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Taxonomic and structural diversity indices predict soil carbon storage better than functional diversity indices along a dieback intensity gradient in semi-arid oak forests

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Key Message: The use of structural diversity indices can be efficient tools to increase understanding of changes in soil carbon storage as a key ecosystem function along the oak dieback intensi

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Abstract

Investigating the relationships between diversity indices and ecosystem functions within the mass-ratio and niche complementary hypotheses is still a challenging issue in terrestrial ecology. These relationships have not been studied along a dieback gradient of disturbance in semiarid forest ecosystems. To fill this gap, we investigated the relationships between a main ecosystem function -soil carbon storage- and various diversity indices along a dieback intensity gradient (no, low, moderate or high dieback intensity) in protected or intensively managed mixed oak forests in western Iran. We used different diversity approaches and calculated the functional divergence index (FDvar), community weighted mean trait values; CWM, taxonomic diversity indices (richness, Shannon–Wiener diversity and evenness) and structural diversity indices (MI: mingling index, HD: height differentiation, DD: diameter differentiation). Soil carbon storage was significantly influenced by the type of management, the intensity of dieback and their interactions and was higher in the protected areas (95.90 ± 4.62 ton ha^{-1}) than in the intensively managed areas (76.52 ± 2.04 ton ha^{-1}). It showed a humped-shaped pattern along the dieback intensity gradient in the protected areas, as it peaked at the low dieback intensity (122.47 ± 10.12 ton ha-1), indicating that soil function was maximized at a low disturbance level. Soil carbon storage was positively and significantly correlated with all structural and taxonomic diversity indices, except for evenness, but negatively with most functional composition indices (CWM of LNC: leaf nitrogen concentration, H: mean of woody species height and LDMC: leaf dry-matter content). It was best predicted by a structural index (Mingling index: R^2=0.214) followed by a taxonomic index (species richness, R^2=0.173) and a CWM index (CWM LDMC, R^2=0.158). Our results emphasize the role played by the diversity indices to predict ecosystem functions in contrasted management conditions and along a dieback gradient. They also provide evidence to support both the mass-ratio and niche complementary hypotheses.

Keywords: Ecosystem function, forest management, biodiversity, woody species.

Introduction

Forest vegetation and soils are major reservoirs of carbon storage which make forests the largest carbon sink in terrestrial ecosystems (Schimel et al., 2001; Zhang et al., 2019; Jhariya, 2017; Qiu et al., 2020) and major contributors in buffering climate change (Aishan et al., 2018; Gordon et al., 2018; Klemm et al., 2020). Forest ecosystems, as atmospheric carbon dioxide filters, have a high potential for storing carbon in wood and other organic matter (Watson et al., 2000) and therefore play an important role in stabilizing the global carbon cycle contributing to the climate stability and preventing global warming (Zhu et al., 2010). However, the amount of carbon stored in soils is about four times the amount of carbon stored in the biomass and 3.3 times the amount of carbon in the atmosphere (Lal, 2004). Therefore, any change in the environmental conditions of the forest ecosystem or in management measures can significantly influence soil carbon and biomass storage and more globally the overall ecosystem carbon flow and atmospheric carbon dioxide content (Han et al., 2008; Brahma et al., 2018; Marques et al., 2019; Ghosh et al., 2020).

Limiting the increase in atmospheric carbon is not just a matter of reducing its emission, and methods favoring the carbon storage in the vegetation and subsoil can also represent cost-effective, simple and practical methods (Richards and Stokes, 2004; Cho et al., 2019). In particular, the protection and restoration of forest areas can play a key role in balancing the carbon cycle as vegetation degradation can reduce carbon storage and increase carbon dioxide emissions. Carbon sequestration potential in forested areas is affected by plant species, climate, and the way biomass is managed, exploited, and used (Singh et al., 2003; Ruiz-Peinado et al., 2017). For example, the capacity of woody plants for carbon sequestration is species-dependent (Thomas et al., 2007). In fact, carbon allocation in the different organs of the woody species is a key factor in the carbon cycle since they have different lifespan and decomposition rates (Pilli et al., 2012). Besides, human actions or natural events leading to site degradation are also crucial factors altering carbon storage of the ecosystem (Ahmad et al., 2018). This applies particularly to large forest dieback.

Indeed, in the last two decades, a widespread phenomenon named tree dieback has been reported in many forest ecosystems over the world (Ibáñez et al., 2017; Ogaya et al., 2020; Sánchez-Salguero and Camarero, 2020). This phenomenon occurred with different intensities in western forests of Iran and affected several major tree species including the Persian oak (*Quercus brantii* Lindl.) (Karami et al., 2018; Shiravand and Hosseini, 2020). In general, this forest decline is attributed to climatic factors and particularly long and recurrent periods of drought but habitat destruction, pests and diseases, as well as non-adaptive management can cause or exacerbate this phenomenon (Kamata et al., 2002; Touhami et al., 2019; Hevia et al., 2019).

However, the effect of site degradation and non-adaptive forest management on the severity of this phenomenon has not received much attention (Haller and Wimberly, 2020). According to the intensity of the dieback, a more or less significant part of the plant decays and disappears, which can lead to the gradual elimination of some plant species and modify the species composition and diversity of the ecosystem (Koepke et al., 2010; Nagel et al., 2019). Numerous studies have examined the effects of disturbances (in particular drought) on tree growth and C storage (Brouwers et al., 2013; Avila et al., 2016; Takahashi et al., 2020), but the effects of different dieback intensities under contrasted management regimes have been more rarely studied.

Among the main factors affecting the carbon storage of land ecosystems species diversity plays a crucial role (Steinbeiss et al., 2008; Sintayehu et al., 2020). Diversity usually includes the number of species (richness) and their abundance but to get deeper insight into the ecosystem processes different functional characteristics of plants must be considered (Díaz and Cabido, 2001). Based on these plant traits, a new group of biodiversity indices, called functional diversity indices, has emerged and has been largely used in numerous ecosystems (Tilman, 2001; Conti and Díaz, 2013; Kuebbing et al., 2018; Wang et al., 2020). They not only consider the abundance of plants within the community but also integrate the value, the range, the distribution and frequency of various functional traits (Díaz et al., 2007). In recent years, functional diversity indices have been used to evaluate different ecosystem functions including carbon storage (Tahmasebi et al., 2017; Häger and Avalos, 2017; Heydari et al., 2020 a) and better results were obtained than by using classical indices (such as Shannon and Simpson diversity index) (e.g. Siebenkäs and Roscher, 2016). For instance, functional traits using height and wood density of tree or shrub species were shown to be directly related to soil biomass and carbon storage, while leaf dry matter content was negatively related to biomass and carbon storage (Tahmasebi et al., 2017; Rawat et al., 2019). Also, higher nutrient uptake rates (such as nitrogen and phosphorus) and higher specific leaf area (SLA) increase photosynthesis and ultimately the plant carbon storage (Herms and Mattson 1992; Poorter and Garnier, 2007; Freschet et al. 2012). Therefore, the use of functional traits of plants can increase our knowledge of changes in ecosystem carbon storage.

In addition, the forest structure often reflects the effect of past management actions or natural disturbances (Heydari et al., 2017; Haber et al., 2020 a) and descriptors of this structure can also be effective in predicting changes in various ecosystem functions, including carbon storage (Zhang et al., 2018; Ali, 2019). Although a great variety of indices has been used to explore many ecosystem functions, we still largely ignore to what extent these indices can be used in forest systems submitted to forest decline and different management conditions. In this study, we used a gradient of forest dieback in semi-arid oak ecosystems under two contrasted types of management to investigate the relationships between taxonomic, functional and structural diversity indices and soil carbon storage. Our assumptions are the following: (1) soil carbon storage is affected by the type of management (conservation vs traditional intense use) and the intensity of dieback, (2) among the indices used, those based on community-weighted mean (CWM) functional traits better predict soil carbon storage changes along the dieback gradient in the two management systems, (3) simultaneous use of all diversity approaches (taxonomic, functional and structural) increases the predictability of changes in soil carbon storage, (4) CWM trait values can better explain the separation between the two types of management than the other approaches.

Material and methods

Sites description

The study area is located in semi-arid mixed oak forests in Ilam county (western Iran). These forests initially hosted a particularly rich flora including many endangered species and are still recognized as a hotspot of biodiversity. However, forests were submitted to long history of human disturbances (e.g. firewood exploitation, grazing and fire) altering main ecological functions and diversity. Two adjacent forest areas with the same physiographic conditions (average slope less than 20 %, same altitude and similar site conditions) were selected (Figure 1). These two areas were initially covered by dense forests centuries ago but were then intensively exploited and degraded due to the high dependence of people's livelihood on forest resources in particular cutting down trees for fuel consumption and charcoal production and livestock grazing. After the implementation of national policies approved 50 years ago in Iran, one of the two areas was protected by the Natural Resources Office from any anthropogenic disturbances (protected area) while the other was left to the traditional intense use (degraded area). The predominant species in these forests is the Persian oak (*Quercus brantii* Lindl.), accompanied by some tree and shrub species such as *Acer monspessulanum* L. subsp. Cinerascens (Boiss. Yaltirik), *Pistacia atlantica* Desf., *Crataegus pontica* K. Koch., *Cerasus microcarpa* Boiss. and *Daphne mucronata* Royle. In the degraded area, only scattered individuals of oaks with large stem diameters and pistachio are found, while the other woody species are very scarce. In contrast, in the protected area oak trees are more frequent and of smaller diameter and mixed with different tree and shrub species.

Usually, the density of woody species in the study area varies from 30 to 100 stems per hectare. The soil of both areas is a shallow calcareous clay loamy soil (average depth: 30 to 40 cm) with abundant small and large stones on the soil surface.

According to long-term statistics of the nearest meteorological station, the mean annual precipitation and the mean annual temperature are 652.6 mm and 17 °C respectively. This region is generally described as sub-Mediterranean with a completely seasonal rainfall distribution which peaks at autumn (Fathizadeh et al., 2017).

Since 2001, a phenomenon known as dieback or sudden death of tree species has occurred leading to drying up of trees partially or totally. Oaks were particularly affected and symptoms of decay were of variable intensity. The causes of this forest decline are still not well known, although some researchers have attributed this phenomenon to the stresses of prolonged drought periods (Goodarzi et al., 2019; Shiravand and Hosseini, 2020).

Experimental design and sampling

In each of the two forest areas, forty sample plots of 1000 m^2 were evenly allocated in each of the four dieback intensity classes (low, moderate, high or no). Classes were defined using visual criteria of dieback as follows:

- High intensity dieback: trees with at least 3:4 of their canopy dry and with deep cracks on most parts of the trunk.
- Moderate intensity dieback: 1:4 to 1:2 of the tree canopy is dry with some cracks and holes on the trunk.
- Low intensity dieback: less than 1:4 of the canopy is dry and no other signs of rot, holes and cracks on the trunk are visible.
- No dieback: healthy trees without signs of dieback.

At each each plot, three soil samples were randomly collected from the 0-30 cm layer, mixed together to produce one composite soil sample. Soil samples (total: 80) were immediately transferred to the laboratory for analysis. Additional undisturbed soil cores were sampled in the 0–30 cm mineral layer andsoil bulk density (BD) was measured (Black and Hartge, 1986). Soil organic carbon (SOC) was determined by the Walky and Black wet oxidation method (Nelson and Sommers, 1982).

The soil carbon storage (CS) was calculated by equation 1 (Qin et al., 2016):

$$\text{CS (t/ha)} = \text{SOC (\%)} \times \text{BD (gr/cm}^3) \times \text{SD (cm)} \times 10^{-1} \qquad \text{(Equation 1)}$$

where SOC is soil organic carbon, BD is soil bulk density and SD is soil depth (30 cm).

Measurements of the functional traits

In order to evaluate functional diversity at the plot level, several traits related to carbon storage were measured (Finegan et al., 2015; Ali and Yan, 2017). For different tree and shrub species, twenty well grown and without damage leaves were collected from the southern direction of the canopy. Samples were put into an ice box and transferred to the laboratory to measure the fresh and dry (48 hours in it at 70 ° C) leaf weight and the leaf area (mm^2). The leaf dry-matter content (LDMC) ($mg\ g^{-1}$) was calculated as the oven-dry mass (mg) of a leaf, divided by its fresh mass (g). Specific leaf area (SLA) was determined as fresh leaf (mm^2), divided by its oven-dry mass (mg) (Perez-Harguindeguy et al., 2013).

For each woody species, we collected one wood sample on ten individuals at 1 m height using a tree corer. These wood samples were dried in an oven at 105 °C for 24 hours (Henry et al., 2010). Wood density (WD) ($g\ cm^{-3}$) of each sample was obtained as the ratio of the dry weight divided by the volume which was measured using the change in volume after immersion in distilled water in a beaker (cm^3). The phosphomolybdic blue colorimetric technique (Anderson and Ingram, 1993) and Kjeldahl method (Bradstreet, 1965) were used to determine P and N concentration in leaves (LPC and LNC, respectively; $mg.g^{-1}$), respectively.

Calculation of taxonomic, structural and functional diversity indices

For the woody species, we calculated at plot level different taxonomic diversity indices including the number of woody species, the Shannon Wiener diversity index (H'), the Richness (S) and the Pielou's evenness (E) using the Ecological Methodology software, version 7.

The community weighted mean (CWM) trait values and the functional divergence index (FDvar) were used to determine the effects of dominant species (selection effect) and diversity (niche complementary effect) (Tahmasebi et al., 2017; Rawat et al., 2019).

CWM were calculated using the trait value of each woody species weighted by its abundance (Equation 2) whereas FDvar was computed using the variance among the traits values of the plant species recorded on a plot and weighted by the abundance of each species in the community (Equation 3) (Mason et al., 2005; Conti and Díaz, 2013; Ali et al., 2017; Wen et al., 2021).

$$CWM_x = \sum_{i=1}^{S} P_i \; T_i \quad \text{(Equation 2)}$$

$$FD_{var} = \frac{2}{\pi} \, arctan\,(5V) \; and \; V = \sum_{i=1}^{S} P_i \; (lnT_i - ln\mathrm{T})^2 \quad \text{(Equation 3)}$$

Where CWM_x is the CWM for trait x, S is the number of species in the community, Ti is the trait value for the i^{th} species, Pi is the relative abundance of the i^{th} species in the community, FDvar is the functional divergence index.

The structural indices of woody species including the mingling index (Equation 4), the height and diameter differentiation indices (Equation 5) were calculated using the following equations (Pommerening, 2002):

$$M_j = \frac{1}{n}\sum_{i=1}^{n} V_{ij} \quad M_j \epsilon \; [0, 1] \qquad \text{(Equation 4)}$$

where M_j is species mingling, n is the number of the nearest neighbors (n=3); $V_{ij} = 1$, if the reference tree j and neighbor tree i are different tree and shrub species and 0 otherwise. High values of this index represent a high species mixture or a high presence of other tree and shrub species.

In each plot, a woody species was randomly selected as the reference tree (i) and the three nearest neighbor woody species (j) were marked to compute the following indices (Equation 5):

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

$$T_{ij} = 1 - \frac{\min(DBHi\ .\ DBHj)}{\max\,(DBHi\ .\ DBHj)} \quad \text{or } T_{ij} = 1 - \frac{\min(Heigh\quad .\ Heightj)}{\max\,(Heighti\ .\ Heightj)} \qquad \mathrm{T_i} \in [0,\ 1] \qquad \text{(Equation 5)}$$

These equations were used for the three pairs of reference woody-neighbor woody species and the Tij indices were calculated as the mean of the three individual calculations. The higher value of the index (close to 1) indicate a higher diversity in terms of tree size.

Statistical analysis

Prior to statistical analysis, the assumptions of normality and homogeneity of variance were checked using the Shapiro-Walk test and Levene test, respectively. The effects of dieback intensity and management (protection vs. degradation) and their interactions on carbon storage were tested using general linear models (GLMs) followed by post-hoc Duncan's multiple range test. Pearson’s correlation coefficients were used to evaluate the relationships between soil carbon storage and structural, taxonomic and functional diversity indices. Stepwise multiple regressions between soil carbon storage and different diversity approaches were produced to predict the main factors affecting carbon storage. A principal component analysis (PCA, using PC-ORD version 5 sofware) using the various diversity indices was performed to visualize plots distribution along the first two axes of the analysis. We wanted to test if the various diversity indices (i.e. functional divergence, functional composition, taxonomic and structural indices) were efficient in segregating the different dieback intensity classes (no, low, moderate or high dieback intensity) in the two areas.

Results

Effect of dieback and management on soil carbon storage

Soil carbon storage was significantly influenced by the type of management, dieback intensity and their interaction (Table 1). Soil carbon stocks were significantly higher in the protected area (95.90 ± 4.62 t/ha) than in the degraded area (76.52 ± 2.04 t/ha) and peaked in the low dieback intensity class of the protected area (122.47 ± 10.12 t/ha), while no difference was found among the intensity classes in the degraded area (Figure 2).

Soil carbon storage was positively correlated with structural, functional diversity (i.e. FDvar of LDMC, H and WD) and taxonomic diversity indices except for species evenness (negative correlation). Similarly, all structural and taxonomic diversity indices with the exception of evenness, positively correlated with CWM of leaf phosphorus content (LPC) and specific leaf area (SLA), and negatively with CWM of LNC, H and LDMC. It was noteworthy that the examination of the correlation values with evenness revealed an exact opposite pattern as that observed with all structural and taxonomic diversity indices (Figure 3).

Models of soil carbon storage

We produced models of soil carbon storage using either functional, taxonomic or structural diversity indices as predictors. We found that all taxonomic diversity and all structural indices were included in the final models as well as almost all of the CWM traits (CWM-LPC, CWM-LNC, CWM-H, CWM-LDMC, and CWM-SLA). In contrast, for the functional divergence, only FDvar-WD was found significant. Considering all the models, FDvar-WD, CWM-LDMC, species richness (S) and mingling index (MI) were the best predictors of soil carbon storage for the different diversity approaches (i.e., functional divergence (FD), functional composition (FC), taxonomic diversity (TD) and structural diversity (SD)). Lastly, the final model taking into account all types of indices (total model) showed that the mingling index (MI) alone was the best model to predict changes in soil carbon storage ($R^2 = 0.173$; P-value = 0.002) along the dieback intensity and management gradients (Table 2).

Results of the PCA

Results of the principal component analysis (PCA) using all types of indices showed that the first two axes of the PCA represented a total variance of 78.37 % (59.48 % for the first axis and 18.89 % for the second axis). Projection of the plots showed that the degraded area was clearly separated from the protected area along the first axis while, there was no clear separation among the dieback intensity classes. Functional traits such as H, LNC, LDMC and species evenness were the most important to identify plots of the degraded area as a group whatever the dieback intensity class, while this role was played by diversity indices (MI, HD and DD) and species richness for plots of the protected area (Figure 4 and Table 3). PCA analyses were also achieved by using only one type of diversity approach (Appendix 1). By this method, we found that each approach was able to separate the protected area from the degraded area but especially when using the structural and CWM indices (Appendix 1a and 1b). In contrast, only the structural indices were able to segregate the different dieback intensity classes, especially in the protected area. Plots belonging to the low and moderate dieback intensity classes were characterized by similar mingling indices (Appendix 1d).

Discussion

Influence of management and dieback intensity on soil carbon storage

Our results clearly showed that soil carbon storage was higher in the protected area than in the degraded area. Carbon sequestration rate is closely related to a large variety of factors including taxonomic and structural characteristics of the forest stands (e.g. density, composition and species diversity), land use change, past management actions (e.g. intense or conservative measures), as well as soil properties (Lal, 2005; Jandl et al., 2007; Hammad et al., 2020; Tong et al., 2020). The woody forest vegetation obviously plays a very important role in soil carbon storage in sequestering atmospheric C in their wood biomass resulting from the process of photosynthesis (Brown and Pearce, 1994). A too intensive forest management can reduce the forest cover and limit the litter inputs, can decrease soil porosity by soil compaction or can enhance soil dryness and leading to erosion of the soil surface. All these processes can impair the forest production cycle and the storage of carbon in the soil (Upadhyay et al., 2005; Li et al., 2017). Land-use change, and particularly deforestation, by changing the predominant type of vegetation also effectively affects C fixation and soil respiration (Post and Kwon, 2000). Soil carbon storage is usually reduced and the soil carbon fluxes also modify due to profound changes in the nature and activity of soil CO_2 emitters (Dixon et al., 1994).We also noted a significant influence of dieback intensity on soil carbon storage. More precisely, the highest amount of soil carbon storage was observed in the low dieback intensity in the protected area wile no change was recorded in the degraded area. In the low dieback intensity class, only a small portion of the crown foliage (mainly leaves and twigs) was lost increasing the inputs in easily decomposable organic matter. This process could have increased soil carbon storage considering that all other environmental factors remained favorable due to the absence of marked disturbances in this protected area. In contrast, when dieback was more pronounced, the photosynthetic activity and growth were reduced which could have limited the amount the stabilized carbon in the biomass and eventually the soil (Ryan et al., 1997; Cook et al., 2008). Besides, in stands showing severe symptoms of dieback (i.e. with a large portion of the canopy dried up), the quantity and quality of litter inputs are likely to be changed (Cobb et al., 2013; Cobb and Rizzo, 2016). Microclimatic conditions are also modified particularly due to the reduction of the canopy cover. In particular, the exposition of the soil surface to direct sunlight is increased and the temperatures are more variable due to a loss of the buffering effect by the overstorey vegetation. These more instable conditions and reduced inputs of organic matter can limit soil microbial activity and decomposition which in turn limit soil carbon storage (Sanji et al., 2020; Karmakar et al. 2016; Berenstecher et al., 2020). Consistent with our results, Pandey et al. (2020) studying oak forests (*Quercus leucotrichophora*) in central Himalaya in degraded and undisturbed conditions, showed that degradation reduced tree density, tree biomass and consequently carbon sequestration up to 73% and total soil carbon storage up to 79%.

The humped-shape pattern of soil carbon storage along the dieback intensity gradient in the protected area is in line with the intermediate disturbance hypothesis (Connell, 1978). According to this hypothesis, ecosystem performance or ecosystem functions (such as soil C sequestration) are maximized at low to medium disturbance intensities, while at the beginning and end of the disturbance gradient (i.e. the control and the high dieback intensity in this study) they are reduced. In our semi-arid oak forests and in absence of marked degradation, a minimal disturbance such as a low defoliation comparable to a moderate natural pruning can reduce intra- and interspecific competition and increase ecosystem function (Lin et al., 2018; Bai et al., 2020).

Modeling soil carbon storage according to different diversity approaches

The establishment of such relationships between species diversity and structural features of the plant community and ecosystem functions is of a high interest to investigate key processes like productivity or nutrient retention (e.g. Chen, 2006). It is noteworthy that the mingling index (a structural index strongly associated with the changes in tree species proportions) (Keren et al., 2020) can be a suitable index in expressing the amount soil carbon change because different woody species have not same potential in litter (quality and quantity) production (Joly et al., 2017; Cakır and Makineci, 2020; Heydari et al., 2020 b). The existence of positive relationships between structural indices (mingling or DD and HD) and soil carbon storage clearly supports the niche complementarity hypothesis and emphasizes the positive role of diversity in forest structural features on ecosystem functions as reported by previous other studies (Lin et al., 2016; Fotis et al., 2018). This result can be explained by considering the influence of the forest structure on soil processes. In fact, soil carbon content is closely related to the composition and activity of microorganisms involved in the decomposition process, which is controlled for a part by the composition and structure of the stand (Van der Heijden et al. 1998; Tedeschi et al., 2006). Forest dieback negatively affects soil carbon storage by eliminating some sensitive species, as shown by a clear variation of mingling index value, and by changing stand structural characteristics as shown by previous studies (Aynekulu et al., 2011; Tenzin and Hasenauer, 2016). Modification of the species composition also implies a variation in biomass accumulation and litter production which affect carbon storage in the ecosystem (e.g. Chen, 2006; Vesterdal et al., 2013). The role played by structural indices is also more clearly visible along a gradient of dieback intensity: when the dieback is pronounced, stand composition and structure are likely to be largely modified (Martin et al., 2015; Renne et al., 2019) and soil carbon storage affected (Spielvogel et al., 2009; Xiong et al., 2011). Similarly, taxonomic diversity indices are more efficient predictors of soil carbon storage along the dieback intensity gradient than functional diversity indices. A possible explanation can be a large functional redundancy among the species in our study area. The role played by a specific species is also supported by other species, consequently the value of the functional index may remain stable even if the species is removed from the community. Under these conditions, the evenness index, which depends on the percentages of presence of the different species, can be more efficient in showing the effect of different dieback intensities on ecosystem functions (Omidipour et al., 2021). However, in the intense dieback intensity class where many species are eliminated, the species richness index also performs well.

Woody species evenness was negatively related to soil carbon storage and previous studies have also reported negative relationships between evenness and various ecosystem functions (Wilsey and Potvin, 2000; Kardol et al., 2010; Vance-Chalcraft et al., 2010; Van Con et al., 2013) while no significant relations were found in other studies (Weiher and Keddy, 1999; van Rooijen et al., 2015). These apparently contradictory results may be explained by the differences in the ecosystems and in the functions under study. In this regard, Omidipour et al. (2021) reported negative relationships between evenness and ecosystem functions in steppe-desert and semi-steppe regions but no significant relationships in Mediterranean rangelands of central Iran. In general, evenness plays a more important role in areas where dominant species have a greater contribution in ecosystem functions (Maestre and Reynolds, 2006; Omidipour et al., 2021). In these areas, the increase in evenness which negatively influences ecosystem functions, is usually controlled by the decrease in the abundance of the dominant species and the increase in the abundance of other plants (Omidipour et al., 2021). These findings are consistent with the mass ratio hypothesis. This hypothesis proposes that the rate of an ecosystem function such as biomass production is primarily determined by the traits of the dominant species. The evenness index is sensitive to variation of frequency rather than the number of species (Chapin Iii et al., 2000; Wilsey and Potvin, 2000). In our study area, oak is the by far the dominant woody species which frequency is primarily affected by the forest dieback, this can explain why evenness is a significant predictor of ecosystem functions (Mulder et al., 2004).

Among all the community-weighted mean (CWM) traits, CWM-LDMC showed a negative relationship with soil carbon storage. In the degraded area with a low soil carbon storage, the dominant oak trees are old and large and produce thick lignin-rich leaves explaining high LDMC values (König et al., 2018). Some studies indicated that high LDMC values in a community are related to the predominance of conservative species growing in a low-production environment similar to the degraded area in this study (Garnier et al., 2004; Finegan et al., 2015). The SLA index was positively correlated with soil carbon storage. Leaf is the most important carbon-stabilizing organ during photosynthesis and therefore leaf properties have a high ability to predict carbon storage (Tahmasebi et al., 2017). Functional characteristics of plants related to photosynthetic such as CWM-SLA play an important role in ecosystem carbon storage and carbon balance (De Deyn et al., 2008; Finegan et al., 2015). Therefore, the high CWM-SLA values of wood species in the protected area at low dieback intensity can be related to an enhanced photosynthetic efficiency explaining a positive effect on ecosystem carbon storage.

The combined use of all diversity assessment approaches was able to separate management conditions (the degraded vs. protected area) but not the different dieback intensity classes. Used separately, each approach –but especially the structural and CWM approaches- was effective in separating protected and degraded areas. However, only structural indicators proved efficient in segregating the different dieback intensities, especially in the protected area. These results put forward that most diversity indices and trait values are primarily influenced by anthropogenic disturbances and management actions while the effect of dieback is less pronounced at least at low intensity.

Conclusion

In this study, we have investigated the predictability of soil carbon storage by taxonomic, functional and structural diversity approaches under different management conditions (protected vs. degraded) and along a dieback intensity gradient. We found that soil carbon storage was clearly improved in the preserved area compared to the degraded area and was the highest in the low dieback intensity class of the protected area. This result emphasizes the positive role played by a moderate disturbance which can reduce intra- and interspecific competition and maximize ecosystem function in line with the intermediate disturbance hypothesis. The structural diversity indices were the best predictors of soil carbon storage followed by the taxonomic diversity and functional composition indices, in contrast to the functional divergence indices. Therefore, the use of such structural diversity indices can be efficient tools to increase our understanding of changes in soil carbon storage which represents a key ecosystem function in semiarid forests. Besides, the positive correlation of the structural, composition and taxonomic diversity indices as well as the negative correlation of species evenness and functional composition (CWM of LNC, H and LDMC) with soil carbon storage provide evidence to support both the mass-ratio and niche complementary hypotheses.

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Authorship contribution statement

Mona Karami: Data curation, Investigation, Writing-original draft; **Ali Sheykholeslami**: Supervision, Investigation, Writing-review & editing; **Mehdi Heydari**: Conceptualization, Methodology, Data curation, Resources, Formal analysis, Software, Visualization, Supervision, Writing -original draft, Writing -review & editing; **Majid Eshagh Nimvari**: Writing -review & editing; **Reza Omidipour**: Formal analysis, Software, Writing -original draft, Writing -review & editing; **Bernard Prevosto**: Writing -review & editing.

Conflicts of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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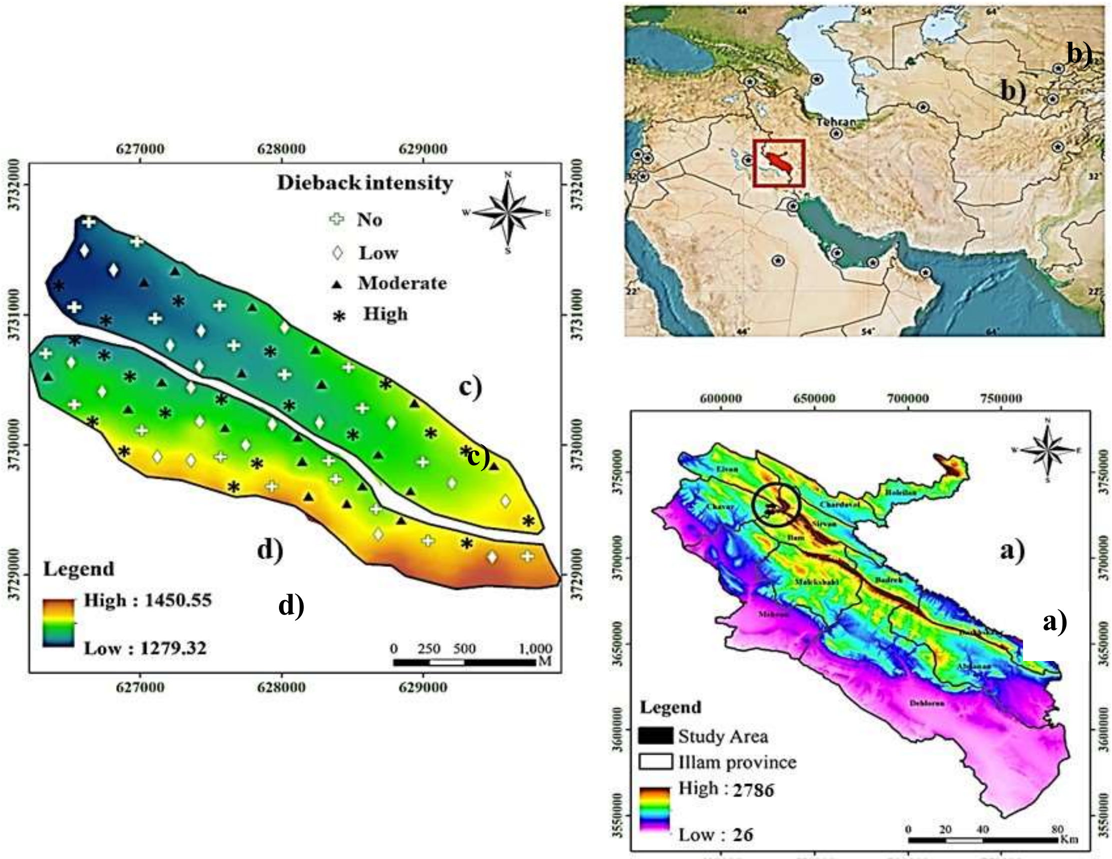


Fig 1. Location of the study area in Ilam province (a), west of Iran (b), the degraded area (c) and the protected area (d).

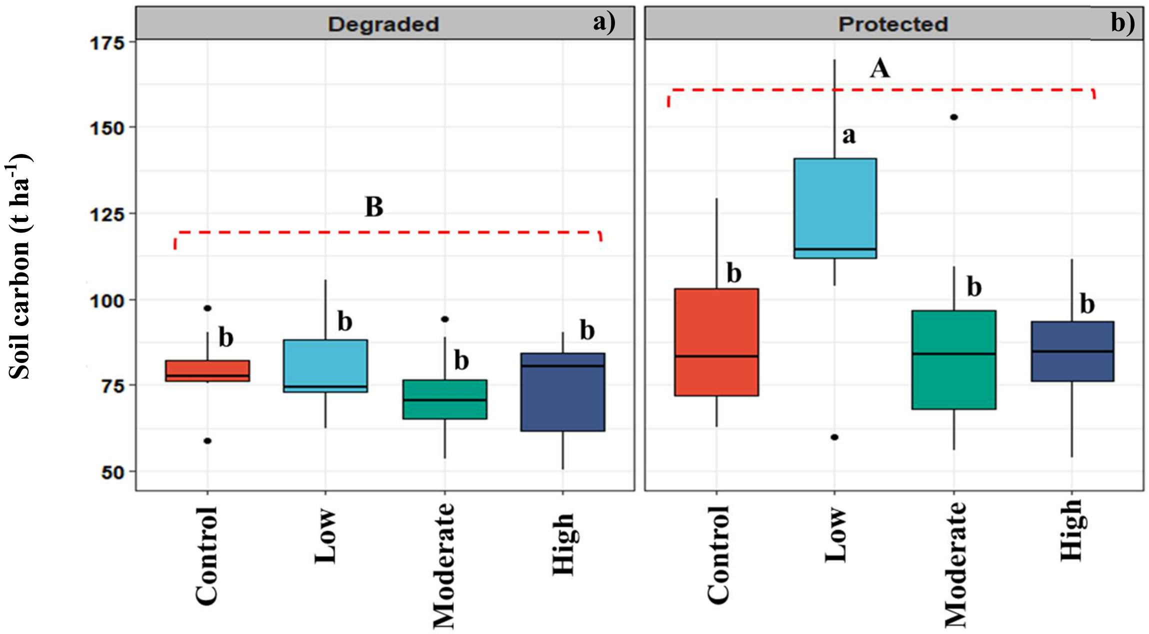


Fig 2. Comparison of the mean soil carbon storage between the different dieback intensity classes in degraded (a) and protected (b) areas. Uppercase letters indicate significant differences between the two areas and lowercase among the intensity classes within the same area (Duncan's multiple range test).

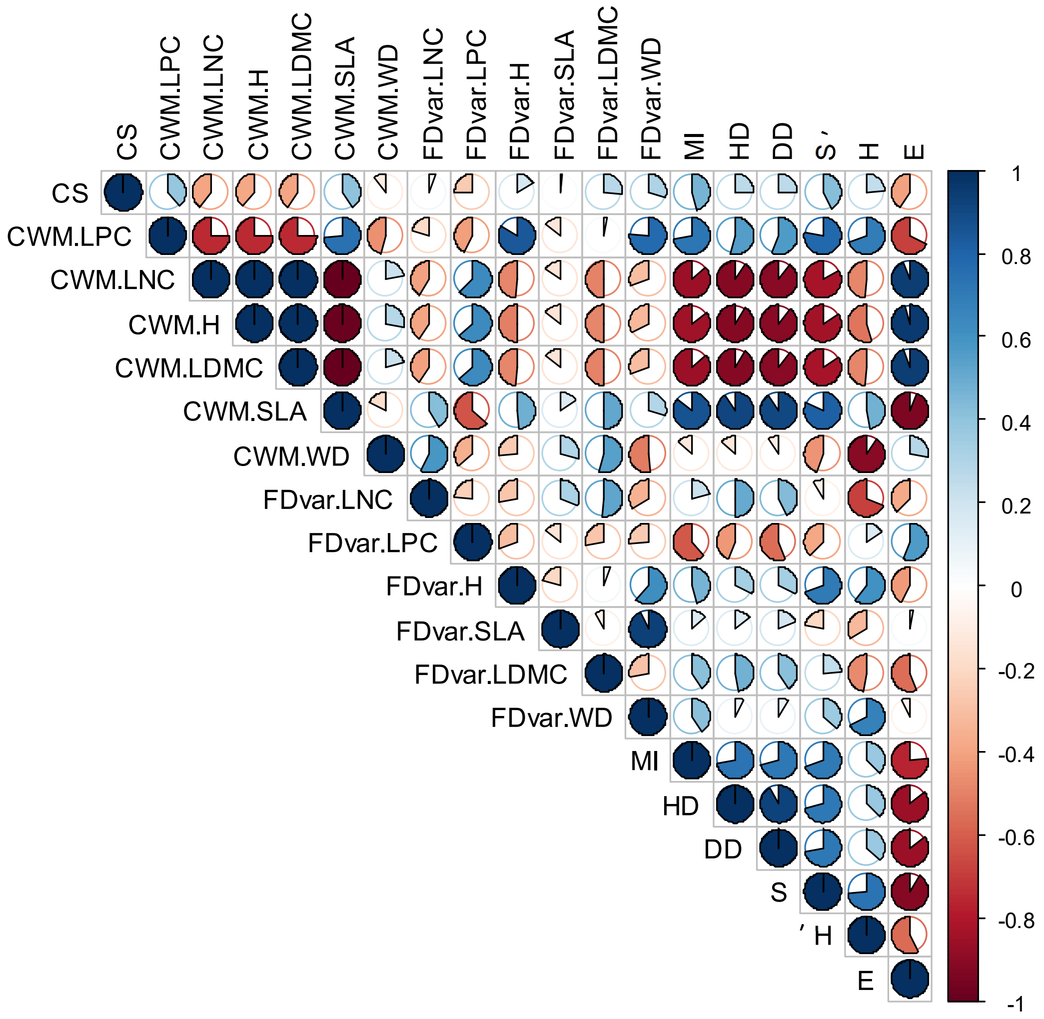


Fig 3. Heat map for Pearson's correlation coefficients between soil carbon storage and structural, taxonomic and functional diversity indices; the color and size of the pie chart denotes the magnitude and direction of the relationship (red and blue circles represent negative and positive correlation, respectively); CS: carbon storage, CWM: community weighted mean, Fdvar: functional divergence, LPC: leaf phosphorus concentration, LNC: leaf nitrogen concentration, H: mean of woody species height, LDMC: leaf dry-matter content, SLA: specific leaf area, WD: wood density, MI: mingling index, HD: height differentiation, DD: diameter differentiation, S: Richness , H′: Shannon–Wiener index and E: evenness

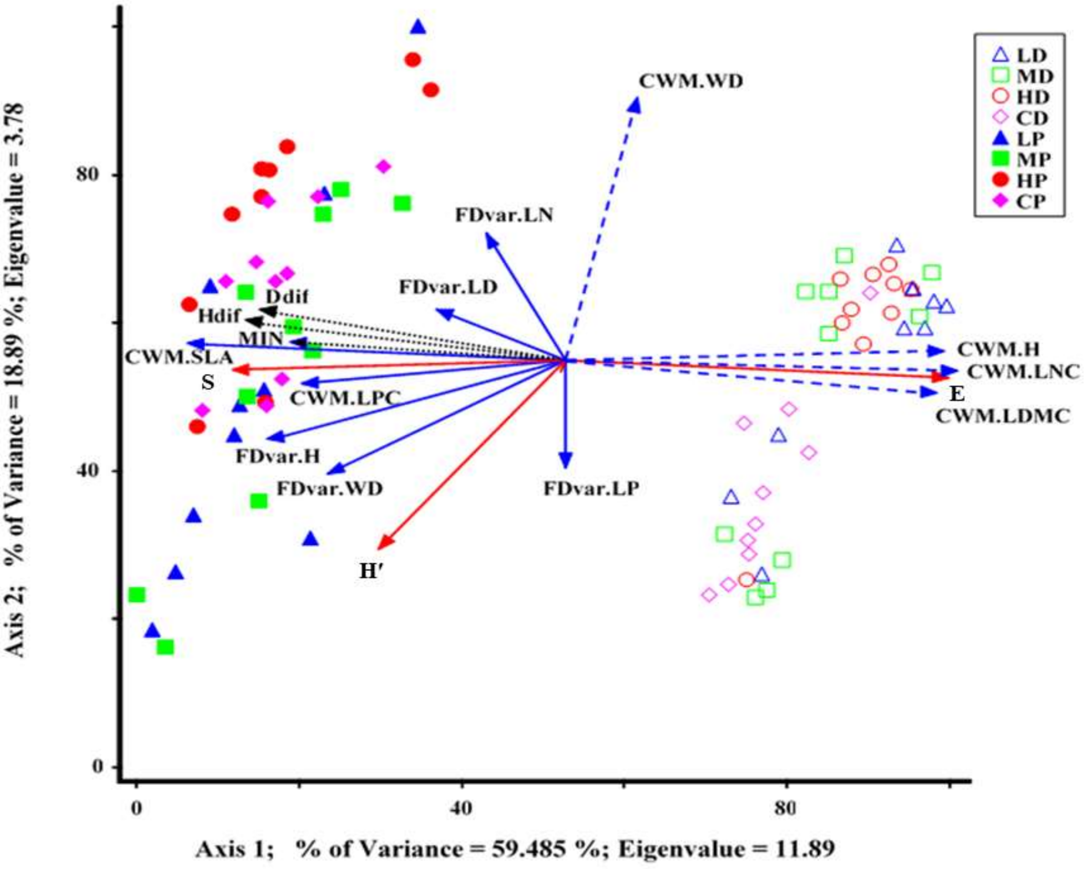
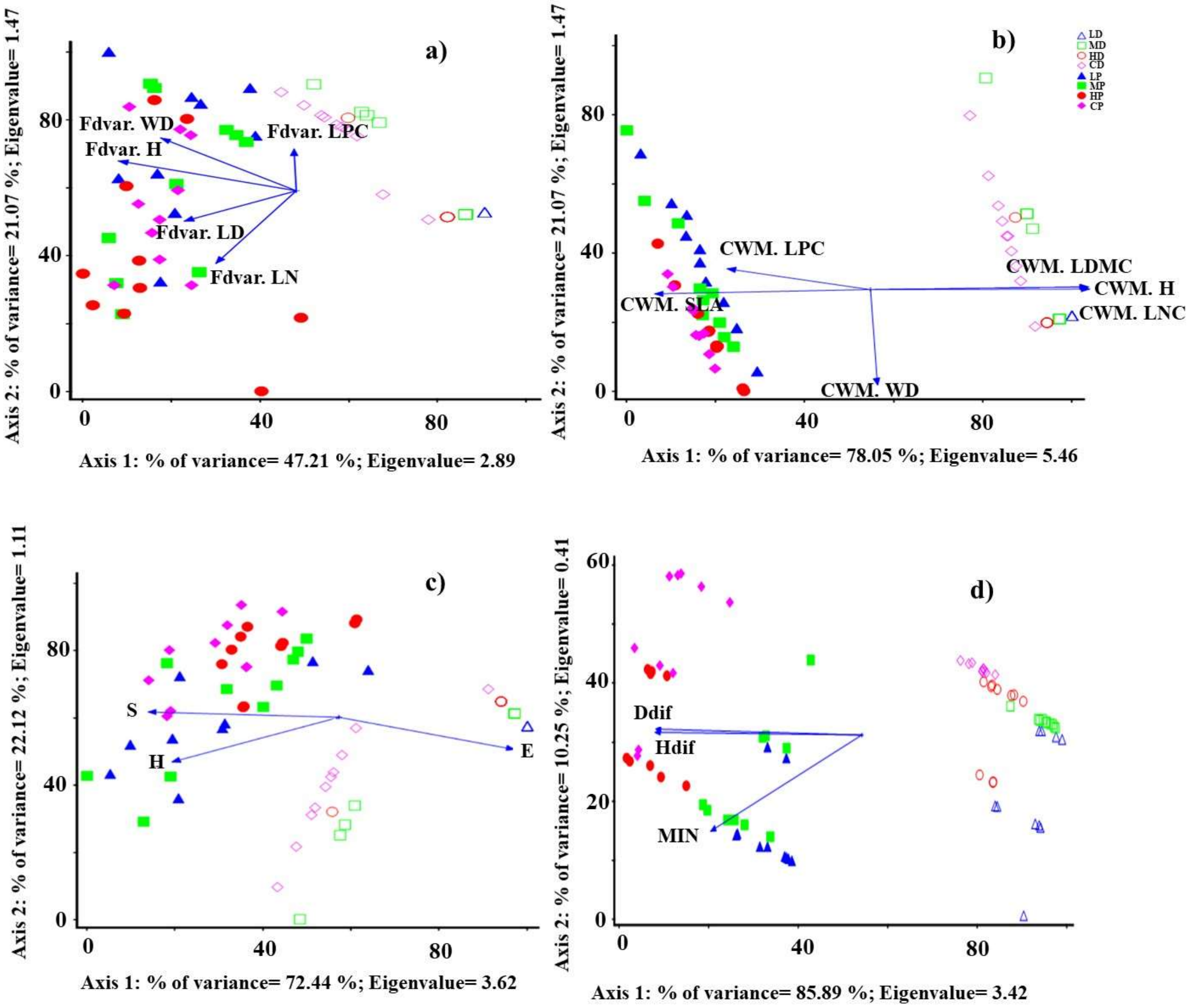


Fig 4. Principal Component Analysis (PCA) ordination diagram showing the distribution of the plots along the first two axes based on all diversity approaches i.e. including functional divergence of woody species (solid blue arrows), functional composition of woody species (blue dotted arrows), taxonomic diversity (solid red arrows) and structural diversity of woody species (black dotted arrows); CWM: community weighted mean, FDvar: functional divergence, LPC: leaf phosphorus concentration, LNC: leaf nitrogen concentration, H: mean of woody species height, LDMC: leaf dry-matter content, SLA: specific leaf area, WD: wood density, MI: mingling index, HDif: height differentiation, Ddif: diameter differentiation, S: Richness , H′: Shannon–Wiener index and E: evenness. Plots are identified by two letters, the first letter refers to the dieback intensity class (L, M, H, C) i.e. low, medium, high or control (no dieback), while the second letter (D, P) refers to the degraded or protected area. Blank and solid symbols indicate degraded and protected areas, respectively.



Appendix 1. Principal Component Analysis (PCA) ordination diagrams showing distribution of the plots along the first two axes when using only one diversity approach; functional divergence (a), functional composition (b), taxonomic diversity indices (c) and structural indices (d); CWM: community weighted mean, Fdvar: functional divergence, LPC: leaf phosphorus concentration, LNC: leaf nitrogen concentration, H: mean of woody species height, LDMC: leaf dry-matter content, SLA: specific leaf area, WD: wood density, MI: mingling index, HDif: height differentiation, Ddif: diameter differentiation, S: Richness , H′: Shannon–Wiener index and E: evenness. Plots are identified by two letters, the first letter refers to the dieback intensity class (L, M, H, C) i.e. low, medium, high or control (no dieback), while the second letter refers (D and P)

to the degraded or protected area. Blank and solid symbols indicate degraded and protected areas, respectively.

Table 1. Results of the GLM with dieback intensity, management and their interaction as fixed factors and soil carbon storage as dependent variables. The statistics are degrees of freedom (df), mean square (MS), F-value (F) and levels of significance (*** P < 0.001, ** P < 0.01, * P < 0.05).

Source of variation	**soil carbon storage**		
	df	**MS**	**F**
Dieback intensity	3	2229.2	5.40***
management	1	7556.7	18.31***
Dieback intensity × Dieback intensity	3	1124.5	2.71 *

Table 2. Results of multiple regressions between soil carbon storage and different diversity approaches (functional divergence (FD), functional composition (FC), taxonomic diversity (TD) and structural diversity (SD))

Diversity approaches	**Variable included in the multiple regression**	**The final model**	**R^2**	**p**
FD	FDvar-WD	CS = 86.27 FDvar-WD + 72.77	0.088	**0.034**
FC	CWM-LPC, CWM-LNC, CWM-H, CWM-LDMC, CWM-SLA	CS = - 0.034 CWM-LDMC + 96.23	0.158	**0.000**
TD	S, H′, E	CS = 6.76 S + 68.76	0.173	**0.000**
SD	MI, HD, DD	CS = 27.21 MI + 74.26	0.214	**0.000**
Total model	**FDvar-WD, CWM-LDMC, S, MI**	**CS = 27.28 MI + 75.28**	**0.173**	**0.002**

CS: carbon storage, CWM: community weighted mean, FDvar: functional divergence, LPC: leaf phosphorus concentration, LNC: leaf nitrogen concentration, H: mean of woody species height, LDMC: leaf dry-matter content, SLA: specific leaf area, WD: wood density, MI: mingling index, HD: height differentiation, DD: diameter differentiation, S: Richness, H′: Shannon–Wiener index and E: evenness

Table 3. Pearson's coefficients of correlation between PCA scores and the different diversity indices

Diversity approache	**Indices**	**PC 1**	**PC 2**
Functinal compositio	CWM.LPC	-0.8 **	-0.25
	CWM.LNC	0.968 **	-0.22
	CWM.H	0.98 **	-0.16
	CWM.LDMC	0.968 **	-0.22
	CWM.SLA	-0.96 **	0.248
	CWM.WD	0.419 *	0.844 **
Functinal divsersity	FDvar.LNC	-0.44 *	0.587 *
	FDvar.LPC	0.001	-0.54 *
	FDvar.H	-0.89 **	-0.35
	FDvar.SLA	-0.14	0.33
	FDvar.LDMC	-0.56 *	0.370
	FDvar.WD	-0.76 **	-0.55 *
Structural diversity	MI	-0.82 **	0.224
	Hdif	-0.88 **	0.305
	Ddif	-0.87 **	0.314
Taxonomic diversity	R	-0.9 **	-0.16
	H′	-0.68 *	-0.72 **
	E	0.956 **	-0.11

Note: * and ** represent significant correlation at 0.05 and 0.01; CWM: community weighted mean, Fdvar: functional divergence, LPC: leaf phosphorus concentration, LNC: leaf nitrogen concentration, H: mean of woody species height, LDMC: leaf dry-matter content, SLA: specific leaf area, WD: wood density, MI: mingling index, HDif: height differentiation, Ddif: diameter differentiation, S: Richness, H′: Shannon–Wiener index and E: evenness