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**mesofauna in semi-arid oak forests** 2

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**Spatio-temporal heterogeneity differently drive the diversity of various trophic guilds of** 28

**mesofauna in semi-arid oak forests** 29

**Abstract** 30

Despite the importance of mesofauna in soil formation, litter decomposition, biological cycles 31
and growth of plants in semi-arid forest ecosystems, the effects of different woody species 32
and seasonality on the abundance, diversity and distribution of mesofauna invertebrates have 33
been little studied. This study has evaluated the effects of different woody species (trees and 34
shrubs) on trophic guilds of soil mesofauna (detritivores vs. predators) composition, 35
abundance and diversity during spring and winter seasons. Moreover, the basic drivers 36
including microclimatic characteristics and soil properties of soil biota abundance, 37
composition and diversity have been identified in semi-arid deciduous broadleaved forests. 38
Woody species types and seasonality affected soil mesofauna abundance, composition and 39
diversity. All the species were present during spring and winter and in all types of woody 40
species, but the mesofauna was differently affected by season and woody cover. Predator 41
abundance was affected by species and seasonality, whereas detritivore abundance was only 42
influenced by woody species. In relation to the season, mesofauna abundance is generally 43
higher in winter compared to spring. Detritivore and predation diversity in soil mesofauna was 44
affected by woody species and seasonality, but not by the interaction of both factors. It has 45
been also demonstrated that the trees understory is a more important biodiversity hotspot 46
compared to shrubs for mesofauna activity; moreover, the detritivores vs. predators 47
mesofauna composition are driven by the seasonality and woody species. Overall, this work 48
has demonstrated that aboveground and belowground relationship (that is, plant and soil 49
organisms) have reciprocal ecological linkages and that aboveground and belowground 50
communities can be powerful mutual drivers. 51

**Keywords:** shrub; tree; soil detritivores; abundance; evenness. 52

## 1. Introduction

The living soil (soil biota) contains a very high diversity of organisms, including 54 microorganisms (i.e., bacteria, fungi) and microscopic and macroscopic fauna (Bardgett and 55 Van Der Putten, 2014; Balestrini et al., 2015). The soil fauna includes macrofauna (having a 56 body size > 2 mm), mesofauna (body size between 100 μm and 2 mm) and microfauna (< 100 57 μm) (Whalen and Sampedro, 2010). The mesofauna consists of small invertebrates that live 58 in soil or litter with different diets such as predators and detritivores (Whalen and Sampedro, 59 2010). These organisms plays an important role in ecosystems multifunctionality and soil 60 quality (Lavelle et al., 2006) playing a vital role in the functioning of terrestrial ecosystems 61 (Wolters et al., 2000; Hossain and Sugiyama, 2019). 62

Soil mesofauna interact with plants and these relationships form the soil's food chain and 63 sustain the services and functions of natural ecosystems, such as carbon and nutrient cycling 64 or water cycle regulation (Motiejūnaitė et al., 2019). Thus, interactions between soil 65 mesofauna and plant are certainly important for growth and establishment of various plant 66 species including trees and shrubs species. In many ecosystems, changes in the diversity and 67 abundance of soil organisms can have significant effects on plant-soil interactions and 68 ecosystem production and functions (Ponge, 2013; Zhao et al., 2013; Agapit et al., 2018). 69 However, soil organisms are sensitive to abiotic and biotic factors both above and below 70 ground, such as climatic conditions, management measures, plant cover and different 71 chemical and physical soil properties (Pritchard, 2011; Wissuwa et al., 2012; Wu and Wang, 72 2019). Mesofauna invertebrates (both mesofauna detritivores and predators) diversity may be 73 affected by several ecosystem features, such as plant cover and biodiversity, which in turn 74 may be directly affected by soil nutrient deficiencies, climate change, forest fires and other 75 biological factors (such as pests and diseases) (Ahmadi et al., 2014; Lieutier and Paine, 2016; 76

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 78 woody species may alter composition of mesofauna invertebrates through for example the 79

quantity or quality of plant debris (Morán- López et al., 2015; Brygadyrenko, 2016). Many 80

studies have examined the effects of tree species, silvicultural operations or shrubs 81 composition on soil fauna (Kataja-aho et al., 2016; Čuchta et al., 2019). For instance, Heydari 82 et al. (2017 a) showed that Shannon-Wiener diversity and Margalef indices of mesofauna 83 richness in soil were significantly related to stand structural indices in a mixed oak (*Quercus* 84 *brantii* Lindl.) forest. Different characteristics of tree and shrub species - canopy architecture 85 and size, and consequently different amount of litter input and root development - can be 86 effective on their effects on soil properties (Vetaas, 1992; Muraoka and Koizumi, 2005; Yao 87 et al., 2017). However, recognizing the effects of different woody species on the abundance, 88 diversity and distribution of mesofauna invertebrates can provide valuable information on the 89 factors contributing to the conservation and enhancement of soil biodiversity at different 90 trophic levels in threaten ecosystems. 91

The different characteristics of soil organisms (such as composition, abundance and diversity) 92 are not randomly distributed, but organise horizontally, following patchy patterns at landscape 93 scale, and vertically, along the soil profile (Frey, 2015). These specific patterns can be largely 94 dependent on site microhabitats (Bayranvand et al., 2017; Heydari et al., 2017 a) and climate 95 seasonal variations (including differences on soil moisture and temperature) (Görres et al., 96 1998; Campuzano et al., 2019). On this context, the role of plant ecosystems or microclimatic 97 characteristics influence on soil mesofauna density is still not completely known (Briones, 98 2018). For instance, a deeper understanding of the effects of forest species on mesofauna 99

detritivores and predators communities may be useful as ecosystems quality indicators, 100

particularly in semi-arid ecosystems in which soil degradation processes are important under 101

the climate change context. 102

Zagros forests are one of the oldest and unique oak habitats in the world. The Zagros forest 103
cover an area of approximately 5 million hectares with highly scattered and occasionally 104
denser oak trees (mostly Brant's oak, *Quercus brantii* var. *Persica*) associated with different 105
shrub and tree species (Sagheb-Talebi et al., 2014). In these oak forests, the effect of individual 106
tree and shrub species on different soil biological and chemical properties throughout the 107
seasons has been little investigated, since most studies have focused on forest stands (Hosseini 108
et al., 2017; Mirzaei et al., 2020). Although one of the major determinants of the spatial 109
distribution of soil fauna diversity in forest ecosystems can be related to the overstory, the 110
current knowledge about the relationships between mesofauna invertebrates and tree species 111
is scarce (Gholami, et al., 2017). This makes difficult for ecologists the application of models 112
describing the structure of soil organism's communities and the comprehension of the 113
distribution of diversity of soil organisms at different scales (Barrios, 2007; Da Silva et al., 114
2015; Kuznetsova et al., 2019). To fill these gaps, this study aims to investigate the spatio- 115
temporal dynamics of soil mesofauna in semi-arid oak forest ecosystems of western Iran. In 116
more detail, the specific objectives of the study were: (i) to analyze the effects of different 117
woody species (trees and shrubs) on trophic guilds of soil mesofauna (detritivores vs. 118
predators) composition, abundance and diversity during spring and winter seasons; and (ii) to 119
identify the basic drivers including microclimatic characteristics and soil properties of soil 120
biota abundance, composition and diversity in semi-arid deciduous broadleaved forests. On 121
this regard, we hypothesized that: (i) the variation of soil mesofauna abundance, composition 122
and diversity are affected by woody species types and season changes; (ii) the trees understory 123
is a more important biodiversity hotspot compared to shrubs for soil biota activity; and (iii) 124
the contribution of mesofauna trophic guilds (detritivores vs. predators) in soil mesofauna 125
composition can be explained by the interaction of season and growth form types (tree vs. 126
shrub). 127

## 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:

$$SRmg = (S-1)/ \ln N \tag{1}$$

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

$$E = H' / \ln (S) \tag{3}$$

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 ($\mu gC\ g^{-1}$ of dried soil) of 0.5 M of $K_2SO_4$ soil extracts using the equation (Vance et al., 1987):

$$SMC = 2.64\ (A) \tag{4}$$

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 $K_2SO_4$ extracts (Brookes et al., 1985). The total N discharge (N extracted

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by the $K_2SO_4$ from the non-fumigated soil subtracted from the fumigated soil) was divided by 203

the KN value (N fraction of the biomass extracted after chloroform fumigation) of 0.54 204

(Brookes et al., 1985). 205

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*2.3. Statistical analysis* 207

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General linear models (GLM) were used to assess the effects of woody species, seasons and 209

their interaction on the soil mesofauna abundance, composition and diversity, including both 210

detritivores and predators. Variables were transformed when necessary to satisfy assumptions 211

of normality and homoscedascity of residues. Duncan's post-hoc tests were used to compare 212

the means of soil mesofauna abundance, composition and diversity among different woody 213

species in the understory. A principal component analysis (PCA) was used to evaluate the 214

relationships between soil mesofauna abundance of various trophic guilds (Detritivore vs. 215

Predator) and the chemical and biological properties of the soil under different species 216

throughout the two seasons (TerBraak and þmilauer, 1998). Moreover, a hierarchical grouping 217

and heat mapping of the 30 soil samples were carried out. A two-way clustering dendrogram 218

was obtained using Euclidean distance with the Ward clustering algorithm and coupled with 219

the heat map relative to the abundances of the nine mesofauna taxa. Differences in soil 220

mesofauna composition between different tree and shrub species were explored using non- 221

metric multidimensional scaling (NMS) as part of the 'vegan' package in R (Oksanen et al., 222

2018). This sorting method, which projects multivariate data in a space with fewer 223

dimensions, was performed on each data set using Bray-Curtis dissimilarity. Unidirectional 224

analysis of variance (ANOVA) was used to identify significant differences in sample plot 225

scores on the NMS axis. All statistical analyses were performed using R 3.5.2 (Main Team R, 226

2018) and CANOCO 5 software. 227

## 3. Results

### *3.1.        Soil mesofauna species and composition*

Nine mesofauna species were found under the tree and shrub species, belonging to two trophic 233 guilds, detritivores (*Pseudosinella octopunctata* Börner, *Folsomides marchicus* (Frenzel) and 234 *Oribatula sp*.) and predators (*Macrocheles glaber* (Müller), *Gaeolaelaps aculeifer* 235 (Canestrini), *Arctoseius cetratus* (Sellnick), *Tyrophagus sp*., *Acanthocreagris iranica* Beier 236 and *Aleochara sp.*) (Fig. 3a and 3b). The heat map splits the six species analysed in two 237 clusters (one for each season), based on mesofauna abundance. However, since soil mesofauna 238 composition was similar, the tree and shrub species were not separated. *Oribatula sp.* (spring)*,* 239 as well as *Tyrophagus sp*. and *Oribatula sp.* (winter) were the most abundant soil mesofauna 240 invertebrates. More specifically, in spring, the most abundant species was *Oribatula sp*. under 241 *Acer monspessulanum* L. subsp. cinerascens (Boiss.), and *Pistacia atlantica* Desf. (Fig. 3a). 242 In winter, *Tyrophagus sp.* and *Oribatula sp*. showed a high abundance under all species. 243 Moreover, *Folsomides marchicus* (Frenzel) and *Pseudosinella octopunctata* Börner were 244 more abundant under shrub species (*Crataegus puntica* C. Koch., *Amygdalus scoparia* Spach., 245 and *Lonicera nummularifolia* Jaub & spach) (Fig. 3b) 246

The NMS shows significant differences in mesofauna composition in spring (F-value = 10.46 248 and P-value < 0.0001 on NMDS axys 1, and F-value = 12.73 and P-value < 0.0001 on NMDS 249 axys 2) (Fig. 4 b, c) and winter (F-value = 23.70 and P-value <0.0001 on NMDS axis 1, and 250 F-value = 4.82 and P-value < 0.05 on NMDS axis 2) among species (Fig. 4 f, g). The 251 mesofauna composition under QU was, as expected, different from the composition detected 252

in other species in both seasons. Mesofauna composition was very similar under AM, PI and 253 CR (in spring), and CR and AM (in winter), as shown by the clear overlapping (Fig. 4 a, e). 254 The contribution of trophic guilds of soil mesofauna in composition under each species was 255 influenced by the interaction of season with vegetative form (tree and shrub), as in spring 256 predators contributes more in mesofauna composition under tree species (Fig. 4 d), while in 257 winter detritivores have a greater contribution in composition beneath shrubs (Fig. 4 h). 258

259

*3.2.      Soil mesofauna abundance and diversity*                                                                  260

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The total abundance of mesofauna was significantly different between the two seasons under 262 all species (Fig. 5). Compared to spring, Lower values were detected under QU and AC in 263 winter, while, in the same season, the abundance was higher under LO and PI . Detritivore 264 abundance was significantly higher in winter compared to spring, except for QU and CR (for 265 the latter the same values were detected in spring and winter). The maximum abundance of 266 detritivores was found under CR in spring ($135 \pm 32$) and winter ($138 \pm 32$), while and the 267 minimum value was detected under LO ($32 \pm 9$) and PI ($32 \pm 6$) in spring. Predator abundance 268 was higher under QU, AC, CR and AM, and lower under PI and LO in spring. The highest 269 abundance of predators was recorded under QU ($124 \pm 13$) and AC ($132 \pm 15$) in spring, while 270 the lowest abundance was surveyed under AM ($19.2 \pm 4$) in winter (Fig. 5). 271

272

The tree and shrub species significantly affected the soil mesofauna diversity indices and 273 abundance of their trophic guilds (i.e., detritivores and predators). Pielou's evenness was an 274 exception, since it was not affected by species. The sampling season had a significant effect 275 on Shannon–Wiener diversity, Margalef's richness and Pielou's evenness of both detritivores 276 and predators diversity. Also in this case, the total mesofauna diversity indices were not 277

significantly affected by season. As regards the trophic guild abundance, only predator 278
abundance was significantly affected by the sampling season (Table 1). The interaction 279
between species and season significantly affected the total mesofauna diversity and evenness, 280
the detritivore diversity and richness, the total mesofauna abundance and the predator 281
abundance (Table 1). No significant differences were detected in the total mesofauna diversity 282
indices between the two sampling seasons. All diversity indices of detritivores were 283
significantly higher in winter compared to spring; conversely, these indices were significantly 284
higher in spring for predators. The comparison of diversity indices between species in spring 285
indicates that diversity and richness indices of total mesofauna, detritivores and predators 286
were the highest under QU and AC and the lowest under shrubs (especially for AM and LO). 287
In spring, only evenness of detritivores got the highest and the lowest values under QU and 288
LO, respectively (Table 2). 289

290

*3.3.      Spatio-temporal variation in mesofauna abundance in relation to soil properties* 291

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PCA provided two main principal components (PCs), explaining more than 49% (PC1) and 293
19% (PC2) of the total variance in soil properties and mesofauna diversity indices under the 294
six species in the sampling seasons (Fig. 6). PC1 indicated that, under soil conditions with 295
higher pH, water content and organic carbon (i.e., under QU and AC in both spring and 296
winter), the activity of predators and microorganisms (higher SMC, MBN, BR and SIR) is 297
higher (see upper left quarter of the chart); moreover, both PC1 and PC2 showed that 298
decreasing organic carbon, water content, pH and microbial activity, and increasing EC 299
(decrease soil fertility) affect a higher activity of detritivores and lower activity of predators 300
under shrubs (CR, AM and LO) in winter. Along the negative direction of PC2 (indicating 301
higher EC, and lower nutrient content and microbial activity) the conditions of understory of 302

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CR, AM, LO and PI in spring are represented by an intermediate presence of both trophic 303

guilds (detritivores and predators) (Fig. 6 and Table 3). 304

All soil properties (except for EC, P = 0.056) showed statistically significant differences 305

among different woody species: pH (P < 0.001), soil organic carbon (P < 0.001), WC (P < 306

0.001), basal respiration (P < 0.001), substrate-induced respiration (P < 0.001), soil microbial 307

biomass nitrogen (P = 0.004), soil microbial biomass carbon (P < 0.001). Soil water content 308

beneath trees was significantly higher than beneath shrubs. It was also significantly higher in 309

spring compared t winter only for *Acer monspessulanum*, *Quercus brantii*, and *Crataegus* 310

*pontica.* In addition, soil organic carbon was higher under trees compared to shrubs. Soil pH 311

was higher in spring compared to winter for trees (*Acer monspessulanum* and *Pistacia* 312

*atlantica*) *and shrub* (*Crataegus pontica* and *Lonicera nummularifolia).* Soil biological 313

attributes (i.e. SIR, BR, SMC, SMN) were significantly higher under tree species compared 314

to shrubs; these attributes were also higher in spring compared to winter (Table 4). 315

316

## 4. Discussions 317

318

Little information about the effects of different woody species (trees and shrubs) on soil 319

mesofauna detritivores and predators composition, abundance and diversity is available. 320

Therefore, these effects have been evaluated during spring and winter seasons in semi-arid 321

deciduous broadleaved forests in Zagros forest. Moreover, we also try to identify the basic 322

drivers (microclimatic characteristics and soil properties) of soil biota abundance (detritivores 323

and predators), composition and diversity in the semi-aridforest of the study area. Among the soil 324

organisms, mesofauna is one of the most important biological components of soil, since it can 325

play an important role in determining soil multifunctionality (Koehler, 1992; Morais et al., 326

2010; Wu and Wang, 2019). However, its role and relationships in many natural ecosystems 327

including trees and shrubs are still poorly understood, especially in arid or semi-arid 328
environments (Taylor and Wolters, 2005; Young et al., 2018). Understanding the different 329
aspects of plant-soil interactions in arid and semi-arid forest ecosystems is very important, 330
because of resource constraints and higher environmental stresses (Schlesinger and Pilmanis, 331
1998; Karmakar et al., 2016). 332

Through this study, the first working hypothesis of our study is confirmed, since woody 333
species types and seasonality affected soil mesofauna abundance, composition and diversity. 334
In more detail, as shown in the abundance heat maps of soil mesofauna invertebrates, all the 335
species were present during spring and winter and in all types of woody species, but the 336
mesofauna was differently affected by season and woody species cover. *Oribatula* sp. and 337
*Tyrophagus* sp. found in *Pistacia atlantica* and *Acer monspessulanum* plots were the most 338
abundant mesofauna species in spring (higher than 60 individuals per $m^2$). *Oribatula* sp., 339
*Tyrophagus* sp., *Pseudosinella octopunctata* and *Folsomides marchicus* species were the most 340
abundant species, but with weak differences among woody species plots, in winter. As regards 341
the mesofauna abundance, GLMs (Table 1) showed statistically significant effects of tree and 342
shrub species and season. Predator abundance was affected by species and seasonality, 343
whereas detritivore abundance was only influenced by woody species. The positive effect of 344
the wet season is shown by the heat map of figure 3, where it is evident that mesofauna 345
abundance is generally higher in winter compared to spring. Water content in soil is an 346
important regulator of soil life, since most biochemical processes, such as the enzymatic 347
activity and reproduction, strictly depend on soil temperature and humidity (Lucas-Borja, 348
2016). Higher soil humidity of wet seasons under plant cover promotes higher availability of 349
chemical nutrients in soil solution, which enhances plant growth, and organic matter inputs to 350
soil, which feed soil mesofauna (Zagatto et al, 2017). As exposed by different authors and in 351
addition to the characteristics of woody species canopy, changes in biological and abiotic 352

factors due to seasonal changes can have directly (e.g., by humidity and temperature changes) 353
or indirectly (production rates) effects on the dynamics of biological activity, including the 354
diversity and richness of soil detritivores and predators (Anslan et al., 2018; Nascimento et 355
al., 2019; Kooch and Noghre, (2019). 356

The highest total mesofauna abundance was found under CR (shrubs species) and in QU, AC 357
(trees species) plots, detritivores species being higher in CR shrubs, and predator species 358
being higher in QU and AC trees, compared to the other woody species plots. Overall, our 359
results are in accordance with previous research about mesofauna abundance. Some studies 360
pointed out that tree canopy abundance and woody species significantly affect soil mesofauna 361
abundance (e.g., Vanbergen et al., 2007). Higher enrichment of carbon and nutrients beneath 362
the canopy of individual woody species with larger canopy size (trees vs. shrubs) can be 363
probably due to higher litter input per unit area and differentiated microclimate conditions 364
along seasons (Yao et al., 2017; Heydari et al., 2017 b; Bayranvand et al., 2017; Salazar et al., 365
2019). These characteristics can differently affect the diversity and composition of fauna 366
invertebrates (Negrete-Yankelevich et al., 2008). Soil invertebrates can benefit from woody 367
species cover, because a litter depth under a deciduous canopy or a dense shrub layer may 368
generate a thick litters (otherwise being thin), which may sustain mesofauna species (Ferguson 369
and Berube, 2004; Schuldt et al. 2008). In addition, Jiménez-Chacón et al. (2018) found that 370
light availability is a main determinant of soil fauna, although the sign of the light effect varied 371
among studies. It is worth to note that in water-limited ecosystems, mesofauna benefits from 372
the higher moisture found in darker microsites (Dhooria, 2016). As Jiménez-Chacón et al. 373
(2018) demonstrated, environmental predictors including light and soil humidity accounted 374
mostly for variation in the abundance of many different mesofauna species (i.e. *Diplopoda,* 375
*Pscoptera, Oribatida, Diptera,* and *Poduromorpha*). 376

In more detail, mesofauna predators were significantly influenced by SMN, WC, SIR, SOC 377 and BR, whereas detritivores by EC. As demonstrated by Liu et al. (2011), soil fauna 378 abundance and richness is highly affected by soil properties and shrubs characteristics. On 379 this context, litter coming from woody species may play a key role on the mesofauna 380 dynamics, since it is the main input of C, N and many other elements to bulk soil. As Thoms 381 et al. (2010) stated, there are direct interactions between soil fauna and plant communities and 382 different vegetal inputs generate variations in initial nutrient concentration and physico- 383 chemical properties of soil. According to Lucas-Borja et al. (2012), plant diversity influences 384 physico-chemical and microbiological soil properties of forest ecosystems. Therefore, the 385 spatial distribution of different wood species on the horizontal surface makes the forest floor 386 conditions heterogeneous in terms of different environmental factors, such as moisture, 387 temperature and litter depth. These agents create various microhabitats (Prescott and 388 Grayston, 2013) that can affect nesting, diversity and activity of organisms within and on soil 389 surface (Tedersoo et al., 2016; Gallé et al., 2017) beside the physical, chemical and biological 390 soil properties (Waring et al., 2016; Hammer, 2019). Thus, the differences related to tree 391 diversity, such as the litter composition, and the variations only indirectly related to woody 392 species composition or tree diversity, such as pH, soil organic matter and EC, might explain 393 the described patterns of soil mesofauna. 394

Our results indicated that detritivore and predation diversity in soil mesofauna was affected 395 by woody species and seasonality, but not by the interaction of both factors. This means that 396 both woody species and season alter at the same extent diversity indexes. For instance, the 397 higher detritivore and predation diversity was generally found in QU and AC (trees species 398 plots) plots, whereas the lowest values were detected in CR (shrubs species plots) plots in 399 spring and winter. This fact seems to corroborate our second and third working hypothesis, 400 which pointed that: (i) the trees understory is a more important biodiversity hotspot compared 401

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 426
2010; Wu and Wang, 2019). 427

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## 5. Conclusions 429

Arid and semi-arid forests, including Zagros forests in western Iran, have high heterogeneity 430
in terms of species composition and canopy structure of woody species. This heterogeneity 431
complicates the study and the comprehension of soil-plant interactions in these ecosystems. 432
However, different conclusions can be derived from this study. This work addresses how the 433
signs and strength of the local determinants of mesofauna abundance, composition and 434
diversity change across woody species gradients. Differences in mesofauna composition, 435
abundance and diversity should be related to the characteristics of woody species and 436
seasonality, in addition to soil conditions mediated by the different shrub and tree species. The 437
high spatial heterogeneity of the forest in the horizontal dimension (such as the different 438
branch and canopy abundance and, as a consequence, the variable forest light and temperature) 439
and vertical variations in the quantity and quality of leaves and woody texture can create 440
different microclimates for the studied mesofauna. 441

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Figure

1    **Figures**

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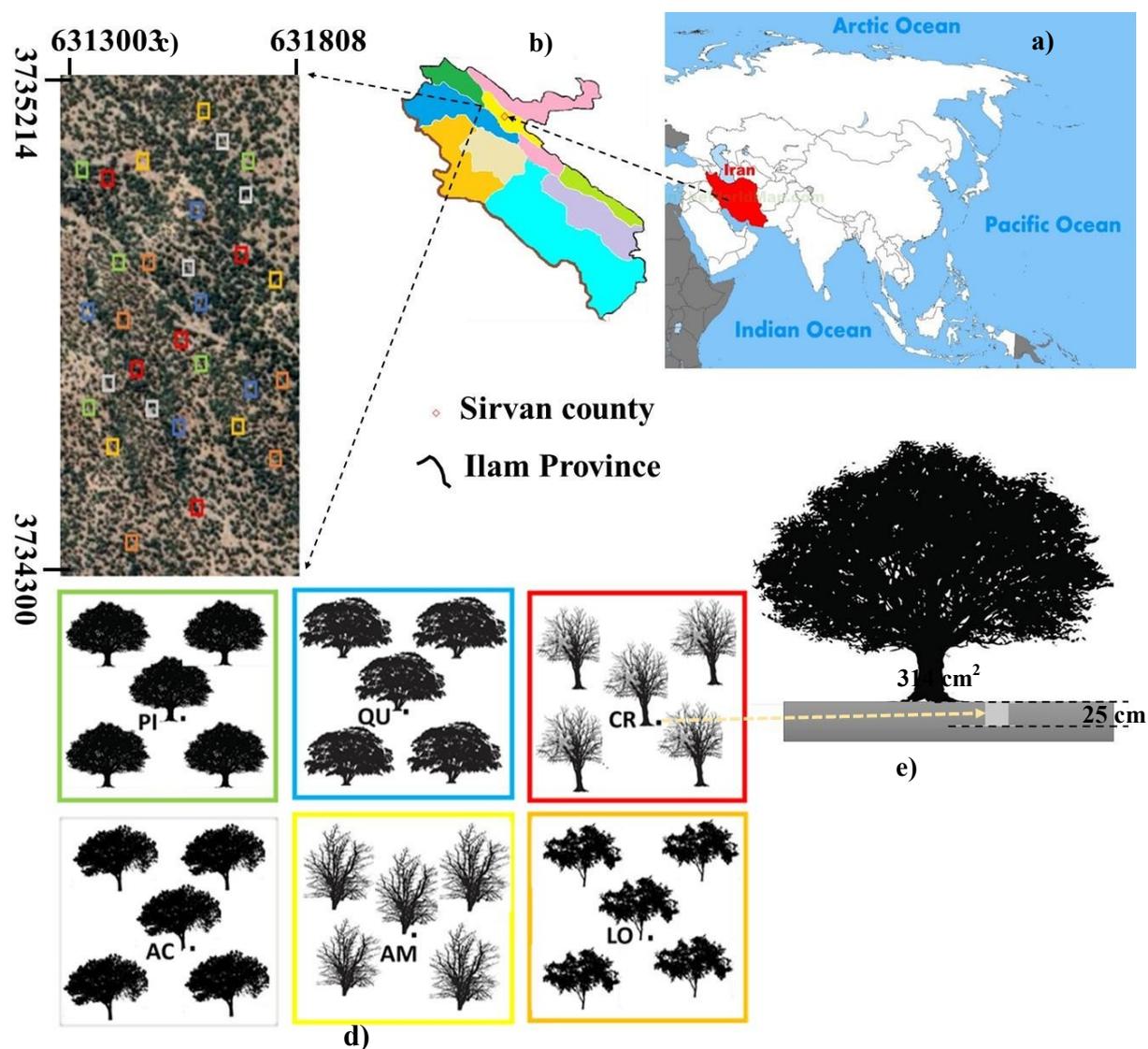


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5    Fig. 1 The study site is located in the Southern Zagros forests in western Iran (a) and Sirvan

6    County (b). For each woody species [QU: *Quercus brantii*), AC: *Acer monspessulanum* L.

7    and PI: *Pistacia atlantica* Desf. and three shrub species, CR: *Crataegus puntica* C. Koch.,

8    AM: *Amygdalus scoparia* Spach. And LO: *Lonicera nummularifolia* Ja ub & spach.] five

9    patches (colored squares) were selected in the study site (c and d). Soil sampling was done

10   in spring and winter 2018 in each patch under the canopy of a central woody species (e) at

11   0-25 cm depth with a sampling area of 314 cm$^2$.

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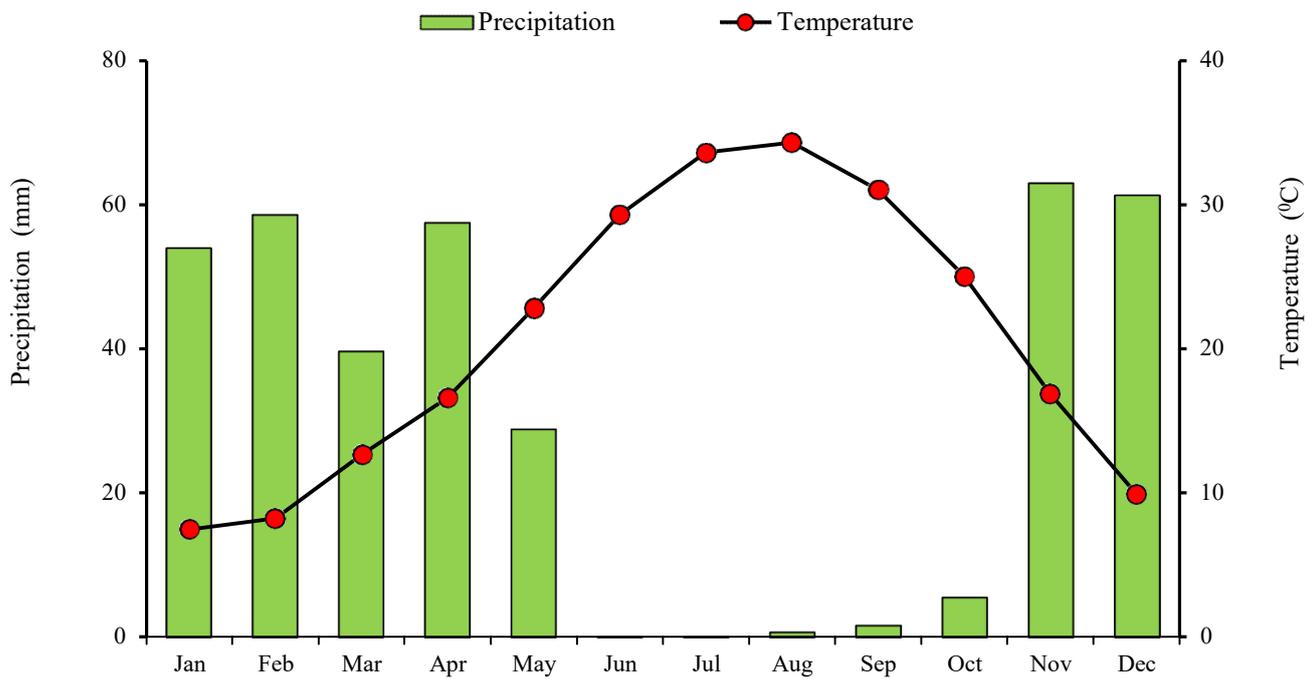
Fig. 2 Ombrothermic diagram of the study site (Southern Zagros forests, western Iran).

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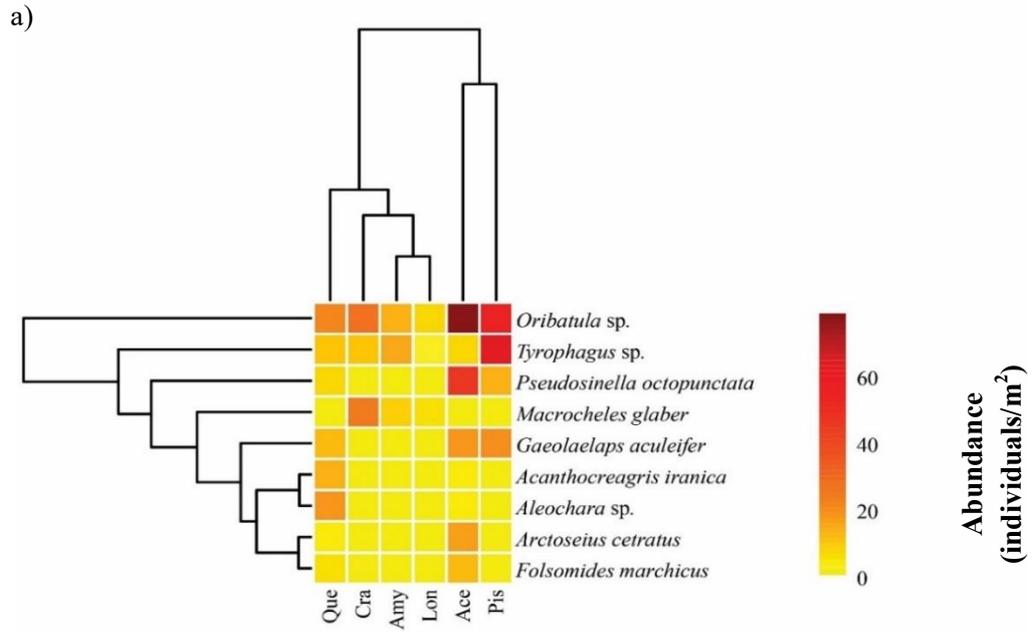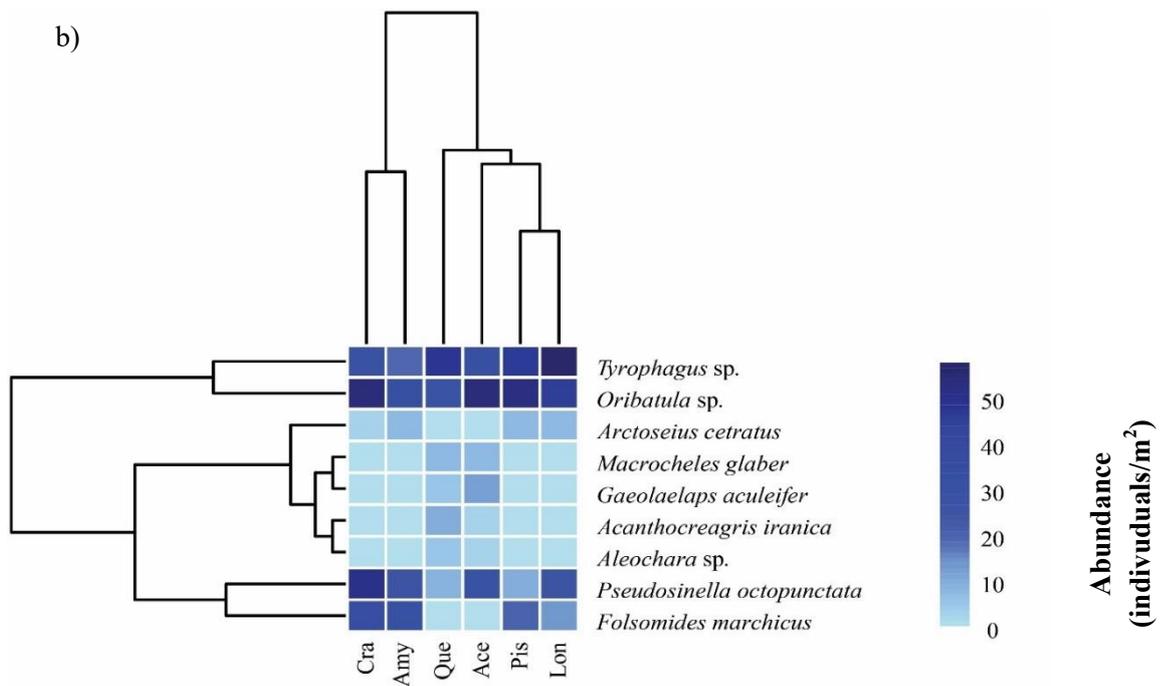
Fig. 3 Abundance heat map of soil mesofauna invertebrates under different tree and shrub species in spring (a) and winter (b) in Southern Zagros forest (western Iran). Que: *Quercus brantii*, Ace: *Acer monspessulanum*, Pis: *Pistacia atlantica*, Cra: *Crataegus pontica*, Amy: *Amygdalus scoparia*, Lon: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

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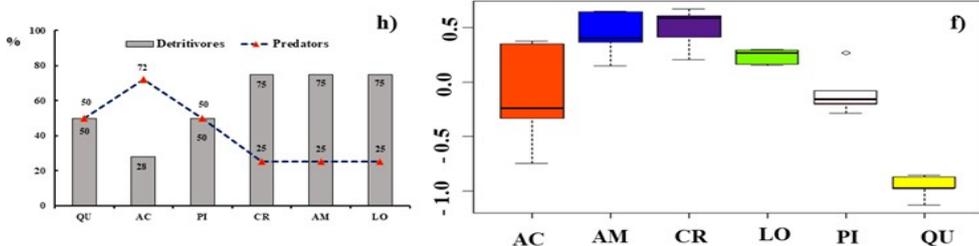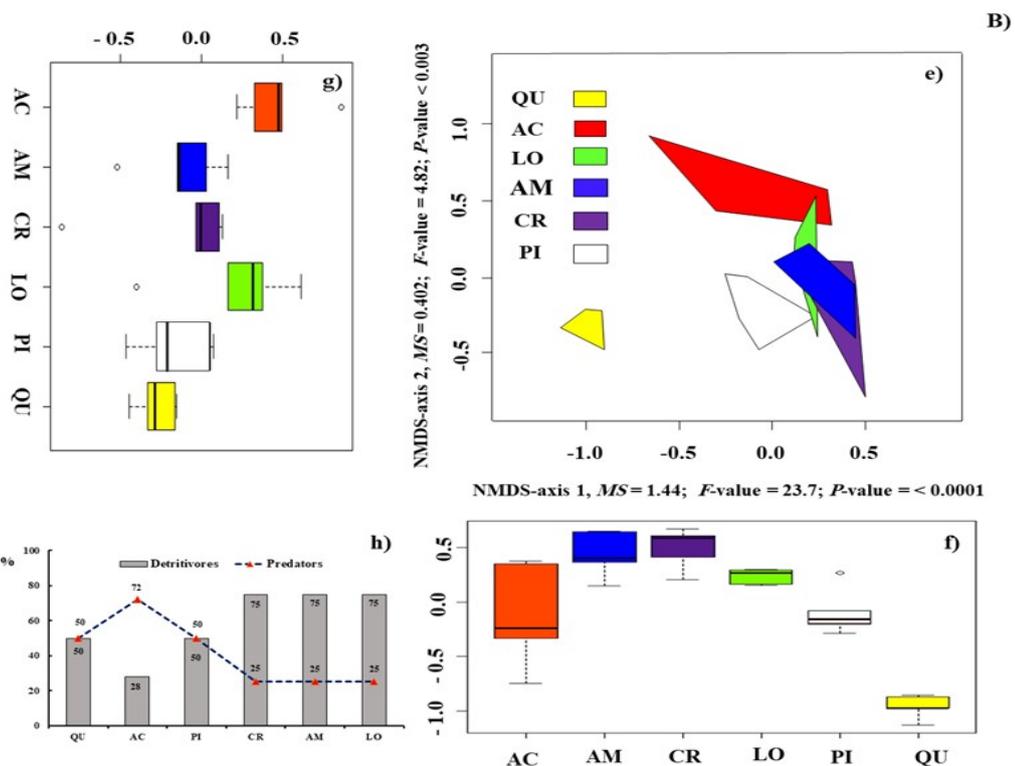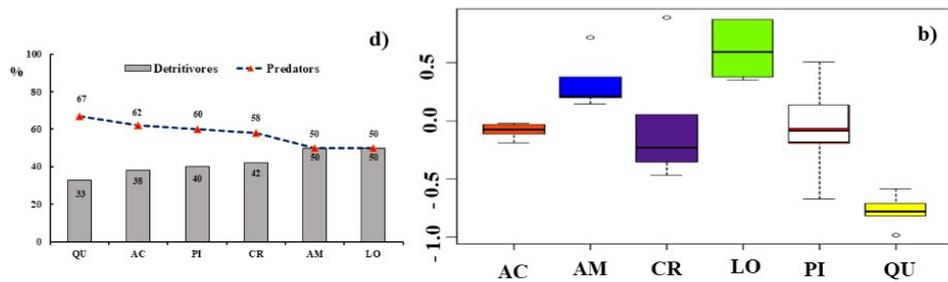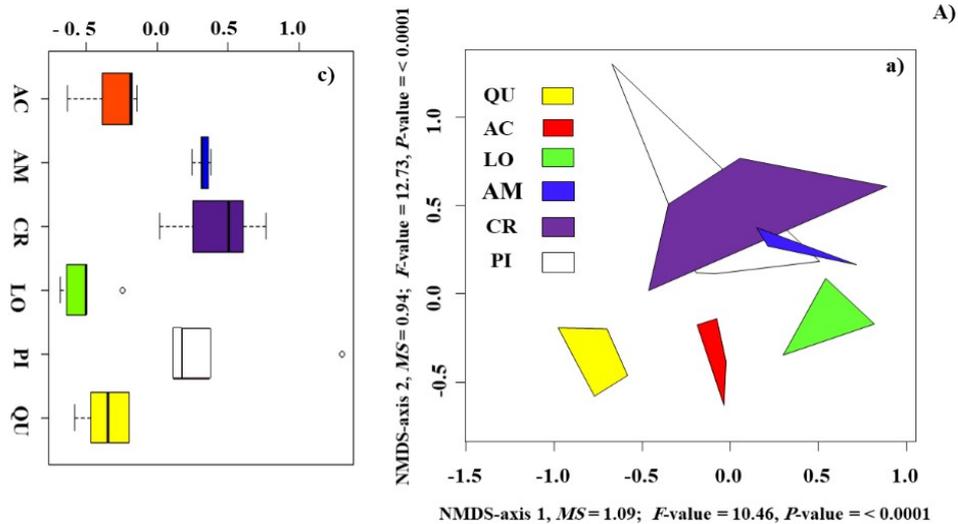
Fig. 4 Non-metric multidimensional scaling (NMS) ordination (a and e) based on Bray-Curtis similarity matrix to identify differences in the mesofauna composition between different tree and shrub species in Southern Zagros forest (western Iran). QU: *Quercus*

*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.

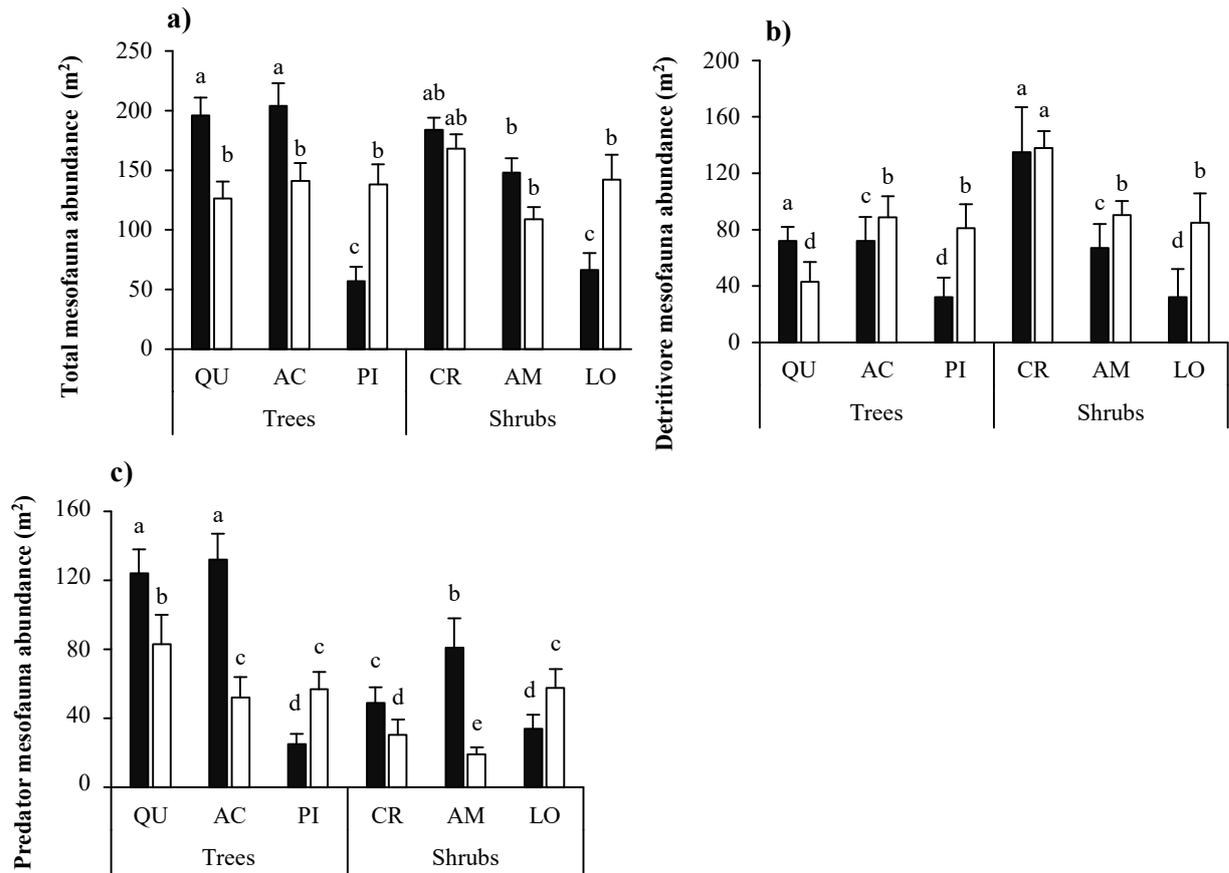Fig. 5 Differences in the abundance (mean ± standard error, individuals/m$^2$) of total mesofauna, detritivores and predators for tree and shrub species (QU: *Quercus brantii*, AC: *Acer monspessulanum*, PI: *Pistacia atlantica, CR: Crataegus pontica*, AM: *Amygdalus scoparia*, LO: *Lonicera nummularifolia*) 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).
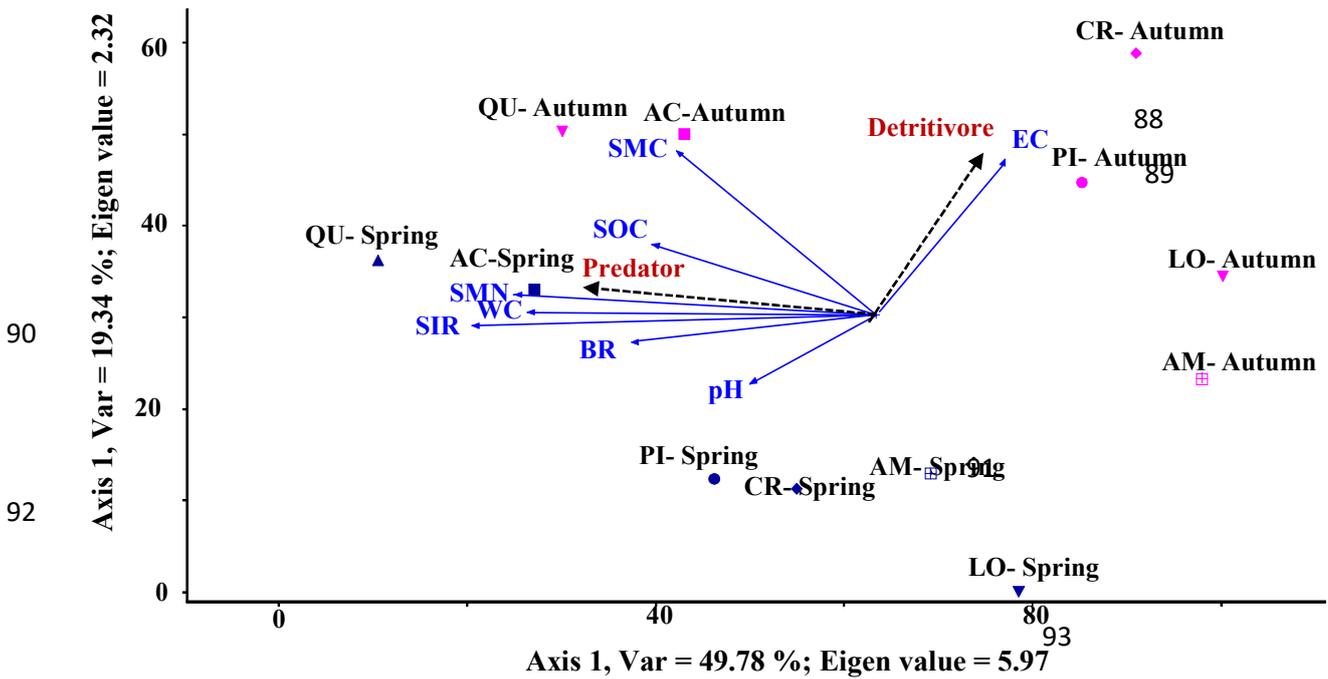
Fig. 6 Principal component analysis (PCA) applied to the tree and shrub species (QU: *Quercus brantii*, AC: *Acer monspessulanum*, PI: *Pistacia atlantica, CR: Crataegus pontica*, AM: *Amygdalus scoparia*, LO: *Lonicera nummularifolia*), soil chemical and biological properties, and water content as well 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).

1    TABLES

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

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| 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 |

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

6 Table 2- Soil mesofauna diversity (mean ± SE) under different tree and shrub species (QU: *Quercus brantii*, AC: *Acer monspessulanum*, PI: *Pistacia*

7 *atlantica, CR: Crataegus pontica*, AM *Amygdalus scoparia*, LO: *Lonicera nummularifol*ia) and seasons (spring and winter) in the topsoil (0–25 cm) in

8 Southern Zagros forest (western Iran).

9 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

| Season | Species | Total mesofauna | | | Detritivores | | | Predators | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | SH | MR | PE | SH | MR | PE | SH | MR | PE |
| | 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 |
| Spring | 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** |
| | 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 |
| Winter | 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** |

10 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

11 evenness.

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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%)

24 Table 4- Mean (± standard error) soil properties under different woody species (QU: *Quercus brantii*, AC: *Acer monspessulanum*, PI: *Pistacia*

25 *atlantica, CR: Crataegus pontica*, AM: *Amygdalus scoparia*, LO: *Lonicera nummularifolia*) and seasons (spring and winter). Lowercase letters

26 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 $kg_{soil-1}$) | 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 |

27 Notes: pH: Soil acidity, EC: electrical conductivity, SOC: soil organic carbon, WC: water content, BR: basal respiration, SIR: substrate-induced respiration, Soil microbial biomass

28 nitrogen (SMN), Soil microbial biomass carbon (SMC).