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ORIGINAL PAPER

Soil functional indicators in mixed beech forests are clearly species-specific

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Abstract Beech stands are considered part of the ancient forest ecosystems in the northern hemisphere. In mixed stands in beach forest ecosystems, the type of associated tree species can significantly affect soil functions, but their influence on microbial activity, nutrient cycling and belowground properties is unknown. Here, we considered forest patches in northern Iran that are dominated by different tree species: *Fagus orientalis* Lipsky, *Quercus castaneifolia* C. A. Mey., *Pterocarya fraxinifolia* (Lam.), *Tilia begonifolia* Stev., *Zelkova carpinifolia* Dippe, *Acer cappadocicum* Gled, *Acer velutinum* Boiss., *Fraxinus excelsior* L., *Carpinus betulus* L., and *Alnus subcordata* C. A. Mey. For each forest patch–tree species, litter and soil samples (25 × 25 × 10 cm, 100 of each) were analyzed for determine soil and litter properties and their relationship with tree species. The litter decomposition rate during a 1-year experiment was also determined. A PCA showed a clear difference between selected litter and soil characteristics among tree species. *F. orientalis*, *Q. castaneifolia*, *P. fraxinifolia*, *T. begonifolia*, *Z. carpinifolia*, *A. cappadocicum,* and *A. velutinum* enhanced soil microbial biomass of carbon, whereas patches with *F. excelsior*, *C. betulus* and *A. subcordata* had faster litter decomposition and enhanced biotic activities and C and N dynamics. Thus, soil function indicators were species-specific in the mixed beech forest. *A. subcordata* (a N-fixing species), *C. betulus* and *F. excelsior* were main drivers of microbial activities related to nutrient cycling in the old-growth beech forest.

Keywords Old-growth forest · Deciduous tree species · Soil fertility · Microbial activities · Carbon and nitrogen cycle

Introduction

Hyrcanian forests are unique forests that have maintained their remnants from the last ice age (Sagheb-Talebi et al. 2014). The Caspian vegetation region on the shores of the Caspian Sea, form a green belt, 110 km wide and 800 km long, of temperate deciduous trees. This ecoregion receives 600 to 2000 mm of rainfall per year. Beech forests are part of the ancient, valuable forest ecosystems in the northern hemisphere because the beech trees have been created by natural regeneration and belong to the third geological period. Based on published statistics, this species alone comprises 23.63% of the number of forests in northern Iran and 29.96% of the volume (Sefidi et al. 2016; Azaryan et al. 2021). In mixed forests, the composition of a mature stand is determined by various dynamic processes that influence the establishing and developing of a stand (Levula et al. 2003). The overstorey composition of trees also significantly affects

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litter quality and topsoil properties (Kemner et al. 2021; Kim et al. 2021; Wang et al. 2021; Qin and Wang 2022).

Soil directly contributes to various ecosystem functions and services including net primary production, climate regulation, nutrient cycle and carbon sequestration (Singh et al. 2018; Parhizkar et al. 2021). Soil is a finite resource because it develops over very long periods of time. On the human timescale, soil can be considered a non-renewable natural resource. Plant community composition at the ground level alters soil processes and functions through a variety of factors including microclimate change, bedding and root secretions, and habitat or resource provisions for soil microbial communities (Lin et al. 2021). Therefore, understanding the impact of plant communities on multiple soil functions is of great value.

The fertility of forest soils is seen in its ability to provide nutrients for forest trees (Nguemezi et al. 2020). The forest canopy cover can affect soil fertility as an important part of forest sites. Amount and quality of litter (Majasalmi and Rautiainen 2020), through-fall and stem flow, rooting patterns, microbial activities and forest floor processes are typically affected by soil fertility, directly or indirectly (de Vries et al. 2021), and result in different levels of forest productivity (Majasalmi and Rautiainen 2020).

Soil quality is promoted through ongoing organic material input and decomposability via microbial activities that generate soil fertility hotspots. These processes lead to an increase in soil microbial diversity and respiration under the tree canopy (Wang et al. 2022) and create a microhabitat for increasing biodiversity (Catenazzi and Donnelly 2007; Rathore et al. 2022). These hotspots of fertility have been hypothesized to form through both biotic and abiotic processes (i.e., litterfall and decomposition) (Charley and West 1977), atmospheric deposition (Fenn et al. 2003) and microbial activity (Žifčáková et al. 2016; Wang et al. 2022) that make feedback loops and fortify high nutrient accumulation (Schlesinger et al. 1996). The attributes of the fertility hotspots will also differ based on factors such leaf quality, species composition and the ecosystem (Alameda et al. 2012). For instance, the canopy cover of trees provides a suitable environment for microbial colonization (Ortiz et al. 2022) and activity by reducing solar radiation, temperature and soil water evaporation (Berry et al. 2013). Changes in forest tree composition due to global climate change also obviously affect ecosystem performance (Mueller et al. 2012). Hence, the impact of trees on biogeochemical cycles has widely been studied, but the results have been inconsistent (Wang et al. 2018, 2021; De Andres 2019).

Beech species can accelerate soil acidification and thus leaching of nutrients, decreasing topsoil fertility. Therefore, the presence of other tree species in beech forest stands may help improve soil characteristics and nutrient cycling (Kooch 2012). In the forests of northern Iran, the contributions of the other tree species that grow with the old-growth beech trees to microbial activity, nutrient cycles, and belowground properties have not been considered yet. Here, we thus assessed the effect of mixed forest stands in composition with different tree species on soil functional indicators in organic and mineral layers. We hypothesized that the soil fertility and microbial hotspots would predominantly correlate with the tree species and litter properties. Our findings on soil functions will serve as a base to optimize forest structure and improve ecosystem services.

Materials and methods

Study area

The Golband region (study site), consisting of 36,855 ha in northern Iran (Fig. 1A), is characterized by uneven-aged stands (i.e., tree diameters between 10–150 cm). The Golband watershed lies between 51°17′ E to 51°46′ E, 36°27’ N to 36°35 N. The mean altitude is 2000 m above sea level, mean total rainfall is 900 mm, and mean annual temperature is 11 °C. The slope of the region varies between 5 and 70%. According to the American USDA Soil Taxonomy classification (Hughes et al. 2017), the soil of the region is Alfisols. The area consists of mixed beech forest dominated by oriental beech (*Fagus orientalis* Lipsky), wingnut (*Pterocarya fraxinifolia* Lam.), oak (*Quercus castaneifolia* C. A. Mey.), lime tree (*Tilia begonifolia* Stev.), maple tree (*Acer velutinum* Boiss.), Caucasian zelkova (*Zelkova carpinifolia* Dippe), ash (*Fraxinus excelsior* L.), hornbeam (*Carpinus betulus* L.), Cappadocian maple (*Acer cappadocicum* Gled), and Caucasian alder (*Alnus subcordata* C.A. Mey.). Less-frequent species (< 10%) are elm (*Ulmus glabra* Huds.), wild cherry (*Prunus avium* L.), and wild service tree (*Sorbus torminalis* Crantz). Herbaceous species such as *Asperula odorata* L., *Hypericum androsaemum* L., *Euphorbia amygdaloides* L., and *Polystichum* sp. cover more than 85% of the forest floors (Anonymous 2018).

Sampling design and laboratory measurements

Patches (hereafter plots) of dominant tree species were identified in the study area. In total, 100 plots (10 replications for each tree species) were considered (see Fig. 1A, B). Each plot includes an individual tree (DBH about 50 cm) of the dominant tree species that are always surrounded by similar tree species. All plots were located between 1000 and 1100 m a.s.l., had a similar aspect (north), slope class (12%–16%), forest management (preserved areas and intact without harvesting) and were at least 1000 m from each other. In September, a litterbag experiment was set up to assess litter decomposition in the field (Wieder and Lang

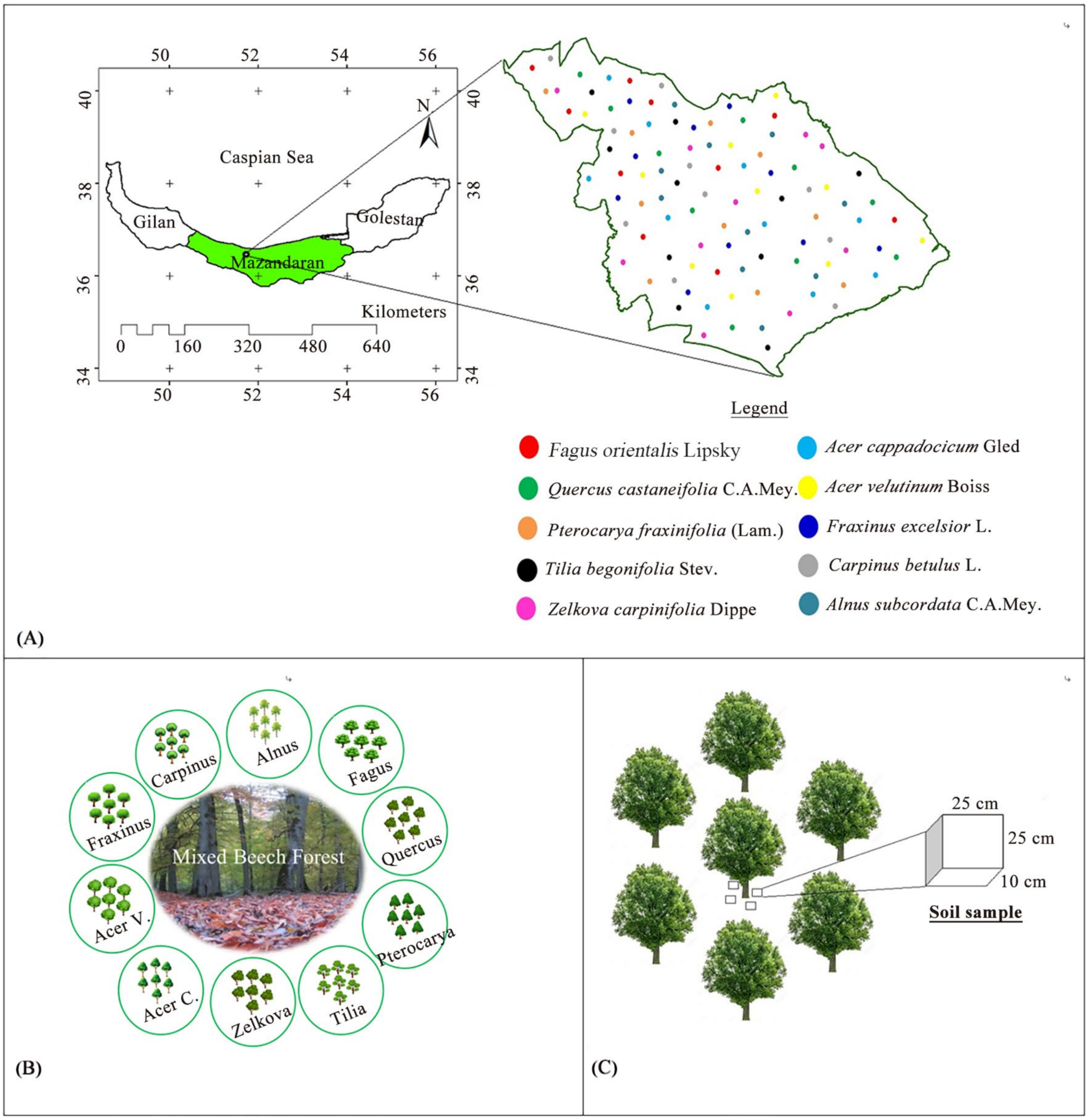

Fig. 1 Location of the study area (Golband Forest) in the Mazandaran Province, northern Iran, with 100 studied patches (plots) of dominated tree species (A, B). Soil samples (0–10 cm depth) were taken in a 25 × 25 cm area under each canopy cover (C). Note: Fagus: *Fagus orientalis* Lipsky, Quercus: *Quercus castaneifolia* C. A. Mey., Pterocarya: *Pterocarya fraxinifolia* Lam., Tilia: *Tilia begonifolia* Stev., Zelkova: *Zelkova carpinifolia* Dippe, Acer C.: *Acer cappadocicum* Gled, Acer V.: *Acer velutinum* Boiss., Fraxinus: *Fraxinus excelsior* L., Carpinus: *Carpinus betulus* L., and Alnus: *Alnus subcordata* C.A. Mey

1982). Four litter traps (1 m × 1 m) were placed in each plot at the four sides of the studied tree species at a distance of one-third of the crown radius from the stem, with 40 bags of laboratory-dried litter from each species within each plot. In August, soil samples (25 cm × 25 cm × 10 cm; see Fig. 1C) were taken at the site of each litter trap. In total, 400 (i.e., 10 tree species × 10 replicated plots × 4 samples) litter and soil samples were gathered, the litter and soil samples within each plot ($n = 4$) were bulked separately to yield one composite litter and one composite soil sample for each plot (total: 100 litter and 100 soil samples) for analysis. In addition, litter (forest floor or O-horizon) thickness was measured at the litter trap sites (Dechoum et al. 2015).

An elemental analyzer (Fisons EA1108, Milan, Italy) was used to measure total C in samples and nutrient components in litter (Parsapour et al. 2018). Bulk and particle densities (BD and PD, respectively) of soils were determined with clod (Plaster 1985) and pycnometer (Blake and Hartge 1986) methods. Soil porosity was computed as 1 − (BD / PD) (Pires et al. 2014). The distribution of aggregate size (0.053 and 0.25 mm for microaggregates and 0.25 and 0.50 mm for macroaggregates) was determined as described by Cambardella and Elliott (1992). Aggregate stability and texture of soils were determined using the Yoder and Bouyoucos methods (Bouyoucos 1962; 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. Soil organic C and total N were determined using the Walkley–Black and Kjeldahl methods (see Allison 1975; Bremner and Mulvaney 1982). C and N sequestrations in this study were computed as C or N sequestration = C or N content × Soil depth × BD × 0.1, where 0.1 is a conversion factor. Particulate organic C and particulate organic N (POC and PON) were measured using physical sundering (Cambardella and Elliot 1992). Dissolved organic C and dissolved organic N (DOC and DON) was analyzed using the procedure of Jones and Willett (2006). Soil extraction solutions were used for the colorimetric determination of NH_4^+ (at 645 nm) and NO_3^- (at 420 nm) concentrations (Li et al. 2014). Soil available K, Ca, and Mg were measured using atomic absorption spectrophotometry (Bower et al. 1952) and available P using spectrophotometry (Homer and Pratt 1961). The separated fine roots (i.e., diameter < 2 mm) were dried at 70 °C, then weighed (Neatrour et al. 2005).

Soil water content and temperature (as soil climate variables) and biota were measured in summer (15 August) and fall (15 November). Soil water content was measured by drying soil samples at 105 °C for 24 h. Soil temperature was measured using a digital probe-thermometer sensor (TFA Dostmann, Model 30.1048, Ottersberg, Germany) in the field (Zancan et al. 2006). Before drying earthworms were picked from the soil samples and categorized into ecological classes based on exterior specifications (Kooch et al. 2014). Extraction and Acari and Collembola counts were obtained using the Berless-Tulgreen funnel method; to obtain mesofauna counts, a certain amount of soil was weighed and placed in the Berless-Tulgreen funnel; after 4 days, mesofauna were collected in 0.5% v/v formalin and counted) (Page 1986). Nematodes were extracted using tray (Whitehead and Hemming 1965) and centrifugation (Niknam 1991) methods, then fixed and transferred to glycerin. Densities of soil protozoa were determined using an extraction method and light microscopy (Mayzlish and Steinberger 2004). Bacterial and fungal counts on nutrient agar and potato dextrose agar were obtained by serial dilution and plate count methods (Kooch et al. 2020). Soil basal respiration (BR) was measured using CO_2 emission method, and CO_2 absorption was measured in an alkaline solution (Alef 1995). Substrate-induced respiration (SIR) (based on CO_2 production; Anderson and Domsch 1990) and microbial biomass C, N and P (i.e., MBC, MBN and MBP) were measured using a fumigation-extraction method (Brookes et al. 1985). The metabolic quotient (qCO_2), microbial ratio or entropy and C availability index were calculated based on the stoichiometry of soil organic C, respiration and microbial biomass C (Insam and Domsch 1988; Anderson and Domsch 1990; Cheng et al. 1996). Soil enzyme activities were calculated using the Schinner and von Mersi (1990) protocol. Soil C and net N mineralization (C_{min} and N_{min}) were measured as described by Raiesi (2012a, b a, b) controlled laboratory conditions.

Statistical analyses

Normality of data was assessed using a Kolmogorov–Smirnov test and homogeneity of variance was checked using Levene's test. One-way analysis of variance (ANOVA) was used to compare litter and soil properties among different tree species; means that differed significantly were analyzed using Duncan's test ($P \leq 0.05$). All analyses were done using SPSS (version 20; IBM, Armonk, NY, USA). In addition, principal component analysis (PCA using PC-Ord version 5.0; Mc Cune and Mefford 1999) was performed to identify any patterns in the changes in litter and soil characteristics between different tree species.

Results

Litter properties

Litter chemistry differed significantly among the various tree species. The contents of NPK, Mg and Ca in the *A. subcordata* litter was highest. Litter thickness was greatest under *F. orientalis* (≈ *Q. castaneifolia*). Litter C was significantly higher under *F. orientalis*, *Q. castaneifolia* and *P. fraxinifolia*, which had the same functional traits. In addition, *F. orientalis* had the highest litter C/N ratio (Table 1). The highest litter decomposition rates after 360 days were found under *Alnus*, but the trend in litter decomposition was the same for all tree species over the experiment. The ANOVA results revealed that significant differences in litter decomposition were due to litter types of the various tree species. At all sites, the litter lost half of its initial mass during the incubation period (Fig. 2 and Table S1).

Soil properties

All soil properties, except soil density, the amount of sand and C sequestration, were affected by the tree species. The most available P and K was found under *Alnus*, whereas litter under *A. subcordata* ≈ *C. betulus* species had the most available Ca and Mg. Soil organic C, POC and DOC were significantly higher at sites having *F. orientalis* and *Q. castaneifolia* than at the other sites, but soil C/N ratio was highest under *F. orientalis*, *Q. castaneifolia* and *P. fraxinifolia*. Fine

Table 1 Mean (±SE; n = 10) of litter properties under different tree species

Tree species	Litter properties							
	Thickness (cm)	C (%)	N (%)	C/N ratio	P (%)	K (%)	Ca (%)	Mg (%)
Fagus	17.36 ± 0.57a	60.32 ± 4.13a	0.90 ± 0.05d	69.00 ± 5.84a	2.41 ± 0.17d	1.32 ± 0.08c	0.92 ± 0.05e	0.34 ± 0.03 g
Quercus	17.14 ± 0.86a	59.13 ± 4.73a	0.91 ± 0.95d	66.42 ± 6.33ab	2.43 ± 0.21d	1.37 ± 0.08c	0.94 ± 0.06e	0.39 ± 0.05 fg
Pterocarya	14.30 ± 0.61b	55.75 ± 1.73a	0.98 ± 0.02d	56.86 ± 2.59b	2.88 ± 0.22d	1.49 ± 0.14c	0.95 ± 0.06e	0.46 ± 0.02efg
Tilia	10.84 ± 0.81c	46.22 ± 2.59b	1.18 ± 0.03 cd	30.71 ± 2.32c	3.66 ± 0.18c	1.58 ± 0.08c	1.31 ± 0.09de	0.51 ± 0.05def
Zelkova	10.70 ± 0.81c	36.06 ± 3.73b	1.25 ± 0.04 cd	29.52 ± 3.69c	3.83 ± 0.14bc	1.94 ± 0.18b	1.57 ± 0.08 cd	0.61 ± 0.06cde
Acer C	10.47 ± 0.69c	35.08 ± 2.19b	1.42 ± 0.15c	27.17 ± 3.20 cd	3.85 ± 0.11bc	2.00 ± 0.12b	1.70 ± 0.11 cd	0.63 ± 0.05bcd
Acer V	10.16 ± 0.74c	34.85 ± 2.71b	1.40 ± 0.10c	26.45 ± 3.18cde	4.04 ± 0.13abc	2.09 ± 0.12ab	1.90 ± 0.24bc	0.69 ± 0.07abc
Fraxinus	9.98 ± 0.40c	29.99 ± 2.51b	1.96 ± 0.17b	16.45 ± 1.99def	4.16 ± 0.28abc	2.11 ± 0.09ab	2.16 ± 0.19b	0.73 ± 0.04abc
Carpinus	8.98 ± 0.60c	29.61 ± 2.62b	2.09 ± 0.16b	15.85 ± 3.21ef	4.24 ± 0.12ab	2.19 ± 0.05ab	2.27 ± 0.15b	0.79 ± 0.05ab
Alnus	6.70 ± 0.72d	26.47 ± 1.78b	2.99 ± 0.28a	9.63 ± 1.10f	4.58 ± 0.10a	2.43 ± 0.20a	3.01 ± 0.21a	0.85 ± 0.06a
Summary ANOVA results								
F test	25.017	18.145	23.867	33.952	18.374	8.916	22.416	9.636
P value	0	0	0	0	0	0	0	0

Different letters in each line indicate significant differences ($P < 0.05$ by Duncan test) between tree species. Bold and italic values indicate significant statistical differences. Fagus: *Fagus orientalis* Lipsky, Quercus: *Quercus castaneifolia* C. A. Mey., Pterocarya: *Pterocarya fraxinifolia* Lam., Tilia: *Tilia begonifolia* Stev., Zelkova: *Zelkova carpinifolia* Dippe, Acer C.: *Acer cappadocicum* Gled, Acer V.: *Acer velutinum* Boiss., Fraxinus: *Fraxinus excelsior* L., Carpinus: *Carpinus betulus* L., and Alnus: *Alnus subcordata* C.A. Mey

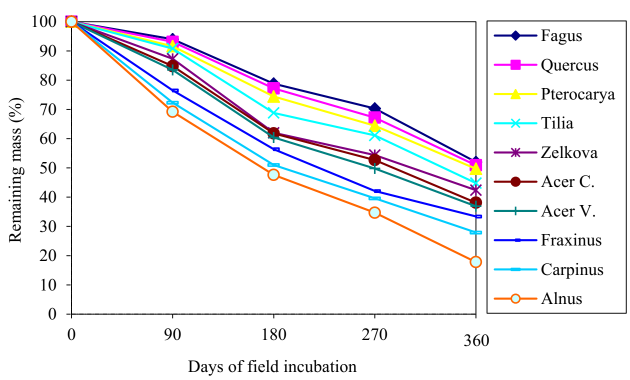

Fig. 2 Litter mass remaining (kg ha^{-1}) under different tree species. Data in details are presented in Appendix 1. Note: Fagus: *Fagus orientalis* Lipsky, Quercus: *Quercus castaneifolia* C. A. Mey., Pterocarya: *Pterocarya fraxinifolia* Lam., Tilia: *Tilia begonifolia* Stev., Zelkova: *Zelkova carpinifolia* Dippe, Acer C.: *Acer cappadocicum* Gled, Acer V.: *Acer velutinum* Boiss., Fraxinus: *Fraxinus excelsior* L., Carpinus: *Carpinus betulus* L., and Alnus: *Alnus subcordata* C.A. Mey

root biomass was highest in the topsoil of *A. subcordata* ≈ *C. betulus* and the lowest under *F. orientalis* (Table 2). In fact, these two species had similar values for some soil characteristics. Overall, the various tree species affected the soil microclimate and biotic characteristics (Table 3). In addition, soil biota population differed significantly among the tree species, and seasonal changes in all traits evaluated were similar among the tree species. The soil water content was higher under *F. orientalis* ≈ *Q. castaneifolia*, with maximum values during the autumn. In the summer, soil temperatures were highest in *A. subcordata* ≈ *C. betulus* ≈ *F. excelsior* stands (Table 3), which have the same function as other species. Except for soil bacteria and fungi, which were more abundant in the summer, the activities of other soil biotas were higher in the autumn when an ideal soil climate (i.e., higher soil water content and lower soil temperature) prevailed for most of the studied soil organisms (Table 3, Fig. 3).

The different tree species exerted significant effects due to the habitat types on the activity of ecological groups of earthworms. Maximum activity was observed under *A. subcordata* trees. The densities of soil acarina were highest under *A. subcordata* ≈ *C. betulus* ≈ *F. excelsior*, whereas greater densities of collembola, nematode and bacteria were observed under *A. subcordata* species. Moreover, higher densities of protozoa were detected under *A. subcordata* and *C. betulus* and more fungi under *A. subcordata* ≈ *C. betulus* ≈ *F. excelsior* ≈ *A. velutinum*. (Table 3). The effects of trees on changes in soil microbial and enzymatic activities were significant (Table 4). Soil BR, SIR, MBN, MBP, qCO_2, urease and acid phosphatase activities were highest under *A. subcordata*. Arylsulfatase activity was highest under *A. subcordata* ≈ *C. betulus* and invertase activity highest under *A. subcordata* ≈ *C. betulus* ≈ *F. excelsior*. The soil under

Table 2 Mean (± SE; n = 10) of soil properties under different tree species

Tree species	Soil properties						
	Bulk density (g cm^{-3})	Particle density (g cm^{-3})	Porosity (%)	Macro aggregate (%)	Micro aggregate (%)	Aggregate stability (%)	Sand (%)
Fagus	1.18 ± 0.03f	2.44 ± 0.07	50.71 ± 2.48a	31.60 ± 2.97e	18.00 ± 1.01d	43.00 ± 1.98c	32.10 ± 3.31
Quercus	1.19 ± 0.05f	2.44 ± 0.10	50.41 ± 2.65a	32.20 ± 2.49e	20.50 ± 2.79 cd	44.14 ± 4.35c	30.00 ± 1.89
Pterocarya	1.23 ± 0.06ef	2.45 ± 0.10	48.74 ± 3.55ab	35.20 ± 1.38e	28.90 ± 3.88bc	49.06 ± 4.13c	30.20 ± 2.01
Tilia	1.37 ± 0.05de	2.46 ± 0.08	43.71 ± 2.75abc	38.00 ± 4.00de	31.90 ± 3.33ab	61.90 ± 5.66b	29.50 ± 1.79
Zelkova	1.39 ± 0.05 cd	2.46 ± 0.09	42.54 ± 2.71abc	39.60 ± 3.01cde	32.40 ± 3.60ab	63.50 ± 5.46b	29.00 ± 3.82
Acer C	1.44 ± 0.03bcd	2.47 ± 0.09	40.65 ± 3.06bc	46.00 ± 1.52 cd	33.30 ± 4.79ab	63.79 ± 3.43b	28.70 ± 2.21
Acer V	1.46 ± 0.02bcd	2.47 ± 0.10	39.73 ± 3.57bc	48.10 ± 2.68bc	33.60 ± 4.53ab	64.79 ± 4.02ab	27.70 ± 3.41
Fraxinus	1.54 ± 0.04abc	2.49 ± 0.08	37.51 ± 3.06c	56.00 ± 3.77ab	35.60 ± 2.00ab	73.04 ± 2.32ab	28.10 ± 4.31
Carpinus	1.58 ± 0.05ab	2.49 ± 0.08	36.23 ± 1.69c	58.10 ± 5.30a	37.20 ± 3.34ab	73.34 ± 1.27ab	26.90 ± 1.49
Alnus	1.61 ± 0.05a	2.51 ± 0.07	34.65 ± 4.32c	62.30 ± 3.17a	40.60 ± 2.30a	75.76 ± 1.75a	25.20 ± 2.66
Summary ANOVA results							
F test	10.215	0.069	3.633	11.94	4.461	10.272	0.453
P value	0	1	0.001	0	0	0	0.902

Tree species	Soil preparation								
	Silt (%)	Clay (%)	pH (1:2.5 H_2O)	Electrical conductivity (ds m^{-1})	Organic C (%)	C in macro aggregates (%)	C in micro aggregates (%)	C sequestration (Mg ha^{-1})	Particulate organic C (g kg^{-1})
Fagus	44.70 ± 3.99a	23.20 ± 2.81d	5.52 ± 0.11d	0.17 ± 0.01d	6.73 ± 0.50a	0.56 ± 0.04a	0.52 ± 0.05a	79.60 ± 5.63	5.07 ± 0.29a
Quercus	45.60 ± 3.43a	24.40 ± 2.97 cd	5.78 ± 0.10 cd	0.17 ± 0.01d	6.70 ± 0.51a	0.55 ± 0.03ab	0.49 ± 0.02ab	79.33 ± 6.34	5.04 ± 0.15a
Pterocarya	43.60 ± 2.74a	26.20 ± 1.20bcd	5.91 ± 0.10bc	0.19 ± 0.01d	6.36 ± 0.59ab	0.51 ± 0.03abc	0.48 ± 0.04ab	79.10 ± 8.37	4.57 ± 0.30ab
Tilia	40.60 ± 2.27ab	29.90 ± 1.65bcd	5.98 ± 0.17bc	0.28 ± 0.02c	5.84 ± 0.37ab	0.49 ± 0.04abc	0.39 ± 0.02bc	80.07 ± 5.62	4.47 ± 0.44ab
Zelkova	40.20 ± 5.15ab	30.80 ± 2.04bc	6.26 ± 0.10b	0.30 ± 0.02bc	5.58 ± 0.37abc	0.45 ± 0.04abc	0.38 ± 0.03bc	77.84 ± 5.54	3.96 ± 0.49abc
Acer C	39.50 ± 2.44ab	31.80 ± 1.78b	6.87 ± 0.21a	0.30 ± 0.01bc	5.39 ± 0.32bc	0.43 ± 0.06abc	0.36 ± 0.04 cd	78.43 ± 5.93	3.73 ± 0.33bc
Acer V	39.90 ± 4.57ab	32.40 ± 1.64b	6.97 ± 0.08a	0.32 ± 0.02abc	5.08 ± 0.52bcd	0.40 ± 0.05bc	0.33 ± 0.02 cd	75.34 ± 9.28	3.62 ± 0.31bcd
Fraxinus	31.40 ± 4.43b	40.50 ± 2.91a	7.01 ± 0.11a	0.34 ± 0.00abc	4.35 ± 0.28 cd	0.39 ± 0.05c	0.30 ± 0.02cde	67.59 ± 5.44	3.12 ± 0.34 cd
Carpinus	30.30 ± 3.37b	42.80 ± 2.65a	7.08 ± 0.14a	0.35 ± 0.00abc	4.11 ± 0.021d	0.38 ± 0.05c	0.26 ± 0.02de	65.41 ± 4.20	2.93 ± 0.37 cd
Alnus	30.30 ± 3.16b	44.50 ± 1.30a	7.16 ± 0.07a	0.37 ± 0.01a	3.95 ± 0.17d	0.36 ± 0.03c	0.20 ± 0.03e	64.23 ± 4.31	2.59 ± 0.36d
Summary ANOVA results									
F test	2.549	11.867	23.5	15.558	6.256	2.332	8.044	1.032	6.034
P value	0.012	0	0	0	0	0.021	0	0.421	0

Tree species	Soil preparation						
	Dissolved organic C (mg kg^{-1})	Total N (%)	N in macro aggregates (%)	N in micro aggregates (%)	N sequestration (Mg ha^{-1})	Ammonium (mg kg^{-1})	Nitrate (mg kg^{-1})
Fagus	81.54 ± 3.75a	0.16 ± 0.01e	0.10 ± 0.01c	0.05 ± 0.01c	1.98 ± 0.13f	15.42 ± 1.33e	26.23 ± 3.31d
Quercus	79.55 ± 5.70a	0.17 ± 0.01de	0.10 ± 0.02c	0.06 ± 0.02c	2.09 ± 0.22f	17.33 ± 1.65de	27.24 ± 2.67d
Pterocarya	75.62 ± 4.49ab	0.19 ± 0.02cde	0.12 ± 0.03bc	0.09 ± 0.02bc	2.34 ± 0.29ef	17.66 ± 1.80de	28.16 ± 2.19d
Tilia	71.11 ± 6.24ab	0.24 ± 0.02cde	0.13 ± 0.02bc	0.11 ± 0.03bc	3.38 ± 0.45def	25.75 ± 2.72 cd	30.26 ± 2.16 cd
Zelkova	6.52 ± 8.14ab	0.24 ± 0.02cde	0.13 ± 0.02bc	0.12 ± 0.04bc	3.42 ± 0.30def	28.16 ± 3.61bc	32.52 ± 3.12 cd
Acer C	64.02 ± 6.25ab	0.27 ± 0.03bcd	0.14 ± 0.02bc	0.12 ± 0.02bc	3.88 ± 0.41de	29.47 ± 2.57bc	35.11 ± 2.00 cd
Acer V	59.14 ± 7.18b	0.29 ± 0.03bc	0.16 ± 0.02bc	0.13 ± 0.02abc	4.21 ± 0.44 cd	32.13 ± 4.18abc	39.61 ± 1.73bc
Fraxinus	36.84 ± 4.86c	0.36 ± 0.03b	0.18 ± 0.05bc	0.15 ± 0.02ab	5.56 ± 0.68c	33.35 ± 4.19abc	45.84 ± 4.77ab
Carpinus	31.25 ± 4.67c	0.50 ± 0.02a	0.22 ± 0.04ab	0.16 ± 0.02ab	7.87 ± 0.39b	37.84 ± 4.10ab	49.24 ± 5.83ab
Alnus	26.96 ± 2.08c	0.57 ± 0.06a	0.30 ± 0.03a	0.21 ± 0.03a	9.46 ± 1.24a	41.07 ± 4.85a	54.22 ± 4.84a
Summary ANOVA results							
F test	13.213	17.219	3.885	3.314	21.061	7.034	7.917
P value	0	0	0	0.002	0	0	0

Table 2 (continued)

Tree species	Soil properties							
	Particulate organic N (g kg^{-1})	Dissolved organic N (mg kg^{-1})	C/N ratio	Available P (mg kg^{-1})	Available K (mg kg^{-1})	Available Ca (mg kg^{-1})	Available Mg (mg kg^{-1})	Fine root biomass (g m^{-2})
Fagus	0.24 ± 0.02d	23.27 ± 1.47d	41.54 ± 3.77a	17.06 ± 0.85e	147.60 ± 12.37e	105.20 ± 8.75c	19.80 ± 1.70f	42.64 ± 4.02e
Quercus	0.25 ± 0.06d	25.55 ± 2.62d	41.10 ± 4.18a	17.59 ± 1.00de	158.80 ± 9.12e	115.60 ± 11.54c	22.10 ± 3.66f	44.41 ± 4.94de
Pterocarya	0.35 ± 0.06 cd	25.97 ± 1.84d	38.62 ± 5.78a	18.18 ± 2.66de	182.50 ± 20.36e	165.10 ± 9.18c	36.00 ± 3.92e	51.96 ± 5.33cde
Tilia	0.39 ± 0.06bcd	27.67 ± 2.60 cd	27.79 ± 4.24b	20.99 ± 1.91de	196.60 ± 18.55e	152.20 ± 18.67c	39.90 ± 2.34de	56.53 ± 10.83cde
Zelkova	0.43 ± 0.04abc	30.74 ± 1.64 cd	23.47 ± 1.61b	22.59 ± 2.23cde	320.90 ± 14.74d	153.40 ± 18.59c	43.10 ± 4.32cde	61.52 ± 7.37cde
Acer C	0.45 ± 0.07abc	31.54 ± 3.09 cd	23.17 ± 3.59b	22.71 ± 1.71cde	325.60 ± 15.13d	157.50 ± 11.12c	47.60 ± 6.22 cd	63.25 ± 4.38bcd
Acer V	0.49 ± 0.05abc	34.52 ± 3.13bc	19.78 ± 2.72bc	23.69 ± 1.59 cd	386.70 ± 21.59c	240.80 ± 10.60b	52.10 ± 1.97bc	67.10 ± 5.47bc
Fraxinus	0.51 ± 0.04abc	40.02 ± 3.20ab	12.99 ± 1.09 cd	27.59 ± 2.58bc	417.50 ± 34.15bc	301.10 ± 29.32d	60.40 ± 1.96ab	81.45 ± 3.45ab
Carpinus	0.54 ± 0.02ab	41.63 ± 2.65ab	8.53 ± 0.74d	31.04 ± 2.46ab	452.40 ± 22.92ab	322.70 ± 28.28a	64.20 ± 1.61a	88.98 ± 7.86a
Alnus	0.58 ± 0.04a	44.04 ± 3.32a	8.10 ± 1.35d	34.73 ± 1.46a	497.50 ± 20.81a	358.40 ± 37.88a	65.50 ± 1.75a	90.32 ± 6.95a
Summary ANOVA results								
F test	5.347	7.656	14.761	9.139	41.75	19.314	24.18	7.202
P value	0	0	0	0	0	0	0	0

Different letters in each line indicate significant differences ($P < 0.05$ by Duncan test) between tree species. Bold and italic values indicate significant statistical differences. Fagus: *Fagus orientalis* Lipsky, Quercus: *Quercus castaneifolia* C. A. Mey., Pterocarya: *Pterocarya fraxinifolia* Lam., Tilia: *Tilia begonifolia* Stev., Zelkova: *Zelkova carpinifolia* Dippe, Acer C.: *Acer cappadocicum* Gled, Acer V.: *Acer velutinum* Boiss., Fraxinus: *Fraxinus excelsior* L., Carpinus: *Carpinus betulus* L., and Alnus: *Alnus subcordata* C.A. Mey.

F. orientalis had a higher MBC, while the highest MBC/MBN ratio was measured for *F. orientalis* or *Q. castaneifolia* stands (Table 4). After 17 weeks of incubation, the soil C mineralization in the litter was differentially affected by the tree species in rank order of *A. subcordata* ≈ *C. betulus* ≈ *F. excelsior* > *A. velutinum.* > *A. cappadocicum.* > *Z. carpinifolia* ≈ *T. begonifolia* > *P. fraxinifolia* ≈ *Q. castaneifolia* ≈ *F. orientalis*. However, soil N mineralization after 35 days, was differentially affected by tree species in rank order of *A. subcordata* > *C. betulus* > *F. excelsior* ≈ *A. velutinum.* > *A. cappadocicum.* ≈ *Z. carpinifolia* > *T. begonifolia* > *P. fraxinifolia* ≈ *Q. castaneifolia* ≈ *F. orientalis* (Fig. 4; Table S2).

Relationship among trees with litter and soil properties

In the PCA analysis of the 70 variables evaluated for litter and soil samples, two principal components (PC1 and PC2) explained over 55% (PC1 = 50.13%, PC2 = 6.90%) of the total variance. The PCA outcomes showed a clear discrimination in the litter and soil properties among tree species due to functional traits or habitat types of trees. Two categories of drivers for soil fertility and microbial activities were revealed Fig. 5. Group 1 (*F. orientalis*, *Q. castaneifolia*, *P. fraxinifolia*, *T. begonifolia*, *Z. carpinifolia*, *A. cappadocicum.* and *A. velutinum.*) enhanced soil microbial biomass of carbon and had a positive effect on soil properties, whereas group 2 (*F. excelsior*, *C. betulus* and *A. subcordata*) showed litter nutrients and enhanced biota activities, C and N cycles (Fig. 3A – C).

Discussion

Litter properties

Our findings clearly indicate litter chemistry and decomposition were differentially affected by the various tree species. In addition to the quality of litter, the availability and content of nutrients that are returned to the soil environment are fundamental for soil fertility and optimum tree growth (Cao et al. 2020). Houle et al. (2015) believed that the type of tree species and the quality of their litter determine the amount of available nutrients and the mechanism of litter decomposition. Chen et al. (2020) pointed to the importance and role of forest species in restoring nutrients to the soil and stated that the litter quality (thickness and litter elements like C, N, K, P, Ca, Mg and C/N ratio) strongly affects decomposition rate and soil fertility. In this study, we showed that *A. subcordata* provides more P, K, Ca, Mg, and total N in the litter than the other species. In addition to the nutrients, the C/N ratio is an important indicator in decomposition dynamics (Goh and Totua 2004; Vesterdal et al. 2012; Kooch and Bayranvand 2019). The litter of *A. subcordata* species had a higher N content than that of the other species. As a consequence, the C/N ratio was lower. We therefore hypothesize that *A. subcordata* releases more C into the soil than the other species do. *A. subcordata* is a pioneer species in Hyrcanian forests that adds new organic substances to the forest soil layers every year (Koupar et al. 2011). It also forms a symbiosis

Table 3 Mean (±SE; n = 10) of soil climate and biota in summer (S) and fall (F) seasons under different tree species

Tree species	Soil climate and biota							
	Water content (%)		Temperature (°C)		Epigeic density (n m^{-2})		Epigeic biomass (mg m^{-2})	
	S	F	S	F	S	F	S	F
Fagus	60.42 ± 4.22a	64.08 ± 4.14a	16.13 ± 1.13d	14.23 ± 0.60c	0.00 ± 0.00c	0.10 ± 0.01d	0.00 ± 0.00c	0.84 ± 0.04d
Quercus	59.91 ± 2.76a	63.79 ± 5.99a	16.34 ± 1.17d	14.47 ± 0.85c	0.00 ± 0.00c	0.10 ± 0.02d	0.00 ± 0.00c	0.95 ± 0.05d
Pterocarya	53.03 ± 4.61ab	62.39 ± 5.00ab	18.43 ± 1.03 cd	16.66 ± 1.09bc	0.00 ± 0.00c	0.30 ± 0.06 cd	0.00 ± 0.00c	2.74 ± 0.52 cd
Tilia	51.87 ± 5.43abc	53.33 ± 6.16abc	20.24 ± 0.65bc	18.14 ± 0.89ab	0.00 ± 0.00c	0.50 ± 0.31 cd	0.00 ± 0.00c	4.46 ± 1.88 cd
Zelkova	45.31 ± 4.08bcd	52.32 ± 4.51abc	20.50 ± 0.87bc	18.16 ± 0.75ab	0.10 ± 0.03c	0.70 ± 0.26 cd	0.76 ± 0.06c	7.21 ± 2.70 cd
Acer C	44.33 ± 4.35bcd	52.08 ± 4.11abc	20.52 ± 0.69bc	18.23 ± 0.84ab	0.20 ± 0.13c	0.90 ± 0.31 cd	1.52 ± 0.32bc	9.18 ± 2.78bcd
Acer V	41.30 ± 4.21bcd	49.66 ± 5.34abc	23.45 ± 1.03ab	18.32 ± 0.55ab	0.40 ± 0.22bc	1.00 ± 0.36 cd	3.77 ± 2.29bc	11.14 ± 3.99bc
Fraxinus	39.98 ± 4.18 cd	48.06 ± 4.74bc	23.92 ± 1.55a	19.87 ± 1.24ab	0.80 ± 0.32b	1.30 ± 0.42bc	6.75 ± 2.48ab	16.91 ± 4.78b
Carpinus	38.78 ± 1.06d	44.69 ± 3.85c	24.33 ± 1.16a	21.14 ± 2.37a	0.90 ± 0.23ab	2.00 ± 0.29b	9.92 ± 2.64a	18.17 ± 2.88b
Alnus	36.39 ± 2.87d	41.21 ± 1.61c	25.14 ± 1.19a	21.28 ± 1.58a	1.40 ± 0.37a	3.70 ± 0.36a	11.64 ± 3.61a	37.18 ± 4.19a
Summary ANOVA results								
F test	4.813	2.864	9.094	4.074	6.438	15.089	5.99	14.057
P value	0	0.005	0	0	0	0	0	0

Tree species	Soil climate and biota							
	Anecic density (n m^{-2})		Anecic biomass (mg m^{-2})		Endogeic density (n m^{-2})		Endogeic biomass (mg m^{-2})	
	S	F	S	F	S	F	S	F
Fagus	0.00 ± 0.00c	0.20 ± 0.03e	0.00 ± 0.00d	1.30 ± 0.09d	0.00 ± 0.00c	0.30 ± 0.02e	0.00 ± 0.00c	2.96 ± 0.19e
Quercus	0.00 ± 0.00c	0.20 ± 0.03e	0.00 ± 0.00d	2.56 ± 0.71d	0.00 ± 0.00c	0.30 ± 0.05e	0.00 ± 0.00c	3.82 ± 1.95e
Pterocarya	0.10 ± 0.01c	0.50 ± 0.16de	0.14 ± 0.04d	5.05 ± 1.71 cd	0.00 ± 0.00c	0.60 ± 0.26de	0.00 ± 0.00c	6.56 ± 2.96de
Tilia	0.10 ± 0.01c	0.60 ± 0.26de	0.32 ± 0.02d	6.24 ± 2.50 cd	0.00 ± 0.00c	0.80 ± 0.20cde	0.00 ± 0.00c	9.08 ± 2.30cde
Zelkova	0.30 ± 0.05c	0.70 ± 0.06cde	3.47 ± 2.02 cd	6.65 ± 2.57 cd	0.00 ± 0.00c	1.10 ± 0.34bcde	0.00 ± 0.00c	11.58 ± 4.21cde
Acer C	0.50 ± 0.12c	0.70 ± 0.21cde	3.61 ± 1.61 cd	7.30 ± 2.29 cd	0.22 ± 0.04bc	1.30 ± 0.33bcd	2.29 ± 1.59bc	16.60 ± 4.45bcd
Acer V	0.60 ± 0.22c	1.20 ± 0.29 cd	6.44 ± 2.27bc	13.07 ± 3.30bc	0.30 ± 0.05bc	1.60 ± 0.26bc	3.34 ± 1.71bc	19.92 ± 3.54bc
Fraxinus	1.20 ± 0.29b	1.50 ± 0.34c	8.67 ± 1.60bc	17.86 ± 4.22b	0.70 ± 0.26b	1.90 ± 0.23b	5.76 ± 1.95bc	24.08 ± 3.42b
Carpinus	1.40 ± 0.30b	3.00 ± 0.25b	11.17 ± 2.18ab	43.91 ± 2.68a	0.70 ± 0.26b	3.80 ± 0.32a	7.78 ± 3.35ab	47.13 ± 4.00a
Alnus	2.10 ± 0.31a	3.80 ± 0.44a	16.12 ± 3.49a	47.85 ± 5.15a	1.40 ± 0.37a	4.50 ± 0.37a	11.33 ± 3.45a	51.07 ± 5.20a
Summary ANOVA results								
F test	12.098	20.975	9.725	32.649	6.91	26.482	4.999	23.035
P value	0	0	0	0	0	0	0	0

Tree species	Soil climate and biota							
	Earthworm density (n m^{-2})		Earthworm biomass (mg m^{-2})		Acarina density (n m^{-2})		Collembola density (n m^{-2})	
	S	F	S	F	S	F	S	F
Fagus	0.00 ± 0.00d	0.60 ± 0.12 g	0.00 ± 0.00e	5.11 ± 2.20 g	17,524 ± 2331c	18,712 ± 8174gg	6356 ± 425e	10,003 ± 301f
Quercus	0.00 ± 0.00d	0.60 ± 0.12 g	0.00 ± 0.00ee	7.34 ± 2.81 g	19,772 ± 6034c	21,133 ± 1545fffg	8330 ± 344de	10,399 ± 346f
Pterocarya	0.10 ± 0.01d	1.40 ± 0.12 fg	0.14 ± 0.04e	14.36 ± 2.30 fg	21,839 ± 6405bc	25,802 ± 2545efg	8604 ± 631de	10,971 ± 495f
Tilia	0.10 ± 0.01d	1.90 ± 0.34efg	0.32 ± 0.02e	19.79 ± 3.53efg	26,799 ± 3910bc	29,119 ± 1630def	9599 ± 326de	13,837 ± 954ef
Zelkova	0.40 ± 0.02 cd	2.50 ± 0.60def	4.23 ± 2.30de	25.45 ± 6.28ef	29,865 ± 7020bc	32,309 ± 2925de	10,803 ± 342d	16,151 ± 898def
Acer C	0.90 ± 0.07 cd	2.90 ± 0.48de	7.20 ± 2.08de	33.09 ± 4.42de	31,210 ± 1670bc	35,641 ± 5276 cd	16,031 ± 1228c	21,582 ± 1034de
Acer V	1.30 ± 0.42c	3.80 ± 0.46 cd	13.56 ± 4.39 cd	44.14 ± 5.97 cd	36,596 ± 4971b	42,055 ± 2936c	16,504 ± 1767c	24,643 ± 3170 cd
Fraxinus	2.70 ± 0.39b	4.70 ± 0.61c	21.18 ± 2.98bc	58.85 ± 8.77c	52,729 ± 7819a	58,310 ± 4949b	19,554 ± 1258b	31,565 ± 4598bc
Carpinus	3.00 ± 0.36b	8.80 ± 0.62b	28.86 ± 4.17b	109.23 ± 7.02b	54,997 ± 4824a	61,380 ± 2902b	200,503 ± 1476b	39,539 ± 4057b
Alnus	4.90 ± 0.75a	12.00 ± 0.71d	39.10 ± 7.03a	136.11 ± 7.44a	60,962 ± 4348a	80,114 ± 3605a	23,509 ± 1551a	50,249 ± 6162a
Summary ANOVA results								
F test	23.563	58.861	18.545	64.11	8.819	42.323	30.082	21.216

Table 3 (continued)

Tree species	Soil climate and biota							
	Earthworm density (n m^{-2})		Earthworm biomass (mg m^{-2})		Acarina density (n m^{-2})		Collembola density (n m^{-2})	
	S	F	S	F	S	F	S	F
P value	0	0	0	0	0	0	0	0

Tree species	Soil climate and biota							
	Total nematode (in 100 g soil)		Protozoa density ($\times 10^2$ g $soil^{-1}$)		Total bacteria ($\times 10^7$ g $soil^{-1}$)		Total fungi ($\times 10^7$ g $soil^{-1}$)	
	S	F	S	F	S	F	S	F
Fagus	146 ± 17.30e	199 ± 9.50f	103 ± 6.43e	133 ± 11.66f	3.37 ± 0.37d	1.03 ± 0.10f	1.40 ± 0.11d	0.88 ± 0.07e
Quercus	148 ± 22.05e	229 ± 12.48f	124 ± 17.65de	139 ± 8.57f	3.49 ± 0.83d	1.14 ± 0.11ef	1.43 ± 0.17d	0.89 ± 0.07e
Pterocarya	264 ± 77.76de	352 ± 24.82e	131 ± 10.38de	159 ± 25.95ef	3.75 ± 0.77d	1.32 ± 0.53f	1.75 ± 0.28 cd	0.94 ± 0.03e
Tilia	306 ± 55.99 cd	404 ± 23.18e	142 ± 16.81de	182 ± 35.81ef	4.41 ± 0.34 cd	1.76 ± 0.29ef	2.32 ± 0.23bc	1.13 ± 0.15de
Zelkova	323 ± 40.59 cd	504 ± 48.08d	148 ± 11.21cde	207 ± 24.61ef	5.10 ± 0.66 cd	1.95 ± 0.20def	2.80 ± 0.25b	1.16 ± 0.06de
Acer C	343 ± 11.93 cd	559 ± 41.37d	188 ± 17.54 cd	221 ± 10.85e	5.56 ± 0.58 cd	2.11 ± 0.31de	3.10 ± 0.30b	1.27 ± 0.07cde
Acer V	437 ± 23.60c	733 ± 53.66c	213 ± 30.09c	389 ± 15.47d	6.09 ± 0.96bc	2.89 ± 0.31 cd	3.98 ± 0.24a	1.44 ± 0.11 cd
Fraxinus	603 ± 70.98b	904 ± 19.25b	319 ± 35.68b	522 ± 34.59c	6.47 ± 0.76bc	3.55 ± 0.33bc	4.08 ± 0.33a	1.62 ± 0.25bc
Carpinus	724 ± 42.57ab	954 ± 29.49ab	395 ± 35.85a	600 ± 35.15b	7.74 ± 0.68ab	4.10 ± 0.33b	4.28 ± 0.41a	1.96 ± 0.22ab
Alnus	808 ± 46.87a	1016 ± 42.51a	438 ± 16.81a	722 ± 29.63a	9.60 ± 0.73a	5.68 ± 0.61a	4.65 ± 0.25a	2.28 ± 0.18a
Summary ANOVA results								
F test	24.86	79.876	29.588	72.571	8.196	19.649	20.018	10.726
P value	0	0	0	0	0	0	0	0

Different letters in each line indicate significant differences ($P < 0.05$ by Duncan test) between tree species. Bold and italic values indicate significant statistical differences. Fagus: *Fagus orientalis* Lipsky, Quercus: *Quercus castaneifolia* C. A. Mey., Pterocarya: *Pterocarya fraxinifolia* Lam., Tilia: *Tilia begonifolia* Stev., Zelkova: *Zelkova carpinifolia* Dippe, Acer C.: *Acer cappadocicum* Gled, Acer V.: *Acer velutinum* Boiss., Fraxinus: *Fraxinus excelsior* L., Carpinus: *Carpinus betulus* L., and Alnus: *Alnus subcordata* C.A. Mey.

with N-fixing actinomycetes and fixes atmospheric N into the soils, increasing soil fertility and providing good quality litter (i.e., lower C/N ratio and higher values of N, P, K, Ca and Mg) (Taleshi et al. 2009; Parsapour et al. 2018). The high N content of *A. subcordata* litter also increases the populations of soil organisms and the mineralization rate of elements (Glaser et al. 2018). The higher C/N ratio in *F. orientalis* litter, compared to the other species, may cause a higher recalcitrance and lower decomposition rate than for litter of the other tree types.

Soil properties

As mentioned earlier, soil properties differ significantly among tree species (Wang et al. 2021). The trees drive biogeochemical regulation in ecosystems via the stabilisation of organic C among other things. The lower amount of organic C under *A. subcordata* and *C. betulus* is the result of a rapid mineralisation (Kooch 2012; Błońska et al. 2018), which is related to the occurrence of fertility hotspots. In comparison to contents in other trees, the higher contents of N of *A. subcordata* and *C. betulus* improve the soil N (Sayyad 2009). The content of soil macro elements is also associated to the release of nutrients by trees and nutrient cycling in the forest floor (Dijkstra and Smits 2002; Osborne et al. 2020). Humus formation and nutrients cycling can also be affected by the canopy of trees (Majasalmi and Rautiainen 2020). *A. subcordata* and *C. betulus* can lead to an increase in soil pH and fertility (Zeng et al. 2014; Majasalmi and Rautiainen 2020), whereas *Q. castaneifolia* and *F. orientalis* species have greater acidifying capabilities (Augusto et al. 2002) than other deciduous trees do.

Soil biological activities were generally lower under *F. orientalis*. At *A. subcordata* stands, the higher quality of the forest floor enhanced soil biota populations (Knops et al. 2002; Osborne et al. 2020). Our data indicated a temporal change in earthworms, acarina, nematodes, protozoa, collembola and densities of fungal and bacterial populations due to seasonal environmental changes (Chaudhuri and Paliwal 2008; Suthar 2012). Soil moisture as an important factor affects the physiology of microorganisms directly, affecting access to water and regulating access to organic matter, which in turn affects macroorganismal and microbial soil populations (Andrade et al. 2017). Soil temperature and

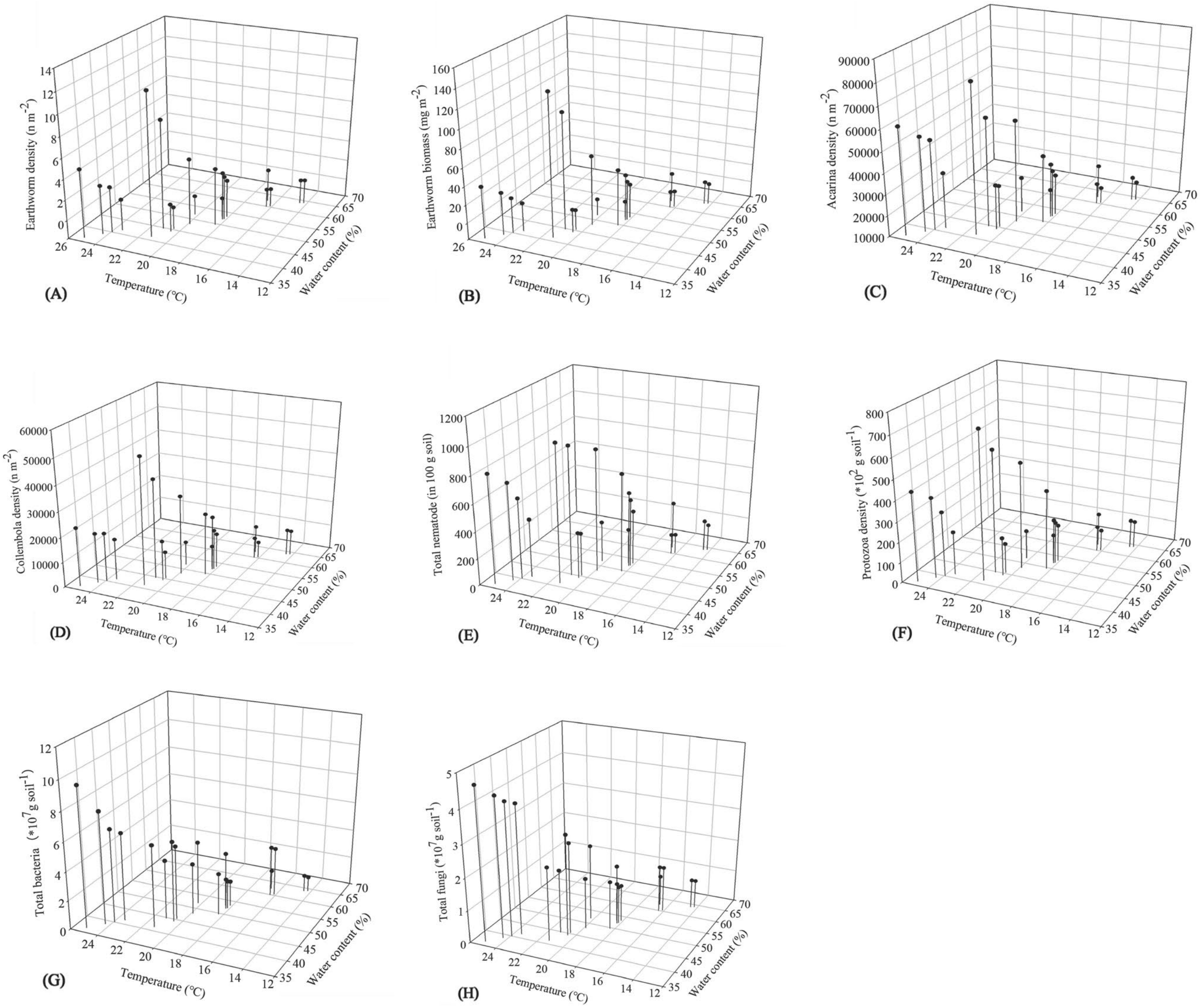

Fig. 3 Variability of soil biota related to soil climate (summer and fall) under different tree species

water content are major drivers of variations in soil biota under different trees (Lozano-Parra et al. 2015). Higher soil temperature and less topsoil water under various tree species are unsuitable for epigeic activity in the summer. The faster reaction of epigeic earthworms than the other ecological groups is due to the higher sensitivity of epigeic earthworms to the soil microclimate compared to anecic and endogeic forms (Lagerlof et al. 2002), which anecic and endogeic groups can move to various soil layers when conditions are favourable (Nuutinen and Butt 2009). Higher soil fauna activities in the fall have also been confirmed (Crumsey et al. 2013; Ren et al. 2018). In the fall season, maximum earthworm activity was recorded among tree species having favourable soil water. The lower earthworm population in the summer is a result of the drier and warmer conditions (see Fig. 2). Crumsey et al. (2013) reported significant effects of soil water on the comparative frequency of earthworm species comparative frequency of earthworm species and that earthworm species richness was mainly regulated by soil water content rather than pH or soil organic C. Similar results were reported by Suthar (2012); low physiological activity and high temperatures in summer limit the activity of soil organisms.

Differences in soil fertility can also be the result of differences in the earthworm, acarina, collembola, nematode and protozoa populations and preferences (Sackett et al. 2013; Sigurdsson and Gudleifsson 2014). Rich stands with more nutrients and litter having a low C/N ratio (Rehschuh et al. 2021) are preferred by earthworms. Several studies (Drouin et al. 2016; Tucker Serniak 2017; Zhang et al. 2020) revealed a crucial influence of the chemical composition of plants (such as N, lignin, and phenols) on soil properties and fauna.

Table 4 Mean (± SE; n = 10) of soil microbial and enzyme activities under different tree species

Tree species	Soil microbial and enzyme activities						
	BR (mg CO_2 g^{-1} day^{-1})	SIR (mg CO_2 g^{-1} day^{-1})	MBC (mg kg^{-1})	MBN (mg kg^{-1})	MBP (mg kg^{-1})	qCO_2 (BR/MBC)	Microbial ratio (MBC/C)
Fagus	0.31 ± 0.08e	1.07 ± 0.05e	811 ± 25.41a	38.93 ± 3.10d	22.20 ± 2.79e	0.37 ± 0.05f	127.89 ± 12.25
Quercus	0.32 ± 0.04de	1.13 ± 0.06e	799 ± 14.34ab	40.12 ± 3.81d	23.90 ± 1.33e	0.41 ± 0.07ef	128.83 ± 15.80
Pterocarya	0.38 ± 0.05cde	1.14 ± 0.14e	782 ± 29.92abc	44.40 ± 4.61c	33.30 ± 3.94de	0.49 ± 0.07def	132.08 ± 12.97
Tilia	0.42 ± 0.05bcde	1.24 ± 0.04de	776 ± 31.90abc	45.25 ± 5.06c	37.00 ± 3.55cdee	0.54 ± 0.04def	137.24 ± 9.87
Zelkova	0.44 ± 0.02bcde	1.29 ± 0.06cde	769 ± 34.18abcd	48.58 ± 4.35c	41.80 ± 8.25cde	0.58 ± 0.04cde	143.71 ± 11.81
Acer C	0.46 ± 0.03abcd	1.32 ± 0.03cde	763 ± 30.66abcd	50.13 ± 3.10c	45.30 ± 7.85 cd	0.61 ± 0.04 cd	148.15 ± 12.60
Acer V	0.48 ± 0.02abc	1.46 ± 0.08bcd	707 ± 20.34abcd	50.79 ± 4.61c	54.70 ± 6.88bc	0.68 ± 0.03bcd	154.04 ± 19.56
Fraxinus	0.53 ± 0.02ab	1.51 ± 0.04bc	693 ± 23.08bcd	55.97 ± 1.64bc	68.80 ± 9.47ab	0.77 ± 0.04abc	167.13 ± 14.80
Carpinus	0.55 ± 0.03ab	1.64 ± 0.05ab	676 ± 18.60 cd	62.85 ± 3.59ab	72.80 ± 5.15ab	0.83 ± 0.05ab	170.62 ± 15.46
Alnus	0.59 ± 0.02a	1.80 ± 0.11a	669 ± 36.29d	68.83 ± 2.90a	78.20 ± 8.19a	0.92 ± 0.07a	171.65 ± 10.63
Summary ANOVA results							
F test	4.384	9.217	2.56	6.561	10.128	8.202	1.524
P value	0	0	0.011	0	0	0	0.151

Tree species	Soil microbial and enzyme activities					
	CAI (BR/SIR)	MBC/MBN	Urease (µg NH_4^+–N g^{-1} 2 h^{-1})	Acid phosphatase (µg PNP g^{-1} h^{-1})	Arylsulfatase (µg PNP g^{-1} h^{-1})	Invertase (µg Glucose g^{-1} 3 h^{-1})
Fagus	0.28 ± 0.06	21.97 ± 1.76a	11.74 ± 0.56e	239 ± 16.60e	109 ± 8.47d	107 ± 10.02c
Quercus	0.30 ± 0.04	21.76 ± 2.69a	12.63 ± 0.63de	252 ± 16.64e	112 ± 7.19d	117 ± 15.86c
Pterocarya	0.49 ± 0.17	20.16 ± 3.00ab	15.39 ± 1.48cde	302 ± 24.78de	129 ± 9.25d	132 ± 12.57c
Tilia	0.36 ± 0.04	19.62 ± 2.56ab	16.46 ± 1.20 cd	327 ± 38.42cde	151 ± 15.35 cd	211 ± 34.27b
Zelkova	0.35 ± 0.02	17.64 ± 2.37abc	17.41 ± 1.35c	370 ± 23.21bcde	157 ± 18.33 cd	216 ± 26.46b
Acer C	0.34 ± 0.02	15.74 ± 1.15abcd	18.71 ± 1.32c	385 ± 21.71bcd	200 ± 21.80bc	262 ± 13.44ab
Acer V	0.34 ± 0.02	15.40 ± 2.14bcd	19.55 ± 2.55bc	396 ± 16.63abcd	225 ± 19.73ab	287 ± 14.74ab
Fraxinus	0.35 ± 0.01	12.48 ± 0.54 cd	23.18 ± 1.27b	446 ± 18.73abc	235 ± 14.07ab	312 ± 18.47a
Carpinus	0.33 ± 0.01	11.18 ± 1.03d	23.26 ± 1.44b	467 ± 11.15ab	269 ± 11.37a	323 ± 14.35a
Alnus	0.34 ± 0.02	9.81 ± 0.65d	29.51 ± 1.47a	522 ± 18.01a	281 ± 18.39a	327 ± 13.66a
Summary ANOVA results						
F test	0.747	4.883	14.224	4.803	10.265	11.524
P value	0.665	0	0	0	0	0

Different letters in each line indicate significant differences ($P < 0.05$ by Duncan test) between tree species. Bold and italic values indicate significant statistical differences. BR: Basal respiration, SIR: Substrate induced respiration, MBC: Microbial biomass C, MBN: Microbial biomass N, MBP: Microbial biomass P, qCO_2: Soil metabolic quotient, CAI: Carbon availability index. Fagus: *Fagus orientalis* Lipsky, Quercus: *Quercus castaneifolia* C. A. Mey., Pterocarya: *Pterocarya fraxinifolia* Lam., Tilia: *Tilia begonifolia* Stev., Zelkova: *Zelkova carpinifolia* Dippe, Acer C.: *Acer cappadocicum* Gled, Acer V.: *Acer velutinum* Boiss., Fraxinus: *Fraxinus excelsior* L., Carpinus: *Carpinus betulus* L., and Alnus: *Alnus subcordata* C.A. Mey

According to our results, the lowest earthworm density and biomass was found at *F. orientalis* plots having a higher C/N ratio. Desirable conditions for earthworms were provided by *A. subcordata*, which had the lowest C/N ratio. Thus, soil bacteria activity was higher in *A. subcordata* plots and more fungi were present in plots with *A. subcordata*, *C. betulus*, *F. excelsior* and *A. velutinum*. Variations in physical properties (e.g., lower aggregate stability) and soil fertility can also alter bacterial and fungal populations in *F. orientalis* and *Q. castaneifolia* plots (Kim et al. 2021). Previous studies showed provisional schemas of soil fungi and bacteria population in various trees and indicated that soil bacteria were more abundant during the summer than the fall (Kuffner et al. 2012; Preusser et al. 2019; Li et al. 2021). Generally, the soil organismal activities in *A. subcordata* plots might be attributable to higher litter quality and more favourable topsoil temperatures (Glaser et al. 2018). Bacteria are more sensitive to a low pH. Therefore, the highest biomass can normally be related to neutral to slightly alkaline conditions of the soil at *A. subcordata* stands (pH > 7). Hence, there is

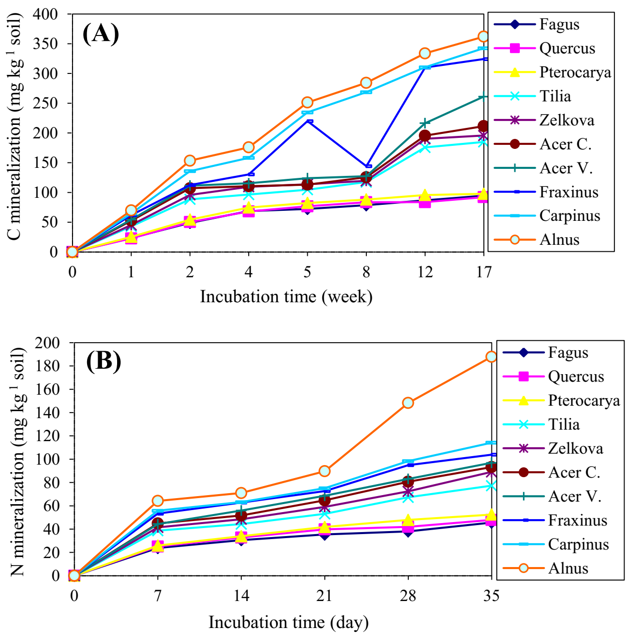

Fig. 4 Mean (±SE; n=10) of soil C and N mineralisation (A, B) under different tree species. Data in details are presented in Appendix 2. Note: Fagus: *Fagus orientalis* Lipsky, Quercus: *Quercus castaneifolia* C. A. Mey., Pterocarya: *Pterocarya fraxinifolia* Lam., Tilia: *Tilia begonifolia* Stev., Zelkova: *Zelkova carpinifolia* Dippe, Acer C.: *Acer cappadocicum* Gled, Acer V.: *Acer velutinum* Boiss., Fraxinus: *Fraxinus excelsior* L., Carpinus: *Carpinus betulus* L., and Alnus: *Alnus subcordata* C.A. Mey

a positive correlation between bacterial biomass and pH. Differences in quantity and quality of the litter influences microbial and enzymatic activities, nutrient accessibility and, thus, all biogeochemical cycles (Zheng et al. 2018). Compared to other species, the highest value of BR, SIR, MBN, MBP, and qCO_2 was recorded in soils at *A. subcordata* stands. Tardy et al. (2014) showed a negative effect of low soil fertility on BR and SIR, similar to our findings. The results of Sasongko et al. (2019) revealed that an increase in forest soil nutrients can lead to higher microbial activities, BR, and SIR in the soil.

Our results showed significant differences in enzymatic activities among the tree species. Soil enzymatic activities are affected by soil management strategies and trees (Silva et al. 2012) and can be used to predict changes in soil quality (Guo and Han 2008; Yao et al. 2020). Higher enzymatic activity causes faster decomposition and higher availability of organic nutrients (Wang et al. 2013). The clay fraction seems to contribute to the accumulation of soil enzymes via their stabilisation and protection (Zhong et al. 2015) under *A. subcordata*. In soils at the *A. subcordata* sites, the activity of urease increases with increasing pH, EC, total N, and nutrients (Cheng et al. 2013) and decreases with higher C/N ratios. Acid phosphatase activities also can significantly differ depending on the tree species (Chodak et al. 2021) and are strongly affected by pH, soil water, total N and organic C content (Wang et al. 2021). The activity of sulfatase is correlated with soil particle size and highest in the clay fraction (Ling et al. 2014) under *A. subcordata*. Greater soil water can reduce the revival oxidation potential anaerobic conditions of the soil that constrain enzyme activities (Brockett et al. 2012) under *F. orientalis*. Low sulfatase activities at the *F. orientalis* stands can also be a result of low soil pH (Wang et al. 2016). Invertase plays a key role in the N and C cycles by hydrolyzing sucrose into glucose and fructose (Zhong et al. 2015). *A. subcordata* gives rise to a higher decomposition rate of litter and accelerates N cycling and invertase activity compared to *F. orientalis* (Zhong et al. 2015). In addition, higher pH (Li et al. 2009) and better fertility (Zhong et al. 2015) at *A. subcordata* stands improves the invertase enzyme activity. According to our findings, the soil at *A. subcordata*, *C. betulus* and *F. excelsior* stands had the highest mineralisation rate of C and N in comparison with other species. Parallel with our data, previous researches (Eickenscheidt et al. 2014; Uri et al. 2014; Tarighat and Kooch 2018) pointed out that mineralization of soil C and N by N-fixing tree species is significantly higher than for non-N-fixing species. In general, some habitat characteristics such as the quality of litter and soil physicochemical characteristics influence the variability of soil C and N mineralisation under various tree species. In general, *A. subcordata* provides better conditions for the mineralization of soil C and N due to the more alkaline soil.

Relationship among tree litter types and soil properties

This study is the first scrutiny that quantifies the impacts of typical trees in the Hyrcanian mixed beech forest on litter and soil properties. The PCA revealed a clear difference in the specific litter and soil properties among the studied trees. The type of broadleaf species also affects spatial variations in nutrient cycling. The better quality of organic matter under *A. subcordata* plots increased the activity of soil fauna/flora, increasing soil fertility. Our comparisons indicate that soil quality increases in order of *F. orientalis* < *Q. castaneifolia* < *P. fraxinifolia* < *T. begonifolia* < *Z. carpinifolia* < *A. cappadocicum*. < *A. velutinum*. < *F. excelsior* < *C. betulus* < *A. subcordata*. Also, *C. betulus* and *F. excelsior* serve an essential role in modifying microbial flora and soil nutrient content. Thus, a mixed natural forest is fundamental to providing soil services in temperate ecosystems and is a pivotal for sustainable forest care. Since the tree species influences litter quantity and quality, forest habitats provide various functions. Therefore, forestry management should be in the direction of ecosystem tolerance and select the most suitable tree species to ensure proper forest care.

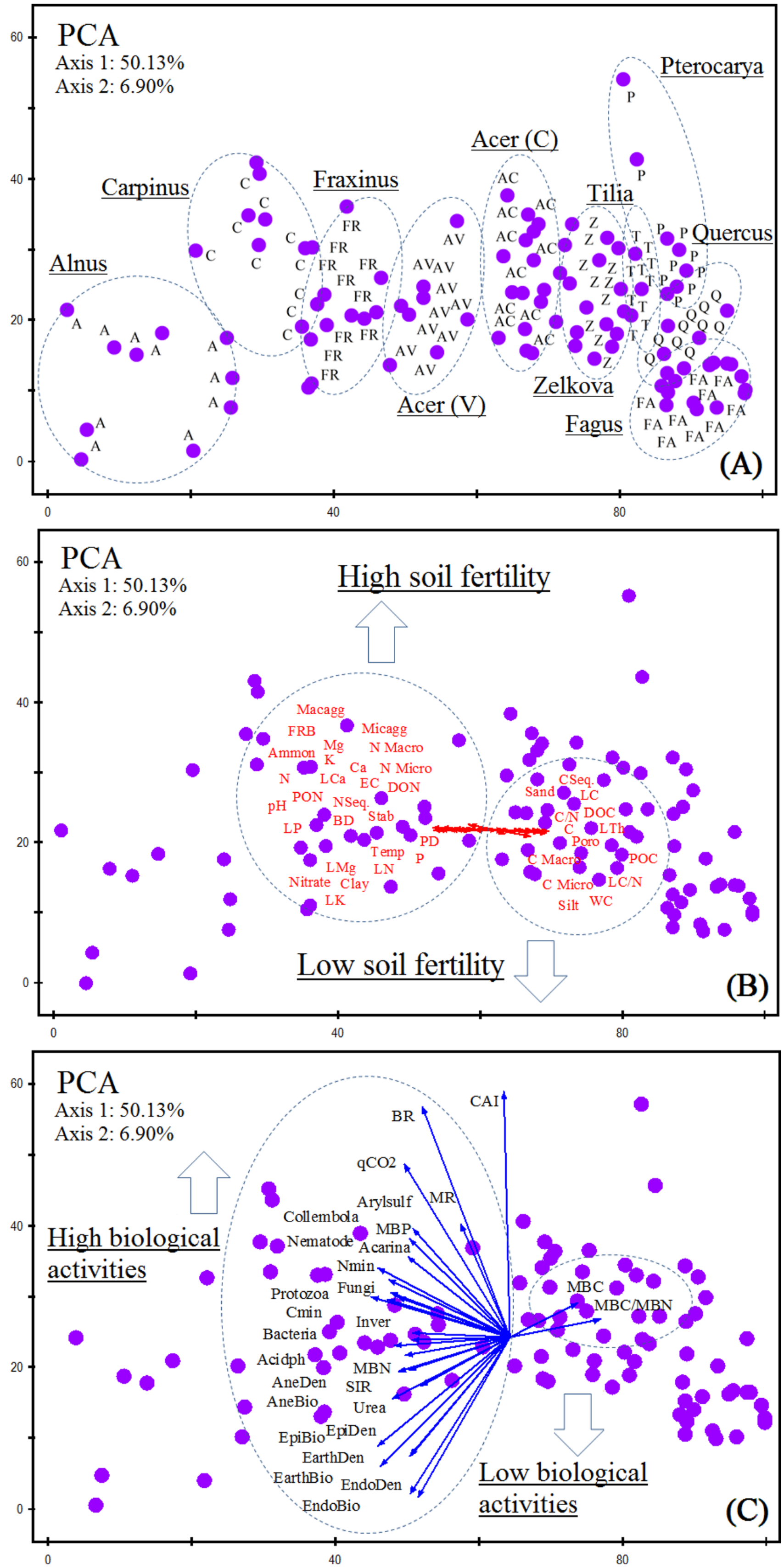

Fig. 5 PCA based on the correlation matrix of the tree species (A), litter and soil properties (B, C). Note: Fagus: *Fagus orientalis* Lipsky, Quercus: *Quercus castaneifolia* C. A. Mey., Pterocarya: *Pterocarya fraxinifolia* Lam., Tilia: *Tilia begonifolia* Stev., Zelkova: *Zelkova carpinifolia* Dippe, Acer C.: *Acer cappadocicum* Gled, Acer V.: *Acer velutinum* Boiss., Fraxinus: *Fraxinus excelsior* L., Carpinus: *Carpinus betulus* L., and Alnus: *Alnus subcordata* C.A. Mey

Conclusions

The tree species in the Hyrcanian mixed beech forests—*F. orientalis*, *Q. castaneifolia*, *P. fraxinifolia*, *T. begonifolia*, *Z. carpinifolia*, *A. cappadocicum*, *A. velutinum*, *F. excelsior*, *C. betulus*, and *A. subcordata*—strongly influence litter and soil properties. Our findings revealed that the differences in basic characteristics of these 10 species resulted in a distinct effect on microbial flora and affected soil nutrient cycling. Soil fertility and microbial hotspots in these forests were clearly species-specific confirming our research hypothesis of soil fertility and microbial hotspots governed by tree species and litter properties. According to our data, *A. subcordata* (as N-fixing species), *C. betulus* and *F. excelsior* species are the main drivers of microbial activities related to nutrient cycling in old-growth beech forests. In fact, the admixture of valuable broad-leaved species with beech stands at fertile sites served as a significant silvicultural system for maintaining soil quality via natural or human-induced soil acidification. These findings improve our knowledge of the impacts of different tree species on the litter and soil properties of deciduous mixed forests and subsequent productivity of the relevant ecosystem.

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Authors' contributions Y K conceived and designed the experiments and analyzed the data; N G and S H performed the experiments; Markus Egli provided editorial advice.

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