

Dieback intensity but not functional and taxonomic diversity indices predict forest productivity in different management conditions: Evidence from a semi-arid oak forest ecosystem postprint

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Abstract

The relationships between different aspects of diversity (taxonomic, structural and functional) and the aboveground biomass (AGB) as a major component of global carbon balance have been studied extensively but rarely under the simultaneous influence of forest dieback and management. In this study, we investigate the relationships between taxonomic, functional and structural diversity of woody species (trees and shrubs) and AGB along a gradient of dieback intensity (low, moderate, high and no dieback as control) under two contrasted management conditions (protection by central government vs. traditional management by natives) in a semi-arid oak (*Quercus brantii* Lindl.) forest ecosystem. AGB was estimated and taxonomic diversity, community weighted average (CWM) and functional divergence indices were produced. We found that the aerial biomass was significantly higher in the intensively used area ($14.57 (\pm 1.60) \text{ t/hm}^2$) than in the protected area ($8.70 (\pm 1.05) \text{ t/hm}^2$) due to persistence of some large trees but with decreasing values along the dieback intensity gradient in both areas. CWM of height (H), leaf nitrogen content (LNC) and leaf dry matter content (LDMC) were also higher in the traditional managed area than in the protected area. In contrast, in the protected area, the woody species diversity was higher and the inter-specific competition was more intense, explaining a reduced H, biomass and LDMC. Contrary to the results of CWM, none of the functional diversity traits (FDvar) was affected by dieback intensity and only FDvar values of LNC, leaf phosphorus content (LPC) and LDMC were influenced by management. We also found significantly positive linear relationships of AGB with CWM and FDvar indices in the protected area, and with taxonomic and structural diversity indices in the traditional managed

area. These results emphasize that along a dieback intensity gradient, the leaf functional traits are efficient predictors in estimating the AGB in protected forests, while taxonomic and structural indices provide better results in forests under a high human pressure. Finally, species identity of the dominant species (i.e., Brant's oak) proves to be the main driver of AGB, supporting the selection effect hypothesis.

Full Text

Preamble

Dieback intensity but not functional and taxonomic diversity indices predict forest productivity in different management conditions: Evidence from a semi-arid oak forest ecosystem

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Abstract: The relationships between different aspects of diversity (taxonomic, structural and functional) and aboveground biomass (AGB) as a major component of global carbon balance have been studied extensively but rarely under the simultaneous influence of forest dieback and management. In this study, we investigate the relationships between taxonomic, functional and structural diversity of woody species (trees and shrubs) and AGB along a gradient of dieback intensity (low, moderate, high and no dieback as control) under two contrasted management conditions (protection by central government vs. traditional management by natives) in a semi-arid oak (*Quercus brantii* Lindl.) forest ecosystem. AGB was estimated and taxonomic diversity, community weighted average (CWM) and functional divergence indices were produced. We found that aerial biomass was significantly higher in the intensively used area ($14.57 (\pm 1.60) t/hm^2$) than in the protected area ($8.70 (\pm 1.05) t/hm^2$) due to persistence of some large trees but with decreasing values along the dieback intensity gradient in both areas. CWM of height (H), leaf nitrogen content (LNC) and leaf dry

matter content (LDMC) were also higher in the traditional managed area than in the protected area. In contrast, in the protected area, the woody species diversity was higher and the inter-specific competition was more intense, explaining a reduced H, biomass and LDMC.

Contrary to the results of CWM, none of the functional diversity traits (FDvar) was affected by dieback intensity and only FDvar values of LNC, leaf phosphorus content (LPC) and LDMC were influenced by management. We also found significantly positive linear relationships of AGB with CWM and FDvar indices in the protected area, and with taxonomic and structural diversity indices in the traditional managed area. These results emphasize that along a dieback intensity gradient, the leaf functional traits are efficient predictors in estimating the AGB in protected forests, while taxonomic and structural indices provide better results in forests under high human pressure. Finally, species identity of the dominant species (i.e., Brant's oak) proves to be the main driver of AGB, supporting the selection effect hypothesis.

Keywords: environmental stress; sudden oak dieback; degradation; conservation; selection effect hypothesis

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1 Introduction

Forests in many regions worldwide are exposed to numerous destructive anthropogenic factors, putting at risk their biomass production and main ecosystem functions. Since 2000, a dangerous phenomenon called oak (*Q. brantii*) decline has occurred in many oak forests globally, especially in the Mediterranean region. In this respect, a gradual dieback of semi-arid oak formations was observed in the Zagros forests of western Iran, which are among the oldest oak forest reserves in the world with remarkable ecological value.

Although the exact cause of this forest dieback has not been determined, most studies have emphasized the role of climate change (particularly prolonged drought periods), habitat degradation (including depletion of soil nutrients and moisture), non-adaptive management, and pest and disease outbreaks. The impact of forest dieback on growth and biomass accumulation is influenced by a wide set of factors, among which species diversity can play a significant role. For instance, severe droughts can significantly reduce tree growth and biomass accumulation, though this effect varies according to tree diversity in different

biomes. In general, most researchers agree upon a positive relationship between forest biomass production and tree species diversity, although changes in direction or absence of a relationship can also occur. This process can be explained by complementarity in ecological traits among species and underlines the concept of functional diversity (FD) that refers to the amount, range, distribution and relative frequency of functional characteristics of species in an ecosystem. In a forest system, functional traits and structural characteristics of forest stands (such as diameter and height differentiation of trees) could influence ecosystem functions (e.g., AGB) along with abiotic factors, human activities and natural disturbances.

However, numerous studies have recorded variation in diversity-ecosystem function relationships based on forest ecosystem type, which can be negative or positive. This apparent lack of consistency indicates that various factors such as heterogeneity of habitat environmental conditions, type and structure of vegetation, geographical scale, management measures, land use change and interactions with climate can affect the relevant mechanisms influencing diversity-ecosystem function relationships.

In general, the relationships between species diversity and traits with different ecosystem functions can be expressed using two main hypotheses: the niche complementarity and the selection effect hypotheses. The niche complementarity hypothesis assumes that communities with functionally diverse species are better able to use limited environmental resources. Differences in functional characteristics reduce species niche overlap in capturing available resources, leading to maximization of matter transformation and energy flux processes. On the other hand, in the selection effect hypothesis, the effects of a species' relative abundance in the community on ecosystem function are predominantly influenced by dominant species that present more efficient functional traits compared with other plants. This implies that ecosystem functions are controlled by the presence or absence of dominant species, whereas addition or elimination of other plants does not greatly influence ecosystem function. Studies supporting these hypotheses have used indices based on frequency and value of functional traits such as functional divergence (FDvar) and community weighted mean (CWM) of trait values. For example, carbon and AGB storage are positively correlated to the CWM of trees with high potential maximum diameter because these trees can use more environmental resources and be more efficient competitors.

Both functional and taxonomic diversity, by reflecting stand structure, can be efficient indicators of AGB. Additionally, forest structure plays a major role in determining ecosystem function, so any factor that changes this structure (including forest dieback) can alter the diversity-biomass relationship, although this point requires further investigation in disturbed forest systems. More research on diversity-ecosystem function relationships in different ecosystems is needed, particularly to understand how these relationships are affected by changing natural forest structure, management practices and natural and anthropogenic disturbances. In this study, we investigate the relationships between functional,

taxonomic and structural diversity of woody species and AGB in a semi-arid oak forest of western Iran. We hypothesize that these relationships can be influenced by dieback intensity and management conditions. More specifically, our questions are: (1) Is the effect of dieback intensity on AGB and biotic indices (taxonomic, functional and structural diversity) affected by management conditions? Two contrasted management conditions were tested: protection vs. traditional management. (2) How much variation in ecosystem production can be explained by taxonomic, functional and structural diversity characteristics along a gradient of dieback intensity under different management conditions? (3) Which is the best combination of multiple metrics of taxonomic, functional and structural diversity regarding dieback intensity under different management conditions? And (4) can the relationships between taxonomic, functional and structural diversity and AGB be expressed by the niche complementarity and selection effect hypotheses?

2.1 Study area

This study was conducted in oak forests of Ilam City in western Iran known as Zagros forests, which are among the oldest continuous oak forests in the world. For this purpose, two adjacent forest areas with the same flat physiographic conditions (altitude range 1279–1450 m a.s.l. and generally flat topography; average slope <20%) were selected and named according to their level of disturbance and management conditions: traditional management by natives and protected area (government protection). Both areas were initially composed of dense forest cover based on documents from the Natural Resources Office and interviews with natives.

The selected forest areas were exposed to human disturbances (e.g., firewood exploitation, grazing and land-use change), but with some differences between the two areas. Before protection enforcement in the protected area, many large trees were cut down to extract large quantities of wood biomass to meet various population needs (particularly by migrant populations, charcoal smugglers and temporary ranchers). In contrast, the traditional managed area has been used by nomads and neighboring rural areas for agriculture and animal husbandry. Management of this forest area followed traditional practices: large trees were preserved mostly because they provided shade for temporary structures (huts and tents), and their high acorn production was used for livestock feeding. In contrast, coppice oak and remaining small woody species like *Crataegus pontica* K. Koch, *Cerasus microcarpa* (C. A. Mey.) Boiss. and *Daphne mucronata* Royle were regularly cut (mostly for firewood and for making livestock hedges).

In the protected area today, degradation was mostly related to war refugees, non-foresters, and wood and coal smugglers. These people did not understand the need to preserve dominant, ancient and large trees such as seed-origin oak and pistachio trees. Consequently, many large trees were cut, gradually developing oak coppice forms. After a period of intense exploitation, ownership conditions changed in the protected area: lands were reclaimed from private ownership by

the Natural Resources Office after implementation of national policies in 1963. Following this, protection measures were applied. The area was fenced and supervised by forest guards to prevent disturbing factors (e.g., fire, grazing and logging). In contrast, the traditional managed area continued to be exploited traditionally by local people and nomads.

The dominant species in these forests is Brant's oak (*Quercus brantii*) associated with different woody species such as *Pistacia atlantica* Desf., *Acer monspessulanum* subsp. *cinerascens* (Boiss.) Yalt., *Crataegus pontica* K. Koch, *Cerasus microcarpa* Andr. ex DC and *Daphne mucronata* Royle. In the traditional managed area, large old oak and pistachio trees were often present, while other woody species were very rare. Since 2001, a phenomenon called oak dieback occurred in the Zagros forests, including our study area, leading to drying of trees, especially oaks, with different intensities. Factors causing this forest decline are not exactly known but are supposed to be linked to climate change, particularly recurrent and prolonged drought periods. Trees with symptoms of decline of different intensities are scattered throughout the study area, with oak being the main affected species.

The most abundant soil types based on FAO classification are Lithosols—shallow soils with low fertility and low water holding capacity. According to climatic data (1999–2015) from the nearest meteorological station (Eyvan station, 33°45' N and 46°21' E; 1320 m a.s.l.), mean annual precipitation and annual mean temperature are 653 mm and 17°C, respectively. This region is described as sub-Mediterranean with high seasonality in monthly precipitation distribution. More than 50% of precipitation occurs in winter, 32% in autumn and 14% in spring, while the summer period (May–October) is particularly dry.

2.2 Experimental design

The two forest areas (traditional managed and protected) were sampled using 80 plots of 1000 m² (40 plots in each area, with distances between plots varying from 500 to 1000 m) distributed across four forest dieback classes (10 plots per class in each area). First, in each plot, the ratio of dried canopy part to total crown of each tree was determined visually as a measure of dieback intensity (I) and then weighted by the frequency (F) of the tree species (percentage of crown cover). Finally, dieback intensity of each plot was determined from the total weighted dieback of all individuals in the plot (Eq. 1) and categorized into four classes: no, low, moderate and high dieback (Table 1; Fig. 2).

$$DI = \sum_i I_i F_i$$

where DI is the total dieback intensity in each plot; I_i and F_i are the dieback intensity and frequency of species i , respectively. The resulting DI values were used to establish four classes: $0\% \leq DI < 10\%$, no dieback; $10\% \leq DI < 35\%$, low dieback; $35\% \leq DI < 65\%$, moderate dieback; $65\% \leq DI \leq 100\%$, high intensity dieback (Table 1).

2.3 Estimation of AGB

We measured diameter at breast height (DBH) and height (H) of all woody species in each plot. In the absence of models to estimate AGB for our species and conditions, AGB of each woody species with DBH ≥ 5 cm was estimated using an allometric relationship (Eq. 2) by Chave et al. (2014). This model covers a wider range of tree sizes (DBH), a site-specific environment stress factor (EF) and wood density ($WD, g/cm^3$). Final AGB was obtained by summing all individuals.

$$AGB = \exp\{-1.803 - 0.976(EF) + 0.976 \times \ln(H) + 2.673 \times \ln(DBH) - 0.0299 \times (\ln(DBH))^2\} \quad (2)$$

EF and climatic water deficit (CWD) were computed using Equations 3 and 4 (Chave et al., 2014).

$$CWD = \min(0, PET - P) / TS$$

where TS is temperature seasonality: the standard deviation (SD) of monthly mean temperature over a year, expressed in degrees Celsius multiplied by 100; PS is precipitation seasonality: the standard deviation (SD) of monthly mean precipitation over a year, expressed in millimeters multiplied by 100; CWD is climatic water deficit computed by summing the difference between monthly precipitation (P_i) and monthly evapotranspiration (ET_i), only when this difference is negative. In our conditions, EF was equal to 2.086.

2.4 Measurement of functional traits

To measure functional diversity at plot level, we selected and measured traits directly related to AGB according to previous studies. For each woody species, two branches from different crown height classes (bottom, middle and top) were selected from the south-facing part of the crown, and twenty well-grown, undamaged leaves were sampled. Leaves were immediately stored in an ice box after labeling for laboratory measurements. In the laboratory, fresh weight and dry weight (48 h at 70°C) were measured (± 0.01 g). Fresh leaf area (mm^2) were measured using a leaf area meter (Model CI-203, CIDBio - Science Inc., Camas, WA). Leaf density was determined as the ratio of dry weight to volume measured using volume change after immersion in distilled water. LPC and LNC (mg/g) were determined using the phosphomolybdic blue colorimetric technique and Kjeldahl method, respectively.

2.5 Measurements of taxonomic, structural and functional diversity indices

To quantify woody species (trees and shrubs) diversity at plot level, we used three indices including species richness (number of woody species per sample or S), Shannon-Wiener diversity index (H'; Eq. 5) and evenness (E; Eq. 6).

$$H' = -\sum_{i=1}^S p_i \ln p_i$$

$-\ln(\sum_{i=1}^S p_i^2)$

where p_i is the proportion of species i and S is the total number of woody species. To distinguish effects of dominant species (selection effect) and diversity (niche complementarity), we used two indices: CWM and FDvar. CWM was calculated as the mean trait value in the community, weighted by species abundance. FDvar was computed using variance among trait values of plant species recorded on a plot, weighted by each species' abundance in the community. Two structural indices of woody species were produced at plot level. The species mingling index was calculated using Equation 7:

$$M_j = \frac{1}{n} \sum_{i=1}^n V_{ij}$$

where M_j is the species mingling index; n is the number of nearest neighbors ($n=3$); $V_{ij}=1$ if reference tree j and neighbor tree i are different species, otherwise $V_{ij} = 0$. Lower values reflect purity or very low presence of other woody species.

Height and diameter differentiation index (T_{ij}) were calculated following Equation 8. In each plot, a woody species was randomly selected as the reference tree (i) and the three nearest neighbor woody species (j) were determined.

$$T_{ij} = \frac{\min(\text{DBH}_i, \text{DBH}_j)}{\max(\text{DBH}_i, \text{DBH}_j)} + \frac{\min(\text{Height}_i, \text{Height}_j)}{\max(\text{Height}_i, \text{Height}_j)}$$

$$T_{ij} = \frac{\min(\text{DBH}_i, \text{DBH}_j)}{\max(\text{DBH}_i, \text{DBH}_j)} + \frac{\min(\text{Height}_i, \text{Height}_j)}{\max(\text{Height}_i, \text{Height}_j)}$$

These equations were used for three pairs of reference-neighbor woody species and T_{ij} indices were obtained as the mean of three individual calculations. Higher values (close to 1) indicate greater diversity in tree size.

2.6 Statistical analysis

After examining normality (Shapiro-Wilk test) and homogeneity of variance (Levene test) preconditions, effects of management (protection vs. traditional management), dieback intensity and their interactions on CWM, FDvar and structural/diversity indices were tested using two-way ANOVA. Post-hoc tests were applied using t-student and Duncan tests. Linear regression was used to predict AGB as a function of structural, taxonomic and functional diversity indices. All variables were standardized ($\min=0$ and $SD=1$) to improve interpretability of regression coefficients. To detect the best combination of AGB predictors including taxonomic (richness, Shannon-Wiener diversity and evenness), functional composition and structural diversity (height, diameter differentiation and mingling) indices and dieback intensity, multiple linear mixed models were produced using nlme R package. To select the best indices in AGB predictors, relative importance was calculated using MuMIn R package and introduced to structural equation modeling (SEM) using lavaan R package. As many sampling plots in the traditional managed area contained only one woody species, FDvar of different traits could not be calculated, so this index was removed from the final SEM in both areas. Dieback intensity was introduced as a fixed factor using four ordinal categories: control (no dieback), low, moderate

and high dieback coded as 1–4, respectively. Best-fit SEMs were assessed using chi-square (χ^2) test ($P > 0.05$), Bentler's comparative fit index and goodness of fit index (CFI and GFI), coefficient of determination (R^2), and root mean square error of approximation (RMSEA). To obtain best-fit SEMs, we selected the two variables with highest relative importance in each category and the best combination using a trial-and-error approach. All statistical analyses were performed using R v3.6.3 software.

3.1 Effects of management and dieback intensity on AGB and diversity indices

AGB was affected by management ($F=14.20$; $P < 0.001$), being higher in the traditional managed area ($14.57 (\pm 1.60) t/hm$) than in the protected area ($8.70 (\pm 1.05) t/hm$). AGB was also significantly influenced by dieback intensity ($F=12.89$; $P < 0.001$), with decreasing values along the dieback intensity gradient in both areas (Fig. 3). However, we found no significant interaction between management and dieback intensity ($F=2.09$; $P=0.109$).

CWM of all functional traits (LPC, LNC, H, LDMC, SLA and WD) were significantly affected by management type, dieback intensity and their interaction (Table 2). In contrast, FDvar of some leaf characteristics (LNC, LPC and LDMC) were only affected by management type, while dieback intensity had no significant effect on any traits.

CWM of LDMC, LNC and H were higher in the traditional managed area, while CWM values of SLA and LPC were higher in the protected area. CWM of LPC was highest in low and moderate dieback intensities in the protected area, while no significant difference existed among dieback intensities in the traditional managed area. There was no significant difference among dieback intensity classes in the protected area for CWM of LNC, LDMC and H. In contrast, the highest CWM values of LNC and LDMC occurred in low dieback intensity class, and for CWM of H in high dieback intensity of the traditional managed area. FDvar of LNC and LDMC were higher in the protected area, while FDvar of LPC was higher in the traditional managed area, with no significant difference among dieback intensities for these attributes.

All taxonomic diversity indices were affected by management, dieback intensity and their interaction ($P < 0.001$). Structural diversity indices were similarly affected by management and dieback intensity, while interaction was only significant for diameter ($F=7.32$; $P < 0.001$) and height ($F=13.65$; $P < 0.001$) differentiation indices.

Woody species richness varied from 1 to 2 (*Q. brantii* or *Q. brantii* and *P. atlantica*) in the traditional managed area, whereas it varied from 2 to 6 in the protected area (*Q. brantii*, *P. atlantica*, *A. monspessulanum* subsp. *cinerascens*, *C. pontica*, *C. microcarpa* and *D. mucronata*). Protection compared to traditional management caused significant increases in richness and Shannon diversity indices, with highest and lowest values recorded in low and high dieback

intensity, respectively. Evenness was higher in the traditional managed area than in the protected area, with the highest evenness value observed in the higher dieback intensity class. In the traditional managed area, all structural diversity indices were significantly reduced. The highest diameter and height differentiation values were observed in high intensity dieback and in the protected area; however, no clear difference existed among dieback intensities in the traditional managed area. Moreover, the highest mingling index values were observed from low to high intensity dieback classes in the protected area.

3.2 Relationships between diversity indices and AGB

We found significant linear relationships for AGB only with functional diversity indices in the protected area. Positive relationships existed between AGB and CWM of traits such as H, LDMC, SLA and WD, and negative relationships with CWM of LPC and FDvar of WD. In the traditional managed area, significant relationships were found only with taxonomic and structural diversity indices, either positive (diameter differentiation and species richness) or negative (evenness).

3.3 Structural equation models

The Shannon-Wiener diversity index, mingling index and CWM of LPC had the highest relative importance in each category of plant diversity, stand structure and trait composition. However, species evenness, mingling index and CWM of LPC provided the best combination of predictors in SEM for the protected area. Results showed AGB was directly and negatively affected by dieback intensity ($\beta=-0.358$; $P=0.006$) and trait composition ($\beta=-0.389$; $P=0.002$). Additionally, dieback intensity positively affected stand structural indices ($\beta=0.363$; $P=0.006$). Moreover, structural indices tended to affect trait composition ($\beta=0.287$; $P=0.068$).

Evenness, diameter differentiation and CWM of LDMC had the highest relative importance in each category of plant diversity, stand structure and trait composition, while the combination of Shannon-Wiener diversity, diameter differentiation and CWM of LDMC provided the best-fit SEM in the traditional managed area. Dieback intensity had only direct effect on AGB ($\beta=-0.586$; $P<0.001$). Additionally, dieback intensity had significant negative influence on taxonomic diversity ($\beta=-0.393$; $P=0.003$) and structural indices ($\beta=-0.272$; $P=0.05$). Structural indices had strong negative effect on trait composition ($\beta=-0.588$; $P<0.001$).

4.1 Effect of management and dieback on diversity and function of ecosystem

We found that biomass amount in the traditional managed area was significantly higher than in the protected area, especially visible in the no dieback class. This

result seems counterintuitive but can be explained by past management actions. In the traditional managed area, old seed-origin oak trees with high biomass were preserved more than those in the protected area (mainly because they provided shade) while other tree species (e.g., *Acer*) and shrub species were exploited for firewood or other uses. Consequently, remaining trees' access to ecosystem resources (light, moisture and nutrients) improved in the absence of competition, leading to increased growth and biomass. In contrast, growth and biomass accumulation were reduced in the protected area due to higher interspecific competition and predominance of oaks in coppice form. Previous studies have shown that coppice-form trees produce less biomass than seed-origin trees in similar semi-arid systems, consistent with these findings.

Evidently, we found biomass amount reduced along the dieback intensity gradient in the traditional managed area and peaked in the no dieback class where both oak and pistachio trees were present. In contrast, no significant biomass change was recorded in the protected area among the three classes with dieback symptoms, indicating that higher diversity induced by protective measures moderated dieback's negative impact on AGB. Besides, tree age (not investigated in this study) is definitely much higher in the traditional managed area; therefore, dieback symptoms may worsen in this area in the future.

CWM values were affected by management type and dieback intensity: CWM of H, LNC and LDMC were higher in the traditional managed area than in the protected area, while CWM of LPC and SLA were higher in the protected area. In the traditional managed area, only old seed-origin oak and pistachio trees (more resistant to historical degradation since large trees are less selected for firewood) were present, explaining increased CWM of H in the community. In this same area, forests exposed to strong human pressure (e.g., harvesting, browsing and grazing) exhibited simplified vertical structure (reduced number of vegetation layers) compared with forests under protective measures. As trees were older in the traditional managed area, they also produced tougher leaves with higher lignin content that increased LDMC. Previous works have shown that higher LDMC values in a community indicate predominance of conservative species growing in low-production environments similar to the traditional managed area in our study. In the traditional managed area, shrubs such as *C. pontica* and *C. microcarpa* were eliminated to benefit oak trees, which developed a more acquisitive resource-use strategy due to absence of competition and better access to ecosystem resources (light, soil moisture and soil nutrients). This explains accumulation of elements such as nitrogen in leaves, leading to higher LNC in this area. Similarly, Boukili and Chazdon (2017) reported prevalence of resource acquisitive traits (such as LNC) in managed forests and conservative traits in old growth forests. Higher CWM values of LPC and SLA in the protected area can be related to higher diversity and richness of woody species with fast nutrient acquisition strategy. In fact, fast-growing species such as wild cherries in this protected area can efficiently capture ecosystem resources in relatively short time.

Contrary to functional composition results (CWM), none of the FDvar were affected by dieback intensity, while only FDvar of LNC, LPC and LDMC were influenced by management (protected vs. traditional managed). In this regard, FDvar values of LNC and LDMC were higher in the protected area than in the traditional managed area, whereas the reverse was true for FDvar of LPC. FDvar generally indicates differences in ecological niches among species. Therefore, reduced tree diversity due to elimination of species most sensitive to human disturbances in the traditional managed area minimized differences in plant nutrient uptake strategies, while protection led to the opposite effect, explaining higher FDvar of LNC and LDMC in the protected area. Similarly, Reich et al. (1995) reported that woody species with different photosynthetic capacities exhibited variations in LNC due to close relationships between photosynthetic capacities and LNC.

We found that management and dieback intensity affected all taxonomic (diversity, richness and evenness) and structural diversity (height and diameter differentiation indices and mingling) indices, such that species richness, Shannon diversity and all structural diversity indices were higher in the protected area than in the traditional managed area, whereas the opposite was true for evenness. Increased richness and diversity and consequently structural diversity in the protected area is associated with positive effects of protection on forest ecosystems, which created conditions for emergence and establishment of plant species usually less tolerant to disturbances. In contrast, only oak and pistachio trees (in the no dieback class) and only oak trees (in other dieback classes) remain in the traditional managed area, explaining higher evenness index under these conditions. In line with this result, increased species evenness is generally reported after disturbances.

Additionally, higher species richness and diversity in intermediate dieback intensity classes in the protected area confirms the intermediate disturbance hypothesis, emphasizing the positive role of moderate-intensity disturbances to reduce competition and maximize diversity. Numerous studies examining effects of various moderate-intensity disturbances such as fire, livestock grazing and land use change have reported positive influences on diversity consistent with intermediate disturbance intensity. However, this study is among the first reports of such an effect along a dieback gradient.

Diameter and height differentiation in the protected area were more pronounced than in the traditional managed area, particularly in no dieback and high dieback intensity classes. There are contrasting patterns of changes in height and diameter differentiation (both u-shaped) and species diversity and richness (both hump-shaped) along the dieback gradient in the protected area. Possibly more intense competition between woody species in no dieback sites could explain more pronounced height and diameter differentiation. Heydari et al. (2017b) and Salehzadeh et al. (2017) also showed that degradation versus protection reduces diversity and density of woody species, leading to reduced values of structural indices for diameter and height differentiation, consistent

with our results.

4.2 Relationships between diversity indices and AGB

We found significant linear relationships between AGB and CWM/FDvar indices in the protected area, and with taxonomic and structural diversity indices in the traditional managed area. This result emphasizes the importance of using various indices to measure biodiversity, allowing more comprehensive understanding of links between biodiversity and ecosystem functions. In the protected area, most functional composition indices (CWM of H, LDMC, SLA and WD) were positively and significantly associated with AGB, clearly supporting the selection effect hypothesis. Similar findings have been widely reported; for instance, Finegan et al. (2015) reported positive relationships between CWM of H and AGB in tropical forests. In contrast, we found a negative relationship between FDvar of WD and AGB in the protected area, contrasting with Ali and Yan (2017) who reported positive relationships between functional divergence of twig WD and AGB in secondary forests. Overall, this relationship between FDvar of WD and AGB, as well as between functional composition (CWM) and AGB, emphasizes the large impact of dominant tree species on biomass production in this semi-arid forest ecosystem. In the protected area, stands where the dominant species prevails (typically oak trees with high WD) present higher biomass than stands with mixtures of oaks and other species with low WD. As previously stated, this result reinforces the selection effect hypothesis.

In the traditional managed area, AGB was positively associated with species richness and diameter differentiation but negatively with evenness. In this area, only oak and pistachio trees are found across different dieback intensity classes. When both species are present, both diameter differentiation and aboveground biomass increase. In contrast, in the protected area, species composition is more stable across dieback intensity classes and only relative abundance changes. Consequently, diameter differentiation remains low and not significantly related to AGB. The negative relationship between AGB and evenness found in this study aligns with numerous previous works reporting similar trends between various ecosystem functions and evenness, confirming the selection effect hypothesis again. In fact, increased evenness indicates reduced abundance of dominant species, leading to reduced roles of these species in ecosystem functions. Our analysis of relationships between different biodiversity indices and AGB provides clear evidence supporting the selection effect hypothesis and emphasizes the importance of dominant species in ecosystem function. In contrast, we found no evidence of positive niche complementarity effects on biomass.

5 Conclusions

The relationships between different aspects of diversity (taxonomic, structural and functional) and AGB (a major component of global carbon balance) have been studied extensively but rarely under simultaneous influence of forest

dieback intensity and management conditions. Our results emphasize that using different approaches for diversity quantification is vital to assess changes in AGB of forest systems subjected to various management intensities and disturbances. Along a dieback intensity gradient, leaf functional traits are efficient predictors for estimating AGB in protected forests, while taxonomic and structural indices provide better results in forests under high human pressure. The results clearly reveal that natural disturbances (here dieback intensity) play a major role in driving ecosystem productivity and biotic conditions. Lastly, our results clearly support the selection effect hypothesis as most biomass accumulation results from the dominant species—Brant's oak.

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