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Structural Dynamics and Successional Trajectories in Zagros Mountain Oak Coppice Forests

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ABSTRACT

Aims: Understanding the structural dynamics of unmanaged oak coppices is crucial, as many of the world's forests remain unmanaged. While previous studies have focused on coppice dynamics in mesic woodlands, there needs to be a more significant gap in understanding these processes in semi-arid regions. The study aims to examine the structural modifications, successional trajectories, and floristic diversity within semi-arid oak coppices in the Zagros Mountains, utilizing a comprehensive dataset obtained from an extensive land survey.

Materials & Methods: The study was conducted in a 175 km strip of Zagros Mountain forests dominated by *Quercus brant ii*. Ninety-four even-aged stands from 14 forests were selected. Structural attributes were evaluated, including tree density, basal area, canopy cover, and floristic diversity measures. A list of vascular flora was documented for each successional stage using the Raunkiær plant life-form classification. Data analysis involved polar ordination, clustering, and multivariate techniques.

Findings: Density, Holdridge complexity index, basal area, and cover were identified as the most influential variables. Two main trajectories, progressive and retrogressive, were identified, with eight successional stages. Significant differences in structural variables were observed across trajectories, with floristic diversity peaking in the middle stages. The later stages of the progressive trajectory showed a significant increase in the relative cover and basal area of *Fraxinus rotundifolia*. The study demonstrates the existence of a progressive successional trajectory in unmanaged coppice forests influenced by disturbances. Stand age, mean diameter of sprout clumps, and flora diversity do not solely determine the successional stages within this trajectory.

Conclusion: While transforming Zagros Mountain oak coppice into high forests is unlikely, there is potential for redirecting succession toward more resilient and diverse ecosystems. We recommend management interventions beyond protection, promoting uneven-aged stands, increasing density and cover, and encouraging species like *Fraxinus*. These strategies can enhance ecological integrity and foster sustainable woodland ecosystems in the Zagros region.

Keywords: Woodland Resilience; Floristic Diversity; Vegetative Regeneration; *Quercus brantii*; Semi-arid Forests.

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Introduction

Coppice forests, characterized by their vegetative regeneration after cutting, are widespread in Mediterranean and semi-arid regions. While managed and unmanaged coppices can potentially develop into high forests [1], the assumption that this transformation is inevitable for unmanaged and abandoned coppices remains debated. Various factors influence the progression towards stands dominated by single-stemmed, seed-originated trees, necessitating a closer examination of coppice dynamics in different ecological contexts[2]. While numerous studies have focused on coppice dynamics in stands and woodlands transitioning into high forests [3, 4], there have also been investigations specifically dedicated to understanding the dynamics of unmanaged and abandoned coppices [3, 5, 6]. Understanding the dynamics of unmanaged coppices is essential because a significant portion of the world's forests remains in this state [7, 8], including millions of hectares of coppices in the Zagros Mountains 10]. Coppices undergo significant structural changes as they age, leading to variations in community composition and species replacement [11]. The dynamics of structural changes in coppices can resemble different ecosystems, and their adaptability to disturbances and climate change is noteworthy. These dynamics may sometimes resemble thicket, savanna, or high-forest ecosystems. These structural dynamics can involve repeated cycles of growth and disturbance without progressing toward a more stable state [8, 12]. In such scenarios, unmanaged coppices are nature's response to persistent disruptive conditions, exhibiting greater adaptability to anthropogenic pressures [13] or climate change [14]. For instance, a significant relationship between the oak tree leaf area index and temperature in the Zagros region partially confirmed the relationship between declining oak trees and increasing temperature [15].

While numerous studies have delved into the dynamics of coppices across a range of forest types, encompassing mesic coppice woodlands, more research still needs to be done on coppice dynamics in arid and semi-arid regions [16]. The significance of studying coppice dynamics becomes particularly pronounced when considering some unique aspects of these ecosystems. These coppices present a distinct advantage due to the relatively short period of shoot growth, which minimizes overlap with potential successional processes [5, 8]. Furthermore, the highly homogeneous nature of these coppices provides an opportunity to determine the progressive order of forest development by examining the characteristics of shoot clumps, including the number, size, and orientation of shoots [17].

The relationship between forest stand structural properties and floristic diversity is critical to ecosystem dynamics, particularly in coppice systems. Previous studies in other forest ecosystems have shown that stand structural complexity often correlates positively with plant species diversity [6, 18]. However, this relationship can be non-linear and context-dependent, varying with forest type, successional stage, and environmental conditions. In Mediterranean-type ecosystems, for instance, moderate levels of canopy cover have been associated with higher understory diversity due to the creation of favorable microhabitats [19].

A notable drawback in studying coppice dynamics in semi-arid regions is the significant variability in resilience under different disturbances, such as grazing and severe drought. This can significantly reduce coppices' resilience, leading to degraded vegetation and lower productivity [20]. Understanding coppice dynamics under constant disturbance in arid and semi-arid climates can provide insights into growth, productivity, and ecological benefits [18].

The Zagros forests in western Iran are

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crucial for forest succession studies due to their unique ecological characteristics and historical continuity. These oak-dominated forests, experiencing common hot semi-Mediterranean conditions, offer diverse microclimates and altitudinal gradients [10, 21]. Their structure is shaped by long-term human influence, resulting in coppiced and even-aged stands [20, 22]. This mosaic of habitats at various successional stages offers valuable insights into ecosystem responses to disturbances and climate change in semi-arid mountain environments.

The primary objective of this study is to examine the structural modifications, successional trajectories, and floristic diversity within semi-arid oak coppices, utilizing a comprehensive dataset obtained from an extensive land survey. The study focuses on one of the world's most extensive unmanaged oak coppice forests in a biogeographic region characterized by a hot summer Mediterranean climate [23]. The analysis includes multiple stages of ecological succession because we carefully selected representative stands from a vast geographic region. The focal goal of this study is to distinguish appropriate indices for each stage of succession to understand their effects on plant community diversity better.

We hypothesize that unmanaged coppice forests undergo distinct structural transformations over time, exhibiting multiple successional trajectories characterized by variations in stand structure. We predict that floristic diversity will increase uniformly across these trajectories as succession progresses. Additionally, we expect that tree species' relative abundance will vary across stages of progressive succession, reflecting improvements in ecological conditions. Furthermore, we anticipate that a combination of structural indices will effectively differentiate between the various successional stages within the Zagros oak coppices.

Materials & Methods

Study Area

The study was conducted in a 175 km long strip of land in the Zagros Mountains forest region, between latitudes 31.3° and 32.5° N and longitudes 49.6° and 51.3° E (Figure 1). The region has a hot-summer Mediterranean climate according to Köppen's classification system or a Mediterranean continental climate according to the Global Bioclimatic classification system [24]. mean annual precipitation ranges from 470 to 990 mm, with an east-to-west gradient. The mean annual temperature is 14.8°C, with fluctuations of 1.5°C due to altitude [25].

The region is characterized by extensive woodlands, historically managed as coppices but largely unmanaged. These woodlands form an interconnected landscape dominated by *Quercus brantii* Lindl, with trees typically growing in multi-stemmed clumps resulting from past coppicing practices [26]. Four other major tree species are present: *Fraxinus rotundifolia* Mill., *Pistacia atlantica* Desf., *Crataegus azarolus* L., and *Acer monspessulanum* L. Other tree species include *Celtis caucasica* Willd., *Cerasus mahaleb* L., *Juniperus excelsa* M.Bieb., *Platanus orientalis* L., *Pyrus syriaca* Boiss., and *Ulmus minor* Mill. are also found in certain parts of the region.

Since the nationalization of forests in Iran in 1963, there have been no wood or charcoal exploitation projects in the study area. However, small livestock have illegally coppiced and grazed the woodlands, resulting in even-aged stands with an mean maximum age of less than a century [20, 21].

Stand selection and data collection

Extensive field travel and record reviews were conducted in the coppiced woodlands to select suitable stands. A total of 14 even-aged forests were selected for the study. Stands were classified as even-aged based on three main criteria: (1) uniform canopy

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structure with minimal vertical stratification, (2) a narrow range of stem diameters, and (3) a normal diameter class distribution for trees with mean diameter >10 cm. The term “forest” in this paper refers to an integrated group of stands on one or different sides of a mountainous terrain. Within these forests, 94 visually 0.5 ha even-aged stands with minimal rockiness and slope were selected (Figure 1 and Table 1).

The structural attributes of the stand evaluated or derived in this investigation encompassed phanerophyte richness (S), density of shoot clumps (density), canopy coverage percentage (cover), mean basal diameter (D), mean height (h), relative density (RD_i) = (individuals of tree species i / total individuals) × 100; relative cover (RC_i) = (cover of tree species i / total cover) × 100; relative dominance (RBA_i) = (basal area of tree species i / total basal area) × 100; relative frequency (RF_i) = (frequency of tree species i / sum of all frequencies) × 100 and importance value index (IVI) = RD + RC + RBA. The basal area (BA) was computed as the cumulative cross-sectional area of shoots. The top height ($_{top}$) was determined by averaging the measurements of the 50 tallest shoot clumps. The standing wood volume (V) was estimated using locally calibrated allometric equations [27]. Additional variables, such as the importance value index (IVI) [28] for each tree species, Holdridge complexity index (HCI) [29], tree diversity (Shannon-Weiner and Simpson diversity, Shannon evenness indices) [30], and tree distribution pattern index [31], were also quantified.

In each stand, vascular plant composition was recorded, and the proportion of the fifth biological spectrum was assessed based on Raunkiær life-form classification, which includes five classes (chamaephytes, cryptophytes, hemicryptophytes, phanerophytes, and therophytes). A botanist identified plant

Table 1) Mean altitude, climatic characteristics, main tree species, and number of stands in the selected forests.

Forest Local Name	Abbreviation	Altitude (m)	Mean Annual Precipitation (mm)	Mean Annual Temperature (°C)	Dominant Tree	Co-dominant Tree	Number Of Stands
Bajgiran	*Ba*	1934	551	13.24	*Crataegus*	*Quercus*	3
Berjooei	*Be*	2115	503	12.07	*Quercus*	*Pistacia*	4
Chahgah	*Cg*	1754	531	14.52	*Quercus*	*Acer*	7
Chebd	*Ch*	1783	990	14.42	*Quercus*	*Crataegus*	5
Chehartagh	*Ct*	2231	519	11.15	*Crataegus*	*Fraxinus*	6
Dvorak	*Dr*	1572	556	15.62	*Quercus*	*Crataegus*	12
Dopolan	*Do*	1686	551	15.11	*Quercus*	*Pistacia*	7
Gandomkar	*Gd*	2029	589	12.63	*Quercus*	*Pistacia*	6
Garab	*Ga*	1823	953	13.97	*Quercus*	*Fraxinus*	8
Helen	*He*	1476	557	16.14	*Quercus*	*Crataegus*	12
Pahnoos	*Pa*	1534	765	15.83	*Quercus*	*Fraxinus*	4
Sarkhoon	*Sa*	1689	603	15.00	*Quercus*	*Pistacia*	6
Shamsabad	*Sh*	1971	470	13.15	*Pistacia*	*Fraxinus*	4
Tarom	*Ta*	1695	849	15.15	*Quercus*	*Crataegus*	10

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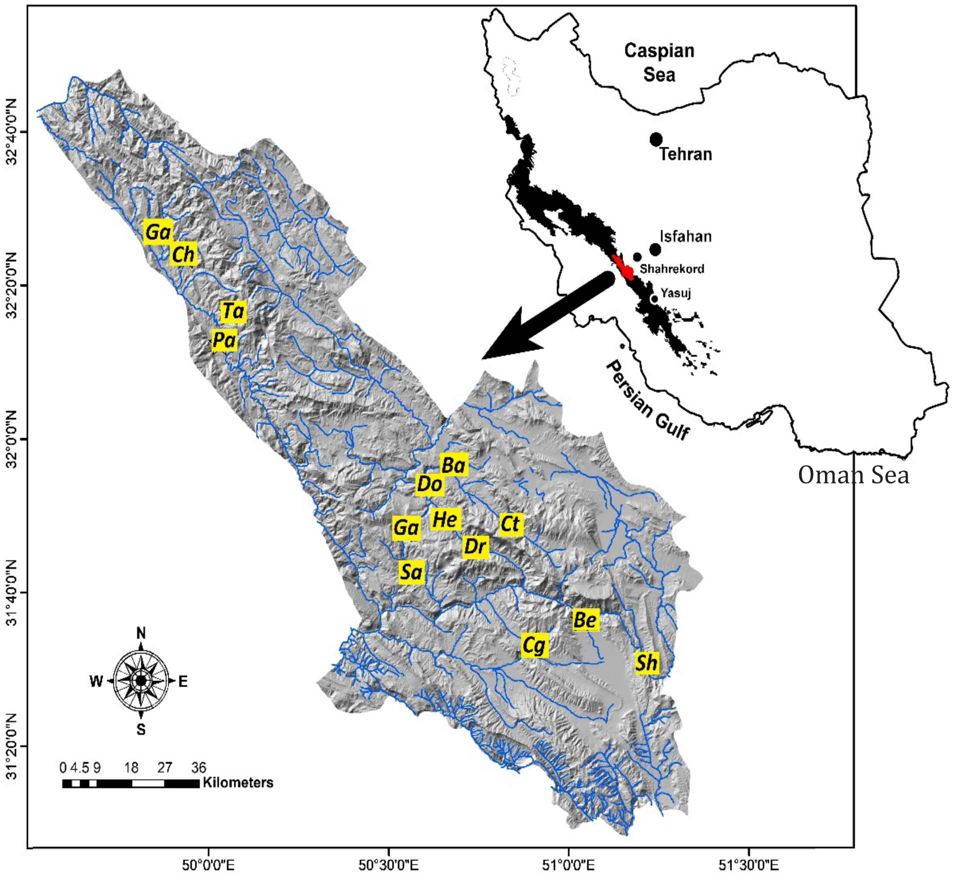

Figure 1) The selected forests, written as two-letter abbreviations (see Table 1), are located in a region of the upper Karun River basin. The area is also part of the Zagros Forests (the black area on the map of Iran).

Table 2) The ranking of the first 14 variables used in the polar ordination of stands based on Kendall rank correlation coefficient (Tau) and coefficient of determination (R^2) along the first axis.

Rank	Variable	Mean ± StD	Tau	R^2	Rank	Variable	Mean ± StD	Tau	R^2
1	Density	135.8±80.5	0.86	0.89	8	Shannon-Weiner	0.5±0.4	0.15	0.02
2	HCI	76.3±141.4	0.85	0.65	9	Distribution	1.8±0.7	-0.13	0.05
3	BA	11.2±8.7	0.63	0.62	10	Simpson	0.2±0.2	0.13	0.02
4	Cover	30.4±19.9	0.60	0.61	11	h	6.5±1	-0.10	0.02
5	V	26.5±15.8	0.56	0.48	12	Evenness	0.3±0.2	0.08	0.01
6	S	5.1±1.9	0.39	0.26	13	h_{top}	10.1±1.7	-0.01	0.00
7	D	17.6±4.3	-0.15	0.05	14	$IVI_{Fraxinus}$	0.1±0.2	0.00	0.01

species using a local flora reference [32]. We measured critical structural attributes: number of shoots per stool (multi-stemmed clump), crown projection area, basal diameter, and height of shoots ≥10 cm. Shoot age was estimated using an exponential relationship between diameter and age [20]. We used the mean number of shoots per stool to indicate stand age (Age index) [33]. In this index, a higher number of shoots indicates a younger stand, while a stand where all clumps are single-stemmed is considered 100% old. This approach allows us to estimate relative stand age without destructive sampling.

Data analysis

Data were standardized using z-score transformation in which z = (x - μ) / σ, where z is the z-score, x is the original value, μ is the mean of the variable, and σ is the standard deviation of the variable. A polar ordination with Sorensen distance measure and variance-regression endpoint selection method was used to determine the most influential variables. Polar analysis is a technique used to explore and visualize the relationships between variables in a circular or polar coordinate system, allowing for the identification of directional patterns, angular dependencies, and asymmetries in multivariate data. The selected variables had the highest absolute Kendall rank correlation coefficient (Tau) and coefficient of determination (R^2) along the first Bray-Curtis axes. The range of each influential variable was divided into three classes, and stands outside the cut-off points were removed from the analysis. In addition, stands that lie above an upper boundary line (the two times standard deviation with maximum flexibility) were excluded from further analysis (PC-ORD statistical software).

Hierarchical cluster analysis using the median linkage and Euclidean distance agglomeration method was performed on the Euclidean distance to group stands based on similarity. The stand age index gradient was added for a chronological perspective. Principal component analysis (PCA) was conducted on influential variables. The scoring values from the first two PCA components and their corresponding age indices were used in a binned scatter plot. To visualize possible progressive or retrogressive trajectories, the stands were scaled by their closest neighbor stands in the PCA scoring plot, but only if they belonged to the same age class. This allowed the stands to be positioned in the plot based on their similarity to neighboring stands of the same approximate age. Additionally, ANOVA (Analysis of Variance) was employed to statistically compare the characteristics of the different successional stages identified through the analysis (Minitab statistical software).

Findings

Polar ordination showed higher variation and distinguished forests along the gradient.

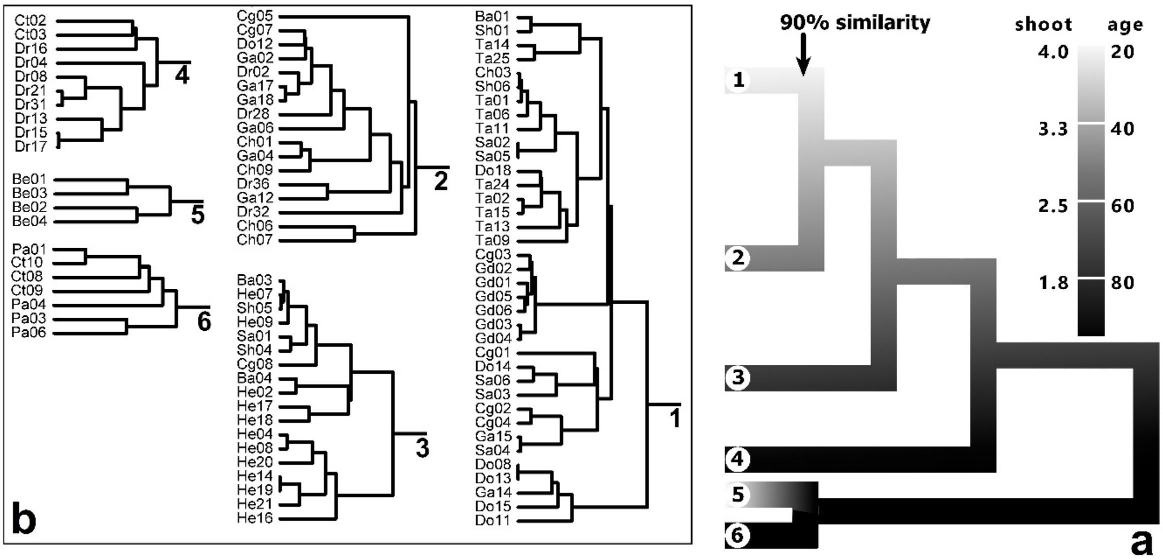

Figure 2) Hierarchical clustering of selected stands based on influential variables. (a) Chronological dendrogram projection using stand age index gradient. (b) Six numbered clusters with 90% similarity as potential successional stages.

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As a result, the ranking was done based on the absolute values of Tau and R^2 coefficients along axis 1, where the top 14 forest variables were ranked, as shown in Table 2. Four variables (density, HCI, BA, and cover) were identified as the most influential.

Using the four most influential variables, the stands were classified into 70, 31, and 6 main clusters based on similarity levels of 99%, 95%, and 90%, respectively. We determined that a 90% similarity level was enough to identify potential successional stages in the dendrogram (Figure 2a). Despite their age, these stands' high density and cover positioned them next to the oldest stands in the 6th cluster (Figure 2b). Therefore, the clustering analysis represented the successional stages and did not indicate the possible chronological paths.

PCA analysis revealed two distinct successional trajectories: progressive and retrogressive (Figure 3a). The distribution of stands along PCA axis 1 showed a general consequential gradient, with older stands typically having higher variable values. However, some exceptions were noted, particularly among young stands in the Be forest and those exhibiting retrogressive trends.

Using a color-ranking technique based on selected variables, we refined our analysis to focus on 81 stands that fit clearly into either progressive or retrogressive trajectories. These stands represented 8 successional stages - 5 in the progressive trajectory and 3 in the retrogressive trajectory. The identified stages aligned well with cluster scores and PCA results (Figure 3b), providing a robust framework for understanding forest succession in this ecosystem.

Table 3) Kendall rank correlation coefficients (Tau) and coefficients of determination (R^2) for the first two components of the principal component analysis based on the four selected variables.

Variables	PCA1		PCA2	
	Tau	R^2	Tau	R^2
HCI	-0.89	0.93	-0.30	0.06
Density	-0.88	0.83	-0.53	0.16
BA	-0.66	0.70	-0.18	0.01
Cover	-0.54	0.69	-0.22	0.01

Precipitation and temperature increased

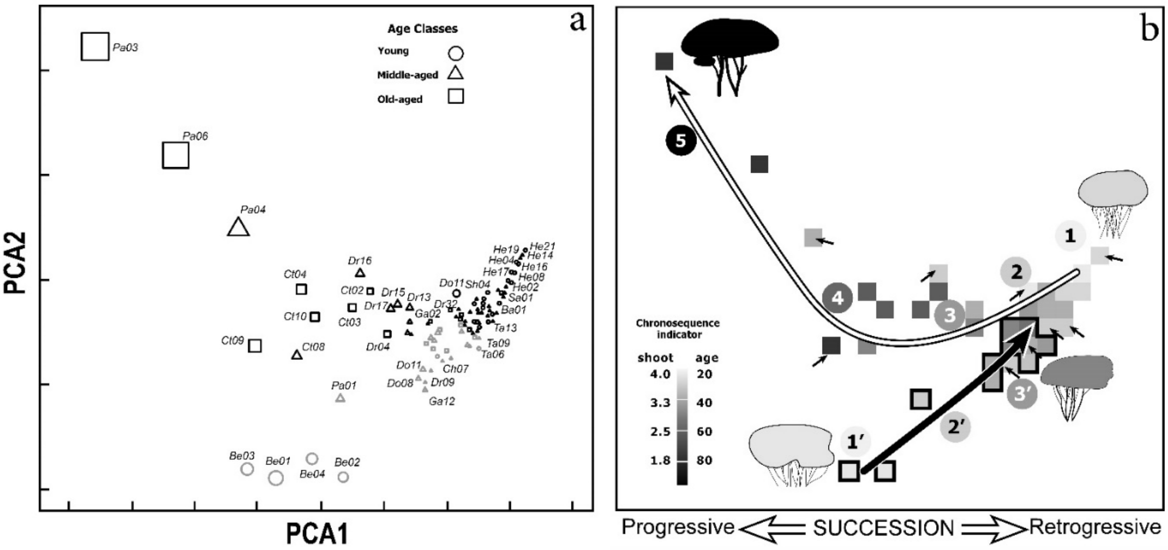

Figure 3) (a) PCA score plot showing stand distribution, weighted by HCI. Stands are classified by age/shoots-per-stool categories. Black and gray points represent progressive and retrogressive trajectories. (b) Identified trajectories based on PCA and cluster scores. Colored numbers indicate successional stages. Prime numbers represent retrogressive trajectory stages.

Table 4) The mean ($\bar{X}$) and standard deviation (StD) of variables measured for the final selected stands are classified into successional stages of (a) progressive and (b) retrogressive trajectories. Significant differences between variables were determined using one-way ANOVA tests to compare the means of each variable across the successional stages. Variables with inter-seral significant differences (one-way ANOVA) are labeled as * for >95% and ** for >99% confidence level. (a) (N = 59, df = 4)

Variable	$\bar{X}$ ± StD	Variable	$\bar{X}$ ± StD	Variable	$\bar{X}$ ± StD	RBA_A	$\bar{X}$ ± StD	Variable	$\bar{X}$ ± StD	Variable	$\bar{X}$ ± StD
Density	109.8 ± 56.7**	V	25 ± 15.8**	RD_{others}	4.2 ± 8.9	RC_{others}	6.4 ± 12.9	IVI_Q	2.3 ± 0.9	S	4.9 ± 1.9*
Cover	28.6 ± 15**	RD_Q	76.2 ± 32.6	RC_Q	80 ± 30.9	RBA_Q	71.7 ± 29.7	IVI_P	0.2 ± 0.3	HCI	57.6 ± 28.8**
D	19.5 ± 5.1**	RD_P	5.9 ± 9.4	RC_P	6.2 ± 9.8	RBA_P	9.1 ± 9.8	IVI_A	0.1 ± 0.1	Shan	0.5 ± 0.2
h	6.4 ± 1	RD_A	2.5 ± 3.9	RC_A	2 ± 3.1	RBA_C	6.2 ± 8.1	IVI_C	0.2 ± 0.2	Simp	0.2 ± 0.1
h_{top}	9.8 ± 1.9	RD_C	8 ± 12.7	RC_C	2.2 ± 3.5	RBA_F	4.2 ± 7.7**	IVI_F	0.1 ± 0.2	Even	0.3 ± 0.0
BA	10.5 ± 8.1**	RD_F	4.9 ± 9.5	RC_F	3.3 ± 7.3*	RBA_{others}	6 ± 11.1	IVI_{others}	0.2 ± 0.3	Dist	1.8 ± 0.6

(b) (N = 22, df = 2)

Variable	$\bar{X}$ ± StD	Variable	$\bar{X}$ ± StD	Variable	$\bar{X}$ ± StD	RBA_A	$\bar{X}$ ± StD	Variable	$\bar{X}$ ± StD	Variable	$\bar{X}$ ± StD
Density	175.5 ± 81.1**	V	23 ± 16.6	RD_{others}	1.5 ± 1.9	RC_{others}	3.2 ± 4.1	IVI_Q	2.4 ± 0.5	S	6.2 ± 1.8**
Cover	36.3 ± 22.5**	RD_Q	81.2 ± 20.4	RC_Q	85.4 ± 15	RBA_Q	76.3 ± 17.0	IVI_P	0.1 ± 0.0	HCI	109.4 ± 58.1
D	16.6 ± 3.9**	RD_P	3.0 ± 2.1	RC_P	3.2 ± 2.2	RBA_P	5.5 ± 2.6	IVI_A	0.1 ± 0.1	Shan	0.5 ± 0.5
h	5.6 ± 1.1	RD_A	3.8 ± 4.1	RC_A	2.5 ± 3.7	RBA_C	6.7 ± 7.7	IVI_C	0.2 ± 0.2	Simp	0.2 ± 0.2
h_{top}	9.1 ± 0.4	RD_C	8.3 ± 11.8	RC_C	3.0 ± 3.4	RBA_F	3.7 ± 4.2	IVI_F	0.1 ± 0.1	Even	0.3 ± 0.2
BA	10.0 ± 6.2**	RD_F	2.1 ± 2.2	RC_F	2.6 ± 2.8	RBA_{others}	3.2 ± 3.1	IVI_{others}	0.1 ± 0.1	Dist	1.5 ± 0.5

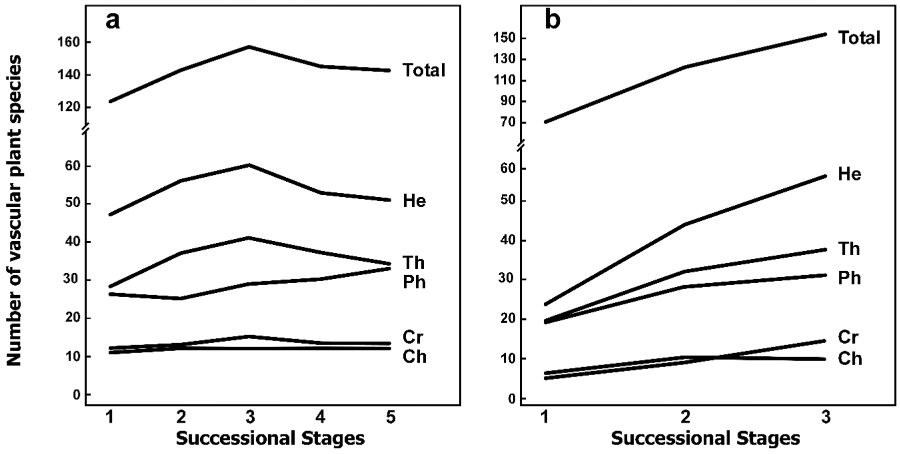

Figure 4) Changes in the total number of vascular plant species along (a) progressive and (b) retrogressive trajectories concerning the Raunkiær plant-life form classification. Ch: chamaephyte, Cr: cryptophyte, He: hemicryptophyte, Ph: phanerophyte and Th: therophyte.

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along the retrogressive trajectory, but no pattern was observed in the progressive trajectory. Significant differences were found in nine variables for the progressive trajectory, with increases in most variables as succession progressed. The retrogressive trajectory showed significant differences in five variables, with decreasing cover, density, and BA as aged (Table 4). Fraxinus's relative cover (RC_F) and relative basal area (RBA_F) have changed significantly in the progressive trajectory, while no change has been observed in the retrogressive trajectory. This differential response suggests that Fraxinus's presence and increased abundance are associated explicitly with improving ecological conditions and forest progression (Table 4).

A total of 185 species of vascular plants were identified in the study area. Phanerophyte richness increased in both trajectories, as did the number of phanerophytes and other Raunkiær plant life forms. In contrast, the number of cryptophytes, hemicryptophytes, and therophytes decreased in the later stages of the progressive trajectory. The number of chamaephytes remained relatively stable in both trajectories (Figure 4).

Discussion

Our study provides novel insights into the complex structural dynamics of unmanaged coppice woodlands in the semi-arid Zagros region, challenging conventional assumptions about coppice succession. By employing a multivariate approach across a wide geographic area, we identified multiple successional trajectories influenced by a combination of factors rather than following a simple, linear path driven primarily by stand age or specific disturbances. This finding contrasts with previous studies that have often focused on stand age or particular disturbance events as the main drivers of succession in coppice systems [5, 6, 12]. Our results suggest that the conventional view of coppices inevitably progressing towards high forest [34] may not apply in these ecosystems. Instead, we observed progressive and retrogressive trajectories, indicating a more nuanced and dynamic successional process.

Our study, in line with previous findings [9, 17], proposes that coppice woodlands do not represent primary stages of successional trajectories leading to high forests. Instead, they are part of a relatively rotating static trajectory. Consequently, despite apparent differences in age and ontogeny, the structural dynamics and stages among these stands may vary significantly. An age-independent structural dynamics analysis could also be applied to high forests [35].

Previous studies of forest community dynamics have used the stepwise selection process [36]. Through multivariate analysis, these 94 stands represented different stages and trajectories of coppice structural dynamics. This study introduces a novel approach where stands do not have to be in the same forest or area. Subsequently, stands whose mean age did not match their successional stage were excluded, resulting in 81 stands. This method can potentially study succession in unmanaged coppice forests and other regularly disturbed even-aged forests in semi-arid regions.

Various structural indices have been proposed to identify different stages of succession in high forests, but they often prove inconclusive, particularly for unmanaged coppices with shorter ontogeny and frequent disturbances. Consistent with previous work [37], the unmanaged oak woodlands in the Zagros region have shown limited species turnover over an extended period, with Quercus dominating for about two thousand years. Our survey of central Zagros protected areas confirms that Quercus remains the dominant tree species, making

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up over 80% of density and cover, except in a few Ct and Sh forests. Therefore, while plant species replacement may occur in Zagros, it is not observed at the level of dominant tree species. Instead, it involves changes in other aspects of plant growth despite rapid climate change in recent decades. In contrast to mesic woodlands, where the decline in stem count corresponds with the growth of shrubs [38], the lack of regeneration and growth constraints in Zagros forests hinder species turnover by undergrowth shrubs.

This study reveals that mean stand height and dominant height remain consistent across all stages of coppice structural dynamics. Without pruning or selective standards, the epicormic shoots in Zagros coppices reach an mean height of 6 to 7 meters, making it unfeasible to differentiate successional stages based on the number of strata [39]. Due to hydraulic limitations and the light requirements of trees in Zagros, a single canopy stratum exists in unmanaged coppices. The lack of variation in mean height contradicts the significant impact of the density index, highlighting the unique characteristics of successional studies in coppices [40]. Density and cover are critical indicators of forest degradation in the region [41], significantly distinguishing successional stages in both progressive and retrogressive trajectories. Early-stage successional stands have low cover, density, eroded soils, shallow topsoil, and a higher proportion of shrubs to trees. BA, mean diameter (D), and density reflects both trajectories' structural deterioration or improvement. BA captures ontogeny and succession, influenced by standing wood volume (V) in progressive trajectories [21,42]. BA is a more comprehensive indicator than shoot diameter, signifying ontogeny and successional progress.

The progressive trajectory demonstrates a notable change in relative cover and basal area (BA) of *Fraxinus*, a nutrient-rich soil-loving mesophyte commonly found in moist and deep soils in the Zagros region. The higher proportion of *Fraxinus* in the later stages of the progressive trajectory indicates an improvement in ecological habitat conditions.

Our results show that phanerophyte richness (S) increases with coppice stand age, regardless of other structural changes. In the progressive trajectory, we observed an increase in phanerophytes, while other vegetation forms and overall flora increased only until the third stage. We propose two possible explanations for this pattern: 1- Higher floristic diversity may occur in the intermediate stages of forest succession rather than in the final stages. However, this may not fully apply to the unmanaged coppices in our study. 2- Floristic diversity changes might be related to temperature and precipitation variations in the retrogressive trajectory, while no such linear relationship was observed in the progressive trajectory. Our findings align with Müllerová et al. (2015) [6], who noted that the dominant tree species composition influences floristic diversity in coppice succession. In diverse woodlands, especially in semi-arid or Mediterranean regions, plant species richness can vary considerably throughout coppice structural development. Plant species richness varies throughout coppice structural dynamics in diverse woodlands, particularly semi-arid or Mediterranean regions. Biodiversity may rise or decline [43] during successional stages without following a specific trend. Fluctuating and humpback [44] patterns of biodiversity changes can occur depending on environmental conditions. This complex pattern of diversity changes highlights the need to interpret successional processes in these ecosystems carefully.

If the selected stands in this study had undergone severe disturbance, the increase in plant biodiversity, especially

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hemicryptophytes (He), would have been unexpected. However, since researchers intentionally chose the stands, they cannot be classified as disturbed forests compared to reports of reduced biodiversity from severe disturbances. The intersection of the progressive and retrogressive trajectories corresponds to stages 3 and nearby 3'. This implies that plant biodiversity peaks before the progressive trajectory's final stages (4 and 5). The alternative view is that the selected stands may have been affected by varying degrees of environmental disturbances before successional processes took place [22]. Ironically, stages 3 and 3' are at a mid-level of protection and exhibit the highest floristic diversity following the intermediate disturbance hypothesis [5, 45].

Conclusion and Management Implications

Our study of unmanaged coppice forests in the Zagros region reveals complex structural dynamics, supporting our hypothesis of distinct structural changes over time. We identified multiple successional trajectories, including both progressive and retrogressive trajectories, confirming our prediction of varied developmental patterns characterized by changes in stand density, basal area, and canopy cover. Phanerophyte richness increased with coppice stand age across both successional trajectories. Contrary to the hypothesis that floristic diversity would increase uniformly with successional stages, other vegetation forms and overall flora diversity peaked at intermediate stages, providing partial support for the intermediate disturbance hypothesis. The expected changes in the relative abundance of tree species along the successional trajectories were supported by a notable increase in Fraxinus's relative cover and basal area during the progressive trajectory's later stages, confirming its potential as an indicator of succession towards more favorable habitat conditions. Additionally, the combination of structural indices, including the Holdridge complexity index, effectively differentiated between the various successional stages, supporting our hypothesis on the utility of these indices in identifying successional stages in unmanaged coppice forests.

While our results suggest a potential for redirecting succession, transforming coppices into high forests is unlikely due to decreased shoot production in densely grown stands. Instead, aging stems in sprout clumps can lead to decline or dieback without rejuvenation measures. Managing coppice forests is complex, especially when biodiversity and climatic conditions do not align with desired successional processes. We recommend management interventions beyond protection, promoting uneven-aged stands, increasing density and cover, and encouraging tree species like Fraxinus. These strategies can enhance resilience and ecological integrity, fostering diverse and sustainable woodland ecosystems in the Zagros Region.

Our findings highlight the need for adaptive management approaches that consider unmanaged coppice systems' unique dynamics in semi-arid regions. Future research should focus on long-term monitoring of these systems to better understand their resilience to climate change and anthropogenic pressures and refine management strategies accordingly.

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