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Tree dieback, woody plant diversity, and ecosystem driven by topography in semi-arid mountain forests: Implication for ecosystem management

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Abstract. Mountain landscapes are highly heterogeneous due to topography, notably positions along slope and slope shapes, which control ecosystem mechanisms. We hypothesized that tree dieback is controlled by topography, selecting productive and less diverse communities in lower slopes, and stress-resistant and more diverse communities on upper slopes. Understanding how this heterogeneity drives vegetation patterns should provide benchmarks for ecosystem management of mountain forest dominated by *Quercus brantii*. Woody communities were sampled along convex vs concave topography (i.e., ridge vs talweg), and with measurements of tree dieback severity, environmental variables (litter depth, soil quality, rock outcrop), stand structure (canopy cover, mistletoe infestation, tree diameter and height, diameter and height differentiations, oaks' number from sprout-clumps or seed-origin), and biodiversity. Slope position was the most significant driver that affected all variables, excepted evenness. Dieback severity was higher on slope shoulders and summits, and lower in lower slopes where trees were the most productive: taller, larger, more homogeneous, and mostly seed-origin. Catena shape affected the diversity and dieback severity, both higher in talwegs, but had no effect on environmental variables and little on stand structure. Outputs indicate that the higher diversity of woody plants is on upper slopes supporting stress-resistant community associated with more severe dieback and mistletoe infection probably because frugivore birds attracted by the shrubs' fruits. Semi-arid forest management must consider the shaped-slope ecosystem heterogeneity by preserving ridges that are more susceptible to tree dieback, and naturally support biodiversity. Restoration measures on lower fertile slopes could be carried out by oak planting or seedlings under the cover of shrubs to counter dieback effects and environmental stresses. In addition, forestry measures can be taken in lower positions for the conversion of coppice to high oak forest to potentially consider a moderate forestry.

Keywords: biodiversity, catena, dieback, landform, forest management, oak forest, slope position, Zagros mountain

1. Introduction

In mountains, forest structure and diversity are driven by micro-scale drivers, e.g., slope, aspect, altitude, bedrock, or moisture (Kovács et al. 2017, Luo et al., 2019; Michalet et al., 2020; Woldu et al., 2020; Deák et al., 2021; Carcaillet et al., 2022). Understanding these natural patterns and associated mechanisms provide valuable benchmarks for the ecosystem management, which aims to reduce the differences between natural and managed landscapes to ensure long-term conservation of ecosystem functions and, thereby, retain the socio-economic benefits (Führer, 2000; Gauthier et al., 2009; Heckwolf et al., 2021). This is helpful knowing that global decline of mountain forests, e.g., tree dieback or biodiversity erosion, results a degradation of ecosystem services (Foley et al., 2007; Laigle et al., 2021; Kaushal et al., 2021).

The tree dieback phenomenon is manifested by reduced growth and vitality and, ultimately, a higher mortality rate. Tree dieback varies in severity notably in temperate and Mediterranean forests and, alters communities' composition and ecosystem functions (Ogaya et al., 2020; Puchi et al., 2021; Sánchez-Moreno and Yuste, 2022). Tree dieback has increased in drought-prone areas during last decades (Gazol et al., 2020). Meanwhile, one million hectares of Zagros forests with the emblematic *Quercus brantii* Lindl. (Brant's oak) has declined in the semi-arid areas of western Iran (Shiravand and Hosseini, 2020; Ghanbari Motlagh et al., 2020), while factors driving of this dieback crisis reducing ecosystem values remain a gap of knowledge.

Acting probably on tree dieback, the location along slope appears crucial in mountain due to trophic processes. A series of different positions along a slope and successive surface roughness is called 'catena' (Wells et al., 2018; Fayyadh et al., 2021). A catena modulates the spatial biotic patterns by controlling their environments and their responses to the environment (Fazlollahi Mohammadi et al., 2022). Along slope, landscape heterogeneity can be driven by micro-scale variability in soil quality and moisture, which are partly controlled by elevation; the higher the altitude, the lower the temperature, the higher the humidity and, thinner the soil depth (see also López-Marcos et al. 2020). These variations can be decisive for plants' structure, productivity, and diversity (Fazlollahi Mohammadi et al., 2022), as well the rate of biotic and abiotic disturbances (Hosseini et al., 2017; Kagezi et al., 2018). Trees may face drought-based stress, sometimes enhanced by thermal stress or biotic disturbances (Schwantes et al., 2018; Zandalinas et al., 2021; Pascual et al., 2022). Topographic structure mitigating these stresses would act as tree refugia (Hampe et al. 2013).

Tree dieback severity varies across species, stand structure and environmental conditions (Hevia et al., 2019; Lakkana et al., 2022). Soil moisture and nutrients' availability, stand structure, competition, tree ages, extreme heat and frequent droughts were found to be effective in the occurrence of dieback (Turner and Lambert, 2005; Gazol et al., 2018; Taccoen et al., 2021). Trees with small crown and root systems would be more susceptible due to less access to water and nutrients (Scott et al., 2013; Hosseini et al., 2014). Further, larger trees were found to suffer less from dieback thanks to their deeper root system to access to soil resources (Mensforth et al., 1994). Conversely, studies found a higher risk of dieback in larger trees due to reduced vigor with age (Worrall et al., 2008), unless the problem concerns tree height: taller trees would be more susceptible due to higher cost of respiration maintenance (Lavigne and Ryan, 1997; Tang et al., 2014; Housset et al. 2021). Forest dieback is often more severe in high-density stands due to between trees competition for resources (Mensforth et al., 1994; Fensham and Fairfax, 2007). Along a gradient of dieback severity, taxonomic diversity and stand structure are highly correlated (Karami et al. 2022). However, tree dieback could be not related to stand characteristics, but to the location in floodplain, where dieback decreased

with increasing water availability (Cunningham et al., 2010) underscoring the role of site quality. The above presented review show that the decline of trees is a complex phenomenon resulting from multiple factors and their interactions in space and time (McDowell et al., 2008; Gazol et al., 2020). Because the processes seem ecosystem specific, environmental or biotic drivers per ecosystem are needed to be used by managers as early warning signal to identify and predict site typologies at higher risk of dieback.

The novelty of the present study is that we analyze a wide range of potential drivers that can be attributed to tree dieback in a heterogeneous mountain environment. We aim to evaluate the relationship between oak dieback severity and ecological characteristics of forest stands in different landforms in a semi-arid oak ecosystem of western Iran, where dieback severity varies within landscapes (Hosseini et al., 2017; Pourhashemi et al., 2017; Zarafshar et al., 2020). It is admitted that the tree dieback in such forests depends on primary macro-scale factors such as drought, increase in temperature and decrease in precipitation, and the increased intensity and duration of fine dust storms (Shiravand and Hosseini, 2020; Yaghmaei et al., 2022). However, we hypothesized that not only macro-scale, but also several micro-scale factors control Brant's oak dieback severity, notably the plant diversity through interspecific interactions and stand structures along slope gradient. Our fine-scale analysis of environmental conditions and their association with the spatial distribution of oak dieback can support the establishment of appropriate forest management policies in mountain environments. In that context, we test the relationship between oak dieback severity and biotic and abiotic characteristics of forest stands. Specifically, we test the ecological and environmental characteristics of Brant's oak stands in different catena shapes and positions on slopes, and how oak dieback pattern is affected by biotic and abiotic factors.

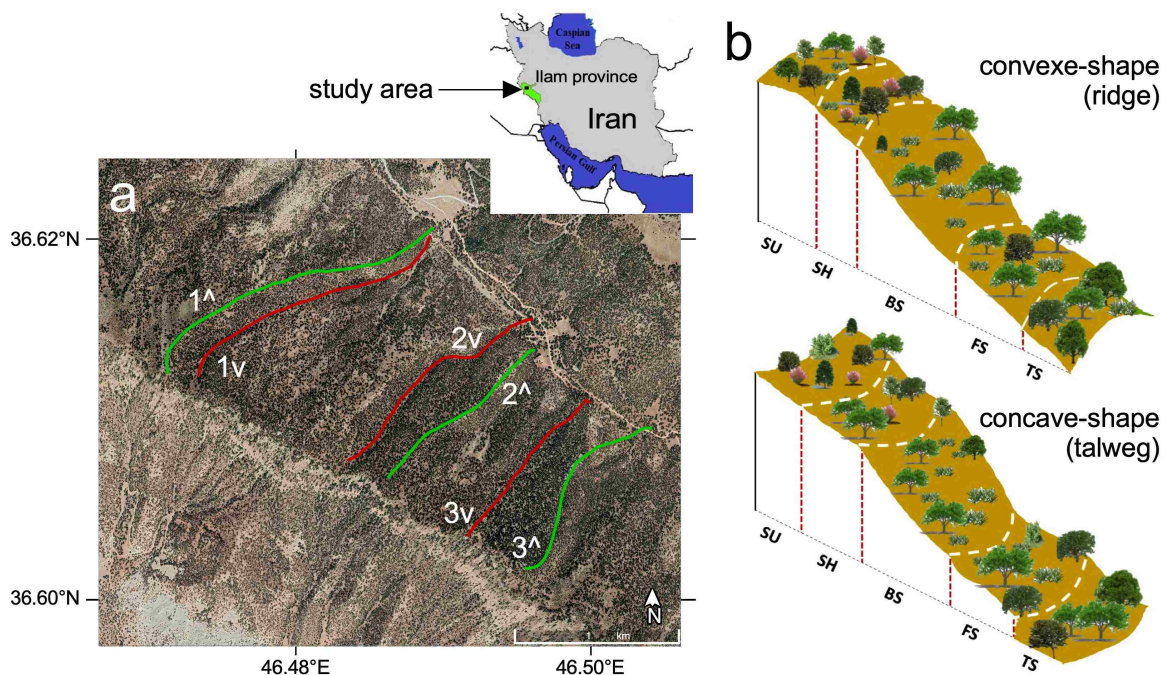


Fig 1. (a) Aerial image of the study area showing the six transects, three on ridges (convex catena; green lines) and three in talwegs (concave catena; red lines). Image date: August 2020; Image©2023 Maxar Technologies. (b) Catena shape and positions on slopes (SU: summit, SH: shoulder, BS: backslope, FS: footslope, TS: toe-slope).

2. Materials and methods

2.1. Site description

Zagros forest is one out five ecological regions of Iran, covering 40% of forests in the Iran west. Protecting soil and water resources and supporting the livelihood of human population are key functions of these semi-arid forests. The study was carried out on northern aspect slope of the Shalem Mountain (46°29'-46°30'E, 33°36'-33°37'N; Fig. 1), which is a protected area of the Ilam Department of Environment. The study ranges from 1750 to 2180 m a.s.l. above sea level (a.s.l.) and slope vary from 15 to 55%, mean values between 19 and 26% (Supplementary Information, Table S1). The semi-arid climate of the study area has a mean annual temperature of 16.7°C and a mean annual precipitation of 591 mm.yr⁻¹ (period of 1986–2021). Soils are sandy clay silt, with alkaline based on limestone bedrocks (pH > 7).

The forest canopy is relatively dense (30-40%) and, is dominated by *Quercus brantii*. Additional woody species distributed along the slope are *Daphne mucronata* Royle, *Lonicera nummularifolia* Jaub. & Spach, *Pistacia atlantica* Desf., *Cerasus microcarpa* C. A. Mey., *Crataegus pontica* C. Koch, *Acer monspessulanum* L., and *Amygdalus scoparia* Spach. Except *A. monspessulanum*, all these species are berry-bearing plants attractive for frugivores animals. Oaks' canopy is commonly parasitized by *Loranthus europaeus* Jacq. (mistletoe), another berry-bearing plants. The understory is covered by annual to perennial grasses and forbs (Heydari et al., 2021), but this diversity and the associated soil functionalities are threatened by repeated wildfires (Mirzaei et al., 2023).

2.2. Experimental design and sampling

The fieldwork was carried out in spring 2021. Three pairs of topography or catena shape, convex (ridge) and concave (talweg), were selected. Six transects with a width of 100 m were established along each catena shape (Fig. 1), and 5 positions per transect were determined: summit (SU), shoulder (SH), back-slope (BS), foot-slope (FS) and toe-slope (TS). In each position, a circular plot of ca 1000 m² was established (radius 17.9 m). Therefore, 30 plots (i.e., 2 catena shapes × 5 positions × 3 replicates) were considered for this study and their coordinates were recorded.

2.2.1. Environmental variables

In each sample plot, a composite soil sample was gathered from 5 cores. Soil physical, chemical and biological properties were measured using standard laboratory methods (detailed methods in Heydari et al., 2017; Eslaminejad et al., 2020): clay, sand, silt, lime, soil acidity (pH), electrical conductivity, organic carbon (OC), total nitrogen (N_{tot}), available phosphorus (P_{ava}), available potassium (K_{ava}), cation exchange capacity (CEC), bulk density (BD), basal respiration (BR), substrate-induced respiration (SIR), microbial biomass carbon (MBC). The total data set was used to determine soil quality index that is based on the collection of indicators selected based on specific characteristics of soil analyzed, such as:

$$SQI = \sum_{i=1}^n W_i N_i \quad \text{Equation 1}$$

where W_i is the weight of each site indicator, and N_i is the score of indicators n . The weight value of each indicator was derived from the communality ratio of each indicator to sum of all indicators communalities. Communality values were inferred from ordination based on Factor Analysis (details in Rahmanipour et al., 2014).

Other environmental variables not included in the SQI were the rock outcrop and the litter depth. The rock outcrop percentage was visually estimated by one person in the sample plots.

Litter depth was measured at 5 points in each plot and, the mean of 5 values was considered as the plot litter depth.

2.2.2. Stand structural variables

In each plot, the diameters at breast height (DBH) of all individuals of trees and tall shrubs were measured using a diameter tape. Their heights (H_{ws}) were measured with a clinometer, and the crown diameter was estimated with a tape measure to calculate the woody-cover percentage (TCC). For individuals with a coppice form (resprouters) and height < 1.30 m, the average diameter of the collar of their stems were measured. In addition, the DBH of all oak stems with coppice form and their height were measured and, the sprout-clumps in each plot were counted. The index value of canopy parasitized by mistletoe (TCIM) of in plot level was visually estimated. Height and diameter differentiation as the structural indices of woody species were obtained (Ruprecht et al., 2010):

$$T_i = \frac{1}{4} \sum_{j=1}^4 (1 - r_{ij}) \quad \text{Equation 2}$$

where $r_{ij} = \frac{\text{Min DBH}}{\text{Max DBH}}$ for diameter differentiation (hereafter ΔD) and, $r_{ij} = \frac{\text{Min Height}}{\text{Max Height}}$ for height differentiation (ΔH). In each plot, a nearest tree to plot center selected as the reference tree (i) and the three nearest neighbor trees (j) were marked. These structural indices, ΔH and ΔD , represent the stand heterogeneity and the competition degree ($0 \leq T_i \leq 1$) between canopy species. Index values of < 0.3 indicate very low differences between-tree shape or large stand homogeneity, whereas > 0.7 represent very large stand heterogeneity.

2.2.3. Diversity

The community diversity was assessed for woody species only, including richness (S) that is the algebraic number of species i per sample. Diversity indices and the evenness were calculated at the plot-scale. The Shannon diversity index (H') is sensitive to rare species (Shannon and Weaver, 1949), such as:

$$H' = \sum_{i=1}^S P_i \ln P_i \quad \text{Equation 3}$$

where P_i is the proportion of species i in the sample and, ranges such as $0 < H' \leq \ln(S)$. The Simpson index (Simpson, 1949) is sensitive to abundant species, such as:

$$D = 1 - \sum_{i=1}^S P_i^2 \quad \text{Equation 4}$$

and vary from $0 \leq D < S$. The Buzas and Gibson's evenness (Buzas and Gibson, 1969) is calculated based on H' and S , as followed:

$$E = e^{H'/S} \quad \text{Equation 5}$$

where E vary from [0 to 1].

2.2.4. Dieback severity

The dieback severity was estimated based on visual criteria of dieback in each plot according to the field method developed by Karami et al. (2022), such as, were recorded the important signs of decline, including the separation of the trunk bark and the sap outflow, the color change of leaves, and the partial or complete drying of the crown.

2.2. Statistical analysis

General linear models (GLM) were used to test the effects of the catena shapes (CS), catena positions (CP) and their interactions on the dependent variables, i.e., environmental variables

(litter depth [LD]; soil quality index [SQI], rock outcrop [RO]), stand structural variables (total canopy cover [TCC], mistletoe-infection [TCIM], diameter at breast-height [DBH], diameter differentiation [ΔD], plant height [H_{ws}], height differentiation [ΔH], oak number of oak originating from sprout-clumps [OSC]; number of seed-originated oak trees [SOO]), diversity measurements (S , H' , D , E), and dieback severity index (DS). Post-hoc Duncan's Multiple Range tests were used to compare the means. The hypothesis that woody species composition differs among different catena positions was considered using non-metric multidimensional scaling (NMDS) as part of the 'vegan' package (Oksanen et al., 2018). This ordination method which projects multivariate data into a space with fewer dimensions, was applied on each dataset using Bray-Curtis dissimilarity. Pearson correlations were performed using GraphPad Prism v6.01 to assess the relationships between diversity indices, environmental variables and dieback severity for each catena shape. The principal component analyses (PCA) were conducted to analyze relationships between ecosystem variables per plot and to highlight the main components. PCA carried out using "FactoMineR" and "factoextra" packages. All statistical analyses were carried out under R environment, version 4.1.0 (R Core Team, 2021).

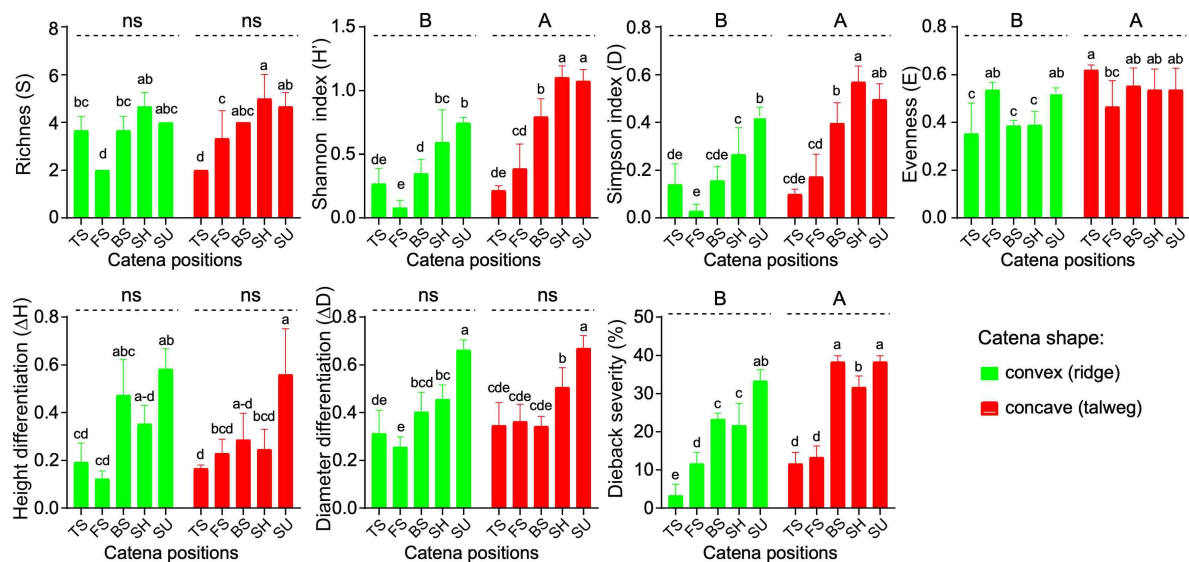


Fig 2. Mean values (\pm SE) of communities' richness (S) and diversity (H' , D) and evenness (E), height (ΔH) and diameter (ΔD) differentiation, and dieback severity according to catena shapes and positions on slopes. Different uppercase letters indicate significant differences between catena shape ($p < 0.05$), and lowercase letters indicate significant differences between catena positions on slope ($p < 0.05$).

3. Results

3.1. Catena shape, slope position and environment and stand structure

All the environmental variables were significantly influenced by the position on slopes ($p < 0.01$) but not by catena shapes (Table S2). However, SQI was significantly influenced by both the position on slopes and, the interaction between catena shape and position on slopes ($p < 0.05$; Table S2). LD and SQI were significantly higher in toe-slope (TS) position ($p < 0.01$) and their values decreased significantly with the elevation along the slope especially at summit (SU) and shoulder (SH), while RO showed the opposite trend ($p < 0.05$; Table S3).

Among stand structural characteristics, H_{ws} , DBH, ΔH and ΔD , TCC were influenced only by the position on slopes ($p < 0.01$; Table S2). ΔH and ΔD raised with increasing slopes; the higher values are observed at SH and SU, whereas lower values are at TS and FS, with the

same pattern in both catena shapes (Fig. 2). Hws, TCC, and DBH were significantly higher in TS position of both catena shapes and their values decreased significantly on upper slope positions especially at SU and SH (Fig. 2, Table S3).

The number of oak sprout-clumps (OSC) and of seed-originated oak trees (SOO) were affected by both catena shape ($p < 0.05$) and position ($p < 0.01$), but their interactions were not significant (Table S2). OSC was significantly higher in concave catena (talweg), while SOO was higher in convex catena (ridge) ($p < 0.05$; Table S3). There was no SOO at the SU and SH positions of the concave catena. SOO was significantly higher ($p < 0.05$) in TS position of both catena shapes compared with the other slope positions. Further, the SOO value decreased significantly ($p < 0.05$; Table S3) upper slope positions especially at SU and SH. OSC also showed increasing trend along both catena shapes and were significantly greater at SU and SH ($p < 0.05$; Table S3). Tree canopy infestation by the mistletoe (TCIM) was significantly influenced by slope position and, the interaction between catena shape and position on slopes ($p < 0.01$; Table S2). TCIM increased with the elevation whatever the catena shapes and, were significantly greater at SU and SH compared to other positions on slopes ($p < 0.05$; Table S3).

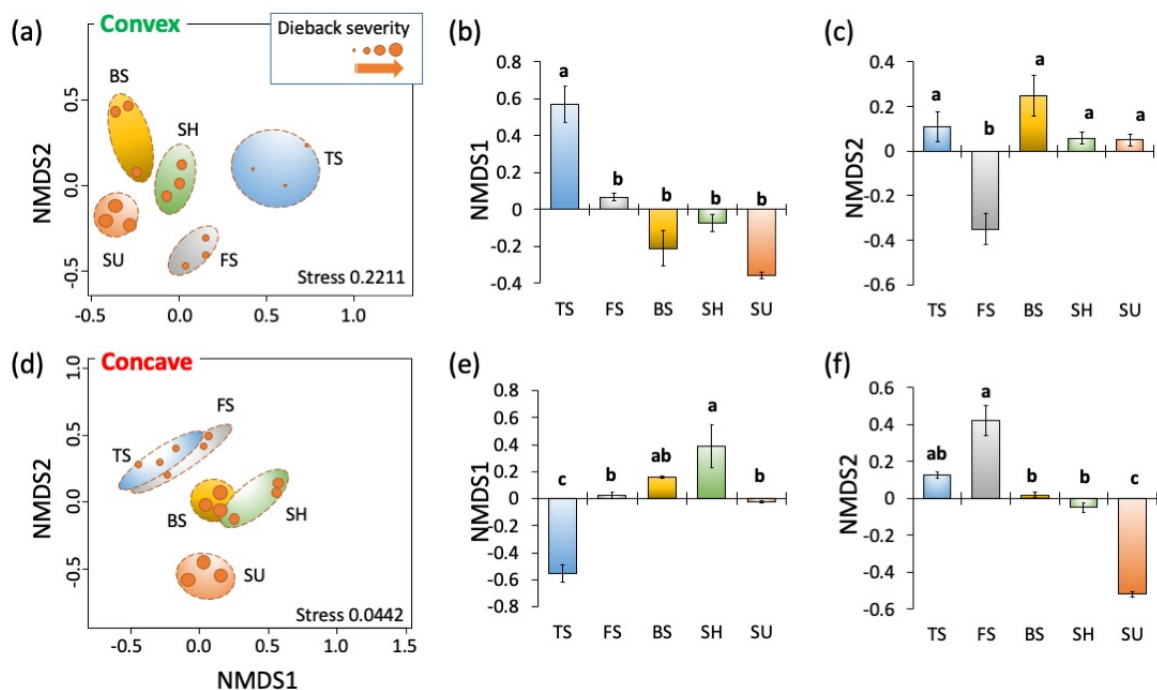


Fig 3. Non-metric Multidimensional Scaling (NMDS) based on Bray-Curtis dissimilarity matrix to highlight the differences of woody plant composition between catena positions in (a) convex catena and (d) concave catena shapes; the dieback severity per plot is projected; (b) means species scores according to position on slopes along convex catena for NMDS-axis 1 ($F=13.38$, $\text{Pr}(>F) = 0.0005^{***}$) and (c) for NMDS-axis 2 ($F = 2.77$, $\text{Pr}(>F) = 0.0471^*$), and along concave catena (e) for NMDS-axis 1 ($F = 4.00$, $\text{Pr}(>F) = 0.0342^*$) and (f) for NMDS-axis 2: $F = 18.73$, $\text{Pr}(>F) = 0.0001^{***}$).

Concerning the community diversity of woody plants, the catena shape, the position on slopes and, their interactions influenced the Shannon and the Simpson indices ($p < 0.01$, except interactions for H' $p < 0.05$). The interaction between catena shape and position on slopes had a significant effect on the richness and the evenness ($p < 0.01$; Table S2). The Shannon and Simpson indices, and the evenness were significantly higher in concave catena (talweg; Fig. 2). In addition, richness, Shannon and Simpson diversity indices increased along

the slope with higher values at the SH and SU and lower values in the TS and FS with the same pattern in both catena shapes (Fig. 2). This means that the communities' structures responded similarly to the topography (ridge or talweg), and tend to the evenness between species, although the concave pattern (talweg) presents higher values (Fig. 2). The richness is not influenced by the catena shape, but SH and SU positions on slopes foster more species per plot (Fig. 2).

Dieback severity (DS) was significantly affected by the catena shape, the position on slopes and, their interactions ($p < 0.01$; Table S2). DS was higher in concave catena (talweg), and increased with elevation, showing higher values at SU in both catena shape and, the SH and the BS but only in concave catena (Fig. 2). Lower values were at TS and FS in both catena shape.

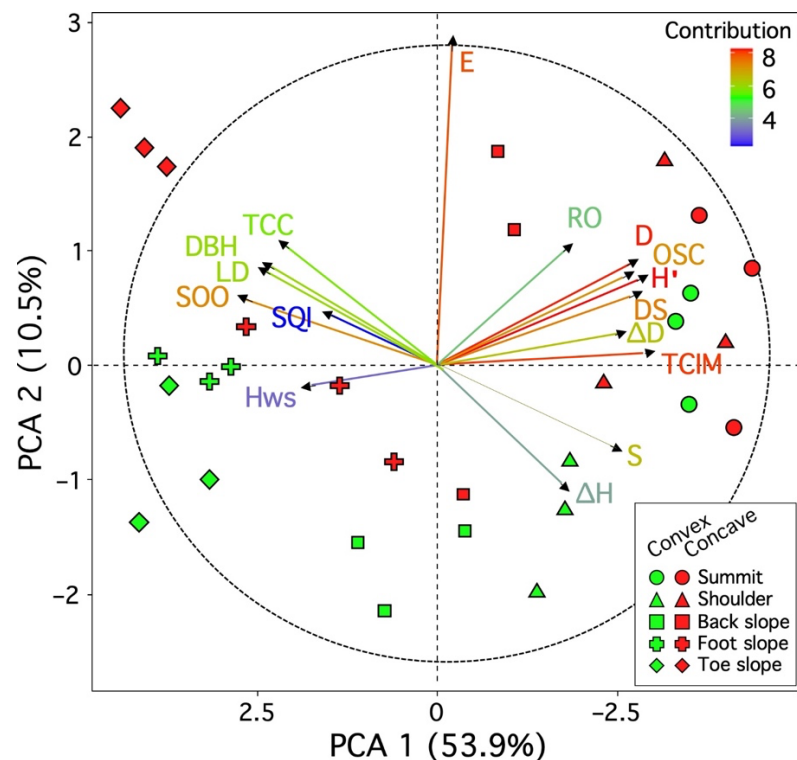


Fig 4. Biplot of principal component analysis (PCA) applied to the catena positions; Richness (S), Shannon diversity index (H'), Simpson diversity index (D) and Evenness (E), dieback severity (DS), tree canopy infestation by the mistletoe (TCIM), height of woody species (Hws), diameter at breast height (DBH), height (ΔH) and diameter differentiation (ΔD), total canopy cover (TCC), number of oak sprout-clumps (OSC) and seed-originated oaks (SOO), litter depth (LD), rock outcrop (RO) and soil quality index (SQI). The length of the arrows is proportional to the importance of variables.

3.2. Woody species composition

NMDS indicated that there are different patterns of woody species composition in different catena positions and shapes. In the convex catena (talweg), ANOVA outputs showed that woody species composition significantly varied among the catena positions (NMDS1: F -value= 13.38, $Pr(>F) = 0.0005$; NMDS2: F -value= 2.77, $Pr(>F) = 0.0471$). In this catena shape, along axes 1 and 2 of the NMDS, the species composition at TS and FS respectively showed a significant difference with other positions on slopes, while these other positions were similar in composition. These two lower elevations, TS and FS, had lower dieback severity than upper elevation on slopes, notably SU that represents highest dieback severity

(Fig 3a-c). In the concave catena (ridge), both TS and FS showed higher similarity of composition (overlap in NMDS) and distinct from other slope positions (NMDS1: F -value= 4.00, $Pr (>F) = 0.0342$; NMDS2: F -value= 18.73, $Pr (>F) = 0.0001$). Further, BS and SH indicated more similarities of plant composition and were clustered together in NMDS. The SU position was significantly separated from the other positions in terms of composition. As on ridge (convex), the dieback severity was lower at the lower elevation (TS and FS), especially SU with higher dieback severity (Fig 3 d-f).

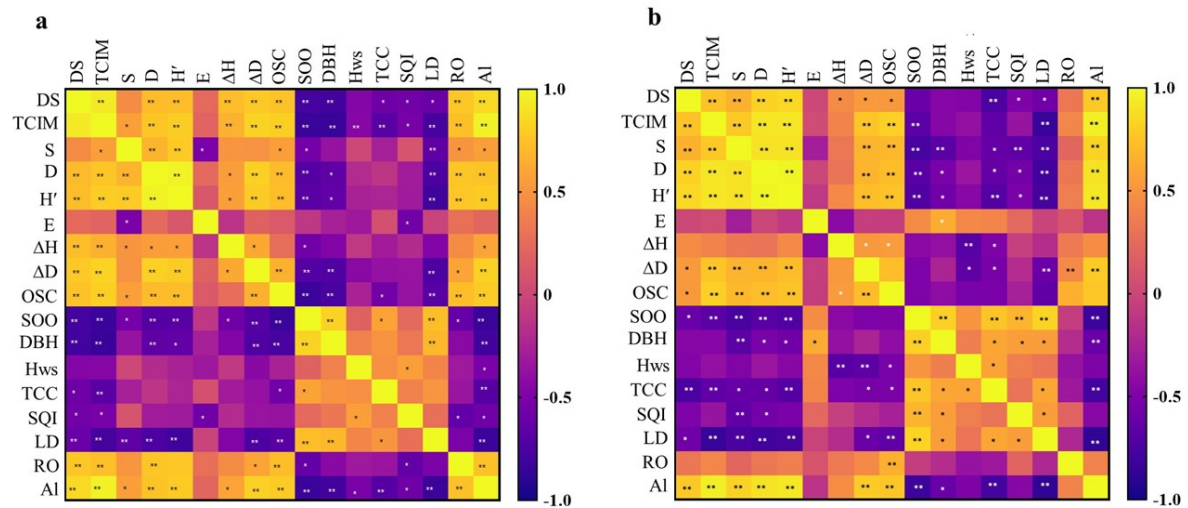


Fig 5. Pearson's correlation coefficients between dieback severity, taxonomic and structural diversity indices and site related features along catena positions; Color chart from yellow to dark violet represents positive to negative correlation in convex (a) and concave (b) catena shapes; Richness (S), Shannon-Wiener diversity index (H'), Simpson diversity index (D,) and Evenness (E), dieback severity (DS), tree canopy infestation by the mistletoe (TCIM), height of woody species (Hws), diameter at breast height (DBH), height (ΔH) and diameter (ΔD) differentiation, total canopy cover (TCC), number of oak sprout-clumps (OSC), number of seed-originated oak trees (SOO), litter depth (LD), rock outcrop (RO), soil quality index (SQI) and altitude above sea level (AI).

3.3. Dieback severity versus ecological and environmental variables

Axes 1 and 2 of the PCA explained 53.9% and 10.5% of the variance in site characteristics along slopes, respectively (Fig. 4). The results of the multivariate analysis indicated that the first PCA axis (PC1) is gradient of plot positions on slopes, while the PC2 opposes plots according to two catena shapes.

Hence, SU in both catena shapes (convex and concave) and SH and BS of concave are at the positive side of PC1 (Fig. 4). The higher value of diversity indices of Shannon (0.89) and Simpson (0.87), richness (0.78), ΔH (0.55), ΔD (0.81), OSC (0.82), RO (0.59), TCIM (0.91) and DS (0.85) are the main variables associated to this group. In contrast, on the negative side of the PC1, the plots of TS and FS of both convex and concave catenas had higher overlapping. This group is characterized by SQI (-0.47), TCC (-0.68), LD (-0.74), SOO (-0.85), DBH (-0.73) and Hws (-0.57; Fig 4). The PC2 that on positive side opposes plots from concave catenas or talwegs is characterized by higher evenness (E) to plots from convex catenas or ridges with lower evenness (Fig. 4).

In convex catena (ridge), dieback severity (DS) correlates positively with TCIM, D, H', ΔH , ΔD , OSC and RO (Pearson's correlation) and negatively with SOO, DBH, TCC, SQI and

LD (Fig. 5). In concave catena (talweg), there are positive correlations between DS with TCIM, S, D, H', ΔH , ΔD , OSC, whereas correlations were negative with TCC, SQI and LD. Therefore, oak dieback present similar pattern of correlation on both catena shapes (Fig 5).

4. Discussion

Study outputs have shown that oak dieback was positively correlated to diversity of woody plants, mistletoe infection, between-tree shape differentiation, resprouting trees, and important rock outcrop. Oak dieback correlated well with the catena shape and the position on the slope, and some of these factors interacted. The topography appears a major driver of ecosystem diversity, structure, and processes. These outputs support our working hypothesis assuming that topography is an important landscape feature that explain the ecosystem functioning of Zagros Mountains forests, and it should be considered in management practices. The following text discusses the interplay between dieback of Brant's oak with topography, disentangles the ecosystem role of this topography on the mistletoe infection, the diversity community, and finally the ecosystem structure. Finally, the conclusion provides some general guidelines for forest management and conservation.

4.1 Dieback severity in relation to catena shape and position

The oak dieback severity was the highest in the upper slope positions (Fig. 2), for trees growing on rock outcrops, resprouting from stumps (Fig. 4) and are more heterogenous in shape (Fig. 4, 5). In these topographic conditions, the canopy is more open, reducing the plant competition probably explaining the highest diversity (Fig. 5). Other arguments to explain this higher diversity is that other plants than oak are more stress-tolerant (*sensus* Grime, 1977). Slope summit and shoulder expose oaks to hydric and nutritional stress enhanced by rock outcrop, and thinner soil and litter. Moreover, the highest density of resprouters indicates higher occurrence or severity of past disturbances on slope summit and shoulder, e.g., wildfires. These resprouting trees seems to have lower fitness either because of their resprout status from fragilized trees by repeated disturbances that decrease ecosystem functionalities (Mizrei et al., 2023), or because these resprouters are too old trees exhausted. Dominant seed-origin oak trees in the lower slopes have wider and taller crowns, and larger trunks, which usually have more developed roots and better access to nutrients and water, which should favour their resistance to stresses such as drought. To sum-up, dieback prone locations are associated with smaller shape trees and greater diversity of woody species on upper slope positions.

Our observations are in line with Karami et al. (2022) who reported the highest rate of oak tree dieback in forest stands with a higher admixture index, as spatial diversity or dissimilarity of tree species in semi-arid areas. Moreover, crown size (Fan et al., 2008), forest structure, and ecological conditions such as soil properties (Turner and Lambert, 2005; Kabrick et al. 2008; Gazol et al., 2018; Cunningham et al., 2010) have also proven to be effective in the occurrence of tree dieback.

Infection by mistletoe that is higher on upper slope positions (Table S3) probably caused the physiological weaknesses of trees and raised their vulnerability to dieback. Unless trees physiologically altered by topographical and soil stress increased their susceptibility to be parasitized by mistletoe, which would appear as an aggravating factor of tree decline (Hosseini et al., 2009).

All these ecosystem variables indicate that the growth conditions of trees control for the intensity of oak dieback in these forests. Finally, the catena shape partly explains the occurrence of oak dieback, notably with more severe effects for concave shape (talweg) and, surprisingly, less severe and more progressive effects on convex shape (ridge) along slopes. The stronger effect of concave shape on tree dieback is counterintuitive, but significant ($p < 0.01$; Table S2). It is counterintuitive because deeper soils, with higher moisture and nutrients resulting from leaching are expected. However, these concave shape presented higher significant density of resprouting oaks (OSC; $p < 0.05$; Table S2), which are more susceptible to stress. This higher density of resprouting oaks could be explained by wildfire behavior that generally spread in talwegs, which channel wind flow into talwegs increasing the fire severity (Povak et al., 2018). Therefore, higher intensity of oak dieback in concave shape would be indirectly linked to topography, but the direct aftermath of more severe wildfires promoted by this topography.

4.2. Mistletoe infection fostered by topography and site conditions

Trees infected by mistletoe dominated on upper slope positions (Table S2), high community diversity, and with high heterogeneity of 'trees' shape (Fig. 5). The presence of berry-bearing shrub species such as *Lonicera nummularifolia*, *Cerasus microcarpa*, *Crataegus pontica*, or *Amygdalus scoparia* on slope summits or shoulders provides a safe shelter and supplies fruits for frugivore birds. Further, the distance of this high-altitude position from the road and recreation areas ensures a safety area for wildlife. The fruit-eaters realize the seed dispersion, notably the endozoochory of mistletoe seeds within their feces. The shorter the distance from foraging areas, the higher the chance of dropping seeds letting conditions to create nuclei for such group of fruiting woody plants (Debussche et al. 1982), including mistletoe (Bilgili et al., 2020; Patil et al., 2022). The late succession favors positive feedbacks to maintain this fruiting species if their life conditions are gathered, notably low cover of highly competitive species as oaks (Debussche et al. 1996). Stands with low tree cover, often associated with lower quality and degraded habitats with smaller tree dimensions, have a higher severity of infection (Tsopelas et al. 2004; Barbu, 2010) because more light availability in these conditions (open crown) increases the germination and establishment success of mistletoe at different crown height (Kumbasli et al., 2011). Because the canopy cover is low and heterogeneous in size and composition due to harsh soil conditions on upper slope positions (Fig. 4), many stress-tolerant plant species can co-habit. This results higher plant diversity (Fig. 2) and favorable conditions for fruiting woody plants that is the home of frugivore birds carrying out the mistletoe dispersion. The initial harsh condition on the top of slopes finally fosters a diversified plant community characterized by fruiting shrubs and trees, attractive for frugivores, and thus a high density of trees infected by mistletoe, which can also foster tree dieback through parasitism.

4.3. Stand structures shaped by topography

The position on slopes in both catena types controls the forest stand structure. The heterogeneity of tree shapes per plot, i.e., height (ΔH) and DBH (ΔD), increased in the upper elevations, and trees are taller and larger trees in average in lower elevations (Fig. 4). These results support studies showing that the positions along the slope, by contrasting soil quality and microclimatic conditions, modify the shape and growth of plant species in mountain areas (Heydari et al., 2021; Rita et al., 2021; Fazlollahi Mohammadi et al., 2022). Rock cover would favor the establishment and distribution of stress-tolerant plants by creating protection

conditions for them in arid areas (Petersa et al., 2008). Here, the increasing variability in DBH and height differentiation in upper positions is related to the higher diversity of woody plants having different growth rates and shapes, notably *D. mucronata*, *L. nummularifolia*, *P. atlantica*, *Q. brantii*, *C. microcarpa*, *C. pontica*, *A. monspessulanum*, and *A. scoparia*. The aftermath of this species diversity is a high stand structural indices in diameter and height differentiation (Vacek et al., 2021).

The proportion of oak seeders (SOO) or resprouters (OSC) varies along slopes, with seeders dominating in lower positions and, resprouters in the uppers. The environmental limitations of the upper positions, such as shallow soil and steep slopes, as well as the more severe occurrence of the phenomenon of dieback and the oak tree infection with mistletoe causes the reduction of seeder oaks in upper positions and supports the occurrence of resprouters (Meier et al., 2012).

4.4. Woody plant diversity driven by landform pattern

In overall, richness, diversity, and evenness of woody species are distributed according to catena shape and position along the slope (Table S2, Fig. 2). Richness is affected by catena shapes solely if position interplays, while diversity indices are strongly controlled by the shape, convex or concave, the position on slopes, and their interactions. Evenness is mainly by catena shapes, and less by the interacts with position on slopes. This means that the abundance of species, and the proportion of both abundant and uncommon species are modified according to topography. In both catena types (convex and concave), the upper positions revealed higher richness and diversity, which supports the findings of many (Wright, 2002; Cui and Zheng, 2016; Woldu et al., 2020) indicating that the community biodiversity peaks on poor soil on elevated slopes. The presence of different woody species at high elevation in the vicinity of rocks is related to their higher establishment and rooting ability in steep slopes with shallow soil. Diverse and heterogeneous microtopography at high altitudes creates micro-habitats for the establishment of stress-tolerant plant (Mirzaei et al., 2017), resulting a higher diversity (Petersa et al., 2008).

The diverse matrix of this rugged area creates various small-scale habitats. The tolerance ranges and even inter-specific competition ultimately leads to significant variations in diversity and species composition based on catena shape and slope position (Fazlollahi Mohammadi et al., 2017).

4.5. Lower elevation along slopes, oaks refuge area

The results showed that lower elevations on slopes present better soil quality (Table S3), i.e., environmental conditions favoring plant productivity. This observation supports classic concept of topography as one of the main factors that control soil genesis through erosion (Isola et al., 2020; Francos et al., 2021). In lower slope positions, soil is more developed (Sun et al., 2014), and the erosion rate and nutrients with runoff is reduced (Gessler et al., 2000; De Alba et al., 2004). Lower slopes thus benefit from accumulation of clay, organic matter, elemental nutrients and percent base saturation (Miheretu and Yimer, 2018). Gentle slopes are the places of water infiltration. In these conditions, primary productivity should be increased. Soil quality index is significantly affected by landscape topography, which is a common observation in terrestrial ecosystems (Moradi et al., 2019; Raiesi and Tavakoli, 2022). In the present arid context, these lower slopes are a protection zone for trees, notably against tree dieback. Further, lower topography can mitigate the regional environmental stress, improves

tree productivity, and reduces the dieback severity (Drohan et al., 2002; Eckhardt and Menard, 2008).

Interestingly, mature seeder oaks dominate lower elevations along slopes (Table S3), probably resulting from better soil quality, including thicker soil and litter that supply more water, nutrients and soil microorganisms (Fig. 5), a phenomenon that matches other observations indicating that ecosystem quality selects seeders against resprouters (Cowling et al. 2018). Associated to the seeder-trees, canopy cover and tree diameters are larger, and trees per plot are more homogeneous, i.e., ΔH , ΔD (Table S3). The larger canopy cover contributes to favor the litter input (Bazgir et al., 2021) and improves the microclimatic conditions on the ground, a crucial positive feedback in semi-arid ecosystem. All these factors should foster organisms' activity (Wang et al. 2017), and thus the recycling of organic matter and nutrients. In overall ecosystem fertility is higher in lower slope position (Ferry et al., 2010; Lawal et al., 2014; Eslaminejad et al., 2020). Moreover, Kooch et al. (2019) named the toe-slope position 'the hotspot of carbon and nitrogen cycles', while others would name this area as 'tree refugia' (Hampe et al., 2013). In conclusion, soil quality in the semi-arid mountain oak forests is closely related to the topography, fostering 'competitive C-type community' (*sensu* Grime 1977) at lower elevation, regardless of the shapes of catena.

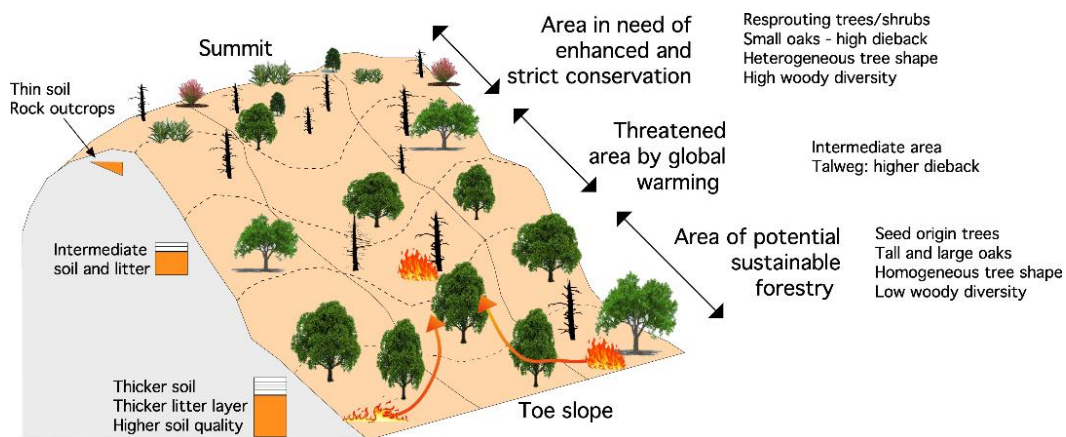


Figure 6. Spatial management guidelines of mountain semi-arid Brant's oak forest considering interplays between ecosystem with topography (slope position, shape of slope) driving soil quality and disturbances pattern, and indirectly plant biodiversity and tree productivity.

4.6. Guidelines for forest management of mountain Zagros forests considering topography

In the Zagros mountain forests, the lower landscape elevations, thanks to their apparent ecosystem productivity, could be eventually used for sustainable forestry practices if they do not alter the forest state (e.g., fuel wood). However, these potential exploitations should remain moderate due to the arid character of these forests at risk of altering for long the ecosystem services of Zagros Mountains (Fig. 6). Restoration measures on lower fertile slopes could be carried out by oak planting or seedlings under the cover of shrubs to counter dieback effects and environmental stresses. In addition, forestry measures can be taken in lower positions for the conversion of coppice to high oak forest to potentially consider a moderate forestry. Considering dieback of Brant's oaks parasitized by mistletoe on the upper slopes, mechanical removal of mistletoe from crowns in conservation areas could be carried out for controlling damage on these iconic trees. Also, in the implementation of conservation and restoration

measures, forest ecosystem management should consider the relationship between vegetation and topography by preserving for biodiversity at upper elevations from all human exploitation, including intermediate slopes to cope global warming and its aftermaths (Fig. 6). Finally, regarding the global warming, the associated risks of wildfires, and the increasing dryness that could affect tree productivity and diversity, tree exploitation in lower landscape elevation remains an issue that the present study cannot solve it-self. Whatever, the upper elevations must be totally protected from any land use regarding their diversity and their usefulness for wildlife, and the intermediate areas corresponding to back slopes must be preserved as well due to risks resulting from global warming, notably the talwegs where trees are more disturbed probably due to higher severity wildfires.

5. Conclusion

The present study showed that topography in forests of the Zagros mountains controls the oak susceptibility to dieback. This control interplays with plant composition and diversity, stand structure and soil quality. We found that slope position is a key driver controlling all variables, but the catena shape, ridge *versus* talweg, is less important, affecting mostly the diversity measurements and variables related to tree dieback. Dieback severity was significantly higher in concave catenas and, varied along the catena with higher values at the shoulder and summit and lower value in the toeslope and footslope. These results are relevant for conservation of semi-arid forests of Zagros mountains, showing that even though tree dieback is high on upper slopes, these positions are crucial for plant diversity and ecosystem functioning (linkage with frugivore birds), where mistletoe infection appears as a proxy of trophic value. Lower elevation, thanks to good soil quality hosts productive oak trees rather preserved from dieback and mistletoe. The dominant landform in the forest areas of western Iran is ridge-valley structures with combined topographic convergence and divergence (catena); therefore, in the implementation of conservation and restoration measures, ecosystem forest management should consider the relationship between vegetation and topography by preserving for biodiversity upper elevations from all human exploitation, including intermediate slopes to cope global warming and its aftermaths.

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Supplementary information

Table S1. Characteristics of the six catena transects, with the altitude above sea level (a.s.l.), elevation between upper and lower altitudes, the length and mean slope of transects.

Transect	Catena type	Upper altitude (m a.s.l.)	Lower altitude (m a.s.l.)	Elevation (m)	Length (m)	Mean slope (%)
1 [^]	Ridge (convex)	2155	1781	374	1995	19
1 ^v	Talweg (concave)	2122	1787	335	1755	19
2 [^]	Ridge (convex)	2131	1846	285	1231	23
2 ^v	Talweg (concave)	2123	1831	292	1516	19
3 [^]	Ridge (convex)	2153	1802	351	1335	26
3 ^v	Talweg (concave)	2126	1848	278	1138	24

Table S2 Results (F-values) of GLMs testing for catena shapes (CS), positions on the slope (CP) and their interaction effects (CS × LS) on the tested dependent variables. * $p < 0.05$; ** $p < 0.01$; ns: not significant. Significant effects are in bold.

Variables	Code	Catena shape (CS)	Catena position on slope (CP)	Shape × Position
<i>Environmental variables</i>				
Litter depth (cm)	LD	6.15 ns	15.21**	0.84 ns
Soil quality index	SQI	2.87 ns	13.91**	4.30*
Rock outcrop (%)	RO	0.37 ns	4.80**	0.54 ns
<i>Stand structure variables</i>				
Total canopy cover (%)	TCC	1.72 ns	12.47**	2.45 ns
Tree canopy infestation by mistletoe (index)	TCIM	1.28 ns	126.28**	9.14**
Diameter at breast height (cm)	DBH	0.132 ns	12.95**	2.59 ns
Diameter differentiation (index)	ΔD	1.18 ns	27.24**	1.17 ns
Height of woody species (m)	Hws	3.67 ns	4.61**	1.03 ns
Height differentiation (index)	ΔH	0.55 ns	5.31**	0.58 ns
Oak sprout-clumps (n)	OSC	7.18*	8.23**	0.37 ns
Seed-originated oak trees (n)	SOO	5.06*	17.40**	2.09 ns
<i>Diversity</i>				
Richness (n)	S	0.81 ns	14.40**	5.13**
Shannon diversity index	H'	42.74**	37.05**	4.17*
Simpson diversity index	D	31.85**	32.19**	5.36**
Evenness (index)	E	15.65**	0.80 ns	5.03**
<i>Dieback severity (index)</i>	DS	57.60**	106.10**	4.60**

Table S3. Mean \pm SE of overstory canopy cover and litter depth across different catena shapes (convex Λ -shaped and concave V-shaped) and positions (SU: summit, SH: shoulder, BS: backslope, FS: foot-slope, TS: toe-slope). Lowercase letters indicate significant differences between catena positions based on Duncan's multiple range test ($p < 0.05$) while uppercase letters indicate differences between catena shapes based on independent t-test

Catena shape	Catena position	TCC	TCIM	Hws
Convex (ridge)	SU Λ	49.47 \pm 0.87 bcd	21.66 \pm 0.88 bc	5.13 \pm 0.48 a
	SH Λ	38.72 \pm 3.16 de	18.33 \pm 0.93 c	5.30 \pm 0.35 a
	BS Λ	42.75 \pm 2.38 cde	13.34 \pm 0.86 d	5.66 \pm 0.40 a
	FS Λ	55.56 \pm 3.40 ab	5.00 \pm 0.34 e	5.36 \pm 0.16 a
	TS Λ	61.92 \pm 2.73 a	0 f	6.10 \pm 0.23 a
	Mean		48.74 \pm 2.10 A	11.66 \pm 0.76 A
Concave (talweg)	SUV	36.24 \pm 1.47 e	25.00 \pm 2.88 ab	4.16 \pm 0.44 b
	SHV	46.18 \pm 4.9 bcde	27.33 \pm 0.78 a	5.43 \pm 0.12 a
	BSV	47.51 \pm 3.89 bcde	10.00 \pm 1.88 d	5.13 \pm 0.29 a
	FSV	50.86 \pm 2.70 bc	0 f	5.30 \pm 0.20 a
	TSV	60.80 \pm 1.86 a	0 f	5.73 \pm 0.26 a
	Mean		51.06 \pm 3.36 A	12.46 \pm 0.68 A
	Catena position	DBH	OSC	SOO
Convex (ridge)	SU Λ	13.63 \pm 0.37 b	8.00 \pm 1.15 abc	0.33 \pm 0.001 c
	SH Λ	16.33 \pm 0.55 b	8.00 \pm 0.57 abc	0.66 \pm 0.005 c
	BS Λ	16.73 \pm 1.82 b	6.33 \pm 0.88 cd	1.33 \pm 0.04 b
	FS Λ	27.00 \pm 2.88 a	4.66 \pm 0.88 d	3.00 \pm 0.21 a
	TS Λ	27.33 \pm 3.17 a	4.33 \pm 0.33 d	3.00 \pm 0.21 a
	Mean		20.20 \pm 2.51 A	6.26 \pm 0.56 B
Concave (talweg)	SUV	16.80 \pm 1.63 b	10.00 \pm 1.52 a	0 c
	SHV	15.50 \pm 0.76 b	9.00 \pm 0.33 ab	0 c
	BSV	17.70 \pm 1.38 b	7.00 \pm 1.50 bcd	1.00 \pm 0.04 b
	FSV	16.03 \pm 1.05 b	6.33 \pm 0.88 cd	1.00 \pm 0.04 b
	TSV	30.46 \pm 4.04 a	5.66 \pm 0.76 cd	3.33 \pm 0.18 a
	Mean		19.3 \pm 2.11 A	7.60 \pm 0.49 A
	Catena position	LD	RO	SQI
Convex (ridge)	SU Λ	2.33 \pm 0.33 cd	23.33 \pm 4.40 ab	0.61 \pm 0.004 e
	SH Λ	2.01 \pm 0.57 d	18.33 \pm 1.66 abc	0.62 \pm 0.005 de
	BS Λ	3.50 \pm 0.28 bc	11.66 \pm 3.32 c	0.65 \pm 0.003 bc
	FS Λ	4.50 \pm 0.28 ab	11.64 \pm 1.65 c	0.61 \pm 0.009 e
	TS Λ	4.16 \pm 0.44 b	8.23 \pm 1.58 c	0.67 \pm 0.001 ab
	Mean		3.30 \pm 0.23 A	14.65 \pm 1.85 A
Concave (talweg)	SUV	2.83 \pm 0.60 cd	25.00 \pm 2.85 a	0.64 \pm 0.001 bcd
	SHV	2.51 \pm 0.50 cd	15.00 \pm 2.78 abc	0.63 \pm 0.004 cde
	BSV	4.33 \pm 0.32 ab	13.33 \pm 1.66 bc	0.61 \pm 0.005 e
	FSV	4.50 \pm 0.50 ab	11.66 \pm 1.23 c	0.63 \pm 0.003 cde
	TSV	5.66 \pm 0.16 a	15.00 \pm 2.23 abc	0.70 \pm 0.005 a
	Mean		3.96 \pm 0.35 A	16.00 \pm 2.21 A

Note: canopy cover (TCC), litter depth (LD), height of woody species (Hws), diameter at breast height (DBH), number of oak sprout-clumps (OSC), number of seed-originated oak trees (SOO), canopy infestation by the mistletoe (TCIM), rock outcrop (RO) and soil quality index (SQI).