Original Articles

Effects of single-tree selection on large-diameter tree retention in old-growth Hyrcanian temperate forests

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Abstract

Large and old trees are key structural components of old-growth temperate forests, yet their persistence under uneven-aged silvicultural systems remains poorly resolved. In many regions, single-tree selection is promoted as a close-to-nature management approach intended to maintain structural complexity, but its long-term consequences for large-diameter tree cohorts remain insufficiently evaluated. We evaluated the effects of repeated single-tree selection on large-diameter tree retention in the Hyrcanian temperate forests (northern Iran) using a landscape-scale case study from the Kheyrud Experimental Forest. Our analysis combined (i) a temporal comparison of permanent inventory plots before harvesting (1982) and after three decades of management (2010) with (ii) a comparison between managed district and adjacent unlogged reference forest, based on a complete inventory covering approximately 1,600 ha. Tree frequency and diameter structure were analyzed with emphasis on large (DBH ≥ 100 cm) and giant (≥ 150 cm) trees. Large-tree density in the managed district declined by 58%, while giant-tree density declined by 83% between 1982 and 2010. Diameter-class distributions further revealed a pronounced truncation of upper-diameter cohorts, whereas stem densities in smaller size classes remained broadly comparable between inventories. In 2010, large-tree density in the managed district remained 63% lower than in the unlogged reference forest. These results indicate that single-tree selection, as implemented in this system, did not maintain the large-tree structure characteristic of mature Hyrcanian forests. Maintaining these structural legacies likely requires explicit retention thresholds for very large trees, longer cutting cycles, and permanent no-harvest areas within managed forest landscapes.

Keywords: diameter-class distributions, forest structure, giant trees, Iran.

Introduction

Old-growth temperate broadleaf forests are ecosystems that have developed over long periods with minimal anthropogenic disturbance, retaining structural and compositional attributes shaped by natural disturbance regimes (Farver et al., 2009; Després et al., 2014). Rather than representing a single developmental stage, old-growth conditions encompass a range of stand structures characterized by high structural complexity (Lorimer & Halpin, 2014; Zenner, 2004), heterogeneous age and size distributions, and the persistence of large and old trees (Lindenmayer & Laurance, 2017; Liu et al., 2022; Wang et al., 2009). Although increasingly rare, such forests provide essential reference conditions for evaluating ecosystem integrity, long-term dynamics, and forest management outcomes (Azaryan et al., 2026; Kucbel et al., 2012).

Among these attributes, the presence and continuity of large and old trees are particularly important (Burrascano et al., 2013). Large trees function as keystone structural elements that disproportionately contribute to biomass (Birdsey et al., 2023), habitat availability (Kozák et al., 2023), and ecosystem resilience (Mildrexler et al., 2023; Piovesan et al., 2022). They also regulate microclimate and hydrological processes (Giambelluca et al., 2009; Martin et al., 2001; Meinzer et al., 2005), and support diverse biotic communities through their structural complexity (Dudinszky et al., 2021; Kozák et al., 2023). Consequently, large-diameter trees are widely recognized as key indicators of structural continuity in mature forest ecosystems (Kozák et al., 2023; Moradi et al., 2012).

In temperate regions, remaining old-growth forests are often confined to landscapes that have escaped intensive land use and repeated harvesting (Burrascano et al., 2013; Wirth et al., 2009). One such region is the Hyrcanian forest belt along the southern Caspian Sea coast of Iran, recognized as a UNESCO World Heritage Site (UNESCO, 2023). These forests represent one of the most diverse temperate ecosystems in Western Eurasia and serve as refugia for Arcto-Tertiary flora (Akhani et al., 2010; Sagheb-Talebi et al., 2014). They support broadleaf stands capable of producing large, long-lived trees, including oriental beech (*Fagus orientalis* Lipsky.), common hornbeam (*Carpinus betulus* L.), and chestnut-leaved oak (*Quercus castaneifolia* C.A.Mey) (Azaryan et al., 2015). Although much of this region has been managed, remaining low-disturbance stands provide rare reference conditions for assessing long-term structural dynamics (Azaryan et al., 2026). These forests therefore offer a unique opportunity to examine how large-tree structural legacies are maintained—or altered—under different management histories.

As old-growth attributes in are increasingly embedded within managed landscapes, understanding how contemporary silvicultural systems influence them is essential. In the Hyrcanian region, forest policy has promoted close-to-nature forestry, which aims to emulate natural disturbance processes while maintaining structural complexity and continuous canopy cover (O'Hara, 2016). Within this framework, forests are typically managed as uneven-aged stands through selection systems, particularly single-tree selection, where trees are harvested across diameter classes while maintaining continuous cover (Collado et al., 2023; Lundqvist, 2017). Although such systems are intended to sustain stable size distributions through continuous recruitment, they present a fundamental challenge: the largest and most commercially valuable trees—those most frequently harvested—are the same structural elements that define old-growth conditions. Consequently, the long-term structural outcomes of selection systems depend strongly on harvest implementation, including marking criteria, harvest intensity, and the retention of large trees. Where such safeguards are insufficient, repeated harvesting may progressively simplify stand structure even when canopy cover is maintained.

Despite widespread adoption of close-to-nature management (Bauhus et al., 2013; Stritih et al., 2026), empirical evaluations of its long-term effects on old-growth attributes remain limited. In particular, few studies combine long-term temporal data with comparisons to unlogged reference stands within the same landscape. Consequently, it remains unclear whether repeated selection harvesting maintains, alters, or erodes upper-diameter tree cohorts central to old-growth structure.

To address this knowledge gap, we present a landscape-scale case study from the Kheyrud Experimental Forest in northern Iran, one of the most intensively studied and professionally managed forest sites in the Hyrcanian region (Etemad et al., 2013). Using complete inventory data covering approximately 1,600 ha, we evaluate the long-term effects of single-tree selection management through two complementary approaches: (i) a temporal assessment of large- and giant-tree abundance within a managed district based on permanent plot inventories conducted before harvesting (1982) and after several decades of management (2010), and (ii) a comparison of forest structure between managed and unlogged districts under comparable environmental conditions. Diameter-class distributions were also analyzed to provide whole-stand structural context for these comparisons. Species-level patterns are presented descriptively to provide ecological context, while statistical inference focuses on plot-level analyses. The objective of this study was to evaluate how three decades of single-tree selection harvesting have influenced diameter-class structure and the abundance of large and giant trees in Hyrcanian forests by comparing pre-harvest conditions, a managed forest district, and an unlogged reference stand within the Kheyrud Experimental Forest.

Method

Area of study. The study was conducted in the Kheyrud Experimental Forest (latitude 36°27’–36°40’ N and longitude 51°32’–51°43’ E), located within the central Hyrcanian forest belt along the southern Caspian Sea coast of northern Iran (Figure 1). The forest covers a total area of approximately 8,000 ha and occupies a humid temperate climatic zone influenced by the Caspian Sea and the Alborz Mountains. It supports mixed deciduous stands typical of the Hyrcanian region, with a mean annual temperature of 9.1 °C and total annual precipitation of 1,350 mm (Keybondori et al., 2025). Elevation across the study area ranges from approximately 350 to 1,380 m a.s.l., with moderate variation in slope and aspect. Soils are generally shallow to moderately deep forest brown soils developed over limestone parent material, reflecting Upper Jurassic geological formations. Most stands have an uneven-aged structure in which new seedlings establish within canopy gaps (Sefidi et al., 2013).

To evaluate the influence of forest management on stand structure, two adjacent forest districts with contrasting management histories were selected for analysis: Namkhane and Gorazbon districts. The Kheyrud Experimental Forest has been managed by the University of Tehran since 1965. Available management records, together with historical information documented by forest managers and researchers through consultations with local communities surrounding the forest, indicate that no commercial logging occurred prior to the establishment of the experimental forest management program (Etemad, 2001). The Namkhane District is divided into 26 management parcels, of which 21 have been subject to harvesting interventions, while five parcels have remained unharvested due to steep slopes and operational constraints and therefore function as internal

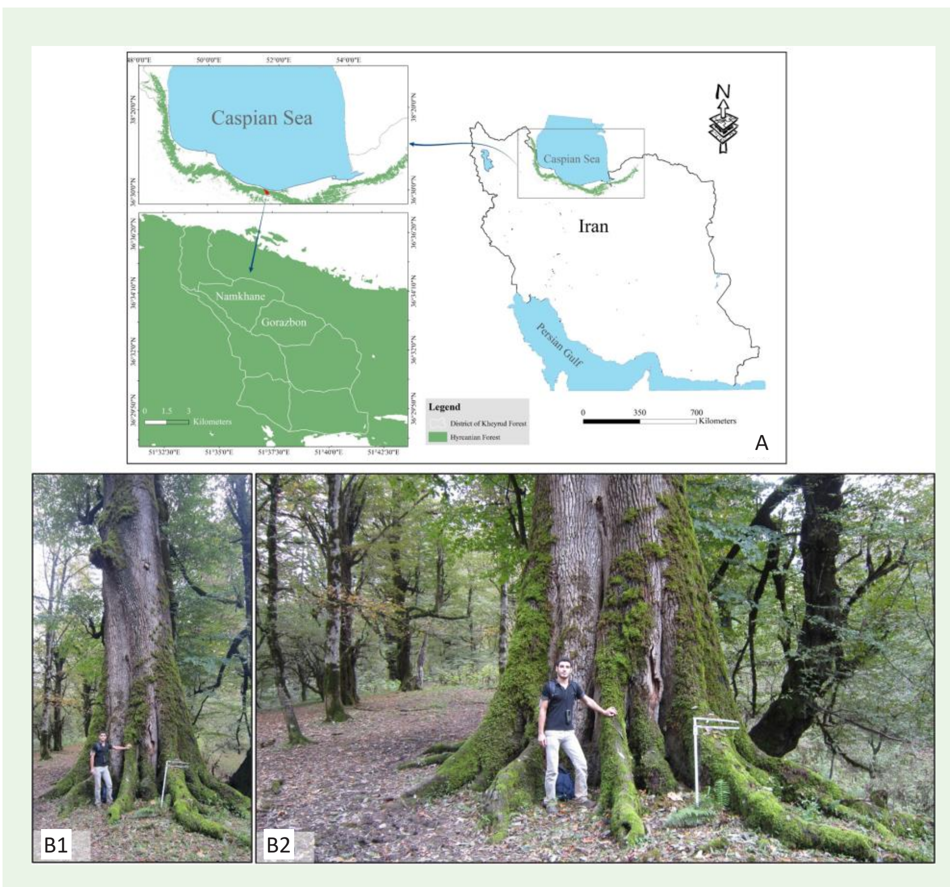

Figure 1. Location map of the Hyrcanian Forest in northern Iran, showing the Kheyrud Experimental Forest and its two study districts, Gorazbon and Namkhane (A). The map highlights the extent of the Hyrcanian Forest (green area) along the southern Caspian Sea coast. Panels (B1) and (B2) show different views of the same chestnut-leaved oak (*Quercus castaneifolia*)—the largest tree recorded in the study area (DBH = 308 cm, height = 48.3 m, crown projection area = 609 m^2)—located in Parcel 224 of the Namkhane District.

control areas. The Namkhane District has been managed under single-tree selection since the early 1980s, with periodic harvest entries conducted between 1983 and 2012. Harvesting interventions typically occur at approximately 10-year intervals, following the cutting cycle established for uneven-aged stands. During each intervention, individual trees are selectively marked for removal based on silvicultural criteria such as tree vitality, stem quality, and stand structural balance rather than exclusively targeting the largest trees.

In contrast, the Gorazbon District has functioned as an unlogged reference area during the study period, with no commercial harvesting recorded prior to data collection. Both districts share comparable climatic conditions, dominant tree species (*Fagus orientalis* and *Carpinus betulus*), geological substrate, and general site characteristics. Key attributes of the two districts, including area, elevation range, climate, geology, and management history, are summarized in Table 1.

Field data collection. Forest structure was quantified using a complete forest inventory conducted in 2010 across approximately 1,600 ha encompassing the two adjacent forest districts within the Kheyrud Experimental Forest (Figure 1a). During this inventory, trees were defined as individuals with a diameter at breast height (DBH) ≥ 7.5 cm (3 inches). All living trees meeting or exceeding this threshold were recorded for species identity and diameter at breast height (DBH, measured at 1.3 m above ground level). Tree height measurements were not available for all individuals and were therefore excluded from the analysis. Because the inventory covered the entire study area, the dataset represents a census-based assessment of forest structure rather than a sample-based plot inventory, thereby allowing a comprehensive characterization of stand structure across both districts.

Following established global and regional conventions (Azaryan et al., 2015; Lutz et al., 2013), trees were classified into two size categories based on DBH: large trees (DBH ≥ 100 cm) and giant trees (DBH ≥ 150 cm) (Table S1). Species-specific thresholds were applied for wych elm (*Ulmus glabra* Hudson.) and Cappadocian maple (*Acer cappadocicum* Gled.), for which giant trees were defined as DBH ≥ 100 cm, consistent with established criteria for

Table 1. Environmental, geographic, and management characteristics of the two study districts within the Kheyrud Experimental Forest, northern Iran. Values represent district-level descriptors derived from published sources and forest management record.

Species	Namkhane*	Gorazbon**
Forestry practices	Single-tree selection	Unlogged***
Harvesting period	1983–2012	–
Dominant species	*Fagus orientalis*, and *Carpinus betulus*	*Fagus orientalis*, and *Carpinus betulus*
Inventory area (ha)	765	848
Elevation (m.a.s.l)	350–1,290 (average 870)	550–1,380 (average: 1,010)
Mean slope (%)	31	33
Latitude (N)	36° 34′ 00″ to 36° 36′ 30″	36° 32′ 30″ to 36° 36′ 30″
Longitude (E)	51° 34′ 00″ to 51° 38′ 30″	51° 36′ 00″ to 51° 41′ 00″
Geology	Upper Jurassic formations; parent material is limestone with alternating hard fractured and softer strata.	Upper Jurassic formations; parent material mainly limestone with alternating hard fractured and softer strata; karstic features enhance infiltration and drainage toward the Kheyrud River.
Soil	Shallow soils developed over limestone; classified as forest brown soils.	Brown forest soils, shallow and on steep terrain; karstic drainage and thin topsoil cause summer drought.
Mean annual precipitation (mm/y)	1,350	1,260
Mean annual air temperature (˚C)	16.1	15.2

* Etemad et al. (2013). ** Marvi Mohadjer et al. (2009). *** The Gorazbon District was logged between 2010 and 2016, prior to the implementation of the forest logging ban project. However, data for this forest were collected in 2010, before harvesting began.

Hyrcanian forests (Azaryan et al., 2015). Analyses focused on eight dominant broadleaved species capable of attaining large diameters, for which complete DBH data were available. Supplementary Figures S1–S7 provide additional photographic examples of giant trees recorded in the study area.

Temporal analytical framework. Historical pre-harvest inventory data were available only for the managed Namkhane District. This inventory was conducted in 1982 prior to the initiation of timber harvesting using a systematic fixed-plot design (Etemad et al., 2013; Marvie Mohadjer et al., 2009). A total of 176 circular fixed-area plots (0.1 ha each) were established across the Namkhane District in 1982, and the same permanent plots were remeasured in 2010, enabling a direct temporal comparison of large- and giant-tree abundance within the managed district.

Comparable historical inventory data were not available for the Gorazbon District, which was therefore used exclusively as a reference representing current unlogged forest structure. Accordingly, the study combined two complementary analytical perspectives. First, a temporal fixed-plot analysis within the managed Namkhane District (1982 vs. 2010) was used to assess long-term changes associated with single-tree selection management. Second, a district-level comparison based on the complete 2010 census inventory was conducted to contrast the abundance of large and giant trees between the managed Namkhane District and the unlogged Gorazbon District under broadly comparable environmental conditions (Table 1). Because both districts were surveyed using the same inventory protocol in 2010, observed differences in forest structure are interpreted primarily in relation to contrasting management histories rather than differences in sampling design.

Diameter-class analysis. Diameter-class distributions were constructed for each district and inventory year using 5-cm DBH class intervals to evaluate whole-stand structural patterns across the full-size range. Stem densities were calculated for each diameter class and plotted on a logarithmic (log10) scale to facilitate comparison of size-class structure among the pre-harvest and post-harvest inventories in the managed district and the unlogged reference district. Because diameter-class distributions describe stand structure rather than species-specific patterns, this analysis was conducted independently of species identity.

Statistical analysis. Temporal variation in the abundance of large- and giant-tree densities within the managed Namkhane District was analyzed using generalized linear models (GLMs) appropriate for count data. GLMs were fitted using the base R function glm, and negative binomial models were implemented using the glm.nb function from the MASS package (Ripley et al., 2013). Logistic regression models were also fitted using the glm function with a binomial error structure.

For the temporal analysis, plot-level tree counts from the permanent plots were modeled as a function of survey year (1982 vs. 2010), which was included as a categorical fixed factor representing pre-harvest and post-harvest conditions. Because only two inventory years were available, survey year was treated as a categorical variable rather than a continuous predictor. To account for environmental heterogeneity, elevation and slope were included as continuous predictors. Because aspect is a circular variable, it was not included as a categorical factor. Instead, aspect was transformed into two continuous orthogonal variables—northness and eastness—calculated as the cosine and sine of aspect (in radians), respectively. These variables were included as continuous predictors in the GLMs. In the interaction models, both northness and eastness were included in interaction with survey year (year × northness and year × eastness) to evaluate whether the influence of topographic orientation on tree abundance differed between the two inventories.

GLMs with a Poisson error structure were first fitted to evaluate model structure and dispersion. For giant-tree counts, which were sparse and dominated by zero values, negative binomial models were subsequently applied to account for overdispersion (Bolker et al., 2009). For large-tree counts, dispersion diagnostics indicated that the Poisson model provided an adequate fit.

To evaluate whether temporal changes varied across environmental gradients, a second set of models including interaction terms between survey year and topographic predictors (year × elevation, year × slope, year × northness, and year × eastness) was fitted. Model selection was based on Akaike's Information Criterion (AIC; Akaike, 2003) and likelihood-ratio tests, and the most parsimonious model was retained for interpretation.

Differences in large- and giant-tree abundance between the managed Namkhane District and the unlogged Gorazbon District in the 2010 inventory (i.e., district-level comparison) were evaluated using GLMs with district (managed vs. unlogged) included as a categorical fixed factor.

For large trees, additional analyses were conducted to examine changes in plot-level occurrence patterns. Tree counts were converted to presence–absence variables to quantify the probability of large-tree occurrence, and logistic regression models were fitted to evaluate the effect of survey year and topographic predictors on the probability of large-tree occurrence. To further examine plot-level trajectories, plots were classified into four change categories (absence in both inventories, loss, gain, and persistence), and logistic regression was used to evaluate the influence of topographic conditions on the probability of large-tree loss between inventories. Species-level results are presented descriptively and were not included as explanatory factors in the statistical models. All analyses were conducted in the R statistical environment (R Core Team, 2024).

Results

Temporal changes in large and giant trees within the managed district (Namkhane, 1982–2010). Based on repeated measurements from 176 permanent plots, the managed Namkhane District exhibited substantial reductions in the abundance of large (DBH ≥ 100 cm) and giant (DBH ≥ 150 cm) trees between the pre-harvest inventory (1982) and the post-harvest inventory (2010) (Table 2). The total density of large trees declined from 56.92 to 23.86 trees per 10 ha, corresponding to a 58.1% decrease over the study period. Across species, large-tree densities declined between inventories, with the greatest reductions observed in *Fagus orientalis* and *Carpinus betulus* (Table 2). Giant trees exhibited an even greater overall reduction, with total density decreasing from 3.70 to 0.64 trees per 10 ha (−82.7%). Across species, reductions in giant-tree abundance were substantial, with several species showing near-complete loss of individuals in the largest diameter class by 2010 (Table 2).

At the plot level, generalized linear models indicated a significant effect of survey year on tree abundance. For giant trees, the negative binomial model detected a significant decline in 2010 relative to 1982 (β = −1.95 ± 0.91 SE, P = 0.032; Table S2), corresponding to an approximate 86% reduction in expected abundance across plots. Elevation and northness were not significantly associated with giant-tree abundance, while slope and eastness showed weak marginal relationships. Models including interactions between year and topographic predictors were not supported (likelihood ratio test, P = 0.885; Table S3), indicating that the relationship between topographic conditions and giant-tree abundance remained consistent between inventories.

Large trees were more widely distributed across plots than giant trees (Table S4), allowing a more detailed assessment of changes along environmental gradients. GLM results indicated a significant negative effect of survey year on large-tree abundance (Table S4). Model comparison showed that inclusion of year × topography interaction terms improved model fit (AIC = 387.42 vs. 393.97; likelihood ratio test χ^2 = 14.55, P = 0.0057; Table S5), indicating that the relationship between large-tree abundance and topographic conditions differed between the 1982 and 2010 inventories. In the interaction model, slope was negatively associated with large-tree abundance, while northness showed a positive association. The interaction between

Table 2. Temporal changes in the number of large (DBH ≥ 100 cm) and giant (DBH ≥ 150 cm) trees per 10 ha in the managed Namkhane District between 1982 (pre-harvest) and 2010 (post-harvest).

Species	Large trees (DBH ≥ 100 cm)			Giant trees (DBH ≥ 150 cm)		
	Pre-harvest (1982)	Post-harvest (2010)	Δ relative to 1982 (%)*	Pre-harvest (1982)	Post-harvest (2010)	Δ relative to 1982 (%)*
Fagus orientalis	33.901	13.511	-60.2	1.347	0.052	-96.1
Carpinus betulus	9.208	2.472	-73.2	0.824	0.079	-90.5
Acer velutunim	6.003	3.989	-33.6	0.366	0.118	-67.9
Quercus castaneifolia	3.388	1.426	-57.9	0.732	0.301	-58.9
Alnus subcordata	2.917	1.491	-48.9	0.170	0.065	-61.5
Tilia platyphyllos	1.400	0.523	-62.6	0.157	0.013	-91.7
*Ulmus glabra***	0.079	0.013	-83.3	0.079	0.013	-83.3
*Acer cappadocicum***	0.026	0.000	-100.0	0.026	0.000	-100.0
Total	**56.920**	**23.856**	**-58.9**	**3.701**	**0.641**	**-82.7**

* Δ relative to 1982 (%) = ((post-harvest − pre-harvest) / pre-harvest) × 100. ** For *Ulmus glabra* and *Acer cappadocicum*, giant trees are defined as DBH ≥100 cm, therefore, their large and giant categories coincide.

survey year and elevation was significant, indicating a shift in the elevational distribution of large trees between inventories.

Predicted occurrence probabilities along the elevation gradient further illustrated this shift in the elevational distribution of large trees (Figure 2). Prior to harvesting (1982), the probability of large-tree occurrence was higher at lower elevations and declined gradually with increasing elevation. In contrast, the post-harvest inventory (2010) showed higher predicted occurrence probabilities at higher elevations.

Differences in large and giant trees between managed and unlogged districts (Namkhane vs. Gorazbon, 2010). Based on the complete 2010 census inventory across approximately 1,600 ha, the abundance of large (DBH ≥ 100 cm) and giant (DBH ≥ 150 cm) trees differed substantially between the managed Namkhane District and the unlogged Gorazbon District (Table 3). When all species were combined, the density of large trees was 23.42 trees per 10 ha in the managed district compared with 63.16 trees per 10 ha in the unlogged district, corresponding to a 62.9% lower density in the managed district. GLM analysis indicated that this difference between districts was statistically significant (P < 0.05).

At the species level, large-tree densities were significantly lower in the managed district for several species, including *Fagus orientalis*, *Carpinus betulus*, *Acer velutinum*, *Alnus subcordata*, and *Ulmus glabra* (Table 3.). No clear differences in large-tree density were observed for *Quercus castaneifolia*, or *Tilia platyphyllos*, and *Acer cappadocicum* was absent from the managed district.

Giant trees showed a similar pattern between districts. Total giant-tree density was 0.64 trees per 10 ha in the managed district and 1.44 trees per 10 ha in the unlogged district, representing a 55.5% lower density in the managed forest (Table 3). GLM results indicated a significant difference in giant-tree abundance between districts (P < 0.05). At the species level, reductions in giant-tree abundance were most evident for *Fagus orientalis*, *Carpinus betulus*, *Acer velutinum*, and *Tilia platyphyllos*, whereas *Quercus castaneifolia* and *Alnus subcordata* showed relatively minor differences between districts. Giant trees of *Acer cappadocicum* were not recorded in the managed district.

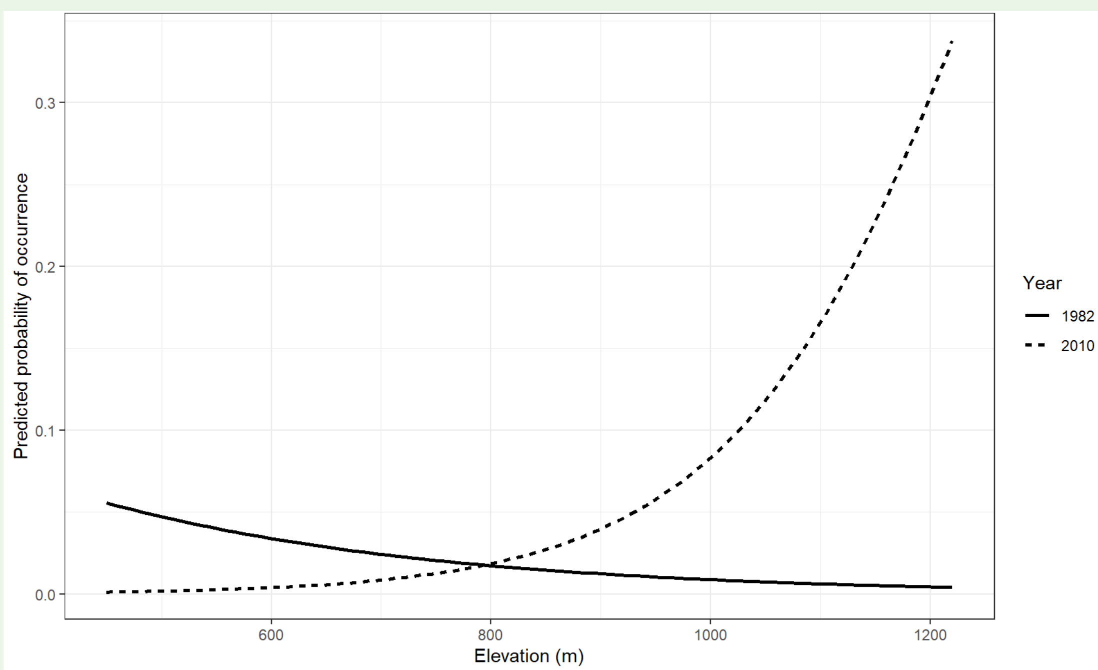

Figure 2. Predicted probability of large-tree occurrence (DBH ≥ 100 cm) along the elevation gradient in the managed Namkhane District of the Kheyrud Experimental Forest. Predictions are derived from the generalized linear model including the interaction between survey year and elevation (Table S5). The solid line represents the pre-harvest inventory (1982) and the dashed line represents the post-harvest inventory (2010). Predictions were generated while holding slope at its mean value and aspect at neutral orientation (northness = 0, eastness = 0).

Table 3. Spatial differences in the number of large (DBH ≥ 100 cm) and giant (DBH ≥ 150 cm) trees per 10 ha between the logged (Namkhane) and unlogged control (Gorazbon) districts of the Kheyrud Experimental Forest, northern Iran.

Species	Large trees (DBH ≥ 100 cm)			Giant trees (DBH ≥ 150 cm)		
	Control district	Logged district	Δ relative to control (%)*	Control district	Logged district	Δ relative to control (%)*
Fagus orientalis	43.565	13.511	-69.0	0.567	0.052	-90.8
Carpinus betulus	6.632	2.472	-62.7	0.130	0.079	-39.5
Acer velutunim	7.623	3.989	-47.7	0.319	0.118	-63.1
Quercus castaneifolia	1.401	1.426	+1.8	0.271	0.30	+10.8
Alnus subcordata	3.363	1.491	-55.7	0.047	0.065	+38.6
Tilia platyphyllos	0.531	0.523	-1.5	0.059	0.013	-77.8
*Ulmus glabra***	0.035	0.013	-63.1	0.035	0.013	-63.1
*Acer cappadocicum***	0.012	0.000	-100	0.012	0.000	-100.0
Total	**63.161**	**23.424**	**-62.9**	**1.440**	**0.641**	**-55.5**

* Δ relative to control (%) = ((logged − control) / control) × 100. ** For *Ulmus glabra* and *Acer cappadocicum*, giant trees are defined as DBH ≥100 cm, therefore, their large and giant categories coincide.

Diameter-class distributions across management histories. Diameter-class distributions showed a progressive decline in stem density with increasing diameter across all stands and sampling periods when plotted on a logarithmic scale (Figure 3). In the managed Namkhane District, stem densities in smaller diameter classes (<40 cm DBH) were generally similar between the pre-harvest (1982) and post-harvest (2010) inventories. Differences between the two distributions became apparent at intermediate diameter classes, with lower stem densities in the post-harvest inventory beginning at approximately 60–70 cm DBH and becoming increasingly pronounced toward larger diameter classes. In the unlogged Gorazbon District (2010), stem density declined gradually across diameter classes and remained consistently higher than values observed in the managed district at larger diameters. Differences among stands were minor in lower diameter classes but increased above approximately 80–100 cm DBH, where stem densities in the post-harvest Namkhane inventory were substantially lower than those observed in both the pre-harvest Namkhane and Gorazbon distributions. In the largest diameter classes (>150 cm DBH), stem densities were low across all stands, but large-diameter stems remained more consistently represented in the unlogged Gorazbon District and in the pre-harvest Namkhane inventory, whereas the post-harvest Namkhane inventory showed markedly reduced representation of these upper diameter classes (Figure 3).

Discussion

Large-tree decline. After more than three decades of contrasting management histories, the two forest districts exhibited pronounced differences in the abundance of large and giant trees. The unlogged Gorazbon District retained substantially higher densities of upper-diameter cohorts, whereas the managed Namkhane District showed marked reductions in both large (≥100 cm DBH) and giant (≥150 cm DBH) trees. Temporal data from permanent plots indicate that this structural change developed during the management period itself: prior to harvesting in the early 1980s, large and giant trees were more abundant in Namkhane, but their densities declined substantially over subsequent decades of repeated selection harvesting. By 2010, large-tree density had decreased by nearly 60% and giant-tree density by more than 80%, leaving the managed forest with markedly fewer upper-diameter trees than the adjacent unlogged district. Together, the temporal and spatial comparisons indicate that this structural deficit reflects long-term management effects rather than pre-existing differences between districts.

Placing these results in a broader ecological context highlights their significance. In mature Hyrcanian beech forests, trees ≥100 cm DBH typically occur at densities of approximately 15–16 stems ha^{-1}, while trees ≥150 cm DBH average about 2 stems ha^{-1} (Azaryan et al., 2026). Although the unlogged Gorazbon District exhibited

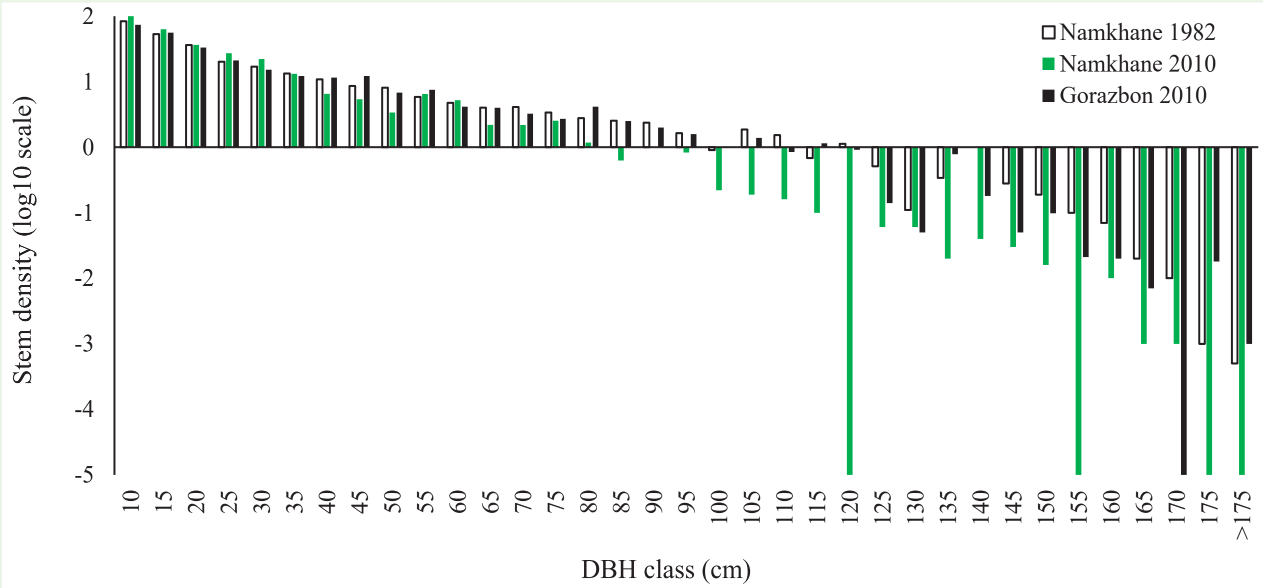

Figure 3. Log-transformed diameter-class distributions of stem density for the managed Namkhane District before harvesting (1982) and after three decades of single-tree selection (2010), and for the unlogged reference Gorazbon District (2010) in the Kheyrud Experimental Forest, northern Iran. Diameter classes represent 5-cm DBH intervals.

lower values than these benchmarks—reflecting its structurally heterogeneous composition—it nevertheless retained substantially higher densities of large trees than the managed Namkhane District. In contrast, the managed forest supported only a small fraction of the large-tree densities reported for mature Hyrcanian forests. Comparable densities have been reported in other temperate old-growth systems; for example, the Yosemite Forest Dynamics Plot contains approximately 19.1 trees ha^{-1} ≥100 cm DBH (Lutz et al., 2012). Taken together, these comparisons indicate that while Gorazbon retains elements of mature structural complexity, Namkhane supports substantially fewer large trees than both regional reference conditions and well-preserved temperate forests elsewhere.

These patterns are consistent with findings from selectively harvested temperate forests worldwide. Studies in North American mixed-conifer forests and European uneven-aged hardwood systems show that repeated selection harvesting can progressively reduce large-tree abundance when harvest entries consistently target the largest merchantable stems (Bauhus et al., 2013; Lindenmayer et al., 2012; Lutz et al., 2013). The magnitude of decline observed here—particularly for giant trees—falls within the upper range reported for these systems, underscoring the vulnerability of upper-diameter cohorts under long-term selection management in the absence of explicit retention thresholds.

Plot-level analyses further indicate that this decline was not restricted to specific environmental conditions within the managed district. GLMs showed a significant negative effect of inventory year on giant-tree abundance, while topographic variables and their interactions with year were not supported. This suggests that reductions occurred broadly across site conditions rather than along particular environmental gradients. Consequently, the observed pattern is most consistent with a generalized structural response to management history rather than with spatial variation in site characteristics.

Diameter truncation. Diameter-class distributions provide further insight into how these structural changes developed over time. In the managed Namkhane District, the post-harvest distribution diverges most strongly from both the pre-harvest condition and the unlogged reference forest at intermediate and large diameter classes (Figure 3). In contrast, stem densities in smaller diameter classes remained broadly comparable between inventories, indicating that regeneration and recruitment processes were not substantially disrupted. In uneven-aged forests managed under selection systems, diameter distributions are typically expected to approximate a reverse-J structure (Hitimana et al., 2004; Li et al., 2024; Westphal et al., 2006), reflecting continuous recruitment into larger size classes. The persistence of high stem densities in the smaller diameter classes therefore suggests that the lower portion of this structure remains intact. However, beginning at approximately 60–70 cm DBH, stem densities decline sharply in the post-harvest distribution relative to both reference conditions, indicating a truncation of the upper tail of the distribution—a structural pattern commonly associated with repeated removal of large individuals.

The persistence of large trees in uneven-aged systems depends on a balance between recruitment into upper diameter classes and removal during harvesting. Although single-tree selection is designed to maintain this balance (Lundqvist, 2017), the pronounced reductions in large and giant trees observed here suggest that this equilibrium has not been achieved. A likely explanation is the concentration of harvesting within commercially preferred diameter classes, particularly stems between 60 and 120 cm DBH, which represent the most valuable merchantable sizes in the Hyrcanian timber market. Such selective pressure can accelerate depletion of upper-diameter cohorts while limiting the progression of smaller trees into the largest size classes over successive cutting cycles.

Comparable structural responses have been documented in uneven-aged systems elsewhere. Studies from temperate forests in North America and Europe show that stands can retain an uneven-aged appearance while progressively losing large trees when harvesting emphasizes minimum cutting diameters without explicitly protecting very large stems (Bauhus et al., 2013; O'Hara, 2014). Similar patterns have also been reported in Hyrcanian forests, where repeated removal of merchantable stems has led to gradual depletion of upper-diameter cohorts (Radaei & Habashi, 2022).

In the present study, the divergence observed above approximately 80–100 cm DBH indicates that repeated selection harvesting reduced the persistence of large stems while leaving smaller diameter classes largely unchanged. From a silvicultural perspective, this suggests that the primary management challenge is the retention of large-diameter trees rather than regeneration failure. Management approaches that explicitly retain a proportion of large stems—such as variable retention or longer cutting cycles—may therefore help maintain the structural characteristics of mature Hyrcanian forests while preserving continuous canopy cover.

Species responses. Species-level patterns provide additional ecological context for how harvesting has influenced forest structure. The largest reductions in both large and giant trees occurred in *Fagus orientalis* and *Carpinus betulus*, the dominant canopy species and primary sources of commercial timber in Hyrcanian forests (Heshmatol Vaezin et al., 2022; Marvie Mohadjer, 2019). Because these species contribute disproportionately to canopy biomass and stand structure (Marvie Mohadjer, 2019), their preferential removal likely played a major role in the decline of upper-diameter cohorts.

In contrast, *Quercus castaneifolia*, *Alnus subcordata*, and *Tilia platyphyllos* showed comparatively smaller reductions in large-tree abundance, likely reflecting differences in harvesting pressure and ecological characteristics. For example, *Tilia platyphyllos* has lower commercial demand and is less frequently targeted, while *Quercus castaneifolia* often occurs in more restricted site conditions, potentially reducing exposure to consistent harvesting (Shahnaseri et al., 2023).

Overall, these patterns suggest that reductions in large and giant trees were concentrated primarily in dominant canopy species targeted during harvesting, which may gradually alter stand structural dominance even when overall species composition remains broadly similar.

Management implications. The results indicate that the current implementation of single-tree selection in the Namkhane District has not maintained the upper-diameter cohorts characteristic of mature Hyrcanian forests. Both temporal and district-level comparisons show substantial declines in large and giant trees under repeated harvest entries, while smaller diameter classes remained broadly comparable between inventories. Diameter-class distributions further indicate that these changes are concentrated in the upper portion of the size structure, where stem densities diverge from both pre-harvest conditions and the unlogged reference forest.

Together with previous studies on structural retention in managed forests, these findings suggest that maintaining large-tree cohorts under selection-based management requires explicit structural safeguards (Edman et al., 2016). This interpretation is consistent with broader evidence highlighting the disproportionate ecological importance of large trees for forest structure and function (Lindenmayer et al., 2014; Lutz et al., 2012). When harvest marking consistently targets dominant canopy trees without retention thresholds for very large individuals, upper-diameter cohorts can decline progressively over successive cutting cycles, leading to reduced structural complexity and loss of key ecological functions (Lindenmayer et al., 2014; Mildrexler et al., 2023; Nolet et al., 2018).

Within the Hyrcanian context, maintaining large-tree legacies may therefore require retention of a defined proportion of trees above large-diameter thresholds, longer cutting cycles to facilitate recruitment into upper size classes, and the designation of permanent retention areas within managed districts. Such approaches align with broader recommendations for conserving large and old trees as critical structural elements supporting carbon storage, habitat availability, and ecosystem resilience (Lutz et al., 2012; Mildrexler et al., 2023).

Growth rates in Hyrcanian beech forests are relatively slow (approximately 1.6 mm yr^{-1}; Mousavisangdehi et al., 2024), indicating that recruitment into large-diameter classes may require several decades. Consequently, the long-term sustainability of uneven-aged systems depends not only on retaining existing large trees but also on maintaining sufficient intermediate-sized cohorts capable of replacing them. Management strategies that support these recruitment pathways—while limiting repeated removal of the largest individuals—are therefore more likely to preserve the structural characteristics of mature Hyrcanian forests under continuous-cover forestry.

Conclusions

This study demonstrates that three decades of single-tree selection harvesting substantially altered the upper-diameter structure of the managed Namkhane District in the Hyrcanian forests. Both temporal comparisons within the managed district and spatial comparisons with an adjacent unlogged reference stand indicate a pronounced decline in large and giant trees under repeated harvest entries.

Diameter-class distributions further reveal that these structural changes were concentrated in the upper portion of the size structure. Stem densities in smaller diameter classes remained broadly comparable between inventories, whereas the abundance of trees above approximately 80–100 cm DBH declined sharply, indicating progressive truncation of upper-diameter cohorts.

Together, these findings suggest that, as implemented in the study area, single-tree selection did not maintain the large-tree structure characteristic of mature Hyrcanian forests. As forest harvesting policies are reconsidered following the 2016–2026 logging moratorium, future uneven-aged management strategies may need to incorporate explicit retention thresholds for large trees, longer cutting cycles that allow recruitment into upper diameter classes, and permanent no-harvest areas that maintain structural reference conditions within the Hyrcanian forest landscape.

Authors contribution

MA, SMMS: conceptualization of the work, formal analysis, supervision, interpretation of results, and writing, and review. AD and VE: formal analysis, interpretation of results, and writing, and review. MVM: writing and review.

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Supporting information

Table S1. Species-specific DBH thresholds for defining giant trees in the Hyrcanian forest (after Azaryan et al. (2015)). For most species, giant trees are defined as DBH ≥150 cm. For *Ulmus glabra* and *Acer cappadocicum*, giant trees are defined as DBH ≥100 cm, meaning their large and giant categories coincide in Table 1.

Species		**Minimum diameter at breast height (cm)**
Scientific name	**Common name**	
Fagus orientalis Lipsky.	Oriental beech	150
Carpinus betulus L.	Common hornbeam	150
Acer velutunim Boiss.	Velvet maple	150
Quercus castaneifolia C.A.Mey.	Chestnut-leaved oak	150
Alnus subcordata C.A.Mey.	Caucasian alder	150
Tilia platyphyllos Scop.	Large-leaved lime tree	150
Ulmus glabra Huds.	Mountain elm	100
Acer cappadocicum Gled.	Cappadocian maple	100

Table S2. Giant-tree occurrence and model dispersion diagnostics based on the permanent plot inventory in the managed Namkhane District of the Kheyrud Experimental Forest. Panel A shows the distribution of giant-tree counts (DBH ≥ 150 cm) across 176 permanent 0.1-ha plots measured before harvesting (1982) and after harvesting (2010). Panel B presents dispersion diagnostics for the Poisson generalized linear model fitted to plot-level giant-tree counts, used to evaluate model assumptions and guide the selection of an appropriate count-data model.

A. Distribution of giant-tree counts across permanent plots		
Giant trees per plot	**Number of plots (1982)**	**Number of plots (2010)**
0	168	174
1	7	2
≥2	1	0
Total plots (n)	**176**	**176**

B. Dispersion diagnostics for Poisson generalized linear model	
Metric	**Value**
Null deviance	126.34
Residual deviance	103.92
Residual degrees of freedom	346
Dispersion ratio*	0.30

*Note: A dispersion ratio substantially below 1 indicates underdispersion relative to the Poisson expectation, supporting the use of a negative binomial model to evaluate factors influencing giant-tree abundance across permanent plots.

Table S3. Results of negative binomial generalized linear models evaluating the influence of survey year and topographic variables on giant-tree abundance (DBH ≥ 150 cm) across 176 permanent 0.1-ha plots in the managed Namkhane District of the Kheyrud Experimental Forest. Panel A presents model coefficients for the negative binomial model relating plot-level giant-tree counts to survey year (1982 vs. 2010) and topographic predictors (elevation, slope, northness, and eastness). Panel B summarizes model comparison statistics used to evaluate whether interactions between survey year and topographic variables improved model fit.

A. Negative binomial model coefficients

Predictor	Estimate (β)	Std. error (±)	z value	*p*-value	Incident rate ratio	95% confidence interval
Intercept	-3.297	2.072	-1.591	0.112	0.037	0.0003 – 3.16
Year (2010 vs. 1982)	-1.947	0.906	-2.150	0.032	0.143	0.017 – 0.767
Elevation	0.00113	0.00213	0.533	0.594	1.001	0.997 – 1.006
Slope	-0.0509	0.0270	-1.883	0.060	0.950	0.875 – 1.007
Northness	-0.106	0.683	-0.155	0.877	0.899	0.177 – 5.61
Eastness	1.888	1.033	1.827	0.068	6.61	1.04 – 103.16

B. Model comparison and goodness-of-fit

Model	Parameters (df)	AIC
Negative binomial (main effects)	7	110.58
Negative binomial (year × topography interactions)*	11	117.43

Likelihood ratio test	Value
χ^2	1.16
Degrees of freedom	5
p-value	0.885

* Note: Interaction terms between survey year and topographic variables were not supported by model comparison, indicating that the relationship between topographic conditions and giant-tree abundance did not change significantly between the pre-harvest (1982) and post-harvest (2010) inventories.

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Table S4. Large-tree abundance and model dispersion diagnostics based on the permanent plot inventory in the managed Namkhane District of the Kheyrud Experimental Forest. Panel A shows the distribution of large-tree counts (DBH ≥ 100 cm) across 176 permanent 0.1-ha plots measured before harvesting (1982) and after harvesting (2010). Panel B presents dispersion diagnostics for the Poisson generalized linear model fitted to plot-level large-tree counts, used to evaluate model assumptions and guide the selection of an appropriate count-data model.

A. Distribution of large-tree counts across permanent plots

Giant trees per plot	Number of plots (1982)	Number of plots (2010)
0	101	139
1	58	34
2	9	3
3	5	0
4≥	3	0
Total plots (n)	**176**	**176**

B. Dispersion diagnostics for Poisson generalized linear model

Metric	Value
Null deviance	361.92
Residual deviance	139.63
Residual degrees of freedom	346
Dispersion ratio*	0.404

* Note: A dispersion ratio below 1 indicates underdispersion relative to the Poisson expectation. The corresponding negative binomial model yielded a very large theta estimate, indicating that the count distribution was adequately described by a Poisson-type model.

Table S5. Results of generalized linear models evaluating the influence of survey year and topographic variables on large-tree abundance (DBH ≥ 100 cm) across 176 permanent plots in the managed Namkhane District of the Kheyrud Experimental Forest. Panel A presents coefficients from the interaction model relating plot-level large-tree counts to survey year (1982 vs. 2010), elevation, slope, northness, eastness, and their interactions with year. Panel B summarizes model comparison statistics used to evaluate whether inclusion of year × topography interaction terms improved model fit.

A. Interaction model coefficients

Predictor	Estimate (β)	Std. error (±)	z value	*p*-value
Intercept	0.309	0.558	0.555	0.579
Year (2010 vs. 1982)	-4.070	1.154	-3.527	<0.001
Elevation	-0.000555	0.000506	-1.098	0.272
Slope	-0.0793	0.0142	-5.604	<0.001
Northness	0.942	0.317	2.973	0.003
Eastness	0.524	0.354	1.482	0.138
Year × elevation	0.00385	0.00106	3.617	<0.001
Year × slope	-0.00165	0.0268	-0.062	0.951
Year × northness	-0.484	0.547	-0.885	0.376
Year × eastness	-0.464	0.633	-0.733	0.464

B. Model comparison and goodness-of-fit

Model	Parameters (df)	AIC
Main effects	7	393.97
Year × topography interaction model*	11	387.42

Likelihood ratio test	Value
χ^2	14.55
Degrees of freedom	4
p-value	0.0057

* Note: The interaction model significantly improved fit relative to the main-effects model, indicating that the relationship between large-tree abundance and topographic setting differed between the 1982 and 2010 inventories, primarily along the elevational gradient.

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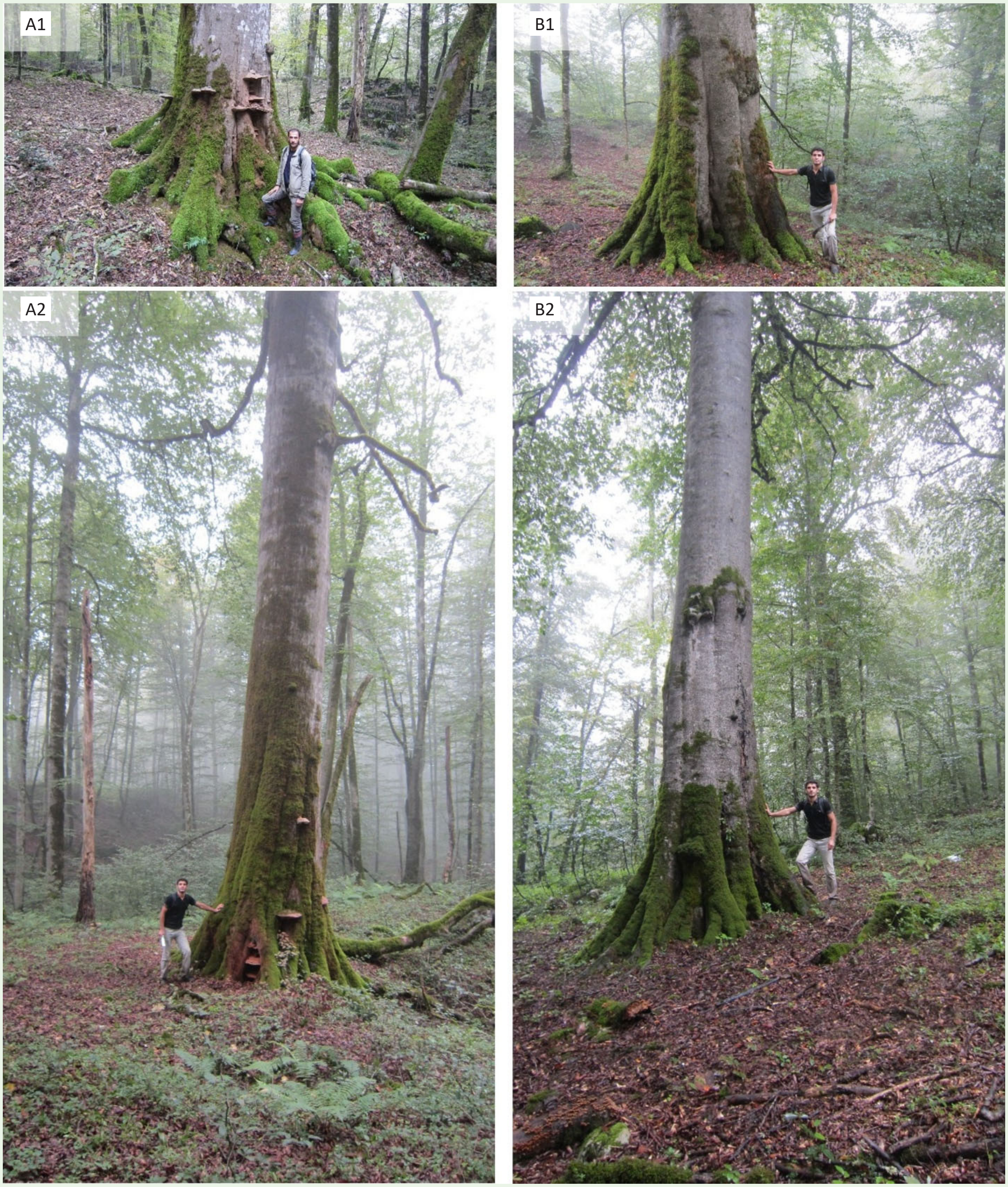

Figure S1. Representative giant *Fagus orientalis* (Lipsky., oriental beech) trees from the Kheyrud Experimental Forest, northern Iran. Panels (A1) and (A2) show Tree A from parcel 211 (DBH = 185 cm; height = 38.3 m; CPA = 214 m^2) from near and far perspectives, respectively. Panels (B1) and (B2) show Tree B from parcel 217 (DBH = 159 cm; height = 34.4 m; CPA = 227 m^2) from near and far perspectives, respectively. DBH, diameter at breast height; CPA, crown projection area.

Figure S2. Representative giant *Carpinus betulus* (L., common hornbeam) trees from the Kheyrud Experimental Forest, northern Iran. Panels (A1) and (A2) show Tree A from parcel 207 (DBH = 175 cm; height = 34.1 m; CPA = 358 m^2) from near and far perspectives, respectively. Panels (B1) and (B2) show Tree B from parcel 206 (DBH = 154 cm; height = 31.3 m; CPA = 314 m^2) from near and far perspectives, respectively. DBH, diameter at breast height; CPA, crown projection area.

Figure S3. Representative giant *Acer velutinum* (Boiss., velvet maple) trees from the Kheyrud Experimental Forest, northern Iran. Panels (A1) and (A2) show Tree A from parcel 211 (DBH = 191 cm; height = 42.6 m; CPA = 200 m^2) from near and far perspectives, respectively. Panels (B1) and (B2) show Tree B from parcel 211 (DBH = 209 cm; height = 35.1 m; CPA = 683 m^2) from near and far perspectives, respectively. DBH, diameter at breast height; CPA, crown projection area.

Figure S4. Representative giant *Quercus castaneifolia* (C.A.Mey., chestnut-leaved oak) trees from parcel 207 (Namkhane District) in the Kheyrud Experimental Forest, northern Iran. Panels (A1) and (A2) show Tree A (DBH = 272 cm; height = 47.9 m; CPA = 432 m^2) from near and far perspectives, respectively. Panels (B1) and (B2) show Tree B (DBH = 294 cm; height = 50 m; CPA = 803 m^2) from near and far perspectives, respectively. DBH, diameter at breast height; CPA, crown projection area.

Figure S5. Representative giant *Alnus subcordata* (C.A.Mey., Caucasian alder) trees from the Kheyrud Experimental Forest, northern Iran. Panels (A1) and (A2) show Tree A from parcel 207 (DBH = 157 cm; height = 37.8 m; CPA = 188 m^2) from near and far perspectives, respectively. Panels (B1) and (B2) show Tree B from parcel 209 (DBH = 163 cm; height = 39.7 m; CPA = 240 m^2) from near and far perspectives, respectively. DBH, diameter at breast height; CPA, crown projection area.

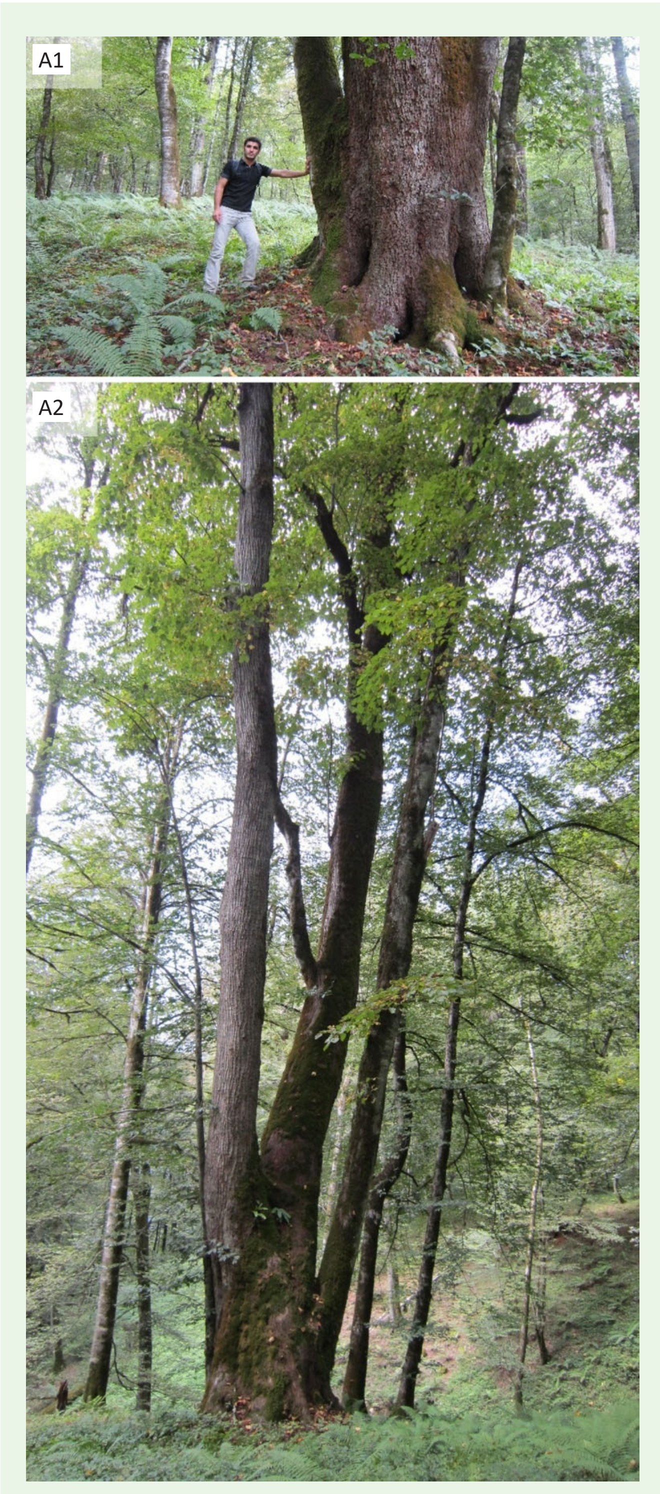

Figure S6. Representative giant *Tilia platyphyllos* (Scop., large-leaved lime tree) tree from the Kheyrud Experimental Forest, northern Iran. Panels (A1) and (A2) show Tree A from parcel 208 (DBH = 182 cm; height = 35.8 m; CPA = 280 m^2) from near and far perspectives. DBH, diameter at breast height; CPA, crown projection area.

Figure S7. Representative giant *Ulmus glabra* (Huds., mountain elm) tree from the Kheyrud Experimental Forest, northern Iran. Panels (A1) and (A2) show Tree A from parcel 222 (DBH = 121 cm; height = 45.4 m; CPA = 254 m^2) from near and far perspectives. DBH, diameter at breast height; CPA, crown projection area.

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