58.33 ± 3.43b	49.80 ± 2.96b	13.569**
	10–20	73.02 ± 2.20a	61.42 ± 3.28ab	52.63 ± 2.07b	15.741**
Sand (%)	0–10	19.06 ± 0.92b	20.40 ± 1.27b	24.46 ± 0.60a	8.360**
	10–20	16.53 ± 0.89b	18.60 ± 1.38ab	22.20 ± 2.10a	3.459*
Silt (%)	0–10	41.13 ± 1.62b	45.66 ± 1.90ab	46.73 ± 1.07a	3.561*
	10–20	47.20 ± 2.18	45.66 ± 3.12	45.20 ± 3.21	0.132 ns
Clay (%)	0–10	39.80 ± 1.20a	33.93 ± 6.25b	28.80 ± 3.32c	19.015**
	10–20	36.26 ± 1.84	35.73 ± 2.50	32.60 ± 2.25	0.799 ns
Water content (%)	0–10	45.10 ± 2.28a	33.98 ± 1.86b	28.39 ± 1.30b	20.879**
	10–20	49.74 ± 2.60a	38.30 ± 1.95b	32.30 ± 1.42b	18.694**
Temperature (°C)	0–10	18.86 ± 0.76b	22.55 ± 0.75a	25.18 ± 0.97a	14.297**
	10–20	16.80 ± 0.46c	19.91 ± 0.27b	22.54 ± 1.10a	16.374**
pH (1:2.5 H_2O)	0–10	6.98 ± 0.06a	6.45 ± 0.15b	6.11 ± 0.17b	9.440**
	10–20	7.04 ± 0.11a	6.64 ± 0.09b	6.26 ± 0.09c	14.539**
Electrical Conductivity or EC (ds m^{-1})	0–10	0.36 ± 0.01a	0.33 ± 0.01a	0.26 ± 0.02b	7.863**
	10–20	0.39 ± 0.01a	0.36 ± 0.01a	0.30 ± 0.01b	7.811**
Organic C (%)	0–10	3.56 ± 0.22a	2.25 ± 0.24b	1.82 ± 0.90b	14.659**
	10–20	1.97 ± 0.12a	1.38 ± 0.09b	1.30 ± 0.11b	11.038**
C in Macro aggregates (%)	0–10	0.34 ± 0.03a	0.25 ± 0.02b	0.17 ± 0.01b	11.272**
	10–20	0.27 ± 0.01a	0.17 ± 0.01b	0.12 ± 0.01b	16.522**
C in Micro aggregates (%)	0–10	0.19 ± 0.02a	0.15 ± 0.01ab	0.12 ± 0.01b	4.703**
	10–20	0.15 ± 0.01a	0.12 ± 0.01ab	0.09 ± 0.01b	6.609**
C sequestration (Mg ha^{-1})	0–10	63.54 ± 4.17a	43.91 ± 5.24b	37.07 ± 4.32b	8.905**
	10–20	36.83 ± 2.07a	28.19 ± 2.13b	28.42 ± 2.43b	4.915**
Particulate organic C or POC (g kg^{-1})	0–10	3.32 ± 0.25a	2.66 ± 0.20ab	2.00 ± 0.24b	7.907**
	10–20	2.52 ± 0.17a	1.75 ± 0.09b	1.04 ± 0.13c	27.930**
Dissolved organic C or DOC (mg kg^{-1})	0–10	73.17 ± 4.80a	58.42 ± 5.54a	33.67 ± 2.78b	19.415**
	10–20	50.92 ± 2.47a	32.60 ± 1.64b	20.72 ± 1.96c	54.509**
Total N (%)	0–10	0.47 ± 0.04a	0.29 ± 0.01b	0.22 ± 0.01b	19.961**
	10–20	0.37 ± 0.03a	0.26 ± 0.01b	0.17 ± 0.01c	19.303**
N in Macro aggregates (%)	0–10	0.12 ± 0.00a	0.08 ± 0.00b	0.07 ± 0.01b	5.995**
	10–20	0.09 ± 0.01a	0.06 ± 0.00ab	0.04 ± 0.00b	6.474**
N in Micro aggregates (%)	0–10	0.09 ± 0.00a	0.06 ± 0.01b	0.05 ± 0.00b	7.443**
	10–20	0.06 ± 0.01a	0.04 ± 0.00ab	0.02 ± 0.00b	6.748**
N sequestration (Mg ha^{-1})	0–10	8.50 ± 0.78a	5.75 ± 0.38b	4.70 ± 0.39b	12.613**
	10–20	7.07 ± 0.62a	5.34 ± 0.44b	3.74 ± 0.26b	12.745**
N mineralization (mg N kg $soil^{-1}$)	0–10	52.95 ± 2.56a	40.75 ± 1.47b	30.92 ± 1.65c	31.866**
	10–20	38.39 ± 3.04a	25.68 ± 1.68b	18.34 ± 0.73c	24.360**
Ammonium (mg kg^{-1})	0–10	30.65 ± 1.65a	22.70 ± 1.16b	16.37 ± 1.15c	28.193**
	10–20	20.05 ± 0.88a	15.95 ± 0.81b	11.88 ± 0.63c	26.976**
Nitrate (mg kg^{-1})	0–10	44.89 ± 2.19a	32.92 ± 2.27b	25.63 ± 1.62c	22.521**
	10–20	25.10 ± 2.77a	17.78 ± 1.46b	13.66 ± 0.96b	9.3544**
Particulate organic N or PON (g kg^{-1})	0–10	0.53 ± 0.03a	0.33 ± 0.01b	0.24 ± 0.01b	31.243**
	10–20	0.48 ± 0.05a	0.31 ± 0.02b	0.18 ± 0.01c	19.280**
Dissolved organic N or DON (mg kg^{-1})	0–10	38.12 ± 1.09a	26.05 ± 1.60b	14.51 ± 0.85c	92.727**
	10–20	29.47 ± 1.65a	18.46 ± 1.75b	9.98 ± 0.449c	47.432**
C/N ratio	0–10	8.41 ± 1.06	8.49 ± 1.24	8.40 ± 1.04	0.002 ns
	10–20	5.88 ± 0.70b	5.67 ± 0.49ab	7.74 ± 0.52a	3.829*
Available P (mg kg^{-1})	0–10	27.27 ± 2.02a	19.51 ± 1.82b	17.79 ± 1.28b	8.435**
	10–20	18.09 ± 0.87a	15.55 ± 1.06a	12.17 ± 0.70b	11.059**
Available K (mg kg^{-1})	0–10	3.58 ± 20.04a	2.88 ± 17.74b	2.14 ± 13.03c	17.591**
	10–20	2.56 ± 22.48a	1.93 ± 14.46b	1.40 ± 9.05b	12.623**
Available Ca (mg kg^{-1})	0–10	2.44 ± 15.78a	2.00 ± 13.70ab	1.64 ± 16.92b	6.554**
	10–20	1.91 ± 12.76a	1.35 ± 7.52b	1.15 ± 9.86b	14.588**
Available Mg (mg kg^{-1})	0–10	65.33 ± 4.71a	46.20 ± 3.58b	37.40 ± 3.37b	13.164**
	10–20	48.46 ± 5.15a	37.46 ± 3.80ab	25.66 ± 1.67b	8.887**

Different letters in each line indicate significant differences ($p < 0.05$ by Duncan test) between land covers. *P < 0.05, **P < 0.01, ns = not significant.

Table 3
Soil biological properties (mean ± standard error) under different land covers.

Land cover / soil properties	Depth (cm)	Forest	Ecotone	Rangeland	*F test*
Fine root biomass (g m^{-2})	0–10	75.60 ± 4.58a	56.60 ± 4.62b	23.00 ± 1.72c	46.806**
	10–20	41.33 ± 3.82a	29.73 ± 4.08b	18.66 ± 0.82b	12.063**
Epigeic density (n m^{-2})	0–10	1.00 ± 0.05a	0.60 ± 0.04b	0.20 ± 0.01c	6.300**
	10–20	0.06 ± 0.02	0.00 ± 0.00	0.20 ± 0.04	1.000 ns
Epigeic biomass (mg m^{-2})	0–10	16.74 ± 2.85a	9.70 ± 1.59b	2.76 ± 0.47c	8.609**
	10–20	0.50 ± 0.03	0.00 ± 0.00	0.00 ± 0.00	1.000 ns
Anecic density (n m^{-2})	0–10	0.66 ± 0.08	0.53 ± 0.05	0.13 ± 0.04	2.333 ns
	10–20	1.06 ± 0.24	0.93 ± 0.03	0.33 ± 0.04	2.731 ns
Anecic biomass (mg m^{-2})	0–10	8.49 ± 0.33a	5.32 ± 0.14b	1.55 ± 0.16c	3.180*
	10–20	13.04 ± 1.03a	11.26 ± 1.07b	3.06 ± 0.75c	3.917*
Endogeic density (n m^{-2})	0–10	0.33 ± 0.05	0.20 ± 0.04	0.06 ± 0.01	1.050 ns
	10–20	1.40 ± 0.09a	0.93 ± 0.08b	0.33 ± 0.06c	3.927*
Endogeic biomass (mg m^{-2})	0–10	4.09 ± 0.61	1.87 ± 0.31	0.31 ± 0.05	1.943 ns
	10–20	18.88 ± 1.85a	11.06 ± 1.29b	3.80 ± 0.17c	4.622**
Earthworm density (n m^{-2})	0–10	2.00 ± 0.27a	1.33 ± 0.36ab	0.40 ± 0.16b	8.316**
	10–20	2.53 ± 0.42a	1.86 ± 0.54ab	0.66 ± 0.30b	4.745**
Earthworm biomass (mg m^{-2})	0–10	29.33 ± 4.17a	16.90 ± 4.43ab	4.63 ± 1.77b	11.367**
	10–20	32.44 ± 5.68a	22.33 ± 6.50ab	6.86 ± 3.34b	5.795**
Acarina density (n m^{-2})	0–10	6.44 ± 3.10a	4.84 ± 2.01b	2.68 ± 3.38c	42.660**
	10–20	3.71 ± 2.14a	3.04 ± 1.53b	1.20 ± 2.67c	71.766**
Collembola density (n m^{-2})	0–10	2.80 ± 1.49a	1.94 ± 7.10b	1.50 ± 8.79c	37.409**
	10–20	1.91 ± 9.35a	1.58 ± 1.25b	1.09 ± 2.91c	19.765**
Total nematode (in 100 g soil)	0–10	5.49 ± 45.79a	4.00 ± 17.68b	2.93 ± 18.30c	18.152**
	10–20	3.31 ± 26.16a	2.37 ± 43.23ab	1.56 ± 13.32b	8.409**
Protozoa density ($\times 10^2$ g $soil^{-1}$)	0–10	3.75 ± 15.84a	2.94 ± 19.01b	1.95 ± 21.39c	22.820**
	10–20	2.82 ± 27.41a	1.63 ± 20.56b	1.03 ± 6.9b	20.390**
Total bacteria ($\times 10^7$ g $soil^{-1}$)	0–10	7.03 ± 0.55a	5.13 ± 0.53b	3.22 ± 0.32c	15.361**
	10–20	4.54 ± 0.27a	3.02 ± 0.21b	1.45 ± 0.09c	53.664**
Total fungi ($\times 10^7$ g $soil^{-1}$)	0–10	4.05 ± 0.31a	2.75 ± 0.26b	2.25 ± 0.19b	12.645**
	10–20	2.03 ± 0.14a	1.75 ± 0.08ab	1.47 ± 0.15b	4.412**
Basal respiration or BR (mg CO_2 g^{-1} day^{-1})	0–10	0.57 ± 0.03a	0.41 ± 0.03b	0.36 ± 0.03b	12.331**
	10–20	0.30 ± 0.02a	0.21 ± 0.01b	0.12 ± 0.05c	22.116**
Substrate induced respiration or SIR (mg CO_2 g^{-1} day^{-1})	0–10	1.57 ± 0.04a	1.26 ± 0.05b	1.15 ± 0.02b	21.060**
	10–20	1.12 ± 0.02a	1.08 ± 0.01a	0.93 ± 0.03b	12.866**
Microbial biomass C or MBC (mg kg^{-1})	0–10	557.93 ± 36.00a	513.73 ± 19.21a	420.20 ± 34.52b	9.336**
	10–20	348.40 ± 19.22a	261.40 ± 34.41b	186.80 ± 20.11c	16.372**
Microbial biomass N or MBN (mg kg^{-1})	0–10	68.02 ± 1.69a	58.46 ± 8.57b	37.09 ± 3.02c	44.396**
	10–20	36.19 ± 3.07a	26.55 ± 1.77b	15.91 ± 0.92c	22.922**
MBC/MBN	0–10	8.31 ± 0.53b	8.83 ± 0.38b	12.37 ± 1.43a	5.894**
	10–20	10.21 ± 0.82	10.56 ± 1.18	12.00 ± 0.99	0.877 ns
Soil metabolic quotient or qCO_2 (BR:MBC)	0–10	1.07 ± 0.09	0.82 ± 0.07	0.96 ± 0.12	1.676 ns
	10–20	0.93 ± 0.09	0.90 ± 0.12	0.69 ± 0.07	1.655 ns
Microbial ratio (MBC:Organic C)	0–10	1.69 ± 16.95b	2.63 ± 26.32ab	2.85 ± 38.71a	4.578**
	10–20	1.90 ± 20.96	1.94 ± 18.43	1.55 ± 15.58	1.349 ns
Carbon availability index or CAI (BR:SIR)	0–10	0.37 ± 0.02	0.34 ± 0.03	0.32 ± 0.03	0.629 ns
	10–20	0.27 ± 0.02a	0.19 ± 0.01b	0.13 ± 0.01b	13.216**
Urease (μg NH_4^+–N g^{-1} 2 h^{-1})	0–10	30.62 ± 2.24a	24.49 ± 1.62b	14.41 ± 0.83c	23.927**
	10–20	21.98 ± 2.85a	12.23 ± 0.33b	9.91 ± 0.49b	14.416**
Acid phosphatase (μg PNP $g^{-1}h^{-1}$)	0–10	6.08 ± 24.47a	5.12 ± 21.54b	4.38 ± 23.91b	13.358**
	10–20	3.26 ± 15.30a	1.91 ± 10.21b	1.18 ± 9.26c	78.265**
Arylsulfatase (μg PNP $g^{-1}h^{-1}$)	0–10	2.61 ± 29.83a	1.84 ± 17.86b	1.19 ± 3.08b	12.506**
	10–20	1.96 ± 10.84a	1.19 ± 10.31b	98.93 ± 6.77b	29.325**
Invertase (μg Glucose g^{-1} 3 h^{-1})	0–10	3.42 ± 28.53a	2.60 ± 25.72b	1.96 ± 11.39b	10.057**
	10–20	2.56 ± 13.69a	1.18 ± 9.72b	94.60 ± 8.21b	65.919**

Different letters in each line indicate significant differences ($p < 0.05$ by Duncan test) between land covers.*$P < 0.05$, **$P < 0.01$, ns = not significant.

have low lignin:N ratios and fast decomposition rates. Low-quality litter under *F. orientalis* species will release less N than the high-quality litter under *C. betulus*, *F. excelsior* and *A. velutinum* tree species; this is because available nutrients are immobilized more rapidly by microbes decomposing low quality, nutrient-poor litter (Giardina et al., 2001). However, in the present study, the soil organic layer has been studied in entirety, since it was not possible to separate plant debris of different species. According to the results of this study, the litter properties (i.e. mass, C, N and C/N ratio) differed significantly among the land covers under study (Table 1 and Fig. 2).

Accordingly, the higher content of carbon in the forest soil compared to other studied land covers is a result of higher inputs of litter mass (see Table 1), especially into surface layers. The study of Vesterdal et al. (2012) on forest litter dynamics showed a correlation between decomposition rates, nutrient cycling and litter quality with soil chemical properties, especially N concentration, C/N ratios of litter and the mineral soil compartment. According to the explanations mentioned, high density of *C. betulus*, *F. excelsior*, and *A. velutinum* tree species in

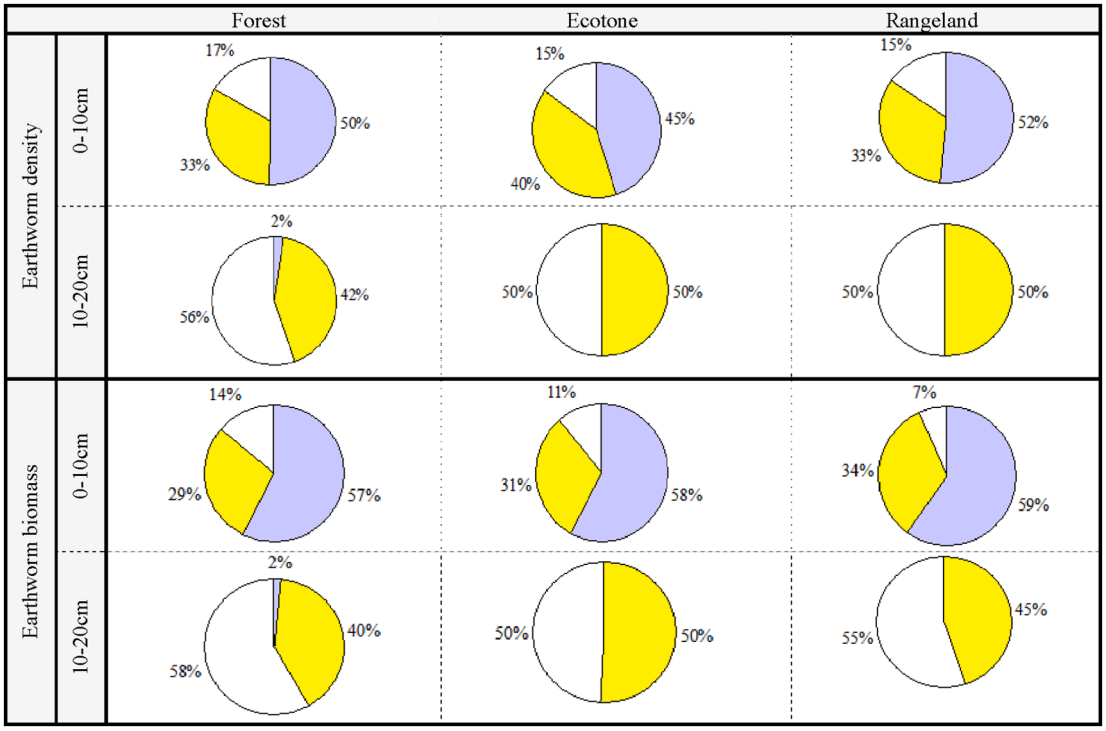

Fig. 3. Contribution of epigeic (blue color), anecic (yellow color) and endogeic (white color) earthworm density and biomass under different land covers. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

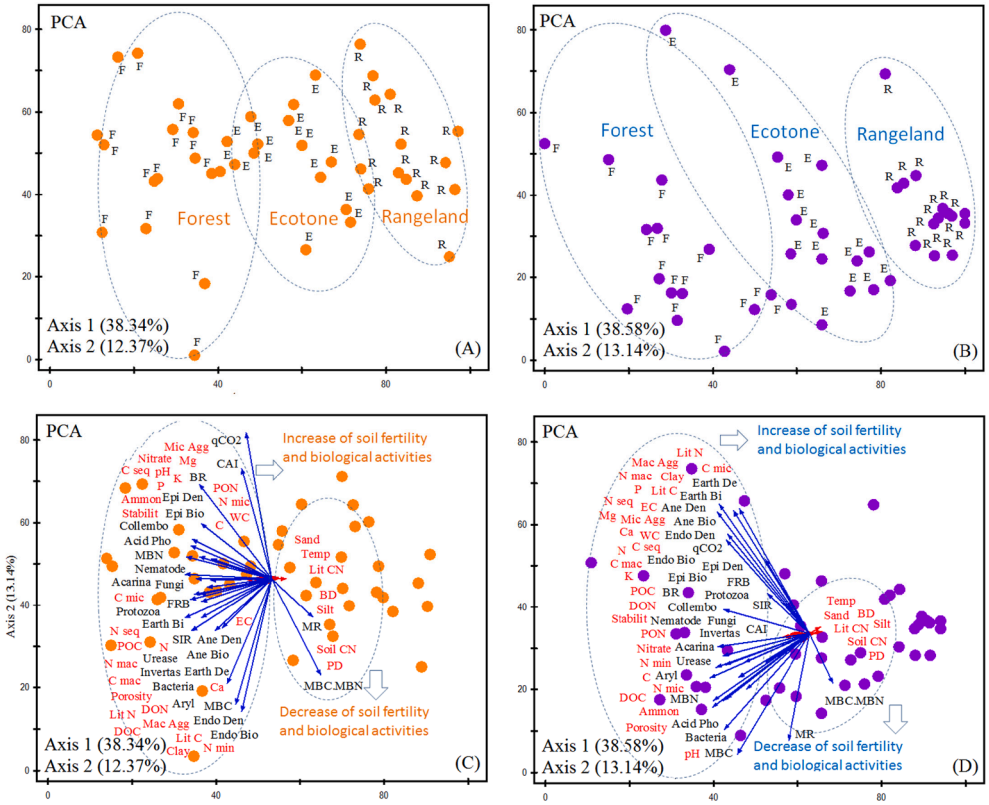

Fig. 4. PCA based on the correlation matrix of the land covers (A: 0–10 cm soil depth; B: 10–20 cm soil depth), and for litter and soil properties (C: 0–10 cm soil depth; D: 10–20 cm soil depth).

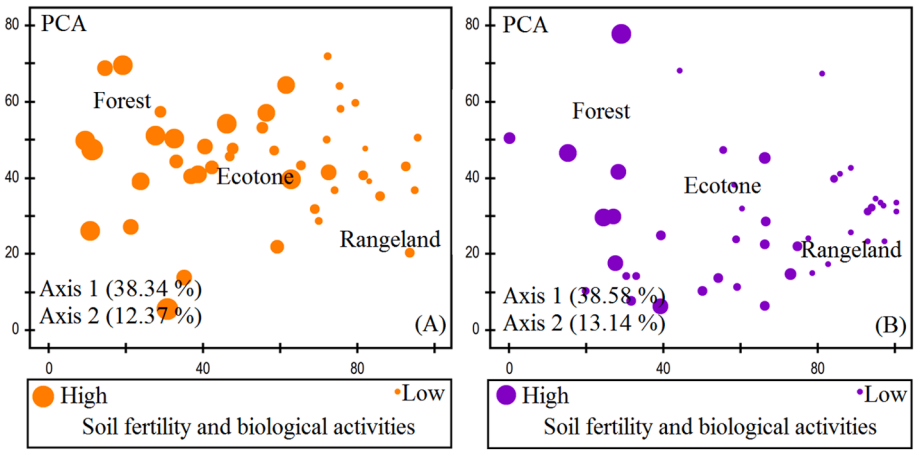

Fig. 5. Heat plots of soil functional indicators (A: 0–10 cm soil depth; B: 10–20 cm soil depth) under different land covers. The size of the dots represents the intensities of soil functions.

forest covers (Table 1) decreased the litter's C/N ratio. Thus, these species played an important role in improving soil microbial activities and nutrient cycles in the mountainous landscape. Parallel to findings of Mendham et al. (2004), our results confirm that different land covers significantly affect labile SOM fractions, including particulate and dissolved organic matter (POM and DOM, respectively) (Table 2). Higher tree density of forest covers increases soil POM (i.e., POC and PON) and DOM (i.e., DOC and DON), as reported by Sleutel et al. (2009). In fact, litter and humus layers are the primary sources of labile SOM (Kalbitz et al., 2000) and the combination of plant residues and organic matter inputs play decisive roles in the amount and concentration of POM and DOM (Laik et al., 2009). As various forms of labile SOM are translocated from the organic layer to the deeper, mineral soil layers, the leaching of fresh litter compounds derived from decomposition processes in the organic layer can, therefore, be primary drivers of change in POM and DOM fractions under different land covers (Kooch and Bayranvand, 2017). The amounts of POM and DOM and the cycling of nutrients can also be affected by the type of canopy structure (Zeng et al., 2014). As the canopy is more open in lands with less (i.e., ecotone) or no tree cover (i.e., range site), the soil leaching rates at these sites are higher (Kooch et al., 2014a), and thus, the contents of soil POM, DOM and nutrients are lower. These findings indicated the decisive role of forest cover in Iran's mountain ecosystems as a result of the increased labile SOM fractions, which are most important for site productivity. In contrast, N mineralization is lower in dry soils because soil microbial activity was limited by water availability (Deenik, 2006). Correspondingly, the lowest N mineralization rate was found in rangeland (Table 2) characterized by drier soil conditions.

Furthermore, this study confirms previous observations that macroaggregates are dynamic in nature and that the size distribution of macroaggregates is influenced by a change of the land cover (Ashagrie, 2004). Because the inputs of specific types of plant biomass, such as litter and fine roots, into the soil are highly variable under different land covers, the resultant aggregate size distribution and fractions of organic C are also different (Liu et al., 2014). Microaggregates have been considered a major factor in the formation of new macroaggregates as a result of the protection of intra-aggregate total C (Aminiyan et al., 2015). Macroaggregates comprise more than 50% of total soil aggregates, which agrees with the observation that macroaggregates were most abundant in forest soils (Li et al., 2016). Litter on the forest floor may provide balanced temperature, and moisture conditions that could increase the activities of earthworms and lead to the production of burrows and casts, thereby increasing the infiltration rate and decreasing runoff which would consequently improve soil aggregation. Additionally, the presence of organic matter at the surface in the form of leaf litter layers and decaying roots exerts significant influence on the physical, chemical and biological properties of soil. Thus, non-humic substances during decomposition are provided which are essential for soil aggregation (Lawal, 2013),enhancing soil macro-aggregation and stability under forest. Furthermore, the formation and stabilization of macroaggregates contributes to the protection and subsequent accumulation of soil C and N (Gama-Rodrigues et al., 2010). In our data, macroaggregates had higher C and N contents than microaggregates under all the different land covers (Table 2). This finding is consistent with a previous study (Aminiyan et al., 2015) where macroaggregates under different vegetation types have been reported to be enriched in C and N compared to microaggregates.

4.2. *Soil biota and enzyme activities*

In this study, the amount of fine root biomass in the forest soils was higher compared to the ecotone and rangeland systems (Table 3). The fully grown, mature trees in the forest ecosystem probably contributed to a comparatively higher fine root biomass (Tamooha et al., 2008). According to Nadelhoffer and Raich (1992), fine root production and above-ground productivity are linked with one another and are affected by similar factors. Dipesh and Schuler (2013) pointed out that younger plant covers have less fine root production than older plants. Fine roots could be easily affected by soil-related factors (Xu et al., 2013), especially the more fertile soils at the forest sites favour fine root production. The high fertility in the upper soil layer may be considered as a vital factor affecting fine roots biomass in forest soils (Wang et al., 2014). This study's results emphasized that the quantity and quality of plant residues are determining the diversity of soil organisms and ecosystem functions. In this regard, Vohland and Schroth (1999) indicated a strong correlation between the amount of plant residues entering the soil and the population density of soil fauna. Accordingly, Liiri et al. (2002) claimed that increasing amounts of organic matter were beneficial to most soil fauna groups. Thus, changes induced by increased input of organic matter and modified soil physicochemical properties following changes in land cover can directly affect soil biota populations and activities (Decäens et al., 2004). In the terrestrial ecosystem, the activity of earthworms is closely related to the quality of litter (Kooch and Bayranvand, 2019). The difference in the quality of the litter provided by the different land covers under study caused significant changes in earthworms' activity (Salehi et al., 2013). Generally, earthworms prefer soils with high contents of nutrients and plant residues with a low C/N ratio (Tucker Serniak, 2017). According to our results, rangeland with a higher C/N ratio in the litter layers had the lowest abundance of several ecological groups of earthworms (Table 3). However, the forest with the lowest C/N ratio provided favourable conditions for the activity of various earthworms. Mariappan (2013) claimed that soil parameters,

namely, pH, EC, organic C, total N, P, K and C/N ratios, greatly influence the abundance of earthworms in various habitats.

Significantly higher densities of epigeic earthworms in 0–10 soil depth can be directly related to the N content of litter. Chaudhuri et al. (2013) indicated that epigeic earthworms feed on organic soil layers and prefer litter rich in N content, whereas anecic earthworms are more active in the mineral soil layers. In general, these species prefer sites with nutrient-rich soils and litter with a low C/N ratio. Earthworms preferentially feed on decomposed plant residues on the soil surface, creating deep vertical holes towards the lower layers, which provide connectivity of surface soil with deeper soil layers (Capelle et al., 2015). Endogeic earthworms had a higher frequency in 0–20 cm depth (Table 3) with a lower C/N ratio and a higher soil pH. The reason could be the capability of endogeic worms to penetrate into deeper soil layers (Uvarov, 2009). Studies by Ayuke et al. (2009) indicated a positive correlation between earthworm groups and N content in forest soils. Such favourable conditions have a positive effect on the density and biomass of earthworms and are considered to be crucial for maintaining soil nutrient supply in continuous plantings at sites in northern Iran. Overall, our results indicated that the type of land cover, from forest to rangeland sites, decreased the activities of soil earthworms, as well as Acarina, collembola, nematodes, protozoa, bacteria and fungi (Table 3). However, high contents of organic matter, a better quality of litter (due to the presence of *C. betulus*, *F. excelsior* and *A. velutinum*), soil properties (higher content of total N and available P, K, Ca, and Mg) and indirect effects by the canopy cover (including amelioration of topsoil temperature and water retention) can play effective roles for the increase of soil biota activities in forest habitats (Bell et al., 2015; Glaser et al., 2018; Phillips et al., 2019).

Soil BR, SIR, MBC, and MBN were higher at the forest sites, followed by the ecotone and lowest in the rangeland (Table 3). High microbial respiration is considered to indicate a high soil quality since more intense microbial respiration is associated with an increased potential microbial activity (Yadav et al., 2017). The high BR in the forest can be attributed to appropriate conditions for microbial activity, including sufficient supply of substrate, especially in the surface soil layers. In the present study, the lowest amount of respiration was observed in rangeland, most probably due to the lower soil water content (Bayranvand et al., 2017; Kooch et al., 2020b). In addition, the results of Singh et al. (2018b) indicated a decreasing trend of soil microbial respiration in rangeland and agricultural lands as compared to a forest, due to the different amounts of organic matter entering the soil. Kooch et al. (2017a) confirmed a negative correlation between the C/N ratio and microbial activities in such systems, indicating the importance of litter quality. According to the results of a study by Forugi Far et al. (2011), the amount of microbial biomass is high in soils with high clay contents. According to Tardy et al. (2014), decreasing contents of soil nutrients can reduce microbial activities, which was consistent with our results. In reverse, Sasongko et al. (2019) indicated that increasing contents of soil nutrients in forest sites could lead to an increase in microbial activities. In fact, the presence of dense vegetation, mostly under tree covers, can lead to the accumulation of organic matter and can stimulate populations and activities of soil microorganisms in the forest floor (Da Silva et al., 2012) since microbial populations are highly dependent upon SOM and overall fertility (Huang et al., 2004). In agreement with previous studies (Ou et al., 2019; Yao et al., 2020), higher enzyme activities in the forest soils (Table 3) can be attributed to higher SOM contents and nutrient concentrations. Urease is considered to play an effective role in urea hydrolysis to carbon dioxide and ammonia and possibly contributes to an increase in soil pH (Martinez-Salgado et al., 2010). The higher contents of soil organic C, N and P, in addition to increased microbial activity in the soil, promote the production and the absorption of enzyme molecules on the surfaces of organic colloids (Kooch et al., 2020b). Thus, it can be assumed that the activity of extracellular enzymes in such systems is mostly stabilized. Correspondingly, acid phosphatase as an extracellular enzyme produced by microorganisms, plant roots, and earthworms is in direct contact with organic matter and controlled by soil water content (Amador et al., 1997). In general, reduced contents of soil organic C and its availability reduce soil enzymatic activity, which is a direct consequence of microbial biomass reduction following a change in soil properties (Hu and Cao, 2006). Arylsulfatase has a main role in the decomposition of S-containing fractions of organic matter and is also known to be sensitive to soil management (Ndiaye et al., 2000). Ling et al. (2014) pointed out that the increase of soil clay content can enhance the activity of arylsulfatase. In this regard, it can be noted that an increased clay accumulation in the soil of forest habitats as in our study area plays a significant role in increasing the activity of this enzyme. Invertase enzyme is decisive for converting sucrose to glucose and ATP fructose. The increased activity of this enzyme in forest soils can be explained by improved fertility indicators under this land cover (Guo et al., 2011). Correspondingly, Zeng et al. (2009) showed a positive correlation between organic carbon, total N, P, and invertase activity. Thus, especially the changes in SOM contents can be considered as the main reason for differences in soil invertase activity among the studied sites. Furthermore, all the differences described above were supported by PCA analysis (Fig. 4), confirming that soil functions were enhanced under the mountain forest ecosystems.

5. Conclusions

The types of land cover (i.e. forest, forest-rangeland, and rangeland) strongly control the properties of soil organic and soil mineral layers at a mountain forest-rangeland mosaic of northern Iran. Most of the litter and soil properties (especially in 0–10 cm compared to 10–20 cm soil depth) differed significantly among the land covers, with mostly the highest values of measured parameters in the forest ecosystem. Confirming our hypothesis, soil biological activity and fertility indices, i.e. SOM and nutrient contents, were enhanced under forest. Although not all parameters followed precisely the same pattern, our study confirms basic principles and dependencies of soil-biological functioning and the impact of land cover changes. In addition, our findings indicate that soil fertility indicators and soil biota abundance and vitality are enhanced under forest ecosystems. This relation is of fundamental importance as it affects the biogeochemistry of nutrients and the fate of organic C compounds and total N contents in vulnerable mountain ecosystems. Based on our findings, soil functional indicators decreased ranked in the order of forest > forest-rangeland ecotone > rangeland, which can be assigned to the lower density of trees, as well as to decreasing litter mass and quality. In this regard, forest covers can be considered as hotspots for nutrient cycles in mountain forest-rangeland systems. It can be concluded that tree cover gains a prominent role in promoting soil functions, which should be considered in the restoration of degraded mountain-rangeland ecosystems.

CRediT authorship contribution statement

Yahya Kooch: Supervision, Writing - review & editing, Software. **Neda Ghorbanzadeh:** Writing - original draft. **Stephan Wirth:** Writing - review & editing. **Agata Novara:** Writing - review & editing. **Atefeh Shah Piri:** Investigation.

Declaration of Competing Interest

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

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