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Abstract

Despite the importance of mesofauna in soil formation, litter decomposition, biological cycles and growth of plants in semi-arid forest ecosystems, the effects of different woody species and seasonality on the abundance, diversity and distribution of mesofauna invertebrates have been little studied. This study has evaluated the effects of different woody species (trees and shrubs) on trophic guilds of soil mesofauna (detritivores vs. predators) composition, abundance and diversity during spring and winter seasons. Moreover, the basic drivers including microclimatic characteristics and soil properties of soil biota abundance, composition and diversity have been identified in semi-arid deciduous broadleaved forests. Woody species types and seasonality affected soil mesofauna abundance, composition and diversity. All the species were present during spring and winter and in all types of woody species, but the mesofauna was differently affected by season and woody cover. Predator abundance was affected by species and seasonality, whereas detritivore abundance was only influenced by woody species. In relation to the season, mesofauna abundance is generally higher in winter compared to spring. Detritivore and predation diversity in soil mesofauna was affected by woody species and seasonality, but not by the interaction of both factors. It has been also demonstrated that the trees understory is a more important biodiversity hotspot compared to shrubs for mesofauna activity; moreover, the detritivores vs. predators mesofauna composition are driven by the seasonality and woody species. Overall, this work has demonstrated that aboveground and belowground relationship (that is, plant and soil organisms) have reciprocal ecological linkages and that aboveground and belowground communities can be powerful mutual drivers.

Keywords: shrub; tree; soil detritivores; abundance; evenness.

1. Introduction

The living soil (soil biota) contains a very high diversity of organisms, including microorganisms (i.e., bacteria, fungi) and microscopic and macroscopic fauna (Bardgett and Van Der Putten, 2014; Balestrini et al., 2015). The soil fauna includes macrofauna (having a body size > 2 mm), mesofauna (body size between 100 μm and 2 mm) and microfauna (< 100 μm) (Whalen and Sampedro, 2010). The mesofauna consists of small invertebrates that live in soil or litter with different diets such as predators and detritivores (Whalen and Sampedro, 2010). These organisms plays an important role in ecosystems multifunctionality and soil quality (Lavelle et al., 2006) playing a vital role in the functioning of terrestrial ecosystems (Wolters et al., 2000; Hossain and Sugiyama, 2019).

Soil mesofauna interact with plants and these relationships form the soil's food chain and sustain the services and functions of natural ecosystems, such as carbon and nutrient cycling or water cycle regulation (Motiejūnaitė et al., 2019). Thus, interactions between soil mesofauna and plant are certainly important for growth and establishment of various plant species including trees and shrubs species. In many ecosystems, changes in the diversity and abundance of soil organisms can have significant effects on plant-soil interactions and ecosystem production and functions (Ponge, 2013; Zhao et al., 2013; Agapit et al., 2018). However, soil organisms are sensitive to abiotic and biotic factors both above and below ground, such as climatic conditions, management measures, plant cover and different chemical and physical soil properties (Pritchard, 2011; Wissuwa et al., 2012; Wu and Wang, 2019). Mesofauna invertebrates (both mesofauna detritivores and predators) diversity may be affected by several ecosystem features, such as plant cover and biodiversity, which in turn may be directly affected by soil nutrient deficiencies, climate change, forest fires and other biological factors (such as pests and diseases) (Ahmadi et al., 2014; Lieutier and Paine, 2016;

Torres- Muros et al., 2017). Moreover, forest characteristics, including forest structure, tree 77

canopy cover, vegetative form (shrub or tree species), abundance and spatial distribution of woody species may alter composition of mesofauna invertebrates through for example the quantity or quality of plant debris (Morán- López et al., 2015; Brygadyrenko, 2016). Many studies have examined the effects of tree species, silvicultural operations or shrubs composition on soil fauna (Kataja-aho et al., 2016; Čuchta et al., 2019). For instance, Heydari et al. (2017 a) showed that Shannon-Wiener diversity and Margalef indices of mesofauna richness in soil were significantly related to stand structural indices in a mixed oak (*Quercus brantii* Lindl.) forest. Different characteristics of tree and shrub species - canopy architecture and size, and consequently different amount of litter input and root development - can be effective on their effects on soil properties (Vetaas, 1992; Muraoka and Koizumi, 2005; Yao et al., 2017). However, recognizing the effects of different woody species on the abundance, diversity and distribution of mesofauna invertebrates can provide valuable information on the factors contributing to the conservation and enhancement of soil biodiversity at different trophic levels in threaten ecosystems.

The different characteristics of soil organisms (such as composition, abundance and diversity) are not randomly distributed, but organise horizontally, following patchy patterns at landscape scale, and vertically, along the soil profile (Frey, 2015). These specific patterns can be largely dependent on site microhabitats (Bayranvand et al., 2017; Heydari et al., 2017 a) and climate seasonal variations (including differences on soil moisture and temperature) (Görres et al., 1998; Campuzano et al., 2019). On this context, the role of plant ecosystems or microclimatic characteristics influence on soil mesofauna density is still not completely known (Briones, 2018). For instance, a deeper understanding of the effects of forest species on mesofauna

detritivores and predators communities may be useful as ecosystems quality indicators, particularly in semi-arid ecosystems in which soil degradation processes are important under the climate change context.

Zagros forests are one of the oldest and unique oak habitats in the world. The Zagros forest cover an area of approximately 5 million hectares with highly scattered and occasionally denser oak trees (mostly Brant's oak, *Quercus brantii* var. *Persica*) associated with different shrub and tree species (Sagheb-Talebi et al., 2014). In these oak forests, the effect of individual tree and shrub species on different soil biological and chemical properties throughout the seasons has been little investigated, since most studies have focused on forest stands (Hosseini et al., 2017; Mirzaei et al., 2020). Although one of the major determinants of the spatial distribution of soil fauna diversity in forest ecosystems can be related to the overstory, the current knowledge about the relationships between mesofauna invertebrates and tree species is scarce (Gholami, et al., 2017). This makes difficult for ecologists the application of models describing the structure of soil organism's communities and the comprehension of the distribution of diversity of soil organisms at different scales (Barrios, 2007; Da Silva et al., 2015; Kuznetsova et al., 2019). To fill these gaps, this study aims to investigate the spatio-temporal dynamics of soil mesofauna in semi-arid oak forest ecosystems of western Iran. In more detail, the specific objectives of the study were: (i) to analyze the effects of different woody species (trees and shrubs) on trophic guilds of soil mesofauna (detritivores vs. predators) composition, abundance and diversity during spring and winter seasons; and (ii) to identify the basic drivers including microclimatic characteristics and soil properties of soil biota abundance, composition and diversity in semi-arid deciduous broadleaved forests. On this regard, we hypothesized that: (i) the variation of soil mesofauna abundance, composition and diversity are affected by woody species types and season changes; (ii) the trees understory is a more important biodiversity hotspot compared to shrubs for soil biota activity; and (iii) the contribution of mesofauna trophic guilds (detritivores vs. predators) in soil mesofauna composition can be explained by the interaction of season and growth form types (tree vs. shrub).

2. Material and methods

2.1. Study area

The study site (covering 60 ha) is the Zagros forests in the Bankol forest region (Sirvan city, western Iran) (Fig. 1). This deciduous forest include broadleaved species dominated by Persian oak (*Quercus brantii* L.) with some associated species, such as *Acer monspessulanum* L. subsp. cinerascens (Boiss.), *Pistacia atlantica* Desf., *Crataegus puntica* C. Koch., *Amygdalus scoparia* Spach., and *Lonicera nummularifolia* Jaub & spach. The presence of individuals or groups of trees/shrubs of small to medium sizes with average overstory canopy cover 35-50 % is recorded. The ground vegetation includes a relatively dense cover of annual and perennial grasses and forbs, such as *Bromus tectorum* L., *Astragalus adscendens* Boiss., *Gundelia turneffortii* L., *Geranium lucidum* L., *Hordeum bulbosum* L., *Alyssum marginatum* Steud. ex Boiss., *Avena wiestii Steud, Medicago radiata* L*., Valerianella vesicaria* Moench and *Neslia apiculata* Fisch. The studied site shows the very similar physiographic conditions (slope < 10% and altitude 1900-2000 m a.s.l.). In the study area, climatic data of the period 2006 to 2017 were collected at the nearest meteorological station (Lomar, 33° 56′ N, 46°82′ E, 850 m a.s.l.). The average annual precipitation was 384 mm and the average annual temperature was 20.6 °C; the dry season is between May and October (Fig. 2). The prevalent soil type (according to the FAO classification) is lithosols with low depth and fertility (Jazirehi and Ebrahimi Rastaghi, 2003) and a sandy clay loam texture.

2.2. Experimental design

A flat area in the studied forest was selected in this study. Soil was sampled under three tree species, including *Quercus brantii* (hereinafter indicated as QU), *Acer monspessulanum* L. (AC) and *Pistacia atlantica* Desf. (PI), and three shrub species, i.e. *Crataegus puntica* C. Koch. (CR), *Amygdalus scoparia* Spach. (AM) and *Lonicera nummularifolia* Jaub & spach. (LO) in mid-spring and in winter 2018. For each tree and shrub species, five individuals within the same diameter class were randomly selected. Individuals of the same species always surrounded selected trees and shrubs species. Thirty individuals were considered for each of the two seasons for a total of 60.

Soil was sampled at a depth between 0 and 0.25 m including litterfall at three points, randomly chosen under each species. Soil samples were extracted using a cylindrical extractor with an area of 0.0314 m^2 and a depth of 0.25 m. The three soil cores were mixed into a composite sample. Immediately after sampling, the samples were stored in plastic bags and brought to the laboratory. Then, the samples were placed into a Berlese funnel to remove the terrestrial arthropods. The species level of the arthropods was identified using standard taxonomic keys and reference slides (Mirab-balou et al., 2011; Ramroodi et al., 2014; Nassirkhani et al., 2017). Richness (SR_{mg}, Margalef, 1958), diversity (*H',* Shannon and Weaver, 1949) and evenness (*J'*, Pielou, 1966) of mesofauna invertebrates were calculated using the following equations:

$$SR\text{mg} = (S\text{-}1)/\ln N \quad (1)$$

$$H' = -\sum_{i=1}^{s} p_i \ln p_i \quad (2)$$

$$E = H' / \ln (S) \quad (3)$$

where p_i is the proportion of cover of species '*i*', *N is* the total number of individuals and *S is* the total number of mesofauna species.

In addition, three composite soil samples of about 0.5 kg were randomly collected from the soil horizon to a depth of 0.25 m under each species, in order to evaluate the chemical and microbial properties of the soil. The soils were sieved through a 2-mm mesh and split into two sub-samples, of which one was stored at 4 °C at its water content, to measure later soil microbial activity (soil microbial biomass carbon, soil microbial biomass nitrogen, soil basal respiration and substrate induced respiration), and a second sub-sample was air-dried, to measure soil chemical properties (soil pH and electrical conductivity and soil organic carbon). The soil water content was determined using the gravimetric method (Famiglietti et al., 1998). Soil organic carbon (SOC) was measured by dichromate oxidation followed by rapid titration (Walkley and Black, 1934). Soil pH and electrical conductivity (EC) were measured in filtered extracts with a glass electrode and a conductivity probe, respectively (Kalra and Maynard, 1991). Soil microbial biomass carbon (SMC) was evaluated by determining organic carbon by dichromate digestion in both chloroform-sprayed and non-fumigated samples (Vance et al., 1987). Soil SMC was estimated from the carbon concentration (μgC g^{-1} of dried soil) of 0.5 M of K_2SO_4 soil extracts using the equation (Vance et al., 1987):

$$SMC = 2.64\ (A) \quad (4)$$

where A is the difference in carbon from fumigated and non-fumigated soils. Soil basal respiration (BR) was determined by trapping and measuring emitted CO_2 over a 5-day period (Alef and Nannipieri, 1995). Substrate-induced respiration (SIR) was measured using glucose (1%) as substrate and evolved CO_2 was measured after eight hours of incubation. Evolved CO_2 was adsorbed by 1 M NaOH and measured by titration of 0.1 M HCl (Anderson and Domsch, 1978). The soil microbial biomass nitrogen (SMN) was determined as total Kjeldahl nitrogen in the same K_2SO_4extracts (Brookes et al., 1985). The total N discharge (N extracted

by the K_2SO_4 from the non-fumigated soil subtracted from the fumigated soil) was divided by the KN value (N fraction of the biomass extracted after chloroform fumigation) of 0.54 (Brookes et al., 1985).

2.3. Statistical analysis

General linear models (GLM) were used to assess the effects of woody species, seasons and their interaction on the soil mesofauna abundance, composition and diversity, including both detritivores and predators. Variables were transformed when necessary to satisfy assumptions of normality and homoscedascity of residues. Duncan's post-hoc tests were used to compare the means of soil mesofauna abundance, composition and diversity among different woody species in the understory. A principal component analysis (PCA) was used to evaluate the relationships between soil mesofauna abundance of various trophic guilds (Detritivore vs. Predator) and the chemical and biological properties of the soil under different species throughout the two seasons (TerBraak and þmilauer, 1998). Moreover, a hierarchical grouping and heat mapping of the 30 soil samples were carried out. A two-way clustering dendrogram was obtained using Euclidean distance with the Ward clustering algorithm and coupled with the heat map relative to the abundances of the nine mesofauna taxa. Differences in soil mesofauna composition between different tree and shrub species were explored using non-metric multidimensional scaling (NMS) as part of the 'vegan' package in R (Oksanen et al., 2018). This sorting method, which projects multivariate data in a space with fewer dimensions, was performed on each data set using Bray-Curtis dissimilarity. Unidirectional analysis of variance (ANOVA) was used to identify significant differences in sample plot scores on the NMS axis. All statistical analyses were performed using R 3.5.2 (Main Team R, 2018) and CANOCO 5 software.

3. Results

3.1. Soil mesofauna species and composition

Nine mesofauna species were found under the tree and shrub species, belonging to two trophic guilds, detritivores (*Pseudosinella octopunctata* Börner, *Folsomides marchicus* (Frenzel) and *Oribatula sp*.) and predators (*Macrocheles glaber* (Müller), *Gaeolaelaps aculeifer* (Canestrini), *Arctoseius cetratus* (Sellnick), *Tyrophagus sp*., *Acanthocreagris iranica* Beier and *Aleochara sp.*) (Fig. 3a and 3b). The heat map splits the six species analysed in two clusters (one for each season), based on mesofauna abundance. However, since soil mesofauna composition was similar, the tree and shrub species were not separated. *Oribatula sp.* (spring), as well as *Tyrophagus sp*. and *Oribatula sp.* (winter) were the most abundant soil mesofauna invertebrates. More specifically, in spring, the most abundant species was *Oribatula sp*. under *Acer monspessulanum* L. subsp. cinerascens (Boiss.), and *Pistacia atlantica* Desf. (Fig. 3a). In winter, *Tyrophagus sp.* and *Oribatula sp*. showed a high abundance under all species. Moreover, *Folsomides marchicus* (Frenzel) and *Pseudosinella octopunctata* Börner were more abundant under shrub species (*Crataegus puntica* C. Koch., *Amygdalus scoparia* Spach., and *Lonicera nummularifolia* Jaub & spach) (Fig. 3b)

The NMS shows significant differences in mesofauna composition in spring (F-value = 10.46 and P-value < 0.0001 on NMDS axys 1, and F-value = 12.73 and P-value < 0.0001 on NMDS axys 2) (Fig. 4 b, c) and winter (F-value = 23.70 and P-value <0.0001 on NMDS axis 1, and F-value = 4.82 and P-value < 0.05 on NMDS axis 2) among species (Fig. 4 f, g). The mesofauna composition under QU was, as expected, different from the composition detected

in other species in both seasons. Mesofauna composition was very similar under AM, PI and CR (in spring), and CR and AM (in winter), as shown by the clear overlapping (Fig. 4 a, e). The contribution of trophic guilds of soil mesofauna in composition under each species was influenced by the interaction of season with vegetative form (tree and shrub), as in spring predators contributes more in mesofauna composition under tree species (Fig. 4 d), while in winter detritivores have a greater contribution in composition beneath shrubs (Fig. 4 h).

3.2. Soil mesofauna abundance and diversity

The total abundance of mesofauna was significantly different between the two seasons under all species (Fig. 5). Compared to spring, Lower values were detected under QU and AC in winter, while, in the same season, the abundance was higher under LO and PI . Detritivore abundance was significantly higher in winter compared to spring, except for QU and CR (for the latter the same values were detected in spring and winter). The maximum abundance of detritivores was found under CR in spring (135 ± 32) and winter (138 ± 32), while and the minimum value was detected under LO (32 ± 9) and PI (32 ± 6) in spring. Predator abundance was higher under QU, AC, CR and AM, and lower under PI and LO in spring. The highest abundance of predators was recorded under QU (124 ± 13) and AC (132 ± 15) in spring, while the lowest abundance was surveyed under AM (19.2 ± 4) in winter (Fig. 5).

The tree and shrub species significantly affected the soil mesofauna diversity indices and abundance of their trophic guilds (i.e., detritivores and predators). Pielou's evenness was an exception, since it was not affected by species. The sampling season had a significant effect on Shannon–Wiener diversity, Margalef's richness and Pielou's evenness of both detritivores and predators diversity. Also in this case, the total mesofauna diversity indices were not

significantly affected by season. As regards the trophic guild abundance, only predator abundance was significantly affected by the sampling season (Table 1). The interaction between species and season significantly affected the total mesofauna diversity and evenness, the detritivore diversity and richness, the total mesofauna abundance and the predator abundance (Table 1). No significant differences were detected in the total mesofauna diversity indices between the two sampling seasons. All diversity indices of detritivores were significantly higher in winter compared to spring; conversely, these indices were significantly higher in spring for predators. The comparison of diversity indices between species in spring indicates that diversity and richness indices of total mesofauna, detritivores and predators were the highest under QU and AC and the lowest under shrubs (especially for AM and LO). In spring, only evenness of detritivores got the highest and the lowest values under QU and LO, respectively (Table 2).

3.3. Spatio-temporal variation in mesofauna abundance in relation to soil properties

PCA provided two main principal components (PCs), explaining more than 49% (PC1) and 19% (PC2) of the total variance in soil properties and mesofauna diversity indices under the six species in the sampling seasons (Fig. 6). PC1 indicated that, under soil conditions with higher pH, water content and organic carbon (i.e., under QU and AC in both spring and winter), the activity of predators and microorganisms (higher SMC, MBN, BR and SIR) is higher (see upper left quarter of the chart); moreover, both PC1 and PC2 showed that decreasing organic carbon, water content, pH and microbial activity, and increasing EC (decrease soil fertility) affect a higher activity of detritivores and lower activity of predators under shrubs (CR, AM and LO) in winter. Along the negative direction of PC2 (indicating higher EC, and lower nutrient content and microbial activity) the conditions of understory of

CR, AM, LO and PI in spring are represented by an intermediate presence of both trophic guilds (detritivores and predators) (Fig. 6 and Table 3).

All soil properties (except for EC, P = 0.056) showed statistically significant differences among different woody species: pH (P < 0.001), soil organic carbon (P < 0.001), WC (P < 0.001), basal respiration (P < 0.001), substrate-induced respiration (P < 0.001), soil microbial biomass nitrogen (P = 0.004), soil microbial biomass carbon (P < 0.001). Soil water content beneath trees was significantly higher than beneath shrubs. It was also significantly higher in spring compared t winter only for *Acer monspessulanum*, *Quercus brantii*, and *Crataegus pontica.* In addition, soil organic carbon was higher under trees compared to shrubs. Soil pH was higher in spring compared to winter for trees (*Acer monspessulanum* and *Pistacia atlantica*) *and shrub* (*Crataegus pontica* and *Lonicera nummularifolia)*. Soil biological attributes (i.e. SIR, BR, SMC, SMN) were significantly higher under tree species compared to shrubs; these attributes were also higher in spring compared to winter (Table 4).

4. Discussions

Little information about the effects of different woody species (trees and shrubs) on soil mesofauna detritivores and predators composition, abundance and diversity is available. Therefore, these effects have been evaluated during spring and winter seasons in semi-arid deciduous broadleaved forests in Zagros forest. Moreover, we also try to identify the basic drivers (microclimatic characteristics and soil properties) of soil biota abundance (detritivores and predators), composition and diversity in the semi-aridforest of the study area. Among the soil organisms, mesofauna is one of the most important biological components of soil, since it can play an important role in determining soil multifunctionality (Koehler, 1992; Morais et al., 2010; Wu and Wang, 2019). However, its role and relationships in many natural ecosystems

including trees and shrubs are still poorly understood, especially in arid or semi-arid environments (Taylor and Wolters, 2005; Young et al., 2018). Understanding the different aspects of plant-soil interactions in arid and semi-arid forest ecosystems is very important, because of resource constraints and higher environmental stresses (Schlesinger and Pilmanis, 1998; Karmakar et al., 2016).

Through this study, the first working hypothesis of our study is confirmed, since woody species types and seasonality affected soil mesofauna abundance, composition and diversity. In more detail, as shown in the abundance heat maps of soil mesofauna invertebrates, all the species were present during spring and winter and in all types of woody species, but the mesofauna was differently affected by season and woody species cover. *Oribatula* sp. and *Tyrophagus* sp. found in *Pistacia atlantica* and *Acer monspessulanum* plots were the most abundant mesofauna species in spring (higher than 60 individuals per m^2). *Oribatula* sp., *Tyrophagus* sp., *Pseudosinella octopunctata* and *Folsomides marchicus* species were the most abundant species, but with weak differences among woody species plots, in winter. As regards the mesofauna abundance, GLMs (Table 1) showed statistically significant effects of tree and shrub species and season. Predator abundance was affected by species and seasonality, whereas detritivore abundance was only influenced by woody species. The positive effect of the wet season is shown by the heat map of figure 3, where it is evident that mesofauna abundance is generally higher in winter compared to spring. Water content in soil is an important regulator of soil life, since most biochemical processes, such as the enzymatic activity and reproduction, strictly depend on soil temperature and humidity (Lucas-Borja, 2016). Higher soil humidity of wet seasons under plant cover promotes higher availability of chemical nutrients in soil solution, which enhances plant growth, and organic matter inputs to soil, which feed soil mesofauna (Zagatto et al, 2017). As exposed by different authors and in addition to the characteristics of woody species canopy, changes in biological and abiotic

factors due to seasonal changes can have directly (e.g., by humidity and temperature changes) or indirectly (production rates) effects on the dynamics of biological activity, including the diversity and richness of soil detritivores and predators (Anslan et al., 2018; Nascimento et al., 2019; Kooch and Noghre, (2019).

The highest total mesofauna abundance was found under CR (shrubs species) and in QU, AC (trees species) plots, detritivores species being higher in CR shrubs, and predator species being higher in QU and AC trees, compared to the other woody species plots. Overall, our results are in accordance with previous research about mesofauna abundance. Some studies pointed out that tree canopy abundance and woody species significantly affect soil mesofauna abundance (e.g., Vanbergen et al., 2007). Higher enrichment of carbon and nutrients beneath the canopy of individual woody species with larger canopy size (trees vs. shrubs) can be probably due to higher litter input per unit area and differentiated microclimate conditions along seasons (Yao et al., 2017; Heydari et al., 2017 b; Bayranvand et al., 2017; Salazar et al., 2019). These characteristics can differently affect the diversity and composition of fauna invertebrates (Negrete-Yankelevich et al., 2008). Soil invertebrates can benefit from woody species cover, because a litter depth under a deciduous canopy or a dense shrub layer may generate a thick litters (otherwise being thin), which may sustain mesofauna species (Ferguson and Berube, 2004; Schuldt et al. 2008). In addition, Jiménez-Chacón et al. (2018) found that light availability is a main determinant of soil fauna, although the sign of the light effect varied among studies. It is worth to note that in water-limited ecosystems, mesofauna benefits from the higher moisture found in darker microsites (Dhooria, 2016). As Jiménez-Chacón et al. (2018) demonstrated, environmental predictors including light and soil humidity accounted mostly for variation in the abundance of many different mesofauna species (i.e. *Diplopoda, Pscoptera, Oribatida, Diptera,* and *Poduromorpha*).

In more detail, mesofauna predators were significantly influenced by SMN, WC, SIR, SOC and BR, whereas detritivores by EC. As demonstrated by Liu et al. (2011), soil fauna abundance and richness is highly affected by soil properties and shrubs characteristics. On this context, litter coming from woody species may play a key role on the mesofauna dynamics, since it is the main input of C, N and many other elements to bulk soil. As Thoms et al. (2010) stated, there are direct interactions between soil fauna and plant communities and different vegetal inputs generate variations in initial nutrient concentration and physico-chemical properties of soil. According to Lucas-Borja et al. (2012), plant diversity influences physico-chemical and microbiological soil properties of forest ecosystems. Therefore, the spatial distribution of different wood species on the horizontal surface makes the forest floor conditions heterogeneous in terms of different environmental factors, such as moisture, temperature and litter depth. These agents create various microhabitats (Prescott and Grayston, 2013) that can affect nesting, diversity and activity of organisms within and on soil surface (Tedersoo et al., 2016; Gallé et al., 2017) beside the physical, chemical and biological soil properties (Waring et al., 2016; Hammer, 2019). Thus, the differences related to tree diversity, such as the litter composition, and the variations only indirectly related to woody species composition or tree diversity, such as pH, soil organic matter and EC, might explain the described patterns of soil mesofauna.

Our results indicated that detritivore and predation diversity in soil mesofauna was affected by woody species and seasonality, but not by the interaction of both factors. This means that both woody species and season alter at the same extent diversity indexes. For instance, the higher detritivore and predation diversity was generally found in QU and AC (trees species plots) plots, whereas the lowest values were detected in CR (shrubs species plots) plots in spring and winter. This fact seems to corroborate our second and third working hypothesis, which pointed that: (i) the trees understory is a more important biodiversity hotspot compared

to shrubs for mesofauna activity; and (ii) the detritivores vs. predators mesofauna composition could be explained by the seasonality and woody species factors. Overall, our result confirm that differences in mesofauna diversity and richness might be related to the characteristics of woody species and the shelters plant species provide. In addition, mesofauna may be also affected by soil properties under shrub and tree species (Liu et al., 2011). Korboulewsky et al. (2016) indicated that mesofauna abundance and diversity is strongly affected by certain tree species; the soil organism community structure is, in most cases, significantly affected by an increase in tree richness or by a mixing effect. Studies developed in the same region as this study demonstrated that soil fauna diversity and abundance were spatially correlated to tree species abundance, diversity. This, highlights that soil properties, tree abundance and plant composition are key driver factors for soil fauna diversity distribution (Gholami et al., 2017). Moreover, our results are in accordance with the findings of the latter authors as we found that different microhabitats generated under different woody species (trees and shrubs) provided the suitable conditions (light, moisture and litter quality) for establishing the mesofauna abundance, composition and diversity. In general, changes in environmental conditions can affect both the composition and the abundance of soil mesofauna, which makes mesofauna a suitable indicator to evaluate the degree of change in site conditions (Davis et al., 2001).

Finally, a correspondence in composition, abundance and diversity of mesofauna and aboveground woody species exists depending on both the nature of the biological interactions between mesofauna and woody species themselves and the spatial and temporal scales of the ecological factors influencing the biology of the organisms (Adeduntan, 2009;). This work has demonstrated that aboveground and belowground relationship (that is, plant and soil organisms) have reciprocal ecological linkages and that aboveground and belowground

communities can be powerful mutual drivers (Battigelli et al., 2004; Harrison and Bardgett 2010; Wu and Wang, 2019).

5. Conclusions

Arid and semi-arid forests, including Zagros forests in western Iran, have high heterogeneity in terms of species composition and canopy structure of woody species. This heterogeneity complicates the study and the comprehension of soil-plant interactions in these ecosystems. However, different conclusions can be derived from this study. This work addresses how the signs and strength of the local determinants of mesofauna abundance, composition and diversity change across woody species gradients. Differences in mesofauna composition, abundance and diversity should be related to the characteristics of woody species and seasonality, in addition to soil conditions mediated by the different shrub and tree species. The high spatial heterogeneity of the forest in the horizontal dimension (such as the different branch and canopy abundance and, as a consequence, the variable forest light and temperature) and vertical variations in the quantity and quality of leaves and woody texture can create different microclimates for the studied mesofauna.

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Figures

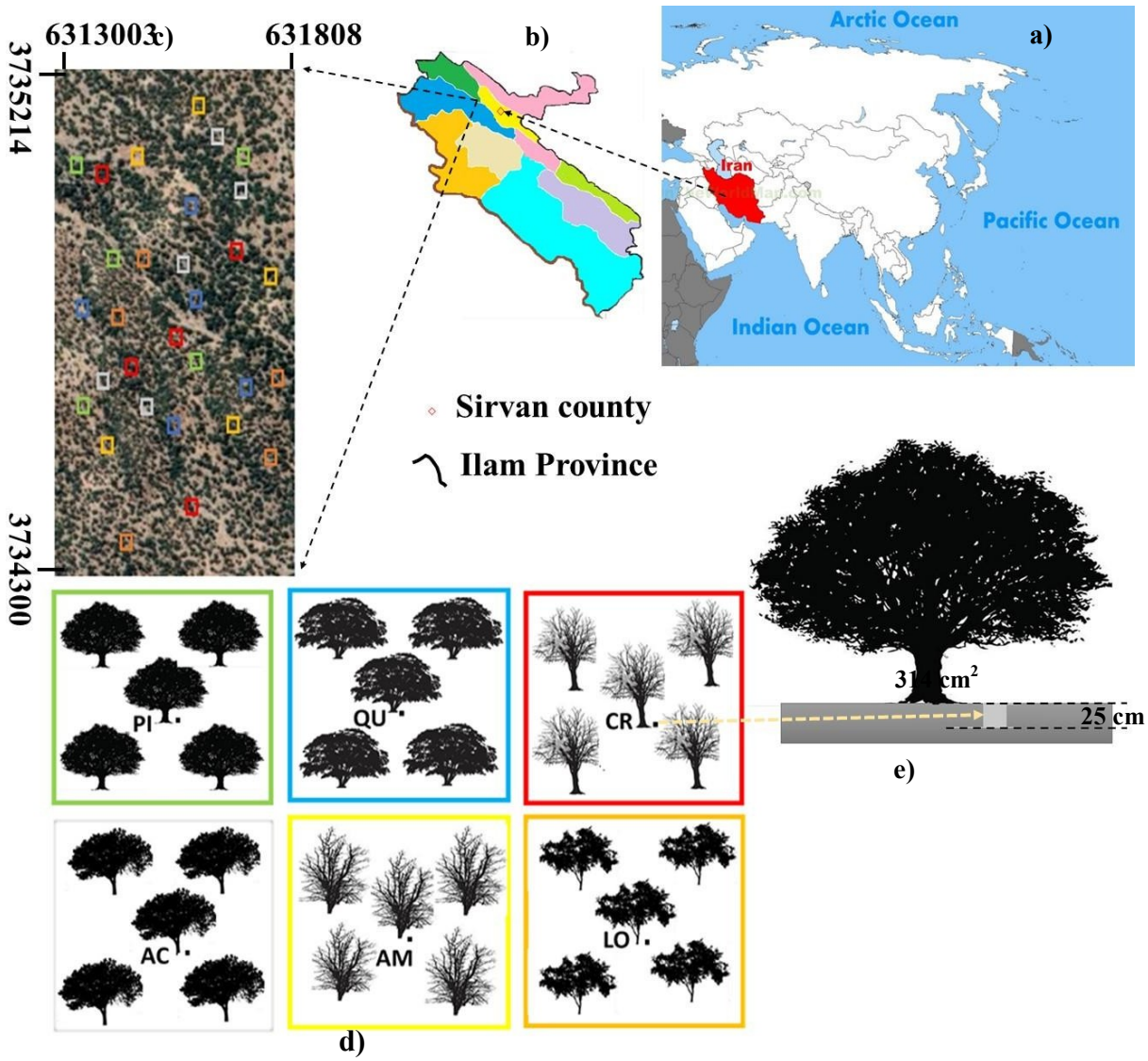

Fig. 1 The study site is located in the Southern Zagros forests in western Iran (a) and Sirvan County (b). For each woody species [QU: *Quercus brantii*), AC: *Acer monspessulanum* L. and PI: *Pistacia atlantica* Desf. and three shrub species, CR: *Crataegus puntica* C. Koch., AM: *Amygdalus scoparia* Spach. And LO: *Lonicera nummularifolia* Ja ub & spach.] five patches (colored squares) were selected in the study site (c and d). Soil sampling was done in spring and winter 2018 in each patch under the canopy of a central woody species (e) at 0-25 cm depth with a sampling area of 314 cm^2.

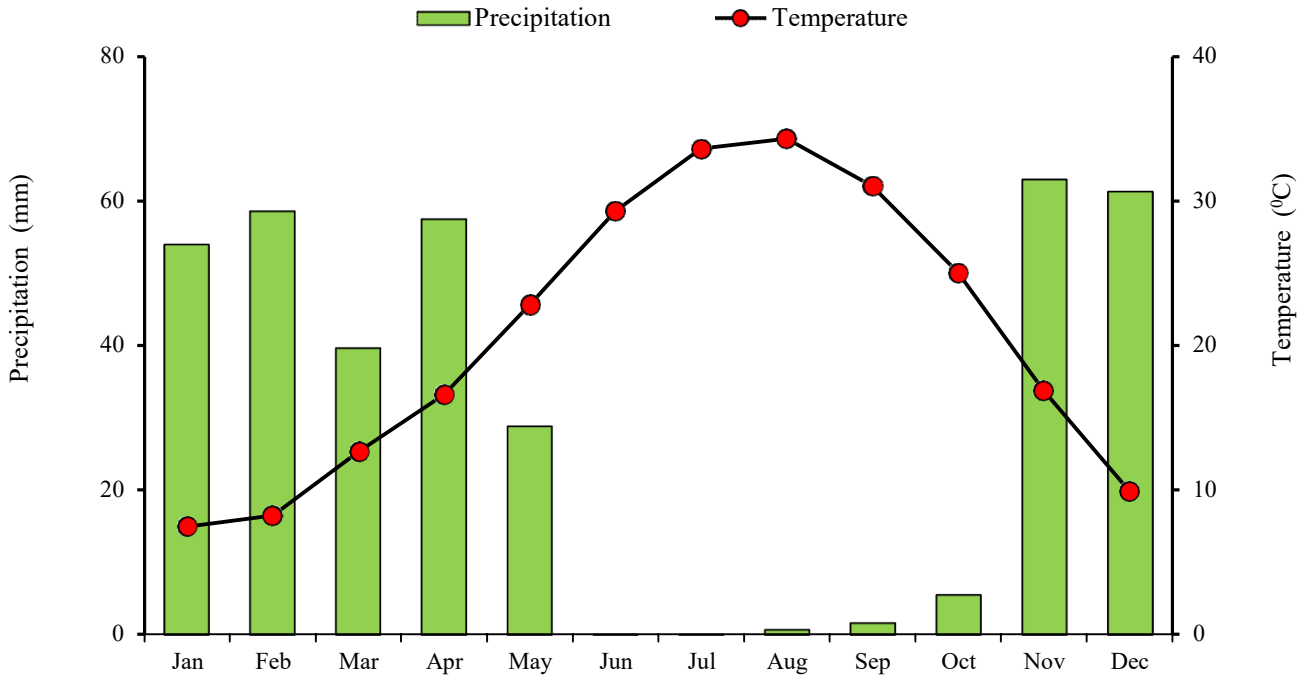

Fig. 2 Ombrothermic diagram of the study site (Southern Zagros forests, western Iran).

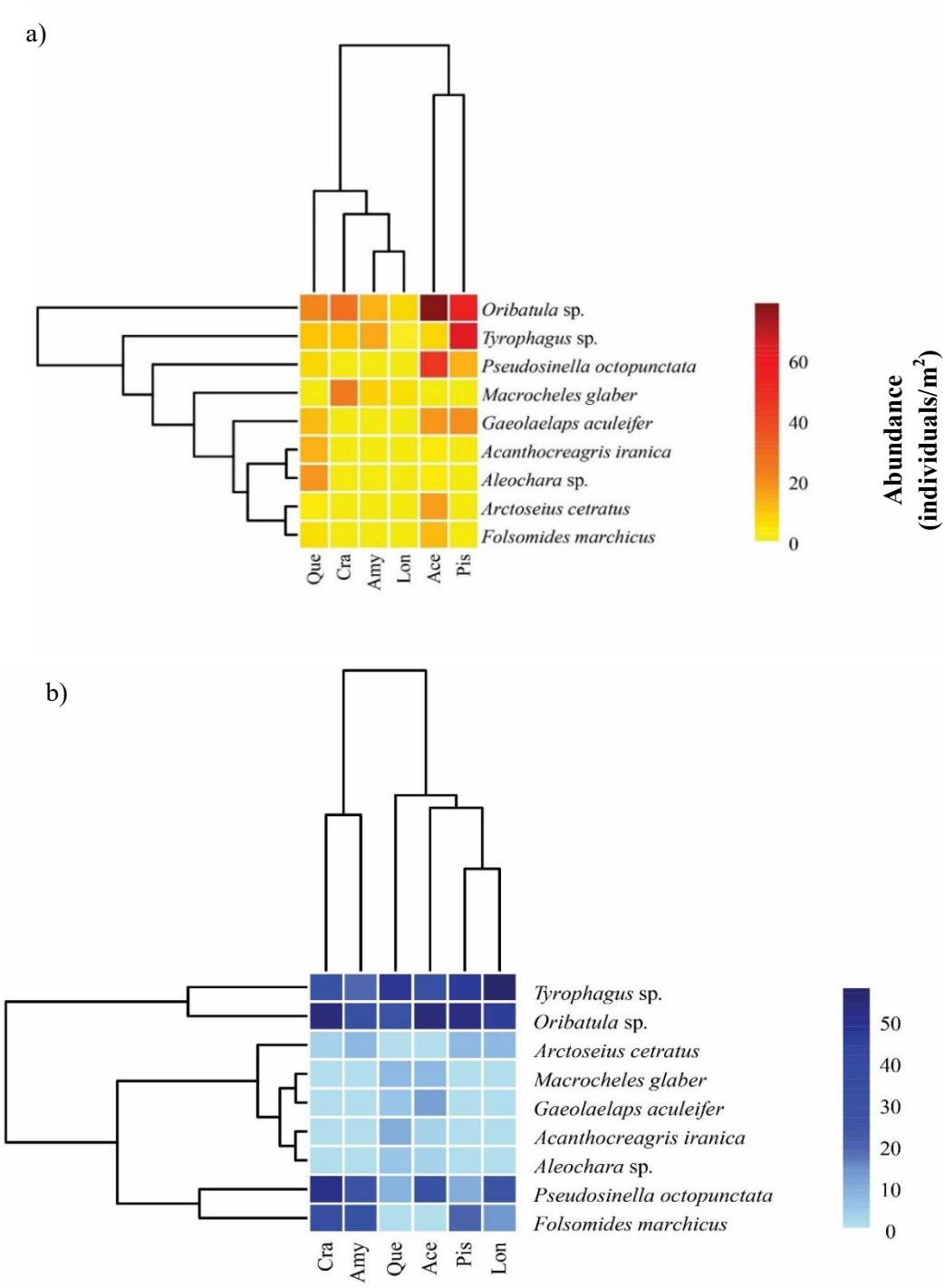

Fig. 3 Abundance heat map of soil mesofauna invertebrates under different tree and shrub species in spring (a) and winter (b) in Southern Zagros forest (western Iran). Que: *Quercus brantii*, Ace: *Acer monspessulanum*, Pis: *Pistacia atlantica*, Cra: *Crataegus pontica*, Amy: *Amygdalus scoparia*, Lon: *Lonicera nummularifolia.* The colour spectrum represents the normalized values of relative abundance.

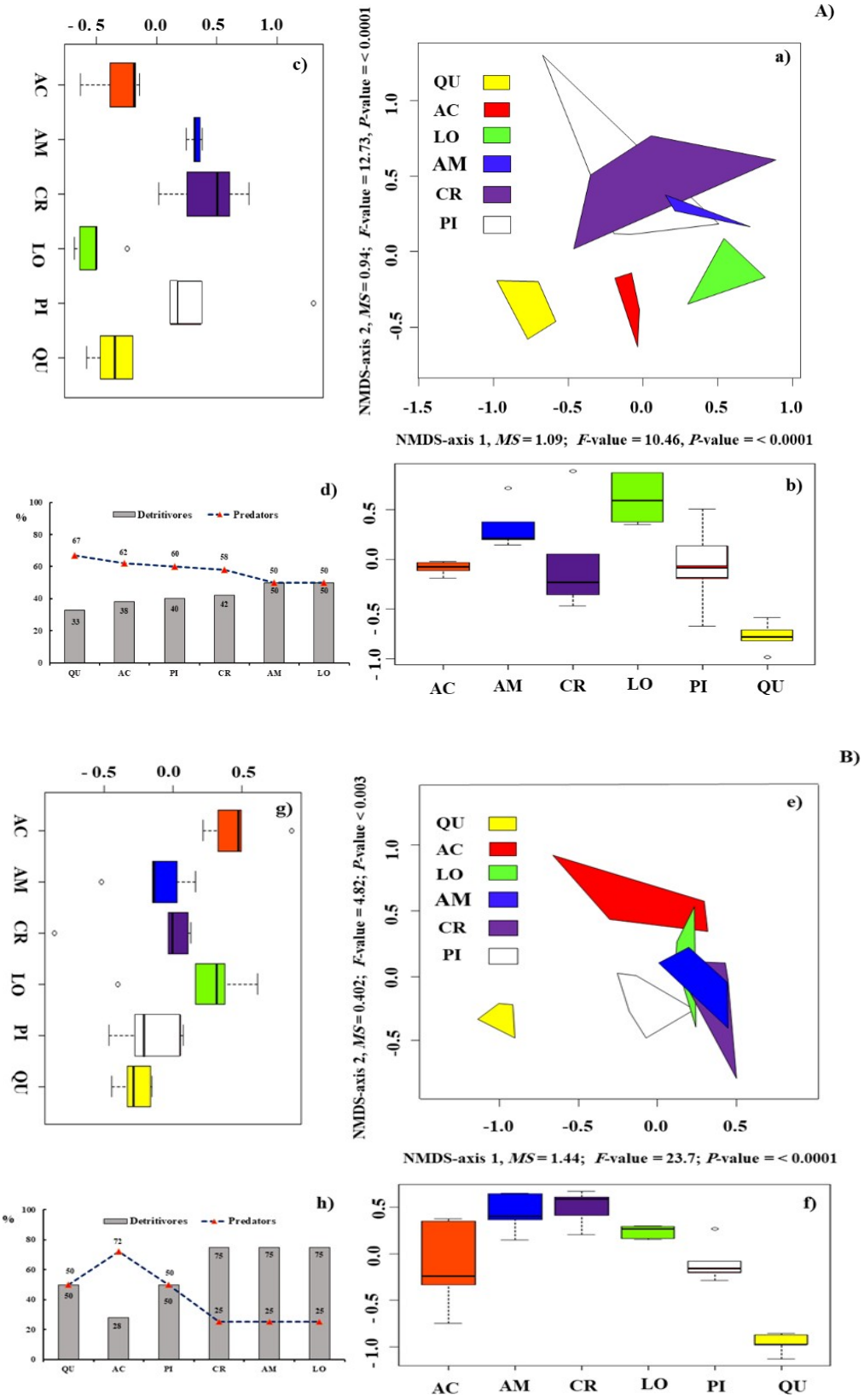

Fig. 4 Non-metric multidimensional scaling (NMS) ordination (a and e) based on Bray-Curtis similarity matrix to identify differences in the mesofauna composition between different tree and shrub species in Southern Zagros forest (western Iran). QU: *Quercus*

brantii, AC: *Acer monspessulanum*, PI: *Pistacia atlantica, CR: Crataegus pontica*, AM: *Amygdalus scoparia*, LO: *Lonicera nummularifolia*) in spring (A) and winter (B); b and c compare means on axis 1 and 2 in spring; f and g compare means on axis 1 and 2 in winter; d and h report the contribution of trophic guilds of soil mesofauna to composition under each species in spring and winter, respectively.

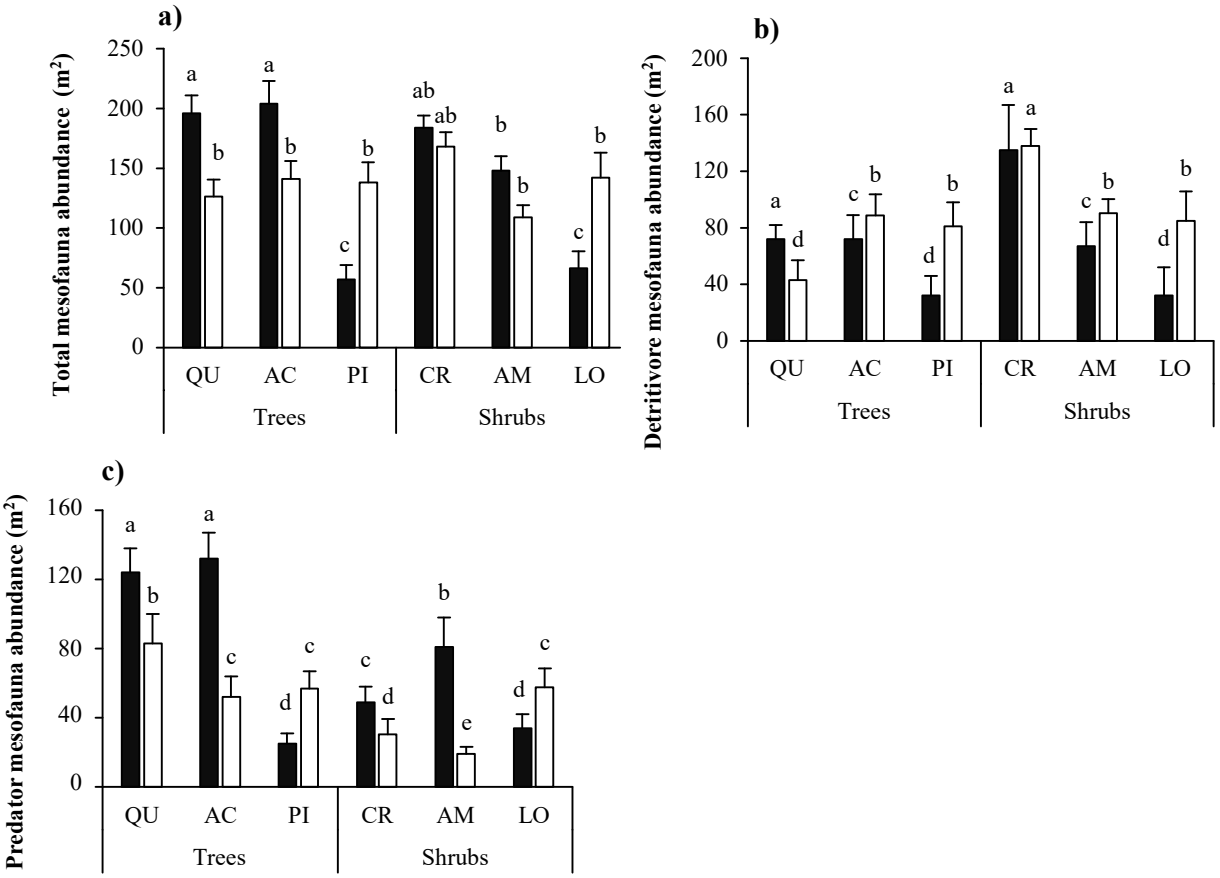

Fig. 5 Differences in the abundance (mean ± standard error, individuals/m^2) of total mesofauna, detritivores and predators for tree and shrub species (QU: *Quercus brantii*, AC: *Acer monspessulanum*, PI: *Pistacia atlantica, CR: Crataegus pontica*, AM: *Amygdalus scoparia*, LO: *Lonicera nummularifolia*) in two sampling seasons (■ spring and □ winter) in Southern Zagros forest (western Iran). Different lowercase and capital letters indicate significant differences ($P < 0.05$) among species and seasons , respectively, after Duncan's test; means and standard errors are calculated on 5 individuals for 6 species (total N = 30)) and 30 individuals for two seasons (totalN = 60).

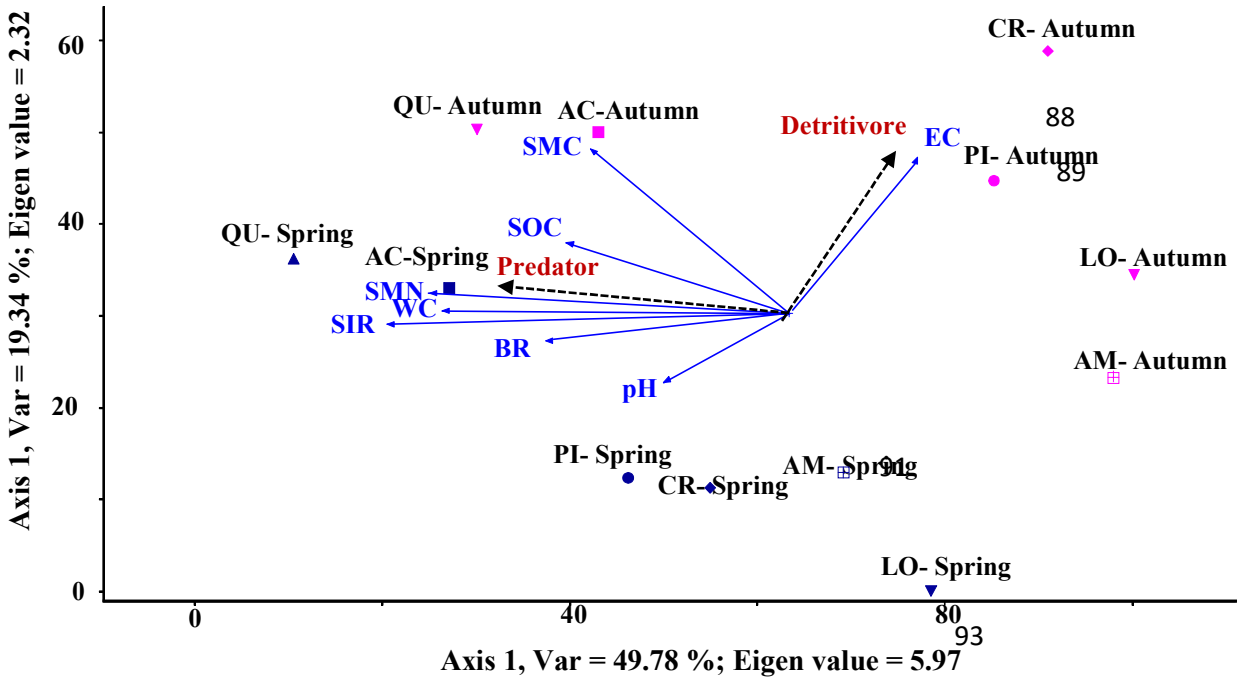

Fig. 6 Principal component analysis (PCA) applied to the tree and shrub species (QU: *Quercus brantii*, AC: *Acer monspessulanum*, PI: *Pistacia atlantica, CR: Crataegus pontica*, AM: *Amygdalus scoparia*, LO: *Lonicera nummularifolia*), soil chemical and biological properties, and water content as well as abundance of trophic guilds (detritivores and predators) in two sampling seasons (winter and spring) (Southern Zagros forest, western Iran); pH: Soil acidity, EC: electrical conductivity, SOC: soil organic carbon, WC: water content, BR: basal respiration, SIR: substrate-induced respiration, Soil microbial biomass nitrogen (SMN), Soil microbial biomass carbon (SMC).

TABLES

Table 1 - Results of GLMs evaluating the effects of tree and shrub species and season on diversity indices.

Diversity and abundance of mesofauna	Tree or shrub species		Season		Species × Season	
	F	p-value	F	p-value	F	p-value
Total mesofauna diversity						
Shannon–Wiener diversity	17.270	0.000	0.400	0.530	1.943	0.104
Margalef's richness	62.337	0.000	0.250	0.620	5.292	0.001
Pielou's evenness	1.637	0.168	0.922	0.342	2.501	0.043
Detritivore diversity						
Shannon–Wiener diversity	6.283	0.000	37.447	0.000	4.377	0.002
Margalef's richness	8.6328	0.000	38.604	0.000	2.610	0.036
Pielou's evenness	2.728	0.030	11.221	0.002	1.629	0.170
Predator diversity						
Shannon–Wiener diversity	10.343	0.000	24.156	0.000	1.317	0.273
Margalef's richness	11.713	0.000	10.513	0.000	1.547	0.185
Pielou's evenness	2.548	0.040	23.657	0.000	0.157	0.977
Mesofauna abundance (individuals/m^2)						
Total mesofauna abundance	4.184	0.003	0.142	0.708	3.935	0.005
Detritivore abundance	5.460	0.000	3.284	0.076	1.340	0.264
Predator abundance	10.661	0.000	12.206	0.001	6.813	0.000

Note: Underlined p-values indicate significant statistical differences at $p<0.05$.

Table 2- Soil mesofauna diversity (mean ± SE) under different tree and shrub species (QU: *Quercus brantii*, AC: *Acer monspessulanum*, PI: *Pistacia atlantica, CR: Crataegus pontica*, AM *Amygdalus scoparia*, LO: *Lonicera nummularifol*ia) and seasons (spring and winter) in the topsoil (0–25 cm) in Southern Zagros forest (western Iran).

Notes: Different lowercase and capital letters indicate significant differences (P < 0.05) among species and seasons, respectively, after Duncan's test; means and standard errors are calculated on five individuals for six species (total N = 30)) and 30 individuals for two seasons (total N = 60); SH: Shannon–Wiener diversity, MR: Margalef's richness: and PE: Pielou's evenness.

Season	Species	*Total mesofauna*			*Detritivores*			*Predators*		
		SH	***MR***	**PE**	***SH***	***MR***	**PE**	***SH***	***MR***	**PE**
Spring	QU	2.03± 0.11 a	2.08± 0.09 a	0.92± 0.03 a	0.94± 0.03a	0.70± 0.04 a	0.85± 0.10 a	1.65± 0.14a	1.47± 0.17 a	0.92± 0.12 a
	AC	1.64± 0.13 b	1.52± 0.07 b	0.84± 0.02 b	0.51± 0.03 b	0.45± 0.01 b	0.62± 0.12 b	1.22± 0.10 bc	0.98± 0.15 b	0.85± 0.10 a
	PI	1.11± 0.05 c	1.16± 0.04 c	0.82± 0.04 b	0.36± 0.03 c	0.42± 0.05 b	0.52± 0.11 c	0.66± 0.04 de	0.63± 0.10 bc	0.73± 0.13 b
	CR	1.21± 0.09 c	0.96± 0.08 cd	0.80± 0.01 b	0.45± 0.03 c	0.45± 0.06 b	0.50± 0.11 c	0.91± 0.04 cd	0.71± 0.12 bc	0.71± 0.14 b
	AM	1.10± 0.07 c	0.72± 0.05 d	0.89± 0.07 a	0.40± 0.03 c	0.28± 0.02 c	0.57± 0.10 c	0.43± 0.04 de	0.35± 0.07 c	0.56± 0.11 c
	LO	0.97± 0.03 c	0.73± 0.06 d	0.93± 0.08 a	0.22± 0.03 d	0.15± 0.03 c	0.31± 0.11 d	0.37± 0.04 d	0.25± 0.04 c	0.54± 0.14 c
	Mean	**1.34± 0.17 A**	**1.19± 0.17 A**	**0.87± 0.04 A**	**0.48± 0.06 B**	**0.39± 0.03 B**	**0.56± 0.08 B**	**0.87± 0.14 A**	**0.73± 0.03 A**	**0.72± 0.11 A**
Winter	QU	1.80± 0.12 a	2.33± 0.16 a	0.82± 0.06 ab	0.85± 0.07 a	0.86± 0.02 a	0.77± 0.13	1.08± 0.12 a	1.34± 0.07 a	0.60± 0.02 a
	AC	1.27± 0.08 c	0.97± 0.05 c	0.88± 0.08 ab	0.69± 0.02 b	0.74± 0.05 b	0.76± 0.11	0.27± 0.07 b	0.14± 0.07 c	0.39± 0.01 bc
	PI	1.18± 0.08 c	1.30± 0.118 b	0.75± 0.07 b	0.58± 0.05 c	0.50± 0.06 c	0.71± 0.10	0.28± 0.05 b	0.43± 0.07 b	0.32± 0.01 bc
	CR	1.16± 0.05 c	0.71± 0.06 cd	0.92± 0.03 a	0.49± 0.02 c	0.62± 0.04 bc	0.74± 0.12	0.207± 0.07 b	0.14± 0.07 c	0.18± 0.01 bc
	AM	1.24± 0.09 c	0.91± 0.08 cd	0.80± 0.05 ab	0.53± 0.04 c	0.58± 0.01 bc	0.78± 0.12	0.00± 0.00 c	0.00± 0.07 c	0.00± 0.00 c
	LO	1.06± 0.05 c	0.78± 0.03 cd	0.89± 0.04 ab	0.52± 0.03 c	0.61± 0.07 bc	0.79± 0.14	0.24± 0.09 b	0.30± 0.07 b	0.139± 0.07 bc
	Mean	**1.30± 0.15 A**	**1.17± 0.15 A**	**0.84± 0.07 A**	**0.61± 0.06 A**	**0.64± 0.06 A**	**0.74± 0.05 A**	**0.34± 0.05 B**	**0.39± 0.08 B**	**0.27± 0.08 B**

Table 3 - PCA applied to the Pearson's correlation coefficient of the soil attributes in the study area

Soil attributes	Axys 1	Axys 2
Detritivores abundance *(*individuals m^{-2}*)*	0.300 ^{ns}	0.341 *
Predators abundance (individuals m^{-2})	- 0.746 **	0.213 ^{ns}
pH	- 0.517 *	- 0.385 *
EC (dS/m)	0.430 *	0.696 **
WC (%)	- 0.860 **	0.081
SOC (%)	- 0.690 **	0.398 *
BR (mg kg_{soil}^{-1} day^{-1})	- 0.683 **	- 0.616 *
SIR (mg kg_{soil}^{-1} day^{-1})	- 0.929 **	- 0.151 ^{ns}
SMC (mg kg_{soil}^{-1})	- 0.692 **	0.622 **
SMN (mg kg_{soil}^{-1})	- 0.876 **	0.207 ^{ns}

Notes: pH: Soil acidity, EC: electrical conductivity, SOC: soil organic carbon, WC: water content, BR: basal respiration, SIR: substrate-induced respiration, Soil microbial biomass nitrogen (SMN), Soil microbial biomass carbon (SMC); ns: No significant, * Significant ($\alpha = 5\%$),** Significant ($\alpha = 1\%$)

Table 4- Mean (± standard error) soil properties under different woody species (QU: *Quercus brantii*, AC: *Acer monspessulanum*, PI: *Pistacia atlantica, CR: Crataegus pontica*, AM: *Amygdalus scoparia*, LO: *Lonicera nummularifolia*) and seasons (spring and winter). Lowercase letters indicate significant differences between woody species based on Duncan's multiple range test ($p< 0.05$).

Soil properties	QU		AC		PI		CR		AM		LO	
	Spring	Winter	Spring	Winter	Spring	Winter	Spring	Winter	Spring	Winter	Spring	Winter
pH	7.56± 0.02 ab	7.60± 0.02 a	7.47± 0.03 bc	7.32± 0.03 d	7.47± 0.03 bc	7.33± 0.03 d	7.55± 0.04 ab	7.44± 0.02 c	7.50± 0.05 abc	7.54± 0.04 abc	7.48± 0.01 bc	7.42± 0.02 c
EC (dS/m)	0.33± 0.01 ab	0.31± 0.01 b	0.24± 0.02 cd	0.35± 0.04 ab	0.25± 0.01 cd	0.35± 0.03 ab	0.22± 0.02cde	0.19± 0.01 e	0.21± 0.01 de	0.19± 0.01 e	0.27± 0.05 c	0.36± 0.02 a
SOC (g/kg dry soil)	5.24± 0.60 a	4.48± 0.30 bc	4.37± 0.02 bc	3.94± 0.04 c	2.20± 0.74 e	1.94± 0.34 e	4.27± 0.42 bc	4.04± 0.19 c	3.10± 0.50 d	2.80± 0.40 d	2.11± 0.11 e	1.98± 0.25 e
WC (%)	69.51± 4.20 a	51.06± 3.28 c	69.57± 5.11 a	44.12± 3.32 d	50.92± 3.15 c	50.80± 5.35 c	60.79± 3.42 b	44.86± 2.12 d	40.40± 4.14 e	38.53± 4.00 e	38.20± 5.00 e	40.72± 3.18 e
BR (mg kg_{soil}^{-1} day^{-1})	53.22± 3.11 a	26.00± 2.50 e	46.00± 2.60 b	24.32± 3.00 e	40.34±3.70 c	23.10± 1.80 e	39.30± 3.50 c	16.65± 2.00 f	41.17± 3.20 c	17.46± 2.40 f	36.11± 2.50 d	18.07± 3.61 f
SMC (mg $kg_{soil\text{-}1}$)	748.14±74.20 a	662.79±45.20a	540.91±70.11bc	538.00±30.18bc	521.53±41.32bc	502.00±53.18bc	551.12±49.18b	322.32±36.32e	370.46±31.30d	269.66±29.15e	372.34±30.01d	320.00±28.17e
SMN (mg $kg_{soil_{-1}}$)	57.92± 6.10 a	48.76± 4.10 b	44.79± 3.45 bc	43.86± 3.45 bcd	46.22± 3.35 b	31.06± 3.92 e	31.80±2.23 e	34.18± 3.00 e	36.40± 2.81 de	29.91± 2.10 e	37.01±2.79cde	32.40± 2.34 e
SIR (mg $kg_{soil_{-1}}$ day_{-1})	60.00± 3.10a	41.97± 2.80b	55.17± 3.12 a	36.60± 2.60 c	57.75±1.92 a	33.03± 1.30 c	43.00± 2.41 bc	28.63± 2.10 d	35.00± 1.46 c	31.06 ±1.50 c	31.60±1.12c	28.47± 1.09 c

Notes: pH: Soil acidity, EC: electrical conductivity, SOC: soil organic carbon, WC: water content, BR: basal respiration, SIR: substrate-induced respiration, Soil microbial biomass nitrogen (SMN), Soil microbial biomass carbon (SMC).