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Interaction between climate and management on beta diversity components of vegetation in relation to soil properties in arid and semi-arid oak forests

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Abstract

This study aimed to investigate the interaction between regions with different climatic conditions (arid vs. semi-arid) and management (protected vs. unprotected) on the turnover and nestedness of vegetation in relation to physical, chemical and biological properties of soils in the Ilam province of Iran. In each of the two regions, we sampled eight sites (4 managed and 4 unmanaged sites) within each of which we established four circular plots (1000 m^2) that were used to inventory woody species, while two micro-plots (1×1 m^2) were established in each 1000-m^2 plot to inventory herbaceous species. In each sample unit, we also extracted three soil samples (0–20 cm depth) for measuring soil properties. The results indicated that the interaction between region and conservation management significantly affected the percent canopy cover of Persian oak (*Quercus brantii* Linddl), soil respiration, substrate-induced respiration, as well as beta and gamma diversities and turnover. The percent canopy cover of oak was positively correlated with soil silt, electrical conductivity, available potassium, and alpha diversity, whereas it was negatively correlated with plant turnover. In addition, plant turnover was positively related to available phosphorus while nestedness was positively related to organic carbon and total N. According to these results, we conclude that physical, chemical and biological characteristics of limited ecological niche generally influence plant diversity. Also, this study has indicated the major contribution of the β-diversity on γ-diversity, especially in the semi-arid region, because of a higher heterogeneity in this area.

Keywords: climatic conditions; conservation; Beta diversity; oak forests

1. Introduction

Forest ecosystems have a critical role to mitigate soil loss and erosion, regulate weather and maintain habitats and biodiversity (Fathizadeh et al., 2017). Forest degradation and/or destruction had many negative effects on plant and soil microorganism diversity and composition (Yacht et al., 2017; Moradi Behbahani et al., 2017) and soil properties (Feng et al., 2017). Conservation management can be a key factor in preventing worldwide destruction of forest ecosystems and promoting the sustainability of these valuable resources.

Biodiversity indices are generally used to assess and evaluate ecosystem degradation (Wilson and Tilman, 2002). However, with the increasing importance of biodiversity conservation, the use of new and effective methods to investigate plant biodiversity has become increasingly popular. Diversity partitioning (additive vs. multiplicative) is one of these methods that was frequently used during the two recent decades by ecologists devoted to biodiversity conservation (Erfanzadeh et al., 2015). According to this method, total regional diversity can be partitioned additively (gamma = alpha + beta; Lande, 1996) or multiplicatively (gamma = alpha x beta) into within (alpha diversity) and among (beta diversity) components across different spatial/temporal scales (Crist et al., 2003). The additive partitioning method has been increasingly used in rangeland and forest studies in relation to plant species diversity (i.e. Chávez and Macdonald, 2012; Zhang, et al., 2014; Erfanzadeh et al., 2015; Schulze, et al., 2016).

Beta diversity is an important biodiversity index that is defined as the variation in community composition from one place to another. Baselga (2010) demonstrated mathematically that beta diversity can be decomposed in two main processes: turnover and nestedness. Spatial turnover is defined as the continuous or sudden replacement of species along an environmental gradient due to environmental pressure, climate change or competition (Baselga, 2010; Lafage et al., 2015). For its part, nestedness refers to communities in which species composing a low-diversity community are a subset of a high-diversity community that was subjected to species migration or extinction (Calderón-Patrón et al., 2013). By analyzing beta diversity components and their respective contribution to the total beta diversity, we can detect the main mechanism involved in changes in community composition.

Semi-arid forests of the Zagros Mountains are dominated by Persian oak (*Quercus brantii* Linddl) and cover an area of about 5 million ha (40% of Iranian forests; Sagheb-Talebi et al., 2014). They form one of the most important ecosystems of Iran due to their high level of biodiversity and the presence of endemic species (Marvi Mohadjer, 2005). The Zagros region has a great impact on people's livelihood due to the dependency of people on local resources (Salehi et al., 2013).

Unfortunately, during the three last decades, the vegetation of the Zagros forests was highly degraded due to incorrect management practices and human activities such as human-caused fire, over-grazing, excessive cutting, firewood harvesting and land use changes (Heydari et al., 2016).

While forest degradation could create important changes in vegetation composition and forest structure, forest soils can also be impacted. Soils are an important constituent of ecosystems and play a critical role in the development of forest vegetation, which, in turn, have noticeable effects on the development of physical, chemical and biological soil properties (Kooch et al., 2007; Onyekwelu et al., 2006; Wang, 2007).

Biodiversity conservation in Zagros forests should take advantage of new management practices to help reduce the progression of its degradation caused by drought-induced oak mortality. Conservation plan including exclosures is one management solution that was effective in Zagros forests (Heydari et al., 2013a). Tárrega et al. (2009) reported that different management regimes in dehesa ecosystems (grazed, ungrazed, ungrazed with shrub cutting) had a critical effect on soil properties and vegetation in oak (*Q. pyrenaica*) stands, and that conservational practices led to improvement in soil fertility. This is in accordance with results indicating that conservational practices (grazed vs. no grazed) had positive effects on soil properties and vegetation (Strandberg et al., 2005). In addition, Sheklabadi et al. (2007) observed that in areas degraded by grazing, the amount of organic carbon, total nitrogen and microbial respiration were lower than in non-degraded areas.

Climate is another factor that has profound effects on vegetation diversity and composition as well as on soil properties (Kardol et al., 2010). Climatic factors, particularly temperature and precipitation, affect the formation and evolution of soils (Binkley and Fisher, 2012), the accumulation of organic carbon (Wang et al., 2013), the cycling rate of nutrients (Auyeung et al., 2013) and the soil biological activity (Sardans and Peñuelas, 2005; Steinweg et al., 2013).

Due to the interaction between soil characteristics, climatic conditions and plant species (von Lutzow & Kogel-Knabner, 2009; Mirzaei and Moradi, 2017; Toure et al., 2015), changes in plant species diversity and composition between regions with different climatic conditions are expected. On the other hand, plant communities and their characteristics such as life form spectra (Raunkiaer, 1934) gradually reach an equilibrium with climatic conditions to form so-called climatic climax communities.

The effects of forest degradation and management strategies on plant diversity and soil attributes have been recently investigated in the Zagros forest of Iran (Parma & Shataee Jouybari, 2010;

Heydari et al., 2017). However, no study has addressed the effects of climate with or without interaction with management practices on diversity components (alpha and beta diversity) as well as on beta diversity components (turnover and nestedness). This study aims to fill this gap by evaluating the effects of climate, management strategies and their interaction on soil physical, chemical and biological properties as well as on biodiversity components.

2. Material and methods

2.1. Study area

This study took place in managed and unmanaged (see details below) forests dominated by Persian oak (*Quercus brantii* Linddl) in western Iran. These forests were located in two regions (Fig. 1) with different climatic conditions. According to the classification system of de Martonne (1925), the climate of these regions are both Mediterranean, but the semi-arid Dalab region is characterized by annual precipitation of 590 mm and mean annual temperature of 16.7 °C, while the mean annual precipitation and temperature of the arid Koshk region are 408 mm and 18.5 °C, respectively. These regions are both part of the Zagros mountains, and the geology and the pedogenesis of the two regions are similar. Calcareous soils with a clay loamy texture, dominate the soils of these regions.

In each region, we selected four managed and four unmanaged sites that were described by Heydari et al. (2013 b). In managed sites, a 20-year period of strict conservation was applied following long-term human disturbances. For their part, unmanaged sites were never protected against long-term anthropogenic land degradation such as tree and shrub cutting for firewood and development of arable lands as well as animal husbandry (Heydari et al., 2013 b). The vegetation of the managed sites of Dalab (MD) was dominated by *Cerasus microcarpa, Daphne mucronata, Acantholimon bromoifoliu, Teucrium polium, Alyssum marginatum, Centaurea depressa, Centaurea amadanensis, Centaurea koeieana*. In the unmananged sites of Dalab (UMD), the dominant vegetation was composed of *Capparis parviflora, Astragalus fasciculifolius, Astragalus (Leucocercis) curviflorus, Bromus tomentellus, Gundelia Tournefortii, Erodium cicotarium, Stellaria media, Valerianella dactylophylla*. In the managed sites of Koshk (MK), the dominant species were *Pistacia khinjuk, Amygdalus lycioides, Populus euphratica, Medicago rigidula, Sinapis arvensis, Trifolium purpureum, Ziziphora capitata, Anthemis pseudocotula*. Finally, in the unmanaged sites of Koshk (UMK), the vegetation was dominated by *Nerium oleander, Vitex* *pseudo-Negundo Medicago rigidula, Sinapis arvensis, Phlomis olivieriv, Crepis katschyana, Scabiosa leucactic* (Aazami, 2016).

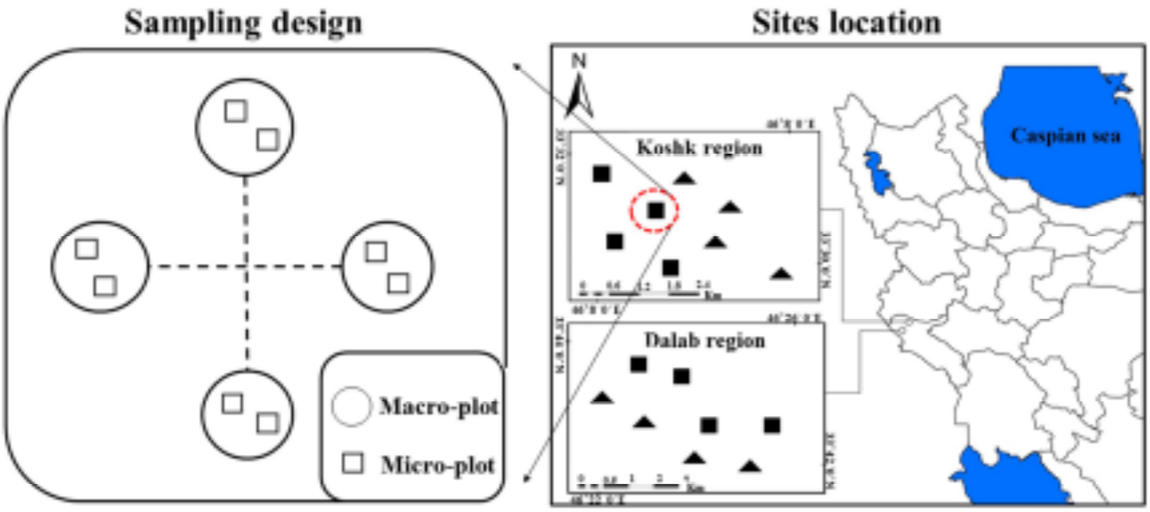


Fig. 1 Study area location and sampling method; ■: : managed and ▲: unmanaged sites; ○: Marco-plot and □: Micro-plot

2.2. Experimental design and data collection

The combination of our two regions (D=Dalab, K=Koshk) with the two types of management (M=managed, UM=unmanaged) results in four treatments (MD, UMD, MK, UMK) and with different climatic conditions (semi-arid Dalab region vs. arid Koshk region). In each treatment, we selected four independent sites that were considered as replicates. However, to decrease variability, geographically adjacent sites were selected in each region. In the center of each site, we used a systematic sampling method to establish a cluster of four circular, 1000-m^2 plots located 100 m apart (Fig. 1). These plots were used to estimate the percent cover of all woody species while two squared 1-m^2 microplots, located within each main plot, were randomly established to inventory herbaceous species (each species was given a value of abundance) in May 2015. In total, we have 16 sampling sites (8 in Koshk and 8 in Dalab), 64 macroplots (1000-m^2) and 128 microplots.

2.3. Soil sampling and laboratory methods

We extracted soil samples at 0-20 cm depth in May 2015. Physical, chemical and biological soil properties were determined from composite samples, each consisting of three sub-samples that were gathered from three randomly selected points in each main plot (for a total of 64 composite soil samples). Soils were sieved (2-mm mesh) to remove roots and debris prior to laboratory analyses and divided into two subsamples.

The first subsample was air-dried for measuring physico–chemical properties. Soil texture was measured using a hydrometer (Bouyoucos, 1962). Soil organic carbon (OC) was determined by dichromate oxidation using the Walkley-Black method (Nelson and Sommers, 1982). Soil pH and electrical conductivity (EC) were determined electrometrically (in H_2O, 2:1 v/m) with a conductivity probe in filtered extracts (Kalra and Maynard, 1991), respectively. Soil cation exchange capacity (CEC) was determined following extraction in buffered sodium acetate (NaOAc, at pH 8.2; Sumner and Miller, 1996). Total nitrogen was measured by Kjeldahl digestion (Bremner, 1996). Available phosphorus (Pava), as ortho-PO_4^{-2}, was determined using the method of Bray and Kurtz (1945). Available potassium (K_{ava}) was determined following ammonium acetate (pH 7) extraction and quantified by flame photometry (Black, 1986). Lime percentage, expressed using the Total Neutralizing Value (T.N.V), was determined using the NaOH titration method.

The second subsample was maintained at field moisture and stored at 4 °C for subsequent measurements of soil microbial activity. Soil basal respiration (BR) was measured by trapping and quantifying CO_2 that was emitted from soil samples over a five-day period (Alef and Nannipieri, 1995). Substrate-induced respiration (SIR) was determined using glucose (1 %) as the substrate and the evolved CO_2 was determined after 8 h incubation. Evolved CO_2 was adsorbed in 1 M NaOH and measured by 0.1 M HCI titration (Anderson and Domsch, 1978).

Additional undisturbed soil cores distributed in the four treatments were collected for the determination of bulk density (BD) in the 0-15 cm mineral layer (Blake and Hartge, 1986). Soils were immediately sieved (2 mm) and kept in a plastic box to avoid evaporation. Soil moisture content or WC (water mass/soil dry mass) was measured gravimetrically (oven-drying at 105 °C for 24 h; Famiglietti et al., 1998)

2.4. Diversity partitioning

To estimate the diversity components, we used the additive partitioning method as shown in equation (1) (Crist et al., 2003):

$$\gamma = \alpha_1 + \sum_{i=1}^{m} \beta_i \quad [1]$$

where γ is the total species diversity, m is the number of scales, α_1 is the average diversity within sample units in each site, and β_i is the beta diversity at each scale *i*. This method enabled us to estimate the total species richness in each region (γ), which was partitioned into α_1 (the mean number of species found per 1 m^2 plot) and β_1 (the difference between α1 and γsite, in which γsite was the total species richness of each site).

Then, we additively partitioned the β-diversity into two components, i.e. the spatial turnover and nestedness. To do this, we used the method suggested by Baselga (2010), which is based on the multiple dissimilarity derived from the Sørensen coefficient of dissimilarity (Baselga 2010). This analysis was performed using the betapart package (Baselga and Orme 2012) within the R software (R Development Core Team 2013).

2.5. Statistical analysis

First, the normality of each variable was verified using the Kolmogorov–Smirnov test as well as variance homogeneity (Levene Test). Mathematical transformations of data were used when necessary to correct deviations from normality and heterogeneity of variance. Then we used two-way ANOVAs to detect significant differences between variable means associated with treatments, regions, and the interaction between treatments and regions. If the two-way ANOVAs detected significant differences, we applied a Duncan test for pairwise comparisons. Pearson correlation coefficients were calculated to investigate possible relationships between oak cover, soil properties and diversity components. Finally, relationships between beta diversity components and soil factors were analyzed using linear regressions. All analyses were performed with the R statistical software (R Core Team 2013).

3. Results

3.1. Effects of management measures and climate

The results showed that management (protected vs. unprotected), climatic conditions (arid vs. semi-arid) and their interaction had a significant (P-value < 0.05) effects on oak canopy cover (Table 1). These variables also produced significant effects on water content, silt, BR and SIR. However, for T.N.V, clay, Pava, Kava, total N and OC, only management and climatic conditions were significant and their interaction was not significant (Table 1). The percent of sand and BD were solely affected by management, while EC and pH were affected only by climatic conditions.

Diversity components (alpha, beta and gamma) and beta diversity components (turnover and nestedness) showed different trends in relation to management, climatic conditions and their interaction (Table 1). We detected significant effects of management and climatic conditions for all diversity components but a significant influence of the interaction was revealed only for beta and gamma diversity as well as turnover. Therefore, the effects of management on alpha diversity and nestedness were similar across the two regions (Table 1).

Table 1 Results of two way-ANOVA (F-value and significance level) testing for regions with different climatic conditions and management on oak canopy cover percentage, soil properties, diversity components (alpha, beta and gamma) and beta diversity components (spatial turnover and nestedness); (EC: electrical conductivity; OC: organic carbon; BD: Bulk density; WC: Water content; T.N.V: total neutralizing Value; N_{tot} :total nitrogen; K_{ava}: available potassium; P_{ava}: available phosphorus; BR: basal respiration; SIR: substrate induced respiration)

	Variable	Management	Climate condition	Management × Climate condition
Oak canopy cover and soil physical properties	Oak canopy cover (%)	11.662**	8.396**	6.04*
	BD (g/cm3)	1.037*	2.846	2.732
	Water content (%)	15.859**	11.017**	5.475*
	Sand (%)	5.988*	0.828	0.198
	Clay (%)	3.562*	0.608*	0.007
	Silt (%)	0.463*	3.795**	0.372*
Soil chemical properties	T.N.V (%)	26.447***	14.393**	2.084
	OC (%)	62.331***	43.721***	0.388
	Pava (ppm)	13.529	394.731***	0.438
	EC (dS/m)	1.752	6.209*	5.1*
	pH	4.134	62.152***	1.145
	N_{tot} (%)	62.331***	43.721***	0.388
	K_{ava} (ppm)	0.219	43.522***	0.005
Soil biological	BR (mg CO_2- C/kg soil/day)	177.92***	368.656***	112.515***

variables	SIR (mg CO_2-C/kg soil/day)	105.622***	162.689***	33.996***
Diversity	Alpha diversity	160.163***	4.379*	0.054
	Beta diversity	136.289***	39.472***	37.768***
	Gamma diversity	370.559***	20.931***	35.477***
	Turnover	11.626**	183.214***	42.374***
	Nestedness	13.636**	4.909*	2.182

*** Significant at *P* = 0.001; ** Significant at *P* = 0.01 and * significant at *P* = 0.05

3. 2. Oak canopy cover and soil physico-chemical properties

Oak canopy cover was significantly higher in the Dalab region than in the Koshk region. This variable was also significantly higher in managed than in unmanaged plots for both Dalab and Koshk regions (Table 2). Available K was higher in the Dalab than in the Koshk region while the reverse was true for P_{ava}.

EC was higher in the unmanaged than in the managed plots of the Koshk region while it was lower in the Dalab region within which no significant differences were found between managed and unmanaged plots. pH was unaffected by management in both regions but was higher in the Koshk than in the Dalab region. Clay content was significantly higher in MD than in the other treatments, whereas silt content was higher in MK. Sand content was higher in unmanaged plots but the difference was significant in the Koshk region only. The treatment order for total nitrogen and organic matter contents was MD> UMD = MK>UMK whereas that of T.N.V was UMK> UMD > MK>MD (Table 2). Water content and bulk density were highest in the managed plots of the Dalab region and in the unmanaged plots of the Koshk region, respectively.

3. 3. Soil biological variables

The mean values of BR and SIR in the Dalab region were higher than those of the Koshk region but the influence of management was significant in both regions with higher values of BR and SIR in managed than in unmanaged plots (Table 2).

Table 2 Oak canopy cover, soil physico-chemical and microbial properties (mean ± SE) measured in the different regions; (EC: electrical conductivity; OC: organic carbon; BD: Bulk density; WC: Water content; T.N.V: total neutralizing Value; N_{tot} :total nitrogen; K_{ava}: available potassium; P_{ava}: available phosphorus; BR: basal respiration; SIR: substrate induced respiration)

Variable	Koshk		Dalab	
	Managed	Unmanaged	Managed	Unmanaged
Oak canopy cover (%)	10.18 ± 2.33 b	7.52 ± 1.32b	20.13 ± 3.92a	8.94 ± 1.22b
BD (g/cm3)	1.37 ± 0.02b	1.48 ± 0.03a	1.36 ± 0.01b	1.38 ± 0.02b
Sand (%)	47.87 ± 1.61b	55.65 ± 2.45a	48.58 ± 1.24b	52.71 ± 2.34ab
Clay (%)	27.71 ± 1.51b	24.43 ± 0.51b	31.04 ± 2.16a	27.04 ± 3.2b
Silt (%)	24.42 ± 1.64a	19.92 ± 2.04b	20.38 ± 1.24b	20.25 ± 0.91b
WC (%)	40.87 ± 0.59b	38.06 ± 0.85b	50.54 ± 3.09a	39.74 ± 0.99b
pH	7.38 ± 0.01a	7.37 ± 0.01a	7.14 ± 0.04b	7.20 ± 0.01b
EC (ds/m)	0.38 ± 0.03 b	0.52 ± 0.03a	0.29 ± 0.01c	0.32 ± 0.01c
Total nitrogen (%)	0.23 ± 0.010b	0.18 ± 0.010c	0.33 ± 0.010a	0.21 ± 0.006b
OC (%)	3.37 ± 0.31b	2.81 ± 0.55c	5.7151 ± 0.32a	3.55 ± 0.11b
T.N.V (%)	43.93 ± 0.91b	52.40 ± 0.47a	35.83 ± 3.39c	48.85 ± 1.87ab
K_{ava} (ppm)	263.09 ± 15.00bc	169.80 ± 8.47c	400.79 ± 17.56a	387.67 ± 39.55a
P_{ava} (ppm)	9.95 ± 0.07a	9.09 ± 0.13a	7.60 ± 0.21b	7.07 ± 0.05b
BR (mg CO_2- C/kg soil/day)	12.21 ± 0.35c	10.49 ± 0.21c	34.01 ± 0.41a	16.40 ± 1.34b
SIR (mg CO_2-C/kg soil/day)	23.61 ± 0.62b	21.84 ± 1.48c	49.40 ± 1.95a	24.58 ± 1.46b

Within rows, means with the same letters do not significantly differ ($p> 0.05$)

3.4. Alpha, Beta and Gama diversity and plant beta diversity components

Alpha, beta and gamma diversity values were higher in managed than in unmanaged plots in both regions. Diversity values were significantly higher (beta and gamma) or similar (alpha) between managed Dalab and managed Koshk whereas no significant differences were detected between the two regions in the unmanaged plots (Fig. 2 a).

Between the two components of the beta diversity, spatial turnover was largely higher than nestedness in each treatment (Fig. 2 b). Turnover significantly decreased according to the following order MD > UMD > UMK > MK. By contrast, nestedness was lowest in MD while there were no significant differences among the other treatments.

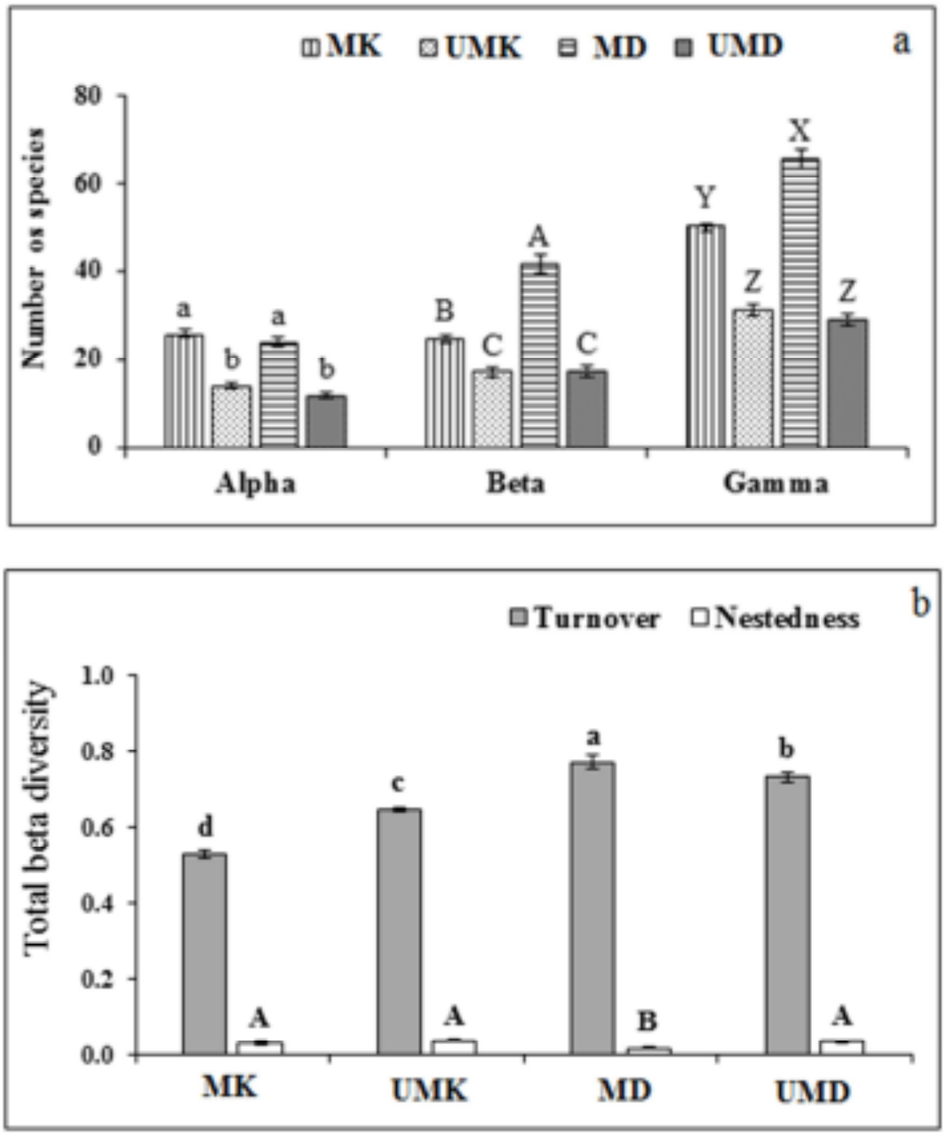


Fig. 2 Variations of the diversity components (mean ± SE) according to the treatments for a) Alpha, Beta and Gamma components and b) Turnover and Nestedness. Means with the same letters for a given diversity component are not significantly different based on Duncan's multiple range test ($p > 0.05$)

3.5. Relationships between oak canopy cover, soil properties and diversity components

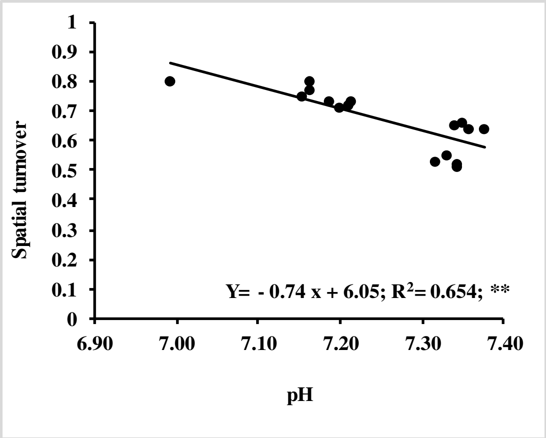
The oak canopy cover was positively correlated with silt, pH, K_{ava} and alpha diversity, while it was negatively correlated with spatial turnover (Table 3).

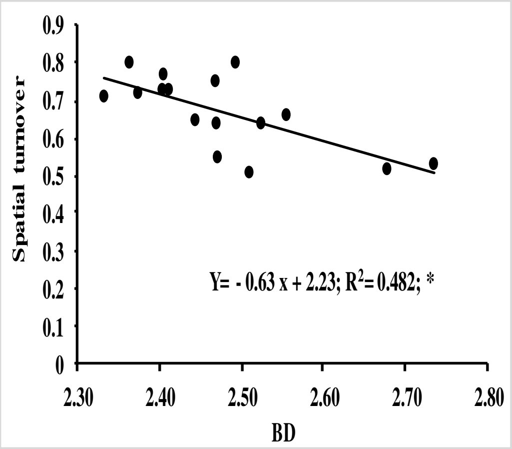
Table 3 Pearson correlation coefficients between the oak canopy cover and soil properties and components of diversity; (EC: electrical conductivity; OC: organic carbon; BD: Bulk density; WC: Water content; T.N.V: total neutralizing Value; N_{tot} :total nitrogen; K_{ava}: available potassium; P_{ava}: available phosphorus; BR: basal respiration; SIR: substrate induced respiration)

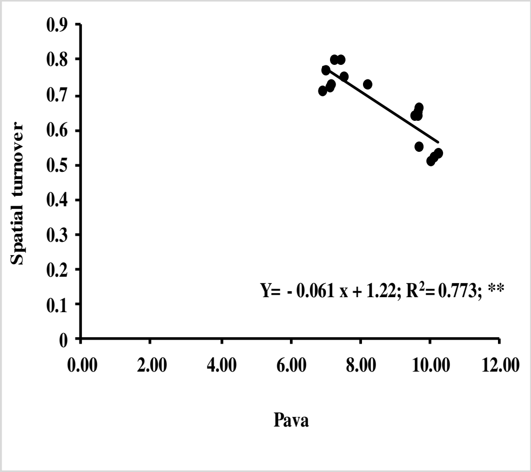
Variables	oak canopy cover	Variables	oak canopy cover	Variables	oak canopy cover
BD (g/cm^3)	- 0.14 ^{ns}	P_{ava} (ppm)	0.14 ^{ns}	Total nitrogen (%)	- 0.02 ^{ns}
WC (%)	- 0.08 ^{ns}	K_{ava} (ppm)	0.36 *	Alpha	0.36 *
Sand (%)	- 0.23 ^{ns}	TNV (%)	0.09 ^{ns}	Beta	- 0.28 ^{ns}
Clay (%)	- 0.03 ^{ns}	BR (mg CO_2- C/kg/day)	- 0.25 ^{ns}	Gamma	- 0.09 ^{ns}
Silt (%)	0.14 *	SIR (mg CO_2-C/kg soil/day)	- 0.28 ^{ns}	Spatial turover	- 0.62 *
pH	0.32 *	EC (dS/m)	0.13 ^{ns}	Nestedness	0.12 ^{ns}

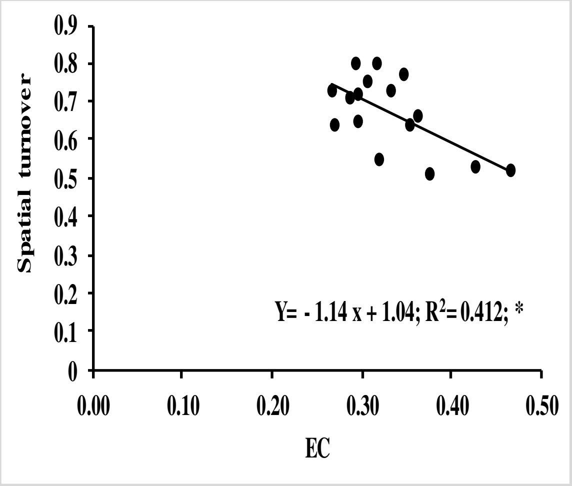
3.6. Linear regressions between beta diversity components and soil properties

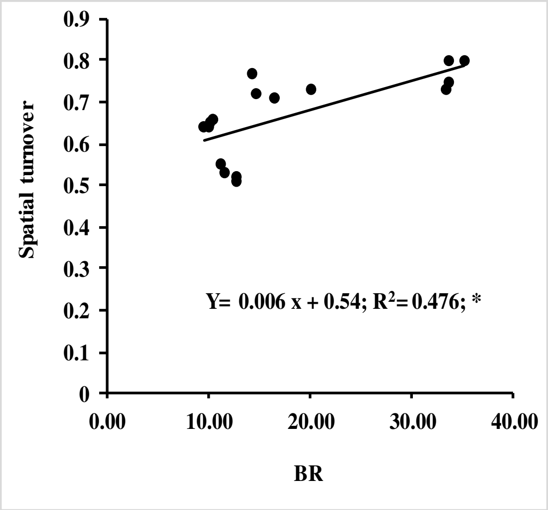
There were strong negative relationships between spatial turnover and BD, EC, pH and P_{ava}. By contrast, spatial turnover was strongly and positively related to Kava, BR and SIR (Fig. 3).

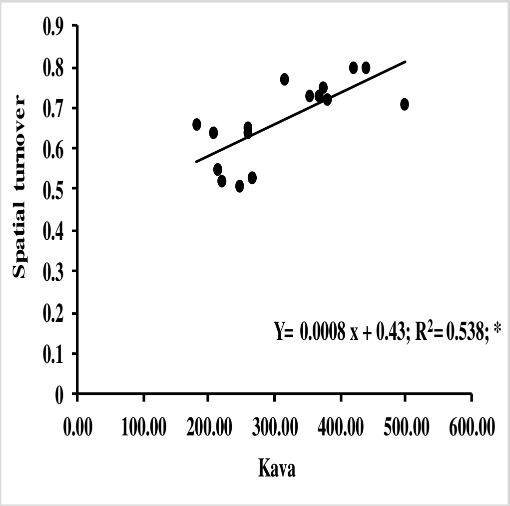

Spatial turnover
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Y= - 0.74 x + 6.05; R^2= 0.654; **
6.90
7.00
7.10
7.20
7.30
7.40
pH


Spatial turnover
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Y= - 0.63 x + 2.23; R^2= 0.482; *
2.30
2.40
2.50
2.60
2.70
2.80
BD


Spatial turnover
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Y= - 0.061 x + 1.22; R^2= 0.773; **
0.00
2.00
4.00
6.00
8.00
10.00
12.00
Pava


Spatial turnover
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Y= - 1.14 x + 1.04; R^2= 0.412; *
0.00
0.10
0.20
0.30
0.40
0.50
EC


Spatial turnover
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Y= 0.006 x + 0.54; R^2= 0.476; *
0.00
10.00
20.00
30.00
40.00
BR


Spatial turnover
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Y= 0.0008 x + 0.43; R^2= 0.538; *
0.00
100.00
200.00
300.00
400.00
500.00
600.00
Kava

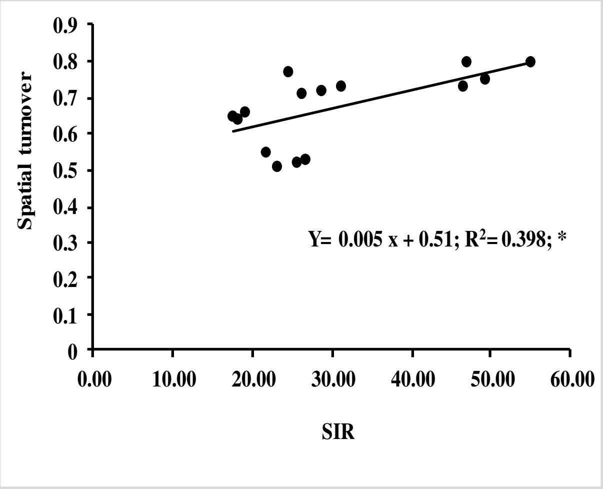


Fig. 3 Simple linear regressions between spatial turnover of plant species and soil properties; * p-value < 0.05 and ** p-value <0.01

The nestedness of plant species was significantly and positively related to T.N.V., and negatively related to WC, OC, N_{tot}, BR, and SIR (Fig.4).

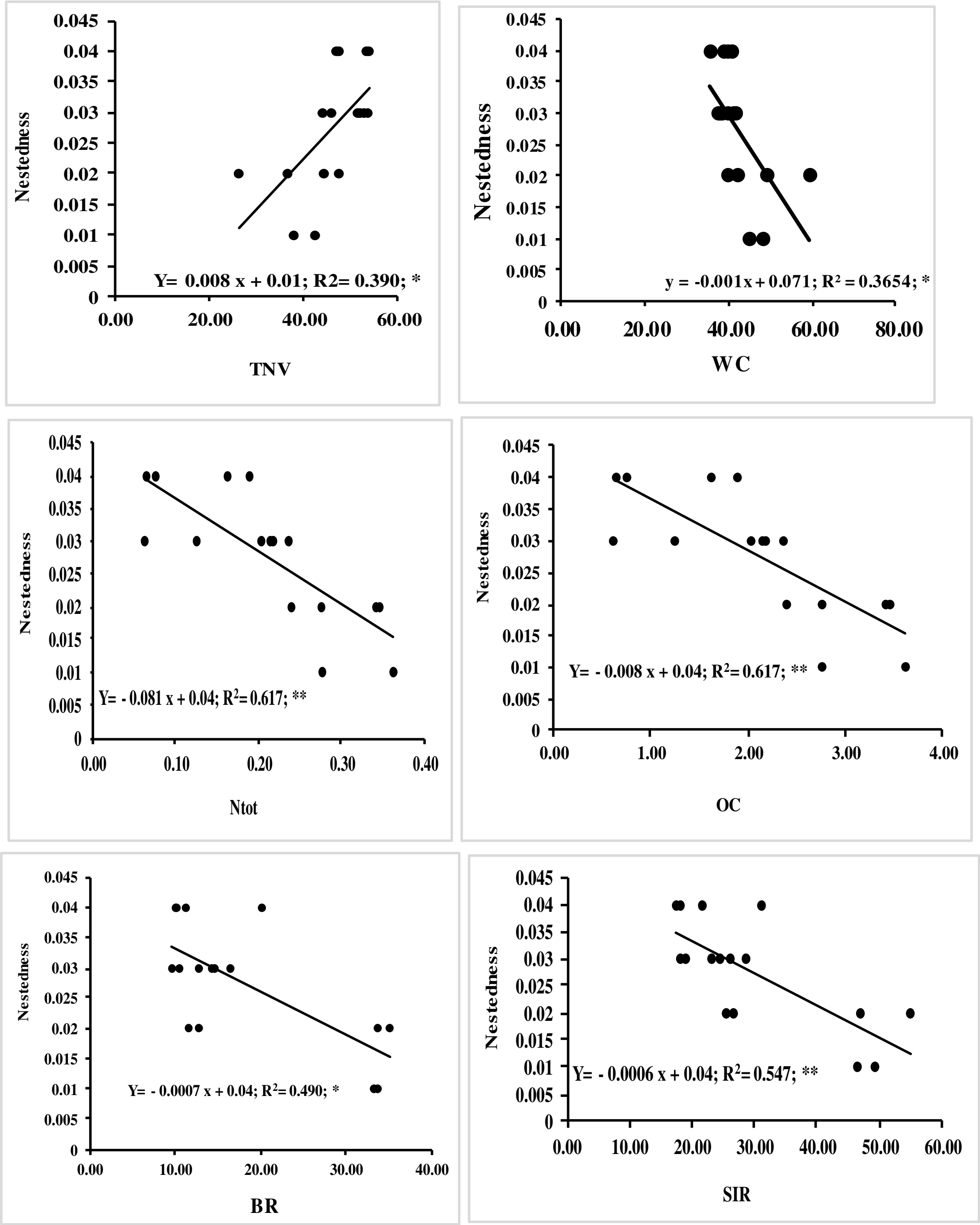


Fig. 4 Simple linear regressions between nestedness of plant species and soil properties; * p-value < 0.05 and ** p-value <0.01

5. Discussion

5.1. Effect of management and climatic conditions on soil properties

We found that some soil attributes were influenced by climatic conditions while others responded to conservation measures. For instance, pH was probably mainly influenced by climatic conditions and showed significantly lower values in the more humid Dalab region than in Koshk. However, we cannot exclude that the higher organic matter content in soils of Dalab has stimulated the microbial activity, in particular respiration, which has led to enhanced carbon dioxide production and the formation of carbonic acid forms reducing soil pH (Brady and Weil, 2008).

Similarly, soil K_{ava} was higher in the semi-arid Dalab region than in the arid Koshk region whereas the reverse was observed for P_{ava}. In accordance, Sardans and Peñuelas (2007) emphasized the influence of climatic conditions, especially drought, in modifying soil phosphorus and potassium accumulation patterns in Mediterranean woodlands.

Total nitrogen and organic carbon were higher in the more humid Dalab region than in the arid Koshk region. Accordingly, climatic conditions influence soil organism activities, which play an important role in improving the soil nutrient cycle (Frossard et al., 2000). For example, temperature affects the decomposition of organic matter and thus influences the physical, chemical and biological soil characteristics (von Lutzow & Kogel-Knabner, 2009). Therefore, the higher organic carbon content in the Dalab region is likely related to soil nutrient availability and thus plays an important role in soil fertility (Bationo et al., 2006). The decrease in nitrogen and organic carbon in unmanaged sites was consistent with the result reported by Dahlgren et al. (2003) and Heydari et al. (2014) who showed that human disturbances and site degradation decreased the amount of organic matter and soil nutrients. Higher cover of woody and herbaceous species in managed sites protects soils from erosion (Mekuria and Aynekulu, 2013) while degradation agents such as livestock grazing in unmanaged Koshk decrease plant biomass accumulation, which in turn affects soil fertility (Savadogo et al., 2007).

EC was higher in the Koshk than in the Dalab region and unmanaged plots were associated with higher EC values in Koshk. Some disturbances, such as overgrazing or tree cutting, reduce the protection of soil by vegetation and tend to dry out the soil surface and increase electrical conductivity (Binkley and Fisher, 2012), a process that is especially pronounced in arid and semi-arid regions (Pan et al., 2014). This explanation also holds for the soil water content, which is higher in managed than in unmanaged areas (Kidron and Gutschick, 2013).

Bulk density was higher in unmanaged than in managed areas although the difference was only significant in the Koshk region. It is well known that soil compaction that is induced by overgrazing and low soil organic carbon increases bulk density (Li et al., 2011, Chaudhari et al., 2013) as observed in the Koshk region.

Finer soil particles (i.e. clay and silt contents) were significantly higher in managed than in unmanaged sites, while sand was higher in unmanaged ones. Due to a higher percentage of bare soil and a lower vegetation cover, soils of unmanaged sites are more exposed to run off and erosion favouring the loss of silt and clay particles (Tessema et al., 2011).

Lime percentage (T.N.V) was higher in unmanaged sites than in managed ones in both arid and semi-arid climates. Accordingly, Celik (2005) showed that the amount of lime increased with forest degradation and land-use change, particularly from forestland to agriculture. Changes in the content of soil lime can also be influenced by other factors such as soil organic carbon, biological activities (soil respiration) and CO_2 pressure (pCO_2). Indeed, higher amounts of soil organic matter enhance CO_2 pressure due to higher heterotrophic and autotrophic respiration and then increase carbonate dissolution (Brady and Weil, 2008).

5.2. Soil biological variables

Basal respiration (BR) and substrate-induced respiration (SIR) in the the Dalab region were higher than those obtained from the Koshk region. More abundant precipitations and lower temperatures in the semi-arid Dalab region compared to the arid Koshk region are favourable to vegetation development and thus increase soil organic matter (Binkley and Fisher, 2012). This process promotes microorganism activities, which can explain the higher BR and SIR values. This result is consistent with the findings of Sardans and Peñuelas (2005) who showed that drought reduces soil enzyme activity in a Mediterranean holm oak forest while more generally, mesic climatic conditions are favourable to the activity of soil organisms (e.g. Qiu et al., 2005; Mansourzadeh & Raiesi, 2012). The same process applies to explain the higher BR and SIR values measured in managed plots compared to unmanaged plots. Indeed, the lower vegetation cover in unmanaged areas caused by human disturbances led to lower organic matter content and reduced respiration values (Cheng et al., 2013).

5.3. Alpha, Beta and Gama diversity and beta diversity components

Alpha and gamma diversity values as well as both components of beta diversity (turnover and nestedness) were significantly affected by management type and climatic conditions and, to a lesser degree, by the interaction between these two variables. This is in accordance with the observations that changes in climatic and management conditions influence species occurrence, diversity and distribution in various ecosystems (Adler & Levine, 2007; van der Putten, 2013), particularly in arid and semi-arid rangelands (Erfanzadeh et al. 2015) .

However, our results clearly indicated that management had a major influence on alpha, beta and gamma diversity (Fig 2a) whereas climatic conditions had no significant effect in our unmanaged Mediterranean ecosystems contrary to the results of some previous studies (e.g. Rodriguez et al., 2017). Conservation management positively affected the different components of species diversity in our study areas likely because it provided sufficient opportunities for vegetation rehabilitation and plant community reconstruction (Miura et al., 2003; Coetzee et al., 2014) as well as preservation of native plant species diversity (Cox and Underwood, 2011).

The fact that beta and gamma diversities were not influenced by climatic conditions when there are no conservation measures indicate that the role of climate on vegetation composition and diversity is considerably reduced compared to the influence of anthropogenic disturbances. In fact, gamma diversity, which corresponds to the number of species in each region, peaked at 65 and 50 in the managed Dalab and Koshk regions, respectively, whereas alpha diversity was approximately the same (24 and 25 respectively in MD and MK). Beta diversity, which represents the difference between the plots diversity (alpha), is therefore of 41 species for Dalab and 25 for Koshk. This indicates that the beta diversity in managed areas of both regions has a similar (Korshk) or a higher (Dalab) contribution to total diversity than alpha diversity. The reduction of the negative impacts of degradation agents by the conservation management strategy resulted not only in a higher diversity at the plot level (alpha diversity; Erfanzadeh et al., 2015) but also increased species composition at larger scales (Hermy and Verheyen, 2007). Our results are consistent with the findings of Tang et al. (2011) who observed a significant positive effect of conservation management on plant species diversity and those of Erfanzadeh et al. (2015) who showed that conservation management can increase plant diversity at the regional scale in arid regions.

Our results emphasize the major contribution of spatial turnover in beta diversity in comparison to nestedness whose contribution was limited in all treatments. These results imply that the variation in species assemblages in the studied regions is less explained by the presence of subsets of species from richer sites than by the high degree of species replacement from one location to the other (Baselga, 2010). First, the more favourable environmental conditions of the Dalab region can explain its higher turnover rate compared to the Koshk region because better soil qualities can positively affect plant species distribution and migration (Harrison et al., 2006; LaManna et al., 2017) and result in increased turnover. Second, the clear influence of conservation measures in both areas suggest that they should be applied more extensively rather than limited to the richest sites (Balsega, 2010).

5.4. Relationships between percent oak canopy cover, soil properties and diversity components

Overstory canopy cover is an important ecological characteristic of Zagros oak forests, which was significantly reduced in disturbed areas (Heydari et al., 2014). Previous studies indicated that canopy cover controls the biological, physical and chemical soil properties as well as the herbaceous coverage, which in turn, influence the seedling recruitment and development (Moradi et al., 2017; Caldeira et al., 2014).

Our results show that oak canopy cover was positively correlated with silt, pH, Kava and alpha diversity while it was negatively correlated with turnover (Table 3). The higher organic matter content in soils under a more developed canopy cover can improve the cation exchange capacity and thus increase the soil pH (Dahlgren et al., 2003). Oak trees, thanks to their deep rooting system, can bring up nutrients from lower soil layers where they can be recycled via leaf litter, a process that can explain higher soil K content with increasing canopy cover (Moreno et al., 2007).

The canopy cover and litter, by creating a suitable microclimate and by limiting leaching, plays an important role in seed storage of plant species and thus increase the diversity of plant species (Arriaga & Mercado, 2004; Heydari et al. 2013 a). This can explain the positive relationship between oak canopy cover and the alpha diversity of plant species. As already observed by Heydari et al. (2015) in the same region, human degradation and lack of protective measures significantly and negatively affect overstory canopy, which, in turn, decrease species diversity.

In contrast, the negative correlation observed between oak canopy cover and turnover of plant species could reflect the modification of the microclimatic conditions below canopy, particularly light availability, which is beneficial to some shade-tolerant species but detrimental to many light-demanding plants (Benítez et al., 2015). Sabatini et al (2014) proposed that the ecological factors driving species composition and turnover, like canopy cover, forest structure or topography, are system-specific and thus vary according to forest types.

Species turnover is negatively correlated with BD, EC, pH and Pava, but positively with Kava, BR and SIR. Turnover means the continuous or sudden replacement of species along an environmental gradient, and that removal or replacement is controlled by environmental variables and competition (Lafage *et al*, 2015; Baselga, 2010). Past studies have shown that the reduction of habitat quality could lead to the elimination of the most sensitive and non-resistant species (extinction) or species with narrow ecological niche range (Tilman and Lehman, 2001). In contrast, the improvement of soil conditions linked to conservation management efforts, can cause increased migration, development and distribution of species (Harrison et al., 2006; LaManna et al., 2017) and may increase the turnover.

Nestedness is observed when species of a specific habitat are a subset of species of a richer habitat (in term of species), and is usually explained by species extinction or selective migration (Calderón-Patrón, et al., 2013; Baselga, 2010). In our study, nestedness is significantly and positively related to TNV, and negatively related to WC, OC, N_{tot}, BR, and SIR. Changes in these factors can lead to limitation in ecological niches -for instance, highly calcareous soils are not adapted to lime-intolerant species- and can increase the nestedness due to extinction of species (Barnes et al., 1998). In contrast, more fertile soils (e.g. with higher NPK or OC contents) may increase the competition and thus species replacement, which can lead to a higher turnover.

Given that turnover was by far a greater contributor to total beta diversity than nestedness, our results support the hypothesis that site productivity (Harrison et al., 2006; LaManna et al., 2017 but see Zemunik et al., 2016) and environmental heterogeneity (Chase and Leibold, 2002; Veech and Crist, 2007; Stegen et al., 2013) promote beta diversity.

6. Conclusion

Our results indicate that conservation management results in positive changes in the physical, chemical and biological soil properties as well as in canopy cover of oak trees, which improve plant species diversity in both studied regions.

This confirms the effectiveness of conservation management to increase plant species diversity independently of the climatic conditions although we have noted a more pronounced effect in the less arid area. More specifically, this study has shown the major contribution of the β-diversity on γ-diversity, especially in the semi-arid region, because of a higher heterogeneity in this area.

Knowledge of the contribution of the components of beta diversity can be a valuable guide for managers in adopting appropriate management decisions. The high spatial turnover and the low importance of nestedness observed in this study imply that conservation measures should be applied to a large number of sites of various qualities rather than to a limited number of the richest sites. Besides, the negative correlation between oak cover and turnover suggests that oak forests could benefit from a silviculture aiming at enhancing micro-environmental heterogeneity, such as the creation of gaps, in order to promote species conservation and diversity.

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