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Abstract

The oak (*Quercus brantii* Lindl.) semiarid forests of western Iran are among the oldest and host a remarkable diversity. However, the originally high forests were largely converted to coppices and submitted to a long history of traditional management and human disturbances. We investigated the effect of past management and forest structure on soil properties and vegetation diversity on two forest systems: coppice-with-standards stands abandoned after an intense period of exploitation (CWS) and high forest stands (HF) submitted to a low intensity of management. We selected in each system three 1-2 ha stands and sampled 30 plots to measure vegetation diversity, forest structure using structural indices and, main soil factors including bulk density, nutrients, organic carbon and porosity. We found a higher species diversity in HF than in CWS with respectively 7 woody species in the former and only 4 in the latter as well as a higher structural complexity. Plant composition differed also between the two systems and multivariate analyses revealed clear associations between vegetation composition and soil factors in particular soil nutrients, soil porosity for HF and bulk density and texture for CWS. In fact, contents in soil nutrients were higher in HF than in CWS for total nitrogen (0.28 vs 0.15 %), available phosphorus (22.82 vs 15.47 ppm), available nitrogen (0.28 vs 0.15 ppm), and organic matter (2.58 vs 1.61 %) whereas soils of CWS showed a higher bulk density (1.39 vs 1.29) and a lower porosity (47.66 vs 51.50 %). This study thus revealed the legacy of the past forest management actions on the different components of the forest ecosystem. We concluded that the conservative management in high forests was more favourable for the protection of soil and vegetation diversity than in the traditional coppicing system.

Keywords: Natural regeneration, plant diversity, semiarid forest ecosystems, soil properties, Coppice

INTRODUCTION

Forest ecosystems sustain different services and functions, such as carbon and nutrient cycling or water cycle regulation, critical for human populations. But at the same time, forests are highly vulnerable to unsustainable forest management and climate change-related disturbances such as wildfires or droughts (Byrnes et al., 2014). Forest management plays an important role in shaping the vegetation composition, plant diversity and forest structure. This influence depends on the intensity, nature, extension in space and time of the management actions as well as the type of the dominant species in the forest ecosystem (Mei et al., 2020; Strubelt et al., 2019; Scolastri et al., 2017; Govaert et al., 2020). It is widely recognized that most forests have been influenced for centuries by traditional activities and transformed to meet the human needs such as the coppice and coppice with standards systems to produce wood and other products (e.g. fodder, fruits, bark) (Dlamini, 2013; Magagnotti et al., 2018).

The coppice stands grow mainly from shoots that emerge from dormant buds on the stumps after the end of the cutting cycle. In each cycle, which lasts approximately between 10 and 30 years, single-stemmed trees scattered among coppice stools are retained (standards). These standard trees are allowed to grow for several coppice cycles, and one-third to one-quarter of them are cut in each cycle. This specific structure is defined as a coppice-with-standards (CWS) and represents a traditional forest system, which allows the production of more diverse wood products than the single coppice systems (CS) as it includes not only wood for fuel (coppice) but also timber for industry (standards). Over time, for various reasons, such as changing market demand or the replacement of wood with fossil fuels, these traditional systems have been willingly or unwillingly abandoned to the benefit of the high forest system (Lo Monaco et al., 2011; Biˇcík et al., 2001; Marchi et al., 2016).

High forests are composed of planted or seed-origin individuals and their cycles last between 50 and 200 years (Van Calster et al. 2008; Venanzi et al., 2019; Becker et al., 2017). Following tree harvesting, forest stands regenerate through interactions among propagules, including seeds in seed banks and those dispersed into a site (Lucas-Borja et al 2017). After this disturbance (tree harvesting), the floor and soil conditions change radically (Lucas-Borja et al., 2020) and are usually more favorable to the development of new seedlings in comparison with preexisting conditions. Canopy characteristics, understory vegetation diversity, site factors and individual species performance were recognized to play crucial roles in natural regeneration forest (Modrý, 2004; Heydari et al., 2017 b). However, natural regeneration is an unpredictable process because of the complex interactions between biotic and abiotic factors determining the success of seedling establishment (Tardos et al., 2018).

The effects of these past management systems and their changes on various aspects of forest diversity and forest structure have not yet been fully investigated. Historical reports indicate that irregular and intense use of coppice and coppice-with-standards has led to degradation in forest stands (Hasel and Schwarz, 2006; Venanzi et al., 2020). It was also shown that forest stands that experienced heavy wood extraction 100 to 200 years ago have undergone major changes in terms of various structural features (Van Calster et al., 2008; Wäldchen et al., 2013). Besides, changes in management regimes such as conversion of coppices to high forests (or the reverse) can have significant effects on plant composition, plant diversity, seedling recruitment as well as on the relationships among these components and with various abiotic factors such as soil factors (e.g. Scolastri et al., 2017)**.** These different changes are closely linked to the modification of the overstorey structure creating various and contrasted environmental conditions or microclimates in the forest floor (Van Calster et al., 2007; Van Calster et al., 2008; Baeten et al., 2009; Heydari et al., 2017; Venanzi et al., 2019). In fact, the management regime deeply influences the dominant canopy cover (e.g. composition, openness, tree dimensions) which in turn modifies the development and composition of the understory (Van Calster et al., 2008). All these changes affect litter inputs in terms of quantity and quality and conditions of litter decomposition due to modifications of light and soil moisture availability. In turn, these processes influence soil nutrients which play a major role in the establishment of the tree regeneration (Heydari et al., 2017). When forest management is intense, physical and chemical soil properties can be negatively affected (e.g. soil compaction after harvesting operations) leading to restrictions on tree growth and natural regeneration (e.g. Marchi et al., 2016) although such negative impacts are not the rule (e.g. Venanzi et al., 2019). In this regard, some researchers have stated that traditional coppicing management is part of the long history of ecosystems, and cannot been seen as a disruption factor as it can support a high level of diversity (Gondard et al. 2006; Bartha et al., 2008; Mattioli et al. 2016; Müllerová et al., 2015; Della Longa et al., 2020). However, some other studies have emphasized the negative effects of repeated cuts on soil properties, plant composition and regeneration (Nave et al., 2010; Marchi et al., 2016).

The oak (*Quercus brantii* Lindl.) forests of western Iran are considered to be among the oldest oak forests in the world. These originally high forests (i.e. regenerated by seeds) were converted to coppices or coppices with standards and were submitted to a long history of traditional management including frequent and traditional cutting, especially for firewood. An abrupt change occurred in the management of these forests with the nationalization policy of forests about 50 years ago (Valipour et al., 2014). Many forest stands came under government protection and the traditional system was abandoned to the benefit of a less intense management. As a consequence, old coppice-with-standards abandoned stands were largely dominant among the different forest types. Such fast changes in the management regime were also documented in European forests during the second half of the 19th century (e.g. Martin et al., 2015).

The effect of species composition on soil properties has been largely studied (Laganière et al., 2012; Waring et al., 2016; Heydari et al., 2020). However, the effects of different management measures, including long-term abandonment of coppice-with-standards, on the plant diversity of the forest floor and on the regeneration of woody species have not received such a large attention. Some studies have shown that active coppices compared to coppices abandoned for more than fifty years exhibit a reduced soil fertility (Martin et al., 2015). However, other studies have shown that 15 years is a sufficient time to recover soil conditions in deciduous forests (Marchi et al., 2016) or that no effect has been noticed on soil properties (Van Calster et al., 2007). Nevertheless, there is still an active debate about the economic and ecological advantages and disadvantages of the different management systems and the impact of the transition of one system to another (e.g. coppices vs high forests). In particular, there is a growing interest in redeveloping coppice systems in some communities mainly for economic reasons, in particular a fast production of biomass or firewood products and an easier regeneration, but also sometimes for ecological purposes such as to favor biodiversity linked to a variety of microhabitats due to the multi-stemmed growth form of the trees (Kirby et al. 2017; Yücesan et al., 2019; Riccioli et al., 2020; Mattioli et al. 2016). In this study, we evaluated various aspects such as forest structure, plant species diversity, regeneration and soil attributes in two forest systems: coppice-with-standards stands abandoned after an intense period of exploitation and high forest stands submitted to a low intensity of management. More specifically, we seek to answer the following two questions: 1) What is the influence of past forest

management on understorey plant diversity and shrubs/trees natural regeneration? 2) To what extent soil properties differ between the two management systems?
We expect that the answers to these questions will help to better manage semi-arid oak forests and restore their remarkable diversity.

MATERIALS AND METHODS

Study area

The forest stands under study were located within the same area (approximately 240 ha) in Zagros deciduous forests of south-western Iran (Fig. 1) and in very similar climatic and physiographic conditions. In this area, mean annual rainfall is 576.4 mm (Izeh meteorological station) with strong seasonal variations (from 0 mm in summer to a maximum of 294 mm in winter) and mean annual temperature is 19.1 °C. This climate can be classified as a semi-arid climate according to the De Martonne's climatic classification. The dominant soil in the study area is Inceptisol (Soil Survey Staff 2014) i.e. shallow calcareous soils with a clay-loam texture. Mean elevation ranges from 1400 to 1650 m a.s.l. and the general topography is flat or moderate slopes (<25%). The area is covered by oak forests with an overstory dominated by the Brant's oak (*Quercus brantii* Lindl.) and an understory with different woody species in particular *Crataegus azarolus*, *Pistacia atlantica*, *Amygdalus orientalis*, *Acer monspessulanum*, A*mygdalus scoparia, Amygdalus lycioides* (Heydari et al., 2017 a). Cover of both strata is less than 25%.

Forest management and sampling

Forests of the study area were submitted to a traditional management which was intense to respond to the strong demand of the population in wood products particularly firewood and charcoal production. At present two main oak forest systems are found: i) old coppices with standards (CWS) and ii) old high forests (HF). The preexisting high forest was converted into a coppice with standards system and submitted to coppicing for centuries. However, in the middle of the 20th century, forests were nationalized and the traditional management was abandoned (Valipour et al., 2014). Instead, forests were protected against intense and frequent cuttings, firewood exploitation and grazing by fencing and a reinforced surveillance by the guards of the Natural Resources Office. Consequently, a shift in the forest structure occurred from young overexploited coppices with a low canopy cover to mature coppices with standards i.e. with trees of greater dimensions and a higher forest cover. The second type of forest structure (High Forests, HF) are derived from some preexisting oak forests which were preserved from the intense traditional management for various reasons. In most cases, these forests were remote from villages or were willingly protected by their private owners. These forests are now composed of old trees and are not intensively exploited.

In this study, our is aim to evaluate the influence of two contrasted past management systems on soil properties, forest structure, plant composition and regeneration. To achieve this objective we have selected a total of six stands (three stands of 1 to 2 ha in each type: CWS and HF) spaced out 250 to 500 m in similar site conditions (in particular a flat topography and comparable soils). With this approach, we have tried to minimize possible confounding factors although we cannot formally exclude pre-existing site differences. Then, two transects of 200 m length and 250 m apart were set up in each stand with a random starting point. Five 20 m×20 m plots, spaced 50 m apart from each other, were placed along each transect i.e. a total of 30 plots in each system (CWS and HF).

Soil properties

In each plot, three soil samples were collected up to 25 cm depth and then mixed in a composite sample. These samples were then sieved (2-mm diameter) and air-dried prior to physical and chemical analyses based on standard methods (see Heydari et al., 2017 a). Soil analyses were carried out 15 days after sampling. Soil parameters included soil texture (contents in sand, silt and clay), soil porosity, soil organic carbon (OC), total nitrogen (Ntot), available phosphorus (Pava), available potassium (Kava), electrical conductivity (EC). Additional undisturbed soil cores were collected for the determination of bulk density (BD) in the 0–15 cm mineral layer (Blake and Hartge 1986).

Vegetation and regeneration measurements

In each plot, the large and small diameter of each tree's crown with a DBH > 7.5 cm were measured to compute the percentage of canopy cover of all woody species. The seedlings (height <1.30 m) were counted for each woody species on a 10m×10m subplot located in the center of the main plot and the cover of herbaceous species was visually estimated using four 1-m^2 subplots located in the four corners of the main plot (i.e. 30×4×2= 240 subplots in each system).

Stand structural indices

In each plot, all trees and shrubs taller than 1.30 m were counted and diameter at breast height (with a tree caliper) and total height (with a Haga altimeter) of all tree species were measured. Then the following structural indices were computed at plot level:

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The species mingling index (MI) was calculated using Eq. 1 (Pommerening, 2002):

$$M_j = \frac{1}{n}\sum_{i=1}^{n} V_{ij} \quad M_j \epsilon\ [0, 1] \qquad \textbf{Equation 1}$$

where M_j is species mingling, n is the number of the nearest neighbors (n=3); V_{ij} = 1, if the reference tree i and neighbour tree j are different tree species and 0 otherwise. Lower values of MI reflected purity or very low presence of other woody species. In each plot, we selected the reference tree as the tree the closest to the plot centre and then we computed the MI value according to Eq. 1. This approach was used because of the low number of trees in the plot (4-5 trees) and to avoid border effects (i.e. selecting a reference tree which neighbours are located outside the plot). Height and diameter differentiation (HD and DD respectively) indices (T_{ij}) were computed using Eq. 2. In each plot, a reference tree (i) was randomly selected as well as its three nearest woody neighbours (j).

$$T_i = \frac{1}{n}\sum_{i=1}^{n} T_{ij}$$

$$T_{ij} = 1 - \frac{\min(DBHi\,.\,DBHj)}{\max(DBHi\,.\,DBHj)} \quad \text{or } T_{ij} = 1 - \frac{\min(Heigh\quad.\,Heightj)}{\max(Heighti\,.\,Heigh\quad)} \quad T_i \epsilon\ [0, 1] \qquad \textbf{Equation 2}$$

These equations were used for the three pairs of reference woody-neighbour species and the Tij indices were calculated as the mean of the three individual calculations. The higher value of the index (close to 1) show the higher diversity in terms of tree size. In addition, total canopy cover (TCC), basal area (BA), tree density and mean height of woody species were also recorded in each plot.

Statistical analyses

The plot was considered as the study unit. Different environmental and stand structural variables such as MI, HD, DD, TCC, BA, density of woody species, mean height of woody species (mean H), sand, silt, clay, bulk density, porosity, OC, Ntot, Pava, K, pH, EC, C/N were surveyed at plot level. Moreover, understory plant composition and shrubs and tree regeneration species were surveyed at plot scale. Differences between CWS and

HF were studied using a resemblance matrix (i.e. a symmetrical 60 × 60 matrix containing the similarities between all pairs of samples) for environmental and stand structural variables (and two biological matrices: understory plant composition and shrubs and tree regeneration species). The resemblance is the general term in PRIMER software used to cover (dis)similarity or distance coefficients between all pairs of samples. All the variables of the environmental matrix were log x+1 transformed and the resemblance matrix was built using the Euclidean distance. The variables included in the biological matrixes were square root transformed and the resemblance matrix was built using the Bray Curtis distance. Then, an analysis of similarities (ANOSIM), described by Clarke (1993), was developed for the environmental and stand structural matrix in order to check differences among environmental variables for each type of forest management. ANOSIM routine was also used for checking differences among understory plant composition or shrub and tree regeneration species between each type (CWS *vs* HF). Secondly, environmental and stand structural variables were analyzed 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 each biological matrix (understory plant composition, shrubs and tree regeneration species). Thirdly, we applied the RELATE routine to check statistical significance of the relation between the environmental and stand structural and the two biological matrixes. Fourthly, the DIVERSE routine was used for calculating richness and different plant diversity indices (Margalef's richness, Pielou's evenness, Shannon and Simpson's diversity). A Spearman correlation analysis was finally made using environmental and stand structural variables, MDS1 and MDS2 of understory vegetation matrix and natural regeneration matrix and biodiversity indices. Statistical analyses were made using PRIMER V6 software (Clarke and Gorley, 2006; Anderson et al., 2008).

RESULTS

Comparison of soil properties and stand structural features

Analysis of similarity (ANOSIM) of the matrices of the physical and chemical soil and stand structural features showed statistically significant differences between CWS and HF (Sample statistic (Global R): 0.98, Significance level of sample statistic: 0.1%). For soil properties, mean values of OC, Ntot, Pava, Kava, sand and porosity were significantly higher in HF than in CWS. In contrast, pH, EC, C/N, silt, clay and BD mean values were significantly higher in CWS than HF. For stand structural features, mean values of all measured variables (except woody species density), i.e. MI, HD, DD, TCC, BA and height of woody species, were significantly higher in HF than in CWS (Table 1).

Understory vegetation and regeneration composition

Analysis of similarity of the understory plant composition matrix and of the tree regeneration species matrix showed statistically significant differences between CWS and HF (Sample statistics (Global R): 0.95 and 0.69 respectively, significance level of sample statistic: 0.1%). In accordance with the pairwise comparison among factors (Fig. 2 and 3), the MDS analyses clearly separated the two forest systems when analyzing each biological matrix indicating that both CWS and HF significantly differed in terms of composition of the understory vegetation and composition of the regeneration in shrubs and trees.

After applying the RELATE routine, we found a statistical significant relationship between the measured variable matrix and both the understory plant composition and woody regeneration species matrixes. More precisely, the environmental and stand structural variables have a significant influence on understory plant diversity (significance level of sample statistic: 0.1 %, (Rho): 0.738) and on the composition of regeneration in woody species (Significance level of sample statistic: 0.1 %, (Rho): 0.477). We found that the composition vegetation of HF and CWS plots were clearly distinct. The HF vegetation composition was associated with higher soil nutrients (Ntot, Pava and Kava), higher soil porosity, as well as higher values of the structural indices (MI, BA, DD and HD). In contrast, the vegetation composition of CWS reflected different soil parameters such as such as higher BD, EC, clay and silt values as well as a higher density of woody species (Fig 2).

Composition of the regeneration in woody species clearly separated along the first axis of the MDS axis1. More precisely, the vegetation composition in HF included *Quercus brantii*, *Acer monspessulanum*, *Crataegus azarolus*, *Pistacia atlantica*, *Amygdalus orientalis*, *Amygdalus scoparia* and *Amygdalus lycioides* and was found on more fertile soils. In contrast, vegetation composition of CWS was less diverse (only *Quercus brantii*, *Crataegus azarolus*, *Amygdalus scoparia* and *Amygdalus lycioides*) and was associated with less fertile soils showing higher BD, EC, pH , clay, silt values and with stands with different structural indices (Fig 3).

Regeneration density and diversity indices

Results of the DIVERSE routine showed statistical differences of the understory vegetation and regeneration diversity indices between the two forest types: all values were higher in HF than in CWS (Table 2). Density of the woody regeneration was significantly higher in HF than in CWS whatever the species (Table 3). Total density was 1.19/m^2 in HF and only 0.43/m^2 all species together. This low density in CWS was explained by the absence of some woody species and a reduced density of the dominant oak species.

Relationships between vegetation composition and environmental and stand structural variables

According to the DISTLIM procedure, the best model for predicting understory plant composition using the environmental and stand structural variables is the model using solely the soil organic matter content (R^2=0.39; AICc=431.49, Table 4). Similarly, the best model (R^2=0.44; AICc=395.51) for predicting the composition of the woody regeneration using the environmental and stand structural variables was a model including soil organic matter (OC), mean height (H) and the mean height differentiation index (HD)(Table 5). According to the Distance-based redundancy analysis (dbRDA) plots generated by the DISTLM procedure, the percentage of variation explained by axis 1 was 99.5% out of the fitted model and 36.5% out of total variation in the case of the understory plant composition (Fig. 4). The model, clearly separated HF and CWS plots according to the OC parameter (Fig. 4). The dbRDA plot (Fig. 5) shows the distribution of the sampled plots of the two forest types (HF, CWS) according to the similarity of the composition of the woody regeneration in the factorial map defined by the two axes. The first axis explains 83.7% of the fitted model and 37.4% of the total variation whereas the second axis explains 15.6% and 6.9% of the fitted and total variation respectively. Plots of the two forest types are clearly separated along the first axis of the ordination plot which is correlated to the environmental and stand structural variables OC, mean H and HD.

Finally, the correlation values among the different environmental and stand structural variables, MDS1 and MDS2 of the plant diversity matrix, and woody regeneration and diversity indices matrices are shown Fig. 6. The multidimensional scaling axes generated using the understory composition (MDS1_Under) and natural regeneration (MDS1_Reg) matrices are positively and significantly ($P<0.05$) correlated with the stand structural indices (except for density), soil fertility (OC, N, P and K) and soil porosity but negatively correlated with soil physical properties (clay, silt and BD), pH, EC and C/N. In addition, we found positive correlations between all diversity indices and stand structural indices (Fig. 6).

DISCUSSION

Soil properties and stand structural features between the two oak forest types

Our results highlighted differences not only in soil properties but also in forest structural features and plant diversity between our two forest types CWS (abandoned coppice with standards stands) and HF (high forests with low management intensity). Indeed, we found that the major soil nutrients (NPK), soil organic carbon, soil porosity were significantly higher in HF than in CWS whereas the bulk density (BD) was higher in CWS than in HF. Moreover, all stand descriptors and vegetation indices (except woody species density) including MI, HD, DD, TCC, BA and the mean height of the woody species were significantly higher in HF than CWS. Centuries of past management have shaped contrasted plant assemblages in the two forest types and more largely have influenced abiotic factors. It is known that plants directly modify the environment of other plants by competing for resources like water or light or by facilitative mechanisms such as amelioration of extreme temperatures or increasing resource availability such as nutrients (Caldeira et al., 2014). Moreover, trees and shrubs have indirect effects on soils through plant remains reaching the soil surface (in particular litter and root exudates) and nutrient uptake, which influence soil biogeochemical processes (Camping et al., 2002; Kooch et al., 2017; Eslaminejad et al., 2020). The higher structural and functional forest complexity found at HF seems to have enhanced litterfall inputs, increased nutrient content and soil organic matter accumulation on the forest floor (Lucas-Borja et al 2016), consequently favoring the nutrient and C cycling functions. Moreover, structural and functional forest complexity may significantly re-route vertical precipitation pathways by canopy interception, throughfall and stemflow, hence clearly affecting the water regulation function (Lucas-Borja and Delgado-Baquerizo 2019). In addition, litter and dead forestry materials above the soil surface perform important ecological functions such as soil protection and nutrition and provide habitat for a large variety of organisms, ultimately contributing to soil fertility and accumulation of soil organic carbon with time (Sangha et al., 2006). Consistent with our results, Van Calster et al. (2007) showed that the conversion of coppices to high forests increased the number of species of the understory vegetation and of soil quality indicators such as nitrogen and soil moisture. Similarly, Heydari et al (2020), comparing high forests to coppice stands in western Iran, found higher amounts and more diverse inputs of litter in high forests which may generate higher quantity of nutrients favoring biomass and diversity of the soil microorganisms. In fact, high forests most often exhibited more diverse and denser woody species with thicker canopy favoring litter accumulation and flow of nutrients, explaining the more fertile soils in this type of forest (Callaway et al., 1991; Klemmedson, 1991; Heydari et al., 2020).

In contrast, in the more simple forest structures like coppices derived from traditional management, soil nutrients and organic matter accumulation are often reduced (e.g. Pyttel et al., 2015). This limited soil fertility can also be explained by the traditional coppice system including too frequent and too intense cuttings, which drastically reduce overstory cover and vegetal inputs reaching soil surface (Van Calster et al., 2008; Poeplau et al., 2011). Such activities can explain the increase of soil bulk density and porosity due to soil compaction, as well as the reduction of soil organic matter (Labelle and Jaeger, 2011; Cambi et al., 2015; Vacca et al., 2017). Moreover, the opening of the forest cover and the biomass removal in CWS have reduced the protective effect of the canopy and accelerated the topsoil erosion (Stott et al., 2001; Borrelli et al., 2017). It has also disrupted the input of organic matter (litter) (Noormets *et al*., 2015) which is the main source of soil nutrients in our systems, reduced soil fertility and accelerated carbon losses (Mallik and Hu, 1997; Vacca et al., 2017).

Effect of forest systems on diversity and composition of plant species and regeneration

In this study, we showed that the forest type (CWS or HF) resulting from contrasted management systems, has a profound influence on vegetation diversity and composition of the overstory, and on the structural characteristics of the stands such as density, diameter, height and canopy. Similar results were also found in temperate forests, in particular after conversion from coppices to high forests, but was more rarely described in semi-arid forests. For instance, Scolastri et al. (2017) showed that the structural characteristics of beech forest stands were significantly affected by silvicultural management and the gradual change of coppices to high forests. Our results indicated that the values of the Shannon diversity indices applied to the forest structure (i.e. using DBH classes, basal area, mean height) were higher in HF than in CWS, while the tree density was the highest in CWS due to the great number of sprouts in this system. This high density in CWS favored the stems' competition for light and space, and over time leads to a more uniform vertical structure of the CWS compared to HF (Fabbio et al., 2006). Such changes illustrate that human disturbances linked to a forest management system such as coppicing can deeply modify the horizontal and vertical structure of the forest as shown by many previous studies (Kirby et al., 1991; Cierjacks and Hensen, 2004; Bruckman et al., 2016; Manetti et al., 2020). This modification of the forest structure then plays a key role in the change of the forest microclimate, soil properties and more largely the future of the forest (Heydari et al., 2017 b; Košulič et al., 2016).

We also showed that the composition, the diversity and richness of the understory vegetation including the regeneration in woody species were significantly higher in HF than in CWS. Such differences between the two systems can be explained by the modification of both the below-ground (soil properties) and the above-ground resources due to change in the forest structure. Forest management involves a set of human activities and disturbances (Van der Maarel 1993; Kulakowski et al., 2017) and is a key factor affecting the environmental factors controlling changes in plant diversity. For example in our study, thinning and frequent cuttings in CWS has increased light availability (Ford and Newbould 1977; Strubelt et al., 2019) and access to soil water and nutrients (Parsons, Knight and Miller 1994). This has favored the competitive exclusion between species and has decreased species diversity (Wilson and Tilman 1993). Because different forest management systems may simultaneously modulate access to different sources such as light and soil nutrients, their effects on biodiversity vary from region to region and according to the type of vegetation. For instance, some plant groups such as graminoids respond more to management operations such as coppicing: their richness and abundance can increase after exploitation operations due to the colonizing capacity of several heliophilous species (Roberts and Zhu 2002; Decocq et al., 2004). Light regime is indeed an important factor in changing the species composition and diversity and the greater light availability after coppicing can efficiently limit the abundance of shade-tolerant species but facilitate the development of light-demanding species (Vild et al., 2013). The higher diversity and species richness in HF compared to CWS can also be related to the more stable canopy conditions in HF over time, i.e. more stable microclimate conditions in the forest floor favorable to shade-tolerant and vernal species (Durak 2012). Similarly, Scolastri et al. (2017) stated that HF stands can offer a wide range of light conditions that support a high plant diversity from strictly shade-tolerant to semi-heliophilous species. The higher diversity and density of woody species in the regeneration of HF can be related to the greater diversity of the overstory in woody species which can provide diverse seeds and offer suitable microhabitats for the seedlings. In contrast, the larger canopy opening in CWS, the simplification of the forest structure as well as the reduced soil fertility, are less favorable for the successful establishment of woody species regeneration (Heydari et al., 2017 a).

CONCLUSION

We compared abandoned coppice with standards stands (CWS) and high forest stands (HF) to understand whether past forest management system can have effects on the forest stand structural features, soil properties and plant diversity, and if so, in what way. Our findings highlighted not only which system has the higher soil nutrient content, soil organic matter, species richness or diversity, but also which was able to preserve the most typical understory species of the oak semiarid forest. HF offered more stable microclimatic conditions over time leading to a higher soil quality and a more diverse ecosystem than CWS. Our results provide the first insights for supporting the conversion of CWS to HF to improve species diversity and soil fertility and maintaining more stable conditions in semi-arid oak forests. In the harsh site conditions of oak forests in western Iran, the more conservative management in HF stands submitted to less frequent cuttings and subsequent disturbances than in the traditional coppicing system was more favorable for the protection of soil and vegetation diversity. This legacy of forest management is still noticeable in the forest composition, structure and soil properties after a long period of abandonment.

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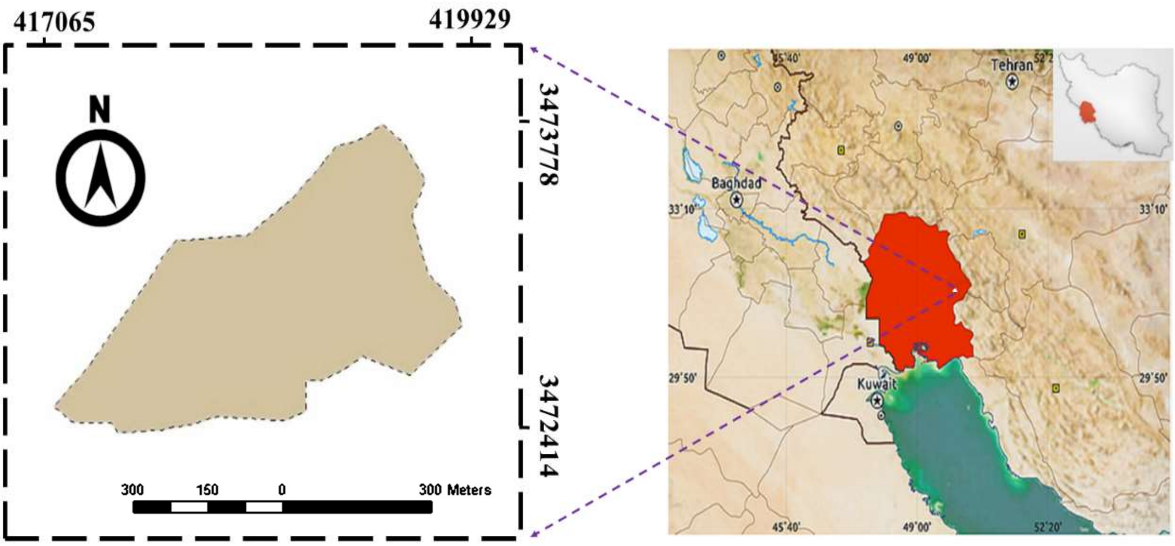

Figure 1. Location of study area in south-western Iran

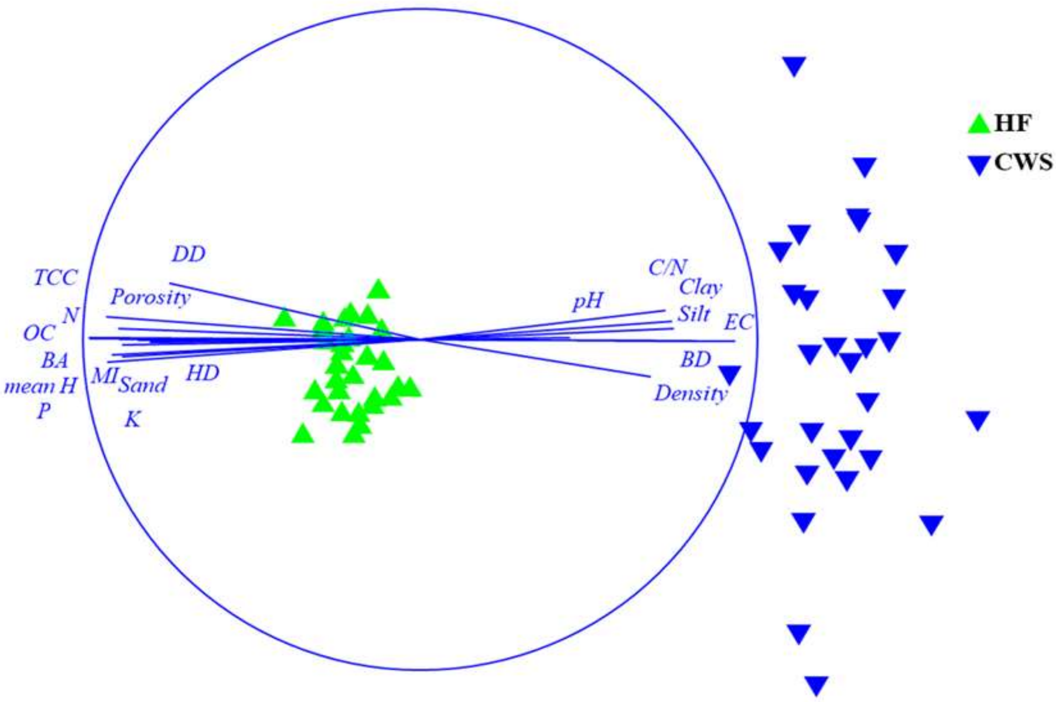

Figure 2. Ordination by multidimensional scaling (MDS) of understory vegetation composition (HF and CWS) showing the environmental and stand structural vectors proportional to the strength of the correlation with the axes. TCC: total canopy cover, BA: basal area, HD: Height differentiation, DD: diameter differentiation, MI: mingling index, Density: tree density; mean H: mean height of woody species, P: available phosphorus, K: available potassium, OC: organic carbon, EC: electrical conductivity, N: total nitrogen, C/N: carbon/nitrogen, BD: bulk density.

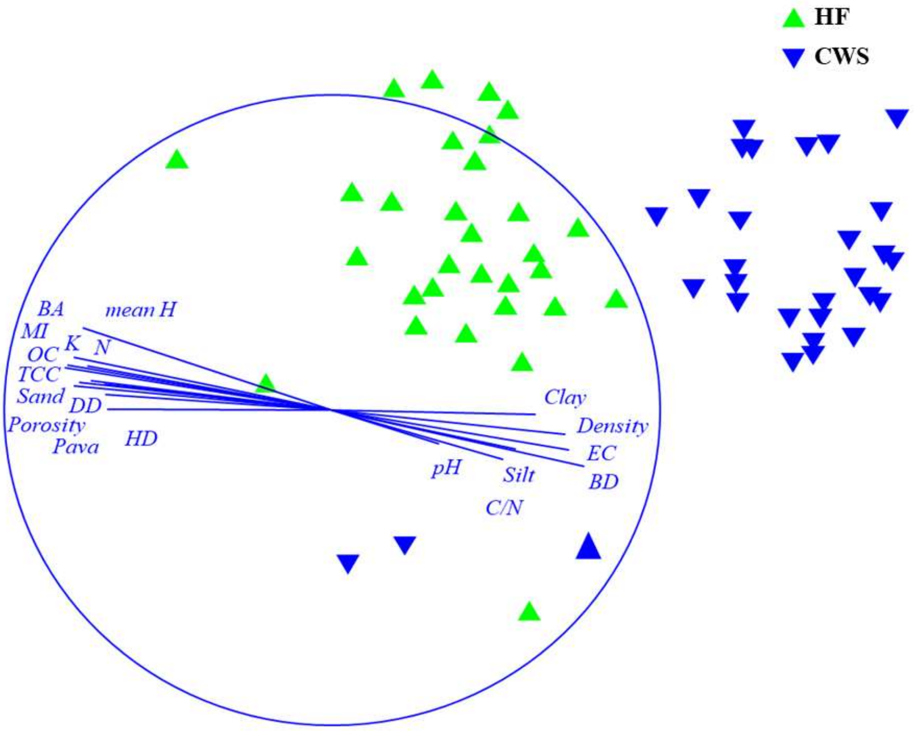

Figure 3. MDS showing the composition of the regeneration in woody species (HF and CWS) and the environmental and stand structural variables.

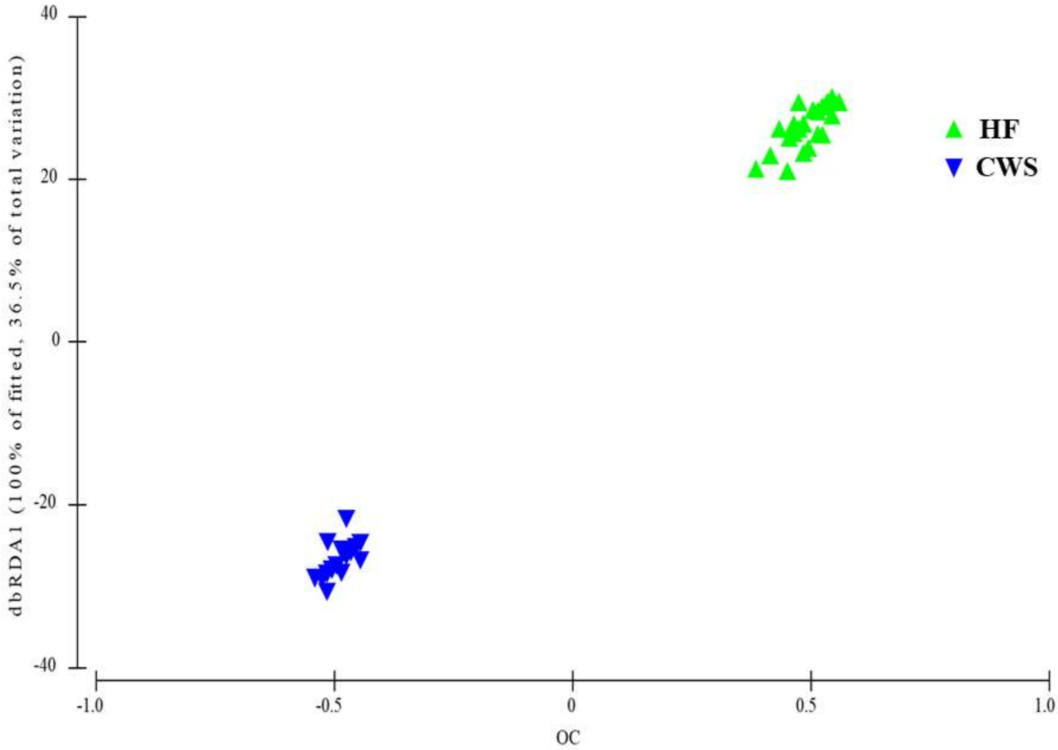

Figure 4. Distance-based redundancy analysis (DbRDA) plot t for understorey vegetation composition showing the distribution of the plots of the two systems (HF, CWS) according to the normalized value of the soil organic carbon (OC).

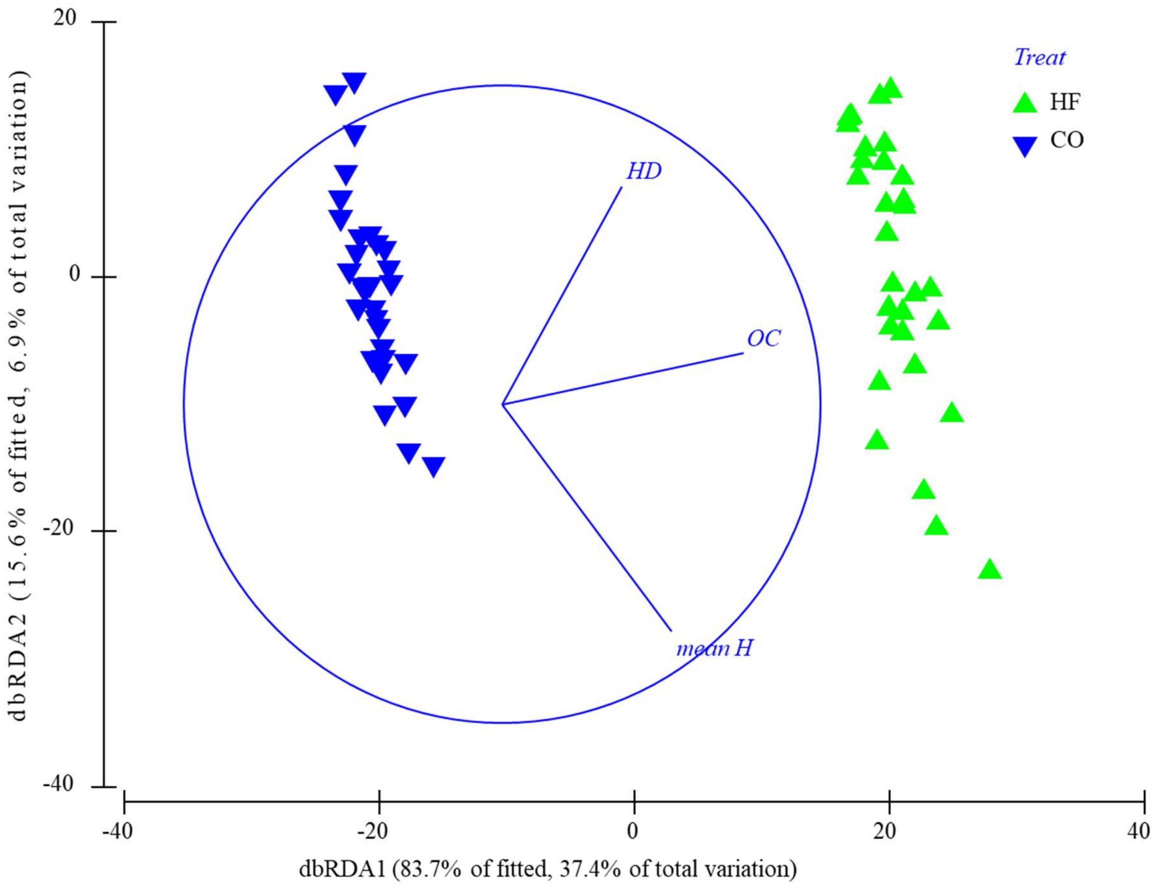

Figure 5. DbRDA ordination plot for composition of the woody regeneration. The environmental and stand structural vectors are indicated in the factorial map as follows: mean H (mean height of woody species); OC (soilorganic carbon) and HD (height differentiation index).

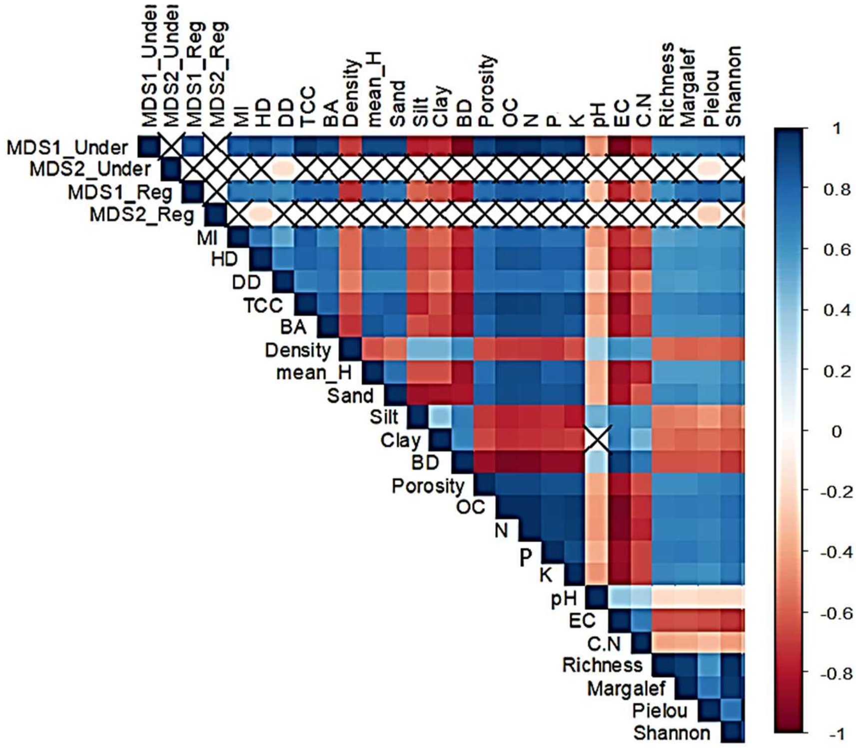

Figure 6. Map of the correlations among the environmental and stand structural variables, the MDS1 and MDS2 of the plant diversity matrix and of the woody regeneration and biodiversity indices matrices. TCC: total canopy cover, BA: basal area, HD: Height differentiation, DD: diameter differentiation, MI: mingling index, Density: tree density; mean H: mean height of woody species, P: available phosphorus, K: available potassium, OC: organic carbon, EC: electrical conductivity, N: total nitrogen, C/N: carbon/nitrogen, BD: bulk density.

Table 1. Comparison of mean (± standard error) soil properties and stand structural features between high forest (HF) and coppice-with-standards (CWS).

	Variables	HF	CWS	t-value
Soil properties	OC (%)	2.58 (0.007)	1.61 (0.004)	112.90***
	Ntot (%)	0.28 (0.001)	0.15 (0.002)	68.94***
	Pava (ppm)	22.82 (0.344)	15.47 (0.129)	19.97***
	Kava (ppm)	314.17 (0.604)	289.93 (0.818)	23.83***
	pH	7.31 (0.006)	7.39 (0.022)	-3.74***
	EC (ds.m-1)	0.36 (0.005)	0.49 (0.003)	-22.74***
	C/N	9.46 (0.103)	10.76 (0.114)	-8.46***
	Sand (%)	41.87 (0.164)	31.23 (0.689)	15.01***
	Silt (%)	29.00 (0.179)	34.63 (0.584)	-9.22***
	Clay (%)	29.13 (0.133)	34.13 (0.587)	-8.31***
	BD (g m^{-3})	1.29 (0.004)	1.39 (0.002)	-21.69***
	Porosity (%)	51.50 (0.215)	47.66 (0.056)	17.31***
Stand structural	MI	0.73 (0.004)	0.13 (0.002)	10.75***
	HD	0.66 (0.002)	0.33 (0.001)	13.03***
	DD	0.64 (0.024)	0.34 (0.021)	9.14***
	TCC (m^2)	234.26 (4.875)	117.32 (2.802)	20.79***
	BA (m^2 ha^{-1})	11.73 (0.350)	5.69 (0.160)	15.67***
	Density (N ha^{-1})	274.07 (4.823)	338.97 (7.074)	-7.58***
	Mean Height of woody species (m)	2.77 (0.053)	1.68 (0.044)	15.73***

***** $p < 0.001$**

Table 2. Mean values (± standard error) of the diversity indices of the understory vegetation and woody regeneration in each forest type.

	Vegetation		
Diversity indices	**HF**	**CWS**	**P-value**
Margalef's richness	2.3(0.1)	1.4(0.1)	<0.001**
Shannon's diversity	1.5(0.05)	0.9(0.05)	<0.001**
Simpson's diversity	0.9(0.02)	0.7(0.02)	<0.001**
Pielou's evenness	0.9(0.01)	0.8(0.01)	<0.001**
	Regeneration		
Diversity indices	**HF**	**CWS**	**P-value**
Margalef's richness	1.16(0.08)	0.62(0.12)	0.001**
Shannon's diversity	0.88(0.06)	0.40(0.07)	<0.001**
Simpson's diversity	0.45(0.02)	0.26(0.05)	<0.001**
Pielou's evenness	0.67(0.02)	0.47(0.08)	0.03*

(**P < 0.01; *P < 0.05)

Table 3. Mean density values (and standard error) (No. in 100 m^2) of the regeneration of the woody species in both forest types.

Species	HF	CWS	P-value
Quercus brantii	8.32 (0.58)	4.1 (0.42)	<0.001**
Pistacia atlantica	0.51 (0.11)	0 (0)	<0.001**
Acer monspessulanum	0.46 (0.11)	0 (0)	<0.001**
Crataegus azarolus	1.00 (0.15)	0.53(0.10)	<0.001**
Amygdalus orientalis	0.30 (0.08)	0(0)	<0.001**
Amygdalus scoparia	0.60 (0.12)	0.46(0.10)	<0.001**
Amygdalus lycioides	0.66 (0.12)	0.23 (0.09)	<0.001**
All species	11.90 (0.68)	4.26 (0.34)	<0.001**

(**P < 0.01)

Table 4. Best DistLM model for predicting understorey plant diversity using all environmental and stand structural variables (R^2=0.39).

Variable	AICc	Pseudo-F	P	Prop.	Cumul.	res.df
+OC	431.49	33.301	0.001	0.36474	0.36474	58

OC: organic carbon

Table 5. Best DistLM models for predicting the composition of the woody regeneration using the environmental and stand structural variables. (R^2=0.44).

Variable	AICc	Pseudo-F	P	Prop.	Cumul.	res.df
+OC	398.6	34.235	0.001	0.37117	0.37117	58
+mean H	396.65	4.107	0.011	4.23E-02	0.41343	57
+HD	395.51	3.2981	0.03	3.26E-02	0.44606	56

OC: organic carbon, mean H: mean height of woody species, HD: height differentiation index