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REGULAR ARTICLE

Plant species and season influence soil physicochemical properties and microbial function in a semi-arid woodland ecosystem

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Abstract

Aims This research investigated the effects of woody plant identity and season on soil physicochemical properties and microbiological function in the semi-arid Zagros forest, one of the old-growth semi-arid oak forests in the world.

Methods Soil sampling was conducted beneath the canopy of six woody (tree and shrub) species in spring and winter. Microbial variables analysed included soil basal respiration (BR), microbial biomass C and N (MBC and MBN), microbial entropy index (MIE), substrate induced respiration (SIR) and enzymatic activities (i.e., urease and alkaline phosphatase). Soil physicochemical properties were also analysed and included pH, electrical conductivity (EC), available calcium and magnesium (Ca^{2+} and Mg^{2+}), organic carbon (OC), total nitrogen (Ntot), lime, water content (WC), bulk density (BD), clay, silt and sand.

Results Results demonstrated significant differences among the woody species (Pseudo-F = 56.31; *p* = 0.001), season (Pseudo-F = 97.37; p = 0.001) and their interaction (Pseudo-F = 2.96; *p* = 0.005) for the matrix of microbiological soil parameters. Differences were species-specific for shrubs and trees with a marked

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effect for tree species such as *Quercus brantii*. Microbial parameters were consistently higher in spring when higher temperature and lower moisture were recorded. Soil OC, Ntot, BD, and WC were important drivers of the soil microbial function.

Conclusions Our results evidenced a strong effect of season and plant species on soil physicochemical and microbiological soil properties in a semi-arid forest ecosystem. Higher values of microbiological soil parameters, including urease and phosphatase activities, were recorded for tree species during spring season.

Keywords Soil enzymes · Soil biomass carbon · Plant diversity · Organic matter: Zagros forest

Introduction

Plant diversity and vegetation type can largely influence the soil microbial community structure and function because of the differences in litter quality, root exudates and nutrient uptake (Dai et al. 2018; Xia et al. 2019; Wu et al. 2019; Estruch et al. 2020). Soil microorganisms play a key role in the functioning of plant communities, e.g. promoting plant-microbe associations and releasing soil nutrients for plant development. In turn, plant remains provide the main carbon and energy source for sustaining microbial activity (Rezende et al. 2017; Di Sabatino et al. 2020). Microbial communities in the soil are directly related to the turnover of carbon, nitrogen, and phosphorus in terrestrial ecosystems (Sandoval-Pérez et al. 2009; Zhang et al. 2018). These organisms are responsible for both organic matter degradation by mineralization and organic matter stabilization by humification, through a wide range of enzymatic activities (Shahbaz et al. 2017; Li et al. 2020).

Soil enzymes such as urease and phosphatase are involved in the decomposition of litter components (Adetunji et al. 2017). These enzymes play important roles in the soil system, e.g. catalysing biological and chemical reactions and promoting the mineralization of soil organic phosphorus and the decomposition of soil organic matter and nitrogen (Zaman et al. 2009; Jarosch et al. 2019). On the other hand, soil microorganism can access the energy and nutrients in complex substrates through the activity of these enzymes (Allison and Vitousek 2005; Avazpoor et al. 2019). Enzymatic activities related to cycles of carbon, nitrogen or phosphorus and microbial indicators such as microbial biomass and respiration, have been proposed as reliable indicators for assessment or soil quality and function (Yang et al. 2012; Hedo et al. 2015; Muñoz-Rojas 2018). Soil respiration reflects the microbial activity level (Rey et al. 2011; Oyonarte et al. 2012), which is sensitive to soil environmental or physicochemical soil variables, such as temperature and humidity, texture, pH, electrical conductivity and soil nutrients (Hursh et al. 2017; Heydari et al. 2019). Furthermore, these soil microbial parameters can be useful for characterizing the extent of aboveground plant influence in soil biological properties (Lucas-Borja et al. 2012a).

Overall, the microbial community is a critical component of sustainable soil-plant systems in forests, including those located in semi-arid areas (Bastida et al. 2008; Ushio et al. 2008; Merilä et al. 2010). Semi-arid regions cover ~15% of terrestrial earth lands and play an important role as potential carbon sinks under elevated CO_2 (Safriel and Adeel 2005; Ahlström et al. 2015). The area occupied by arid and semi-arid ecosystems is increasing due to global warming and advanced desertification (Teimouri et al. 2018). In these ecosystems, climatic conditions, forms of vegetation and low levels of organic matter may promote erosion processes, reducing soil fertility (Khalyani and Mayer 2013; Bracken et al. 2019). Thus, plants and soil feedbacks in these semi-arid regions need to be thoroughly understood in order to preserve and promote higher soil and ecosystem functionality in current and future global change scenarios (Ostle et al. 2009; Sardans and Peñuelas 2013). Different woody species can create diverse microclimate conditions (Ayres et al. 2009; Lucas-Borja et al. 2012b; Scheibe et al. 2015; Heydari et al. 2017b), and generate a varied quantity and quality of litter inputs and root exudates which are major carbon source for microorganisms (Grayston et al. 1997; Cheng et al. 2013; Wan et al. 2015). These differences can affect the spatially dependent soil enzymatic activities together with the soil physicochemical and biological characteristics (Mungai et al. 2005). Despite the importance of these processes, the ability of soil enzymes to reflect nutrient and microbial hotspots under different tree and shrub species and climatic conditions has not been thoroughly studied (Lucas-Borja et al. 2012a; Yao et al. 2019; Zuccarini et al. 2020).

The effects of season on the soil and ecosystem functioning can be critical, particularly in arid and semi-arid ecosystems (Jia et al. 2020). Contrasting effects in the degradation of soil organic compounds through soil moisture and temperature regulation, can simultaneously affect the soil microbial community response and enzymatic activities (Kang et al. 2009; Huang et al. 2016). Previous studies have shown that seasonality significantly affects soil enzymatic activity. For example, Zuccarini et al. (2020) showed a significant decrease in soil enzyme activities during summer due to warming and limited soil moisture whereas Wallenstein et al. (2009) reported a decrease of soil enzyme activity due to winter cold temperatures in semi-arid climate areas. Overall, seasonal variation may generates different patterns of microbial processes depending on the availability of different substrates, variation in soil temperature and moisture (Kaiser et al. 2011). In semi-arid ecosystems, the availability of water, plant biomass, litter and soil nutrients is modulated by the occurrence of precipitation, which mainly occurs in autumn and winter (Snyder and Tartowski 2006). Despite an increase of studies focused on the impacts on climate on semi-arid forests, our understanding regarding the effects of season on soil microbial and physicochemical characteristics for specific woody plant species is still limited in semi-arid ecosystems.

In this study, we aimed to investigate these processes in the Zagros forest in western Iran, which is one of the oldest semi-arid oak forests in the world influenced by the Mediterranean climate. Zagros has lost abundant forest area over the last 30 years due to economic expansion but these forests are critical because they supports several ecosystem services such as food, timber, water, carbon storage, air purification, wildlife habitat and social and cultural benefits (Heidarlou et al. 2019). Our main objective was to evaluate the effects of plant species and season on soil physicochemical properties and microbial function, e.g. soil respiration, microbial biomass and enzymatic activities. For this study, six woody species representative of the semi-arid Zagros forest were selected. We hypothesized that tree and shrub growth forms will have different effects on soil patterns, which can be attributed to mass action effect (e.g. differences in quantity and quality of plant remains and organic matter) and the availability of water, plant biomass, litter and soil nutrients during winter. In addition, trees and shrubs may generate patchy microclimate conditions which may modulate the microbial functional response in semi-arid forest. These heterogeneous conditions would have a relevant response in the activity and function of soil microbial communities.

Material and methods

Study area

This study was conducted in a 60-ha area in the central part of the Zagros Mountain (Sirvan city, western Iran, 33° 44′ 55“ N; 46° 25’ 19” E, Fig. 1) with homogeneous physiographic conditions (slope < 10% and altitude 1900–2000 m.a.s.l.). Forests in this area are typically formed by relatively spare woody overstorey (basal area 11 ± 5.2 m^2 ha^{-1}) with patchy distribution. Tree and shrub species in the area include *Quercus brantii* Lindl., *Pistacia atlantica* Desf., *Acer monspessulanum L. subsp.* cinerascens (Boiss.) Yaltirik., *Crataegus puntica* C. Koch., L., *Amygdalus scoparia* Spach., and *Lonicera nummularifolia* Jaub & spach. In the study area, the age of shrub and tree species is approximately 30–70 and more than 150 years old, respectively. The understory vegetation is relatively dense and comprised of annual and perennial grasses and forbs such as *Alyssum marginatum* Steud. ex Boiss*., Astragalus adscendens* Boiss*., Geranium lucidum* L.*, Medicago radiata* L.*, Valerianella vesicaria* Moench*, Neslia apiculata* Fisch.*, Hordeum bulbosum* L.*, Gundelia turneffortii* L. and *Bromus tectorum* L. Mean annual rainfall and temperature are 428.8 mm and 18.55 °C respectively (Sarableh climate station, 2009–2018). Precipitation usually occurs during October–May with a maximum during December to April. During June to September, effective precipitation is very sparse and rarely recorded (Fig. 2). Soil in the Zagros Mountains is generally calcareous shallow (Jazirehi and Ebrahimi 2003). Soil across our study area was classified as a sandy clay loam. The soil type in the study area is Calcisols based on FAO classification.

Experimental design and soil sampling

This study focused on three tree species, i.e. *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* Ja ub & spach. (LO). Five patches were sampled for each species (total of 30

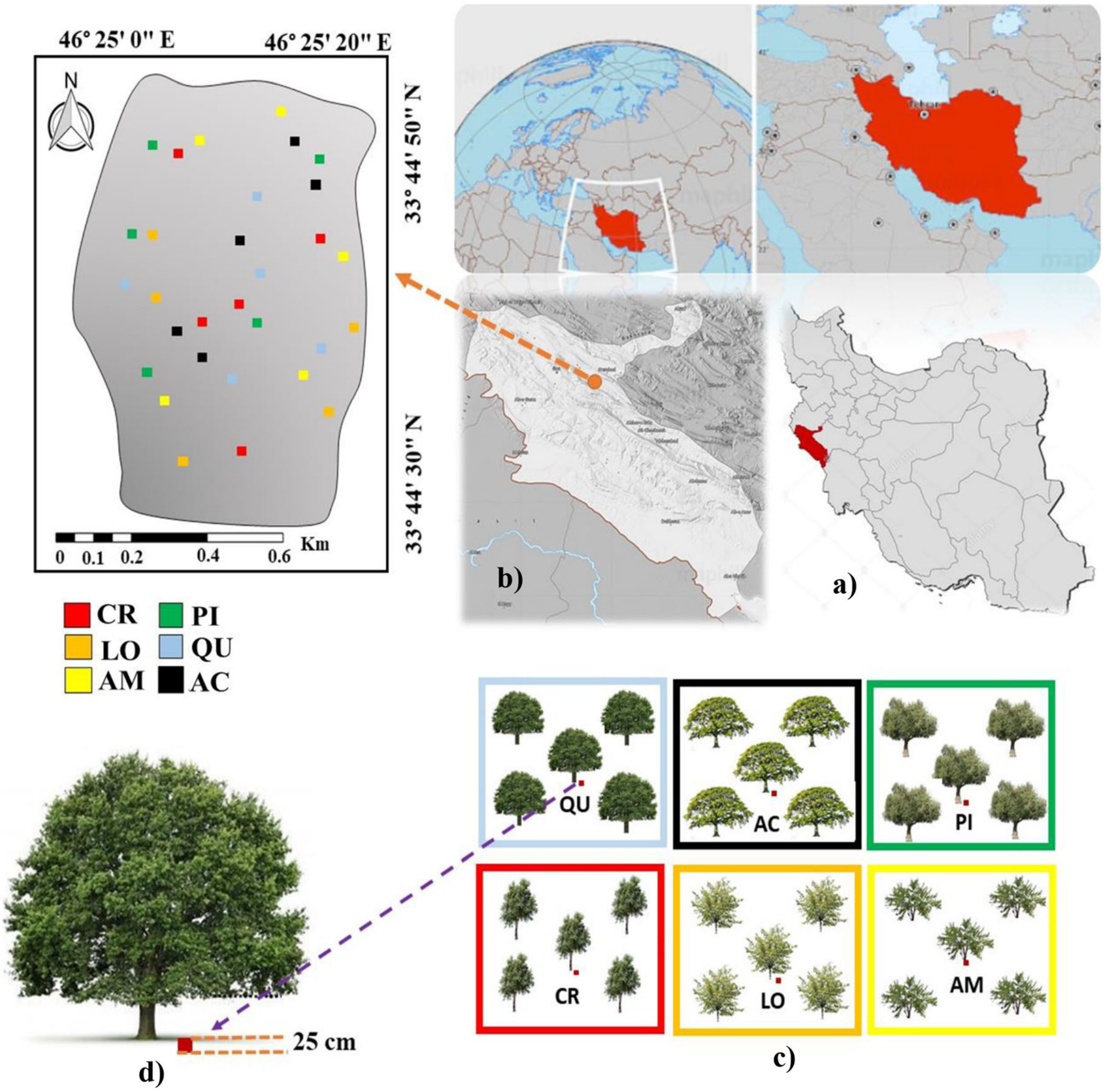
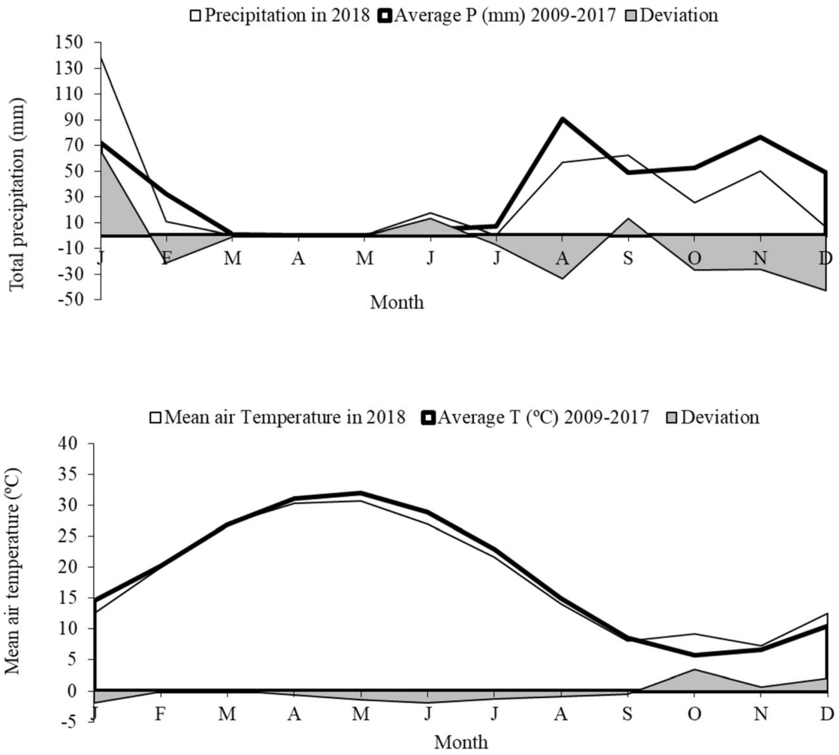


Fig. 1 The study area is located in the Southern Zagros forests in western Iran (**a**) and Ilam province, Sirvan County (**b**). For each woody species [QU: *Quercus brantii*), AC: *Acer monspessulanum* L. and PI: *Pistacia atlantica* Desf. and three shrub species, CR: *Crataegus puntica* C. Koch.,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

patches), which consisted in small groups of individuals of the same species and same size (Bayranvand et al. 2017). The minimum distance between two adjacent patches was 40 m. Vegetation patches (≈ 55–240 m^2 canopy cover) included 4–5 individuals of the same woody species, and the size between patches was kept as less variable as possible. One composite soil sample ($n = 30 \times 2$ seasons) was randomly collected beneath the canopy of the central woody species for each patch from the uppermost 25 cm layer using a cylindrical extractor with an area of 314 cm^2 in spring (May) and winter (December) in 2018 (Bayranvand et al. 2017; Heydari et al. 2017b). We focus on this soil depth as soil chemical and biological conditions in the semi-arid environments is restricted to this uppermost soil layer (Yao et al. 2019). Soils were placed in hermetic boxes and immediately taken to the laboratory. Soil samples were then divided into two subsamples; one was kept in the

Fig. 2 Average annual temperature and precipitation regime in the study area for comparison between conditions during the experiment (light black line, January 2018 to December 2018) and historic records from the local meteorological station (thick black line, from 2009 to 2017). The difference is represented as a grey shadow (deviation)



refrigerator (+4 °C) for one 30 days before measuring microbial and biochemical properties, and the other was air-dried and passed through a 2 mm sieve to measure the physical and chemical properties. Additional undisturbed soil cores were taken for the determination of bulk density (BD) in the 0–25 cm mineral layer (Blake and Hartge 1986).

Laboratory measurements

Soil texture was measured using a hydrometer (Bouyoucos 1962) and soil water content (WC) was determined using the gravimetric method (Famiglietti et al. 1998). Soil pH was measured electrometrically (in soil: water suspension), while electrical conductivity (EC) was determined with a conductivity probe in filtered extracts (Kalra and Maynard 1991). Dichromate oxidation followed by rapid titration was used for soil organic carbon (OC) determination (Walkley and Black 1934). Lime content as the total neutralizing value (TNV) were determined by titration with NaOH (Black 1986). Available calcium and magnesium were determined using atomic absorption and complexometric titration (Botha and Webb 1952). Soil microbial biomass carbon (MBC) and microbial biomass nitrogen (MBN) were analysed by dichromate digestion in both chloroform-sprayed and non-fumigated samples (Vance et al. 1987). Soil MBC 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): MBC = 2.64 (A); where A is the difference in carbon from fumigated and non-fumigated soils. To obtain the MBN, fumigated and non-fumigated soil samples were extracted with K_2SO_4 and the filtered extract was measured for total Nitrogen using the Kjeldahl digestion method (Brookes et al. 1985). 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 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). Urease activity was measured according to Tabatabai and Bremner (1972) using a water-urea solution as a substrate. This activity was determined by the NH_4^+ released after a 2-h incubation at 37 °C. The soil alkaline phosphatase was measured based on the detection of p-nitrophenol (PNP) released after incubation (37 °C, 1 h) (Tabatabai and Bremner 1969).

Statistical analyses

Resemblance-based methods were used to analyse multivariate data in the context of more complex sampling structures and experimental designs (Clarke and Gorley 2015). Since microbiological soil parameters used in this study, i.e. (soil enzymes, soil respiration, SIR, MIE, MBC and MBN) did not meet the assumption of normality, we analysed the data using a resemblance matrix for environmental variables (physicochemical soil properties) and biological data (microbiological soil parameters). Factor studied were woody species (QU, AC, PI, CR, AM, LO) and season (spring and winter). The routines used were first PERMANOVA (Permutational MANOVA) in which biological data (urease and phosphatase activities, BR, MBC, MBN, MIE and SIR) were square root transformed and the resemblance matrix was built using the Bray-Curtis distance. The sums of squares type were type III (partial) and woody species and season were considered as fixed effects. The permutation method used was unrestricted permutation of raw data and the number of permutations was 999. Secondly, physicochemical soil data was analysed using non-metric Multi-Dimensional Scaling (MDS) and the Kruskal stress formula (minimum stress: 0.01) for visualizing the level of similarity of individual cases of a dataset. Previously to MDS, an analysis of similarities (ANOSIM), described by Clarke (1993), was developed for soil physicochemical properties, and multivariate resemblances were analysed according to the factors woody species and season. Thirdly, we made a Similarity Percentages (SIMPER) routine for identifying the physicochemical soil variables primarily discriminating between woody species. Fourthly, a comparative (Mantel-type) test on both physicochemical soil properties and soil microbiological parameters similarity matrices (RELATE) was developed to identify statistical relationships between environmental and biological data. Finally, Distance-based linear models (DISTLM) and distance-based redundancy analysis (dbRDA) were applied to the biological data being the criterion AICc used for selection of best model flowing the step-wise procedure. Statistical analyses were made using PRIMER V6 software (Clarke and Gorley 2015; Anderson et al. 2008).

Results

Permanova analyses showed significant statistical differences among the different woody species (Pseudo-F = 56.31; $p = 0.001$), season (Pseudo-F = 97.37; $p = 0.001$) and their interaction (Pseudo-F = 2.96; $p = 0.005$) for the matrix of microbiological soil parameters (urease and alkaline phosphatase activities, BR, MBC, MBN, MIE and SIR) (Table 1). Most microbial soil parameters varied among woody species and seasons and higher values of microbiological soil parameters were generally observed for tree species, i.e. QU, AC and PI, and during the spring season (Figs. 3 and 4). Similarly, soil microbial factors were higher during the spring season under shrub species (AM, CR and LO) although differences between seasons were lower compared to tree species (Figs. 3 and 4). Specifically, BR was significantly different between seasons across all species with significant larger values in spring ($P < 0.05$, Fig. 3). Similarly, SIR was higher in spring, but differences were only significant for tree species ($P < 0.05$, Fig. 4). Overall, the effect of season on the microbial parameters was stronger compared to the plant identity (Table 1).

The ANOSIM analyses showed statistically significant differences in soil physicochemical properties among woody species levels (Global R: 0.86, significance level of sample statistic: 0.1%) and between seasons for each woody specie (Global R: 0.43, Significance level of sample statistic: 0.1%) (Table S1). The NMDS analyses clearly separated all woody species (Fig. 5a) and season levels within species (Fig. 5b). Tree species QU and AC clustered and were largely explained by variation in total N, OC and nutrients. Shrub species such as CR were driven mostly by soil texture parameters, e.g. clay, silt and sand, C:N, lime and BD (Fig. 5).

The Similarity Percentages analyses showed the most important soil properties contributing to the average square distance for each woody species level (Table 2). The average square distance for QU plots was 3.74 and the soil physicochemical properties that most contributed to similarity of QU plots were BD, Mg^{2+}, pH, sand and clay properties. In the case of AC plots, the average square distance was 3.44 and the soil properties that most contributed to similarity of AC plots

Table 1 Permanova and pair-wise test for woody species and season factors in relation to microbiological soil parameters matrix (urease and phosphatase activities, BR, MBC, MBN, MIE and SIR)

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Species	5	1945.80	389.15	56.31	0.001	999
Season	1	672.95	672.95	97.37	0.001	998
Interaction	5	102.37	20.47	2.96	0.005	998
Residual	48	331.72	6.910			
Total	59	3052.8				
Pair-wise test among woody species depending of the season						
	Spring				Winter	
Groups	t	P(perm)		Groups	t	P(perm)
QU, AC	4.532	0.012		QU, AC	2.5069	0.009
QU, PI	3.7143	0.011		QU, PI	3.7865	0.012
QU, CR	10.561	0.006		QU, CR	11.138	0.008
QU, AM	15.598	0.013		QU, AM	7.977	0.005
QU, LO	9.2527	0.014		QU, LO	8.0263	0.010
AC, PI	2.9008	0.008		AC, PI	2.7299	0.007
AC, CR	3.0216	0.011		AC, CR	7.8803	0.006
AC, AM	4.7651	0.009		AC, AM	6.1261	0.008
AC, LO	4.4887	0.006		AC, LO	5.8542	0.007
PI, CR	4.3405	0.012		PI, CR	6.6326	0.009
PI, AM	5.7974	0.011		PI, AM	5.7532	0.007
PI, LO	3.9124	0.009		PI, LO	4.3076	0.007
CR, AM	5.6785	0.008		CR, AM	2.2077	0.01
CR, LO	4.8657	0.008		CR, LO	4.9066	0.007
AM, LO	2.8324	0.011		AM, LO	3.5351	0.013

QU, *Quercus brantii*; *AC*, *Acer monspessulanum*; *PI*, *Pistacia atlantica*; *CR, Crataegus pontica*; *AM*, *Amygdalus scoparia*; *LO*, *Lonicera nummularifolia*

were BD, silt, Mg^{2+}, pH and clay properties. In the case of PI plots, average squared distance was 13.44 and the soil properties that most contributed to similarity of PI plots were pH, clay, sand, silt and EC. Average square distance was 3.25 in case of CR plots, being BD, lime, WC, Mg^{2+} and Ca^{2+} the most important variables; and 3.42 for the LO plots, being sand, pH, clay, Mg^{2+} and Ca^{2+} the most important variables. Finally, average square distance was 2.21 in case of AM plots, being BD, lime, WC, Mg^{2+} and Ca^{2+} the most important variables (Table 2).

The matched resemblance matrices test (RELATE test) indicated that soil physico-chemical properties significantly correlated with microbiological soil parameters (Rho: 0.43; significance level of sample statistic: 0.1%). According to the distance based linear models (DistLM), marginal test and sequential test for physicochemical soil variables indicated that almost all physicochemical soil variables influenced soil microbiology when considered isolated (Table 3).

The best model for predicting microbiological soil parameters was composed by BD, OC, WC, lime, Mg^{2+}, pH, Ca^{2+} and Clay % ($R^2 = 0.75$, AICs = 173.56; Table 4). The RDA analysis for the microbiological soil parameters showed that the percentage of variation explained by axis1 was 72.0% out of the fitted model and 54.2% out of total variation whereas the percentage of variation explained by the axis 2 was 16.8% out of the fitted model and 12.6% out of total (Fig. 6). The dbRDA1 axis clearly discriminated trees from shrub species. There was a positive correlation between microbial parameters, e.g. BR, SIR, MBC and MBN which accounted for a large variation in the distribution of samples along axis 1 (Fig. 6a). Samples did not show a clear clustering for season (Fig. 6b).

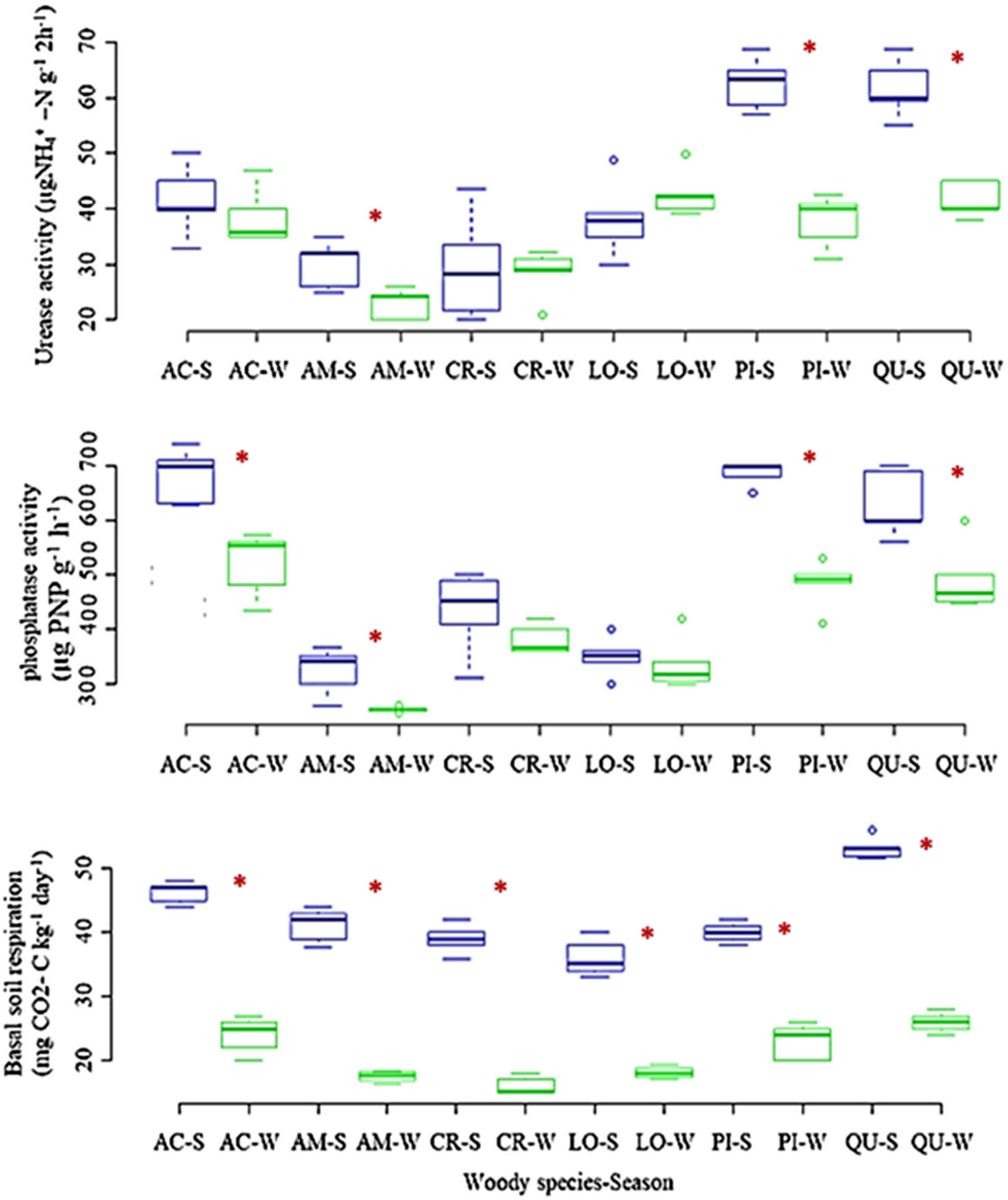
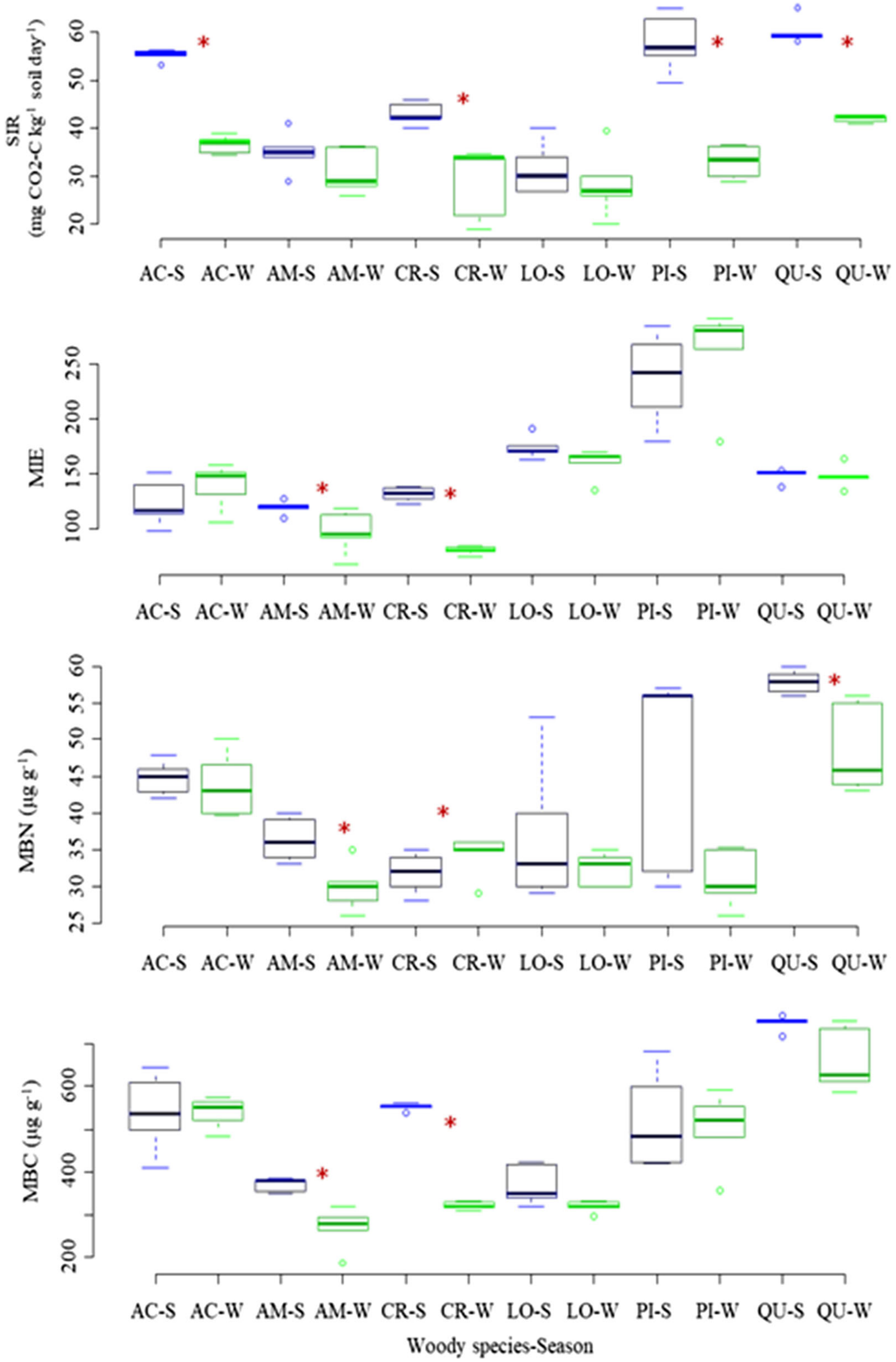


Fig. 3 Boxplots for each microbiological soil parameters according to factors (woody species and season). Urease activity (µgNH_4^+ –N g^{-1} 2 h^{-1}), phosphatase activity (µg PNP g^{-1} h^{-1}) and basal soil respiration (mg CO_2-C kg^{-1} soil day^{-1}) among woody species (QU: *Quercus brantii*, AC: *Acer monspessulanum*, PI: *Pistacia atlantica, CR: Crataegus pontica*, AM: *Amygdalus scoparia*, LO: *Lonicera nummularifolia)* and season (S: spring, W: winter). Asterisk indicating significant statistical differences between seasons among species (P(perm) <0.05). A blue and a green boxplot with the meaning of spring and winter, respectively

Discussion

Overall, our results showed that woody species had a strong influence on the soil microbial and physicochemical properties, which confirmed our first hypothesis. Specifically, we found a clear contrast in the enzymatic activities (i.e. urease and phosphatase), BR and SIR between trees and shrubs. Woody plants have an undeniable role in soil processes and generates different microclimates conditions that facilitate processes such as surface runoff reduction and seed trapping efficiency (Aerts et al. 2006). All these processes promote the


SIR (mg CO2-C kg-1 soil day-1)
20
30
40
50
60
*
*
*
*
*
AC-S
AC-W
AM-S
AM-W
CR-S
CR-W
LO-S
LO-W
PI-S
PI-W
QU-S
QU-W
MIE
100
150
200
250
*
*
AC-S
AC-W
AM-S
AM-W
CR-S
CR-W
LO-S
LO-W
PI-S
PI-W
QU-S
QU-W
MBN (µg g-1)
25
30
35
40
45
50
55
60
*
*
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AC-S
AC-W
AM-S
AM-W
CR-S
CR-W
LO-S
LO-W
PI-S
PI-W
QU-S
QU-W
MBC (µg g-1)
200
400
600
*
*
AC-S
AC-W
AM-S
AM-W
CR-S
CR-W
LO-S
LO-W
PI-S
PI-W
QU-S
QU-W
Woody species-Season

◀ **Fig. 4** Boxplots for microbiological soil parameters according to factors (woody species and season). SIR: substrate-induced respiration (mg CO_2-C kg^{-1} soil day^{-1}), MIE: microbial entropy, MBC: microbial biomass carbon (mg kg $soil^{-1}$), MBN: microbial biomass nitrogen (mg kg $soil^{-1}$); QU: *Quercus brantii*, AC: *Acer monspessulanum*, PI: *Pistacia atlantica,* CR*: Crataegus pontica*, AM: *Amygdalus scoparia*, LO: *Lonicera nummularifolia* and season (S: spring, W: winter). Asterisk indicating significant statistical differences between seasons among species (P(perm) < 0.05). A blue and a green boxplot with the meaning of spring and winter, respectively

formation of 'fertile islands', assisting the establishment and survival of seedlings in degraded sites (Heydari et al. 2017b; Avendaño-Yáñez et al. 2018; Urza et al. 2019). Although the effects of particular plant species on soil properties have been broadly reported (Ayres et al. 2009; Waring et al. 2015) few studies have examined the factors that control these aspects. (Bayranvand et al. 2017; Heydari et al. 2017a).

Our results highlight the effect that woody species identity can exert on important soil physicochemical and microbiological parameters and point to the factors driving these differences. Firstly, the distribution of soil nutrient is influenced by plant structure, as shown by the progressive increase in litter content with tree age or forest management (Lucas-Borja et al. 2016). The higher organic matter accumulation in unmanaged and older forests in comparison with younger plant ecosystems may allow higher soil microbiological activity (Lucas-Borja et al. 2019a). Secondly, a stronger effect of plant identity can be expected as a consequence of the irregular distribution of soil nutrients nearby plants in arid and semi-arid ecosystems (Koch et al. 2007; Allison

Fig. 5 Non-metric multidimensional scaling (NMDS) plot according to physicochemical soil variables for woody species (**a**) and seasonality (**b**)

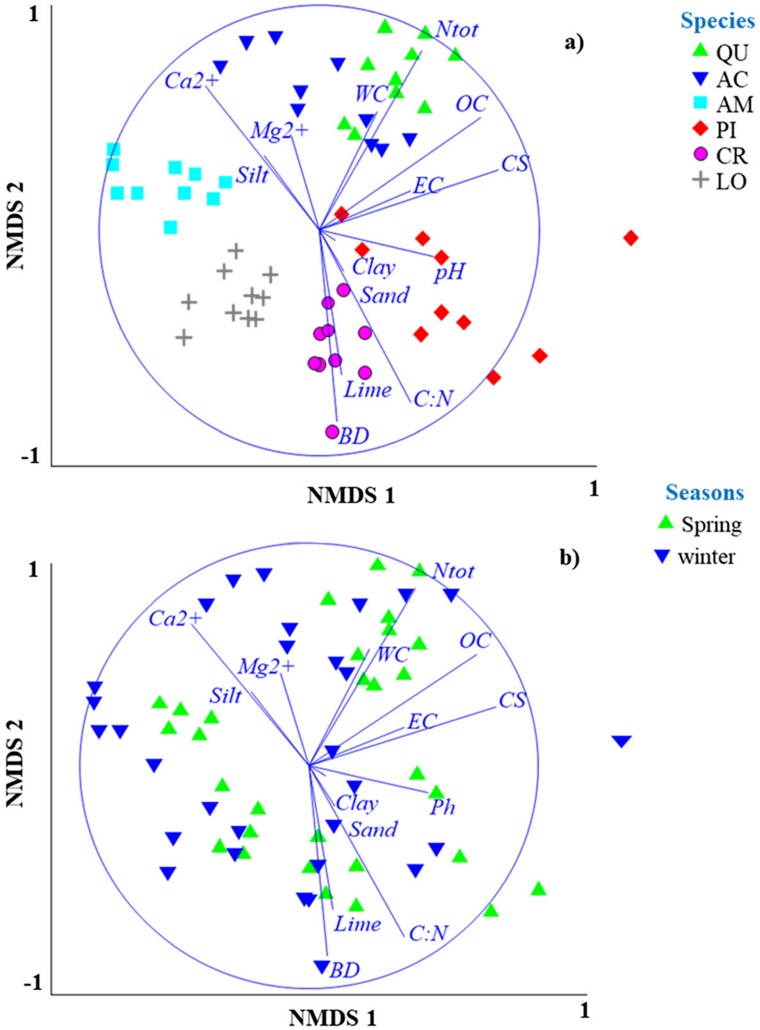

Table 2 Results of the similarity percentages and soil properties contributions to similarity percentages for each tree diversity level

Group QU	Average squared distance = 3.47		Group LO	Average squared distance = 3.42	
Species	Contrib%	Cum.%	Species	Contrib%	Cum.%
BD (g cm^{-3})	8.56		BD (g cm^{-3})	7.64	
Mg^{2+} (meq Lit^{-1})	13.03	21.59	Lime (%)	8.42	16.06
pH	14.3	35.89	WC (%)	16.28	32.34
Sand (%)	15.77	51.66	Mg^{2+} (meq Lit^{-1})	17.25	49.59
Clay (%)	28.13	79.79	Ca^{2+} (meq Lit^{-1})	17.82	67.41
Group AC	Average squared distance = 3.44		Group CR	Average squared distance = 3.25	
Species	Contrib%	Cum.%	Species	Contrib%	Cum.%
BD (g cm^{-3})	6.34		Sand (%)	9.55	
Silt (%)	11.19	17.53	pH	11.16	20.71
Mg2+ (meq Lit^{-1})	11.75	29.28	Clay (%)	12.53	33.24
pH	14.91	44.19	Mg^{2+} (meq Lit^{-1})	13.52	46.76
Clay (%)	28.11	72.3	Ca^{2+} (meq Lit^{-1})	15.05	61.81
Group PI	Average squared distance = 13.44		Group AM		Average squared distance = 2.71
Species	Contrib%	Cum.%	Species	Contrib%	Cum.%
pH	4.25		Silt	10.17	
Clay (%)	5.9	10.15	Ca^{2+} (meq Lit^{-1})	10.43	20.6
Sand (%)	13.99	24.14	Lime (%)	11.37	31.97
Silt (%)	20.81	44.95	C:N	12.25	44.22
EC (dS/m)	42.83	87.78	pH	22.93	67.15

Table 3 Marginal test for microbiological soil parameters matrix according to physicochemical soil matrix. Significant variables in bold

Variable	SS (trace)	Pseudo-F	*P*	Prop.
pH	174.67	3.52	**0.050**	0.06
EC	18.90	0.36	0.790	0.01
Mg^{2+}	121.00	2.39	**0.090**	0.04
Lime	419.89	9.25	**0.001**	0.14
OC	532.07	12.24	**0.001**	0.17
Ntot	960.46	26.62	**0.001**	0.31
C:N	971.29	27.06	**0.001**	0.32
Ca^{2+}	548.22	12.70	**0.001**	0.18
Sand	78.82	1.54	0.210	0.03
Clay	181.14	3.66	**0.040**	0.06
Silt	23.20	0.44	0.680	0.01
BD	1287.90	42.32	**0.001**	0.42
WC	992.01	27.92	**0.001**	0.32
CS	386.51	8.41	**0.001**	0.13

OC, Organic carbon; *Ntot*, Total nitrogen; *EC*, electrical conductivity; *Ca*$^{2+}$, available calcium; *Mg*$^{2+}$ *, available magnesium; BD*, Bulk density; *WC*, Water content; *CS*, Carbon sequestration

et al. 2008; Li et al. 2014). This effect has been attributed to the diverging carbon and nitrogen enrichments beneath shrub and tree canopies (via litter and rhizodeposition) driven by the diverse species (Perroni-Ventura et al. 2006; Chen et al. 2020). In this study, tree species, i.e. *Quercus brantii*, and *Acer monspessulanum* and *Pistacia atlantica* showed higher rates of enzymatic activity, SIR and MBC compared to shrubs. These microbial parameters were strongly correlated to nutrient levels, and particularly related to total nitrogen, organic carbon and the C:N, in agreement with other studies (Thompson et al. 2006). Soil water content and bulk density were among the most significant physicochemical variables driving the activity of microbes and enzymes in the Zagros forests. Specifically, we found a negative correlation between bulk density and carbon and nitrogen, and higher bulk density was found in shrubs compared to trees. Our findings agree with recent studies that also found a significant connection between bulk density and microbial diversity and activity (Muñoz-Rojas et al. 2016; Liu et al. 2018; Ramírez et al. 2020). Moreover, the higher BD under the shrubs is certainly caused primarily by the lower SOC (Lucas-Borja et al. 2019b). These relationships reflect the

Table 4 Sequential test for microbiological soil parameters matrix according to physicochemical soil matrix

Variable	AICc	SS(trace)	Pseudo-F	*P*	Prop.	Cumul.	res.df
BD	207.10	1287.90	42.32	0.001	0.42	0.42	58
OC	195.38	365.95	14.91	0.001	0.12	0.54	57
WC	186.05	246.40	11.97	0.001	0.08	0.62	56
Lime	182.53	108.01	5.69	0.001	0.04	0.66	55
Mg^{2+}	180.12	81.67	4.58	0.010	0.03	0.68	54
pH	178.64	62.78	3.70	0.040	0.02	0.71	53
Ca^{2+}	175.66	80.92	5.14	0.010	0.03	0.73	52
Clay	173.56	63.97	4.32	0.030	0.02	0.75	51

OC, Organic carbon; *BD*, Bulk density; *WC*, Water content; Ca^{2+}, available calcium; Mg^{2+}, available magnesium

positive effect of an improved soil structure and associated lower rates of surface runoff and soil erosion, on the soil microbial communities (Xiao et al. 2017). Although several studies have pointed to pH as a regulator of microbial activity and composition (Rousk et al. 2010), we did not find a strong relationship between pH and the soil microbial parameters in tree species. This can be explained by the calcareous nature of the substrate found at the study site, so that soils are very well buffered and any acidification by organic activity is not detectable (Certini 2005).

Our results also evidenced the critical role of season as a factor modulating soil microbial properties and enzymatic activities, which corroborated our second hypothesis. Both urease and phosphatase activities were significantly different between spring and winter. Specifically, we found higher values in spring where higher temperatures and lower precipitations were recorded. Nevertheless, differences among shrubs and trees were species-specific with a marked effect for tree species. Several studies have documented seasonal variations in soil enzymatic activity, attributed mostly to patterns in temperature and/or moisture (Bloem et al. 2005; Brockett et al. 2012). Temperatures in different seasons can largely affect organic matter, decomposition of litter and soil acidity and thus enzymatic activity (Fekete et al. 2011; Baldrian et al. 2013). However, variation reported in the overall enzymatic activities across seasons has been largely inconsistent among enzyme types, soil properties and ecosystems (Salazar et al. 2011; Veeraragavan et al. 2018). Specific woody species producing different amounts of plant residues and tree canopy cover (Geisseler et al. 2011; Maillard et al. 2019) can in fact change the microclimate conditions such as understory temperature and humidity (Koch et al. 2007). Moreover, these differences in litter can result in different microbial carbon biomass that in turn will affect the soil enzymatic activity (Singh et al. 2017).

Basal respiration was consistently higher in spring (with higher temperature and lower moisture compared to winter) across all the studied species. In semi-arid ecosystems, water availability is a crucial factor regulating soil respiration and moderating the influence of other factors on soil respiration such as temperature and substrate availability (Yan et al. 2014; Muñoz-Rojas et al. 2016). The intra- and inter-annual variation of this water availability is directly connected to the intensity and frequency of precipitations (Fang et al. 2017). Projected climate scenarios in dryland regions such as the Zagros forests in Iran, predict extended dry periods and more irregular rainfall events (Vaghefi et al. 2019). From our results we can then assume that this increased warming would have large impacts on the enzymatic activity and soil respiration in these semi-arid ecosystems. In fact, an increase in soil temperature and a decrease in soil moisture would negatively impact soil microbial activity (Muñoz-Rojas et al. 2016).

Overall, our results highlighted the importance of soil microbial and enzyme activities to assess the variation of soil characteristics and functions and soil-plant associations across woody plant species. Soil microbial parameters and enzyme activities have been proposed as relevant indicators to assess ecosystem recovery following restoration (Muñoz-Rojas 2018). In our study region, the use of criteria evaluation and relevant indicators has been identified as a priority for a sustainable forest management (Nazariani et al. 2017). Thus, the outcomes of this study may have practical significance for restoration and conservation management for the Zagros forest. Our study evidence that enzyme activities and soil microbial

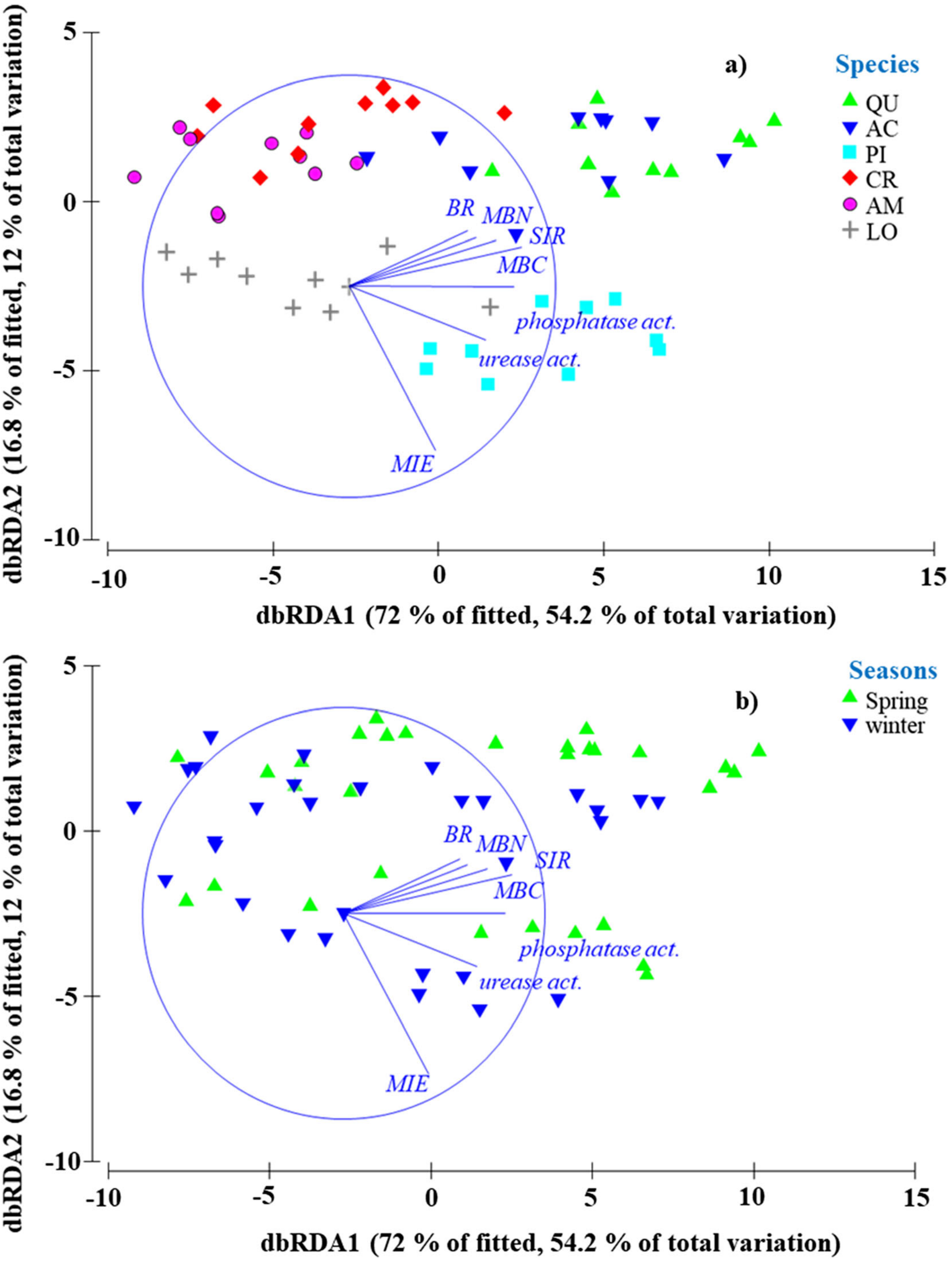

Fig. 6 Redundancy analysis (RDA) analysis graph for microbiological soil parameters matrix according to microbiological soil matrix (**a**) and different seasons (**b**); MIE: microbial entropy, BR: basal respiration, MBC: microbial biomass carbon, MBN: microbial biomass nitrogen, SIR: substrate-induced respiration; QU: *Quercus brantii*, AC: *Acer monspessulanum*, PI: *Pistacia atlantica, CR: Crataegus pontica*, AM: *Amygdalus scoparia*, LO: *Lonicera nummularifolia*

parameters can serve as effective indicators of soil function at landscape or ecosystem scale, but they are also sensitive to intra-annual changes and plant-specific rhizospheres. We found that both urease and phosphatase activities could be useful to identify hotspots of biological activity and soil nutrient in semi-arid ecosystems, which can assist ecosystem recovery (Hu et al. 2016). This is particularly relevant in areas like the Zagros forest (Arekhi et al. 2010; Komprdová et al. 2016), where high dependence of human population on forest resources has caused severe land degradation through deforestation processes (Heydari et al. 2014; Amiraslani and Dragovich 2011).

Adequate forest management strategies need to be implemented in arid and semi-arid forests, including our study area in western Iran. These forests present a high ecological heterogeneity in terms of woody species composition and canopy structure, which guarantees diverse ecosystem services and a high biodiversity level (Assal et al. 2016; Heydari et al. 2019). However, the high level of human pressure due to the strong livelihood dependence of people on forest resources generates different anthropogenic disturbances (i.e. alteration on vegetation composition or excessive grazing pressure), which are accentuated by climatic and land-use changes (Plieninger et al. 2011; Heydari et al. 2019). Having solid information about plant-soil interactions can help to effectively manage these arid and semi-arid environments.

Conclusion

Our results evidenced a strong effect of season and plant species on soil physicochemical and microbiological soil properties in semi-arid forest ecosystems. Soil nitrogen, carbon and bulk density were the most significant variables driving the activity of microbes and enzymes in the Zagros forests. Higher values of microbiological soil parameters, e.g. microbial biomass and enzymatic activities were generally observed for tree species, particularly *Quercus brantii*, and *Acer monspessulanum*. Soil microbial function parameters, including urease and phosphatase activities were higher during the spring season under shrub species although differences between seasons were lower compared to tree species. This study highlights the importance of soil microbial parameters and enzyme activities to assess soil function and soil-plant interactions. Furthermore, it provides essential information for maintaining ecosystems' health and quality through appropriate restoration and conservation management of semi-arid ecosystems such as the Zagros forests.

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