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

Masoud Jafarzade 1, Hooman Ravanbakhsh 2*, Alireza Moshki 1 and Maryam Mollashahi 1

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 TWINSPLAN 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, Querco-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; Chytry 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

![Study area along with sample plots](image-url)
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
| Group | 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 % | Average height (m) |
| 1     | 336.4                    | 18.2         | 4.8  | 0  | 0  | 118.7       | 50        | 6.2 | 0  | 0  | 196.4       | 6.9        | 6.5 | 0  | 0  | 0  |
| 2     | 184.1                    | 100          | 3.3  | 0  | 0  | 20.0        | 0.8       | 5.9 | 0  | 0  | 18.0        | 0.1       | 6.9 | 0  | 0  | 0  |
| 3     | 72.3                     | 39           | 1.8  | 984.1 | 676 | 1070       | 45.0      | 4.2 | 688.7 | 57.8 | 6268       | 22.2      | 4  | 682.1 | 28.6 | 10.0 − 770.0 | 32.7 |
| 4     | 118.7                    | 4.8          | 0  | 0  | 118.7       | 50        | 4  | 187.5 | 15.7 | 1505.4      | 53.3      | 4.3 | 1210.7 | 50.7 | 0  | 0  | 0  | 0  |
| 5     | 0  | 0  | 0  | 0  | 35.0        | 15        | 4.9 | 28.7  | 2.4  | 2339       | 8.3       | 5  | 607.7 | 25.0 | 15.0 | 3.8 | 250.0 |
| 6     | 0  | 0  | 0  | 0  | 518         | 18        | 3.8 | 429.1 | 18.1 | 0  | 0  | 0  | 0  | 0  | 0  | 0  |
| 7     | 118.7                    | 5.0          | 4  | 0  | 228.7       | 19        | 2.8 | 239.3 | 10.0 | 0  | 0  | 0  | 1500.0 | 59.1 |
| 8     | 32.5                     | 1.4          | 0  | 0  | 234.1       | 16.1      | 2.9 | 230.0 | 7.1  | 0  | 0  | 0  | 0  | 0  | 0  | 0  |
| 9     | 1364.4                   | 7.4          | 1.6 | 23.0 | 0.1       | 6.25       | 0.3      | 1.5 | 0  | 0  | 10.7        | 0.4       | 1.8 | 0  | 0  | 0  |
| 10    | 1.2                      | 0            | 0  | 0  | 0  | 0  | 1.2        | 0.1       | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  |
| 11    | 377.3                    | 2.0          | 4.5 | 0  | 0  | 1.5        | 0.6      | 1.1 | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  |
| 12    | 45.5                     | 2.5          | 2.0 | 72.7 | 5.0       | 33.0       | 13.9     | 2.0 | 52.5 | 4.4  | 23.2       | 0.8       | 2.9 | 73.2 | 3.1  | 5.0 − 150.0 | 64 |
| 13    | 0  | 0  | 0  | 0  | 32.5        | 14        | 2.8 | 12.1  | 0.1  | 35.7       | 1.3       | 2.8 | 25.0 | 10  | 0  | 0  | 15.0 |
| 14    | 0  | 0  | 0  | 0  | 0  | 2.5        | 0.2       | 5.4  | 18.0 | 0.1       | 1.5        | 0  | 0  | 10.0 | − 0  | 0  | 0  |
| 15    | 0  | 0  | 0  | 0  | 2.5        | 0.1       | 5  | 0  | 0  | 17.8       | 0.6       | 5.7 | 10.7 | 0.4  | 0  | 0  | 0  |
| 16    | 0  | 0  | 0  | 0  | 50  | 2.1        | 0  | 0  | 0  | 42.9       | 1.5        | 2  | 0  | 0  | 0  | 0  | 0  |
| 17    | 602.3                    | 32.6         | 1.5 | 1470 | 10.1      | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  |
| 18    | 34.1                     | 1.8          | 1.3 | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  |
| 19    | 4.5                      | 0.2          | 2.9 | 11.4 | 0.8       | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  |
| 20    | 4.5                      | 0.2          | 3.0 | 0  | 0  | 1.2        | 0  | 3.0 | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  |

Table 1: Composition of stands and regeneration rates in various groups.
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
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

![Figure 4](image)

**Fig. 4** Distribution of trees in diameter classes in three groups (group 1—coniferous plantation without the establishment of broadleaf trees, group 2—coniferous plantation with the relative reestablishment of broadleaf species, and group 3—coniferous plantation with the reestablished indigenous broadleaf forest) (a–d). e Tree distribution in diameter classes of dominant species in group 3

| 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<sup>a</sup> | 10.0 ± 1.9<sup>b</sup> | 12.2 ± 2.0<sup>a</sup> | 96 ± 0.5<sup>b</sup> |
| Simpson index | 0.86 ± 0.03<sup>a</sup> | 0.84 ± 0.04<sup>a</sup> | 0.86 ± 0.03<sup>a</sup> | 0.85 ± 0.03<sup>a</sup> |
| Shannon index | 2.22 ± 0.21<sup>a</sup> | 2.06 ± 0.21<sup>a</sup> | 2.22 ± 0.17<sup>a</sup> | 2.03 ± 0.18<sup>a</sup> |
| Menhinick index | 1.43 ± 0.10<sup>a</sup> | 1.31 ± 0.16<sup>bc</sup> | 1.51 ± 0.16<sup>a</sup> | 1.20 ± 0.12<sup>c</sup> |
| Margalef index | 2.48 ± 0.4<sup>a</sup> | 2.19 ± 0.34<sup>b</sup> | 2.68 ± 0.41<sup>a</sup> | 2.07 ± 0.21<sup>b</sup> |
| Sheldon index | 0.82 ± 0.05<sup>a</sup> | 0.81 ± 0.05<sup>a</sup> | 0.77 ± 0.07<sup>a</sup> | 0.80 ± 0.09<sup>a</sup> |
| Pielou index | 0.92 ± 0.19<sup>a</sup> | 0.90 ± 0.21<sup>a</sup> | 0.89 ± 0.15<sup>a</sup> | 0.90 ± 0.07<sup>a</sup> |

Different letters in the same rows show significant difference (p < 0.05) amongst vegetation 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 (Paritis and Aizen 2008; Bremner 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 3: Comparison of the mean (± SD) amongst vegetation groups regarding environmental variables

| Environmental variables | Group 1       | Group 2       | Group 3       | Group 4       |
|-------------------------|---------------|---------------|---------------|---------------|
| Sand (%)                | 38.2 ± 10.3 a | 29.9 ± 8.7 ab | 31.6 ± 6.5 ab | 27.7 ± 7.9 b  |
| Silt (%)                | 30.6 ± 5.9 a  | 31.7 ± 3.8 a  | 31.6 ± 4.9 a  | 33.7 ± 6.1 a  |
| Clay (%)                | 31.1 ± 5.7 b  | 38.3 ± 4.1 a  | 37.4 ± 3.3 a  | 387 ± 2.5 a   |
| Organic carbon (%)      | 2.7 ± 1.5 b   | 3.7 ± 1.0 a   | 3.8 ± 1.4 a   | 2.9 ± 0.6 ab  |
| pH                      | 7.7 ± 0.3 a   | 7.5 ± 0.4 a   | 7.5 ± 0.3 a   | 7.4 ± 0.3 a   |
| Total N                 | 0.24 ± 0.11 a | 0.31 ± 0.09 a | 0.30 ± 0.09 a | 0.25 ± 0.07 a |
| Available P (mg/kgsoil) | 5.6 ± 2.3 b   | 8.9 ± 5.0 a   | 7.5 ± 2.3 ab  | 4.7 ± 2.3 a   |
| Available K (mg/kgsoil) | 245 ± 61 b    | 379 ± 70 a    | 354 ± 72 a    | 391 ± 60 a    |
| Litter depth (cm)       | 0.6 ± 0.2 b   | 1.4 ± 0.4 a   | 1.6 ± 0.3 a   | 0.5 ± 0.0 b   |
| Humus depth (cm)        | 0.0 ± 0.0 b   | 0.4 ± 0.3 a   | 0.6 ± 0.3 a   | 0.0 ± 0.1 b   |
| Litter coverage %       | 28 ± 11 b     | 54 ± 16 a     | 69 ± 25 a     | 24 ± 5 b     |
| Tree crown cover %      | 41 ± 22 a     | 35 ± 16 a     | 48 ± 27 a     | 3 ± 4 b     |
| Shrub crown cover %     | 29 ± 17 b     | 60 ± 21 a     | 62 ± 21 a     | 18 ± 24 b     |
| Ground vegetation cover % | 43 ± 27 b     | 42 ± 22 b     | 43 ± 18 b     | 100 ± 0 a     |
| Moss coverage %         | 35 ± 29 a     | 30 ± 25 a     | 17 ± 21 a     | 25 ± 7 a     |
| Altitude (m a.s.l)      | 791 ± 30 a    | 809 ± 37 ab   | 831 ± 31 bc   | 851 ± 10 c   |
| Aspect (degree)         | 106 ± 23 a    | 85 ± 38 a     | 77 ± 40 a     | 81 ± 20 a     |
| Slope %                 | 64 ± 17 a     | 34 ± 15 b     | 30 ± 13 b     | 58 ± 22 a     |

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

### 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 |
| 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.
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.
Carpinus is effective, both to escape from density, or persal (large-scale distance effect). The wind dispersal of indigenous Hyrcanian forests, which facilitated seed dis-

Adams, 2004) provides valuable and detailed informa-

Petrusev et al. 2017). Adding to the experimental work, a study by Petrušev et al. (2017) revealed that the presence of Rh. pallasii was associated with increases in seedling emergence. The authors concluded that Rh. pallasii is a light-demanding species that thrives 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 ef-
fact). 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, Carpinus 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. Rhamnus cathartica has been shown to require disturbed sites along steep slopes (Oyama et al. 2018). 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
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 (Khila 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 Hycranian 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 Mollahash: 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.

Author details
1Department of forestry, Faculty of Desert Studies, Semnan University, Semnan, Iran. 2Research institute of Forests and Rangelands, Agricultural Research, Education and Extension Organization (AREEEO), Tehran, Iran.

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References
Alday JG, Etebereria E, Ametzaga I (2017) Conversion of Pinus radiata plantations to native forest after harvest operations: a north Iberian Peninsula case study. Eur J Forest Res 136(5):801–810. https://doi.org/10.1007/s10342-017-1071-2
Assadi M (1988–2020) Flora of Iran, no. 1–149. Research Institute of Forests and Rangelands, Tehran, Iran. Babaei F, Jalali SG, Sohrabi H, Shirvany A (2016) Physiological responses of seedlings of different Quercus castratifolia CA Mey. provenances to heterogeneous light environments. J Forest Sci 62(10):485–491. https://doi.org/10.17221/56/2016-JFS
Balapour S, Kazemi SM (2012) Effects of climate variables (temperature and precipitation) on annual growth of Zelkova carpinifolia. Iran J Wood Paper Sci Res 27(1):69–80
Barbier S, Gosselin F, Balandier P (2008) Influence of tree species on understory vegetation diversity and mechanisms involved— a critical review for temperate and boreal forests. Forest Ecol Manag 254(1):1–15. https://doi.org/10.1016/j.foreco.2007.09.038
Bennett LT, Adams MA (2004) Assessment of ecological effects due to forest harvesting: approaches and statistical issues. J Appl Ecol 41(4):585–598. https://doi.org/10.1111/j.1113-0343.2004.00094.x
Bergé S, Leiss T, Avon C, Martin H, Rochel X, Dauffy Richard E, Cordonnier T, Dugouey JL (2017) Response of understory plant communities and traits to past land use and coniferous plantation. Appl Vegetation Sci 20(3):468–481. https://doi.org/10.1111/avsc.12296
Bíró J, Földi T, Deák G, Štockel A, Farkas M, László J, László G, Böck C (2018) Zelkova carpinifolia. The IUCN Red List of Threatened Species of threatened 2018. https://doi.org/10.2305/IUCN.UCN. UK2018-2.RLTS.T130331166773.en
Binley D (1995) The influence of tree species on forest soils, processes and patterns. In: Proceedings of the trees and soil workshop, vol 7. Agronomy Society of New Zealand Special Publication, Lincoln University Press, Canterbury
Bond BJ (1989) The tortoise and the hare: ecology of angiosperm dominance and gymnosperm persistence. Biod J Linnean Soc 36(3):227–249. https://doi.org/10.1111/j.1095-8312.1989.tb00492.x
Borji M, Ravanbakhsh H, Hamzehlou B, Amiri M (2018) A comparison of environmental and vegetation variables between Carpinus betulus and C x schusschensis stands in Naghibdeh and Mazdeh forests (Sari, Mazandaran) and introducing a new hornbeam association. Iran J Forest Poplar Res 26(2): 189–201. https://doi.org/10.22092/JFPR.2018.116748
Braun-Blanquet J (1946) Pflanzensoziologie. In: Grundzüge der Vegetationskunde, 3nd edn. Springer, Wien, New York
Bremer LL, Fairley KA (2010) Does plantation forestry restore biodiversity or create green deserts? A synthesis of the effects of land-use transitions on plant species richness. Biodivers Conserv 19(14):3893–3915. https://doi.org/10.1007/s10531-010-9936-4
Brown S (2002) Measuring carbon in forests: current status and future challenges. Environ Pollut 116(3):363–372. https://doi.org/10.1016/S0269-7491(01)00212-3
Burrows CJ (1994) Fruit types and seed dispersal modes of woody plants in Burrows CJ (1994) Fruit types and seed dispersal modes of woody plants in

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Chen FS, Zeng DH, Fahey TJ, Liao PF (2010) Organic carbon in soil physical fractions under different-aged plantations of Mongolian pine in semi-arid region of Northeast China. Appl Soil Ecol 41(1):42–48. https://doi.org/10.1016/j.apsoil.2009.09.003
Chytry M, Otyjyková Z (2003) Plot sizes used for phytosociological sampling of European vegetation. J Veg Sci 14(4):563–570. https://doi.org/10.1111/j.1121-060X.2003.tb02183.x
Chytry M, Tichý L, Holt J, Botta-Dukát Z (2002) Determination of diagnostic species with statistical fidelity measures. J Veg Sci 13(1):79–90. https://doi.org/10.1111/j.1121-060X.2002.tb02025.x
Cusack D, Montagnini F (2004) The role of native species plantation in recovery of understory woody diversity in degraded pasturaleands of Costa Rica. Forest Ecol Manag 188(1–3):1–15. https://doi.org/10.1016/S0378-1127(03)00302-5
Dijkstra FA (2001) Effects of trees species on soil properties in a forest of the Netherlands. Wageningen University, United States
Doolman JC, Stelhert E, van Vuuren DP, Tabeau A, Hof AF, Braakhekke MC, Gemaat DEH, Berg M, Zeist W, Daogtou V, Meijl H, Lucas PL (2020)
Afforestation for climate change mitigation: Potentials, risks and trade-offs. Global Change Biol 26(3):1576–1591. https://doi.org/10.1111/gcb.14887
Forbes AS, Allen RB, Herbert JW, Kohiti K, Shaw WB, Taurua L (2021) Determining the balance between active and passive indigenous forest restoration after exotic conifer plantation clear-fell. Forest Ecol Manag. https://doi.org/10.1016/j.foreco.2020.118621
Gholizadeh H, Najinezhad A, Chytry M (2020) Classification of the Hycrcanian forest vegetation, Northern Iran. Appl Veget Sci 23(1):107–126. https://doi.org/10.1111/avsc.12469
Hill MO (1979) TWINSPAN: A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell Ecology Programs Series. Cornell University, Ithaca, NY
Humphrey J, Hall K, Broome AC (1998) Birch in spruce plantations: management for biodiversity. Forestry Commission Technical Paper 26. Forestry Commission, Edinburgh
Jafarzade M, Ravanbakht H, Moshti A, Mollahashi M (2021) Vegetation Data-Iran, Mazandaran. [dataset]. V3. Science Data Bank. https://doi.org/10.11922/sciencedb.01099
Kent M, Coker P (1994) Vegetation description and analysis: a practical approach. Wiley-Blackwell, New Jersey
Khilfa R, Angers DA, Munson AD (2020) Understory species identity rather than Ellenberg indicator values in vegetation analyses. J Veget Sci 23(3):419–431. https://doi.org/10.1111/1654-1103.2020.0021x
Kuvaždev E, Connor SE (2005) Zelkova carpinifolia (Pallas) K. Koch in Holocene sediments of Georgia, an indicator of climatic optima. Rev Palaeobot Palynol 138(1-2):69–89. https://doi.org/10.1016/j.revpalbo.2004.09.002
Lozano YM, Hortal S, Armas C, Pugnaire FI (2014) Interactions among soil, plants, and microorganisms drive secondary succession in a dry environment. Soil Biol Biochem 78:298–306. https://doi.org/10.1016/j.soilbio.2014.04.007
Mingzuo W, Dongfeng Y, Xuefeng Z, Jun M, Zenglu L (2004) A study on adjacent competition effect of forestry community of mountainous area in western Henan Province Acta Agriculturae Universitatis Henanensis 38(4):409–413
Morrison EB, Lindell CA (2011) Active or passive forest restoration? Assessing restoration alternatives with avian foraging behavior. Restoration Ecol 19(2011):170–177. https://doi.org/10.1111/j.1526-100X.2010.00725.x
Nagamatsu D, Seiwa K, Sakai A (2002) Seedling establishment of deciduous trees in various topographic positions. J Veget Sci 13(1):35–44. https://doi.org/10.1111/j.1654-1103.2002.tb02021.x
Oyama H, Fuse O, Tomimatsu H, Seiwa K (2018) Variable seed behavior increases recruitment success of a hardwood tree, Zelkova serrata, in spatially heterogeneous forest environments. Forest Ecol Manag 415:1–9. https://doi.org/10.1016/j.foreco.2018.02.004
Pantis J, Aizen MA (2008) Effects of exotic conifer plantations on the biodiversity of understory plants, epigeal beetles and birds in Nothofagus dombyi forests. Forest Ecol Manag 255(5-6):1575–1583. https://doi.org/10.1016/j.foreco.2007.11.015
Pelláez Silva JA, León Pelláez JD, Lema Tapias A (2014) Conifer tree plantations for forest regeneration in the tropical seasonal rain forest of Xishuangbanna, SW China. Revista de Biología Tropical 59(1):455–463
Togodzide P (2011) Typology of East Georgian open Juniper woodlands. Bull Georgian Nat Acad Sci 5(3):103–106
Wang B, Liu GB, Xue S, Zhu B (2011) Changes in soil physico-chemical and microbiological properties during natural succession on abandoned farmland in the Loess Plateau Environ Earth Sci 62(5):915–925. https://doi.org/10.1007/s12665-010-0577-4
Whittaker RH (1977) Evolution of species diversity in land communities. Evol Biol 10:1–67
Wozniowa B, Michalska-Hejduk D (2011) Impact of land use changes and dynamic vegetation changes on vascular flora diversity in Maldow-Bartchów (the Warta river valley). Folia Geobotica 7:125–138. https://doi.org/10.1016/j.j.egco.2011.07.009-0020-3
Zaraffshar M, Bazar S, Matinizadeh M, Bordbar SK, Rousta MJ, Kooch Y, Enayati K, Abbasi A, Naghdarabesh M (2020) Do tree plantations or cultivated fields have the same ability to maintain soil quality as natural forests? Appl Soil Ecol. https://doi.org/10.1016/j.apsoil.2020.103536
Zeleny D, Schaffers AP (2012) Too good to be true: pitfalls of using mean Ellenberg indicator values in vegetation analyses. J Veget Sci 23(3):419–431. https://doi.org/10.1111/j.1654-1103.2011.01366.x

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