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Recolonization by Indigenous broadleaved species of a conifer plantation (*Cupressus* spp.) in Northern Iran after 25 years

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Abstract

Key message: A vegetation analysis revealed the extent of recolonization by native vegetation of a 25-year-old *Cupressus* spp. plantation in northern Iran. A young indigenous *Quercus-Carpinus* community replaced the conifers in the low-slope areas with deeper, heavier, and more fertile soils.

Context: Reforestation of degraded or clear-cut-harvested lands can modify site conditions, facilitating succession and reestablishing native forests. It is critical to investigate the plantation in terms of vegetation, natural regeneration, and environmental variables to better understand ecological restoration.

Aims: This study examines the recolonization of a Cypress plantation by native vegetation in the deforested Hyrcanian broadleaf forests and determines which edaphic, topographic, and structural variables are correlated to the degree of reconstitution.

Methods: A systematic random sampling method was used to establish 55 plots in a 25-year-old *Cupressus* plantation, followed by plot classification using TWINSpan and environment-vegetation analysis using CCA. The classification groups were compared using an analysis of variance. Tested variables included floristic composition, stand structure, regeneration, topography, and soil parameters.

Results: Four vegetation groups were identified based on an analysis of floristic composition. The first group demonstrated the least degree of native forest reconstitution, as planted conifers (*Cupressus* spp.) were established alongside pioneer broadleaf shrubs, enhancing *Zelkova carpinifolia* (Pall.) K.Koch regeneration. While most conifers disappeared in the third group, *Carpinus betulus* L., *Zelkova carpinifolia*, and *Quercus castaneifolia* C.A. Mey became dominant. The most influential environmental factors in reestablishing indigenous communities were a low-slope, heavier soil with a higher organic carbon and potassium content.

Conclusion: On low-slope lands with fertile soils, the Hyrcanian native broadleaf forest can recolonize the coniferous plantation; however, on steep lands with poor sandy soils, planted *Cupressus* trees as well as relatively xerophytic shrubs in the understory may establish.

Keywords: Hyrcanian, *Quercus-Carpinetum*, Restoration, Species-environment analysis, Succession

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1 Introduction

Human exploitation of natural resources has increased due to population growth, scientific advancement, and technological development, and as a result, forests are being degraded worldwide, with developing countries experiencing the highest deforestation rates. Afforestation through plantation is one method of rehabilitating degraded lands, protecting soil and water, combating desertification, preparing wood, and increasing carbon storage (Chen et al. 2010; Lozano et al. 2014; Doelman et al. 2020). By improving site conditions, the plantation can accelerate the succession process (Cusack and Montagnini 2004). Trees and canopies can positively affect ecosystem changes (Dijkstra 2001), and because of tree leaves decomposing on the forest floor, soil ecosystems can change (Binkley 1995). Trees and other forest plants with extensive roots influence the microbial biomass of soil by regulating the carbon cycle between the atmosphere and the soil (Brown et al. 2002). Plantation results in biological diversity and changes in species composition due to various factors such as upper-story plant structure and composition (Tao Lu 2011), light transmission, chemical characteristics of litter, stem flow (Barbier et al. 2008), and succession history. The current composition of understory species in temperate forests results from previous management actions (Poirier et al. 2016).

One of the most critical aspects of the plantation is species selection. Improper species selection can lead to substantial economic and ecological costs. At regional and local scales, replacing indigenous forests with non-indigenous species can result in significant changes in the diversity and composition of plant communities (Woziwoda et al. 2011). Conifer species can be used as pioneer plants to expedite succession, paving the way for establishing plant communities and restoring biological diversity to degraded ecosystems. Numerous studies indicate that planting conifers alters the soil's physical-chemical properties and mineral cycle, resulting in long-term adverse changes in regional ecosystems. Bergès et al. (2017) demonstrated that conifer plantation slows the process by which post-agricultural forests revert to their ancient broadleaf forest conditions. On the other hand, Humphrey et al. (1998) stated that the plantation of conifer species prepares the environment for the emergence of indigenous plants and animals. Additionally, they emphasized the benefits of conifer planting in terms of increasing the diversity of indigenous species. Furthermore, according to Peláez Silva et al. (2019), conifer plantations favored the rehabilitation process by altering the structure of native understory vegetation and soil ecological properties. Shakespeare (2020) demonstrated in a study of 50-year-old conifer plantations that regions with the greatest species diversity have the

least understory cover or pine tree density as well as the highest *Rhamnus cathartica* L. population as an aggressive species. Nowadays, it is critical to investigate the effects of conifer and broadleaf plantations on biodiversity, vegetation, and regeneration to better understand reestablishment stages, ecological restoration, and biodiversity conservation (Zeleny and Schaffers 2012).

In northern Iran, Hyrcanian forests are temperate deciduous broadleaf forests and date from the Tertiary geological period (Sagheb Talebi et al. 2014). These forests sparsely contain only five conifer species naturally occurring in the Hyrcanian flora (Assadi 1988–2020). However, since the 1960s, some non-indigenous species have been introduced into these forests, and in some regions, following years of tree harvesting, they have been used for plantation. Understanding the establishment of plantations in temperate broadleaf forests, the succession process, and ecosystem rehabilitation can significantly help in understanding current conditions and future plans and in determining appropriate approaches if necessary.

In this study, we analyzed the vegetation and stand structure of a 25-year-old coniferous plantation to determine the extent of recolonization by native broad-leaved species and then examined the relationship between recolonization degrees and several environmental variables. The primary research objectives were (a) to determine whether *Cupressus* spp. or other species have established themselves in this plantation 25 years after clear-cutting native forest and planting, (b) whether the reestablished vegetation is homogeneous or consists of distinct groups, (c) classifying those groups according to their characteristics (plant composition, diversity, and stand structure), and (d) identify edaphic, topographic, and structural variables that are correlated to the degree of reconstitution.

2 Methods

2.1 Study site

This research was conducted in Mazandaran Province, Iran, in series 11, region 48, 22 km from the city of Royan. This area has a humid temperate climate with an average annual temperature of 16.35 °C. Annual precipitation averages between 1307 and 864 mm at the nearest weather stations. *Quercus castaneifolia* C.A. Mey, *Carpinus betulus* L., and *Parrotia persica* C.A. Mey are the dominant species in natural forests in this region. In 1993, 50 ha were cleared and planted with two conifer species: *Cupressus sempervirens* L. and *C. arizonica* Greene (2 × 2 m spacing). These areas were typically enclosed for approximately two decades, and livestock was prohibited; however, livestock has entered the stand infrequently in recent years due to fence failures in some parts. As a result, the study area has a consistent succession history and forest management.

2.2 Data collection

The survey was conducted using a 70 × 30 systematic random sampling method. Then, a primary field survey was used to control the dispersion of sample plots, yielding a total of 55 plots measuring 20 × 20 m (Kent and Coker 1994; Chytrý and Otpková 2003) (Fig. 1). Fifty plots were located within the enclosed plantation area, while five additional plots were located outside the plantation, on open land adjacent to the enclosed plantation area. The understory, overstory, and ground plant species, their abundance-dominance (Braun-Blanquet 1946), the diameter at breast height (dbh), the height, and crown canopy of trees, as well as their density, regeneration, and environmental factors (topography and soil variables) were recorded in each plot. Each of these plots had four randomly selected soil samples taken from a depth of 0–30 cm (using an auger device). Each plot’s samples were combined and transported to the laboratory for testing (Jafarzade et al. 2021). The flora of Iran (Assadi 1988–2020) and flora Iranica were used to identify plant samples (Rechinger 1963–2005).

2.3 Analysis method

TWINSPAN (Hill 1979) was used to analyze the vegetation data, and different degrees of reconstitution of native broadleaved forests and diagnostic species were identified. The diagnostic value of species was determined using the fidelity concept and JUICE (ver. 7.0) (Chytrý et al. 2002).

The classified groups were then compared in terms of vegetation structure, plant species diversity, and environmental variables. The comparison was conducted using analysis of variance and mean comparisons in SPSS 22 software.

Since three plots (i.e., 1, 2, and 11) had few old uncut trees (*Parrotia*, *Carpinus*, and *Quercus*), they were excluded from the analysis to eliminate the direct effect of distance on seed dispersal.

The Shannon Wiener index (Shannon and Weaver 1949), Simpson index (Simpson 1949), Menhinick and Margalef richness indices (Whittaker 1977), Pielou evenness index (Pielou 1975), and Sheldon evenness index were used to determine the species diversity. Moreover, the CCA (canonical correspondence analysis) was used to define the variation gradient, species–environment relationship, and environmental factors affecting the establishment or reestablishment of indigenous forests. PC-Ord 4 and Canoco 4.5 were used in this analysis.

3 Results

3.1 Floristic composition and classification of vegetation

There were 98 plant species identified (Fig. 2), 22 of which were trees and shrubs (Phanerophyte). The most abundant life forms in the studied area were hemicryptophytes and phanerophytes. The plots investigated were classified into four distinct groups (Fig. 2). Group 1 consisted of conifer trees with some broadleaf understory

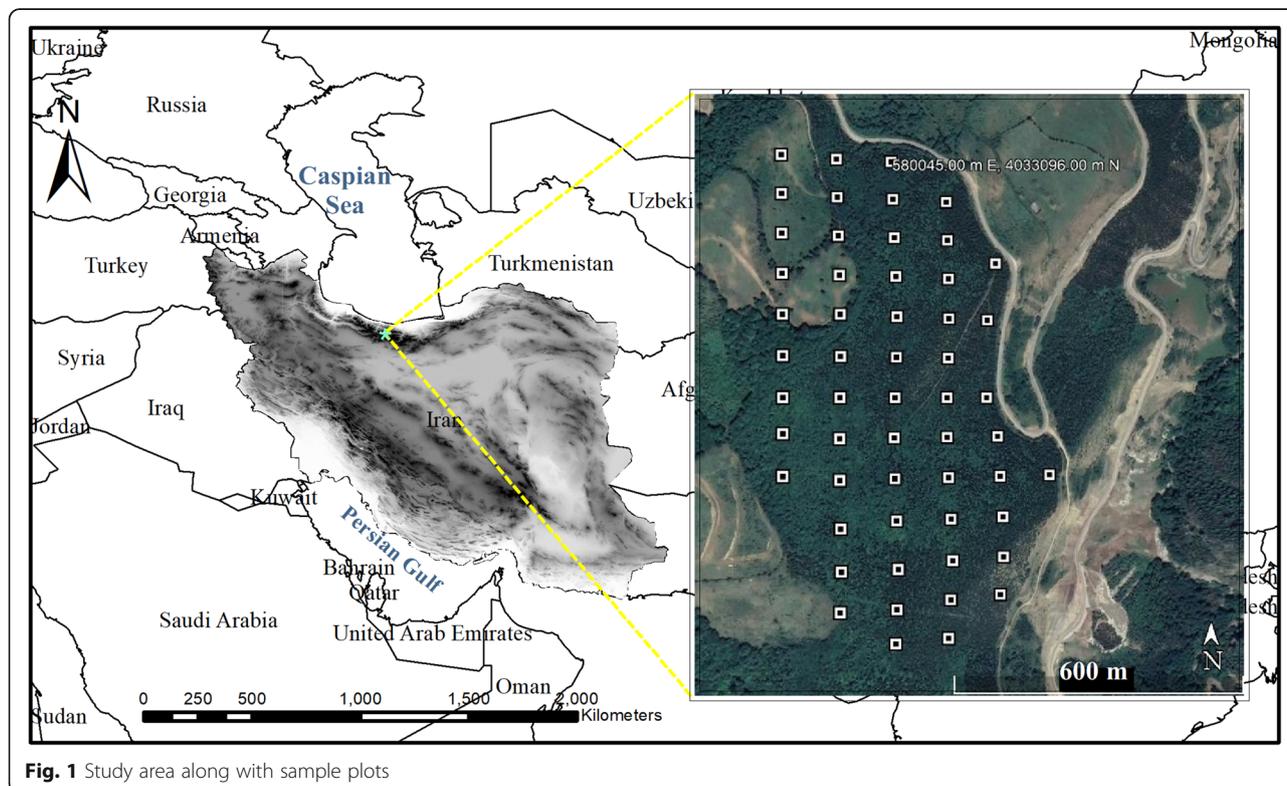
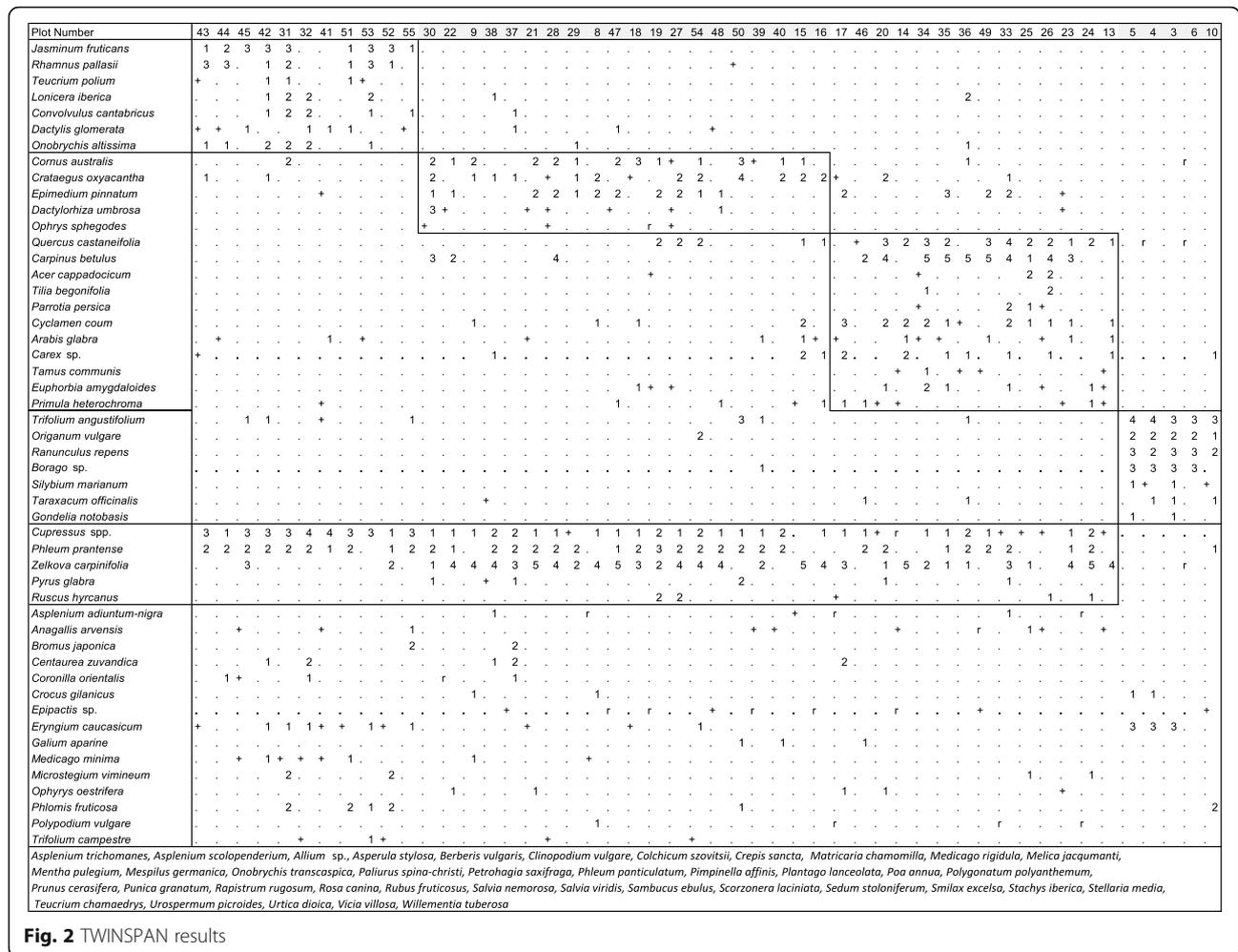


Fig. 1 Study area along with sample plots



shrubs (*Jasminum fruticans* L., *Rhamnus pallasii* Fisch. and C.A. Mey, *Lonicera iberica* M. Bieb, and *Teucrium polium* L.). Group 2 included a mixture of coniferous and broadleaf trees (*Cupressus* spp. and *Zelkova carpinifolia* (Pall.) K. Koch), as well as *Crataegus oxyacantha* L. and *Cornus australis* C.A.Mey. Group 3 was dominated by broadleaf tree species (*Quercus castaneifolia*, *Carpinus betulus*, among others), while group 4 was dominated by herbaceous species, with five plots outside the plantation area.

3.2 Stand formation and regeneration

Based on the results, conifers dominated in group 1, accounting for 520 trees per hectare, while broadleaf trees were scarce, and some shrubs were identified as understory species (Table 1). *J. fruticans*, *Rh. pallasii*, and *L. iberica* were the dominant shrub species, accounting for 1115 individuals/ha. *Zelkova carpinifolia* and *Crataegus oxyacantha* had the highest natural regeneration rates in this group, respectively (Table 1).

The density of conifers was reduced to 139 trees per hectare in group 2, while the density of broadleaf tree species had significantly increased, primarily of young trees with an average height of 4.5 m (Table 1). In this group, the most regeneration occurred in *Z. carpinifolia*, *C. oxyacantha*, and *Carpinus betulus*, respectively.

Broadleaves reached a density of 1877 individuals/ha in group 3. On the other hand, the number of conifers planted per hectare had decreased to 199 trees. *C. betulus*, *Z. carpinifolia*, and *Q. castaneifolia* were dominant tree species, while *Ruscus hyrcanus* Woronow and *Crataegus oxyacantha* were dominant shrub species. *Z. carpinifolia*, *C. betulus*, *C. oxyacantha*, and *Q. castaneifolia* had the highest regeneration rates, respectively (Table 1). Group 4 was dominated by herbs, but some tree and shrub species had established themselves. *C. oxyacantha* and *Z. carpinifolia* had the highest regeneration rates, respectively (Table 1).

The degree of reconstitution of native broadleaved forests was explained using the results of vegetation classification and the survey of stand formation and

Table 1 Composition of stands and regeneration rates in various groups

Group	1				2				3				4					
	Woody species composition		Regeneration		Woody species composition		Regeneration		Woody species composition		Regeneration		Woody species composition		Regeneration			
	Individual (stem/ha)	Mixture grade %	Average height (m)	Individual (stem/ha)	Mixture grade %	Average height (m)	Individual (stem/ha)	Mixture grade %	Individual (stem/ha)	Mixture grade %	Average height (m)	Individual (stem/ha)	Mixture grade %	Individual (stem/ha)	Mixture grade %			
<i>Cupressus sempervirens</i>	336.4	18.2	4.8	0	0	118.7	5.0	6.2	0	0	196.4	6.9	6.5	0	0	0	0	
<i>C. arizonica</i>	184.1	10.0	3.3	0	0	20.0	0.8	5.9	0	0	1.8	0.1	6.9	0	0	0	0	
<i>Zelkova carpinifolia</i>	72.3	3.9	1.8	984.1	67.6	1070	45.0	4.2	688.7	57.8	6268	22.2	4	682.1	28.6	10.0	7700	32.7
<i>Carpinus betulus</i>	0	0	-	0	0	118.7	5.0	4	187.5	15.7	1505.4	53.3	4.3	1210.7	50.7	0	0	0
<i>Quercus castaneifolia</i>	0	0	-	0	0	35.0	1.5	4.9	28.7	2.4	233.9	8.3	5	60.7	2.5	15.0	25.0	1.1
<i>Parrotia persica</i>	0	0	-	0	0	0	0	-	0	0	51.8	1.8	3.8	42.9	1.8	0	0	0
<i>Crataegus oxyacantha</i>	25.0	1.4	2.9	234.1	16.1	591.2	24.8	2.8	228.7	19.2	46.4	1.6	2.8	239.3	10.0	0	13900	59.1
<i>Lonicera ibetica</i>	136.4	7.4	1.6	2.3	0.1	6.25	0.3	1.5	0	0	10.7	0.4	1.8	0	0	0	0	0
<i>Prunus divaricata</i>	22.7	1.2	2.2	0	0	0	0	-	1.2	0.1	1.8	0.1	4	0	0	0	0	0
<i>Rhamnus pallasii</i>	377.3	20.5	1.5	4.5	0.3	2.5	0.1	1.1	0	0	0	0	-	0	0	0	0	0
<i>Cornus australis</i>	45.5	2.5	2.0	72.7	5.0	330.0	13.9	2.0	52.5	4.4	23.2	0.8	2.9	73.2	3.1	5.0	1500	6.4
<i>Pyrus sp.</i>	0	0	-	0	0	32.5	1.4	2.8	1.2	0.1	35.7	1.3	2.8	25	1.0	0	15.0	0.6
<i>Mespilus germanica</i>	0	0	-	0	0	0	0	-	2.5	0.2	5.4	0.2	3	23.2	1.0	0	0	0b
<i>Rosa canina</i>	0	0	-	0	0	0	0	-	0	0	1.8	0.1	1.5	0	0	10.0	0	0
<i>Acer cappadocicum</i>	0	0	-	0	0	2.5	0.1	5	0	0	17.8	0.6	5.7	10.7	0.4	0	0	0
<i>Tilia begoniifolia</i>	0	0	-	0	0	0	0	-	0	0	16.1	0.6	4.9	17.9	0.7	0	0	0
<i>Ruscus hyrcanus</i>	0	0	-	0	0	50	2.1	-	0	0	42.9	1.5	-	2	0	0	0	0
<i>Jasminum fruticans</i>	602.3	32.6	1.5	147.0	10.1	0	0	-	0	0	0	0	-	0	0	0	0	0
<i>Punica granatum</i>	34.1	1.8	1.3	0	0	0	0	-	0	0	0	0	-	0	0	0	0	0
<i>Paliurus spinachristi</i>	4.5	0.2	2.9	11.4	0.8	0	0	-	0	0	0	0	-	0	0	0	0	0
<i>Berberis vulgaris</i>	4.5	0.2	3.0	0	0	1.2	0	3.0	0	0	0	0	-	0	0	0	0	0

dominant tree species. Group 1: coniferous plantation with a predominance of established conifers (Fig. 3). Group 2: coniferous plantation with a relative proportion of indigenous broadleaf species; group 3: coniferous plantation with the reestablishment of indigenous broadleaf species and natural conifer removal (Fig. 3); and group 4: clear-cut lands that have been abandoned without plantation and previously used for grazing.

3.3 Structure of stands

Figure 4 depicts the distribution curves for the diameter classes of the major species within each group. *Z. carpinifolia* curves were uneven-aged in all three groups, but group 1 had a higher regeneration rate than the other two. *C. betulus* and *Q. castaneifolia* had comparable diameter distributions; however, *Q. castaneifolia* exhibited a decrease in smaller diameters and regeneration in group 3. *Cupressus* curves demonstrated an even-aged form, and a comparison of three groups revealed a decline in this species' density in the region. Broadleaf species were uncommon in group 1, occurring primarily in seedling or sapling stages. As a result, no broadleaf stand formed, and the tree distribution curve in diameter classes could not be plotted.

3.4 Plant diversity

The results indicated that the third group had the most significant species richness, while the Shannon and Simpson diversity indices did not differ significantly (Table 2).

3.5 Comparison of environmental variables in different groups

The results indicated that the average percentages of organic carbon (OC) and potassium (K) in the soils of groups 2 and 3 were significantly higher than those in group 1. Phosphorus and nitrogen levels in this group's soil were higher, though the differences were insignificant (Table 3). According to the results, group 1 had a

significantly lower average percentage of soil clay than groups 2, 3, and 4 (as well as a higher average percentage of soil sand). In other words, the soil was significantly lighter in groups 1 (conifers) than in groups 2 and 3 (broadleaves). There was a significant difference between groups regarding the litter layer, with groups 2 and 3 having a greater depth and coverage percentage than groups 1 and 4. Additionally, group 1 had a significantly higher slope than groups 2 and 3 (Table 3).

3.6 Vegetation-environment analysis

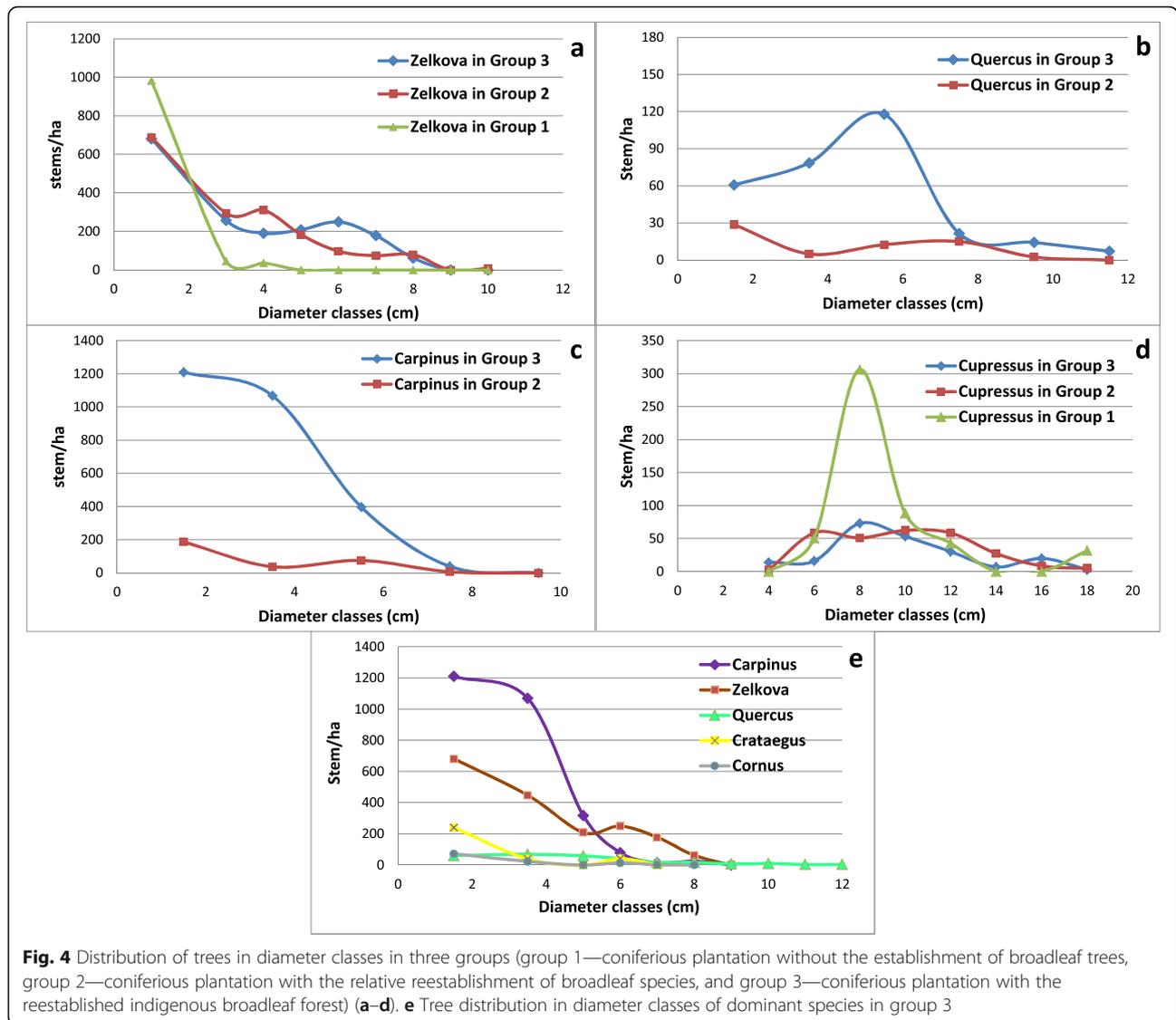
At the 0.01 level, the CCA eigenvalues and ordination results (Table 4) demonstrated that the first and second axes were significant and interpretable. The first three axes account for 72% of the variance in the species-environment relationship. CCA analysis revealed a strong positive correlation between the first axis and the slope variable and a negative correlation between the first axis and the soil OC and K parameters (Fig. 5). The second axis showed a strong positive correlation with altitude and clay content but a strong negative correlation with sand content. The position of species and plots along the aforementioned environmental factor gradient is depicted in Fig. 5. Sampling plots associated with conifer establishment were primarily located in the positive direction of the first axis and the negative direction of the second axis (plots 31, 32, 42, 44, 52, 53, 51, 55, 45, 43, 46, and 43). In contrast, plots associated with broadleaf species reestablishment were primarily located in the negative direction of the first axis (plots 20, 23, 26, 49, 47, 35, 34, 17, 46, 24, and 36).

4 Discussion

Nowadays, the demand for reforestation of degraded lands using former indigenous species has increased (Forbes et al. 2021). Natural regeneration and indigenous broadleaf species can help restore the ancient broadleaf forests' conditions (Bergès et al. 2017). On the other hand, passive restoration is based on natural regeneration with minimal human intervention (Morrison and



Fig. 3 A view of forest stands in group 1 (left side) and group 3 (right side)



Lindell 2011). Certain areas of Hyrcanian forests have been clear cut and replanted with conifer saplings. The condition of parts of these plantations after 25 years was investigated in this study. As a result of these findings,

portions of these coniferous plantations have been naturally replaced by native broadleaf species (group 3). On the other hand, coniferous species remained dominant in other regions (group 1). Several parts had a condition

Table 2 Comparison of the average diversity indices (± SD) in each group

	Group 1	Group 2	Group 3	Group 4
Mean of species no. in each plot	11.3 ± 1.9 ^{ab}	10.0 ± 1.9 ^b	12.2 ± 2.0 ^a	9.6 ± 0.5 ^b
Simpson index	0.86 ± 0.03 ^a	0.84 ± 0.04 ^a	0.86 ± 0.03 ^a	0.85 ± 0.03 ^a
Shannon index	2.22 ± 0.19 ^a	2.06 ± 0.21 ^a	2.22 ± 0.17 ^a	2.03 ± 0.18 ^a
Menhinick index	1.43 ± 0.10 ^{ab}	1.31 ± 0.16 ^{bc}	1.51 ± 0.16 ^a	1.20 ± 0.12 ^c
Margalef index	2.48 ± 0.4 ^{ab}	2.19 ± 0.34 ^b	2.68 ± 0.41 ^a	2.07 ± 0.21 ^b
Sheldon index	0.82 ± 0.05 ^a	0.81 ± 0.05 ^a	0.77 ± 0.07 ^a	0.80 ± 0.09 ^a
Pielou index	0.92 ± 0.19 ^a	0.90 ± 0.21 ^a	0.89 ± 0.15 ^a	0.90 ± 0.07 ^a

Different letters in the same rows show significant difference ($p < 0.05$) amongst vegetation groups

Table 3 Comparison of the mean (\pm SD) amongst vegetation groups regarding environmental variables

Environmental variables	Group 1	Group 2	Group 3	Group 4
Sand %	38.2 \pm 10.3 ^a	29.9 \pm 8.7 ^{ab}	31.6 \pm 6.5 ^{ab}	27.7 \pm 7.9 ^b
Silt %	30.6 \pm 5.9 ^a	31.7 \pm 3.8 ^a	31.6 \pm 4.9 ^a	33.7 \pm 6.1 ^a
Clay %	31.1 \pm 5.7 ^b	38.3 \pm 4.1 ^a	37.4 \pm 3.3 ^a	38.7 \pm 2.5 ^a
Organic carbon %	2.7 \pm 1.5 ^b	3.7 \pm 1.0 ^a	3.8 \pm 1.4 ^a	2.9 \pm 0.6 ^{ab}
pH	7.7 \pm 0.3 ^a	7.5 \pm 0.4 ^a	7.5 \pm 0.3 ^a	7.4 \pm 0.3 ^a
Total N	0.24 \pm 0.11 ^a	0.31 \pm 0.09 ^a	0.30 \pm 0.09 ^a	0.25 \pm 0.07 ^a
Available P (mg/kgsoil)	5.6 \pm 2.3 ^{ab}	8.9 \pm 5.0 ^a	7.5 \pm 2.3 ^{ab}	4.7 \pm 2.3 ^b
Available K (mg/kgsoil)	245 \pm 61 ^b	379 \pm 70 ^a	354 \pm 72 ^a	391 \pm 60 ^a
Litter depth (cm)	0.6 \pm 0.2 ^b	1.4 \pm 0.4 ^a	1.6 \pm 0.3 ^a	0.5 \pm 0.0 ^b
Humus depth (cm)	0.0 \pm 0.0 ^b	0.4 \pm 0.3 ^a	0.6 \pm 0.3 ^a	0.0 \pm 0.1 ^b
Litter coverage %	28 \pm 11 ^b	54 \pm 16 ^a	69 \pm 25 ^a	24 \pm 5 ^b
Tree crown cover %	41 \pm 22 ^a	35 \pm 16 ^a	48 \pm 27 ^a	3 \pm 4 ^b
Shrub crown cover %	29 \pm 17 ^b	60 \pm 21 ^a	62 \pm 21 ^a	18 \pm 24 ^b
Ground vegetation cover %	43 \pm 27 ^b	42 \pm 22 ^b	43 \pm 18 ^b	100 \pm 0 ^a
Moss coverage %	35 \pm 29 ^a	30 \pm 25 ^a	17 \pm 21 ^a	25 \pm 7 ^a
Altitude (m a.s.l)	791 \pm 30 ^a	809 \pm 37 ^{ab}	831 \pm 31 ^{bc}	851 \pm 10 ^c
Aspect (degree)	106 \pm 23 ^a	85 \pm 38 ^a	77 \pm 40 ^a	81 \pm 20 ^a
Slope %	64 \pm 17 ^a	34 \pm 15 ^b	30 \pm 13 ^b	58 \pm 22 ^a

Different letters in the same rows show significant difference ($p < 0.05$) amongst groups

between these two states (group 2). The establishment of broadleaf species resulted in a relative increase in species richness, although this increase was not statistically significant for Shannon and Simpson diversity indices. However, the composition of species and their density varied significantly between groups. After 27 years in temperate forests, the absence of vegetation management in coniferous plantations has increased ground vegetation richness and deciduous broadleaf trees' dominance (Khlifa et al. 2020). Although conifer plantation altered the species composition in Mongolia, it had no discernible effect on plant diversity and richness (Sukhbaatar et al. 2018). According to the findings of numerous studies, coniferous plantations can either increase (Humphrey et al. 1998) or decrease species diversity (Paritsis and Aizen 2008; Bremer and Farley 2010) depending on a variety of factors such as plant species and succession stage.

According to the results, the plants with the highest regeneration rates in the studied area were *Zelkova*

carpinifolia, *Crataegus oxyacantha*, and *Carpinus betulus*. *Z. carpinifolia* had the highest regeneration density in coniferous stands, while *C. betulus* (along with *Quercus castaneifolia*) had the highest regeneration density in broadleaf stands. Unlike the other groups, the third group (broadleaf) saw a considerable increase in *C. betulus* individuals (Fig. 4c). As illustrated in Fig. 4e, *Z. carpinifolia* outnumbered *C. betulus* in diameters greater than 5 cm, while *C. betulus* outnumbered *Z. carpinifolia* in diameters less than 5 cm. This indicates that *Z. carpinifolia* was dominant in the past and early stages of reestablishment (as seen in coniferous stands), but with time and the proper environmental conditions, *C. betulus* became dominant in the subsequent stages. This is due to the changes in the ecosystem following broadleaf trees and shrubs' development, the gradual decline of coniferous species, and the establishment and development of *C. betulus* and *Q. castaneifolia*. Oak regeneration occurred concurrently with common hornbeam (*C.*

Table 4 Eigenvalues and correlation coefficients for species-environment interactions along three major axes of the CCA

		Axis 1	Axis 2	Axis 3
Eigenvalue		0.45 ^{**}	0.30 ^{**}	0.13 ^{ns}
Cumulative percentage variance explained	of species data	11.4	19	22.2
	of species-environment relation	36.8	61.6	72.0
Pearson correlation		0.87 ^{**}	0.76 [*]	0.72 ^{ns}
Kendall (rank) correlation		0.56 ^{**}	0.50 [*]	0.41 ^{ns}

The results of Monte Carlo test: ^{**}Significant at $p < 0.01$ level, ^{*}Significant at $p < 0.05$ level

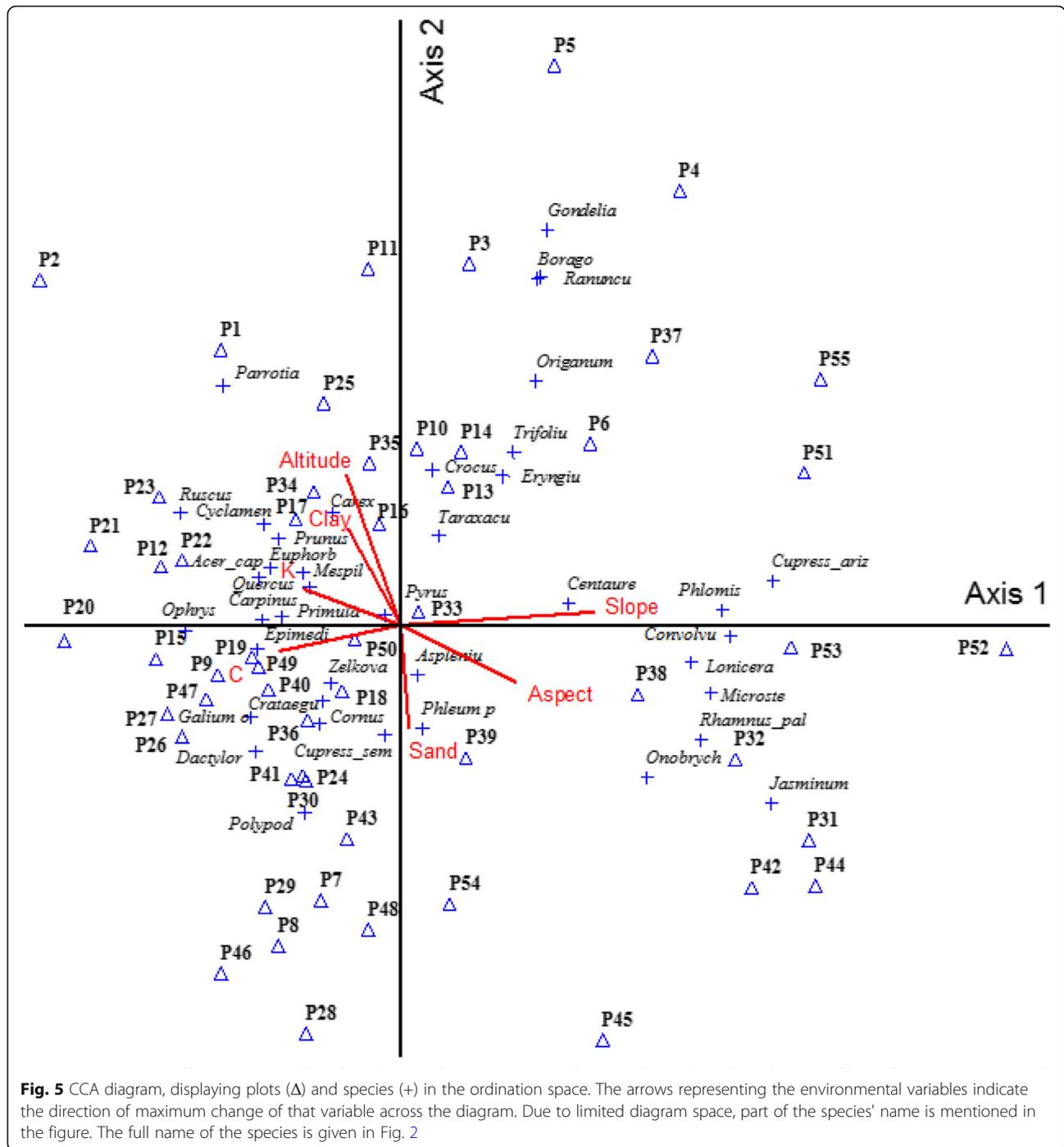


Fig. 5 CCA diagram, displaying plots (Δ) and species (+) in the ordination space. The arrows representing the environmental variables indicate the direction of maximum change of that variable across the diagram. Due to limited diagram space, part of the species' name is mentioned in the figure. The full name of the species is given in Fig. 2

betulus) but at a slower rate. It is worth noting that *C. betulus* seeds are small and winged, whereas oak seeds were heavy and oversized. Wind, gravity, or frugivory are used to disperse light seeds in tree species, whereas only frugivory and gravity are used to disperse heavy seeds in tree species (Burrows 1994). As a result, *Q. castaneifolia* seeds disperse and establish more slowly than *C. betulus* seeds (Sikkema et al. 2016). The oak did not regenerate naturally in group 1 and had a low

regeneration rate in group 2, whereas it had a relatively high rate of regeneration in group 3 (61 stems/ha) (Table 1). In conjunction with an increase in the number of *C. betulus* trees in the region, this phenomenon indicates the succession stages and return of coniferous stands to the *Q. castaneifolia*-*C. betulus* community as a Hyrcanian climax community (Borji et al. 2018; Gholizadeh et al. 2020). This is also confirmed by the TWINSPAN results, which classify *Q. castaneifolia* and *C.*

betulus and several other significant Hyrcanian trees such as *Parrotia persica*, and floor plants such as *Cyclamen coum* Mill., *Euphorbia amygdaloides* L., *Carex* sp., *Primula heterochroma* stapf, and *Tamus communis* (L.), as group 3 diagnostic species (Fig. 2). *C. betulus* and deciduous oaks are the forest community's dominant species in European mixed broadleaf forests, particularly in lowlands (Sikkema et al. 2016). The *Q. castaneifolia*-*C. betulus* community is one type of climax forest found in Hyrcanian forests (Sagheb Talebi et al. 2014). Additionally, *Q. castaneifolia* had a relative decrease in lower diameters and regeneration in group 3, as illustrated in Fig. 4b. Since *Q. castaneifolia* is a light-demanding tree (Babaei et al. 2016), regeneration has slightly decreased as the canopy in group 3 has become denser (Table 1) and less light reaches the forest floor.

In group 1, shrub species such as *Jasminum fruticans*, *Rhamnus pallasii*, *Lonicera iberica* and *Teucrium polium* were considered diagnostic species (Fig. 2) as they were abundant in the understory beneath the conifer trees. The shrub species mentioned above are tolerant of harsh conditions and thrive in harsh environments (Ravanbakhsh and Moshki 2016; Togonidze 2011). Thus, these species can be considered pioneer species for establishing an indigenous broadleaf forest instead of a coniferous plantation. Other studies have demonstrated that conifer plantations (pine) increased the number of xerophytes and light-demanding species in the understory (Bergès et al., 2017; Sukhbaatar et al. 2018). An increase in regeneration of light-demanding species such as *Zelkova carpinifolia* and *Rhamnus pallasii* was observed in the conifer plantation. In similar results, *Rhamnus cathartica* has developed in 50-year-old pine plantations in the Huron natural area in the eastern US (Shakespeare 2020). Based on the preceding, reestablishment stages from planted conifer stand to reestablished broadleaf forest in the area are depicted in Fig. 6.

Possessing a time course of the plantation's changes with permanent plots (BACI-design: Bennett and Adams, 2004) provides valuable and detailed information; thus, this type of plan is recommended for future studies.

The study area was surrounded by a vast habitat of indigenous Hyrcanian forests, which facilitated seed dispersal (large-scale distance effect). The wind dispersal of *Carpinus* is effective, both to escape from density, or

distance, dependent high mortality and to increase the chance of arriving at canopy gaps, where seedling survival rate is high (Shibata and Nakashizuka 1995). The mature fruits of *Zelkova* fall with the entire twig (shoot-seed), and the still attached dried leaves acted as a parachute. Shoot-seeds are successfully established in disturbed sites along steep slopes (Oyama et al. 2018). Additionally, there are some uncut old trees in the western part of the research area, suggesting that these old trees may be necessary for seed distribution to achieve quick and successful reestablishment of broadleaf forests within the nearby group 3 plots (small-scale distance effect). As a result, it seems that wind dispersal is initially responsible for the regeneration of trees and shrubs in the study area (*Zelkova* and *Carpinus*). However, after the tree's growth and crown formation, birds play a role in this process, as *Crataegus oxyacantha*, *Cornus australis*, *Jasminum fruticans*, *Rhamnus pallasii*, and *Lonicera iberica* all produce fleshy fruits that birds can consume. Furthermore, some deciduous trees in the secondary forest area reach seed-bearing age after approximately 10 years. For example, *C. betulus* has a minimum seed-bearing age of 10–30 years (Pijut 2008).

When the CCA results are compared, it is evident that *Cupressus arizonica* and *Rhamnus pallasii* are located in the positive direction of the first axis, implying a steeper slope and a lower concentration of OC and K in the soil. On the other hand, broadleaf species such as *Q. castaneifolia*, *C. betulus*, *Parrotia persica*, and *Acer cappadocicum* occur in the negative direction of the first axis, indicating that the first axis has a lower slope and soils with a higher content of OC, K, and nitrogen. *Rh. pallasii* is a tolerant shrub that thrives on slopes with nutrient-deficient and immature soils (Ravanbakhsh and Moshki 2016). Zarafshar et al. (2020) investigated oak forests and concluded that while planting *Cupressus arizonica* does not increase soil nitrogen or richness, establishing oak forests does. In Europe, the oak-hornbeam community is a classic example of a temperate forest with fertile soils (Sikkema et al. 2016).

On the second axis of the CCA diagram, it can be observed that *Cupressus sempervirens* and *Z. carpinifolia* are oriented negatively on lighter soils (with a higher amount of sand). Simultaneously, *P. persica*, *Q. castaneifolia*, and *A. cappadocicum* are located in the positive direction of the second axis, indicating that they are

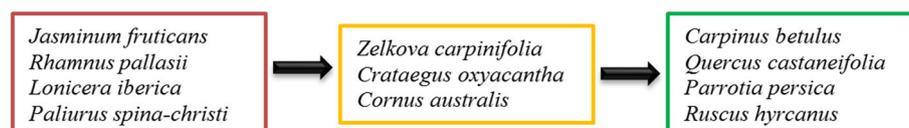


Fig. 6 Stages of vegetation reestablishment, from conifer plantations into indigenous broadleaf forest

established on heavier soil. Furthermore, *C. betulus* exhibits an intermediate condition in terms of soil texture. According to other studies, *Z. carpinifolia* prefers well-drained soils with greater dispersal ability on light sandy soils (Bétrisey et al. 2018). *C. betulus*, on the other hand, grows in a variety of soil types, from heavy clay to sandy light soils, and is only intolerant of acidic soils (Sikkema et al. 2016). The soils in the studied region were all calcareous, and the results indicated that the pH values of the various groups did not differ significantly.

The research conducted in coniferous plantations in southern-east Canada demonstrated that controlling and eradicating indigenous vegetation decreased the soil's exchangeable K without affecting the soil's nitrogen storage (Khlifa et al. 2020). This paper's findings demonstrate that gradually replacing coniferous plantations with indigenous vegetation can significantly increase soil K without affecting nitrogen or phosphorus levels (Table 3).

By examining the positions of plots on the CCA diagram, the environmental gradient that determined whether broadleaf species were replaced or not in the coniferous plantations could be soil texture and slope. Conifers have established themselves on steep lands with poor sandy soils due to reduced competition from broadleaf species (Table 3 and Fig. 5). Broadleaf species dominated conifers on low slopes with heavier soil textures and richer soils. While the number of conifers in group 3 is small, their average height (6.5 m) is greater than that of conifers in group 1, which is 4 m, indicating that group 3 has more prosperous environmental conditions.

According to local residents and the forestry administration, and based on available field evidence (dead trees and stumps), the coniferous plantation thrived for the first 10 years after planting but has since begun to disappear due to the recolonization of indigenous broadleaf species in some locations of the area. Conifers appear to have been eradicated due to their inability to compete with broadleaves on low slopes with heavier, richer soils. In other words, broadleaves performed better in the environment mentioned above. Gymnosperms are restricted to areas where growth of angiosperm competitors is limited, for example, due to cold or nutrient scarcity. Biogeographic evidence supports this prediction, since conifers are largely confined to high latitudes and elevations or soils deficient in nutrients (Bond, 1989). According to Mingzuo et al. (2004), while needle leaf species are oppressed in the middle-age community, broadleaf species prioritize the natural community success process.

In the study area, *Zelkova carpinifolia* regeneration was abundant in coniferous stands (group 1). This species has regenerated in coniferous understory stands with less diversity and density than other

species. However, because broadleaf species cannot compete with conifers in this group (steep slopes with poor sandy soils), the majority of *Zelkova* saplings have naturally been eliminated. As a result, they have remained in the regeneration stage for the last two decades. Similar research found that while *Z. serrata*'s regeneration density was high on slopes beneath the crown canopy, its survival rate was higher in gaps (Nagamatsu et al. 2002). *Z. serrata* developed primarily on disturbed sloped sites in Japan (Oyama et al. 2018), indicating the species' tolerance for harsh environmental conditions is similar to those found in our study region. *Z. carpinifolia* and *Castanea* developed in Georgia during the warmest period of the mid-Holocene (Kvavadze and Connor 2005). However, an investigation of 78-year-old *Z. carpinifolia* trees in the Hyrcanian Region revealed that while temperature had little effect on growth, February precipitation had a significant positive effect on annual growth rings (Balapour and Kazemi 2012). Thus, the development of *Zelkova* can be viewed through the lens of climate change, which requires additional investigation.

Group 4 pastures were formed due to clear-cutting indigenous forest trees, which occasionally resulted in removing saplings and twigs. After clear-cutting the primary forest, there was no coniferous plantation on these lands, and the reestablishment line differed. *Crataegus oxyacantha* and *Zelkova carpinifolia* regeneration were the precursors to the emergence of woody species, and *Jasminum fruticans* was absent. The plants' diversity in this group was comparable to those in group 3, but richness (as measured by the Menhinick and Margalef indices) was significantly lower than group 3 (Table 2).

By examining the CCA diagram, it was discovered that plots of these lands (3, 4, 5, 6, and 10) tended toward the positive direction of the second axis, indicating a higher altitude and heavier soils, and were environmentally similar to plots of group 3 (Table 3). Regarding organic carbon and fertility, group 4 soils were intermediate and did not significantly differ from the other groups. The establishment of indigenous species on abandoned agricultural lands gradually increases the soil's organic carbon, total nitrogen, phosphorus, and potassium content (Wang et al. 2011). However, succession remained at the primary stage in group 4 of the studied area due to grazing, sapling removal, high grass species density (100% herb-layer cover), and competition, environmental conditions such as soil condition and plant composition remained stable, while species richness decreased. The vegetation that occurs as a result of succession in coniferous plantations can aid in establishing and restoring native trees and shrubs following exploitation (Alday et al. 2017).

5 Conclusion

Native broad-leaved Hyrcanian species can recolonize planted areas in low-slope lands with fertile soils where topographic and edaphic conditions allow them to compete with planted conifers. However, after 25 years of coniferous plantation, Cypress trees are established along with relatively xerophytic shrubs on steep lands with poor sandy soils, where conditions are not optimal for temperate deciduous trees.

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Authors' contributions

Masoud Jafarzade: methodology, field study. Hooman Ravanbakhsh: methodology, field study, formal analysis and investigation, writing—original draft preparation. Alireza Moshki: methodology, field study, soil analysis, revision—original draft preparation. Maryam Mollashahi: methodology. All authors read and approved the final manuscript.

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Availability of data and materials

Materials described in the manuscript, including all relevant raw data, could be freely available to any researcher wishing to use them for non-commercial purposes: <https://doi.org/10.11922/sciencedb.01099>

Declarations

Ethics approval and consent to participate

We confirm that this work, which is submitted to "*Annals of Forest Science*" Journal, is original and has not been published elsewhere (in any form or language, partially or in full), nor is it currently under consideration for publication elsewhere. We confirm that our work has not been split up into several parts to increase the quantity of submissions and submitted to various journals or to one journal over time. Our results are presented clearly, honestly, and without fabrication, falsification, or inappropriate data manipulation (including image-based manipulation). Authors adhered to discipline-specific rules for acquiring, selecting and processing data. No data, text, or theories by others were presented as if they were the author's own ('plagiarism').

Consent for publication

All authors whose names appear on the submission (1) made substantial contributions to the conception or design of the work; or the acquisition, analysis, or interpretation of data; or the creation of new software used in the work; (2) drafted the work or revised it critically for important intellectual content; (3) approved the version to be published; and (4) agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

Competing interests

All authors declare that they have no competing interests.

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