Journal of Insect Biodiversity and Systematics
ISSN: 2423-8112
2026 | 12 (04), 705–723
Website: https://jibs.modares.ac.ir
Contents list: https://www.biotaxa.org/jibs
https://doi.org/10.48311/jibs.12.04.705

Original Article

Macrofauna and mesofauna in Hyrcanian Protected Forest: Seasonal patterns of the arthropod diversity and community structure across soil depths

Mahmood Mehrafrooz Mayvan [1,2] | Masoumeh Shayanmehr [1]

1 Department of Plant Protection, Faculty of Crop Sciences, Sari University of Agricultural Sciences and Natural Resources (SANRU), Sari, Iran.

2 Institute of Soil Biology and Biogeochemistry, Biology Centre of the Czech Academy of Sciences, Na Sádkách 7, 370 05 České Budějovice, Czech Republic; Email: mahmood_mehrafrooz@yahoo.com

Corresponding author: Masoumeh Shayanmehr | ✉ m.shayanmehr@sanru.ac.ir

https://zoobank.org/urn:lsid:zoobank.org:6B3B5205-4F60-4EE8-8A5F-8AA698620AEB

Academic Editor
Elaheh Daghighi

Received
May 24, 2026

Revised
August 05, 2026

Accepted
August 06, 2026

Published online
August 30, 2026

ABSTRACT. Hyrcanian forests are considered among the oldest forests in the world, and due to their temperate and humid climate and fertile soil, they have rich fauna and flora. Soil-dwelling arthropods play essential roles in forest ecosystem functioning, contributing to litter decomposition, nutrient cycling, and soil structure maintenance. This study assessed the diversity and vertical distribution of macrofauna and mesofauna in Semeskandeh Forest, a protected Hyrcanian Forest in northern Iran, across different soil depths (leaf litter, 0–3 cm, 3–6 cm) and seasons over one year. Over 10,000 individuals were collected, representing diverse taxonomic groups, including ants, millipedes, springtails, mites, pseudoscorpions, and diplurans. Population densities and species diversity were consistently highest in the litter layer and declined with increasing soil depth, with clear seasonal peaks observed during the study period. Ants dominated the macrofauna, while mites and springtails were the most diverse mesofaunal taxa. The study revealed clear seasonal and vertical patterns in the density and diversity of soil faunal communities in the Hyrcanian forest ecosystem. These findings provide baseline information for biodiversity conservation and future monitoring of soil fauna in Hyrcanian forests. Thereby, conserving litter quality, maintaining habitat integrity, and monitoring soil faunal diversity are critical for sustaining forest ecosystem functions in such a globally valuable and inherited region.

KEYWORDS: Abundance, Community composition, Conservation, Faunal diversity, Iran, Leaf litter

Citation: Mehrafrooz Mayvan, M. & Shayanmehr, M. (2026) Macrofauna and mesofauna in Hyrcanian Protected Forest: Seasonal patterns of the arthropod diversity and community structure across soil depths. *Journal of Insect Biodiversity and Systematics*, 12 (04), 705–723.

INTRODUCTION

Forests are among the most valuable natural resources on Earth and play an important role in climate regulation, provision of food and shelter, prevention of soil erosion, biodiversity conservation, regulation of surface water and groundwater recharge, soil protection and formation, as well as supporting industrial production (Ghomi-Avili et al. 2020; Zahriban Hesari et al. 2020; Truffer et al. 2025; Stritih et al. 2026). The Hyrcanian Forest, with its diverse vegetation, is recognized as one of the most valuable temperate broad-leaved deciduous forests in the world (Hosseini 2006; Haghdoost et al. 2011; Mehrafrooz Mayvan et al. 2015; D'Haese et al. 2025). It extends as a narrow green belt, 850 km in length and 20–70 km in width, from the southern shores of the Caspian Sea to northern Iran (Mohammadi et al. 2017; Waez-Mousavi 2017; Kooch et al. 2019; Homami Totmaj et al. 2021). These forests provide diverse habitats that support a wide range of soil invertebrate communities, linking the above-below ground ecosystem. Soil-dwelling arthropods are among the first organisms to have colonized terrestrial environments and are the most abundant animals on Earth, occurring in most

ISSN 2423-8112 – **Published by** Tarbiat Modares University | **Owner** The Entomological Society of Iran

ecosystems. Their species richness is generally higher in forests than in other habitats (Zhang 2011; Eckert et al. 2023; Hébert 2023). Soil fauna plays crucial ecological roles in soil processes, food web dynamics, and overall ecosystem health (Chahartaghi et al. 2009; Domene 2016; Cayuela et al. 2020; Kooch & Noghre 2020; Ma et al. 2019; Coleman et al. 2023). Their contributions include litter decomposition, nutrient cycling (e.g., nitrogen and carbon), enhancement of soil quality and structure, serving as reliable indicators of soil environmental function, and indirectly contributing to the regulating microclimate and local hydrological processes, representing just a portion of the ecosystem services provided by arthropods (Guo et al. 2020; Lin et al. 2019; Berry et al. 2020; Domínguez et al. 2020; Gonçalves et al. 2020; Kooch et al. 2020; Menta & Remelli 2020; Sánchez-Montoya et al. 2020; Yang et al. 2020; Wang et al. 2021). Invertebrate communities that constitute the soil fauna are classified into three groups based on body size: macrofauna, mesofauna, and microfauna (Zagatto et al. 2017; Wu & Wang 2019; Marsden et al. 2020; Zagatto et al. 2020). Soil macrofauna are relatively large, with body sizes ranging from 2 to 20 mm (e.g., millipedes, insects, and earthworms). Mesofauna measure between 0.2 and 2 mm (e.g., springtails, mites, pseudoscorpions, some millipedes, oligochaetes, and several insect orders). Microfauna, including nematodes and protozoa, are smaller than 0.2 mm (Lavelle et al. 1997; Xin et al. 2012; García-Segura et al. 2018; Cayuela et al. 2020; Marsden et al. 2020; Zagatto et al. 2020).

Investigating soil-dwelling arthropod diversity provides valuable insights into environmental conditions because these organisms have limited mobility and highly specific microhabitat requirements (Heydari et al. 2020; Nacif et al. 2020). Sustainable forest management should prioritize biodiversity conservation. Human activities, including habitat loss and fragmentation combined with high pesticide inputs, are now recognized as major drivers of global biodiversity loss (Tilman et al. 2001; Tscharntke et al. 2005; de Pedro et al. 2020). The importance of biodiversity in supporting ecosystem services is increasingly acknowledged, and substantial experimental evidence demonstrates its positive influence on ecosystem functioning (Hector & Bagchi 2007; Tresch et al. 2019; O'Donnell & Wright 2021). Accurate characterization of biodiversity and a thorough understanding of dynamic ecological processes are both essential for the effective assessment and management of ecosystems (Decaëns et al. 2006; Valencia-Cuevas et al. 2020). In this context, understanding diversity patterns and their ecological relationships is particularly critical for conservation and for maintaining ecosystem functions (Xu et al. 2020).

The Hyrcanian forests in northern Iran exhibit complex patterns of species diversity and ecosystem structure that can be optimally managed only through comprehensive knowledge of this ecosystem. Although the biodiversity of vascular plants and vertebrates has been relatively well documented, recent studies indicate that soil arthropods, particularly Collembola, remain considerably understudied in these forests (Mehrafrooz Mayvan et al. 2015; D'Haese et al. 2025). Recent investigations have also demonstrated that Hyrcanian forests support highly diverse soil arthropod communities with a high proportion of endemic and potentially undescribed species, while substantial knowledge gaps remain regarding their diversity, community structure, spatial distribution, and ecological patterns across different habitats and protected areas (Shayanmehr et al. 2025; Tully et al. 2025). Consequently, below-ground taxa have received relatively limited ecological attention, highlighting the need for quantitative studies assessing soil faunal diversity across different soil depths and microhabitats to improve our understanding of forest ecosystem functioning and to support evidence-based conservation and sustainable forest management. Accordingly, the objectives of this study were to assess the seasonal variations in the density and diversity of soil-dwelling arthropods, investigate their vertical distribution across different soil depths, and evaluate the implications of these patterns for biodiversity conservation and sustainable ecosystem management in a protected Hyrcanian forest.

MATERIALS AND METHODS

Study Area. The study was conducted in the Semeskandeh Forest, a part of the Hyrcanian Forest in Mazandaran Province (Fig. 1). The Hyrcanian Forest forms a green belt along the northern slopes of the Alborz Mountains, extending to the southern coast of the Caspian Sea. It spans five provinces (North Khorasan, Golestan, Mazandaran, Gilan, and Ardabil), and covers approximately 1.9 million hectares up to 2800 m above sea level (Akhani et al. 2010; Nakhutsrishvili et al. 2015).

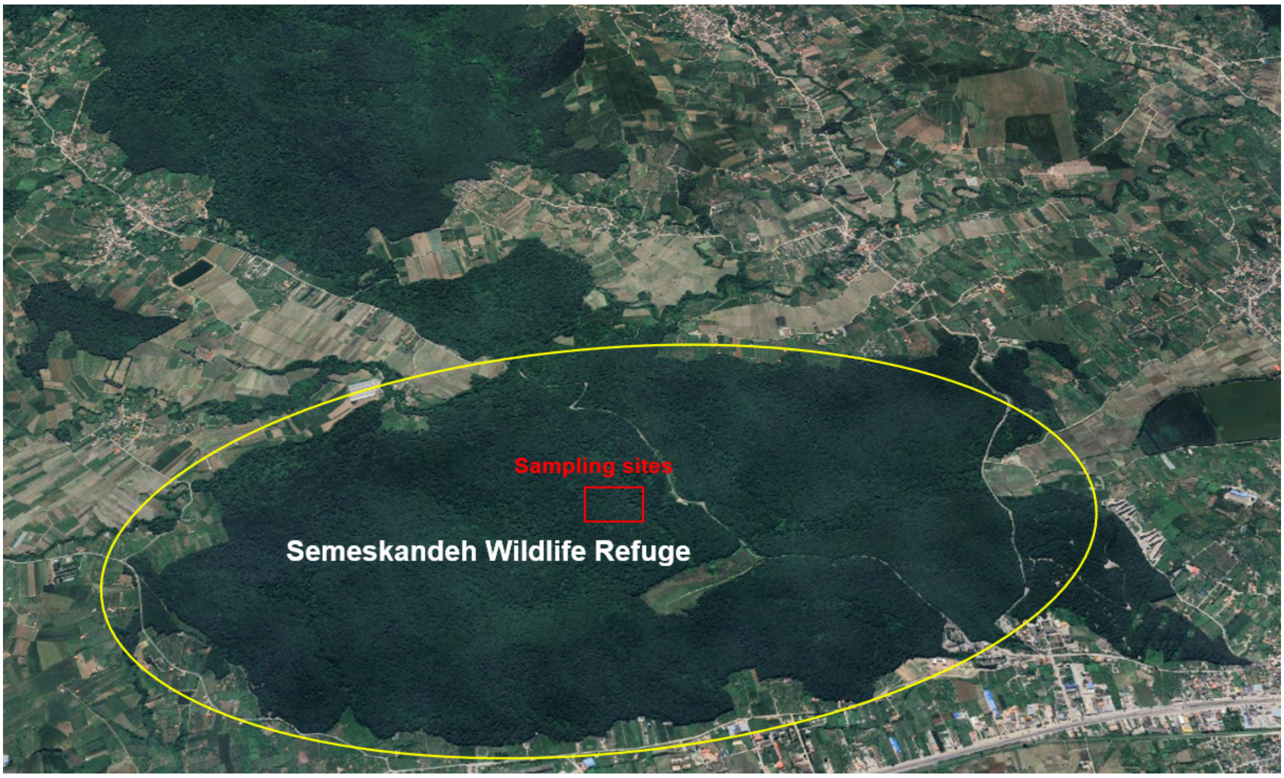

Figure 1. Semeskandeh forest in Mazandaran Province, northern Iran. The yellow outline indicates the boundary of the study forest, whereas the red rectangle indicates the sampling plots where soil arthropod samples were collected.

The forest exhibits diverse tree species, including Persian maple (*Acer velutinum* Boiss.), Cappadocian maple (*Acer cappadocicum* Gled.), Oriental beech (*Fagus orientalis* Lipsky), Caucasian alder (*Alnus subcordata* C.A.Mey.), European alder (*Alnus glutinosa* (L.) Gaertn.), chestnut-leaved oak (*Quercus castaneifolia* C.A.Mey.), Persian ironwood tree (*Parrotia persica* (DC.) C.A.Mey.), common hornbeam (*Carpinus betulus* L.), Scots elm (*Ulmus glabra* Huds.), field elm (*Ulmus minor* Mill.), white mulberry (*Morus alba* L.), European ash (*Fraxinus excelsior* L.), wild service tree (*Aria torminalis* (L.) Beck), Caucasian elm (*Zelkova carpinifolia* (Pall.) K.Koch), and Caucasian walnut (*Pterocarya fraxinifolia* (Lam.) Spach) (Gholizadeh et al. 2019; Ghorbanalizadeh & Akhani 2022). Semeskandeh Forest, covering approximately 1,041 hectares, is located in Mazandaran Province, 5 km southeast of Sari city along the Sari–Neka Road (36°32'–36°34'N, 53°07'–53°11'E) at an elevation of 50–90 m above sea level. The area has a temperate sub-humid climate, characterized by mild, humid winters and warm, relatively dry summers, with an average annual temperature of 15°C and mean annual precipitation of about 650 mm (Moradi et al. 2016). Soil types in the area include silty clay loam, silty loam, clay, silty clay, and clay loam, with a pH ranging from 6.2 to 7.9, close to neutral (Mehrafrooz Mayvan & Shayanmehr 2016).

Sampling methods. To sample soil-dwelling arthropods, specimens were collected from leaf litter (OL, F, H horizons) and soil at depths of 0–3 cm and 3–6 cm (Ah horizon). Eight samples, spaced at least 20 m apart, were taken in July, September, and November 2012, and in January, March, and May 2013, at two-month intervals. Samples for macrofauna were collected using a steel corer of 20 cm diameter (314 cm²), while mesofauna were sampled with a 5 cm diameter corer (19.625 cm²) (Kounda-Kiki et al. 2004; Chahartaghi et al. 2005, 2006; Palacios-Vargas et al. 2007). The corers were inserted into the soil, and the upper 10 cm of soil was collected and subsequently separated into the leaf litter, 0–3 cm, and 3–6 cm layers. Arthropods were extracted using a modified Berlese–Tullgren funnel consisting of individual plastic extraction units equipped with a wire mesh to support the soil samples and a 40-W incandescent lamp positioned above each sample to create a gradual heat and moisture gradient, forcing arthropods into collecting containers beneath the mesh, and were preserved in 75% ethanol. Specimens belonging to different groups were sent to the experts for precise species determination.

Taxonomic identification was carried out using available taxonomic keys, monographs, and regional faunal references relevant to each arthropod group. Insect larvae were treated as a separate category because they could not be reliably identified to order or family level. Specimens of Curculionidae (Coleoptera) were identified by Patrick Weil (Maison de la Nature et de l'Environnement, Pau, France), Carabidae (Coleoptera) by Ron Felix (Naturalis Biodiversity Center, Leiden, the Netherlands), Staphylinidae (Coleoptera) by Sinan Anlaş (Manisa Celal Bayar University, Manisa, Turkey), Formicidae (Hymenoptera) by Donat Agosti (Plazi, Bern, Switzerland), Isopoda by Stefano Taiti (Research Institute on Terrestrial Ecosystems, National Research Council, Florence, Italy), Diplopoda by Sergei Golovatch (Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia), Diplura by Alberto Sendra (Universidad de Alcalá, Madrid, Spain), and Pseudoscorpiones by Mehdi Nasirkhani (Shahid Bahonar University of Kerman, Kerman, Iran). These taxa were identified to the species level. Collembola specimens were identified mainly using the keys provided by Bretfeld (1999), Potapov (2001), Thibaud et al. (2004), Fjellberg (2007), and Jordana (2012) and were identified to the species level. Due to the extremely high diversity and taxonomic complexity of mites (Acari), as well as limitations in available diagnostic resources for many groups, mites were identified mainly at the family level by Mahdi Jalaeian (Rice Research Institute of Iran, Rasht, Iran).

Statistical Analysis. The data were recorded in Microsoft Excel. Diversity of soil macrofauna and mesofauna was calculated according to Shannon–Wiener as $H' = -\Sigma\, pi \ln pi$, with pi the ratio between the number of the ith species and the total number of species for each soil depth per sampling date (Pielou 1971; Ardakani 2007). Analysis of variance was used to analyze variations in the number of soil fauna species with sampling date and soil depth. Means were compared using the least significant difference (LSD) multiple range test at $p < 0.01$. Prior to statistical analysis, data were inspected for homogeneity of variance using the Levene test and log (x+1) transformed if necessary. Statistical analyses were performed using IBM SPSS Statistics version 21.0 (IBM Corp., Armonk, NY, USA) and Minitab Statistical Software version 16.0 (Minitab Inc., State College, PA, USA). The density values presented in Tables 3 and 4 represent monthly mean densities (mean ± SD) for each sampling month. The density ranges reported in the results refer to the minimum and maximum monthly mean densities observed during the sampling period.

RESULTS

Species composition

Soil macrofauna. A total of over 5,000 soil macrofauna individuals, representing various taxonomic groups, including insects (class Insecta), centipedes (class Chilopoda), millipedes (class Diplopoda), spiders (class Arachnida), and isopods (order Isopoda), were collected across different seasons and soil depths. Among them, Hexapods exhibited the highest density, followed by millipedes, while the lowest density was observed in spiders (Fig. 2). The class Insecta assemblage included several orders such as Blattodea, Heteroptera, Hymenoptera, and Coleoptera. Hymenoptera dominated the insect assemblage, with the family Formicidae accounting for 52% of individuals, followed by Coleoptera (44%), and Diptera (3%). Overall, a total of 70 soil-dwelling macrofauna species, belonging to 58 genera, 14 families, and 4 orders, were collected and identified from Semeskandeh Forest (Table 1).

Soil mesofauna. A total of over 6,400 mesofauna individuals were collected. The mesofauna community included mites (subclass Acari), springtails (class Collembola), proturans (class Protura), diplurans (class Diplura), psocids (class Insecta: order Psocoptera), and pseudoscorpions (class Arachnida: order Pseudoscorpiones). Among these groups, mites (45%) and springtails (40%) were the most abundant taxa (Fig. 3). Within subphylum Hexapoda, a total of 19 Collembola species, belonging to 17 genera and 10 families, were identified (Table 2). Additionally, 2 Diplura species (1 genus, 2 subgenera, 2 species) and 3 Psocoptera species (3 genera, 3 species) were recorded. Excluding Hexapoda, 4 pseudoscorpion species were collected. Also, mites comprised 33 species from 16 families within the orders Oribatida (superorder Acariformes), Mesostigmata (superorder Parasitiformes) and Trombidiformes (superorder Acariformes). The families within the Mesostigmata order included Uropodidae, Macrochelidae, Rhodacaridae, Phytoseiidae, Veigaiidae, Pachylaelapidae, Laelapidae, Parholaspididae, and Epicriidae.

The families within the Trombidiformes order included Trombidiidae, Cunaxidae, Pseudocheylidae, Bdellidae, Erythraeidae, Labidostomatidae, and Caligonellidae. Within Mesostigmata, Uropodidae was the most abundant family (16%), while Epicriidae was the least abundant (1%) (Fig. 4). In Trombidiformes, Cunaxidae showed the highest abundance (17%), whereas Labidostomatidae was the least numerous (1%).

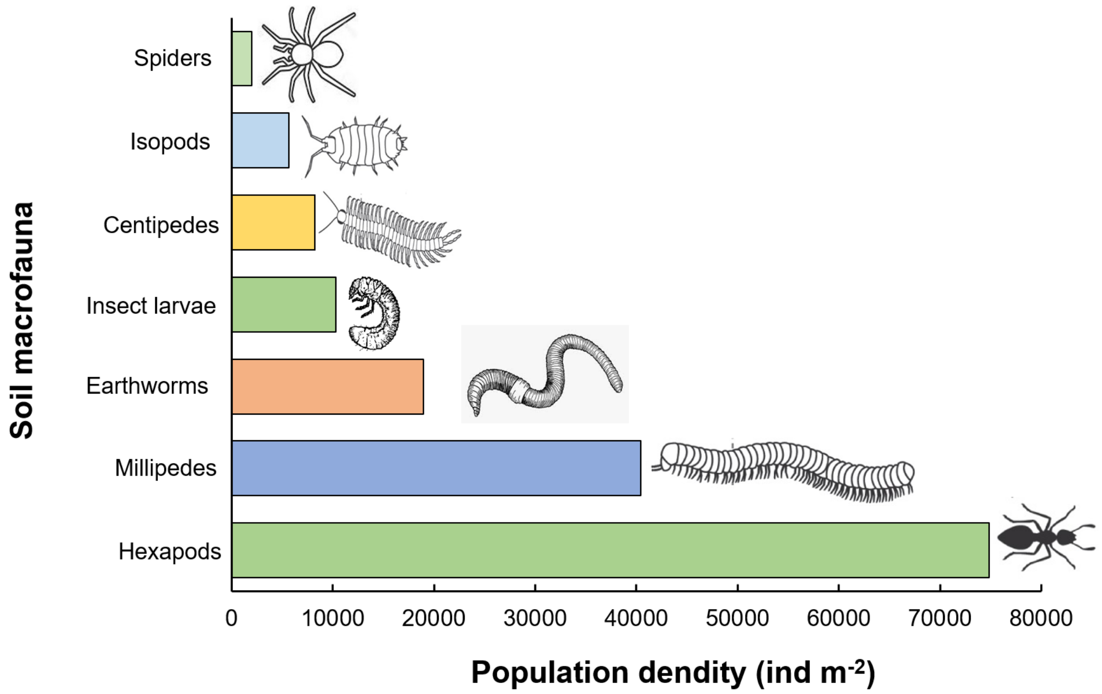

Figure 2. Composition and population density of macrofauna collected from different soil layers in Semeskandeh Forest (Mazandaran Province, Iran).

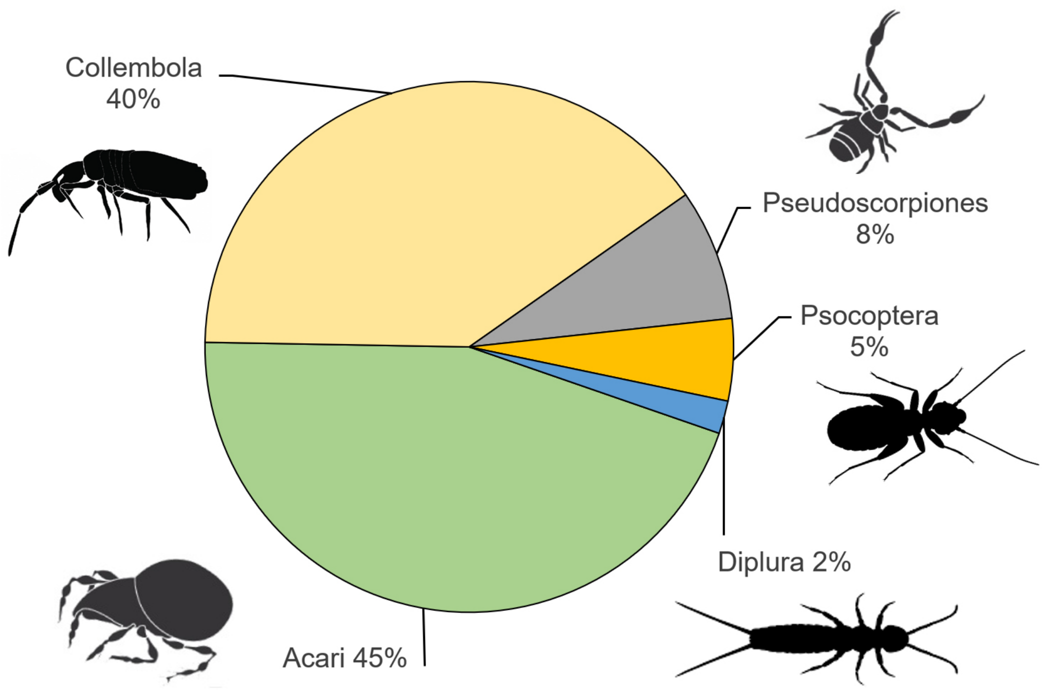

Figure 3. Abundance percentage of soil mesofauna collected from different layers of Semeskandeh Forest soil.

Table 1. Soil macrofauna recorded in the Semeskandeh Forest (Mazandaran Province, Iran).

Categories	Family	Species
Class Chilopoda	Dignathodontidae	*Henia bicarinata* (Meinert, 1870)
	Lithobiidae	*Lithobius chalusensis* Matic, 1969
		Lithobius forficatus (Linnaeus, 1758)
Class Diplopoda	Blaniulidae	*Nopoiulus iranicus* Enghoff, 1984
	Julidae	*Amblyiulus* sp.
		Cylindroiulus treptoflagellum Read, 1992
		Leptoiulus sp.
	Lophoproctidae	*Lophoproctus lucidus* (Chalande, 1888)
	Paradoxosomatidae	*Strongylosoma kordylamythrum* Attems, 1898
	Polydesmidae	*Brachydesmus ferrugineus* Lohmander, 1936
Order Isopoda	Porcellionidae	*Brevurus masandaranus* Schmalfuss, 1986
	Trachelipodidae	*Trachelipus pieperi* Schmalfuss, 1986
Order Coleoptera	Attelabidae	*Neocoenorrhinus* (*Schoenitemnus*) *minutus* (Herbst, 1797)
	Carabidae	*Acinopus laevigatus* (Ménétriés, 1832)
		Acupalpus maculatus (Schaum, 1860)
		Amara aenea (De Geer, 1774)
		Amara apricaria (Paykull, 1790)
		Amara familiaris (Duftschmidt, 1812)
		Amara ovata (Fabricius, 1792)
		Anchomenus dorsalis (Pontoppidan, 1763)
		Bembidion (*Phyla*) *incommodum* Netolitzky, 1926
		Brachinus brevicollis (Motschulsky, 1844)
		Broscus karelini (Zoubkoff, 1837)
		Carabus (*Shodristocarabus*) *adamsi* (Adams, 1817)
		Chlaenius festivus (Panzer, 1796)
		Chlaenius tristis (Schaller, 1783)
		Cicindela monticola Ménétriés, 1832
		Cylindera germanica (Linnaeus, 1758)
		Cymindis andreae (Ménétries, 1832)
		Distichus planus (Bonelli, 1813)
		Ditomus calydonius oriens (Dvorak, 1993)
		Harpalus convexus Faldermann, 1836
		Harpalus rufipes (De Geer, 1774)
		Harpalus smyrnensis medicus (Kataev, 1993)
		Odontocarus asiaticus (Chaudoir, 1852)
		Parophonus planicollis (Dejean, 1829)
		Poecilus cupreus (Linnaeus, 1758)
		Sphaerotachys hoemorrhoidalis (Ponza, 1805)
		Stenolophus proximus (Dejean, 1829)
		Stenolophus abdominalis persicus Mannerheim, 1844
		Syntomus obscuroguttatus (Duftschmid, 1812)
		Trechus quadristriatus (Schrank, 1781)
	Curculionidae	*Asproparthenis punctiventris* (Germar, 1824)
		Bagous bagdatensis Pic, 1904
		Larinus centaurea Oliver, 1807
		Lixus angustatus (Fabricius, 1775)
		Lixus (Broconius) rubicundus Zoubkoff, 1833
		Polydrusus (*Scythodrusus*) *inustus* Germar, 1824
		Sitophilus granarius (Linnaeus, 1758)
		Sitophilus oryzae Hustache, 1930
		Sitophilus zeamais (Motschulsky, 1855)
		Sternuchopsis karelini (Boheman, 1844)
	Staphylinidae	*Physetops tataricus* (Pallas, 1773)
		Gauropterus sanguinipes (Reitter, 1889)
		Ocypus curtipennis Motschulsky, 1849
		Quedius mixtus Eppelsheim, 1890
		Paederus balcanicus Koch, 1938
		Astenus klapperichi Coiffait, 1980

Categories	Family	Species
Order Hymenoptera	Formicidae	Aphaenogaster subterranea (Latreille, 1798)
		Formica cunicularia Latreille, 1798
		Formica sanguinea Latreille, 1798
		Lepisiota semenovi (Ruzsky, 1905)
		Messor denticulatus Santschi, 1927
		Myrmica bergi Ruzsky, 1902
		Paratrechina longicornis (Latreille, 1802)
		Pheidole pallidula (Nylander, 1849)
		Ponera sp.
		Tapinoma karavaievi Emery, 1925
		Temnothorax parvulus (Schenck, 1852)

Table 2. Soil mesofauna recorded in the Semeskandeh Forest (Mazandaran Province, Iran).

Category	Family	Species
Order Pseudoscorpiones	Chthoniidae	*Chthonius* (*Chthonius*) *shelkovnikovi* Redikorzev, 1930
		Chthonius (*Ephipiochthonius*) *tetrachelatus* (Preyssler, 1790)
	Neobisiidae	*Roncus corimanus* Beier, 1951
		Roncus viti Mahnert, 1974
Class Collembola	Dicyrtomidae	*Dicyrtoma ghilarovi* Bretfeld, 1996
		Dicyrtoma sp.
	Entomobryidae	*Heteromurus major* (Moniez, 1889)
		Heteromurus nitidus (Templeton, 1836)
		Lepidocyrtus sp.
		Pseudosinella octopunctata Börner, 1901
	Hypogastruridae	*Ceratophysella stercoraria* Stach, 1963
	Isotomidae	*Folsomia penicula* Bagnall, 1939
		Isotomiella minor (Schäffer, 1896)
		Isotomurus italicus Carapelli, Frati, Fanciulli & Dallai, 1995
	Katiannidae	*Sminthurinus elegans* (Fitch, 1863)
	Neanuridae	*Persanura hyrcanica* Mehrafrooz Mayvan, Shayanmehr, Smolis & Skarżyński, 2015
	Onychiuridae	*Heteraphorura japonica* (Yosii, 1967)
	Sminthuridae	*Caprainea marginata* (Schött, 1893)
		Lipothrix lubbocki (Tullberg, 1872)
		Paralipothrix cf. *natalicius* (Ellis, 1974)
		Sminthurus ghilarovi Stebaeva, 1966
		Sphaeridia sp.
	Tomoceridae	*Tomocerus vulgaris* (Tullberg, 1871)
Class Diplura	Campodeidae	*Campodea* (*Campodea*) *fragilis* Meinert, 1865
		Campodea (*Dicampa*) *sprovierii* Silvestri, 1932
Order Psocoptera	Ectopsocidae	*Ectopsocopsis cryptomeriae* (Enderlein, 1907)
	Trogiidae	*Lepinotus reticulatus* Enderlein, 1904
	Liposcelididae	*Liposcelis paeta* Pearman, 1942

Population density and biodiversity

Macrofauna. The total density of soil macrofauna ranged from 32,746 to 42,312 individuals m^{-2} in the litter layer, from 11,776 to 14,408 individuals m^{-2} in the 0–3 cm soil depth, and from 7,784 to 12,267 individuals m^{-2} in the 3–6 cm soil depth (Table 3). In the litter layer, the highest density was observed in autumn, particularly in September. After January, macrofaunal density increased with rising temperatures, reaching a peak in September. In the 0–3 cm layer, the highest densities were recorded in July and November, with numbers remaining relatively stable throughout the year, except for minor increases in July and November. The 3–6 cm layer, which had the lowest densities among the three layers, reached its highest density in January. The highest diversity value was recorded in the litter layer during autumn (September) (Table 3), whereas the lowest value occurred in the 3–6 cm soil depth in March. Throughout the year, diversity values in the litter layer were consistently higher than in the two deeper layers, except in January, when the 0–3 cm layer exhibited a slightly higher diversity value than the litter layer.

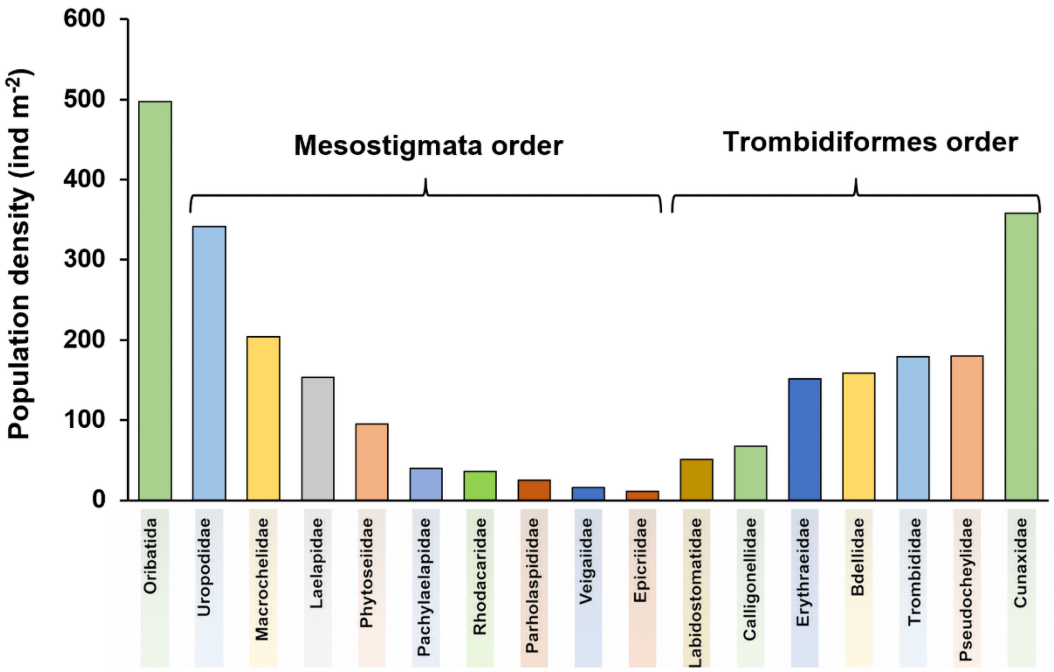

Figure 4. Population density of soil mites (Oribatida, Mesostigmata and Trombidiformes orders) in Semeskandeh Forest.

Table 3. Seasonal changes in density and diversity of soil macrofauna at three soil depths recorded in the Semeskandeh Forest (means ± SD).

	January	March	May	July	September	November	Average
Density (ind. m^{-2})							
Leaf litter	1831±455	820±67	764±46	2512±534	3213±1335	1429±360	1761±466
0-3 cm	860±215	788±199	776±110	1441±458	951±188	1441±458	1042±271
3-6 cm	784±250	243±51	271±40	426±183	701±279	744±209	528±168
Total	3475±920	1851±317	1811±196	4379±1175	4565±1802	3614±1027	3331±905
Diversity (*H´*)							
Leaf litter	1.48±0.13	1.91±0.33	1.99±0.31	1.85±0.31	2.32±0.23	1.79±0.25	1.89±0.29
0-3 cm	1.54±0.14	1.32±0.41	1.51±0.33	1.83±0.37	1.79±0.41	1.60±0.27	1.60±0.34
3-6 cm	1.10±0.17	0.95±0.27	1.41±0.31	1.22±0.59	1.83±0.51	1.13±0.54	1.27±0.43
Total	4.13±0.44	4.19±1.01	4.92±0.95	4.91±1.27	5.96±1.15	4.53±1.06	4.77±1.07

Table 4. Seasonal changes in density and diversity of soil mesofauna at three soil depths recorded in the Semeskandeh Forest (means ± SD).

	January	March	May	July	September	November	Average
Density (ind. m^{-2})							
Leaf litter	847±116	1070±160	903±99	995±177	1078±164	839±211	988±154
0-3 cm	473±125	672±80	637±123	453±107	720±176	417±93	562±117
3-6 cm	441±90	477±88	445±88	238±88	350±67	417±93	395±86
Total	1763±332	2221±329	1986±311	1687±372	2149±408	1675±398	1913±358
Diversity (*H´*)							
Leaf litter	2.29±0.13	2.38±0.21	2.29±0.13	2.11±0.38	2.34±0.11	2.24±0.21	2.27±0.19
0-3 cm	2.03±0.14	2.21±0.17	2.02±0.43	1.88±0.33	2.29±0.31	1.97±0.19	2.06±0.26
3-6 cm	2.01±0.17	2.14±0.18	2.11±0.23	1.59±0.35	1.51±0.15	1.97±0.19	1.88±0.21
Total	6.33±0.44	6.73±0.56	6.42±0.79	5.5±1.06	6.14±1.57	6.18±0.59	6.23±0.66

Among the soil macrofauna, ants (family Formicidae) exhibited the highest population density and community diversity across all soil depths. Their density ranged approximately from 120 to 1,470 individuals m^{-2} in the litter layer, from 175 to 400 individuals m^{-2} in the 0–3 cm soil depth, and from 110 to 690 individuals m^{-2} in the 3–6 cm layer. The highest densities were recorded in the litter layer during autumn, particularly in September (Fig. 5A), after which it declined with decreasing temperatures. The lowest densities across the three soil depths occurred in the 3–6 cm layer during spring (May).

Diversity showed seasonal variation, with the highest values observed in the litter layer in September and the lowest in the 0–3 cm layer during winter (January). Throughout the year, diversity in the litter layer remained higher than in the deeper soil depths, except in January (winter), when the 0–3 cm layer exhibited a slightly higher value than the litter layer (Fig. 5B). Millipedes exhibited variable densities across soil depths. Their densities ranged approximately from 220 to 770 individuals m^{-2} in the litter layer, from 170 to 740 individuals m^{-2} in the 0–3 cm soil depth, and from 90 to 150 individuals m^{-2} in the 3–6 cm depth (Fig. 5C). Peaks of density were recorded in July during the summer, while density decreased significantly in May (Fig. 5C). The results indicate that millipede species in this study remained active throughout the year in Semeskandeh Forest. Vertical distribution analysis showed that millipedes were relatively evenly distributed across all soil depths during different seasons, although their density was generally higher in the litter layer, except in November, when densities in the 0–3 cm layer exceeded those in the litter and 3–6 cm layers. Diversity followed a similar pattern, with the highest values observed in the litter layer in September and the lowest in the 3–6 cm layer in January (Fig. 5D). Soil-dwelling centipedes exhibited densities ranging from approximately 51.41 to 142.08 individuals m^{-2} in the litter layer, from 56.34 to 120.03 individuals m^{-2} in the 0–3 cm soil depth, and from 29.39 to 51.44 individuals m^{-2} in the 3–6 cm layer. Peak densities occurred in September during autumn, whereas density declined significantly in March and May. The results also indicated that the three species recorded in this study were active throughout the year in Semeskandeh Forest. Vertical distribution analysis showed that centipedes were relatively evenly distributed across all soil depths throughout the seasons, although they generally showed higher densities in the litter layer, except in July and January, when densities in the 0–3 cm layer exceeded those in the litter and 3–6 cm layers (Fig. 5E). Diversity patterns mirrored these trends, with the highest value observed in the 0–3 cm layer in July (summer) and the lowest in the 3–6 cm layer during the same month. Overall, diversity in the litter layer remained higher than in the other layers throughout most of the year, except in January and July, when the 0–3 cm layer exhibited slightly higher diversity than the litter layer (Fig. 5F).

Mesofauna. Densities of soil mesofaunal arthropods ranged from 839.81 to 1,077.66 individuals m^{-2} in the litter layer, from 417.83 to 720.38 individuals m^{-2} in the 0–3 cm soil depth, and from 238.85 to 477.71 individuals m^{-2} in the 3–6 cm layer (Table 4). Overall, mesofaunal arthropod densities remained relatively stable across seasons in Semeskandeh Forest. Peak densities were recorded in the litter layer and in the 0–3 cm soil depth during autumn (September). In the 0–3 cm soil depth, densities showed moderate seasonal fluctuations, with the highest value recorded in September and the lowest in November. The lowest densities among the three soil depths were observed in the 3–6 cm depth during July (summer). The diversity of mesofaunal arthropods ranged from 2.11 to 2.38 individuals m^{-2} in the litter layer, from 1.88 to 2.29 individuals m^{-2} in the 0–3 cm soil depth, and from 1.51 to 2.14 individuals m^{-2} in the 3–6 cm soil depth (Table 4). The highest diversity value was observed in the litter layer during March and September, whereas the lowest diversity occurred in the 0–3 cm soil depth in July. Throughout the year, diversity values in the litter layer were consistently higher than those in the deeper soil depths and remained relatively stable across all months. The density and diversity of the most abundant mesofaunal groups, including Collembola, Acari, Diplura, and Pseudoscorpiones, were further examined across different soil depths and seasons.

Density of Collembola ranged approximately from 1,800 to 5,500 individuals m^{-2} in the litter layer, 1,250 to 2,500 individuals m^{-2} in the 0–3 cm depth, and 750 to 3,100 individuals m^{-2} in the 3–6 cm depth. Their density peaked during the cold seasons, with the highest density recorded in the litter layer in winter (January). In the 0–3 cm depth, the maximum density was also observed in January, while overall fluctuations remained relatively stable throughout the year, except for a decline in May, followed by an increase in July and September (Fig. 6A).

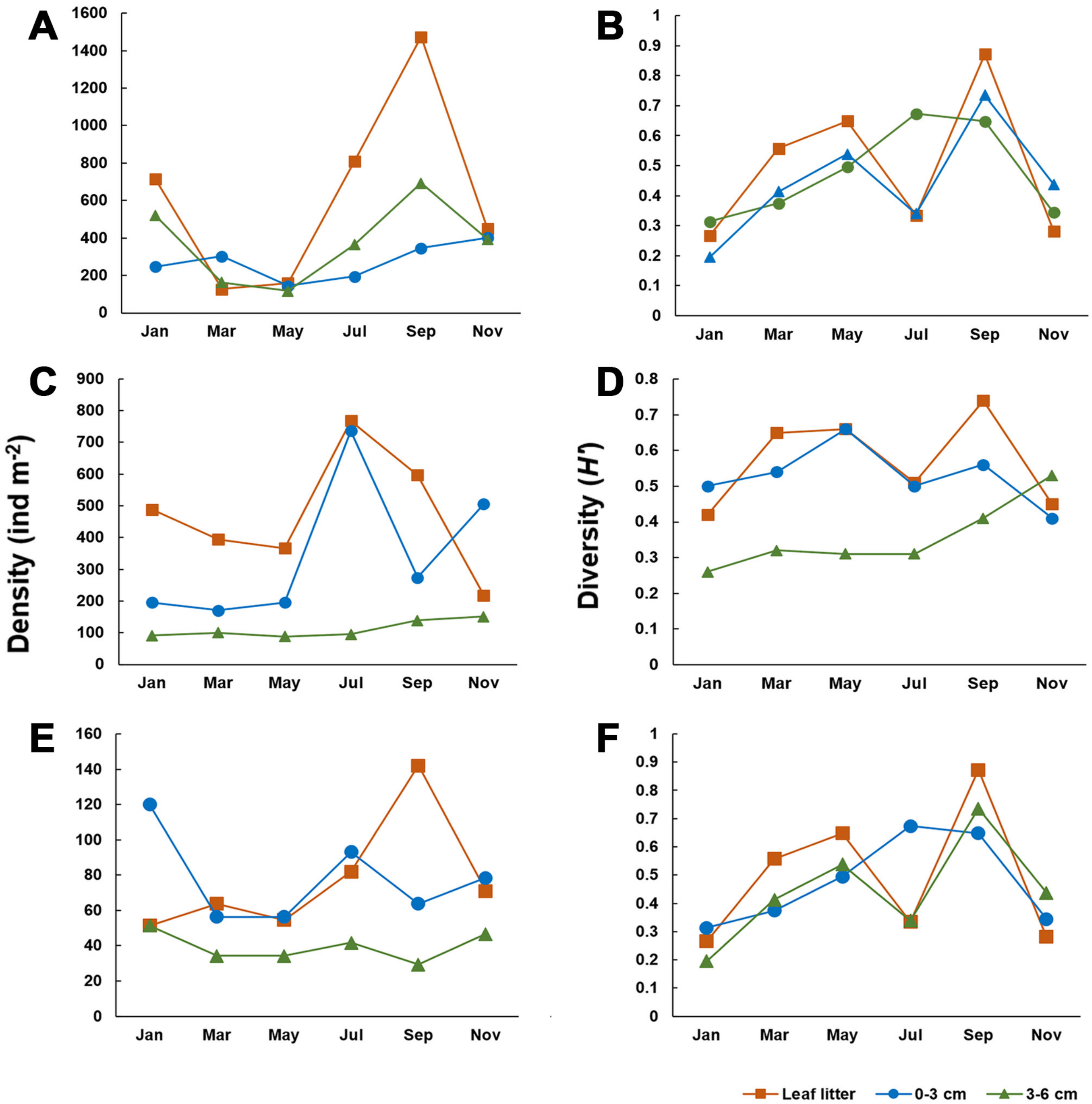

Figure 5. Seasonal changes in density (ind. m^{-2}) (A, C, E), and diversity (B, D, F) at different soil depths. **A–B.** Formicidae; **C–D.** Diplopoda; **E–F.** Chilopoda. Samples were taken at bimonthly intervals in the leaf litter (OL, F, H), 0–3 and 3–6 cm soil depths.

The lowest density across all depths occurred in the 3–6 cm depth during July (summer). In general, higher densities in the 0–3 cm depth were associated with cold and humid periods, particularly in January and September. Also, community diversity of springtails ranged from 0.86 to 1.50 in the litter layer, 0.61 to 1.07 in the 0–3 cm layer, and 0.55 to 1.04 in the 3–6 cm depth. The highest diversity value was recorded in the litter layer during January and March, whereas the lowest value occurred in the 0–3 cm depth in July (Fig. 6B). Overall, diversity in the litter layer remained relatively stable throughout the year, except in September, when the 0–3 cm depth exhibited a slightly higher diversity value. Density of soil-dwelling mites ranged approximately from 770 to 2056 individuals m^{-2} in the litter layer, 573 to 1046 individuals m^{-2} in the 0–3 cm depth, and 425 to 861 individuals m^{-2} in the 3–6 cm depth. Density remained relatively stable across months, with the highest values recorded in the litter layer during March and September (Fig. 6C). In the 0–3 cm depth, density peaked in September and was lowest in May, while in the 3–6 cm depth the lowest density occurred in January.

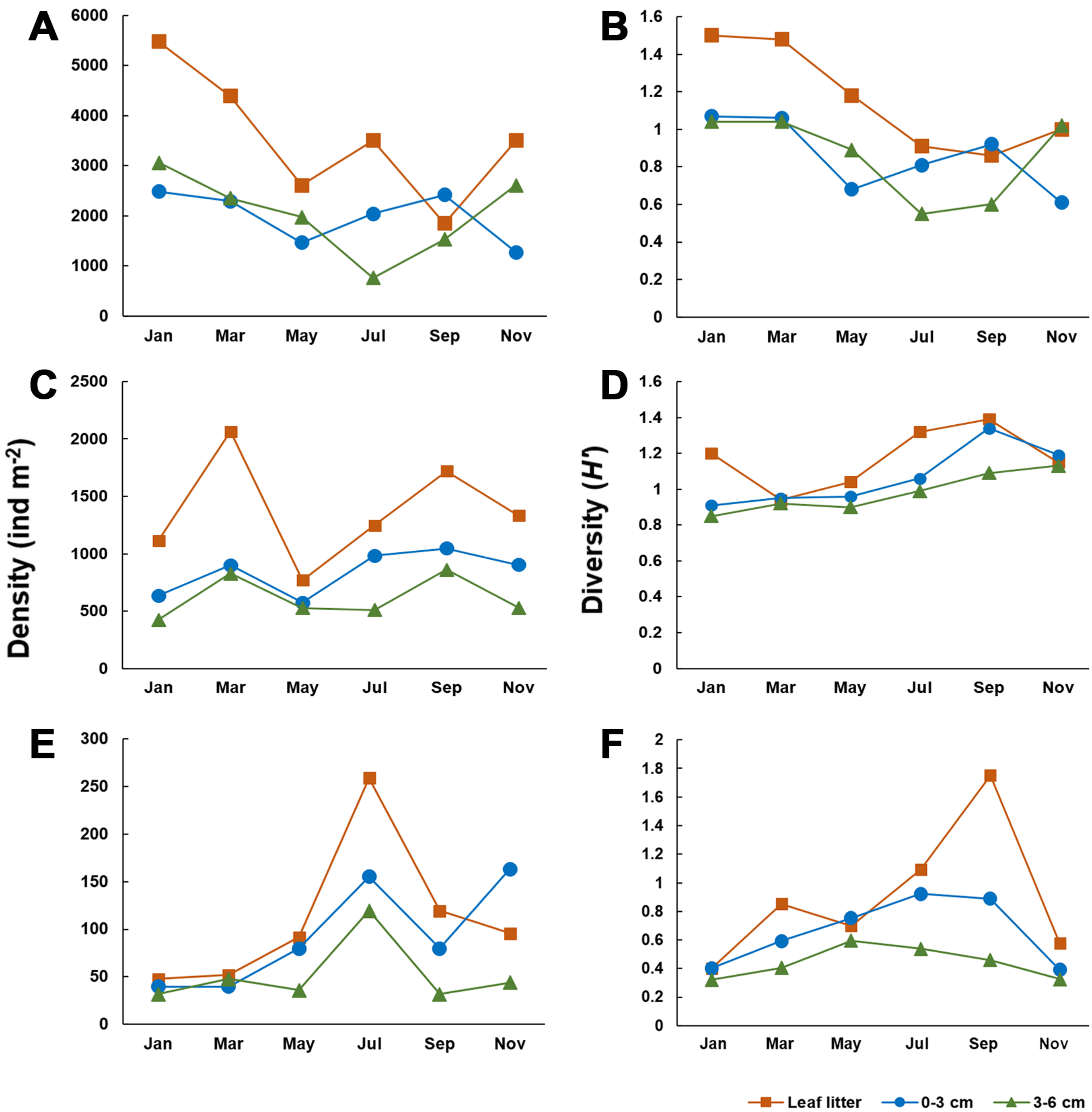

Figure 6. Seasonal changes in density (ind. m^{-2}) (A, C, E), and diversity (B, D, F) at different soil depths. **A–B.** Collembola; **C–D.** Acari; **E–F.** Pseudoscorpiones. Samples were taken at bimonthly intervals in the leaf litter (OL, F, H), 0–3 and 3–6 cm soil depths.

The diversity value of soil mites was highest in September in the litter and 0–3 cm depths, whereas the lowest value was recorded in the 3–6 cm depth in January. In this deeper depth, diversity remained almost constant throughout the year (Fig. 6D). The highest density of pseudoscorpions was recorded in the litter layer in July (Fig. 6E). In the litter layer, their density peaked in July, while the lowest densities were observed in January. Following May, density increased sharply, reaching a peak in July. After September, densities declined toward November. A similar seasonal trend was observed in both the 0–3 cm and 3–6 cm soil depths, with the lowest values in January and March. The highest diversity of pseudoscorpion assemblages was observed in the litter layer during September, while the lowest was recorded in the 3–6 cm depth in January (Fig. 6F). Community diversity increased gradually from March, reaching its peak in September in the litter layer, and then declined again with decreasing temperatures. In contrast, the 0–3 cm and 3–6 cm depths showed no significant differences in diversity across months, maintaining a relatively stable trend throughout the year (Fig. 6F).

DISCUSSION

Over 10,000 individuals of various soil-dwelling animal groups were collected in the present study. Our results align with previous studies, showing that the highest densities occurred in the litter layer. The litter plays a pivotal role for soil invertebrates' populations, functioning as a protective cover against erosion, regulating soil moisture and temperature, and serving as a major source of organic matter (Gomyo & Kuraji 2016; Li et al. 2017; Marsden et al. 2020; Zhang et al. 2023; Liang 2024). In general, old-growth forests, due to their structural complexity, richer litter composition, and favorable microclimatic conditions, provide habitats that support higher soil faunal density and diversity (Burton & Eggleton 2016; Pereira et al. 2017; Pestana et al. 2020; Venuste 2020; Adiningrat et al. 2025). In particular, mites and collembolans were the most diverse mesofaunal taxa, and ants were dominant in the macrofauna community (Takeda & Abe 2001; Gagnarli et al. 2015; Ghiglieno 2020). The high density of ants may be attributed to their notable tolerance to environmental stress and even chemical pollution, allowing them to maintain large populations under varying soil conditions (Hasin & Booncher 2020). Semeskandeh Forest, as part of the ancient Hyrcanian forests, has been protected for more than four decades with limited human disturbance. Comparable studies on seasonal and vertical distribution patterns of both soil macrofauna and mesofauna in the Hyrcanian forests remain very limited. Therefore, the present study provides baseline information on the composition, density, diversity, and seasonal dynamics of soil arthropods in this unique forest ecosystem. Nevertheless, anthropogenic impacts such as industrial logging, heavy machinery traffic, agricultural expansion, and chemical inputs remain important pressures in the Hyrcanian forests and may adversely affect soil fauna communities (Jourgholami et al. 2019).

The present study revealed clear seasonal and vertical patterns in the density and diversity of soil fauna across different soil depths. Previous studies have shown that environmental factors such as vegetation type, rainfall, soil pH, and microclimate can influence the density and composition of soil fauna (Kelleher & Choi 2020). Plant cover has also been reported to affect both resource availability and habitat structure, with changes in plant community composition leading to shifts in soil arthropod assemblages (Kelleher & Choi 2020). Likewise, diverse vegetation generally supports more abundant and diverse soil fauna by providing food resources and suitable habitats for reproduction (Utami et al. 2019). Seasonal precipitation and soil moisture are among the major drivers of soil faunal dynamics, particularly for mesofaunal groups such as collembolans, which often reach peak densities during wetter periods, whereas mite populations may decline under dry conditions (Wiwatwitaya & Takeda 2005; Palacios-Vargas et al. 2007). Extreme temperature fluctuations may also influence soil fauna, especially epigeic taxa inhabiting the litter layer. In addition, population dynamics are often density-dependent, with periods of high density followed by declines associated with food limitation, intra-specific competition, predation, or parasitism (Sibly & Hone 2002; Pequeno et al. 2020). According to previous studies, soils in Semeskandeh Forest are slightly acidic to nearly neutral (pH 6.2–7.9), a condition that may influence the distribution of certain taxa, as some groups, such as isopods, are known to prefer neutral to alkaline soils (van Straalen 1998).

The seasonal density patterns observed in the present study suggest that vertical redistribution may have occurred in some soil arthropod groups in response to seasonal changes in environmental conditions. In particular, Collembola exhibited the clearest pattern, with a marked decline in litter layer density during September accompanied by a relative increase in the 0–3 cm soil depth, which may reflect a downward movement in response to changes in soil temperature or moisture. A similar but less consistent pattern was observed for Chilopoda. In contrast, Acari, Pseudoscorpiones, Diplopoda, and Formicidae generally showed parallel seasonal fluctuations across soil depths rather than reciprocal changes between adjacent horizons, providing little evidence for consistent vertical migration. Overall, these observations suggest that vertical redistribution, where present, was taxon-specific and likely represented a behavioral response of certain groups rather than a general pattern across the entire soil fauna community. Beyond these seasonal shifts, vertical stratification further shaped community patterns, with both density and diversity of soil fauna decreasing sharply with increasing soil depth. The litter layer, as the main entry point of organic matter into the soil, sustains the highest densities. While the reduction in organic matter content with depth partly explains this pattern, other factors such as microclimatic shifts and habitat constraints also contribute (Berg 2012; Moradi et al. 2020). Interestingly, in line with Frouz et al. (2004), our results showed that the diversity of some soil faunal groups increased in deeper depths during colder months, supporting the taxon-specific patterns of vertical redistribution observed in the present study rather than a general refuge strategy across the entire soil fauna community.

Beyond biodiversity assessment, the observed seasonal and vertical patterns of soil fauna are important for forest soil health and sustainable soil management. Soil fauna contribute to litter fragmentation, decomposition, nutrient cycling, and microbial activity, which helps maintain soil structure and soil ecological functions (Zan et al. 2022; Zhang et al. 2023; Angst et al. 2024). In forest ecosystems, these processes are closely linked to carbon cycling because soil fauna can affect both the release of carbon and nitrogen from decomposing litter and the formation and stability of more readily decomposed and more stable soil organic matter (Anthony et al. 2023; Zhang et al. 2023; Angst et al. 2024). Therefore, conserving litter layers and reducing human disturbances such as soil compaction, intensive logging, and litter removal should be considered important management strategies for maintaining soil faunal diversity, soil health, and the carbon storage potential of Hyrcanian forest soils. Future studies should integrate soil faunal diversity with measurements of soil organic carbon fractions, microbial community structure, enzyme activities, soil respiration, and physicochemical soil properties to better clarify the mechanisms linking soil fauna, soil health, and carbon storage under seasonal and environmental changes.

Considering the key role of soil fauna in maintaining ecosystem health, assessing changes in soil faunal diversity and species composition in the valuable Hyrcanian forests is of great importance. In the present study, soil samples were collected across different soil depths and seasons over one year, revealing that even small volumes of soil harbor numerous macrofaunal and mesofaunal groups at various depths. The protected status of Semeskandeh Forest and the lack of human disturbance significantly contributed to high density and diversity values. In contrast, most Hyrcanian forests remain unprotected and are heavily impacted by human activities, which can severely reduce soil fauna populations and disrupt ecosystem balance. The observed seasonal patterns suggest that changes in soil moisture and temperature may have influenced the population dynamics of forest soil fauna. Previous studies have shown that forest age, management practices, and vegetation diversity directly influence soil fauna density and diversity, which in turn play a crucial role in improving soil physicochemical properties, promoting plant growth, and sustaining overall forest ecosystem health. Given the ecological importance of soil fauna and the vulnerability of unprotected forests, targeted efforts to study and conserve these organisms and their habitats are essential.

AUTHOR CONTRIBUTIONS

The authors confirm their contribution to the paper as follows: M. Mehrafrooz Mayvan: Investigation, Methodology, Data curation, Formal analysis, Visualization, and Writing – original draft; M. Shayanmehr: Conceptualization, Methodology, Supervision, Validation, Project administration, and Writing – review & editing. The authors read and approved the final version of the manuscript.

FUNDING

This research received no specific grant from any funding agencies.

AVAILABILITY OF DATA AND MATERIAL

All source data used in this study are cited in the Materials and Methods section. The specimens listed in this study are deposited in Sari University of Agricultural Sciences and Natural Resources (SANRU) and are available from the curator upon request.

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This study only included arthropod material, and all required ethical guidelines for the treatment and use of animals were strictly adhered to in accordance with international, national, and institutional regulations. No human participants were involved in any studies conducted by the authors for this article.

CONSENT FOR PUBLICATION

Not applicable.

CONFLICT OF INTERESTS

The authors declare that there is no conflict of interest regarding the publication of this paper.

GENERATIVE AI STATEMENT

The authors used ChatGPT (OpenAI) solely for English language editing and grammatical correction. Generative AI was not used for content generation, data analysis, or interpretation of the results.

ACKNOWLEDGMENTS

The first author is most grateful to Sari Agricultural Sciences and Natural Resources University (SANRU) for financial support during his Master of Science dissertation.

REFERENCES

Adiningrat, D.P., Siegenthaler, A., Schlund, M., Wang, T., Skidmore, A.K., Rousseau, M. & Heurich, M. (2025) Effect of forest structural attributes on soil microbial diversity in mixed temperate forests. *Plant Soil*, 517, 867–885. https://doi.org/10.1007/s11104-025-07907-4

Akhani, H., Djamali, M., Ghorbanalizadeh, A. & Ramezani, E. (2010) Plant biodiversity of Hyrcanian relict forests, N Iran: An overview of the flora, vegetation, palaeoecology and conservation. *Pakistan Journal of Botany*, 42, 231–258.

Anthony, M.A., Bender, S.F. & van der Heijden, M.G.A. (2023) Enumerating soil biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, 120 (33), e2304663120. https://doi.org/10.1073/pnas.2304663120

Angst, G., Potapov, A., Joly, F.X., Angst, Š., Frouz, J., Ganault, P. & Eisenhauer, N. (2024) Conceptualizing soil fauna effects on labile and stabilized soil organic matter. *Nature Communications*, 15, 5005. https://doi.org/10.1038/s41467-024-49240-x

Ardakani, M.R. (2007) *Ecology*. University of Tehran Press, Tehran. 340 pp.

Berg, M.P. (2012) Patterns of biodiversity at fine and small spatial scales. In: Wall, D.H., Bardgett, R.D., Behan-Pelletier, V., Herrick, J.E., Jones, T.H., Ritz, K., Six, J., Strong, D.R. & van der Putten, W.H. (eds) *Soil Ecology and Ecosystem Services*. Oxford University Press, UK, pp. 136–152. https://doi.org/10.1093/acprof:oso/9780199575923.003.0014

Berry, G., Tanruean, K., Napiroon, T., Saetang, W., Penpo, M., Duangrod, S. & Poolprasert, P. (2020) The community structure of beneficial and harmful arthropod fauna in rice field ecosystems in lower Northern Thailand. *The Journal of Applied Science*, 19 (1), 1–12. https://doi.org/10.14416/j.appsci.2020.01.001

Bretfeld, G. (1999) Synopses on Palaearctic Collembola. V. 2. Symphypleona. *Abhandlungen und Berichte des Naturkundemuseums, Görlitz*, 71 (1), 1–318.

Burton, V.J. & Eggleton, P. (2016) Microhabitat heterogeneity enhances soil macrofauna and plant species diversity in an ash - field maple woodland. *European Journal of Soil Biology*, 75, 97–106. https://doi.org/10.1016/j.ejsobi.2016.04.012.

Cayuela, M.L., Clause, J., Frouz, J. & Baveye, P.C. (2020) Interactive Feedbacks between soil fauna and soil processes. *Frontiers in Environmental Science*, 8, 14, https://doi.org/10.3389/fenvs.2020.00014

Chahartaghi, M., Langel, R., Scheu, S. & Ruess, L. (2005) Feeding guilds in Collembola based on nitrogen stable isotope ratios. *Soil Biology and Biochemistry*, 37 (9), 1718–1725. https://doi.org/10.1016/j.soilbio.2005.02.006

Chahartaghi, M., Scheu, S. & Ruess, L. (2006) Sex ratio and mode of reproduction in Collembola of an oak-beech forest. *Pedobiologia*, 50 (4), 331–340. https://doi.org/10.1016/j.pedobi.2006.06.001

Chahartaghi, M., Maraun, M., Scheu, S. & Domes, K. (2009) Resource depletion and colonization: A comparison between parthenogenetic and sexual Collembola species. *Pedobiologia*, 52 (3), 181–189. https://doi.org/10.1016/j.pedobi.2008.08.003

Coleman, D.C., Geisen, S. & Wall, D.H. (2023) Soil fauna: occurrence, biodiversity, and roles in ecosystem function. In: Paul, E.A. & Frey, S.D. (eds) *Soil Microbiology, Ecology and Biochemistry*, 5th ed. Elsevier, Amsterdam, Netherlands, pp. 131–159. https://doi.org/10.1016/B978-0-12-822941-5.00005-3

de Pedro, L., Perera-Fernández, L.G., López-Gallego, E., Pérez-Marcos, M. & Sanchez, J.A. (2020) The effect of cover crops on the biodiversity and abundance of ground-dwelling arthropods in a Mediterranean pear orchard. *Agronomy*, 10 (4), 580. https://doi.org/10.3390/agronomy10040580

Decaëns, T., Jiménez, J.J., Gioia, C., Measey, G.J. & Lavelle, P. (2006) The values of soil animals for conservation biology. *European Journal of Soil Biology*, 42 (1), 23–38. https://doi.org/10.1016/j.ejsobi.2006.07.001

D'Haese, C., Shayanmehr, M., Yoosefi Lafooraki, E. & Tully, T. (2025) An initial assessment of the Collembola (Hexapoda) fauna of the Bula Hyrcanian Forest (Iran) at the interface of two biodiversity hotspots. *Soil Organisms*, 97, 211–245. https://doi.org/10.25674/451

Domene, X. (2016) A critical analysis of meso- and macrofauna effects following biochar supplementation. In: Ralebitso-Senior, K.R. & Orr, C.H. (eds) *Biochar Application: Essential Soil Microbial Ecology*. Elsevier Inc., Amsterdam, pp. 268–292. https://doi.org/10.1016/b978-0-12-803433-0.00011-4

Domínguez, M.V.S., González, E., Fabián, D., Salvo, A. & Fenoglio, M.S. (2020) Arthropod diversity and ecological processes on green roofs in a semi-rural area of Argentina: Similarity to neighbor ground habitats and landscape effects. *Landscape and Urban Planning*, 199, 103816. https://doi.org/10.1016/j.landurbplan.2020.103816

Eckert, M., Gaigher, R., Pryke, J.S., Janion-Scheepers, C. & Samways, M.J. (2023) High trait diversity among soil arthropods allows their survival in a heterogeneous eco-agricultural mosaic. *Soil Biology and Biochemistry*, 186, 109180. https://doi.org/10.1016/j.soilbio.2023.109180

Fjellberg, A. (2007) The Collembola of Fennoscandia and Denmark. Part II: Entomobryomorpha and Symphypleona. *Fauna Entomologica Scandinavica*, 42, 1–264. https://doi.org/10.1163/ej.9789004157705.i-265

Frouz, J., Ali, A., Frouzova, J. & Lobinske, R.J. (2004) Horizontal and vertical distribution of soil macroarthropods along a spatio-temporal moisture gradient in subtropical central Florida. *Environmental Entomology*, 33 (5), 1282–1295. https://doi.org/10.1603/0046-225X-33.5.1282

Gagnarli, E., Goggioli, D., Tarchi, F., Guidi, S., Nannelli, R., Vignozzi, N., Valboa, G., Lottero, M.R., Corino, L. & Simoni, S. (2015) Case study of microarthropod communities to assess soil quality in different managed vineyards. *Soil*, 1, 527–536. https://doi.org/10.5194/soil-1-527-2015

García-Segura, D., Castillo-Murrieta, I.M., Martínez-Rabelo, F., Gomez-Anaya, A., Rodríguez-Campos, J., Hernández-Castellanos, B., Contreras-Ramos, S.M. & Barois, I. (2018) Macrofauna and mesofauna from soil contaminated by oil extraction. *Geoderma*, 332, 180–189. http://dx.doi.org/10.1016/j.geoderma.2017.06.013

Ghiglieno, I., Simonetto, A., Orlando, F., Donna, P., Tonni, M., Valenti, L. & Gilioli, G. (2020) Response of the arthropod community to soil characteristics and management in the Franciacorta Viticultural area (Lombardy, Italy). *Agronomy*, 10 (5), 740. https://doi.org/10.3390/agronomy10050740

Gholizadeh, H., Naqinezhad, A. & Chytrý, M. (2019) Hyrcanian Forest Vegetation Database. *Phytocoenologia*, 49 (2), 209–210. https://doi.org/10.1127/phyto/2018/0315

Ghomi-Avili, A., Akbarinia, M., Hosseini, S.M., Talebian, M.H. & Knapp, H.D. (2020) Fuzzy and Boolean operation based modelling for evaluation of ecological capability in the Hyrcanian Forests. *Journal of Forest Science*, 66 (4), 170–184. https://doi.org/10.17221/130/2019-JFS

Ghorbanalizadeh, A. & Akhani, H. (2022) Plant diversity of Hyrcanian relict forests: An annotated checklist, chorology and threat categories of endemic and near endemic vascular plant species. *Plant Diversity*, 44 (1), 39–69. https://doi.org/10.1016/j.pld.2021.07.005

Gomyo, M. & Kuraji, K. (2016) Effect of the litter layer on runoff and evapotranspiration using the paired watershed method. *Journal of Forestry Research*, 21 (6), 306–313. https://doi.org/10.1007/s10310-016-0542-5

Gonçalves, F., Nunes, C., Carlos, C., López, A., Oliveira, I., Crespí, A., Teixeira, B., Pinto, R., Costa, C.A. & Torres, L. (2020) Do soil management practices affect the activity density, diversity, and stability of soil arthropods in vineyards? *Agriculture, Ecosystems and Environment*, 294, 106863. https://doi.org/10.1016/j.agee.2020.106863

Guo, X., Bian, Z., Wang, S., Wang, Q., Zhang, Y., Zhou, J. & Lin, L. (2020) Prediction of the spatial distribution of soil arthropods using a random forest model: A case study in Changtu County, Northeast China. *Agriculture, Ecosystems & Environment*, 292, 106818. https://doi.org/10.1016/j.agee.2020.106818

Haghdoost, N., Akbarinia, M., Hosseini, S.M. & Kooch, Y. (2011) Conversion of Hyrcanian degraded forests to plantations: Effects on soil C and N stocks. *Annals of Biological Research*, 2 (5), 385–399. https://www.researchgate.net/publication/275333499

Hasin, S. & Booncher, K. (2020) Change in ground-dwelling arthropod communities in different agroecosystems in Wang Nam Khiao, Nakhon Ratchasima province, Thailand. *Agriculture and Natural Resources*, 54 (2), 139–149. https://doi.org/10.34044/j.anres.2020.54.2.04

Hébert, C. (2023) Forest arthropod diversity. In: Allison, J.D., Paine, T.D., Slippers, B. & Wingfield, M.J. (eds) *Forest Entomology and Pathology*. Springer, Cham, pp. 45–90. https://doi.org/10.1007/978-3-031-11553-0_3

Hector, A. & Bagchi, R. (2007) Biodiversity and ecosystem multifunctionality. *Nature*, 448 (7150), 188–190. https://doi.org/10.1038/nature05947

Heydari, M., Eslaminejad, P., Kakhki, F.V., Mirab-balou, M., Omidipour, R., Prévosto, B., Kooch, Y. & Lucas-Borja, M.E. (2020) Soil quality and mesofauna diversity relationship are modulated by woody species and seasonality in semiarid oak forest. *Forest Ecology and Management*, 473, 118332. https://doi.org/10.1016/j.foreco.2020.118332

Homami Totmaj, L., Ramezani, E., Alizadeh, K. & Behling, H. (2021) Four millennia of vegetation and environmental history above the Hyrcanian forest, northern Iran. *Vegetation History and Archaeobotany*, 30, 611–621. https://doi.org/10.1007/s00334-020-00813-y

Hosseini, S.M. (2006) Death of Elm trees in the Hyrcanian forests of Iran. In: IUFRO Working Party 7.03.10. *Proceedings of the Workshop 2006*. Gmunden, Austria Vienna, pp. 183–186.

Jordana, R. (2012) Capbryinae and Entomobryini. In: Dunger, W. & Burkhardt, U. (eds) *Synopses on Palearctic Collembola. Soil Organisms*, 84 (1), 1–391.

Jourgholami, M., Labelle, E.R. & Feghhi, J. (2019) Efficacy of leaf litter mulch to mitigate runoff and sediment yield following mechanized operations in the Hyrcanian mixed forests. *Journal of Soils and Sediments*, 19, 2076–2088. https://doi.org/10.1007/s11368-018-2194-x

Kelleher, E.M. & Choi, Y.D. (2020) Role of plant diversity on arthropod communities in a restored tallgrass prairie of the U.S. Midwest. *Restoration Ecology*, 28 (6), 1464–1474. https://doi.org/10.1111/rec.13238

Kooch, Y. & Noghre, N. (2020) The effect of shrubland and grassland vegetation types on soil fauna and flora activities in a mountainous semi-arid landscape of Iran. *Science of the Total Environment*, 703, 135497. https://doi.org/10.1016/j.scitotenv.2019.135497

Kooch, Y., Moghimian, N. & Kolb, S. (2019) Microbial hotspot areas of C and N cycles in old-growth Hyrcanian forests top soils. *Forest Ecology and Management*, 446, 93–104. https://doi.org/10.1016/j.foreco.2019.05.022

Kooch, Y., Ehsani, S. & Akbarinia, M. (2020) Stratification of soil organic matter and biota dynamics in natural and anthropogenic ecosystems. *Soil & Tillage Research*, 200, 104621. https://doi.org/10.1016/j.still.2020.104621

Kounda-Kiki, C., Vaçulik, A., Ponge, J.F. & Sarthou, C. (2004) Soil arthropods in a developmental succession on the Nouragues inselberg (French Guiana). *Biology and Fertility of Soils*, 40, 119–127. https://doi.org/10.1007/s00374-004-0749-z

Lavelle, P., Bignell, D., Lepage, M., Wolters, V., Roger, P., Ineson, P., Heal, O.W. & Dhillion, S. (1997) Soil function in a changing world: the role of invertebrate ecosystem engineers. *European Journal of Soil Biology*, 33 (4), 159–193.

Li, X., Xiao, Q., Niu, J., Dymond, S., McPherson, E.G., van Doorn, N., Yu, X., Xie, B., Zhang, K. & Li, J. (2017) Rainfall interception by tree crown and leaf litter: an interactive process. *Hydrological Processes*, 31, 3533–3542. https://doi.org/10.1002/hyp.11275

Liang, K. (2024) The role of leaf litter in forest soil fertility and microbial diversity. *Molecular Soil Biology*, 15 (3), 99–108. https://doi.org/10.5376/msb.2024.15.0011

Lin, D., Wang, F., Fanin, N., Pang, M., Dou, P., Wang, H., Qian, S., Zhao, L., Yang, Y., Mi, X. & Ma, K. (2019) Soil fauna promote litter decomposition but do not alter the relationship between leaf economics spectrum and litter decomposability. *Soil Biology and Biochemistry*, 136, 107519. https://doi.org/10.1016/j.soilbio.2019.107519

Ma, C., Yin, X. & Wang, H. (2019) Soil fauna effect on *Dryas octopetala* litter decomposition in an Alpine tundra of the Changbai Mountains, China. *Alpine Botany*, 129, 53–62. https://doi.org/10.1007/s00035-018-0215-4

Marsden, C., Martin-Chave, A., Cortet, J., Hedde, M. & Capowiez, Y. (2020) How agroforestry systems influence soil fauna and their functions - a review. *Plant Soil*, 453, 29–44. https://doi.org/10.1007/s11104-019-04322-4

Mehrafrooz Mayvan, M. & Shayanmehr, M. (2016) An investigation of soil Chilopoda from Semeskandeh forest (Sari, Mazandaran, Iran). *Taxonomy and Biosystematics*, 7 (25), 1–12. https://dor.isc.ac/dor/20.1001.1.20088906.1394.7.25.2.2

Mehrafrooz Mayvan, M., Shayanmehr, M. & Scheu, S. (2015) Depth distribution and inter-annual fluctuations in density and diversity of Collembola in an Iranian Hyrcanian forest. *Soil Organisms*, 87 (3), 239–247. https://soil-organisms.org/SO/article/view/293

Menta, C. & Remelli, S. (2020) Soil health and arthropods: from complex system to worthwhile investigation. *Insects*, 11 (1), 54. https://doi.org/10.3390/insects11010054

Mohammadi, J., Shataee, S., Namiranian, M. & Næsset, E. (2017) Modeling biophysical properties of broad-leaved stands in the hyrcanian forests of Iran using fused airborne laser scanner data and ultraCam-D images. *International Journal of Applied Earth Observation and Geoinformation*, 61, 32–45. http://dx.doi.org/10.1016/j.jag.2017.05.003

Moradi, H., Naqinezhad, A., Siadati, S., Yousefi, Y., Attar, F., Etemad, V. & Reif, A. (2016) Elevational gradient and vegetation environmental relationships in the central Hyrcanian forests of northern Iran. *Nordic Journal of Botany*, 34, 1–14. https://doi.org/10.1111/njb.00535

Moradi, J., John, J., Vicentini, F., Vesela, H., Vicena, J., Ardestani, M.M. & Frouz, J. (2020) Vertical distribution of soil fauna and microbial community under two contrasting post mining chronosequences: Sites reclaimed by alder plantation and unreclaimed regrowth. *Global Ecology and Conservation*, 23, e01165. https://doi.org/10.1016/j.gecco.2020.e01165

Nacif, M.E., Kitzberger, T. & Garibaldi, L.A. (2020) Positive outcomes between herbivore diversity and tree survival: Responses to management intensity in a Patagonian forest. *Forest Ecology and Management*, 458, 117738. https://doi.org/10.1016/j.foreco.2019.117738

Nakhutsrishvili, G., Zazanashvili, N., Batsatsashvili, K. & Montalvo Mancheno, C.S. (2015) Colchic and Hyrcanian forests of the Caucasus: similarities, differences and conservation status. *Flora Mediterranea*, 25 (Special Issue), 185–192. https://doi.org/10.7320/FlMedit25SI.185

O'Donnell, P.P. & Wright, W. (2021) Assessing the conservation and enhancement value of revegetated strips on arthropod assemblages in a pasture landscape. *Journal of Environmental Management*, 278, 111522. https://doi.org/10.1016/j.jenvman.2020.111522

Palacios-Vargas, J., Castaño-Meneses, G., Gómez-Anaya, J., Martínez-Yrizar, A., Mejía-Recamier, B.E., & Martínez-Sánchez, J. (2007) Litter and soil arthropods diversity and density in a tropical dry forest ecosystem in Western Mexico. *Biodiversity and Conservation*, 16, 3703–3717. https://doi.org/10.1007/s10531-006-9109-7

Pequeno, P.A.C.L., Franklin, E. & Norton, R.A. (2020) Determinants of intra-annual population dynamics in a tropical soil arthropod. *Biotropica*, 52, 129–138. https://doi.org/10.1111/btp.12731

Pereira, J. de M., Segat, J.C., Baretta, D., Vasconcellos, R.L. de F., Baretta, C.R.D.M. & Cardoso, E.J.B.N. (2017) Soil macrofauna as a soil quality indicator in native and replanted *Araucaria angustifolia* forests. *Revista Brasileira de Ciênciado Solo*, 41, 1–15. https://doi.org/10.1590/18069657rbcs20160261

Pestana, L.F.A., de Souza, A.L.T., Tanaka, M.O., Labarque, F.M. & Soares, J.A.H. (2020) Interactive effects between vegetation structure and soil fertility on tropical ground-dwelling arthropod assemblages. *Applied Soil Ecology*, 155, 103624. https://doi.org/10.1016/j.apsoil.2020.103624

Pielou, E.C. (1971) *An Introduction to Mathematical Ecology*. Wiley and Sons, New, 300 pp.

Potapov, M. (2001) Isotomidae. In: Dunger, W. (ed.) *Synopses on Palaeartic Collembola*. Vol. 3. Abhandlungen und Berichte des Naturkundemuseums Görlitz, 73 (2), pp. 1–603.

Sánchez-Montoya, M.M., Tockner, K., von Schiller, D., Miñano, J., Catarineu, C., Lencina, J.L., Barberá, G.G. & Ruhi, A. (2020) Dynamics of ground-dwelling arthropod metacommunities in intermittent streams: The key role of dry riverbeds. *Biological Conservation*, 241, 108328. https://doi.org/10.1016/j.biocon.2019.108328

Shayanmehr, M., Mehrafrooz Mayvan, M., Yoosefi Lafooraki, E., Kahrarian, M., Yahyapour, E., Daghighi, E., Jordana, R., Arbea, J., Potapov, M., D'Haese, C., Tully, T., Skarżyński, D., Smolis, A., Galli, L., Sendra, A., Gioia Cipola, N., Molero, R. & Kováč, L. (2025) Arthropod diversity in Iran: Subphylum Hexapoda Latreille, 1825, Basal Hexapod Taxa. *Journal of Insect Biodiversity and Systematics*, 11 (4), 1085–1114. https://doi.org/10.48311/jibs.11.4.1085

Sibly, R.M. & Hone, J. (2002) Population growth rate and its determinants: An overview. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 357 (1425), 1153–1170. https://doi.org/10.1098/rstb.2002.1117

Stritih, A., Lecina-Diaz, J., Mohr, J., Schattenberg, C., Ammer, C., Anselmetto, N., Bauhus, J., Bončina, A., Garbarino, M., Hlásny, T., Lindner, M., Lingua, E., Knific, E., Krüger, K., Marangon, D., Morresi, D., Mulec, K., Nagel, T.A., Potterf, M., Stritih, J., Thom, D., Welling, D. & Seidl, R. (2026) Can "Closer-to-Nature" forest management sustain biodiversity and ecosystem services in an uncertain future? lessons from Central Europe. *Current Forestry Reports*, 12, 1. https://doi.org/10.1007/s40725-025-00264-6

Takeda, H. & Abe, T. (2001) Templates of food-habitat resources for the organization of soil animals in temperate and tropical forests. Ecological Research, 16 (5), 961–973. https://doi.org/10.1046/j.1440-1703.2001.00450.x

Thibaud, J.M., Schulz, H.J. & da Gama Assalino, M.M. (2004) Hypogastruridae. In: Dunger, W. (eds) *Synopses on Palaearctic Collembola*. Vol. 4. Abhandlungen und Berichte des Naturkundemuseums Görlitz, 75 (2), pp. 1–287.

Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D. & Swackhamer, D. (2001) Forecasting Agriculturally Driven Global Environmental Change. *Science*, 292 (5515), 281–284. https://doi.org/10.1126/science.1057544

Tresch, S., Frey, D., Le Bayon, R.C., Zanetta, A., Rasche, F., Fliessbach, A. & Moretti, M. (2019) Litter decomposition driven by soil fauna, plant diversity and soil management in urban gardens. *Science of the Total Environment*, 658, 1614–1629. https://doi.org/10.1016/j.scitotenv.2018.12.235

Truffer, O., Lieberherr, E., Van Ruymbeke, K., Chimisso, C., Rowe, T., Vranken, L. & Ohmura, T. (2025) Mapping the Research of Forest Ecosystem Services in Europe: A Review. *Forest Policy and Economics*, 181, 103663. https://doi.org/10.1016/j.forpol.2025.103663

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity-Ecosystem service management. *Ecology Letters*, 8, 857–874. https://doi.org/10.1111/j.1461-0248.2005.00782.x

Tully, T., Shayanmehr, M., Yoosefi Lafooraki, E., Ghajar Sepanlou, M. & D'Haese, C. (2025) Diversity and community structure of Collembola (Hexapoda) across sites and microhabitats in the Bula protected area, a UNESCO-listed Hyrcanian forest at the crossroads of two biodiversity hotspots (Iran). *bioRxiv* 2025.05.20.650270. https://doi.org/10.1101/2025.05.20.650270

Utami, S., Kurniawan, A. & Muslimin, I. (2019) Arthropod diversity on forest stands in South Sumatra, Indonesia. *IOP Conf. Series: Earth and Environmental Science*, 394, 012003. https://doi.org/10.1088/1755-1315/394/1/012003

Valencia-Cuevas, L., Rodríguez-Domínguez, A., Mussali-Galante, P., Ramos-Quintana, F. & Tovar-Sánchez, E. (2020) Influence of edaphic factors along an altitudinal gradient on a litter arthropod community in an Abies-Quercus forest in Mexico. *Acta Oecologica*, 108, 103609. https://doi.org/10.1016/j.actao.2020.103609

van Straalen, N.M. (1998) Evaluation of bioindicator systems derived from soil arthropod communities. *Applied Soil Ecology*, 9 (1–3), 429–437. https://doi.org/10.1016/S0929-1393(98)00101-2

Venuste, N. (2020) Impacts of forest and agricultural land use on soil and litter arthropod assemblages in Southern province of Rwanda. *Rwanda Journal of Engineering, Science, Technology and Environment*, 3 (1), 1–16. https://dx.doi.org/10.4314/rjeste.v3i1.7

Waez-Mousavi, S.M. (2017) Humus systems in the Caspian Hyrcanian temperate forests. *Applied Soil Ecology*, 123, 664–667. http://dx.doi.org/10.1016/j.apsoil.2017.09.022

Wang, B., Verheyen, K., Baeten, L. & De Smedt, P. (2021) Herb litter mediates tree litter decomposition and soil fauna composition. *Soil Biology and Biochemistry*, 152, 108063. https://doi.org/10.1016/j.soilbio.2020.108063

Wiwatwitaya, D. & Takeda, H. (2005) Seasonal changes in soil arthropod abundance in the dry evergreen forest of north-east Thailand, with special reference to collembolan communities. *Ecological Research*, 20, 59–70. https://doi.org/10.1007/s11284-004-0013-x

Wu, P. & Wang, C. (2019) Differences in spatiotemporal dynamics between soil macrofauna and mesofauna communities in forest ecosystems: The significance for soil fauna diversity monitoring. *Geoderma*, 337, 266–272. https://doi.org/10.1016/j.geoderma.2018.09.031

Xin, W.D., Yin, X.Q. & Song, B. (2012) Contribution of soil fauna to litter decomposition in Songnen sandy lands in northeastern China. *Journal of Arid Environments*, 77, 90–95, https://doi.org/10.1016/j.jaridenv.2011.10.001

Xu, G., Zhang, Y., Zhang, S. & Ma, K. (2020) Biodiversity associations of soil fauna and plants depend on plant life form and are accounted for by rare taxa along an elevational gradient. *Soil Biology and Biochemistry*, 140, 107640. https://doi.org/10.1016/j.soilbio.2019.107640

Yang, X., Shao, M. & Li, T. (2020) Effects of terrestrial isopods on soil nutrients during litter decomposition. *Geoderma*, 376, 114546. https://doi.org/10.1016/j.geoderma.2020.114546

Zagatto, M.R.G., Niva, C.C., Thomazini, M.J., Baretta, D., Santos, A., Nadolny, H., Cardoso, G.B.X. & Brown, G.G. (2017) Soil Invertebrates in different land use systems: How Integrated production systems and seasonality affect soil mesofauna communities. *Journal of Agricultural Science and Technology*, 7, 158–169. https://doi.org/10.17265/2161-6264/2017.03.003

Zagatto, M.R.G., Filho, L.C.I.O., Pompeo, P.N., Niva, C.C., Baretta, D. & Cardoso, E.J.B.N. (2020) Mesofauna and macrofauna in soil and litter of mixed plantations. In: Bran Nogueira Cardoso, E., Gonçalves, J., Balieiro, F. & Franco, A. (eds) *Mixed Plantations of Eucalyptus and Leguminous Trees*. Springer, Cham, pp. 155–171. https://doi.org/10.1007/978-3-030-32365-3_8

Zahriban Hesari, M., Shataee, S., Maghsoudi, Y., Mohammadi, J., Fransson, J.E.S. & Persson, H.J. (2020) Forest variable estimations using TanDEM-X Data in Hyrcanian Forests. *Canadian Journal of Remote Sensing*, 46 (2), 166–176. https://doi.org/10.1080/07038992.2020.1763790

Zan, P., Mao, Z. & Sun, T. (2022) Effects of soil fauna on litter decomposition in Chinese forests: a meta-analysis. *PeerJ*, 10, e12747. http://doi.org/10.7717/peerj.12747

Zhang, L., Liu, J., Yin, R., Xu, Z., You, C., Li, H., Wang, L., Liu, S., Xu, H., Xu, L., Liu, Y., Wang, Y. & Tan, B. (2023) Soil fauna accelerated litter C and N release by improving litter quality across an elevational gradient. *Ecological Processes*, 12, 47. https://doi.org/10.1186/s13717-023-00459-4

Zhang, Z.Q. (2011) Animal biodiversity: An introduction to higher-level classification and taxonomic richness. *Zootaxa*, 3148 (1), 7–12. https://doi.org/10.11646/zootaxa.3148.1.3

بندپایان درشت‌خاک‌زی و میان‌خاک‌زی جنگل‌های حفاظت‌شده هیرکانی: الگوهای فصلی تنوع و ساختار اجتماعی بندپایان در عمق‌های مختلف خاک

محمود مهرافروز مایوان [۱،۲] و معصومه شایان‌مهر [۱]

۱ گروه گیاهپزشکی، دانشکده علوم زراعی، دانشگاه علوم کشاورزی و منابع طبیعی ساری، ایران.
۲ مؤسسه تحقیقات زیست‌شناسی و بیوشیمی خاک، مرکز زیست‌شناسی آکادمی علوم جمهوری چک.

نویسندهٔ مسئول: معصومه شایان‌مهر | m.shayanmehr@sanru.ac.ir

ویراستار علمی
الهه دقیقی

دریافت: ۰۳ خرداد ۱۴۰۵
ویرایش: ۱۴ مرداد ۱۴۰۵
پذیرش: ۱۵ مرداد ۱۴۰۵
انتشار: ۰۸ شهریور ۱۴۰۵

چکیـده: جنگل‌های هیرکانی به عنوان یکی از قدیمی‌ترین جنگل‌های جهان در نظر گرفته می‌شوند و به دلیل اقلیم معتدل و مرطوب و خاک‌های حاصلخیز خود، دارای تنوع زیستی غنی هستند. بندپایان ساکن در خاک نقش‌های اساسی در عملکرد اکوسیستم جنگل ایفا می‌کنند و به تجزیه برگ‌ها، چرخه مواد مغذی و حفظ ساختار خاک کمک می‌کنند. این مطالعه تنوع و توزیع عمودی ماکروفون و مزوفون را در جنگل سمسکنده، یک جنگل حفاظت‌شده هیرکانی در شمال ایران، در عمق‌های مختلف خاک (برگ‌های ریخته شده، ۰–۳ سانتی‌متر، ۳–۶ سانتی‌متر) و فصول مختلف در طول یک سال ارزیابی کرد. بیش از ۱۰،۰۰۰ فرد جمع‌آوری شد که نمایانگر گروه‌های تاکسونومیک متنوعی از جمله مورچه‌ها، هزارپاها، دم‌فنری‌ها، کنه‌ها، شبه‌عقرب‌ها و دم‌چنگالان بودند. تراکم جمعیت‌ها و تنوع گونه‌ها به طور مداوم در لایه برگ بیشترین مقدار را داشت و با اوج‌های فصلی واضحی که در طول دوره مطالعه مشاهده شد با افزایش عمق خاک کاهش یافت. مورچه‌ها گروه غالب در ماکروفون بودند، در حالی که کنه‌ها و دم‌فنری‌ها متنوع‌ترین گروه‌های مزوفون بودند. این مطالعه الگوهای فصلی و عمودی واضحی را در تراکم جمعیت و تنوع جوامع جانوری خاک در اکوسیستم جنگل هیرکانی نشان داد. این یافته‌ها اطلاعات پایه‌ای برای حفاظت از تنوع زیستی و نظارت آینده بر جانوران خاک در جنگل‌های هیرکانی فراهم می‌کند. بنابراین، حفظ کیفیت برگ‌ها، حفظ یکپارچگی زیستگاه و نظارت بر تنوع جانوران خاک برای حفظ عملکردهای اکوسیستم جنگل در این منطقه‌ای به عنوان میراث ارزشمند جهانی، بسیار حیاتی است.

واژگـان کلیدی: فراوانی، ترکیب جامعه، حفاظت، تنوع جانوری، ایران، خاک‌برگ